Drifting Ethologists.

by

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Statutory Declaration
(on Authorship of a Dissertation)

I, Claus Ludl, hereby declare that I have written this PhD thesis independently, unless where clearly stated otherwise. I have used only the sources, the data and the support that I have clearly mentioned. This PhD thesis has not been submitted for conferral of degree elsewhere.

I confirm that no rights of third parties will be infringed by the publication of this thesis.

Bremen, November 03, 2015
Abstract

The present dissertation thesis understands itself as epistemological case study for the principles of scientific change. It presumes that the modern sciences established distinguishable subsystems of human culture yet, in principle, are still sharing culture’s inner reproductive dynamics. To evince this dynamic, it shall be asked for the formative impulse it might possibly yield in the life-histories of individual protagonists in a deliberately selected epistemic community.

Both the choice of the scientific object and the applied comparatist methodology are guided by two deliberate considerations. At first, transformation in human thought systems eventually can be conceived as a cyclical process in course of which periods of synthetization alternate periodically with phases of polarization whereby the “turns” might be fairly abrupt. Second, in contrast to other, more object-oriented, theories and approaches of cultural change (Cultural Transfer, Cultural Transmission and Memetics), this study assumes that it is the human organism which is the primary interface in the process of knowledge production and re-production. By adopting the findings obtained by behavioural geneticists and life course sociologists, namely that cognitive and personality-related life-history traits seem to be plastic in youth and early adolescence, while they increasingly gain stability in later stages of life, a working hypothesis for this study can be formulated: Life courses of researchers covering abrupt turnovers, in particular cases, might reveal structural peculiarities in so far as the formation of their scientific orientation involves a process of merging together different epistemic realms of scientific inquiry quite independent whether they experience their academic socialization in a period of cultural polarization and the breakthrough of their disposition coincides with a general synthetic movement or vice versa. This dissertation thesis examines and compares the intellectual life-histories of two behavioural scientists, Nikolaas Tinbergen (1907–1988) and Gustav Kramer (1910–1959), whose trajectories are supposed to belong to this sample in so far as they cover both the movements to and away from the extended synthetic complex of biological theorizing which generated both the Modern Synthesis of Evolution and, as will be shown, a complementary Ethological Synthesis in the mid-thirties of the 20th century. In doing so, these researchers contributed to the establishment of a scientific community whose epistemic foundation had been laid by Ch. Darwin one time layer before but until the 1930s did not become a real reproductive social entity.

The focus on “behaviour”, both as a phenomenon and a scientific concept, thereby appears to be particularly promising since behaviour scientists not only made behaviour the subject of their research (scientization of behaviour) – their manifestations also include an additional communicative function which can be interpreted as implicit second-order reflections of the reproductive dynamics taking place within their epistemic community. Raising this latent communicative dimension thus eventually provides a unique opportunity to gain insight into the performative modes that keep going the process of knowledge production and re-production within an epistemic community: In how far do particularly the performative forms of knowledge organization with help of which researchers present and represent their findings reveal how they relate to other scientific orientations in course of their life and, if so, in how far do their utterances express “movements” within the epistemic space of their scientific community?

In order to answer these research questions, the presented thesis proceeds in three major steps: In a first step, it develops both an adequate reference system and a tool to place a researcher’s scientific expressions within the epistemic space provided by his particular scientific community relative to the point of time in his (possibly also her) life. In the main part, the intellectual life-histories of the two chosen behaviour researchers will be recon-
structured on basis of their scientific publications and additional archival sources. Thereby it will be taken care that the transitions shaping the trajectories of both life courses are presented in a chronologically synchronized way. In a third step, the results of the study and the specific comparative setting they imply – namely that N. Tinbergen’s and G. Kramer’s paths of life cover complementary trajectories within the given reference system while simultaneously the major transitions of their lives reveal a high degree of supra-individual coincidence – shall be tentatively used to grasp the particular forms of epistemic variability guiding the transformation of the epistemic community in question in the given period of time (ca. 1930–1975). In doing so, the results will be summarized in a graphical form at first. Then, the forms of epistemic variability, which are supposed to shape the transformation of scientific ideas inside the epistemic community, are tentatively “encircled” through comparative variability decomposition. Finally, a brief outlook will be given how both textual and transtextual representations of epistemic schemata regulate the interaction across different coexistent, and possibly competing, epistemic communities.
Drifting Ethologists

Claus Ludl

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2015
Dedicated to My Mother
Ending a research project that shaped the rhythms of my everyday life for quite a long time gives cause to think over the distance that had to be covered. In particular, the closer and wider environment of my research work seems worthwhile some concluding reflection. Starting a research project on the history of a scientific field kept together by the mental concept of “behaviour” from a contemporary historian’s perspective soon turned out to be a risky undertaking in many respects. Finally, however, the subject provided some astounding insights into the means of scientific and cultural change – at least this is what I believe. Certainly, that my dissertation project was not meant to be integrated in one of the prominent research institutions science historians can call at in Germany was of disadvantage with respect of financial support as well as communication and networking. Isolation, however, offered a “more of”, on the other hand. The ideal of unrestricted academic freedom, supported by my advisor and defended by Jacobs University, the at least theoretical possibility to get into contact directly with the members of the natural science faculty and the opportunity to devote my attention exclusively to the thesis proved to be the advantages of a small private research university of which I still believe they shaped the outcome of this dissertation thesis in a strictly positive way.

At the beginning of my research endeavour, I was convinced that behaviour is not a scientific object in a narrow sense like the skeleton, the moon or any technical device. Behaviour, understood as a mental concept, by contrast, seemed to have a different quality for its denotations were closely connected to the notion of observable action. In both the highly specialized language of the academic professionals and our everyday language speaking about “behaviour” refers to movements in time and space and thus implies a relation between the organism and its particular conditions of life. Hence, I thought, “behaviour” is a “relational” term, more “wave” and less “particle” and thus more subject of a history of relations and less of scientific objects that seemed to be one of the predominant linking elements of the network-identity shared by science historians in Germany at that time.

In the meantime I changed my mind to a certain degree, since the longer I worked on the project the more I came to realize that the core dimensions of the phenomenon “behaviour” itself and consequently the main lines of its scientific investigation within the various areas of behaviour study are – at least metaphorically
– the ones of the three-dimensional Euclidean space to which the perceptual capacities of us humans seemingly are adapted so perfectly well. From that viewpoint, a history of behaviour, at least in a first step, could be reconciled with a history of scientific objects in so far as behaviour could be approached as multi-facetted quasi-geometrical mental object consisting of various dimensions which, in their turn, seem to be characterized by a high degree of arbitrariness – so to say – as their constitutive quality.

At this point, however, a new difficulty appeared. The increasing scientization of behaviour as a phenomenon which, as I believe, went hand in hand with the evolution of the epistemic space, within which the modern sciences seem to be partly placed, by no means took place within one single scientific discipline. Quite the opposite. The increasingly scientific treatment of phenomena related to the concept of “behaviour” in course of the 19th century resisted – at least to a certain extent – the process of disciplinary diversification of Natural Philosophy into biological, psychological and anthropological sub-branches each of which being concerned with behaviour with varying emphases. As a result, the study of behaviour – following across transdisciplinary lines – appears to be something which is to be addressed less as a particular theme, subject, or topic, rather than something which is coextensive with the notion of space itself. If we put a piece of space into a box and then imagine to put the box away, we need to have a tool, some kind of artificial language, to describe this something which is left – this something of which I think that it can be addressed as “behaviour” in the Humanities and Social Sciences. In order to solve this problem I suggested to make use of a simple observation, namely that the three dimensions of the geometric space precipitated into the mental concept “behaviour”, as three different conceptual dimensions, which can be described in form of discrete levels of larger paradigmatic epistemic units which I – following L. Nyhart – use to call “scientific orientations”.

The result of this act of translation was a methodological approach which allowed seeking systematically for the structural reconfigurations taking place in the different dimensions of a scientific orientation over time. It allowed me to ask for the varying forms of expressions taken by the sub-entities that turned out to be the constitutive parts of a scientific orientation. And it was possible to ask for the different epistemic schemes or epistemic reference systems on basis of which or within which one particular theorem was dealt with in course of its history such as the concepts of “instinct” or “ritualization”. In sum, all these forms of epistemic variability – as soon as their appearance was correlated with the parameter “time” – turned out to be valid means for writing a piece of historical epistemology. How other people will read my dissertation thesis is certainly up to them. I, for my own part, would like to see it as no more than a case study, testing the possibilities and constraints of a methodological approach within a field of historical research that is concerned with the reconstruction of people’s biographies, namely by reconstructing and systematically comparing the intellectual life-histories of two protagonists of animal behaviour study in the 20th century: Nikolaas Tinbergen and Gustav Kramer.

A preface of a treatise is the place to thank all those (and only those) who supported my dissertation project. In particular, the efforts taken by my primary advisor, Pro-
fessor Dr. Johannes Paulmann (Institute for European History, Mainz), to make possible this dissertation project at all, deserve my utmost appreciation and thankfulness. Professor Dr. Margit Szöllösi-Janze (LMU, Munich) supported the project in its initial phase. Prof. Dr. Immacolata Amodeo (Jacobs University Bremen), Prof. Dr. Julia Angster (University of Mannheim), and Prof. Dr. Dominic Sachsenmaier (Jacobs University Bremen) finally were prepared to become members of my dissertation committee. I’d like to express my whole-hearted gratefulness for their assistance and helpfulness. Professor Dr. Günther Zupanc (now Northeastern University, Boston, MA) commented my project in its incipient phase and although it changed a lot since then I’d like to thank him for his unprejudiced and benevolent cooperativeness beyond disciplinary lines. Moreover, my thankfulness owes to Jacobs University (former International University Bremen) for providing me with a three-year fellowship that allowed full-time research work on my dissertation project during that period. A short term fellowship of the German Historical Institute, London (GHIL) enabled me to see the source material in various archives in Oxford, Cambridge (UK) and London. Many thanks to Professor Dr. Hagen Schulze, Professor Dr. Andreas Gestrich, and Dr. Benedikt Stuchtay for their unbureaucratic support. Many archivists assisted me in collecting the data for my thesis, in particular, Dr. Marion Kazemi, Bernd Hoffmann, and Dirk Ullmann (Archive of the Max-Planck-Society, Berlin), as well as Paul Cartwright (Bodleian Library, Oxford) and Mandy Wise (University College London, UCL, Special Collections). The Jacobs University librarians deserve my utmost gratitude for fulfilling my wishes over now several years. W. Steenken-Eisert granted access to many ornithological rarities in the magazine of the library of the Übersee-Museum, Bremen. Barbara Leyhausen allowed me to have a glance at the personal papers of her husband, Paul Leyhausen, and although the part of my project I finally submitted as dissertation thesis side-lines the circle of researchers around K. Lorenz and E. v. Holst, I, nonetheless, would like to thank Mrs. Leyhausen for her assistance and hospitality. Alyssa Honnette’s patient, kind and highly reliable cooperativeness is the reason why I was able to include some parts of the Julian Huxley archives into my thesis. Furthermore, I would like to thank Dr. Wilhelm Füßl (Archive of the German Historical Museum, Munich) for his moderating influence, his profound recommendations concerning academia and for giving me the opportunity to work with him. The experiences I collected while treating the archive material turned out to be extraordinary useful in course of my own research work in the archives. My personal thanks owes to Buffy and Chris Mellor for their overwhelming kindness and hospitality during my visit in London, Joanna, John and the other Newsons for providing me with accommodation in Oxford and the exciting opportunity to get into contact directly with one of the exponents of British autism-research in the 1970s. Many, many thanks to Ines Eben v. Racknitz, Kathi Behrens, and Andreas Steinsieck for the unforgettable evenings in London Town. Last but not least, I would like to thank my sister, Christine, and my dear mother for their patience and their mental support over the rather long period of time it has taken to complete my dissertation project. After all, my thesis has been submitted in April 2013, accepted by the dissertation committee in September and, finally, successfully defended in December 2014.
Preface

The dissertation committee has not made anything a condition for publication. Nonetheless, in those cases I considered the reviewers’ hints correct and useful I tried to reflect on them in the final version of my thesis. Due to the rather long period of time that elapsed between submitting and oral defense I felt a necessity to bring the research literature up to date. The main line of argument and the core contents are identical with the ones outlined in the submitted version.

Thierhaupten, November 03, 2015
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**Preface**

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Introduction

a) Behaviour, Cycles, and Biographical Representation

My dissertation thesis puts forward the hypothesis that scientific change is the outcome of a reproductive process with its own inherent dynamics. To carve out the principles of this dynamics in a case study is the main objective of my thesis. Historical case studies, in contrast to other mere narrative accounts, claim to proceed in a more reflected manner when it comes to choose their methodology or scientific objects. From this perspective it can be asked why I have picked the study of animal and human behaviour as a topical field of my inquiry. The answer to the question why I have shaped the topic of the my thesis like I did lies within the Janus face of the Behaviour Sciences in the 20th century: Behavioural scientists not only made behaviour an object of their scientific accounts and therefore subject of scientization, they also left us an unspoken legacy inasmuch as their utterances serve an additional communicative purpose: They contain information how researchers place themselves within the epistemic space of their scientific community or “move” between various different scientific orientations. This additional communicative function of their – at first sight – merely objective statements sug-


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gests that 20th century behavioural scientists might have brought under “cognitive” control the regularities of cultural evolution earlier and in a more elaborate manner than the representatives of other contemporary branches of research. For the time being, I am not yet capable to measure how universal or widespread the epistemic practices in question are nor how “deliberate” their application actually was or still is. What can be claimed for certain, however, is that information related to the reproduction of knowledge might be articulated primarily in a non-explicit way but, on the other hand, reveals a high degree of sophisticated organization which, as I believe, cannot be explained by common theories of human (and animal) culture that are based on “pure” transmission. To raise the deeper lying, most likely, organismic dimension of scientific speech in a historical case study thus promises to gain insight into the dynamics of scientific transformation processes, in particular, and eventually of cultural variability in general. Altogether, my thesis therefore makes an attempt to go beyond all those studies which so far examined the formative role social practices, in general, and textual practices, in particular, play in the process of knowledge-production: What seems to produce knowledge is the regular reproduction of the particulate heuristic dispositives which constitute(s) a particular epistemic community.

I presume that scientific action is a special case of human culture and as such is underlying cyclical wave-movements which – in analogy to business cycles – will be called “cultural cycles” or, more specifically, “knowledge cycles” in my study. This includes the presumption that intellectual history in Europe and North America since the mid-1700s at the latest (in the United States eventually later) reveals fluctuations in course of which periods of synthetization are succeeded by phases

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3 As it seems, what early ethologists eventually would have called the “plasticity of the human genome” might be a possibility to address this dimension in future transdisciplinary research. As a teaser see here S. Weigel’s courageous account, S. Weigel. “An der Schwelle von Kultur und Natur. Epigenetik and Evolutionstheorie”. In: V. Gerhard et al., eds. Evolution in Natur und Kultur. Berlin et al.: De Gruyter, 2010, 103–123.


of polarization and vice versa. When researchers were interested in the synthetic movements they were tempted to emphasize different part-narratives or singular epistemic trajectories: For instance, those science historians in Germany who have operated with knowledge cycles so far have tried to grasp the periods of synthesis around 1830/1850 and 1930/1950 by applying the concept of “experimentalization” and, in doing so, refused to take into consideration that in other scientific communities or contexts these “hypes” (Prof. J. Angster’s quite fitting term) became manifest primarily in terms of upgrading various forms of ultimate causation.

Another example to approach the cycles in question from a particular angle might be seen in the attempt to divide modernity into periods by applying the concept of “derealization” – that is, the idea that speaking about “reality” slipped into periodically reoccurring and self-amplifying crises. A more biased and, most interestingly, more biographical attempt to describe a particular synthesis may be M. Ash’s account of the emergence and the genesis of Gestalt Psychology in Germany during the period between the two world wars. Yet, in addition to that, as for the second half of the 20th century, I am thinking of the (auto-) biographical studies related to N. Luhmann’s life and research, as well.

On the other hand, however, it is, in principal, also possible to focus upon the opposite movement – the polarization. Altogether, one may say that the perception of periodically reoccurring scientific orientations forced both us science historians and the representatives of
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the primary sciences themselves to find more abstract concepts to address the respective “homological” positions within an epistemic space. To this canonical vocabulary belong concepts such as “vitalism” and “holism”, one the one hand, and “mechanism”, “sensualism”, “environmentalism” or “atomism”, on the other.\footnote{See hereto, for example, W. Metzger. “Atomismus”. In: J. Ritter et al., eds. Historisches Wörterbuch der Philosophie. Vol. 1 (A-C). Basel et al.: Schwabe, 2001, 603–605; J. C. Gregory. A Short History of Atomism. From Democritos to Bohr. London: A. and C. Black Ltd., 1931.}

In particular, the periodic reactivation of these semi-abstract concepts, at least in a first
approximation, suggests that the great western thought- and value-systems faced several waves of Enlightenment which, as I also believe, used to coincide with political and social revolutions yet, after having reached their peak, faced their own transient breakdown just to be rebuilt once more in a later time layer. Until now, it is well known that these cycles comprise a fusion of separately running strains of discourse (1), moreover, that these convergences can coincide with a process of textualization (semiosis) of extra-textual cultural practices and (partly traumatic) experiences (2), that the newly emerging intellectual configurations eventually can be subject to secondary transformation processes (3) and, finally, that the resulting syntheses can “decay” inasmuch as their underlying commonly accepted paradigms break up into their original constituents and, in so doing, re-establish the initial (for some individuals) traumatic situation. Although Cultural anthropology, in general, as well as theory of trauma and narration, in particular, turned out to be highly promising approaches to enlighten various aspects scholars of literature and history connect with the concept of “semiosis”, the actual causes of these cyclic dynamics are still unknown and to clarify their origins would possibly require to exceed by far the boundaries of the humanities. 


14 For (1) and (4) see explicitly M. Middell. “Kulturtransfer und Weltgeschichte. Eine Brücke zwischen Positionen um 1900 und Debatten am Ende des 20. Jahrhunderts”. In: H. Mitterbauer et al., eds. Ent-grenzte Räume. Kulturelle Transfers um 1900 und in der Gegenwart. (Studien zur Moderne 22). Wien: Passagen Verlag, 2005, 63. For (2) and (3) see, particularly, A. Koschorke. Körperströme und Schriftverkehr. Mediologie des 18. Jahrhunderts. 2. durchgesehene Auflage. München: Fink, 2003 [1999], 259–262. In the fairly abstract, semiotic model suggested by the latter, (4) eventually appears to be a potentially asymmetric and facultative process. The results of my thesis eventually suggest that (1) and (2) must be separated conceptually, that (3) encompasses several epistemologically distinguishable processes and, finally, that (4) is a potentially symmetric form of cultural transformation – with respect of both an entire epistemic community and maybe also of single individuals (which is not part of my thesis). 

15 Some historians questioned whether this widening of our perspective is eligible. See M. G. Ash.
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cyclical dynamics accelerated so vehemently in western civilizations during the 20th century and why the cycles partly synchronized globally in the forefield of the breakdown of the economic expert systems in the first decade of the 21st century. As a result, I'd like to keep the question of the knowledge cycle's causal origins and their statistical assessment in the background and tackle their existence on basis of those reductions of complexity that can be drawn on a mere phenomenological level of the cultural appearances themselves. In doing so, I see several different ways to evince the dynamics of knowledge cycles: Cultural and social historians might eventually want to begin with raising their own quantitative data. If this is not possible they still could work with historical sources that include quantitative information by themselves (which is rather likely, for instance, in technical history or history of demography). In both mentioned cases practices of quantification would yield the finer developmental nuances of which I think they could make evident the dynamics in question. The way I have chosen is more qualitative. I am primarily interested in the question how the intellectual life-histories (to be understood as compound of “intellectual history” or “history of ideas” and the life-history approach) of those researchers belonging to one particular epistemic community interpret or “inscribe” themselves within the overall cyclical dynamics. Being granted that it is possible to represent the life courses of researchers in an adequate reference system it can be presumed that the trajectories of those persons whose biographies cover the more or less abrupt turning points of the cycles display topographic peculiarities. How is that? If we open a contemporary handbook of Behavioural Genetics we will probably find the information that the old controversy of nature vs. nurture has become obsolete and also that the phenotypic appearance of a living organism, including man, must be thought as the outcome of a complex interaction between environmental impact factors, on the one hand, and various kinds of inherited and acquired dispositions, on the other. Moreover, we will learn that during a human being’s ontogeny the relative impact of the “nurture”-factor especially upon the development of cognitive abilities decreases, while the proportion of genetic influences increases. This does certainly not exclude the

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18 For the increase of heritability see R. Plomin et al. Gene, Umwelt und Verhalten. Einführung
possibility that also later stages in an individual’s life course might be affected by secondary environmental modifiers such as stress, effects of ageing, illness or even the selective pressures exerted inside a particular social community – not to mention the fact that genetic effects by themselves might vary from stage of life to stage of life.\(^\text{19}\) In other words, behavioural geneticists tend to believe that during an individual’s ontogenetic development we face the breakthrough of a person’s inherited (and also acquired ?) dispositions.\(^\text{20}\) With a view upon the biographies of researchers whose life courses cover major more or less abrupt turning points within the cyclical reproductive dynamics of an epistemic community we may therefore infer that there will be a certain amount amongst them whose later scientific development will – so to speak – undermine their academic socialization by – as I will show – merging together epistemic realms which hitherto had been bound together in quite different, in some cases even antagonistic, scientific orientations. So far I have examined carefully the intellectual life-histories of four researchers of whom I believe they belong to this sample of persons. The behavioural scientists, I speak about, K. Lorenz, E. v. Holst, N. Tinbergen and G. Kramer, all belong to the epistemic community of neo-Darwinians (in the wider extended understanding of the concept) whose inherent structure had been anticipated already by Ch. Darwin one time layer before in his *Origin of Species*.\(^\text{21}\) However, Darwin’s foundation was to be fleshed out with “reproductive life” only since the thirties of the 20\(^{th}\) century.

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\(^\text{19}\) D. F. Alwin et al., for instance, describe six different phenotypic models of human stability, namely a persistence model, the lifelong-openness model, the increasing persistence model, the impressible-years model, the midlife-stability model and, finally, the decreasing persistence model. See Alwin et al., “Generations, Cohorts, and Social Change”, 36–38 and Shanahan et al., “Biological Models of Behavior and the Life Course”, 610.

\(^\text{20}\) This implies that social representations of dispositions may develop a certain social inertia.

\(^\text{21}\) R. J. Richards has devoted almost a life-time of research to reconsider the epistemic place of Darwin’s research outside the tradition established by the so-called “architects” of the Modern Synthesis. Richards criticized that the neo-Darwinian reception of Darwin is directed backwards and, beyond that, made an attempt to explain the genesis of Darwin’s work more in a neo-romantic framework. See, for instance, R. J. Richards. “Darwin on Mind, Morals and Emotion”. In: J. Hodge et al., eds. *The Cambridge Companion to Darwin*. Cambridge: Cambridge University Press, 2003, 92–93 and R. J. Richards. “Darwin’s Place in the History of Thought: A Reevaluation”. In: *PNAS* 106 Suppl. 1 (2009), 10056–10060. My opinion is that on basis of a careful examination of the various scientific orientations Darwin’s works covered over time – that is the composition of the epistemic frameworks as a whole – it cannot be claimed that Darwin’s place in the history of thought might be *within* the old Cartesian system of thought. However, I think, Richards is perfectly right when he claims that the neo-Darwinian reception of Darwin’s work was highly selective and concentrated primarily upon the core theorems of Darwin’s conceptual amalgam of otherwise partly adverse conceptual schemes. This selective reception led to a neglect of Ethology as a chronologically and structurally complementary synthetic movement in the 1930s. My project, by contrast, started with a careful examination of
when a group of so-called “architects” began to re-construct his original foundation by integrating the latest achievements of those sciences that were concerned with the heredity and variation of living organisms (Mendelism, statistical population genetics, allopatric speciation).\textsuperscript{22} It is one of the core-hypothesis of my thesis that Ethology originated as a conceptual fusion of divergent epistemic frameworks \textit{simultaneously and complementary} to the Modern Synthetic Theory of Evolution which, for its own part, established an epistemic amalgam consisting of both Population and Ecological Genetics.\textsuperscript{23} As a result, one may say that my dissertation

\textsuperscript{22} Those scholars who want to make explicit (alleged) connections to certain core-theorems of Darwin’s work – quite independently whether or not they have a critical attitude towards these theorems – tend to speak of “neo-Darwinism” or “neo-Darwinian Revolution”, while mainly the North American architects preferred the nominal phrases “(Modern) Synthetic Theory” or “Evolutionary Synthesis” in order to distance their approach to evolution from any forms of social Darwinism and other distortions of Darwin’s work. See for the usage of the various different concepts M. Ruse. \textit{Darwin and Its Discontents}. Cambridge: Cambridge University Press, 2006, 21, and W.-E. Reif et al. “The Synthetic Theory of Evolution: General Problems and the German Contribution to the Synthesis”. In: \textit{Theory in Biosciences} 119.1 (2000), 43–45. For a more extensive conceptual history see, T. Junker. \textit{Die zweite Darwinistische Revolution. Geschichte des synthetischen Darwinismus in Deutschland 1924 bis 1950}, (Acta Biohistorica. Schriften aus dem Museum und Forschungsarchiv für die Geschichte der Biologie 8). Marburg: Basilisk-Presse, 2004, 27–67. Further common descriptions are “second Darwinian Revolution” or “Synthetic Darwinism”. I tend to use the terms “neo-Darwinism”, “Modern Synthesis” (MS) and “Synthetic Theory of Evolution” synonymously in order to refer to the epistemic framework and its concrete expression which were both shaped in this new synthetic movement. This might seem problematic insofar as particularly E. Mayr claimed that researchers should not use the term “neo-Darwinism” to refer to the MS because it was G. J. Romanes who had coined the phrase decades before in order to disavow a scientific position which was conceptually quite different from Darwin’s, notably A. Weismann’s doctrine of the separation of somatic and germ lines – a notion which fundamentally contradicted Romanes’ Lamarckian attitude.

thesis makes, or must make, a contribution to a highly topical discussion which is ongoing at present amongst evolutionary biologists, namely whether and how the Modern Synthesis – even if it is conceived in its wider understanding – should be extended still by additional theorems which eventually even belong into those epistemic realms Darwin had declared “problematic” in his *Origin of Species*.24 As a first more concrete approximation to the topic of my thesis it might be said that three of the persons I have mentioned above, K. Lorenz, E. v. Holst, and N. Tinbergen, represented – either in a transitional (N. Tinbergen) or a final (E. v. Holst, K. Lorenz) stage of their intellectual life-history – the epistemic framework provided by Classical Ethology or the Classical Ethological Synthesis, whereas the two constitutive domains of G. Kramer’s behaviour research coincided more with the framework provided by the Modern Synthesis itself.25 Moreover, it is necessary to understand that for two of the named behaviour scientists, namely N. Tinbergen and, as I will show, also G. Kramer, this “double-synthesis” consisting of Modern Synthesis and Classical Ethology only marked a transitional stage during their overall intellectual development since N. Tinbergen and his work group at Oxford University successively but inexorably drifted towards Behavioural Ecology, Human Ecology or Functional Ethology in general, while G. Kramer, as I intend to show, more or less simultaneously might have changed into a pioneer of Cognitive Ethology and or, at least, what he himself called “Bio-climatology”. N. Tinbergen and G. Kramer are the two persons whose intellectual life-histories I will examine more carefully in this comparative case study. There are several reasons which let me choose these two behavioural scientists. At first, G. Kramer’s and N. Tinbergen’s trajectories together eventually cover the complete tableau of scien-

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24 P. Beurton has shown that the group of persons often called architects can be distinguished in two different – in the last consequence mutually irreducible – epistemic schools (theoretical population geneticists and naturalists) whose epistemic conviction even guided whether or not they addressed themselves as adherents of the Modern Synthesis although both realms turned out to be intertwined with each other or researchers switched from one into the other school. See P. Beurton, “Was ist die Synthetische Theorie?” In: T. Junker et al., eds. *Die Entstehung der Synthetischen Theorie in Deutschland*. Beiträge zur Geschichte der Evolutionsbiologie 1930–1950. (Verhandlungen zur Geschichte und Theorie der Biologie 2). Berlin: VWB – Verlag für Wissenschaft und Bildung, 1999, 80–92, 93–94. Partly contrary to Beurton, I tend to identify the mere coexistence of both schools and their intertwining as major characteristic of the MS. My understanding of the MS thus is epistemological. Beurton’s seems to be historical. For the integration of still wider areas of biological inquiry see M. Pigliucci, “Do We Need an Extended Evolutionary Synthesis?” In: *Evolution. International Journal of Organic Evolution* 61.12 (2007), 2743–2749 and M. Pigliucci et al. “Elements of an Extended Evolutionary Synthesis”. In: M. Pigliucci et al., eds. *Evolution – The Extended Synthesis*. Cambridge (Mass.): MIT Press, 2010, 3–17. For a general historical survey of how the MS was conceived by different people in different periods of the 20th century and especially the challenges the theory had to face since the 1970s see Smocovitis, *Unifying Biology* [1996], chapter two, “A ‘Moving Target’”, 19–44, particularly 34–44.

25 G. Kramer’s part in establishing the MS apparently has been totally forgotten, even by those who knew him personally. See Mayr, “Thoughts”, 23–28. Also J. Harwood does not mention Kramer. See J. Harwood, “Genetics and the Evolutionary Synthesis in Interwar Germany”. In: *Annals of Science* 42.3 (1985), 279–301.
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tific orientations constituting the epistemic community within which their research work was located. Second and however, in doing so, their life courses might be complementary in a sense that they, in principle, do not interfere with each other. Structural similarities in their scientific development therefore possibly point to supra-individual dynamics. Third, both life courses reveal the peculiarity that their earlier stages of life (early academic socialization and subsequent breakthrough of dispositions) are supplemented by a third phase which is characterized by a “drifting” movement and whose explanation eventually is not totally wrapped up in the mere double-logic of socialization and breakthrough of individual dispositions. Finally, both researchers conceived themselves as parts of an international scientific community. This aspect, together with the fact that covering the antagonistic derivatives which, since ca. 1955, branched off from the above mentioned Extended Synthesis yielded additional conflicts not only inside but also between or across different epistemic communities (a consequence of three), provides the opportunity to examine these conflicts on an international, maybe, even a global level without presupposing any geographic boundaries. Altogether one may therefore say that the two trajectories I aim to reconstruct represent major lines of development within the neo-Darwinian community (in a wider sense) as a whole so that my thesis also proves that this community becomes a living reproductive unit next to and in competition with both an older, in the last consequence, Cartesian epistemic community and a third structurally deviating unit of behaviour research. The foundations of the latter two most likely have been laid by C. Darwin’s works, that is on the one hand, his studies on transmutation which led to his *Origin of Species*, and, on the other hand, his reasoning on mind and behaviour, which established another partly deviant epistemological space and particularly culminated in his later works *The Descent of Man* and *The Expression of the Emotions in Man and Animals*. I think the latter foundation gained much topicality by E. O. Wilson’s sociobiological synthesis since the mid-1970s. However, I believe that this

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26 My thesis therefore points the way to a global history of knowledge-based social systems beyond national and transnational history the latter of which suffers from the logical paradox that it presupposes the national boundaries in a first step it aims to surpass in a second. The problematic is well known and therefore need not be regurgitated once more. And: There is no doubt that epistemic regimes are virulent regardless of whether or not researchers are able to find a match between scheme and theme! All these approaches, in the last consequence, seem operate with a conception of space A. Einstein tried to express when he made use of the metaphor of the “container”, that is the notion of classical geometry that space has an absolute character. That is they presuppose spatial entities no matter how small or large, or how extended they are defined. See A. Einstein, “Relativität und Raumproblem”. In: Idem. Über die spezielle und die allgemeine Relativitätstheorie. 23rd ed. Berlin et al.: Springer, 1988 [1917], 92–93. See also A. Einstein, “Raum, Äther und Feld in der Physik”. In: J. Dünne et al., eds. Raumtheorie. Grundlagentexte aus Philosophie und Kulturwissenschaften. (stw 1800). Frankfurt a. Main: Suhrkamp, 2006 [1930], 99.


28 I think that R. J. Richards’ studies on the emergence of the behaviour sciences in the 19th century started with a reception of those of Darwin’s work’s which were related to “mind” and “behaviour” and the question why Darwin tackled these issues in public only with some delay in

\(^{29}\) The delay with which the epistemic communities which Darwin had founded with his major works became filled with life usually is discussed amongst science historians under the catchphrase “the eclipse of Darwinism”. See M. A. Largent. “The So-Called Eclipse of Darwinism”. In: J. Cain et al., eds. *Descended from Darwin*. (Transactions of the American Philosophical Society 99.1). Philadelphia: American Philosophical Society, 2009, 3–21, here 1. On basis of this information, Prof. J. Paulmann has drawn the further leading conclusion that the history of Ethology therefore contributed to the pluralization of epistemic communities in the 20th century (oral information, 05/02/2013). I would even go so far as to say that the principles of cultural and scientific change I aim to evidence in my thesis, in the last consequence, have the function to maintain and increase desperately needed (cultural) variability.

\(^{30}\) For a critical reassessment of the concepts “generation” and “cohort” see Alwin et al., “Generations, Cohorts, and Social Change”. According to F. Alwin’s and R. J. McCammon’s suggestion, the term “cohort” refers to a group of persons sharing the same birth date. The members of a birth cohort share similar or same experiences (social history, life cycle, the cohort itself), so-called “cohort-effects”, but, according to Alwin and McCammon, these shared experiences still do not make a “cohort” a “generation” (Ibid., 26). The concept of “generation” can be understood in a “kinship sense” and a “historical sense”, meaning “groups of people who share a distinctive culture and / or a self-conscious identity by virtue of their having experienced the same historical events at roughly the time in their lives” (Ibid., 27). The latter usage exceeds the definition of both “cohort” and “cohort-effects” by either bringing in the criterion “shared historical experiences”, or by including an ontogenetic nuance (“at roughly the same time in their lives”) and, if I have understood correctly, by demanding a more of “shared identity” (Ibid., 27–28, 41–42) or “style recognized from outside and from within” (Ibid., 27, literally quoting H. White’ thesis whose reference can be found on page 49). I will use both concepts primarily when I examine the works of N. Tinbergen’s pupils and here both the term “cohort” (similar birth date plus shared cohort effects) and the more specific concept “generation” (shared identity, here being subject of Tinbergen’s practice of academic socialization) apply particularly well. As will become clear later in my thesis, I think that Niko’s two generations of pupils can be distinguished by the epistemic framework within which they were socialized and the behavioural patterns of their response to this socialization.
show that this new synthetic wave of biological inquiry encompassed a much wider range of heterogeneous scientific orientations. While examining G. Kramer’s and N. Tinbergen’s life courses I will in particular ask for the transitions that were shaping each trajectory in its own way and how the respective pathway fits into what – in alluding to C. H. Waddington’s concept of “epigenetic landscape” – might be called the overall “epistemic landscape”. The “epistemic landscape” established by both life-histories together, in turn, might be interpreted as a form of bio–graphical representation of the cyclical dynamics of transformation I have in mind when I speak of “knowledge cycles”.

b) Accounts of Others and Desiderata

If taken for granted that the mid-20th century knowledge cycle as defined in the preceding subchapter is the main thematic focus of this treatise, then the research literature published so far can be sorted along the preshaped lines. Thus, since the end of the 1960s a considerable amount of publications put emphasis on the origins and early development of biological behaviour research. Here again, older studies dated the beginnings of Ethology in the Germany of the 1930s. These studies tended to be scientific-immanent and very often – though not exclusively – originated within the epistemic milieu of the biological sciences themselves.


The Edinburgh embryologist C. H. Waddington coined the concept “epigenetic landscape” to illustrate that the differentiation of homogeneous cell populations into different cell types might occur in canalized pathways that is under the control of stabilizing forces such as the norm of reaction provided by a gene, gene-gene interactions and gene-environment interactions. For Waddington’s model of ontogenetic development see L. van Speybroeck. “From Epigenesis to Epigenetics. The Case of C. H. Waddington”. In: Annals of the New York Academy of Sciences 981 (2002), especially 72–73. For the manifold lines of epigenetic research and modelling see J. Baedke et al. “Die andere Epigenetik: Modellbildungen in der Stammzellenbiologie und die Diversität epigenetischer Ansätze”. In: V. Lux et al., eds. Kulturen der Epigenetik: Vererbt, codiert, übertragen. Berlin et al.: De Gruyter, 2014, 23–41. I adopted Waddington’s topographic concept deliberately loosely and ambiguously: I am interested in the latent forces underlying human development (symbolized in the slope-like shape of the model) yet believe that the interaction between human organisms and their environments should be more adequately conceived in terms of agency and less environmental causation (that is more the hillocks rather than the valleys in the model). In addition to that, I am wondering whether all transitions in an individual’s life course are actually triggered by “epi-genetic” mechanisms.

More recent investigations, on the contrary, tend to take a European perspective by putting emphasis on precursors and prehistories.\textsuperscript{34} Further studies underscore the existence of early ethological research in the United States at the beginning of the 20\textsuperscript{th} century and put the main protagonists into a comparative perspective.\textsuperscript{35} In sum, there is a trend to broaden the view on wider chronological and geographical contexts of Ethology’s commencement. Moreover, science historians reveal a stronger propensity to consider the possibility of parallel innovation relatively independent from direct impacts.


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In general, one may say that scholars who were interested in the further history of biological behaviour studies approached the main trajectories of research by putting emphasis on single representatives, their lives and contributions to the institutionalization of their disciplines. On the one hand, we can therefore rely on a comparatively large number of autobiographical accounts written by time witnesses who – though directly involved in their stories – nonetheless tend to bring in the objectivistic view they used to practice in course of their lives as researchers. Science historians agree with many biologists that transformation, development and creation of knowledge might primarily be a mental, cognitive and constructive process at whose centre is first of all the human being. The popularity of biographical accounts in combination with their heuristic value resulted in numerous historiographical examinations of individual lives, in particular, of the three Noble Prize Winners of 1973, whereby the authors of these texts were coming both from within and the outside of the primary scientific discipline. The colourful personality of K. Lorenz and the many facets of his life thereby surely attracted both us historians and the biologists with a historical interest at the foremost.


Thus, next to a series of general biographical accounts, there are also a number of specialized studies dealing with K. Lorenz and his fame as popularizer of his science as well as political figure of public life and environmental activist.\(^{39}\) Besides his own life the biographies of Lorenz’s “teachers”, that is mainly O. Heinroth and E. Stresemann, attracted the attention of science historians and historically interested time-witnesses.\(^{40}\) Apart from being mentioned in a few earlier accounts, K. v. Frisch became the object of us science-historians’ interest only in very re-

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cent years – particularly in T. Munz’s research.41 His life-history might eventually reveal the existence of pre-sociobiological research which may lead to a more comprehensive understanding of the epistemic communities involved in the history of the comparative behaviour sciences in the 20th century. In comparison to Lorenz, N. Tinbergen’s biography was much less in the centre of historical interest – unjustly I am inclined to say since his turn to Behavioural Ecology contributed much to the vivid apparency of the neo-Darwinian epistemic community we regard self-evident nowadays.42 In addition to the biographies of the Nobel laureates, the lives


of a number of further protagonists of 20th century animal behaviour study such as, for instance, E. v. Holst, J. Huxley, Ch. Elton, J. B. S. Haldane and B. Rensch, went into shorter biographical accounts.\textsuperscript{43} Next to the “pure” biographies and auto-biographies there are a number of quasi-biographical accounts which have a wider research interest in as much as they interpret the examined trajectories as representative for the development of an entire research branch. These studies either take individual life-histories as a starting point and place these life courses within the overall development and / or are composed as comparative biographical investigations. The latter case in particular applies to the relationship between K. Lorenz and N. Tinbergen by which historians of science aimed to approach the mutual diversification of Classical Ethology and Behavioural Ecology.\textsuperscript{44} In particular, R. W. Burkhardt’s examinations here reveal a high degree of differentiation in focusing on certain relevant aspects such as aggression, subjective experience and “place”.\textsuperscript{45} Studies with more extensive non-person-oriented research foci either have chosen scientific schools and disciplines as their primary investigative units or put emphasis on regional and / or national contexts so that many of them tended to neglect the deeper-lying epistemic constitution of the scientific community.\textsuperscript{46}


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trate on the epistemic community directly related to the foundation of Ethology we may in conclusion infer that two of the three main areas of biological behaviour research are represented fairly well in historiography, namely Classical Ethology and the branching-off of Functional Ethology. What has been neglected so far from a purely intra-scientific point of view is the existence of a profound sub-branch of ethological research leading towards Cognitive Ethology and related fields such as Neurobiology and Neuroethology. I personally see further desiderata in a detailed and more systematic examination of the origin of Behavioural Ecology, its relation to earlier more Lamarckian orientations and its dissemination in Germany (W. Wickler), Great Britain and the United States. In particular, besides a few obit-


48 An attempt to trace the origins of Behavioural Ecology in Ethology has recently been made
uaries and some brief references in historical accounts there is no extensive study of G. Kramer’s intellectual life-history and his pioneering work. As I will show, it was his works on avian orientation and navigation which most likely anticipated the rise of Cognitive Ethology just as his study of relative growth at least pointed the way to a theory of evolution beyond the Modern Synthesis – a position which, in S. J. Gould’s words, might be called provocatively “the return of the ‘Hopeful Monsters’”. Moreover, by no means we have a complete picture of the transformation process Classical Ethology itself underwent from the mid-1930s to the mid-1970s beyond the emphasis on the main protagonists. The fact that powerful new lines of behaviour study branched-off from Ethology (while adopting theorems covered by the Modern Synthesis) does not mean at all that the epistemic framework provided by Classical Ethology ceased to exist. In particular, there is no study on the successive emergence of Human Ethology including P. Leyhausen’s, H. Prechtl’s and I. Eibl-Eibesfeldt’s research work on cats, infants and native ethnic groups. What is desperately needed in my opinion simply is a thorough history of the MPI for Behavioural Physiology which was founded in 1954 as double-institute for K. Lorenz and E. v. Holst and henceforth was growing steadily both by the integration of further and the finer bifurcation or specialization of already existing departments. Moreover, histories on biological behaviour research have situated their fields of interest only insufficiently within the larger framework of evolutionary theory. On the other hand, those historians who were concerned with the reconstruction of the Modern Synthetic Theory did not realize at all that the epistemic areas covered by the Modern Synthesis in sum establish only a reduced research program if it is compared with the full tableau of epistemic fields Darwin had outlined in his *Origin of Species*. In other words, the fact that Classical Ethology originated both simultaneously and complementary to the Modern Synthesis – as I will show in my comparison of G. Kramer’s and N. Tinbergen’s life history – has not been realized at all so
far.\textsuperscript{51} This only shows that the epistemic constitution of the scientific community or communities which were concerned with the biology of behaviour in the 20\textsuperscript{th} century has not been understood up to now. In general, there is still a tremendous lack of epistemological research locating the various schools of behaviour studies within the field of the natural sciences.\textsuperscript{52} If we widen our perspective beyond the core-community which is subject of my investigation, we may soon realize that there might coexist a second Darwinian epistemic community in which still other branches of comparative behaviour sciences originated and flourished. This community has received some attention in as much as E. O. Wilson’s sociobiological synthesis became subject of several historical accounts.\textsuperscript{53} What has not been examined carefully enough so far is the possibility that sociobiological research might have had precursors already in the first half of the 20\textsuperscript{th} century.\textsuperscript{54} I think that a careful epistemological study of K. v. Frisch’s life course and his works on Insects and Fish in combination with the paths his “descendants” in a narrower and wider sense (e. g. M. Lindauer, B. Hölldobler, H. Autrum, H. Markl) have taken would prove the coexistence of two Darwinian epistemic communities related to the study of behaviour.\textsuperscript{55} And I think it possible that G. Tembrock’s bioacoustic research program in the former German Democratic Republic might belong to this thought system although this hypothesis should be clarified in a more detailed separate study as soon as his private archives are available for us science historians.\textsuperscript{56}

What can be the contribution of my thesis against the backdrop of this research overview? First of all, my emphasis upon the epistemic community as a whole leads to a more systemic view upon the history of Ethology and its derivatives without necessarily giving up the special focus on representative protagonists which has turned out to be extraordinary fruitful. Thus I can claim that the two life-histories

\textsuperscript{51} As far as I can see M. Weber mostly concentrates upon the synthesis of Population and Ecological Genetics and therefore does not mention Ethology. Junker, for instance, explicitly excludes K. Lorenz from his sample of architects due to the latter’s typological approach and the fact that his attempt to link his phylogeny of behaviour with modern genetics remained mere program. See Junker, \textit{Die zweite Darwinistische Revolution}, 150–153.

\textsuperscript{52} See here W. Schleidt’s critical annotation to recent histories of Ethology: W. Schleidt. “The Founding of Ethology”. In: \textit{Perspectives in Biology and Medicine} 49.3 (2006), 461.


\textsuperscript{55} I was hoping that T. Munz would raise this field of historical research. For a promising start see T. Munz, “The Bee Battles: Karl von Frisch, Adrian Wenner and the Honey Bee Dance Language Controversy”. In: \textit{Journal of the History of Biology} 38.3 (2005), 535–570.

\textsuperscript{56} P. Bateson recently honoured G. Tembrock as one potential co-founder of modern animal behaviour study. See P. P. G. Bateson. “Behavioural Biology: The Past and a Future”. In: \textit{Ethology} 118.3 (2012), 216.
I have put in the centre of my inquiry not only cover the realms of Classical Ethology or the path to Functional Ethology (including Behavioural Ecology, Functional Physiology and Human Ecology) but also the Modern Synthesis and the path to Cognitive Ethology. Maybe, for the first time the major lines of the bigger picture of the entire epistemic community including its inherent reproductive dynamics will become comprehensive. Especially my account of G. Kramer’s trajectory will fill a gap since his life and work have not been treated in a historical study before. Second, my emphasis upon the more conservative deeper-lying strata of scientific change in combination with the particular setting of the comparison will carve out the particular forms of epistemic variability which make the epistemic community as a whole a vivid and reproductive thought system. Thirdly, my thesis presupposes the coexistence of at least three epistemic communities which were concerned with the study of behaviour in the 20th century and which became partly mutual competitors as soon as they began to change into actual social systems. By picking core-Ethology and its derivatives as a starting point my thesis will show that conflicts between these communities emerged at predictable points of friction and, beyond that, might have taken another form of social interaction, too. The fact, that these epistemic areas of interaction and conflict can possibly materialize themselves in geographic regions all over the world in combination with the observation that the discrete positions within an epistemic community are mostly arbitrary in terms of nations and nation states, allows to read my thesis also as a contribution to a global history of expert systems or expert cultures beyond national and transnational history. My argument actually includes two steps. At first, I do agree that in some areas of historical research such as, for instance, the history of the sciences it seems more promising to focus upon smaller investigative units below the level of nations, nation states and the wider extended transnational entities of historical inquiry, simply because the prototypical roots of the epistemic communities within which the modern sciences take place can be traced back at least into the 17th century, that is, an age when, at least in the area of the German territories, there were existing no nation states yet. Epistemic communities are therefore at least chronologically pre-national phenomena. Moreover, epistemic communities, as I aim to define them for my heuristic purposes, are most likely too diversified internally to address them (as a whole or in parts) stably with national stereotypes such as “Dutch Ethology” or “German Biology” while internal complexity most likely even applies to the discursive fields within which national identities are negotiated. Revealing internal complexities and mutual deconstruction of value systems legitimately raises the question of “discursive intertwinement”, the epistemic preconditions of this intertwinement, and the various forms of cultural manifestation these epistemic dispositions can be expressed with – sometimes quite independent of national boundaries. The establishment of a scientific community of behaviour scientists that went hand in hand partly with the genesis of the modern sciences most likely was a

58 Several historians focused on processes of nationalization in science and the intertwinement of both spheres, e.g., J. Harwood. “National Styles in Science. Genetics in Germany and the
more international endeavour right from the start. To examine cross-references and to avoid misreading (in H. Bloom’s sense) requires a both relativistic and pluralistic approach that allows to switch between and delve playfully into various different scientific positions. My approach is therefore definitely nothing else but a plea for the peaceful coexistence of and a more playful interaction between often substantially deviating ideological machineries – well knowing that virtually all of them contribute to the recreation of culture. If one’s own research cannot escape its own frames this, certainly, would force us to choose reference systems that allow and promote this pluralism. Second, I also do agree with some science historians that it is particularly the national boundaries loosing their importance in our seemingly so globalized world which seem to show that (regional) research centres actually do exist and, moreover, that they are not distributed randomly over the surface of the earth but, instead, that they are connected with each other in epistemic communities and larger systems of knowledge production and reproduction. Whether or not the accumulation of particular scientific orientations including the corresponding set of epistemic practices being cultivated by the researchers in question necessarily have to have a spatial or geographical correlate, I think, is facultative. Finally, my study does not treat biographies of researchers as isolated appearances or for their own sake but as representations of a more general cyclical dynamics of transformation – a wider realm of historiographical inquiry which can be interpreted as a sort of environment for the life courses I aim to reconstruct. To address this environment, right from the start, eventually other concepts of “milieu” must be found than the ones used by those who were following and thinking ahead L. Fleck’s, P. Bourdieu’s and T. S. Kuhn’s social theories of scientific change: Being granted that researchers primarily “construct” their social and / or institutional environment, evincing the mere fact of “structural coupling” does not reveal the principles underlying this creative process. My thesis traces biographical trajectories in order to highlight the particular spatio-temporal distribution of the epistemological reference systems within which the representatives of an epistemic community placed their research at a given point of time in their psychophysical development. In future studies, it has to be asked what socio-biological dynamic can incite this distribution? To understand these dynamics might be of interest beyond the boundaries of the history of the sciences. Moreover, in order to understand human culture, future research endeavours

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59 For the existence of non-randomly distributed geographical centres of research see H. C. R. Henke et al. “Sites of Scientific Practice: The Enduring Importance of Place”. In: O. Amsterdam et al., eds. The Handbook of Science and Technology Studies. 3rd ed. Cambridge (Mass.): MIT Press, 2008, 355. Contrary to that, some contemporary theories of practice postulate that knowledge based behavioural routines (i.e. scientific practices) are “interobjective” – i.e. related to specific scientific objects and independent of space and time. See A. Reckwitz. “Grun-delemente einer Theorie sozialer Praktiken”. In: Idem, ed. Unscharfe Grenzen. Perspektiven der Kultursociologie. Bielefeld: Transcript-Verlag, 2008, 117–118, also 126–127. My concept of “scientific orientation” (which will be explained below) allows to think both propositions in one. Researchers either sharing the same scientific orientation or being eager to oppose a particular orientation find each other no matter where their geographic location currently is on planet earth!
eventually must try to shape a new synthesis which covers both the plasticity of the human organism and a theory of cyclical social change, as well as the mutual intertwining of both realms. I further postulate that this synthesis cannot be built on basis of mere discourse analytic approaches and their derivatives since they are primarily interested in the transmission of knowledge from one to another generation rather than in generating promising matches between observation-based data and adequate reference systems of which I believe that it is one of the heuristic prerequisites to form a synthesis of cultural inquiry. My thesis concentrates upon the former of the two realms of inquiry. It is more what K. Lorenz once playfully called “pure Leicology”: It wants to reduce complexity on basis of meticulous observations which, for their part, intend to refine the abstractions that resulted from rather extensive preparatory studies.

c) Chosen Sources and “My Methodology”

To me it seems quite obvious that the developmental shading of my topic, that is the intention to reconstruct scientific manifestations upon an individual time axis, requires a type of historical sources which fulfills several requirements. Firstly, the type of sources I need must have been generated in periodical intervals and therefore must have a serial character. Moreover, it must be possible to date the sources exactly. Secondly, they must be more or less particulate though representative epistemic units. That is, their content, or more general, the information they contain must be reducible to scientific positions or standpoints. Finally, and closely connected with the previous point, in one way or another they must include some kind of inner organization which allows me to recognize and position a respective scientific statement within the overall reference system (which will be outlined soon below). All these demanded characteristics let appear published sources as one of the most suitable type of source for my research endeavour. However, it cannot be neglected that scientific publications also have some essential disadvantages. At first, publications always appear with some delay in time. This is simply due to the fact that scientific publishing establishes hurdles which to surpass requires additional efforts. A considerably amount of correspondence in the personal papers of researchers is devoted to this issue proving how time consuming the practice of publishing actually was in earlier times and still is. As a result, scientific publications are lagging somewhat behind a researcher’s actual intellectual development which they are meant to represent. Second, research belongs to those cultural practices which intend to convert uncertain to certain and confirmed knowledge. This may sound like a triviality but it has the effect that large parts of the creative process in course of which a researcher develops her or his ideas is excluded or remains unrepresented. For instance, in G. Kramer’s publications we will not find the information that he tested a theory according to which solar activity affects the flocculation of the blood – a hypothesis which finally turned out to be false but nonetheless might tell us something about Kramer’s interests or his way of shaping ideas. To avoid or balance these negative side effects I have used archival sources, at first, without any presupposed preferences then more and more with a special focus on my own interests. In general, the personal papers of researchers include documents we might
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not expect at all at first sight such as the lots of correspondence which is concerned with obtaining experimental animals, food for animals and the maintenance of the stock. Another part of correspondence is related to negotiation of dates for meetings, travels and their financing, or administrative issues of all kinds. I still believe that all these different types of sources can be of value if we are able to find the right research question. For my investigative purpose the following sorts of documents turned out to be most informative. Depending on correspondent there are quite a number of letters especially in G. Kramer’s papers which contain information about own research endeavours (e.g. reports on orientation experiments) or discussion of the works published by others. Very promising is the constellation when members of the same work group are spatially separated so that they needed to exchange their ideas in letters. For instance, U. v. St. Paul and K. Hoffmann, two pupils of G. Kramer’s, carried out navigation experiments with pigeons in the United States and England while Kramer himself dwelt at his institute in Wilhelmshaven. In this case I found significant documents. On the contrary, despite the fact that the members of N. Tinbergen’s famous Animal Behaviour Research Group (ABRG) at Oxford University cultivated an highly elaborate peer-to-peer tutoring system it is difficult to make evident the effect of this scientific interaction because it happened through direct communication which isn’t likely to have left many written traces.

Besides the letters sometimes the manuscripts of lectures or popular presentations have been preserved. This sort of document is often more explanatory than highly condensed academic papers – especially in case of G. Kramer’s publications which usually were highly reduced though extraordinarily reflected and organized research reports. In addition to that I found informative proposals for research grants, accompanying correspondence and evaluations of both the researcher who was about to start a project and the research project itself. This type of document is of utmost interest because of its prospective character and also because it reveals that research usually begins with a much wider range of possible ideas than finally appears in the ultimate publication. As to the time span the sources of the personal papers I have worked through are covering, one can say that in general the period after the Second World War is represented better. One of the reasons explaining this matter of fact might be that the two persons my thesis is primarily concerned with took over advanced administrative functions primarily after 1945 either as lecturers and professors, on the one hand, and / or as head of a department in a research institute, on the other. In case of N. Tinbergen’s papers science historians have to face the problematic that he destroyed much of his correspondence with friends and colleagues except those documents which still were of value for him when he had grown old. To this scope of preserved sources belongs, for instance, the correspondence he maintained while he was engaged with early childhood autism that is during the period shortly before and after his retirement. H. Kruuk’s biography of Niko Tinbergen is of great value for me not least because he made the attempt to compensate this gap by using many interviews with Niko’s contemporaries and pupils. When historians are confronted with silent periods in a researcher’s personal papers they still have the option to search the holdings of those institutions the respective individual was affiliated with in his life or approach the correspondences from the side

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of the other correspondent and try to find complementary letters. I have made use of this option in singular cases yet have not exhausted it. For instance, I tried to compensate N. Tinbergen’s lost correspondence by taking into account the letters he exchanged with J. Huxley from the mid-1940s to shortly before Huxley’s death. However, my primary focus was lying on publications and the personal papers. Some readers of my thesis will be wondering why I elaborate on my methodology after I have described my source material. The reason for this move is that my methodology has grown step by step over the years while I was examining the effects of epistemic cycles in scientific communities related to the study of animal and human behaviour across various different time layers ranging from the 17th, over the 19th to, finally, the 20th century. My methodology therefore has the character of an abstraction and less of an artificial model although this certainly does not mean to imply that, from time to time, I felt great pleasure when I was able to connect my research with the views of others. I think that reconstructing the life courses of researchers – in the last consequence, on basis of epistemic practices and their dispositions – requires both an adequate overall reference system and a tool that allows to locate the cultural and scientific expressions of a person within this reference system.

The largest basic structural entity I should like to introduce is the epistemic community.

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more intrinsic dynamics of production and reproduction of knowledge. This process of knowledge reproduction, in turn, seems to be based partly on behaviours in general or, more precisely, on epistemic practices, in particular. Scientific or cultural practices are usually defined as shared latent precondition of explicit cultural manifestations as implicit, tacit or even subversive complement of knowledge and its conscious manifestations. In psychoanalytic theory practices even turn out as “the other side” of our selves, another self which has a both material, informal and behavioural nuance, which is connected to bodily routines or is artefact, yet is not situated in the environment itself. For my argumentative purpose, it is important to detach the idea of practice from particular scientific positions and learn to understand them as ordering performances that can be both the expressions of deeper-lying dispositives and the tool to modify these dispositions. In other words, the type of practices I have in mind can act in service of a norm as well as they can alter and establish this norm in the first place - no matter what this norm may be. From a structural point of view the epistemic community, to be understood as overall reference system, consists of sub-entities which I call “scientific orientations”, a concept I have adopted from L. Nyhart. According to L.


65 Defining “scientific orientation” as subunit of a larger heuristic entity, the epistemic community, implies that the orientations are connected with each other. See here for the network character of orientations W. Stegmaier. “Grundzüge einer Philosophie der Orientierung. Ein Forschungs-
Nyhart, who has introduced the concept into the history of sciences in her study on 19th century Morphology in Germany, “orientation” can be defined as a certain area of study related to a group of people sharing the same “philosophical attitudes accompanying the cluster of problems they are working on.” Beyond that, “orientation” is used similarly loosely as “school” but in contrast to the latter does include also more indirect impacts of a wider milieu beyond the narrow, direct and individual interaction between teacher and pupil – the latter not being excluded. Moreover, as a rough translation of the German word “Richtung” (lit. “direction”, “line of thought”), according to Nyhart, “orientation” refers to a sort of vision which is both less codified and less self-consciously articulated than is implied, for instance, by “research program”. Finally, “orientation” means something less institutionally solidified and epistemologically deeper-lying than do the concepts of “disciplines”, “sub-disciplines”, and “sub-specialities”, which are defined more concretely, by chairs, institutes and teaching appointments. The history of Ethology shows that scientific orientations can but need not become manifest in the structure of scientific institutions. In sum, the concept of “orientation”, as I would like to use it, encompasses the wider, looser, though deeper-lying, practical and mental dispositions being characteristic of single members or part-groups within an epistemic community which can but need not be materialized in schools, programs or institutions. I think I go beyond Nyhart’s understanding of the concept when I add to her general definition a more specific and structural one. In my view, a scientific orientation turns out to be a scientific paradigm, in a very literal (here linguistic and eventually non-Kuhnian) sense in as much as the larger investigative unit “orientation” can be decomposed into further subunits. Over the years I studied these entities, I realized that a scientific orientation in principle always consists of two different “realms” or “registers” and at least three different “levels” or “dimensions”. As a result, one scientific orientation in principal is built by at least six


There is a long-lasting debate in the history and philosophy of the sciences about what to understand by “primary” and “secondary” qualities of things. And I think, the hypothesis should
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different subunits which I call “epistemic scheme” or, synonymously, “epistemic pattern”, “reference system” (following N. Bischof) or “frame” (adopted from W. James). The reason why “behaviour” as a concept is discussed by distinguishing at least three different dimensions probably lies within the fact that “behaviour” as a phenomenon observable in living organisms is closely related to the idea of motility within a three-dimensional space. Conversely, it might well be, that human beings would not be able at all to perceive three-dimensional space without objects moving within this space, at least not without objects being extended in space. As a result, the idea of three-dimensional space is closely intertwined with both the phenomenon and the concept of “behaviour”. I cannot answer the question with definite certainty why our understanding of behaviour is so closely related with the idea of geometric space. What can be claimed for certain is that the three dimensions which establish our perception of geometric space precipitated into the concept of behaviour as three discrete semantic, thematic, or contextual levels. These dimensions are related to the ideas of variability, causality and complexity whereby the epistemic schemata located on each level can become manifest in manifold expres-

be tested whether this discussion does not refer to what I’ve called “registers” or “realms”. For a first approximation to the problematic see A. D. Smith. “Primary and Secondary Qualities”. In: The Philosophical Review 99.2 (1990), particularly 221–222 and 230.


My interest tackles the quest for a common theory of behaviour. A minimal consensus here seems to be that behaviour refers to all aspects (movements, sensations, etc.) by which an organism mediates its relationships with its environment. See here R. D. Alexander. “The Search for a General Theory of Behaviour”. In: Behavioral Science 20.2 (1975), 77.

E. Jablonka and M. J. Lamb, for instance, distinguish between four dimensions of evolution and the information that is of utmost interest for my argument is that “behaviour” is discussed as a phenomenon with three dimensions. See E. Jablonka et al., eds. Evolution in Four Dimensions. Genetic, Epigenetic, Behavioral and Symbolic Variation in the History of Life. With Illustrations by Anna Zeligowski. Cambridge (Mass.): MIT Press, 2005. However, I would like to stress at this point that my understanding of “dimension” deviates from Jablonka’s and Lamb’s, which seems to be inspired by H. Maturana’s radical constructivist approach to the phylogenetic development of human cognition, inasmuch as my definition of “dimension” combines the conceptions of “three-dimensional space” and “behaviour”. I feel supported in choosing this more conservative conception by the research of John O’Keefe, May-Britt Moser and Edvard Moser who were awarded the Nobel Prize for Physiology and Medicine in 2014 for their achievements in explaining the physical mechanisms of animal orientation: Like early ethologists have postulated, organisms seem to mirror their spatial environment directly in their bodily structure and I am wondering whether this findings do not only apply to physical space but (mediated by the ideas of “motion” and “behaviour”) to epistemic space, as well. If this question could be answered in the affirmative it would have drastic consequences for the study of human culture inasmuch as cultural change not only involves mere transmission but also a number of organismic parameters establishing rules and constraints for building and maintaining human tradition.

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sions. For instance, the question of variability can be discussed in terms of nurture vs. nature, whether variation is gradual and continuous or abrupt and discontinuous, whether boundaries are exceeded or maintained, whether organic appearances are flexible or static, or whether they are special or general.\textsuperscript{71} The second level is related to causation. Behavioural scientists, over several centuries, learnt to distinguish between direct (proximate) and indirect (ultimate) causes.\textsuperscript{72} There are many, more or less metaphorical, and beyond that, sometimes arbitrarily used circumscriptions of this conceptual field.\textsuperscript{73} One of them is related to the dualism of observation and experiment, another to the question whether behaviour studies


take place in the field or within a laboratory. In both autobiographies and biographies of K. Lorenz and his friend, N. Tinbergen, we find repeatedly the dualism of the “farmer” (Lorenz) and the “hunter” (Tinbergen) – the one who goes into the wild and adapts to an environment in contra distinction to the one who takes nature into one’s own possession and cultivates it. Ultimate causation is therefore closely connected with the idea of “adaptation” and since Darwin therefore also with the notion of “selection”, while – particularly in ethological reasoning – proximate or mechanical causality often is described in terms of “dysfunction”. The third level can be approached best by describing it in M. Foucault’s words as the “anthropolog...
ical” dimension of behaviour.\textsuperscript{77} It is always related to some kind of vertical relation, for instance, in R. Descartes’ method of doubt, when S. Kracauer speaks of the “historian’s journey” or in Foucault’s own conception of “dream”.\textsuperscript{78} The anthropological dimension of behaviour is also related to the idea of hierarchy, (academic) discipline and the aspect of institutionalization. That complexity was and still is discussed highly arbitrarily within the area of behaviour sciences most obviously becomes evident in the researchers’ view on animals: Whereas some tended to seek for physiological roots even in human behaviour (zoomorphism) others, on the contrary, were prepared to point out intellectual and even moral qualities in animals (anthropomorphism).\textsuperscript{79} The question whether or not researchers, research groups or


\textsuperscript{79} The relationship or boundary between man and animal recently gained enormous attention in history and historical anthropology. To my sense, the studies in question often neglected the deeper-lying cultural and scientific dimension the relation is \textit{expression} of. Not so G.
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Schools can be reduced to so-called “model organism” or “emblematic animals” is related to the scientific practices of researchers and their anthropological dimension but – if the existence of “model organisms” is simply presupposed uncritically and in a statistically untested way – it also shows how blurred the methodology of science historians sometimes can be with the primary object (here the reduction to one particular scientific object) they wanted to examine in the first place. Beyond that, the anthropological dimension of behaviour pervades into the problematic of scientific methodology of researchers. Although these terms are used arbitrarily (even already in the works of R. Descartes), concepts such as “analysis” and “synthesis” usually may imply a vertical spatial dimension and – pending on usage and author – either mean the progressive increase or the reduction of complexity. Since the middle of the 19th and especially in the following 20th century the problematic of order and disorder was possibly more and more expressed in the vocabulary provided provided

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For instance, H. Spencer in his Principles of Psychology most likely arranged the phenomena he discussed along particular curves in a mathematical system of coordinates with four quadrants. These corresponded with four major heuristic procedures he called “General Analysis”,
by thermodynamic theory. In popular accounts of thermodynamics, as well as in scientific handbooks, “entropy” is described as a parameter for disorder: The higher the disorder, the higher the entropy – ultimately heading to a state of complete disorder, which is “appropriately called heat death”. In later information theoretical re-conceptions of the principles of thermodynamics “entropy” turned out to be a measure for heuristic uncertainty. Order, by contrast, is associated with heuristic certainty and – if thermodynamic theory is applied to the sphere of organic growth and development – with life. To mark the difference between living organisms and inorganic matter, E. Schrödinger in his treatise *What is Life?* (1944) underlined: “Life seems to be orderly and lawful behaviour of matter, not based exclusively on its tendency to go over from order to disorder, but based partly on existing order that is kept up”. Order, Schrödinger continues, is preserved by organisms via extracting order from its environment or – as he paraphrases his thesis – by getting rid of the positive entropy it is forced to produce as long as it lives. “Thus the device” – he summarizes – by which an organism maintains itself stationary at a fairly high level of orderliness ( = fairly low level of entropy) really consists in continually sucking orderliness from its environment. This conclusion is less paradoxical than it appears at first sight. Rather could it be blamed for triviality.

The theory of thermodynamics, in general, and its information theoretical interpretation, in particular, is one of the conceptual contexts that heavily pervaded ethological theorizing especially in the works of K. Lorenz. For instance, in one of his later books, namely *Die acht Todsünden der zivilisierten Menschheit* (Civilized Man’s Eight Deadly Sins), he connected the hyperbolic seek for pleasure, on the one hand, with a loss of emotionality, on the other, by using the vocabulary of thermodynamics: Literally, Lorenz spoke of “Heat Death of Emotionality” by which he – in accordance with the heuristic double-logic of his hypothetical realism – meant to say that the loss of constraints and their perception might prevent humans from experiencing emotions such as the “pleasure” and the “lust” humans sense when they have successfully surpassed a problem or, more precisely, have removed

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an obstacle.\textsuperscript{86} Altogether it’s not quite a simple undertaking to find the common denominator of all three dimensions of behaviour and the epistemic frames being located upon them. However, one common aspect seems to be that all frames define prototypical relations between an object and a human’s body. For instance, when behavioural scientists argue on the level of causality they discuss whether the vector of the behaviour in question points \textit{away from} or \textit{into} the direction of a body independent whether this body is located in the centre of the reference system. The plasticity of a behaviour is related to the spatial extension and the motility of a body, whereas the anthropological dimension of behaviour is essentially connected with a vertical dimension of space. Moreover, since Ch. Darwin’s epistemological interventions into the previously prevailing scientific paradigm, the epistemic frames on each level of the scientific orientation appear to be \textit{freely combinable} and this matter of fact, in my opinion, is one of the reasons for the fact that the epistemic space, within which the behavioural sciences of the 20\textsuperscript{th} century developed, is a three-dimensional space. Each epistemic pattern on any level of a scientific paradigm is combinable with any other just like – at least if we want to fall back into the modes of presentation for the geometric space – any point on any axis in a system of coordinates can be combined with any point on every other axis – the logical precondition for being allowed to place the axes of a coordinate system perpendicular to each other. On basis of this general considerations a general problematic becomes evident with which all behaviour scientists including us science historians are confronted. The medium “text” is inadequate to represent three-dimensional motions because of its linear nature.\textsuperscript{87} As a result, we have to do with a heuristic process in course of which movements in time and space are translated into writ-


\textsuperscript{87} I think it would be a further leading exciting research question to assess the extensive usage of film material by ethologists, both for the sake of behavioural analysis and popularization, from this angle. For a first attempt to consider the practice of filming see G. Mitman, ed. \textit{Reel Nature. America’s Romance with Wildlife on Film}. Cambridge (Mass.): Harvard University Press, 1999. For a possible data basis for a project on film see W. Schleidt et al. “The ‘Konrad Lorenz Duck Film Collection’: A Monument to Methodology and History of Science Re-discovered”. In: \textit{Journal of Ornithologie} 152.2 (2011), 505–506. From T. Munz’s epistemological assessment of ethologists’ usage of films we can infer that motion-picture provided several heuristic advantages, for example, that a (wider) audience could become eye-witness of experiments or the (seemingly) unrestricted and uniform repeatability of behavioural bouts. See Munz, “Die Ethologie des wissenschaftlichen Cineastes”, 53, 65–66. Besides the increase of intersubjective verification and the presentation of animal behaviour as lawful scientific object, it might be possible, that the usage of a particular medium can serve as valuable identification signal of a researcher’s scientific orientation. T. Munz’s paper seems to be on the right track.
ten text and from there, while reading these texts, need to be resurrected in the reader’s imagination. Especially the latter part is difficult and must be trained. Both the information contained in my source material and my own experiences gathered during oral presentations show that the ability to evolve a multi-dimensional mental space cannot be presupposed self-evidently in us humans. The tree of life, as Darwin claimed in one of his notebooks, must be erected not pressed on paper.  

However, the evolvement of three-dimensional mental spaces remains a, though challenging, makeshift.

The more my research moved from the 16th and 17th over the 19th into the 20th century the more it became obvious that what I have termed “epistemic pattern” or “frame” so far has an “inner life”. This made my methodology more complex yet, on the other hand, provided the possibility to develop a typology of epistemic schemata. In December 2003, on the occasion of K. Lorenz’s hundredth birthday, N. Bischof, one of E. v. Holst’s pupils, delivered a memorial lecture in which he suggested to evaluate the scientific achievements of former generations of researchers not so much by the criterion whether or not their statements can still claim direct or material validity from a nowadays perspective rather than by the question whether or not they provided deeper-lying, more rudimentary epistemic foundations for the future generations of researchers to come after them. In doing so, he introduced a concept of “reference system” which he in its original form had adopted from T. S. Kuhn but henceforth developed further from a bivalent to a trivalent epistemic framework.

From Bischof’s lecture we can infer that a reference system consists of a more obvious dualism in the foreground and a less obvious or latent entity in the background, namely the background itself. The latter entity in the following I will call “overtone”, a concept I have picked up in W. James’ Principles of Psychology. Although Bischof’s lecture is a very rare case where a member of the community made the “reference systems” of an ethologist’s thinking the explicit theme of a metalinguistic statement, I think, it is not an accident that exactly a psychologist whose academic career started in Seewiesen made retrospectively the attempt to approach the findings of his teacher generation by a trivalent epistemic concept since it can be demonstrated that ethological theorizing itself is utterly pervaded by this structural moment. And this proposition applies not only to K. Lorenz’s work, but also to N. Tinbergen’s, E. v. Holst’s and G. Kramer’s ways of knowledge organization. For instance, after Lorenz had left behind the epistemic framework of his early mentor, O. Heinroth, the former translated his theorizing into a more gestalt theoretical frame-

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89 Whether this is due to my own more refined perception or a matter of fact, I cannot tell.


91 Reference systems in their triangular form have recently received considerable attention. See E. Eßlinger et al., eds. Die Figur des Dritten. Ein kulturwissenschaftliches Paradigma. (stw 1971). Frankfurt a. Main: Suhrkamp, 2010. Most interestingly, Bischof’s presentation is the only place that I know of where an ethologist explicitly reflected on triangular forms of knowledge organization.
work which seemed to be more compatible with K. Bühler’s teaching with whose
institute Lorenz was affiliated at that time. In accordance with the newly adopted
frame, Lorenz now suggested to define instinctive action patterns as intercalation
of a more flexible, initial and directing component (following W. Craig the “ap-
petence”), on the one hand, and a final and static constituent (the “consummatory
act”), on the other. Since the system as a whole was meant to address fixed action
patterns, we may infer that the entire frame’s overtone was more like the second
component. My second example traces the roots of our modern idea of “adaptive-
ness”. Darwin’s understanding of “adaptation” through “selection” by no means
was a uniform concept, since he discussed natural selection in combination with a
second type of selection, sexual selection, whose primary characteristic was, and
still is, that it (paradoxically) partly suspended the principle of primary adaptedness
through natural selection. The heuristically so enormously productive constellat-
ion was that evolutionary biologists from Darwin to modern handicap theoreticians
were not prepared to give up the idea that “adaptiveness” guided the natural system
as whole so that they, in countless circumscriptions, tried to resolve the paradox
how a seemingly dysfunctional appearance might be adaptive, nonetheless. How
can it be that an organic structure like the deer’s antler which requires a so enor-
mous amount of organic investment is still functional? How can it be that the over-
conspicuous colouration of tropical birds which must decrease their survival value
is still adaptive? Is not, after all, the risk the organism takes while developing such
seemingly maladaptive body structures a quantitative measure which indicates the
amount of selective pressure which the respective organism faces in order to claim
and maintain its niche and therefore its further existence? These two examples – I
will examine many more in course of my thesis – may suffice to demonstrate the in-
er architecture of reference systems. According to my current state of knowledge,
a reference system consists of a primary entity, a secondary entity and a background
or overtone the latter of which seems to tend always to either side. In order to ob-

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92 See V. Hofer. “Konrad Lorenz als Schüler von Karl Bühler. Diskussion der neu entdeckten
Quellen zu den persönlichen und inhaltlichen Positionen zwischen Karl Bühler, Konrad Lorenz
und Egon Brunswick”. In: Zeitgeschichte 28.3 (2001), 135–159. For a history of Gestalt
Psychology as an alternative intermediate foundation in-between the humanities and the (natural)
sciences, idealistic philosophy and positivism, see Ash, *Gestalt Psychology in German Culture*,
3, especially 8 and passim. Further information on Bühler’s institute can be found in M. G.
Ash. “Die Entwicklung des Wiener Psychologischen Instituts 1922-1938”. In: A. Eschbach,
und Theoriegeschichte des Wiener psychologischen Instituts 1922-1938*. Wien: WUV-

93 For a general history of the “instinct”-concept see W. K. Köck. “Zur Geschichte des Instinktbe-
griffs”. In: O. Breidbach et al., eds. *Das Gehirn – Organ der Seele? Zur Ideengeschichte der
the concept see I. Brigandt, “The Instinct Concept of Early Konrad Lorenz”. In: *Journal of
the History of Biology* 38.3 (2005), 571–608 and also I. Brigandt. “Gestalt Experiments and
Inductive Observations. Konrad Lorenz’s Early Epistemological Writings and the Methods of
Classical Ethology”. In: *Evolution and Cognition* 9.2 (2003), 157–170. For further details
concerning K. Lorenz’s contact to W. Craig see Burkhardt, *Patterns of Behavior*, 33–59.

94 When I speak of “Darwin’s paradox” in the subsequent sections of my thesis I mean this end-
paradox framework.
tain a more precise understanding I suggest to concentrate less upon the “figure” as a whole but the semantic and conceptual relations which generate the overall system in the first place. Thus it seems that there exists a linear or chrono-logical relation between the primary and the secondary element. This becomes evident in the fact that Lorenz’s instincts are what he and several of his pupils after him, called “Zeitgestalt” that is they are a linear though ordered – and in this organized structure repeatable – form of behavioural progression.\textsuperscript{95} Darwin may have understood sexual selection as a secondary derivative of natural selection. The fact that the overtone of a reference system apparently drifts to either side creates the co-existence of both a tautological and a paradox conceptual relation.\textsuperscript{96} The fact that there are always both types of relation within one reference system is not vital per se. My analyses of these systems revealed that it is of crucial importance when it comes to classify them whether the tautological relation is at the beginning and the system is paradox at the end or vice versa. Lorenz’s “Zeitgestalten” are based upon an end-tautological system, while Darwin’s “adaptiveness”-system rests upon an end-paradox epistemic pattern. Besides, direction and conceptual relations there is a third parameter which to understand is of great importance for the differentiation of epistemic systems: The phenomenon of hierarchy. The dignity of a reference system’s constituents is a relative phenomenon, that is, the value of one constituent can only be determined relative to the other. Thereby I claim that it is especially the paradox relation in which the hierarchies become manifest. Thus it seems that


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in Darwin’s “adaptiveness”-frame the overtone is simultaneously the dominant element which – so to say – superimposes (i.e. “suffuses” in W. James’ words) the secondary element thus creating a paradox in the final subaltern constituent: A sort of quasi-non-adapted morphological appearance, an only seemingly dysfunctional structure, or a dysfunctional phenomenon which is functional nonetheless. As a rule, not only the Bird swallows the Fly but also the hierarchy creates the paradox.\(^97\) Thereby it is not always the overtone which is the prevailing element. By no means! Sometimes it is one of the subaltern elements which superimposes the overtone – so to speak – from beneath in which case the overtone is more an undertone and the paradox moves into the position of the third element.\(^98\) For instance, as soon as Ethology had reached its final advanced theoretical constitution, Lorenz’s “Zeitgestalten”, by no means, were as rigid as it was the case in the infant days of Ethology and his taxonomic reductions faded somewhat indefinitely in the deep dark lower end of a shaving brush.\(^99\) In other words, in contradistinction to their reputation classical ethological reductions are “soft” forms complexity reduction. Hierarchical shifts, in my opinion are a crucial moment in the developmental course to both the Ethological and the Modern Synthesis but they are extraordinary difficult to make evident since this requires to observe carefully how the paradox changes its location within the reference system. A final aspect, or more precisely, two final aspects I’d like to mention in my description of the epistemic reference systems is their reducibility and the consequences of this reducibility, on the one side, and their repeatability, on the other.\(^100\) The manifold examples I have mentioned above when I tried to distinguish the various different dimensions of a scientific orientation already indicate that one and the same epistemic pattern can become manifest in different concrete expressions.\(^101\) This must be so if they want to be abstractions of concrete phenomena. However, the reverse possibility that one and the same concrete expression, for instance the concept of “instinct” (i.e. the mere signifier), can


\(^99\) Lorenz used the shaving brush as a graphical and metaphorical illustration to communicate his revised idea of taxonomic reduction which is implied in a tree of life.

\(^100\) P. E. Griffiths and K. Stotz, in their draft of an Experimental Philosophy of Science, suggest to gather “empirical data on how scientific concepts are understood by particular scientific communities”. In doing so, they seem to examine distributions of statistically independent characteristics being denoted by core concepts such as “innateness” or the “gene”. See P. E. Griffiths et al. “Experimental Philosophy of Science”. In: Philosophy Compass 3.3 (2008), 507 for the quote, as well as 514–515. I, by contrast, want to scrutinize the distribution of epistemic dispositions related to concepts and practices within and in-between epistemic communities.

\(^101\) The linguist E. Oksaar argued convincingly in her culturem theory that just like in language, where one single concept can be expressed in various signifiers (e.g. tree, Baum, arbre etc.), also cultural behaviours – Oksaar speaks of “behavioremes” – can be analyzed as concrete manifestations of more abstract entities Oksaar termed “culturemes”. See E. Oksaar. “Kultureme
A study like mine, which is primarily interested in the question how the deeper-lying preconditions of scientific transformation processes change by themselves must naturally focus upon the latter possibility without neglecting the former. To distinguish both forms of variability, however, it is essential to differentiate between various different levels of abstraction which might even correspond with different strata of more or less conservative transformation. At this point I’d like to mark only the provisional extreme poles. To use the idea of a vertical order one might say that on the utmost top there is the stratum of the concrete phenomena, the concrete cultural appearances or scientific manifestations, the words and their signifier, the models, the drawing and the lines. I call this the “phenomenological sphere”. At the opposite end of the scale there is the sphere which is “ruled” by the epistemic schemes. I call this the “epistemological level”. At the end of my thesis there will stand a couple of principles which seem to have structured not only N. Tinbergen’s but also G. Kramer’s intellectual life-history upon this epistemological level. In other forms of epistemic variability both life courses seem to differ. In the long run my wish would be that I, sometime, will be able to answer the further leading question what the actual causes might be for each type of epistemic variation. This, however will require more advanced methodological approaches which can only emerge if science historians, and historians in general, are willing to cooperate with medical history as well as the social, psychological and the biological sciences. Moreover, to answer this question requires a fairly huge amount of both archival sources and quantitative data actively raised by us historians. Next to the variability which is caused by the manifold expressibility of reference systems in concrete manifestation, epistemic schemes appear to be reproducible as such in so far as they can reappear as particulate entities both in different epistemic constellations on one and the same time layer and at structurally identical (“homological”) positions of the overall reference system across the various layers of time. This repeatability or reproducibility is one of the strongest indicators suggesting that scientific innovation might be conceived more adequately as reproductive process rather than as mere outcome of social interaction. Several theories are traded in the Humanities and the Social Sciences which, in the last consequence, deal with re-occurrences of discrete cultural entities in changing spatial and chronological constellations. One of these approaches which has been discussed particularly in the historical sciences is related to the

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103 The latter of the two aspects I have already tackled by pointing to semi-abstract concepts (vitalism, sensualism, mechanism, etc.) which seem to gain topicality in periodically reoccurring waves and very often in combination with the prefix “neo-”.
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concept of “Cultural Transfer”. Another example can be seen in the theories of
“Cultural Transmission” that have been launched particularly in Cross-cultural Psy-
104 chology. Finally, there is “Memetics” – an approach to culture which has been
105 founded by R. Dawkins in his best seller The Selfish Gene and since S. Blackmore’s
book The Meme Machine became both more and more popular and the object of
extensive debates. I am not fully capable to profile my approach against these
theories yet. In general, it seems as if many common theories of cultural represen-

104 For the methodological debates in the background of this approach see, for instance, S. Con-
rad. “Vergleich, Transfer, transnationale und globalgeschichtliche Perspektiven. Geschichte
der Geschichtsschreibung jenseits des Nationalstaats”. In: J. Eckel et al., eds. Neue Zugänge
zur Geschichte der Geschichtswissenschaft. Göttingen: Wallenstein Verlag, 2007, 230–254,
F. Celestini et al., eds. Ver-schobene Kulturen. Zur Dynamik kultureller Transfers. (Stauffenburg
Discussion 22). Tübingen: Stauffenburg Verlag, 2005, H. Kaeblle et al., eds. Vergleich und
Transfer. Komparativistik in den Sozial-, Geschichts- und Kulturwissenschaften. Berlin et al.,
Campus-Verlag, 2003, M. Werner et al. “Vergleich, Transfer, Verleihung. Der Ansatz der Hi-
S 105 stoire croisée und die Herausforderung des Transnationalen”. In: Geschichte und Gesellschaft
Vergleich am Beispiel der französischen und amerikanischen Geschichtswissenschaft während
mann. “Internationaler Vergleich und interkultureller Transfer: Zwei Forschungsansätze zur
649–685, and in particular H. Mitterbauer et al., eds. Ent-grenzte Räume. Kulturelle Transfers
um 1900 und in der Gegenwart. (Studien zur Moderne 22). Wien: Passagen Verlag, 2005. Ex-
plicit applications to knowledge are L. Jordan et al., eds. Nationale Grenzen und internationaler
Austausch. Studien zum Kultur- und Wissenschaftstransfer in Europa. (Communicatio. Studien
zur europäischen Literatur- und Kulturgeschichte 10). Tübingen: Niemeyer, 1995, and more re-
cently R. Mayntz et al., eds. Wissensproduktion und Wissenstransfer. Wissen im Spannungsfeld

105 A. Bisin et al. “Cultural Transmission”. In: S. N. Durlauf et al., eds. The New Palgrave
also U. Schönplflug, ed. Cultural Transmission. Psychological, Developmental, Social, and
Methodological Aspects. (Culture and Psychology). Cambridge: Cambridge University Press,
2009 and D. Matsumoto et al. “Toward a New Generation of Cross-Cultural Research”. In:
Perspectives on Psychological Science 1.3 (2006), 234–250. Furthermore the introductions of
and the Evolution of Human Behaviour”. In: Philosophical Transactions of the Royal Society,
U. Schönplflug. “Introduction: Cultural Transmission – A Multidisciplinary Research Field”. In:

106 R. Dawkins circumscribed meme as follows: “We need a name for the new replicator, a noun
that conveys the idea of a unit of cultural transmission, or a unit of imitation. ‘Mimeme’ comes
from a suitable Greek root, but I want a monosyllable that sounds a bit like ‘gene’. I hope my
classicist friends will forgive me if I abbreviate mimeme to meme. [...] Examples of memes
are tunes, ideas, catch-phrases, clothes fashions, ways of making pots or of building arches.
Just as genes propagate themselves in the gene pool by leaping from body to body via sperms
or eggs, so memes propagate themselves in the meme pool by leaping from brain to brain via
a process which, in the broad sense, can be called imitation”. See R. Dawkins. The Selfish
Darwinizing Culture. The Status of Memetics as a Science. Oxford: Oxford University Press,
Seriously: Memetics Will Be What We Make It”. In: R. Aunger, ed. Darwinizing Culture. The
tation – regardless whether they’ve their origin within the cultural studies or the biological sciences – are based on what C. J. Lumsden and E. O. Wilson call “pure cultural transmission”. And at least to me it seems now almost beyond doubt that this matter of fact is most likely the reason why these theories failed to explain the cyclical dynamics of human culture and in particular were not capable to foresee the breakdown of the economic, social and political systems of values in the first fifteen years of the 21st century. I’d like to mention some points where I feel considerable unease or even have doubts. At first, all the three theories mentioned above are phenomenology- or, if you prefer, phenotype-centred approaches inasmuch as they presuppose categorically that culture is a more or less self-enclosed system of variability independent from the organisms who perform culture including their mind, their physical bodies and the development of both. However, as, for instance, C. H. Waddington remarked earlier and recent findings particularly in the field of Epigenetics suggest, this distinction does not hold at all as soon as human culture is understood as *behavioural expression of human organisms* who certainly are already the product of *both* nature and nurture, to put it simply. Second, all three theories, despite their differences which should not be neglected, seem to be object- or element-centred inasmuch as they assess the re-occurrence of definable “cultural goods” (Transfer), “preferences, beliefs and norms of behaviour” (Cultural Transmission) or presume the existence of an additional particulate “replicator” (Meme) whose “virulence” is thought in analogy to, but otherwise, independently from genes. In doing so, these theories – as do the gene-centred, quantitative and often hypothetical concepts of gene-culture coevolution standing close to Sociobiology – tend to neglect that scientific output is generated or processed by human organisms who, in my opinion, need to be conceived as varying interface between various different “systemic fields of forces” of which the interaction of disposition (including

107 “Pure cultural transmission” is defined in contradistinction to “pure genetic transmission” and “gene-culture transmission”. For example, see C. J. Lumsden et al. “Translation of Epigenetic Rules of Individual Behavior into Ethnographic Patterns”. In: *Proceedings of the National Academy of Sciences, USA* 77.7 (1980), 4382.

108 According to E. Jablonka and M. J. Lamb the word “epigenetics” was coined by C. H. Waddington in order to capture his theory of ontogenetic development but soon was also used to refer to “epigenetic inheritance” most likely because it includes the modern term “genetics” which was not part of the ancient concept “epigenesis” from which Waddington’s term was derived. The prefix “epi” which means “upon” or “over” thereby indicates the necessity to consider secondary processes beyond the gene. Nowadays the term is applied in both its wider and its narrower meaning. See E. Jablonka et al. “Evolutionary Epigenetics”. In: C. W. Fox et al., eds. *Evolutionary Genetics. Concepts and Case Studies*. Oxford: Oxford University Press, 2006, 253. For the relatively young area of genetic research the term “epigenetics” refers to see G. Felsenfeld. “A Brief History of Epigenetics”. In: D. C. Allis et al., eds. *Epigenetics*. Cold Spring Harbor (NY): CSHL Press, 2007, 15–22. Jablonka et al., *Evolution in Four Dimensions*, especially, 113–154, and 245–284 and T. Tollefsbol. “Epigenetics: The New Science of Genetics”. In: Idem, ed. *Handbook of Epigenetics*. The New Molecular and Medical Genetics. San Diego: Academic Press, 2011, 1–6. Epigenetics has also raised interest in cultural studies. Here representatives want their studies to be understood as corrective to the mere quantitative assessment of human culture by (natural) scientific members of the newly emerging field of research and, beyond that, ask in how far Epigenetics itself already became subject of cultural discourse. See here once more S. Weigel’s account quoted in fn. 3, page 2 and the reflections in V. Lux et al. “Einleitung”. In: Idem, ed. *Kulturen der Epigenetik: Vererbt, codiert, übertragen*. Berlin et al.: De Gruyter, 2014, xiii–xxviii.
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phylogenetic heritage and changing ontogenetic condition) and environment is only one of them.\textsuperscript{109} As a tentative result, I think it possible that the act of transmission which is the primary formative force of cultural expression occurs in a realm researchers, especially in the humanities, haven’t even thought of and that it might be more fruitful if we tried to grasp human culture as an act of expression on basis of this underlying dynamics whereby secondary environmental impulses in fact are a mandatory player.\textsuperscript{110} Yet, these brief remarks show that, if we take seriously the question which parameters are actually driving on scientific transformation, we would have to exceed by far the fields of research that are up to date conceived as canonical areas of enquiry particularly in the Humanities (less in the Social Sciences which don’t reveal the same fear to get into contact with other sciences but, in my opinion, often lack the introspective sensitivity for cultural phenomena). My tentative solution to this dilemma in this account, which is primarily devoted to cultural representations rather than the underlying dynamics they interpret much more directly and sensitively than imagined, consists of pursuing a phenomenological epistemology. That is, I aim to begin with cautious phenomenological observations and from thence dig deeper and carve out approximatively the causal regularities of scientific change in a researcher’s intellectual biography.\textsuperscript{111} Thereby readers have to accept that there are legitimately existing styles of scientific thought which turn out to be extreme at both ends, that is to say, in some model sciences such as genetics, the molecular or the nuclear sciences choosing an ever finer resolution reversely allows a more of abstraction to spring forth. In case of this thesis, raising data in itself is not entirely inductive since the fine-grained observations I make intend to verify and refine the methodological categories I have introduced hypothetically in this subsection of my thesis and the overall reference system they establish. As a provisional result I’d like to suggest the following figure which is meant to illustrate the reference system in which I intend to place my data (Fig. 1.1).

\textsuperscript{109} For this pivotal position the individual subject takes in sociological processes related to production, storage and transmission of knowledge see Kretschmann, “Biographie und Wissen”, 73, including further leading references. In contrast to Kretschmann, who is following Th. Luckmann at this point, I am not able to presuppose the social constructiveness of the individual subject any more, yet question it, that is, I’m interested in when and how it becomes (or can become) effective. So-called “constructivist” theories, at least if they emphasize the constructiveness of the subject, indirectly ascribe to the social environment the role of a proximate cause. The insights obtained by the life-sciences in the late 20\textsuperscript{th} and beginning 21\textsuperscript{th} century contradict this view. Recent approaches to bridge the gap between between nature and nurture can be found in various research field such as “Epigenetics”, “Gene-Culture Coevolution” or, more recently, “Human Social Genomics”. Helpful review articles might be S. A. Tammen et al. “Epigenetics: The Link between Nature and Nurture”. In: Molecular Aspects of Medicine 34.4 (2013), 753–764, C. T. Ross et al. “New Frontiers in the Study of Human Cultural and Genetic Evolution”. In: Current Opinion in Genetics & Development 29 (2014), 103–109, G. M. Slavich et al. “The Emerging Field of Human Social Genomics”. In: Clinical Psychological Science 1.3 (2013), 331–348 and S. W. Cole. “Human Social Genomics”. In: PLoS Genetics 10.8 (2014), 1–7. DOI: doi:10.1371/journal.pgen.1004601. (Accessed on Feb. 4, 2015).

\textsuperscript{110} Most interestingly, V. B. Smocovitis, in her highly inspiring study of the Evolutionary Synthesis, introduces the concepts “epistemic framework” and “packaging” as components of a “positivist theory of knowledge as the legitimating background of inherited values (many of which are silent) against which evolution and biology would emerge as legitimate sciences”. “This is in direct response to interpretations”, she continues, “that would legitimate science in terms of immediate social ’interests’”. See Smocovitis, Unifying Biology [1996], 14–15.
Chosen Sources and “My Methodology”

Fig. 1.1

Reference System for the Study of Epistemic Communities. The constituents are named arbitrarily. “Tm” and “tm” stand for “transmutation” or simply gradual and continuous variability. “M” and “m” for discontinuous variability. “Fct” and “fct” stand for “function” and represent the different forms of ultimate causation. “C” and “c” represent the different variants of proximate causality. “Asc” stands for “ascending” development and the increase of complexity, while “desc” may be read as an abbreviation for the “reduction of complexity”. “R1” and “R2” are abbreviations for the “registers” or “realms” of a single scientific orientation.

The figure shows that my thesis does not begin at zero any more. Previous examinations of epistemic communities have shown that there are involved at least four central scientific orientations plus several transitional forms which are not integrated in my illustration. Two of these orientations are homogeneous inasmuch as they combine different variants of either continuous (tm) or discontinuous variability (M). The other two levels behave analogously. The remaining two orientations are heterogeneous inasmuch as they combine, in slightly modified form, the epistemic schemata of one realm (viz. one $R_1$ and one $R_2$ each) of each homogeneous orientation. One of these heterogeneous orientations builds the epistemic tableau underlying the Modern Synthesis of Evolutionary Theory, while the complementary synthetic complex represents the structural outline of Classical Ethology. For me it is not a question any more whether or not G. Kramer’s and N. Tinbergen’s life courses proceeded within this reference system but how they did it. As a result, one may say that my thesis aims to confirm a presupposed hypothesis (i.e. the reference system as a whole) but that it also goes beyond inasmuch as it asks for the “how” and, to a limited extent, the “why”. A final question remains to be answered: Which epistemic entities are represented preferably by what concrete manifestations – so far as I can know? On basis of my current state of knowledge my impression is that

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Other orientations might not be represented at all because of the fact that biographical trajectories eventually must make a selection.

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textual expressions usually coincide with what I have called “register” or “realm”. As I will show in the following paragraph, they represent epistemic entities which can be reduced due to the form of knowledge organization they exhibit as a result of their tradition. But there are veritable exceptions to this general impression: For instance, as I will show later, N. Tinbergen’s techniques to socialize his PhD students were based upon practices that went beyond but included mere textual performative acts. Furthermore, I believe that the controversy triggered by R. J. Richards about the epistemological placement of Ch. Darwin’s works might be resolvable by bringing in a wider biographical and practice-oriented scope. A human being, by contrast, seems to encompass always and in principal two realms or the scientific orientation as a whole (at a given point of time). However, it should be kept in mind that not every realm must be equally represented in each phase of an individual’s life course. Some researchers seem to push one realm into the background during a certain period of life or oscillate between the two realms. Others, like G. Kramer, used to cover both realms all over their entire life in a more balanced manner. An intellectual life-history can be defined as the series of scientific orientations covered by one person in course of her or his life. On basis of this more precise information my concept of “scientific orientation” can be redefined as the smallest heuristic constituent within the reference system of an epistemic community which is not reducible or whose inherent double-nature resists the dynamics of triangular reduction of complexity. The primary emphasis of my thesis lies upon scientific orientations and series of orientations in time, especially individual lifetime. I have argued that the methodology I need must consist of both an adequate reference system and a tool that allows to place scientific and cultural expressions within this system. What might this tool be? I think it has already become clear that placing cultural expressions in a reference system requires adequate techniques to reduce their complexity and therefore that this is possible at all. I am inclined to argue that the latter requirement is fulfilled as soon as cultural and scientific manifestations (of all kind) include some sort of orderly performance or organization in general – and maybe this is their very nature. In case of the sample of researchers whose publications I have examined more carefully it can be claimed with certainty that the before mentioned orderly performance consists of applying

113 To have raised this research question is, I think, G. Beale’s merit.
114 At least, R. J. Richards’ “delay-hypothesis” refers to wider transtextual realms of research.
117 Triangular schemata seem to be more liable to allow the reduction of complexity. See Koschorke, “Ein neues Paradigma der Kulturwissenschaften”, 18.
highly sophisticated, mostly performative forms of knowledge organization: The publications of K. Lorenz and E. v. Holst, and especially, of N. Tinbergen and G. Kramer are organized compositions whose ordering principle is based on practices of recursively applied differentiation: On closer inspection, each textual representation thus turned out as tree of theorems and propositions which unfolds a particular theme from the title (i.e. the root of a text) into ever finer peripheral proposition which – if read into the reverse direction, that is from the bottom to the top (or from the top to the bottom if readers prefer a vee-like shape) – substantiate the overall message of the text. The significant insight I gained over time is that behaviour scientists not only differentiate propositions like they classify specimens but also that they, in doing so, observe principles which make their seemingly objective scientific statement simultaneously an expression of a particular overall epistemic frame. The particular constitution of these schemes, in turn, established relationships to other statements of the same person or statements of others so that – in the last consequence – a particular scientific expression could be located precisely within the epistemic space of a researcher’s scientific community. The fact that behaviour scientists ordered things not by mere arbitrary differentiation but instead by observing principles is the reason why I have claimed in the introductory section of my thesis that they, in contrast to, and earlier than the representatives of other research branches brought under control the principles of cultural transformation. In order to carve out these principles I suggest to apply several different techniques

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118 For an attempt to raise performative action as historical source see the chapter titled “Symbolische Handlungen als 'Quelle': Der 'performative turn’” in S. S. Tschopp et al. Grundfragen der Kulturgeschichte. (Kontroversen um die Geschichte). Darmstadt: WBG, 2007, 111–122.

119 V. B. Smocovitis has pointed to the various cultural and religious contexts in which the metaphor of the tree is used and, moreover, made an attempt to describe the formative function of the metaphor in evolutionary reasoning. “Bearing special signification for religious systems of thought”, she says, “this metaphor herein represented an end to conventional Judeo-Christian thought: a secular, yet meaningful evolutionary humanism had thus emerged”. See Smocovitis, Unifying Biology [1996], 150–151, here 151, including further leading references. Tree shapes also attracted the attention of those biologists and science historians who wanted to stress the narrative character of scientific accounts or claimed that tree-thinking is something to be trained with. See R. J. O’Hara. “Telling the Tree: Narrative Representation and the Study”. In: Biology and Philosophy 7.2 (1992), 135–160, R. J. O’Hara. “Population Thinking and Tree Thinking in Systematics”. In: Zoologica Scripta 26.4 (1998), 323–329, H. Sandvik. “Tree Thinking Cannot Taken for Granted: Challenges for Teaching Phylogenetics”. In: Theory in Biosciences 127.1 (2008), 45–51 and T. R. Gregory, “Understanding Evolutionary Trees”. In: Evolution: Education and Outreach 2.1 (2008), 121–137. In addition to that “Recursive Partitioning Analyses” belong to the methodological repertoire of Statistics and enjoy great popularity not only in Evolutionary Biology but also in Psychology, Genetics and Bioinformatics. For a brief introduction see C. Strobl et al. An Introduction to Recursive Partitioning. (Ludwig-Maximilians-University, Department of Statistics, Technical Report 55). Munich: LMU, Dep. of Statistics, 2009. URL: http://epub.ub.uni-muenchen.de/10589/1/partitioning.pdf (accessed on Aug. 15, 2014). Finally, recursive bifurcation has been used as model for assessing the evolutionary history of (human) knowing. For this line of reasoning see H. R. Maturana et al. The Tree of Knowledge: The Biological Roots of Human Understanding. Revised Edition. Boston: Shambala, 1992. I am particularly interested in the cognitive potential of tree-like forms of knowledge organization and, furthermore, tend to use it as a heuristic tool for my own textual analyses!

120 I tend to interpret these rules of differentiation as some kind of self-imposed orderly constraints. “Discipline” thus seems to emerge through discipline.
Introduction of perceiving cultural manifestations (both textual and non–textual). The first technique is intuition. When reading a scientific statement both the representatives of the primary sciences themselves and us science historians (including myself) obtain a more or less vague impression whether the respective writer is a “vitalist”, a “materialist”, a “neo-Darwinian”, a “neo-Lamarckian” or a “neo-Kantian”. But what entitles us to classify these writers in a way that even other recipients agree with our verdict? At least the possibility, or even the fairly high degree of intersubjective conformity these verdicts obtain, can eventually be read as an indicator that humans can sense intuitively what the relationship is like between their own “epistemic constitution” and the one of others. However, as we all know, intuition is liable to errors of perception and, beyond that, might lead to inadequate reductions. For instance, I doubt that all the writers we call “neo-Kantian” covered this position all over their life – not to mention that the great I. Kant himself, including the genesis of his work, certainly has a history on his own. The type of reduction I suggest is therefore more punctual inasmuch as it concentrates on singular cultural manifestations upon the time axis of a person’s individual development and, beyond that, intends to supplement mere intuition with more reflected techniques of complexity reduction. In order to achieve this objective I have often applied a method that can be circumscribed with terms such as “binominal analysis” or “repetitive partitioning analysis”.

To explain the method I, once more, refer to a prototypical example. In 1958, G. Kramer, together with his workmates, J. G. Pratt and U. v. St. Paul, published a research paper which was concerned with the so-called “direction effect” in pigeon homing. Pigeons had shown different home finding performances depending on the release site from which they were sent up. The reasons for these release-site related performance differences were unknown and therefore became subject of extensive testing. The order of the paper can be illustrated in the following diagram (Fig. 1.2).

In general, carrying out a binominal analysis consists of cautiously reading, especially reading the clues that contain information about the underlying organization. These clues can be both explicit and implicit. By explicit clues I mean all kinds of metalinguistic utterances which inform the reader about the way a written text is structured. However, especially the shorter forms of publications very often do not contain any outlines. In this case order is the sole product of performative forms of knowledge organization. To this set of clues first of all belong graphical and syntac-

121 This approach is a compromise because it primarily rests upon carefully reading and writing. Students of culture who were inspired by poststructuralist text theories applied other techniques such as the analysis of metaphors or beginnings. My private opinion is that these techniques contain a “Versprechen” in a very literal sense, namely, the possibility to infer from one part, or single parts, to the entirety. At first sight, this seems legitimate in epistemologically extraordinary homogeneous accounts (like poststructuralist texts themselves) but fails eventually in cases of textual accounts that bear in themselves a fair amount of epistemological heterogeneity. For some nice thoughts concerning the coincidence of parts and entirety in reasoning about metaphors see R. Gasché. “Metapher und Quasi-Metaphorizität”. In: A. Haverkamp, ed. Die paradoxer Metapher. (Edition Suhrkamp, N.F. 940). Frankfurt a. Main: Suhrkamp, 1998, 250. Altogether, I therefore believe that the “problem of reduction” is unsolved. As a result, my readings sometimes grow too long since they must be aimed at completeness.

Fig. 1.2

G. Kramer, *Neue Untersuchungen über den “Richtungseffekt”* (1958), Binominal Analysis
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tical hints. For instance, in my example-publication the first major section has no heading, while all others do have one. Amongst the sections which do have headlines, again, there are some being numbered, while others apparently are not subject to any quantitative or sequential ordering principle. The numbered sections build the main part of the paper. Next to graphical and syntactical clues there are semantic or “content-related” ones, too: Within the main part the major share of sections is related to the description of the experiments, while section “V. Discussion” provides a reduction insofar as it reflects the obtained results. The related experiments, one level below, are classified in so far as some of them tested the parameter “distance” (I. Direction Effect in Case of Very Short and Very Long Distances). Within this sample we find once more a bifurcation, namely in short-distance and long-distance releases whereby the linear succession, from close to remote distances, is significant. To some readers this might be too far-fetched but my impression is that G. Kramer was highly sensitive for these details. Besides the experiments which are classified by release distance we find those being classified by location, either the release site or the location of the home loft. From G. Kramer’s observer position, which was Wilhelmshaven at that time, the experiments carried out by his colleague in Durham (USA) are remote tests, while the tests carried out around Wilhelmshaven were close (IV. Releases Easterly and Westerly of Wilhelmshaven). The aspect of distance also seems to guide the differentiation of the experiments conducted in the United States: Montville and Richmond are more remote places in relation to Durham than the location of the “Baucom loft” which was actually one of the two home lofts of Duke University. As a result, we may see that implicit differentiation not only makes use of syntactic and graphical but also semantic clues. The regulation of distance, which is one of the primary social functions of animal and human behaviour, thereby is one of the most significant aspects which is translated – so to speak – upon a methodological level of the paper. I should like to mention two further aspects which turned out to be relevant while carrying out binominal analyses. The one of them is what I’d like to call “performative coincidences” and “linkages”. By the former two I mean that sometimes the structure of subordinate parts can coincide with larger structural units above (or vice versa). For instance, the authors I have dealt with very often take care that the introduction including its epistemic outline coincides, or can coincide, with the epistemic pattern of the entire text as a whole. The same very often applies to a paper’s or book’s final section. Moreover, sometimes we find that a chapter ends with a theme that is picked up at a discrete position in one of the following sections. These cross-references which partly touch what linguists in Germany might call “Thema-Rhema”-structures also play an essential role in how and why we understand scientific publications as an organized whole. Finally, all paths of a tree of propositions can be read with a view upon all three dimensions of behaviour. The problematic of “distance regulation” primarily refers to what I have called the level of “variability”. But Kramer’s highly differentiated way of presenting his results also has causal implications. For instance, it is not an accident that he treated releases easterly of Wilhelmshaven before he dealt with releases westerly of Wilhelmshaven: Pigeons released westerly performed less well although east-west differences in general were less drastic than north-south dif-
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ferences. These correlations can be called “linkages”. Their alternation is one of the structural modifications which were leading both to the Modern and the Ethological Synthesis. The last aspect I’d like to discuss might be called “disambiguating by meta-concepts”. Binominal analyses sometimes end in structural ambiguities. For instance, when a research publication has three major parts, introduction, main part and conclusion, the question pops up whether introduction and main part built a unit which is separate from the conclusion or the other way round: Main parts and conclusion establish a unit which as a whole is separate from the introduction. In this case meta-concepts might come in which clarify the situation. For instance, G. Kramer, while affiliated with the KWl for Medical Research, picked up the medical concept of “differential diagnosis”. Differential diagnosis is a sort of heuristic program physicians apply when they do not know the physical cause of a certain disease. In this cases they begin with a declaration of a desideratum or what they do not know but in a second step widen their view upon all possible explanations. Within this wide range of possibilities they, in a second step, try to isolate the proper explanation in course of a process of empirical and gradual reduction. Altogether, at least as Kramer seems to have applied it, the heuristic machinery which is implied in the concept of “differential diagnosis” contains two separate steps. A primary extension from the known (the not known) to the unknown (the possibilities) and a secondary reduction within the latter sphere. The text-example I have mentioned above includes such a diagnostic scheme inasmuch as a “nameless” introduction is supplemented by a section with experiments within which the description leads to a critical discussion of the results: That is, uncertainty is translated into certainty. In case of my text-example my binominal analysis thus leads to the conclusion that the presented information is ordered inasmuch as it fulfils what Kramer himself called “Komplex-Qualität” – a form of non-reductive holistic reduction which is not identical with Lorenz’s Gestalt theorem. Many if not all the academic publications I have dealt with can be read by applying the method I have introduced in this section. As soon as researchers begin to apply a procedure of recursive differentiation, texts can always be read back to their roots.

Although I have not put this aspect in the centre of my argumentation, I think, that behavioural scientists also conceived social relationships with peers, colleagues and pupils in form of the above mentioned reference systems. This refers to the wide range of transtextual representations of epistemic schemata which can eventually be arranged alongside the three dimensions of behaviour, too.123 For instance, the question whether or not and how researchers see themselves as part of an international scientific community or whether they allow scientific transfers as an essential moment of their research, I think, can only be answered relative to the respective individual and, maybe, even more relativistically, by referring to a particular stage of her or his life course.124 The question whether researchers function as popularizers

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123 This eventually implies that there must be a distinction between several types of practice. See to this W. Detel. “Wissenskulturen und epistemische Praktiken”. In: J. Fried et al., eds. Wissenskulturen. Beiträge zu einem forschungsstrategischen Konzept. (Wissenskultur und Gesellschaftlicher Wandel 1). Berlin: Akademie Verlag, 2003, 119–132.

124 For instance, K. Lorenz describes the inventions of his colleague E. v. Holst as highly original and detached from any kind of mainstream. See K. Lorenz. “Erich von Holst”. In: Die
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of their science or, more general, whether and how they provide or acquire scientific resources seems to be correlated with the aspect of causation and therefore refers to a level of scientific practice which must be conceived independent from questions of internationalization and scientific originality. Finally, the question how biologists address the relation between man and animal, how they discuss the human predicament or the development of human civilization, in general, appear to be themes related to the anthropological dimension of behaviour. I am inclined to treat these aspects, which all cover their own domains within the cultural and the social sciences, less from a mere thematic point of view rather than as various different epistemic practices which, too, might be ruled by deeper-lying epistemic reference systems. But in contrast to textual representation they are more difficult to make evident because this would require adequate source material. Where I see connection points in my thesis I will mention them. But it is too early to answer definitely the question whether or not a researcher’s behaviour is coherent in all social systems she or he is part of.

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125 N. Tinbergen, by contrast, is said to have moved to Oxford in 1949 because he wanted to propagate his science in the Anglo-American world. G. Kramer, as many other ornithologists, conceived himself as part of an international scientific community which even persisted the turbulences of the Second World War and thus does not belong to those branches of research which were entering a period of isolation after the war.


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Outline and Other Conventions

The outline of my own thesis can be described as follows: I have divided the main part into two sections. The first of these two main parts will be empirical and clarify how the intellectual life-histories of my two main protagonists, G. Kramer and N. Tinbergen, proceeded and how they fit in the overall reference system I have outlined in my chapter on methodology. Within these parts I will proceed in chronological order. Both subchapters in this part differ in so far as I worked with a limited number but representative selection of N. Tinbergen’s publications, whereas in case of G. Kramer’s life course my account rests upon a more or less complete sample of his scientific publications. The second major part discusses the main results and, beyond that, carves out the forms of epistemic variability which characterize the life courses. In a first step it provides a condensed presentation of the two life courses by applying the methodological tool of “epistemic landscapes”. In a second step I aim to carve out the very nature of the mechanisms governing the intellectual development of both researchers by making use of different and deliberate sets of comparison. These comparisons refer both to processes of scientific transformation within the epistemic community as a whole and to forms of interaction between different epistemic communities, that is, the question how the reproductive neo-Darwinian community interfered with other coexisting epistemic communities. In the final conclusion I will summarize the results and finally enter the question of causality.

Several formal aspects of my thesis turned out to be problematic and therefore need to be clarified explicitly. At first, due to the fact that several behaviour scientists wrote historical accounts, biographies and autobiographies, the boundary between primary and secondary literature becomes blurred. There are different possibilities to solve the conflict. First of all, it would be possible to differentiate between different genera of textual sources (autobiography, biography, histories) and define the status in each case by convention in which case the classification would be based on more or less arbitrary criteria. A second option would be to emphasis the status of the author of the source and let his status decide about whether a scientific expression or statement is to be classified as primary or secondary source: Statements – written or spoken – of authors who at least a certain period in their lives were directly engaged with the biological sciences and thus belong to the same epistemic community as my two target persons then would have to be classified as primary sources. A final possibility, the one I favour, would be to determine what is primary and what is secondary source from case to case and relative to my research question and how I have used the respective document, that is, functionally. Since my thesis focuses upon two main protagonists but my research interest lies upon the epistemic community as a whole I am inclined to treat those historical accounts that have been written by biologists but address the field as a whole as secondary sources, whereas their biographies and autobiographies on singular researchers would appear to be primary sources. For instance, W. H. Thorpe’s treatise *The Origins and Rise of Ethology* (1979) and N. Tinbergen’s retrospective account bearing the title “Etho-

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et al., eds. *Frosch und Frankenstein. Bilder als Medium der Popularisierung von Wissenschaft. (Science studies).* Bielefeld: Transkript-Verlag, 2009, 79–89.
**Introduction**

... (1969) would have to be classified as secondary sources, while J. Autrum’s autobiography *Mein Leben* would be primary source. Autrum’s encyclopaedia article for R. Hesse in *Neue Deutsche Biographie*, by contrast, would be a piece of secondary literature because I used it as auxiliary background information and not a primary piece of historical information with which I built my argument. The second problematic refers to the usage of the tenses in my own account. My thesis not only reconstructs historical events of the past but also analyses historical sources whereby the propositions that I put forward sometimes obtain the character of universals or are still valid at present. For instance, when I introduce a literal quotation with “it reads ...” or “N. Tinbergen writes ...”, this is to say that the act in which the information can be drawn from the source text or is provided by the text occurs right now. In those sections of my thesis in which I analyze source material I therefore use Present Tense, while in all other sections dedicated to the reconstruction of historical events I use Past Tense, Present or Past Perfect. As a rule archival sources are quoted as a combination of three components, the reference to the archive, the reference to the respective holding, and the reference to the respective file or, pending on how sorted the respective holding is, the location within the holding. In addition to that, I specify the quoted document by providing the information what type of document it is (i.e. “ms.”, “letter” etc.) and a further piece of information to specify a single document. For example, in case of letters I mention the correspondents, plus date. Manuscripts are specified by author, title and date. The date is quoted in British style, that is following the template “dd/mm/yyyy”. In case the author is identical with the person in whose personal papers the document is located I drop the author. The question of capitalization needs to be clarified, too. As a rule, I write general terms, names of scientific disciplines, names of animal classes and species in capital letters. In doing so, my intention is to avoid ambiguities. For instance, behaviour scientists sometimes use the term “ethology” ambiguously since they either refer to the discipline or to the behaviour repertoire of an animal as a starting point for further enquiry. It makes a difference whether someone says the “ethology of the chimpanzee...”, or the “history of ethology comes of age”, not to mention, that “Ethology” is a concept with its own history. In the former of the three cases I do not use capital letters in the latter two cases I do, thereby using quotation marks for metalinguistic references. Inside headlines and reference titles in English language everything is written in capital letters except prepositions, articles, “and”, and “or”.

Lastly, the ways I will address the main protagonists of my study is guided by economical considerations. For the sake of shortness, I therefore often write “Niko” for Nikolaas Tinbergen or simply use an author’s last name only which is often the case when I am referring to Gustav Kramer.

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a) Niko Tinbergen (1907–1988)

I have argued that the history of Ethology cannot be understood without taking into account the reproductive dynamic which revealed itself in the establishment of the neo-Darwinian-ethological double synthesis but, in a second step, was further perpetuated by those scientific orientations which began to deviate from this synthetic complex of scientific paradigms. N. Tinbergen and G. Kramer, as I will show, are, each in his own way, representatives of this group of researchers. Their intellectual life histories, again each in its own way, reveal both movements to and away from the heterogeneous orientations being characteristic either for neo-Darwinians or ethologists. The specificity of their paths shall be examined in the following two subchapters. In doing so, I should like to answer the further leading research question which part of the double movement consisting of convergence and divergence is based on scientific socialization and which by the breakthrough of a researcher’s disposition. For instance, was Lorenz’s admiration for O. Heinroth, one of his early mentors, or E. v. Holst’s purely physiological education (his dissertation thesis) a result of academic or scientific socialization and the synthesis they subsequently established an act of “subversion”? This would be a difference to J. B. Watson’s and W. McDougall’s life course because here the socialization took place in direction of the heterogeneous orientation and the abrupt breakthrough of the homogeneous orientations were most likely acts of subversion based on disposition. If K. Lorenz’s and E. v. Holst’s life course consisted primarily of merging together theorems drawn from antagonistic scientific positions, this specific quality of their scientific socialization – so to speak as a reverse conclusion – would eventually also explain why their early interests were spread over various antagonistic orientations. But how do things look like in case of N. Tinbergen’s and G. Kramer’s life course? From my reading of G. Beale’s thesis I got the impression that Tinbergen’s life-history paralleled the one of classical ethologists (early Tinbergians) but in addition since ca. 1959 developed into a truly ecological orientation (late Tinbergians) not least by acquiring theorems that had been refined before in the Modern

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In claiming that Classical Ethology originated in a synthetic process parallel and next to the Modern Synthesis of Evolution (MS) my thesis also takes position in the recent debate whether or not there is a need for an “Extended Evolutionary Synthesis” (EES). Please see Pigliucci, “Do We Need an Extended Evolutionary Synthesis?”
Synthetic Theory of Evolution.\textsuperscript{2} If the first of the two stages was already an act of “subversion” initiated by the researcher’s disposition – so to say as a subsequent response to Niko’s own socialization into the academic community of the early 20\textsuperscript{th} century –, the second could be due to a sort of late (reverse) socialization triggered by major impacts coming from his own pupils and also, for instance, scientific controversies. This is why I like Beale’s approach and the extension of his focus on Tinbergen’s pupils. Despite the fact that I appreciate G. Beale’s approach, I’ll keep my focus narrow because I’d like to learn more about the type of scientific variability which urged on Tinbergen’s shift to “pure functionalism” in his later intellectual life-history. In contrast to Beale, I am therefore much more interested in the effect the research results of his pupils had upon him rather than in the pupils themselves. 

Asides G. Beale’s differentiation in research of “early” (i.e. 1948–ca. 1958) and “later Tinbergians” (i.e. 1958–1974) periodizations of N. Tinbergen’s research have been suggested by D. R. Röell and H. Kruuk. Röell’s study on the origins of Dutch Ethology operates with a time-frame between 1920 and 1950 and therefore can be read complementary to Beale’s emphasis on N. Tinbergen’s research group during his Oxford period (1948–1974). If I have understood correctly, according to D. R. Röell, Tinbergen’s scientific development between his birth in 1907 and his move from Leiden to Oxford in 1948 can be separated in three major periods.\textsuperscript{3} Thus Röell speaks of an early “naive” phase in which Tinbergen’s approach to animals was mainly observational and mediated by photographing as the primary scientific practice (1907–1930). In a second period Tinbergen’s course was characterized by a process scientization triggered both by the Dutch Youth Association for Nature Study Tinbergen was a member of and his university studies (1930–1936). Around 1936, finally, Tinbergen began to develop a theoretical frame for his research and, according to Röell, this move was also initiated by the contact with K. Lorenz from whom he borrowed for instance the concept of the innate releasing schema (later “innate releasing mechanism”, (IRM)). Tinbergen’s theorizing reached a provisional peak in 1942 when he published An Objectivistic Study of Behaviour and the scientific dispute with vitalist psychologists reached a highpoint. H. Kruuk underlined that a major caesura in N. Tinbergen’s scientific development occurred during his trip to Greenland in 1932 / 1933.\textsuperscript{4} Beyond that, the more or less decade-wise composition of his biography suggests that he identified the outbreak of the Second World War and Tinbergen’s imprisonment in a National Socialist hostage camp in 1942, his move to Oxford in 1948, the turn to Ecology in 1959 and, finally, the Nobel Prize in 1973 and his retirement in 1974 as the major turning points and events in his teacher’s life-history.\textsuperscript{5} As a provisional hypothesis, I’d like to suggest a periodical model with four major turning points. At first, I do believe that

\textsuperscript{2} For Beale’s differentiation between “early” and “later Tinbergians” see Beale, “Tinbergian Practice, Themes and Variations”, headlines of chapter three and four, passim.

\textsuperscript{3} Röell, The World of Instinct, 87.

\textsuperscript{4} See Kruuk, Niko’s Nature, 59–69.

Tinbergen’s research interests from the very beginning were divided in more observational and more experimental queries which during his early scientific socialization were situated in entirely different practical fields yet more and more merged together to a heterogeneous, yet closely intertwined, epistemic model – a process which can be made evident also in trajectories of other behaviour researchers such as E. v. Holst and K. Lorenz.\(^6\) I interpret N. Tinbergen’s dissertation thesis which was published in German under the title *Über die Orientierung des Bienenwolf* in 1932 as the end-point of this transformation process. Second, I would like to pick up H. Kruuk’s suggestion and ask whether Tinbergen’s experiences in Greenland initiated a turn-over of the causal architecture in his scientific orientation. If so, Tinbergen’s joint research with K. Lorenz in 1937 can be interpreted eventually as the provisional end-point of this particular epistemic shift. Thirdly, I ask since when Tinbergen articulated the typical ethological set of epistemic values which led to the paradigm of Classical Ethology and when this paradigm became partly obsolete for Tinbergen. My provisional hypothesis here is that Tinbergen’s first journey to the United States in 1938 and the contact to E. Mayr eventually had a major impact leading to the characteristic epistemic re-evaluations. Moreover, it apparently was also the environmental impact of innovative research results of some members of his research group (especially E. Cullen, nee Sager) and the counterarguments put forward against Classical Ethology in course of the so-called Lehrman controversy which triggered N. Tinbergen’s functional turn in 1959. In sum, one may eventually say that Tinbergen between 1938 and 1959 adhered to the paradigm of Classical Ethology. Thereby it must be kept in mind that this long period of almost twenty years can be differentiated in smaller units which take into account the circumstances of the respective time and place. As such I suggest to treat the period between 1938 and 1942 (self-establishment in Leiden), between 1942 and 1945 (time of internment), between 1945 and 1948 (Leiden after 1945) and, finally, between 1948 and 1959 (early Oxford research group) as estimable chronological units within a larger epistemic cross-section otherwise characterized by structural continuity. Finally, I follow the opinion of most historians of Ethology that N. Tinbergen’s research after his functional turn in 1959 (1962 at the latest) obtained a different quality which eventually reshaped his research fundamentally till his retirement in 1974 and beyond.\(^7\) Again I would like to put emphasis on the different phases this major period consisted of and which coincided with different places, objects and interests of research without giving up the major epistemic frame which

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\(^6\) G. Beale lately underlined that N. Tinbergen’s research agenda covered two different spheres which he identified as the *laboratory* and the *field*. See Beale, “Tinbergian Practice, Themes and Variations”, 21–23. My approach to differentiate epistemic patterns which can become manifest in various different phenomenological expressions supports Beale’s dualistic view but allows me to open my account theoretically for a wider range of structurally similar phenomena.

\(^7\) See Kruuk, *Niko’s Nature*, 6–7, 189–193, 211–218, Burkhardt, *Patterns of Behavior*, 411–434, and Beale, “Tinbergian Practice, Themes and Variations”, Chapter Four: The later Tinbergians in laboratory and field, 151–202. In contrast to G. Beale, who tends to argue that both spheres, the laboratory and the field, were equally affected by the Tinbergians’ turn to Behavioural Ecology (Ibid., 199), my hypothesis is that the realm which was covered by N. Tinbergen the teacher and advisor must be supplemented by another sphere of his research, namely the one which was dedicated to his theorizing. Although Beale makes several exciting observations, his study suffers sometimes (not genuinely) from the fact that he presupposes simple correlations.
Intellectual Life-Histories

is my primary focus. As such the years between 1959 and 1963 yielded an early ecological research agenda which in the works of the “Maestro” himself became manifest mainly in a thorough study of the so-called “egg shell removal behaviour” of the Black-headed Gull and finally culminated in his famous landmark paper On Aims and Methods of Ethology (1963). From this early ecological research which was also connected mainly with Ravenglass as a site of scientific observation the establishment of the so-called Serengeti Research Institute in Tanzania must be distinguished since Behavioural Ecology here was mainly concerned with mammals. Finally, since 1968 Tinbergen more and more began to apply ethological methods to humans – an interest which finally culminated in his books on childhood autism. In the following I will try to make evident all four major turning points.

i) Synthesizing Classical Ethology

Merging Divergent Interests

N. Tinbergen was born in The Hague on the 15th of April 1907 as the third child of altogether six children five of which survived: Jan (*1903), Jacomiena (*1905), Niko (*1907), Dik (*1909) and Luuk (*1915). Niko’s parents were Dirk Cornelis and Jeanette Tinbergen (nee van Eak). His father was teacher for Dutch and had written a Dutch grammar book. His mother is remembered as a warm-hearted and impulsive woman. She had worked as a maths teacher, spoke German, French and English, and was well-read. The Tinbergen family was Calvinist and, according to H. Kruuk, belonged to the liberal Dutch middle class. Like his older brother Luuk took a career as zoologist and obtained positions as lecturer (since 1949) and professor (since 1954) for Zoology at the University of Groningen. Ac-

between, for instance, the field and innate, on the one hand, and the laboratory and learnt, on the other (e.g. Beale, “Tinbergian Practice, Themes and Variations”, 13) – in other words, he distinguishes not between epistemic levels or dimensions which – especially with a view of a neo-Darwinian epistemic community – partly leads to an incoherent argumentation. In contrast to Beale’s emphasis on Tinberian Practice I think the more drastic shift might have taken place in Niko’s theorizing, while I, in addition to that, suggest to take into account that the causal turn which characterized ethological practice and theorizing since the mid-1930s already implied a first shift towards ecological research – and this exactly in the realm Beale addresses in terms of “Tinberian Practice”. My view therefore agrees with J.-S. Bolduc’s standpoint according to which Behavioural Ecology inherited from Ethology two “distinct but complementary approaches” or “inference-building schemes”, as he puts it, namely an “adaptationist” and a “comparative” approach. About the transformation of the latter of the two “inference schemes” he writes: “Ever since, the approach permitted the quantification of some phylogenetical relations, it allowed both the grounding of historical inferences into available phylogenies, and the grounding of adaptationist inferences into evolutionary histories”. See Bolduc, “Behavioural Ecology’s Ethological Roots”, 675, 678, 681–682, and 682 for the quotation.


Niko Tinbergen (1907–1988)

According to Kruuk, both brothers were at the foremost J. Verwey’s pupils. Moreover, alike to Niko, Lukas suffered from severe (presumably endogenous) depressions which most likely were also the reason for his suicide in 1955. Jan Tinbergen studied mathematical statistics at the University of Leiden where he obtained a doctor’s degree in 1929. In 1933 he was appointed extraordinary professor of statistics, mathematical economics and econometrics at the Netherlands School of Economics in Rotterdam where he also was appointed full professor in 1956. Together with R. Frisch, Jan was awarded with the first “Noble Prize of Economics” in 1969 – four years before his younger brother Niko became Nobel laureate for Medicine together with K. Lorenz and K. v. Frisch. When it comes to reconstruct the impacts which allegedly shaped Niko’s career it is this erudite liberal Dutch middle class milieu which is said to have provided the initial environment for his scientific development: Niko is said to have observed animals on the beaches of Scheveningen from his early childhood, yet, while being a school boy (i.e. 1920–1925), his desire for being in the open field and his passion for studying the wildlife were fostered especially by Dr. A. Schierbeek, teacher for botany and zoology at the “2nd HBS” (Higher Burgher School) which was a government grammar school in the Stadhouderslaan in The Hague. Moreover, Tinbergen remembers the fascination E. Heimans’ and – to an even greater extent – J. P. Thijsses’s popular accounts such as “Our Blond Dunes”, “Our Rivers”, or “Our Flowers and their Insect Friends” evoked in him. Even his dissertation thesis on bee-hunting Digger Wasps seemed to be inspired in parts by Thijsses’s articles. “There is nothing much original in these papers”, Tinbergen writes later in the introductory part of the English translation of his *Philanthus*-studies and continues, the Frenchmen Henri Fabre and Charles Ferton the American Phillip Rau and the great Dutch naturalist Jac. P. Thijsses work had shown me the power of simple experiments in as natural conditions as possible; and Mathilde In a later letter to J. Huxley, Niko describes himself as pupil of J. Verwey and K. Lorenz. See Woodson Research Center, Fondren Library, Rice University [quoted as: WRC-RU Fondr. Lib.], Julian Sorell Huxley Papers [quoted as: MS 50], box 41, file 6, letter N. Tinbergen to J. Huxley (20/06/1967).

For an attempt to bring in a medical history approach see Mysterud, “Niko Tinbergen’s Life and Work”, especially 547–550. I. Mysterud speculates that a “nutrient hypothesis (fatty-acid deficiency and / or protein intolerance) would explain the apparent absence of any systematic social reasons for the blues [...][CL. although psychosocial stress seemed to lower the threshold for or aggravate his illness [...]” (Ibid., 548).


On A. Schierbeek’s impact see also Tinbergen, “Watching and Wondering”, 437. For some more details concerning his life and profession see in particular Röell, *The World of Instinct*, 43–44. Schierbeek had devoted his life’s work to the preservation of the Meyendel, an area of dunes between The Hague and Wassenaar, by stimulating ecological studies of the habitat and recording its biological diversity. N. Tinbergen was involved in this “Meyendel research” (Ibid., 44).


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Hertz’s work on the vision of bees – to me still a model of imaginative experimentation – had inspired my first steps.\textsuperscript{17}

Asides popular literature, the impact of teachers and the annual family summer vacation to Hulshurst, N. Tinbergen’s pre-scientific socialization was also mediated by the Nederlandse Jeugdbond voor Natuurstudie (NJN) which was part of a broader youth movement that had taken shape in pronounced demarcation from the urbanization movement of the 1920s. The NJN organized leisure activities outside home and provided the opportunity for playful learning, teaching and pre-scientific research but also intended to convey humanitarian and democratic values. The NJN edited a journal – the *Amoeba* – which (asides *De levende natuur*) was also the forum for Niko’s early publications upon ornithological and other observations.\textsuperscript{18} In 1925 Niko still was undecided about his later professional career so that A. Schierbeek and Prof. P. Ehrenfest, Jan’s mentor at Leiden University, encouraged Niko’s parents to send him on a several-month visit to the “Vogelwarte Rossitten” whose director at that time was J. Thienemann. The “Vogelwarte” was one of the first European field stations to examine the migration of birds and thus one of the number one addresses for practical ornithological research. Most likely these experiences enforced Niko’s wish to study Biology.\textsuperscript{19} In 1925, when Niko arrived at Leiden University, studies in Biology encompassed five years and began broad, that is, N. Tinbergen attended lectures in taxonomy, morphology, physiology, geology, paleontology, chemistry and physics. After two years and the “candidate” exam, students spent another year with practicals in various fields and, only after that, specialized in one main subject (fourth year) and two additional subsidiaries (half of the fifth year each).\textsuperscript{20} The Zoology Department which represented Niko’s primary interest had changed and was about to change structurally insofar as the department had taken over additional responsibilities for teaching medical students in morphology and comparative anatomy in 1917.\textsuperscript{21} According to D. R. Röell’s account, this development occurred under the auspices of P. N. van Kampen’s directorate (1916-1931), was the result of the so-called Limburg Law (1917) and upgraded Comparative Anatomy to one of the most important subjects at the department. Later in 1926, a study course reform made animal physiology an integrative part of zoological training at Leiden University. This initiative seemed to be mainly the brain child of H. Boschma who replaced the comparative anatomist P. N. van der Kampen as head of the department due to the latter’s serious illness in 1931 yet himself was


\textsuperscript{18} The magazine *De levende natuur* was founded in 1896 by Heimans and Thijsse in collaboration with J. Jaspers Jr. All three were head teachers in Amsterdam and devoted to the rediscovery of living nature. For further details concerning their efforts to popularize the study of nature see Röell, *The World of Instinct*, 41–43.


\textsuperscript{20} Kruuk, *Niko’s Nature*, 38.

\textsuperscript{21} For the (changing) institutional environment see Röell, *The World of Instinct*, 59–69.
succeeded by C. J. van der Klaauw as department director in 1934. According to H. Kruuk old Comparative Morphology dominated zoology in Leiden in the late 1920s and early 1930s. Physiology was on the verge to be integrated and, according to Röell’s view, Boschma, with whom “Tinbergen was closely involved”, was well aware “that this would have to be at the cost of the purely morphological subjects”. The trend continued under C. J. van der Klaauw yet in contrast to Boschma the latter – whose own research remained within the traditional framework of comparative anatomy and classical phylogeny – seemed to have a stronger interest in Theoretical Biology and the disciplinary unity of Biology. Although he opened the curriculum for new fields such as experimental physiology, applied Biology, field Biology, Ecology and Ethology he interpreted these more practical concerns as “appetizer” for and within the frame of his “organismological” and “holistic teleological” conception of Biology. Asides G. J. Tijmstra who furthered the scientization of Niko’s ornithological passion outside academia, the person who formed Niko’s interest most during his university studies since the mid-1920s, was J. Verwey. Verwey, with whom Niko was connected by the ties of a life-long friendship, covered a position as research assistant at P. N. van Kampen’s chair (January 1926 till November 1927) and was responsible for supervising the students. Later, in 1927, he left for the Dutch East Indies and in 1931 he was appointed director of the Zoologische Station at Den Helder in northern Holland. Verwey, whose interest in animal behaviour rested upon the Biology of pair formation in the Heron, broke with Comparative Anatomy and is considered as one of the founding fathers of Dutch Ecology and Comparative Physiology. It was Verwey, with whom Niko shared

22 For this information see Kruuk, *Niko’s Nature*, 38. Röell’s account seems to differ slightly from Kruuk’s at this point: According to his treatise, animal psychology was first introduced at Leiden in 1927 (represented by A. Schierbeek), genetics in 1929 (taught by A. L. Hagedoorn), experimental plant physiology in 1931 (by appointment of Professor L. Baas Becking), and – most important – comparative physiology in 1928 (taught and promoted by H. Boschma and J. Verwey since 1927). See to this Röell, *The World of Instinct*, 61–62, and fn. 7.

23 Ibid., 61, and 62 respectively. According to Röell, H. Boschma realized the necessity to integrate physiological studies yet did not follow the trend by heart – eventually one of the reasons why he gave up his position at the Zoological Laboratory to become director of the *Rijksmuseum van Natuurlijke Historie*.

24 On C. J. van der Klaauw see ibid., 63–67. Roell writes: “These subjects had little in common except that they all involved studying living animals in relation to their environments. Van der Klaauw lumped them all together as ‘ecology’ and characterized the new subject in his theoretical work as the study of the relations between an organism and its environment and of supra-individual relationships” (Ibid., 66).

25 On J. Verwey see ibid., 49–54, 63. Tijmstra, former captain of the royal army in the Dutch East Indies who had become headmaster and maths teacher at a private school, had been asked by Thijsse to write something about the island of De Beer. Tijmstra for his part approached N. Tinbergen and his NJN friend G. v. Beusekom and delegated some research on dune movements to Niko, a subject he was already familiar with from his visit at Rossitten. According to D. R. Röell’s account, the contact to Tijmstra, who himself was an observer of animal behaviour, resulted in the fact that Niko “adopted a more scientific attitude” and: “His observations became more systematic, and focused on a specific subject” (Ibid., 48).

the inclination to field study and the passion for ornithology and who drew Niko’s attention to the animal’s social behaviour. Niko’s final exam papers concentrated on “The Biology of Mating in the Common Tern”, the phylogeny (mostly taxonomy) of echinoderms (that is, sea-urchins and starfish), a literature study on gall-wasps and galls and, finally, the “Phenology of the Digger Wasps”.\footnote{Niko’s study on the common terns mating rituals was performed formally under H. Boschma, yet actually supervised and inspired by J. Verwey. The paper was later published in the Tijdschrift der Nederlandse Ornithologische Unie. See N. Tinbergen, “Zur Paarungsbioogie der Flussseeschwalbe (Sterna hirundo hirundo L.)”. In: Ardea 20.1/2 (1931), 1–18.} The “Phenology of the Digger Wasp”, that is, the latter of the altogether four research projects which Niko completed in order to obtain his degree eventually was the most important one:\footnote{Phenology stands for the study of inter-annual and seasonal variations.} It was supervised by van der Klaauw and later became also the topic of Niko’s dissertation thesis though in a modified form. Both research projects which resulted in academic publications, the biology of mating behaviour and the phenology of the Digger Wasp were part of the major subject, Zoology, Niko had chosen for his degree.\footnote{Röell, The World of Instinct, 68.} They formally encompassed Physiology (with Boschma) and Ecology (with van der Klaauw). Altogether, one may say that the biographic accounts on N. Tinbergen tend to reconstruct his life-history primarily on the basis of his socialization as a young naturalist and the background of a back to nature movement which was nourished by the contradistinction to urban growth, technocracy and experimentalism. In my opinion this is only half way true. Tinbergen’s scientific orientation originated in a process of merging together epistemic values from different positions and this is an indicator both for a more ambivalent early scientific socialization as well as for the fact that shaping his way must be conceived – at least on a more deep structure level – less as a process of acquiring rather than withdrawing from epistemic values, theorems and corresponding scientific practices. On the one hand, I am very sure, that Niko’s early contact with Biology was shaped to a large extent by the neo-vitalistic whole animal movement which spawned both the Comparative Morphology underlying for instance O. Heinroth’s maturation studies and Lorenz’s systematic approach of social behaviours. On closer inspection, however, N. Tinbergen primarily was not interested in keeping and taming animals – not interested in surpassing the biological constraints, that is in other words, the habit which generates the epistemic practices of taming and breeding animals in captivity as well as, for instance, E. L. Thorndike’s problem solving experiments or the testing of a bird species’ homing ability: “Zoos and natural history museums had always bored him”, A. R. Leen writes.\footnote{A. R. Leen. “The Tinbergen Brothers”. In: Nobel Prize in Economics Documents 1969.4 (2004), U R L: http://econpapers.repec.org/paper/risnobelp/1969_5f004.htm (accessed on Aug. 11, 2011), 4. See also Kruuk, Niko’s Nature, 91.} By contrast, Niko’s early primary access to nature was mediated by precisely observing in the wild and writing about these observations or – even more significant – by photographing which, according to his own accounts, served him as a surrogate for hunting.\footnote{Science historians have ascribed different functions to early ethologists’ use of photography. “Photography”, D. Röell writes, “was seen as a sport, not only in the sense that it was a physical pastime, but in the competitive sense as well”. See Röell, The World of Instinct, 43–49, here 99. R. E. Kohler describes photography more as a tool used by “new naturalists” to import a more} Both behaviours share...
the same scheme since they put a moving object actively and abruptly to a state of rest either in form of the animal’s death or the picture. On the other hand, if we look carefully at Niko’s youth we see that natural history was not the only starting point for a potential career. Niko also was a talented and devoted hockey player having the option to take the career of an athlete. The status of a competitive sportsman, however, requires the readiness to advance both one’s own body and the interaction within a team. In other words, in Niko’s passion for competitive team sports we might eventually see an early and rudimentary form of an “experimentalist attitude”. Yet it is important to keep in mind that Niko’s access to sports was primarily a collaborate and social one as well as it was related to play. Moreover, it is also important to notice that what I have called “experimentalist attitude” primarily has not the quality or thrust of labour work, in a sense of sacrificing oneself for the benefit of a greater good – an attitude which we can find much more definitely developed in Jan’s life who, together with his future wife, decided to “dedicate their lives to the goals of the Social Democratic Labor Party”. Correspondingly, it is told that Niko out of rivalry to his older brother rejected quantitative methods in his early research. In sum, when H. Kruuk tends to identify Niko’s socialization as a young naturalist with a typical “Dutch upbringing” I am inclined to see the typical fallacy of a national history to fuse a specific scientific orientation with an entire national identity. Even the comparison of Niko’s path with the ones of his brothers reveals that the Dutch pre-war society was heterogeneous and therefore offered various ways of intellectual and personal development. The crucial question for me is what the specific values were in which Niko saw represented his personality. And his life-history shows that this process was not only one of adopting but more likely of rejecting cultural values. As a result, one may say Niko’s way into an academic profession combined a more empirical attitude to experimentalism with what K. Lorenz later and with modified causal implications should call metaphorically “Analyse in breiter Front” or “pure Leicology”. It would be an interesting research question whether the integration of more physiologically oriented research into the zoological department of Leiden University did not match with Tinbergen’s and also with Verwey’s development which was based on epistemic shifts that were tolerated and furthered though not shared by the older generation of zoologists at the institute. A brief glance at Niko’s major subjects reveals that it was mainly his experimental attitude which became absorbed in his university studies – either as part of an independent separate Physiology or as appetizer for more: His dissertation project. The latter of the two projects eventually still was underlying stronger van der Klaauw’s intention to push Niko’s academic socialization in his own sense. And this hypothesis might be also an adequate starting point for reading N. Tinbergen’s scientific works.

32 Leen, “The Tinbergen Brothers”, 1.
34 A. R. Leen remarks: “Except for gymnastics and drawing, in which he excelled, he [Niko] had poor marks in all other subjects”. See Leen, “The Tinbergen Brothers”, 2.
Transition One. (R1) Like in my other readings of scientific sources my primary interest in N. Tinbergen’s paper *Die Paarungsbiologie der Flussseeschwalbe* is aimed at the epistemic deep structures which turned out to be an adequate criterion to place a researcher’s stage of development within the epistemic and social space of a scientific community. From a perspective like that one may eventually say, the general tenor of Tinbergen’s paper eventually is the observation that the behaviour of a species does not appear entirely uniform yet multiple in terms of seasonal variation and daily rhythms. The basic assumption thereby seems to be that the socially living Common Terns abandon parts of their social life as soon as they respond to their mating mood. “Howard (1920) hat festgestellt”, Tinbergen writes, dass viele unserer Vögel ausserhalb der Brutzeit gesellig leben. Seine Ausführungen beziehen sich hauptsächlich auf die Singvögel, aber auch auf andere wie z.B. Kiebitz und Uferschnepfe. Der “Herdeninstinkt” (Groos 1930) oder “gregarious instinct” wird in der Fortpflanzungszeit in seinen Äusserungen vom sexuellen Instinkt verdrängt.

Howard (1920) has stated that our birds live gregariously outside the mating season. His statements refer primarily to song birds but also to others such as the Peewit and the Black-tailed Godwit. The “Herdeninstinkt” (Groos 1930) or “gregarious instinct” will be replaced in its expressions by the sexual instinct during the mating period. [*transl. CL]*

Niko’s topic is the relation between the two states and the modes of transition from one state into the other. In general, one may say that Niko thinks the transition between “social” and “individual” life of common terns in both directions but puts emphasis on the transformations from social to the sexual in as much as their number increases gradually in course of the breeding season. Moreover, Niko’s account eventually reveals that both types of transition have a different quality. While the transition to social life appears to be a more abrupt process which is based upon mutual excitation, Tinbergen tends to describe the transformation of social by sexual instincts as non-abrupt. [*transl. CL]*

Furthermore, the social and the individual state are not entirely discrete here insofar as they overlap with each other. It is of some interest for my argumentation that Niko in this respect deviates explicitly from E. Howard whose emphasis on strict functional separation (division of labor, sex roles) is described as “schematisch”. “Der Übergang vom sozialen zum sexuellen Leben erfolgt nicht plötzlich”, Tinbergen underlines,

sondern es herrscht während einiger Zeit bald das Eine, bald das Andere vor. Howard beschreibt für mehrere Singvögel, wie sie im Anfang einen grossen Teil des Tages noch im Trupp vereinigt bleiben. [Bei unseren Flussseeschwalben sehen wir etwas ähnliches. Allmählich wird die Zeit, die in der Truppe verbracht wird kürzer und nehmen die sexuellen Äusserungen mehr Zeit in Anspruch. Man muss sich diese Abwechslung von sozialem und individuellem Leben nicht so schematisch vorstellen wie es Howard tat; wenn die Seeschwalben in grossen Gesellschaften auf dem Strande sitzen, sehen wir wie gelegentlich sexuelle Handlungen ausgeführt werden

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35 Tinbergen, “Zur Paarungsbiologie der Flussseeschwalbe”, 2. Eventually one may say that the sexual instincts have a three-fold valency: (1) They are the objective in a chrono-logical sense, that is, reproduction is the target of the breeding season. (2) Beyond that sexual instincts superimpose the normal daily routine which is characterized by social relations. (3) Finally, the non-sexual state eventually prevails conceptionally in as much the breeding season is an extraordinary though common phenomenon.

36 Similar to K. Lorenz, N. Tinbergen had observed that social behaviours rest upon accumulation of mutual excitation. For his thesis that the transition to social life is a more abrupt process based on mutual excitation, see *ibid.*, 3.
From a perspective like that the course of the breeding season corresponds with an increasing number of transitions from the social to the sexual state. In putting emphasis on measurable time (and also the number of transitions) Tinbergen’s approach thus turns out to be quantititative as well as the course of the breeding season appears as gradually changing process. Tinbergen’s conception of the mating season thus is non-schematic just in the same way the transformation of social by sexual instincts is non-schematic. The alternation of the various modes of life which K. Lorenz some years later tried to grasp with J. v. Uexküll’s concept of the “companion” in Tinbergen’s mating behaviour study thereby is introduced on different levels. These levels become evident best in those parts of the paper where Tinbergen is concerned with the transition from social to individual life, that is, mainly – though not exclusively – in “II. Beschreibender Teil” and “III. Diskussion”. One of these levels is spatial: Non-sexual birds stay together with others in what Tinbergen calls “Trupp” (literally troop), while terns with prevailing sexual instincts choose separate breeding areas, that is, a “Kolonie” (colony). One of the decisive aspects of a colony, in Tinbergen’s view, is that it is conceived by the birds as “territory of the community” (Howard) and defended collectively. “Wie ich schon sagte”, writes Tinbergen,

37 Ibid., 2–3. “Schematisch” in Howard’s sense eventually means that both partners choose an individual territory which they defend together to the outside yet which is ruled by strictly sex-determined division of labour to the inside. See also ibid., 17.

38 Or: sexually conditioned transformations of the usual daily rhythms in favour of the sexual life.

39 I have described this epistemic figure as performative coincidence. Moreover, in Tinbergen’s critique of Howard’s schematism we might see a move analogous to the one K. Lorenz performed with his critique in J. v. Uexküll.

40 See ibid., 3–4.
kommern die Vögel in den ersten Tagen nicht auf den Boden herunter, sondern fliegen fortwährend umher. Dass sie ihr künftiges Brutgebiet doch schon mit anderen Augen ansehen als jedes andere Gebiet, dass sie darin also ihr gemeinschaftliches Territorium ("territory of the community" Howard’s) erblicktn, ersieht man in der Weise, wie sie auf Menschen reagieren. Wenn ich die Kolonie durchquerte, hörte ich schon ziemlich oft den Alarmruf, ein langgezogene: Tji-èrrrrr! Zwar sammelte sich nicht, wie in der Brutzeit, eine grosse Anzahl Vögel über mir, aber das Rufen war erheblich stärker als über dem Meeresstrande, wo nur gelegentlich ein einziger Vogel alarmierte.

As I already said, the birds do not come down to the grounds during the early days but instead circle continuously. Yet that they see their future breeding area already with different eyes than any other area, that is, that they interpret it as their collective territory (Howard’s “territory of the community”) can be seen in the way they respond to humans. When I passed through a territory, I often heard rather soon the alarm call, a long: Tjèrrrrr! Although a great number of birds did not assemble over me like in the mating season, the calls were considerably stronger than over the beach where just one bird performed the alarm call now and then.[transl. CL] 41

Another aspect is causality: In contrast to silvery Gulls whose daily rhythms are adjusted to the tides, the variation of behaviours in terns seems not adapted directly to environmental factors. Tinbergen speaks of “Stunden sexuell bedingten Lebens” (hours of sexually conditioned life) and though he goes not into detail we may estimate he eventually thought more about the physiology of sexual interaction.42 An aspect which reveals Tinbergen’s physical understanding of pair bondings is the individual recognition of both partners and between parents and offspring.43 Although his paper does not provide a fully elaborated theory of individual recognition we see from his account that Tinbergen primarily thinks about acoustic and olfactory factors which are likely to establish the relationships. Insofar the bondings are conceived as physically conditioned.44 Moreover, Tinbergen describes symbolic actions such as mutual feeding less as functional in themselves (i.e. as relevant for nourishment) but within a behavioural frame that is both ruled by and directed towards establishment and maintenance of stable pair bondings.45 Insofar the original purpose of the behaviours appears more or less superimposed by the sense of sexual reproduction. In this context, Tinbergen ascribes an “exciting effect” to the symbolic actions in question.46 He writes:

Wir müssen den verschiedenen oben beschriebenen Bewegungen und Zeremonien unbedingt eine erregende Wirkung zuschreiben. Sie sind alle imstande, die Tiere entgegengesetzten Geschlechtes zu reizen, damit sie allmählich mehr “Geschlechtsstier” und weniger “soziales Tier” werden.

[We must absolutely ascribe an exciting effect to the various movements and ceremonies de-

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42 See ibid. Endocrinological factors, which would also be plausible, do not play any role in Tinbergen’s argumentation.
43 Ibid., 14–15.
44 This implies a proximate form of causation.
45 See ibid., 14. It is of great interest for my argumentation that Tinbergen in a later additional paper published in 1938 after what I have called “causal turn” puts more emphasis upon the aspect that feeding has not only a symbolic biological meaning but also the function to provide the partner with food. See N. Tinbergen. “Ergänzende Beobachtungen über die Paarbildung der Flussseeschwalbe (Sterna h. hirundo L.).” In: Ardea 27.3/4 (1938), 247.
46 Which is a paradox construction from an epistemological point of view.
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scribed above. They are all capable to arouse sexually the animals of the opposite sex so that they gradually become more “sexual animal” and less “social animal”. [transl. CL]47

From his account we may eventually also infer that transition to sexual life corresponds with raised mutual sexual desire which becomes manifest also symbolically, for instance, in begging for food.48 J. Verwey formulated more precisely than N. Tinbergen the causal frame of symbolic actions in his study of the heron’s courtship behaviours: “Wir haben keinen einzigen Grund zu der Annahme”, he writes,

dazu der Fischreiher, der geschlechtlich erregt ist, seinen Paarungskr gen hören läßt, damit ein Weibchen diesen hört und zu ihm kommt, sondern wir können die Handlungen der Vögel besser verstehen wenn wir annehmen, daß der Paarungslockruf nur ausgestoßen wird als Reaktion auf einen inneren Trieb, den Geschlechtstrieb, ohne daß der Vogel beabsichtigt, sich ein Weibchen zu suchen.

[We have not one single reason to believe that the heron who is aroused from time to time exhibits his mating call, so that a female hears it and comes to him, but we can understand the behaviours of the birds better if we presuppose that the mating call is only uttered as a response to an inner excitation, the sexual instinct, without the bird having the intention to find a female for him.][transl. CL]49

Verwey’s causal understanding of the heron’s courtship behaviours presupposes a sexual instinct in the first place and interprets the bird’s behaviours as immediate reaction to this drive. Moreover, the relation between the two stages is thought to be direct, unmediated and placed within a context of preconscious sexual agitation. He states:

Wenn wir einen Fischreiher lange studieren, dann kommen wir zur festen Überzeugung, daß jede Handlung des Tieres eine direkte Folge der Sinneswahrnehmung ist, also anders als bei uns, wo die Handlung ganz indirekt der Wahrnehmung folgt und wir also die sog. Überlegung finden.

[When we study a heron long we come to the conclusion that every action of the animal is a direct consequence of the sensory perception, that means differently than in us humans where the action very often follows the perception quite indirectly and we therefore find so-called reasoning.][transl. CL]50

From Verwey’s statement we can therefore conclude that the sexual state of life in birds was conceived in non-functional but proximate terms. Finally, the stability of pair bondings is of primary concern for Tinbergen. While the relationship of non-married pairs is more plastic the one of married pairs is steady in the sense of a reproductive association. In Tinbergen’s view, establishing relationship means transgressing a boundary, that is, creating a continuous and enduring relationship between an individual A and B. An advanced bonding thus is mutual. For instance, he argues that one of the behaviours belonging to the repertoire of sexual instincts is mutual feeding. The more mutual feeding is established the more “perfect” a relationship is. Thereby it is important to keep in mind that N. Tinbergen contradicts the widespread opinion that it is always the male individual which feeds the female.51

48 See to this also the chapter on “Lautäußerungen”, ibid., 11.
50 Ibid.
51 Tinbergen, “Zur Paarungsbiologie der Flussseeschwalbe”, especially 5, 13. According to Tinbergen, his deviating observations were also the trigger for publishing his results. Moreover,
His main argument thereby consists in the observation that mutual feeding develops gradually from a behaviour he calls “Fischflug”, that is, a playful symbolic action in course of which an individual “B” without fish aims to lead an individual “A” (with a fish in its beak). In differentiating several intensity levels of feeding behaviour Niko writes:


In order to corroborate his view that sexual pair bondings are characterized by reciprocity Niko also puts forward the notion that there is no sex determined division of labour for instance in hatching the eggs. He goes even so far to question whether

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52 Tinbergen, “Zur Paarungsbiologie der Flussseeschwalbe”, 4–7, for the playful character see pages 13–14.
53 Ibid., 7.
54 Both sexes alternately hatch and fish. See ibid., 8.
the roles of both sexes might be not fixed during copulation either.\textsuperscript{55} Finally, it is important to keep in mind that N. Tinbergen had chosen a scientific object which turns out quite beneficial for his argumentation: Common terns show hardly any sexual dimorphism and thus can be distinguished by the observer from distance only with difficulty unless the birds stay in or around the area of the nest.\textsuperscript{56} Altogether we may therefore infer that N. Tinbergen’s main intention is to make evident that the sexual life of the common terns is a nice example for what he calls with J. Huxley “mutual courtship”. “Zusammenfassend können wir also sagen”, N. Tinbergen writes in a concluding remark,

\textit{dass Sterna h. hirundo L. ein schönes Beispiel einer Vogelart ist mit “mutual courtship” in der “premating period” (Huxley (1923). Es gibt keinen einzigen Laut und keine einzige Bewegung bei den Paarungseinleitungen, die nicht beiden Geschlechtern eigen sind. Die Ankunft auf dem Brutgebiet erfolgt bei beiden Geschlechtern zur gleichen Zeit. Die Vögel sind dann noch nicht gepaart. Zur Paarbildung stimulieren sich die beiden Geschlechter gegenseitig. [In summary we can therefore say that Sterna h. hirundo L. is a nice example for a species of Bird with “mutual courtship” in the “premating period” (Huxley (1923). There is not one single call and not one movement in the introduction of the mating behaviours which is not possessed by both sexes. The arrival at the mating territory occurs simultaneously in both sexes. The birds are not yet mated at this point. To establish a bonding between the partners both sexes stimulate themselves mutually. ](transl. CL)\textsuperscript{57}

If we want to interpret Tinbergen’s paper from an epistemological point of view me might eventually say that its general thrust is to replace Howard’s schematism with a non-schematic framework which is based on continuous variability but maintains the overwhelming idea of mutual and therefore non-one-sided behavioural interaction.\textsuperscript{58} This becomes evident both in details, for instance in pointing out the mutuality of the symbolic actions at the onset of the mating season, and on the

\textsuperscript{55} Ibid., 16–17. Tinbergen’s model of pair bonding therefore is characterized both by continuity and uncertainty (in an information theoretical sense).

\textsuperscript{56} Ibid., 8, 16.

\textsuperscript{57} Ibid., 17. In his early ornithological studies J. S. Huxley, in addition to the pure-Darwinian framework consisting of natural and/or sexual selection, put forward an evolutionary model in course of which primary functional and sex-specific behavioural bouts could be mutually transferred to both sexes while gaining mere “symbolic” meaning. This means, in Huxley’s view, species of Bird with no or reverse sexual dimorphism and arbitrarily exhibited courtship displays had developed secondary forms of symbolic interaction which, in a final state, could lose their “active symbolism” and – now being associated with pleasurable and exciting emotions – can change into merely pleasurable self-exhausting processes. See to this J. S. Huxley. “The Courtship-habits of the Great Crested Grebe (Podiceps cristatus); With an Addition to the Theory of Sexual Selection”. In: \textit{Proceedings of the Zoological Society of London} 35 (1914), 496–497, 506–507, J. S. Huxley. “The Courtship of the Red-throated Diver”. In: \textit{Discovery. A Monthly Popular Journal of Knowledge} 3.26 (1922), 45, 47, 48 and J. S. Huxley. “Courtship Activities in the Red-throated Diver (Columbus stellatus Pontopp.); Together with a Discussion of the Evolution of Courtship in Birds”. In: \textit{Journal of the Linnean Society of London, Zoology} 35.234 (1923), 253, 268, 272–273, 278. For more background details concerning Huxley’s position see also M. M. Bartley. “Courtship and Continued Progress: Julian Huxley’s Studies on Bird Behavior”. In: \textit{Journal of the History of Biology} 28.1 (1995), 91–108. I think it is the epistemic framework underlying Huxley’s evolutionary model which attracted N. Tinbergen in his own early ornithological studies and, beyond that, might also have been the starting point for his reasoning about “ritualization”.

\textsuperscript{58} Tinbergen terms his observations in chapter “II. Beschreibender Teil” as “schematisch” (Tinbergen, \textit{Zur Paarungsbiologie der Flussseeschwalbe}, 13). This matter of fact seemingly contra-
more abstract levels of Niko’s argumentation such as his view that the course of the breeding season can be described as gradually shifting equilibrium system of transitions between the social and the sexual life of the birds which, despite all continuity, can be divided in periods. The overtone of the entire epistemic reference system is therefore paradox.

(R2) According to H. Kruuk, it is not entirely clear why N. Tinbergen began to be obsessed with digger-wasps in his final exams. An impact might have come from J. P. Thijssse, H. Fabre’s and K. v. Frisch’s works. What is known for certain is that Niko’s interest in *Philanthus triangulum Fabr.* shifted from its phenology (final exam paper) to the animal’s orientation skills (dissertation project) and as such constituted a research project which expanded over several breeding seasons (1931, 1934–1937). As far as I can see mainly four papers originated from Niko’s perennial *Philanthus*-research each of which was originally published in German language either in the *Zeitschrift für vergleichende Physiologie* (Journal of Comparative Physiology) or the *Biologisches Zentralblatt*. The dates of the publications suggest that Niko’s *Philanthus*-research eventually covers a period of major epistemic shifts. The comparison of the papers thus might reveal quite well the way Tinbergen interpreted the turning points of his early scientific development. This is the more likely since the three later publications (of the years 1935 and 1938) pick up more detailed topics upon which Tinbergen had already elaborated in his dissertation thesis (published in 1932). My hypothesis is, that Niko’s dissertation thesis provides a first approach to the topic and beyond that rests upon the classical causal architecture whilst the succeeding three publications of the years 1935 and 1938 provide detailed insight in the two main types of orientation Niko had already introduced in 1932 yet do so on basis of the causal turn which can be made evident in both the life courses of other ethologists and the transformation process

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dicts the overall tenor of the paper but would make sense if we took into account the overall composition of the text. That “objectivist” epistemic frames can actually encompass “subjectivist” and / or “anthropomorphic” passages is supported by G. Beale’s dissertation thesis, especially the parts where he analysis Tinbergen’s field notebooks. See Beale, “Tinberian Practice, Themes and Variations”, 31–76. Please note that in Beale’s dissertation thesis the page references of the table of contents do not always match with the actual page numbers. I refer to the latter. Kruuk, *Niko’s Nature*, 50.

D. R. Röell his identified a major impact in J. P. Thijssse’s studies on wasps which included taxonomic aspects, their behaviour and life cycles as well as their “homing practice”. See Röell, *The World of Instinct*, 69–70. Methodologically Tinbergen’s study reflects K. v. Frisch’s spirit whose works he had “devoured” while being a student in Zoology and whose experiments he will later recall as “methodologically faultless and in their sophisticated simplicity beautifully elegant”. See Tinbergen, “Watching and Wondering”, 440 and in addition Röell, *The World of Instinct*, 71–72.

Phenology is the study of those appearances in living organisms which are dependent on seasonal changes.

Darwin’s ideas underwent one time layer before. I will therefore analyze at first Niko’s dissertation thesis and return to the additional parts II., III., and IV. of his overall *Philanthus* study when I examine later how the known causal intervention became manifest in N. Tinbergen’s research around the year 1933. *Philanthus* is a wasp-like hymenopteron whose female representatives dig holes in the sand in which they lay their eggs during the summer months. To feed their offspring they prey living bees which they kill with a precise sting and after that dispose inside the tubes they have dug into the sandy ground before. Since each tube is furnished with more than one bee the digger-wasps have to return to their nest several times. Both approaching the bee which is the preferred and almost exclusive prey animal of the digger-wasp and returning to the nest are faculties which Tinbergen subsumes under the term “orientation” and as such require the capacity to recognize a schema of the respective target object. A first hint how to receive Tinbergen’s *Philanthus*-studies from a more epistemic point of view may be his understanding of orientation which he interprets apparently less in terms of the classical problem-solving experiment (opening accidentally a puzzle-box and being rewarded) but as more or less abrupt change from a state of disorientation into a state of orientation. Other aspects of his study seem to coincide with this analytical scheme of thought: For instance, Tinbergen had observed that young imagines produce several unfinished holes before they can dig complete orderly nests. He explains this matter of fact with an awakening digging instinct or drive which in the first days is not yet directed and connected purposefully with other acts. Moreover, it is important to keep in mind that *Philanthus*, in contrast to bees, is a solitary living insect which implies that orientation primarily cannot be achieved by gregarious instincts or even communication. Tinbergen’s interest in orientation thus refers to the individual, species-specific or even sex-specific faculty to recognize both inorganic and organic environmental objects. Finally, in a first approximation, one may eventually say, the entire act of bee-hunt encodes also an epistemic pattern insofar as it consists of two rather discrete part behaviours, namely the act of taking prey, on the one hand, and the act of homing and storing the bee, on the other. With respect of Tinbergen’s way to articulate the causal dimension in his thesis it is of some interest that *Philanthus* after having stung the bee begins immediately to take away the bee’s honey. Furthermore, it is not quite irrelevant that the digger-wasp disposes the taken prey in the nest-tube dead and not alive which would favour a more paradox epistemic constellation. It could be made evident that the way how N. Tinbergen organized and presented his knowledge in his thesis as a whole recapitulates the epistemic pattern in question in form of an analytical scheme in course of which empirical data is reduced to a set of both physiological and observational results. The main part of the empirical preparatory works which later serve as basis

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64 On Tinbergen’s observation that honey bees are almost exclusively the sole prey animal of *Philanthus*, see ibid., 308.
65 Ibid., 307.
66 Tinbergen’s study is related to female digger-wasps only. See ibid., 306. That his study concentrates on a solitary living hymenopteron can be inferred from the research overview he provides in chapter “III. Die Heimkehrfähigkeit der Hymenopteren”. See ibid., 310–312.
67 Ibid., 308.
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for conclusions consist of making evident that both part acts – that is homeing, on the one hand, and making prey, on the other – reveal two different sensory types of orientation. “Diese beiden Arten der Orientierung, das Heimfinden und das Erkennen der richtigen Beute”, Tinbergen writes,

können in grundverschiedener Weise vor sich gehen. Es ist also notwendig, die beiden Fragen einzeln zu untersuchen.

[These two kinds of orientation, the homeing and the recognition of the right prey object can basically proceed in different manner. It is therefore necessary to scrutinize both questions separately.] (transl. CL)

The faculty to recognize a nest in fact is a result of what Tinbergen calls “orientation flight” (Orientierungsflug), that is, a specific flight-behaviour pattern during which the insect flies with increasing radius and height around a nest thereby memorizing adequate landmarks which are perceived mainly optically. Tinbergen describes the capacity to memorize landmarks with A. Kühn’s concept of “Mnemotaxis” that is orientation takes place by means of stimuli stored within the memory and not by stimuli transmitted by the present object itself. Mnemotaxis thus allows to orient towards more remote objects. Memorizing optical stimuli, in Niko’s view, therefore is the prevailing factor in the homing ability of Philanthus triangulum. The

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69 Ibid., 307–308.
releaser to prey a bee, by contrast, appeared to be the contact of the digger-wasp’s antenna with the bee. The fact that the antennas include the insect’s smell organ let Tinbergen suppose that recognizing a bee is also olfactory by nature. In how far does N. Tinbergen’s experimental examination of both orientation types reveal different epistemic schemes, in particular, on the causal level of argumentation? In general, one may say that N. Tinbergen’s experimental examination of the digger-wasp’s homing ability is based on the conditioning method (Dressurmethode). That means the insect is made familiar with a specific environmental setting by habituation and tested for reactions to changes of this setting in the second place. The intention of the procedure thereby is to isolate single optical qualities. “Nach den Untersuchungen von v. Frisch (12, 13, 14)”, Niko underlines,

The “isolation” of the visual stimuli occurs in fact by comparing an experiment with a corresponding control-experiment in each of which the insect could choose between the original nest and a pseudo- or dummy-nest. While in the first case the modification affected the dummy-nest, it is the original nest which was modified in the control-experiment. If in both cases the modified setting was chosen – that is the dummy nest in the experiment and the original nest in the control-experiment – Tinbergen felt entitled to infer that *Philanthus* prefers the more refined setting of visual stimulation over the original setting and this was said to hold quite independent from the location of the nest and its environment. In order to illustrate Tinbergen’s conditioning method I quote a longer passage in which he describes his first experiments. He writes:


73 For the contact as releaser see, ibid., 308. On the olfactory nature of proximate orientation see ibid., 310.
74 Ibid., 312. See also Röell, *The World of Instinct*, 72.
es war also ganz egal, ob ich in der Umgebung des richtigen Nestes etwas änderte oder nicht, denn beim Kontrollversuch wurde nur der Zapfenkreis verlegt.

[For reasons that will be explained further below I used pine cones for proving optical orientation. These were lying around on the sandy ground in masses so that they apparently could be used as a natural quality [for the recognition of the nest]. I conditioned wasps to a circle consisting of 20 cones around the nest entry which I have built in the morning between 8 and 10 o’clock. In course of the afternoon then the following experiment was carried out. If the wasp had flown out to fetch a bee I built a “dummy nest” in a distance of around 30cm from the nest by fairly precisely imitating the sand spot and the entry. The real nest was kept intact or I altered the sandy ground but the entry of the nest always remained intact. The cone circle was laid around the dummy nest. When the wasp returned with a bee and settled down on one of the two nests I drove it carefully off – so that it did not drop the bee – and let it choose once more anew.

After I had made at least five observations in this way, I at once performed the control test by placing back the pine cones around the right nest. Also in this setting I let choose the wasp at least five times. By this control test I isolated the characteristic of the entire complex of stimuli being connected with the “cone circle”; as a result it was entirely irrelevant whether I changed something in the environment of the original nest or not because in the control experiment only the cone circle was displaced.]

N. Tinbergen’s method to examine visual orientation can be called “discrimination experiment”. Its intention is to correlate definitely one or an entire setting of visual stimuli with a reaction. This method also implied the possibility of successive comparisons of ever more refined experimental settings. While in Tinbergen’s first experiments, as the quotation above shows, the entire setting “Zapfenkreis” was isolated as relevant (i.e. discriminative stimuli), later experiments intended to determine which of the setting’s qualities are more liable to release a response than others. Just in the same way the procedure of a single experiment is reductive, the entire set of experiments conducted by Tinbergen thus seems reductive as well. Thus I believe that chapter “IV.A. Dressur auf den Reizkomplex ‘Zapfenkreis’” and chapter “IV.B. Dressur auf optische Merkmale” provide the sufficient argument for Niko’s hypothesis that it is mainly the optical stimuli which have discriminative value: Whenever optical discriminative values are applied, that is, the insect has been conditioned on visual qualities, they – but eventually not they alone – have the decisive effect. De facto this requires eliminating olfaction as possible relevant parameter of the animal’s homing ability. In contrast to Tinbergen’s later studies and his image of a pure “field observer” this intention also implied vivisectional methods such as the amputation of the insect’s antenna where the experimenter had localized the insect’s scent organs. The amputation of smell organs apparently had no impact upon the digger-wasp’s homing ability – a result which confirmed Tinbergen’s hypothesis. In a concluding remark it reads:

Aus den vorhergehenden Versuchen geht überraschend eindeutig hervor, daß die optischen Merkmale in der Nähe des Nestes für die Nahorientierung ausschlaggebend sind. Die Wespen sind ja leicht auf optische Merkmale zu dressieren und aus der Tatsache, daß keine einzige Wespe sich auch nur einmal “geirrt”, d.h. sich auf andere Merkmale orientiert hat, dürfen wir schließen, daß eine andere Orientierungsweise hier kaum in Betracht kommt. Daß eine olfaktorische Orientierung nicht sehr wichtig sein kann, zeigen uns die Versuche 2, 3 und 4, Der 4. Versuch

76 Ibid., 314–315.
77 Ibid., explicitly 316, passim.
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beweist außerdem – und das ist für die Verwertung späterer Versuche wichtig –, daß nach Amputierung der Antennen die optische Dressur erhalten bleibt, daß also von einer schweren allgemeinen Schädigung, einer Schockwirkung nicht die Rede sein kann.

[From the previous experiments, it can be inferred surprisingly unambiguously, that the optical characters near the nest are crucial for the orientation in close distances. The wasps, in fact, can be conditioned easily to optical clues and from the fact that not one single wasp has made a mistake, that is, has become oriented through other clues, we may infer that another form of orientation cannot be taken into consideration here. That olfactory orientation cannot be very important, is shown by the experiments 2, 3 and 4. The fourth test proves in addition – and this is important for the later use of the experiments – that after the amputation of the antennas the possibility of conditioning to optical clues was till preserved so that one does not have to consider any severe general damage or shock effect.]

Chapter “IV.C. Dressur auf olfaktorische Merkmale”, on the contrary, provides the necessary argument by excluding the discriminative value of olfactory stimuli (logically by negating the proposition that not only visual but also olfactory stimuli can have a discriminative effect).

Visual stimuli and visual stimuli only, thus the implicit conclusion, have a decisive effect on the digger-wasp’s ability to recognize its nest. In addition, Tinbergen excludes the effective relevance of color perception (chapter “IV.D.1. Dressur auf Farbplatten”) and reveals that recognition through visual mnemotaxis applies predominantly within a radius of about 200 cm around the nest and not beyond (chapter “IV.D.2. Die Grenze zwischen Fernorientierung und Nahorientierung”). To mark this inner area whose radius might be subject to individual variation as well, Tinbergen speaks of “Nestumgebung” (surrounding of a nest). Within this area Philanthus is guided by the modes of “Nahorientierung” (proximate orientation, short-distance orientation) (Tinbergen’s emphasis). It is characterized by the insect’s ability to choose between different nests. With respect of the area beyond this boundary he speaks of “Fernorientierung” whose mechanisms have not been subject of his thesis.

At the end of the discriminative procedure in course of which Tinbergen drew tighter and tighter the circle of relevant sensory factors (exclusion of non-optical factors, if visual then exclusion of non-adequate factors such as colour or landmarks outside a critical range) there stands a conclusion: “Über die Natur der optischen Mnemotaxis des Philanthus läßt sich weiter folgendes sagen”, Tinbergen summarizes.

Die Wespen orientieren sich weder auf eine bestimmte Zapfenzahl, noch auf die genaue Form des Kreises, sondern auf einen nicht scharf begrenzten Reizkomplex, den wir(d)\textsuperscript{1} den optischen Reizkomplex Zapfenkreis nennen müssen. Daß dieses nicht vom Bau der Rezeptoren, sondern psychisch bedingt ist, geht aus den Ergebnissen der Versuche 7–10 hervor.

[About the mnemotaxis of Philanthus the following can be said: The wasps are neither oriented by a certain amount of cones nor the exact form of the circle but instead by a not clearly defined complex of stimuli which we have to call the optical stimulation complex cone circle. That this

\textsuperscript{78} Ibid., 316.
\textsuperscript{79} See ibid., 317–319. The fact that Tinbergen describes his attempts to condition the insect upon olfactory sensations as failed, from a more epistemological point of view, implies that these sensations are linked with a notion of “dysfunctionality” in the present experimental setting.
\textsuperscript{80} Ibid., 319–322, 322–323.
\textsuperscript{81} Ibid., 322.
\textsuperscript{82} Ibid., 323.
is not a result of the physiological structure of the receptors but has psychic origins, is suggested by the results of the experiments 7–10.

The quotation reveals that Niko’s conclusion of the digger-wasp’s capability to recognize its nest is topographic and partly exclusive. Neither pure form nor a numerical factor determines the insect’s homing ability yet a complex of stimuli whose unity is traced back to a higher (i.e. psychic) level of integration.

The hunting behaviour of *Philanthus*, in contrast to its ability to recognize the nest, is not only guided by an alternative type of orientation, from an epistemological point of view its experimental examination is also based upon a different epistemic pattern. While Tinbergen’s account on optical mnemotaxis was obviously reductive and mainly observational by nature, the examination of the digger-wasp’s ability to approach and prey follows much more a classical experimentalist scheme insofar as initial tests (chapter “V.A. Beobachtungen” and chapter “V.B. Versuche”) are supplemented by succeeding histological examinations (“VI. Der Bau der antennalen Sinnesorgane”). In the following, my analysis mainly concentrates upon the former of the two aspects. While approaching his subject “bee-hunt”, Tinbergen must have had in mind a dualism between a “normal” (V.A) and a non-normal (V.B) test setting. However, on closer inspection, it turns out that what Tinbergen terms “normal behaviour” (in V.A) was not observed under entirely natural conditions either since he put his experimental animals under a bell jar. From an epistemological point of view, we have therefore to do with a paradox experimental setting in chapter V.A. (“Observations”), that is, quasi-natural environmental conditions. According to Tinbergen’s observation, the digger-wasp’s hunting behaviour itself consisted of a multistage action pattern in course of which *Philanthus* needs to get interested in its prey in the first place but ultimately is prepared to sting the bee only under the precondition that the wasp has touched the bee before with its antennae. From this Niko inferred that asides visual stimulation another additional olfactory stimulus must be involved in the digger-wasp’s prey hunt. “Ich gewann also aus diesen Beobachtungen die nachfolgende Vorstellung”, Tinbergen writes and continues:

As the quote above reveals, Tinbergen had in mind a bipartite procedure for his

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84 See chapter “V. Die Bienenjagd” of N. Tinbergen’s *Philanthus*-study. See ibid., 324–328.
85 Ibid., 325.
86 Ibid.
Niko Tinbergen (1907–1988) experiments, too, namely both the elimination of the olfactory stimulus through vivisection and what he calls “isoliertes Darbieten” (isolated presentation) of the stimulus in question. “Man kann nun den Geruch in zwei Weisen isolieren”, Tinbergen explains,

und zwar erstens durch Amputierung der Antennen, also durch Ausschaltung des Geruchsreizes, und zweitens indem man anderen, normaliter von Philanthus verweigerten Insekten Bienenduft als Merkmal beigt.

[One can isolate the scent factor in two ways and that is, firstly, by amputation of the antennas, that is, by extirpation of the scent organ and, secondly, by attaching insects which are normally refused by Philanthus with the scent of the bees.] [transl. CL]

In both cases the experiments again were performed under the bell jar (Glasglocke) but in contrast to Tinbergen’s observations included manipulative interferences, either through severe causal intervention in form of extirpation or, less rigorously, by the attachment of an object animal with a scent. Thus, the extirpation of the antennas (chapter “V.B.1 Versuche mit antennenlosen Wespen”) suggested that the final recognition of a bee is dependent on the function of the smell organs whose gradual extirpation apparently corresponded with a gradually changing quantity of digger-wasps performing the final sting. Moreover, in order to confirm his hypothesis that the final killing act of the digger-wasp was triggered by the smell-organs located in the antennas and not, for instance, by mere touch, Tinbergen conducted experiments without amputations (chapter “V.B.2. Versuche mit bienendufttragenden Fliegen”). The results confirmed his hypothesis in principle: Insects which usually do not belong to the prey animals of Philanthus were grasped to be stung as soon as Tinbergen had transferred the bee’s scent upon their bodies. However, Tinbergen mentions that none of the manipulated insects was actually killed since Philanthus apparently realized its mistake. This brought him to the conclusion that the digger-wasp finds its prey through visual stimuli but tests its prey by means of its olfactory sensory organs before a final killing act is performed. In sum, we may eventually say that Tinbergen’s experimental examination of the digger-wasp’s hunting behaviour as well as the practices underlying the study of the optical mnemotaxis follow a particular characteristic scheme. While Tinbergen’s examination of the digger-wasp’s homing ability was reductive, the experimental approach to the insect’s hunting behaviour extended or supplemented initial observations and once more reductive experiments with additional histological data. A brief glance at the causal level of the epistemic schemes applied particularly in chapter V. which also seem to mirror the way Tinbergen ordered and presented his knowledge in his thesis as a whole reveals that his early scientific studies were grounded on a classical causal architecture which combines the experimental variation of environmental settings with manipulative interferences and thus a non-functional, proximate and direct form of causality (as applied, for instance, in V.B.1), whereas reduction corresponds with an ultimate form of causality: The idea of discrimination is linked with the idea of choice, right choice, to be more precise. The latter aspect becomes
evident for instance in Tinbergen’s thesis that the optical orientation of a digger-wasp within its restricted “Nestumgebung” is characterized by its ability to *choose* between various nests which implies selective perceptual and that means psychic “mental” capacities. In other words, in pre- or non-Darwinian scientific orientations the discrimination of sensory stimuli is functional. This constellation will change as soon as Niko chose a Darwinian course.

**Causal Interventions 1932/1933–1938**

Transition Two. Niko had finished his dissertation thesis in early 1932 and was appointed Doctor of Philosophy on the 12th of April. Two days later he married Elisbeth Amélie Rutten. At that time the young couple was already busy planning a trip to Greenland which also was meant to be their honeymoon. With the help of his friend G. J. Tijmstra Niko had managed to be chosen as one of six members for a meteorological expedition to Greenland which was part of the International Polar Year 1932–1933 and funded by the Dutch government. Niko’s official task was to collect ethnographic material for the School Museum in The Hague, plants for the Leiden Herbarium and animal specimens (mainly birds) for the Rijksmuseum van Natuurlijke Historie. Despite the fact that Niko’s official work was not directly related to his expertise, H. Kruuk has connected the year in Greenland (01/08/1932–10/09/1933) with critical changes in Niko’s scientific work. “But more significantly still”, he writes,

I believe that the Greenland work marked a watershed for Niko the scientist: he came of age. Greenland conferred a maturity that began to show in the papers on the bird work during the second part of their stay. He also began to publish in English, and after Greenland, he began to theorize. His views of animals had changed, and he became confident of his scientific approach to animal behaviour.

In addition, I. Mysterud has argued that changed eating habits during the journey to Greenland might have put Niko’s depression into another light or even lessened its severity. For the moment I would like to stay still on a more phenomenological level of argumentation and ask in how far the experiences made during his year in Greenland might coincide with fundamental epistemological shifts on the deep-structure level and especially the causal dimension of N. Tinbergen’s scientific reasoning. Several sources document the Tinbergens’ stay in the area of Angmagssalik.

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91 For the biographical details mentioned in the following and the details about Niko’s trip to Greenland see mainly Kruuk, *Niko’s Nature*, 59–69. On Niko’s trip to Greenland, in addition to Kruuk’s account, see also Roell, *The World of Instinct*, 76–77, 81–85.
92 Ibid., 81.
94 See Mysterud, “Niko Tinbergen’s Life and Work”, 549. In a later letter to his colleague, the Italian psychotherapist M. Zappella, Niko himself seems to argue exactly in this direction. See Bodleian Library, Special Collections and Western Manuscripts, Oxford University [quoted as: Bod. Lib.], Nikolaas Tinbergen Papers [quoted as: N. Tinbergen Papers], Ms.Eng. c. 3146, D 47, letter N. Tinbergen to M. Zappella (16/02/1982). The New York psychologist M. Welch who analyzed N. Tinbergen’s depressive condition in a letter, however, seems to have made responsible other than purely nutritional factors for Niko’s depressions as well (early childhood, traumatic experience during war and imprisonment etc.). See ibid., Ms.Eng. c. 3146, D 45, letter M. Welch to N. Tinbergen (21/11/1982), and also Niko’s response ibid., Ms.Eng. c. 3146, D 45, letter N. Tinbergen to M. Welch (02/12/1982).
Niko Tinbergen (1907–1988)

(now Tassiusaq) which is located on the south-east coast of Greenland. Niko began to document his observations in a diary, he wrote two scientific and a bunch of popular articles and finally published a book in Dutch language with the title “Eskimoland”.

After the members of the expedition landed in Angmagssalik, Niko and Lies separated from them to move up the fjord and take a base in Kungmiut, a small settlement whose community had been founded by Karale seventeen years before the Tinbergens arrived. Karale who belonged to a family of shamans taught Niko how to use a kayak, how to hunt and fish, and survive in the cold. Moreover, he passed on to Niko what he knew about animals and people. Following H. Kruuk’s account Niko began to view his environment with the eyes of a native Inuit whose intimate relationship with nature (especially animals) he reverently awed. “The hunting experience affected him deeply”, Kruuk underlines and continues:

His own diary showed that Niko threw himself into his new existence with complete abandon, and the Tinbergens would talk about their time in Greenland until the end of their lives. They dressed the part, had no problems in living on a diet of ship-biscuits, seal meat, and fish, and honed their field skills.

Moreover, according to Kruuk it was in particular the Inuit’s habit to treat animals as objects (though with respect) which “went to the heart of Niko’s views of the animal world and therefore of his science”. “Animals were not accredited with the subjective feelings that we have ourselves”, he writes and continues: “they were objects, highly complicated yet objects, as are plants. This view of nature was very different from what Niko had grown up with, but it became an important aspect of his scientific, ethological approach to his animal subjects”. I do share Kruuk’s view that Niko’s approach to natural objects, especially animals, often had the character of a direct relation. For my argumentation, however, it is even more important that this “objectivist” attitude was mediated primarily by the practice of hunting which implied foraging in and adjustment to the wild. Insofar the modified objectivist attitude Tinbergen most likely began to develop in Greenland contradicted partly the experimentalist objectivism he had already been familiar with through the physiological training which had been part of his zoological studies and which he had applied eagerly for instance in the vivisectionist parts of his *Philanthus*-study.

Nor was the idea of complex social relationships in animal aggregations a new one as his paper on the mating behaviour of common terns reveals clearly. My analyses...

95 For the time being, I will focus on the scientific publications of Niko’s which originated in the period between 1932 and 1933. However, I am convinced that a historical account which is aimed at finding out the causes for the epistemic shifts Niko’s works experienced around that time must take into consideration these additional sources. For a first approximation to N. Tinbergen’s autobiographical accounts see N. Tinbergen. *Wo die Bienenwölfe jagen. Neugierige Forscher in freier Natur*. Mit einem Geleitwort v. Konrad Lorenz. Aus dem Englischen und Holländischen von Amélie Koehler. Berlin et al.: Parey, 1961, chapter two, “Arktisches Zwischenspiel”, and three, “Schneemännern und Odinshühnchen”, 24–40 and 41–52, respectively.


97 Ibid., 63–63.

98 Ibid., 64.

99 See also ibid., 69. I think Kruuk mixes too much “mechanism” with “objectivism” a linkage which does not hold within a neo-Darwinian framework.

100 According to Röell, Niko was gradually becoming aware of the difference between proximate and ultimate behavioural factors in this time and began to give priority to the question of...
of the scientific papers which I have put in the centre of my interest therefore are guided by the questions how Niko’s objectivism became modified and – secondarily – in how far this intervention which most likely took place on the causal level of his scientific orientation might have been affected his later reasoning on orientation as it became manifest in his renewed reassessment of the Digger Wasps’ hunting and homing after his trip. Altogether, I am therefore interested how both realms of Niko’s personality changed during and after his Greenland experience. From their base in Kungmiut the Tinbergen set off for long camping trips into the Torsssukaataq-fjord (one of the smaller side-fjords of the Angmagssalik-fjord) in order to observe birds, especially Snow Buntings and Phalaropes, which later became the objects of the two scientific papers Niko published after his return to Leiden. Both papers are not only connected with each other through their enumerative titles “Field Observations [...] CL I” and “Field Observations [...] CL II” but also through a common topic, territoriality, which N. Tinbergen continued to reassess and reinterpret in his Greenland studies in terms of non-spatial categories. Moreover, his papers on Phalaropes and Snow Buntings continue his reasoning about the arbitrariness (i.e. uncertainty in epistemic terms) of sex-roles and now, in addition to that, bring in the question of adaptedness and a stronger emphasis on natural and sexual selection. Yet both studies pursue this objective from a slightly different perspective which becomes clear if we take into account the different types of scientific object and the presuppositions with which these objects are treated. One of these presuppositions is that the differences in plumage which cause sexual dimorphism correspond with different adaptive values, that is, “dull” colouration, as Tinbergen puts it, has protective value, while “conspicuously coloured structures” may be of value during...
courtship and fighting. Second, in cases of extreme division of labour where one sex mainly courts and the other does the incubation, according to Tinbergen, there are two tendencies: The courting partner will be the one which displays obviously coloured parts, while the incubating partner tends to be camouflaged. Finally, differences in morphological structures may correlate with corresponding behaviours. The Red-necked Phalarope, a species of wading birds, was reasonably chosen as an object of scientific observation by N. Tinbergen because of its reverse sexual dimorphism.\(^{104}\) In many bird species the male is brightly coloured, while the female is the less conspicuous partner. Not so in Phalaropes: Here the male is the drab sex, while the female displays coloured parts and defends a territory. Phalaropes are therefore an example for marked arbitrariness of morphological sexual characters and Niko’s question was whether the inverse sexual dimorphism is correlated with corresponding courtship and territorial behaviours. Snow buntings, by contrast, reveal only little sexual dimorphism and Tinbergen’s observations suggested that territorial behaviour here is variable both with respect of the temporal succession in the breeding season and with respect of single courtship ceremonies. In the first case he realized that the habit to claim and defend territories wanes in course of the breeding season when the birds “roamed widely in search of food for their growing young”, a result which contradicted M. E. Nicolson’s views.\(^{105}\) The latter apparently had observed Snow Buntings only later in the season and thus came to the conclusion that arctic Snow Buntings in contrast to their British relatives display at best only a very slack territorial behaviour. The question how Snow Buntings recognize and react towards other intra- and extra-specific individuals entailed, finally, a common principle which Niko later generalized to further species such as the Stickleback, the Robin, Storks, Gulls, Lizards, Bitterlings and the Cuttlefish:\(^{106}\) Especially in species with relatively slight sexual dimorphism the first reaction of the “male” towards a foreign individual is hostile and triggered independently whether this individual is male or female. In a second step, which is dependent on the response of the newcomer, the male’s reaction pattern bifurcates in either fight (reaction to a male response) or courtship (reaction to a female response). In the latter of the two cases the aggressive tendencies against the other individual are suppressed by the friendly ones. Both steps seem to be correlated with corresponding mechanisms inside the animal’s sensory apparatus, which to carve out was more the task of the Phalarope paper. In sum, one may eventually say, N. Tinbergen continued his aim to evince the arbitrariness of courtship behaviours in the two studies he performed during his year in Greenland. In the one case he asked for the behavioural correlates of reversed sexual dimorphism, while in the other case he put emphasis on the linear transformation of the behaviours on both the macro- and the micro-level of his observations. How did he come to his results in each case? And in how far are both

\(^{104}\) On the Phalarope’s reverse sexual dimorphism see Tinbergen, “Field Observations of East Greenland Birds I [1935]”, 4, 6-7, especially 18, 21, and 25.

\(^{105}\) See Tinbergen, “Watching and Wondering”, 442.

\(^{106}\) N. Tinbergen. The Herring Gull’s World. A Study of the Social Behaviour of Birds. Reprint. London: Collins, 1971 [1953], 89–90. It would be a nice further leading research question in how far Lorenz’s Special Phylogeny of Releaser was inspired by the double logic of this principle or the other way round.
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studies documenting an intervention on the causal level of Tinbergen’s reasoning? In comparison to Niko’s study of Snow Bunting his observations of the Phalaropes seemed to have more the character of an interlude.\textsuperscript{107} Moreover, the study cannot be called quantitative since it refers to the behaviour of “one female and of one male which paired with her”.\textsuperscript{108} Furthermore, Niko’s case study of more or less one single pair is said to have been made from a more psychological perspective. “Though the Phalarope is a valuable object for the study of the natural history of bird-courtship, and the purpose of my studies was primarily the ‘Biology’ of the Phalarope’s courtship”, he points out, yet I have tried to look at it from a more psychological point of view too, as to my opinion close observation of the behaviour of any bird will reveal many new facts, tending to throw light on the vast field of the psychology of birds, which, in spite of much work done, still may be said to be almost undiscovered country.\textsuperscript{109}

In this introductory statement we are also informed about the general thrust of the study: Close observations of the wading bird’s courtship behaviours (to be made in the first place) ought to entail some insight into the psychology of the specific sexual display. In other words, observed behaviours should disclose correlations with Phalarope’s reverse sexual dimorphism on a more psychological level. Although it appears difficult to reconstruct with definite certainty the way how N. Tinbergen organized his findings in his Phalarope-paper, I think, the study as a whole mirrors the reductive general thrust inasmuch as a general overview of the bird’s breeding cycle (“2. Description of the courtship and the formation of pairs”) seems to be supplemented by a more elaborate account of four particulate problems whose critical reassessment (chapters 3.–6.), in turn, paves the way for a more general conclusion as to the psychological nature of the behaviours in question (as outlined in chapter “7. Discrimination of the other sex”): Thus, for the time being, I believe that chapter three (“Territory and ceremonial flight”) reactivates Tinbergen’s non-spatial and behaviour-based understanding of the “territory”. Chapter four (“The stimulating actions”) argues that both sexes are, so to say, ad hoc in the need of sexual stimulation. Chapter five (“The functions of the male and female”) concludes that no parameter other than the bird’s \textit{behaviour} can be reasonably correlated with the morphological feature of “camouflage”. Chapter six (“‘Functionless’ courtship and the supposed polyandry”), finally, seems to contradict accounts according to which the female Phalarope is liable to polyandry and thus suggests that the birds can recognize the respective other sex. All these argumentative parts point into the direction of a more energetic model of behavioural motivation. For my argumentative purpose it is sufficient to give a brief overview of the linear succession of Phalarope’s reproductive behaviour in the first place and then pick out two relevant epistemic complexes whose causal architecture shall be examined in detail.

N. Tinbergen’s account of Phalarope’s reproductive cycle can be read as succession of altogether four different stages. Thus, a first period covers the wader’s courtship

\textsuperscript{107} This is suggested by the relatively short period of time the Tinbergens invested in these observations. Niko speaks of ca. 140 hours divided over 22 days. See Tinbergen, “Field Observations of East Greenland Birds I [1935]”, 2.
\textsuperscript{108} Ibid.
\textsuperscript{109} Ibid., 3.
before the pair mates.\textsuperscript{110} It is characterized mainly by a first indifferent approach of the female which is directed to any newcomer independent of its sex (and species). This behaviour pattern is supplemented in a later stage of the interaction by behaviours which are directed towards a potential partner and have the function to attract the male (love-call / ceremonial flight, gestures of devotion, and rattling of wings expressing sexual desire) or which are directed against other females and reveal more and more hostility. Altogether the first period of the Phalarope’s reproductive cycle thus is meant to establish an isolated territory which is mainly the result of the female’s signal behaviours. “Concluding”, N. Tinbergen ascertains, we may say that all sexual activity (ceremonial flight, fighting, building etc.) is shown especially and nearly exclusively within the territory, which is taken in possession and defended by the female. The ceremonial flight expresses desire for the sex partner, and has a stimulating (attracting) influence on the other sex, and therefore acts as a means to bring the sex-partners together.\textsuperscript{111}

The second period is termed the “short period of mated life” by N. Tinbergen.\textsuperscript{112} It consists of mainly two behavioural complexes, namely the copulation itself and the building of the nest. The copulation is characterized by the female’s hostility against the male following the act of copulation. The behaviour of nest-building reveals a transformation process which begins with initial \textit{symbolic} nesting and ends with building \textit{real} nests through mutual cooperation of both partners. Copulations which occur all over this period become less and less hostile. Altogether, the second phase thus reveals a trend towards more harmony and mutuality. The female does not exhibit the ceremonial flight during this period. The third phase is characterized by what Tinbergen calls “egg-ceremony”:\textsuperscript{113} It consists of the female’s love-call (which is now uttered again and has the function to guide the male to the nest) and the laying of the egg, on the one hand, and additional action patterns which are meant to stimulate the pair bonding-despite an increasing trend to a division of labour. The fourth period of the reproductive cycle is related to incubation and thus increasingly reveals the different roles of both sexes.\textsuperscript{114} On this stage there are also behaviours which have the function to continue and maintain the relationship of both partners (e. g. finding a lost partner). The general biological meaning of this stage however seems to be the trend to “institutionalize” the division of labour which is a result both of the different morphological structures and the different functions of the sexes: Breeding is up to the clay-coloured male only, while the female exhibits ceremonial-flights and eventually disappears to produce another clutch. From a more epistemological point of view, Tinbergen’s way to give his observations an order reveals a pattern which by no means is accidental and which obviously is based upon the theorems of distance regulation such as whether signals are \textit{affine} or \textit{diffuge}, their linear order and the modes how one theorem superposes the other. Thus, my impression is that the former two of the four stages are ruled by and directed to the notion of sexual union, while the latter two

\textsuperscript{110} Ibid., 3–8, 29–30.  
\textsuperscript{111} Ibid., 18.  
\textsuperscript{112} Ibid., 9–12, here 9.  
\textsuperscript{113} Ibid., 12–13, especially 13.  
\textsuperscript{114} Ibid., 13–14.
are both directed to and underlie the notion of sexual difference which becomes manifest in form of the division of labour. The latter epistemic complex eventually coincides with the scheme of the reproductive cycle as a whole and, not unlikely, with the order of the entire paper. In the following I will examine mainly two epistemic complexes and ask how they are construed in terms of causality. Niko’s account on “The stimulating actions” thus turns out to be an elucidative example for the functional tenor of the behaviours in question.\textsuperscript{115} “It is unnecessary to say”, N. Tinbergen writes,

that the pairing behaviour of birds largely consists of instinctive actions, urged by innate drives, which cause the bird to react in a purposive way on its surroundings; insight in the purpose consists, if at all, surely in a very small degree, and the role of learning by experience is restricted, though in certain special cases remarkable.\textsuperscript{116}

On the one hand, the paragraph reveals the inner structure of the action patterns in question. They consist of mainly two heuristic components, that is, an initial physical drive and a succeeding reaction. Both aspects seem to be related to each other in a linear succession (mutuality not being excluded). On the other hand, we are also informed how this conceptual unit is understood in terms of causality. Thus, Tinbergen describes the physical drive as “cause” and the reaction as “purposive”. In addition, the entire frame of the concept turns out to be \textit{functional} as well. This is suggested by the fact that what is purposive and what dysfunctional is made plausible by the environmental “surroundings” – in Tinbergen’s account especially the bird’s social environment with which the individual communicates via behaviours. This, however, is an ecological force which does not act upon the reproductive unit through the individual’s insight. In other words, Niko’s notion of purposive action, in contrast to McDoucall’s view, does not involve a subject yet presupposes functional reasoning in terms of preconscious and object-centred correlations. If we compare the functional model applied to the stimulating actions of Phalarope with his earlier study on common terns the shift in his causal reasoning becomes evident: While the former study, following Verwey’s heron paper, was concerned with the physiological causes of sexual stimulation through symbolic behaviours, Niko’s Phalarope-research pushes into foreground the ecological function of these behaviours by interpreting them (amongst other effects) in service of establishing a territory. As a result, the causal reconfiguration of underlying epistemic schemes since ca. 1933 favoured the notion that behaviour has a protuberant \textit{social function} inasmuch as it yields a communicative effect upon other individuals of a group. Amongst other consequences this contributed to establish the research field of “animal communication”.

The chapter on “The Discrimination of the other sex”, by contrast, is a good example for what E. Crist, regarding the causal reasoning typical for \textit{classical ethologists}, called “mechanomorphism” or “mechanomorphic portrayal of animals” and which here becomes manifest more in form of Niko’s specific \textit{psychic sensualism}.\textsuperscript{117} Sig-

\textsuperscript{116} Ibid., 19.
\textsuperscript{117} For Crist’s usage of the term “mechanomorphism” see Crist, “The Ethological Constitution”, 62–63, 69, 71, 76, 81–82, 84–85, 90, 99.
significantly, we find the chapter divided in two parts. It starts with Niko’s observation that the female’s initial approach to other specimens is indefinite in terms of sex and species. This observation makes him contemplate about the psychic causes of this indiscriminate perception. In order to isolate the relevant causal parameters he himself applies a discrimination procedure similar to the one he had applied earlier in his Philanthus-Study. In a first step, he feels urged to exclude possible olfactory factors of the wader’s sensual discrimination and put emphasis on visual parameters only. Once this decision is made he states that no lack of physiological visual capacities can be relevant for the bird’s perceptive constraints since the visual faculties of birds are said to be even better than in humans. “We have ample evidence to conclude”, Tinbergen argues, “that birds are able to recognize other birds sharply by means of their capacities of observation, and we may suppose, that the explanation of cases where they appear or seem to fail, has to be sought in psychological peculiarities”. Moreover, no inborn hostile schemata as a result of species-specific competition can be responsible for the wader’s specific visual discrimination since Phalarope is not exposed to this competition neither with respect of food resources nor of breeding places. Correspondingly, the only potential competitor of Phalarope, the Snow Bunting, does not seem to be covered by the wader’s hostile schemata. The visual constraints therefore must emerge from psychic factors and therefore have the quality of a perception error which is based upon corresponding emotional states. The stronger the sexual desire of a bird the wider the scope of objects it appeals to and the less discriminative (i.e. less selective) its visual powers appear. “It appears from this”, N. Tinbergen writes, that it would be very difficult to determine exactly the nature of these situations, which lead the bird to respond. The situation does not need to be the same under different circumstances, dependent on the emotional state of the bird. When action under the influence of strong sexual desire, a bird will respond to a much wider range of objects, than he would otherwise do.

Based on the assumption that a bird’s discriminative power is hampered by its emotional state Tinbergen develops a typology of causes for maladaptive perceptions which serves to place the behaviour of Phalarope more precisely. Either, he argues, the loss of discriminative power results from the birds which have been reared by humans in captivity or there is a fundamental lack of adequate objects which make the animal exhibit its drives with replacement objects. “The difference between the first and the second group perhaps could be best expressed in the following way”, Tinbergen summarizes:

in the first case the birds prefer an inadequate object, in the other case they content themselves with an inadequate object. Only the second case seems to be comparable with the behaviour of the Phalarope, and the abnormal behaviour is only observed in individuals, who are in a state of

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119 Ibid., 31.
120 The surplus of food resources and the neglect of Snow Buntings, in Niko’s view, thus contradicts E. Howard’s theory of ecological competitors – in my opinion a reformulation of what Darwin had called “sports”. See ibid., 31–32.
121 Ibid., 35.
122 Without mentioning it explicitly N. Tinbergen apparently referred to the phenomenon of sexual imprinting when he describes the former of the two cases. See ibid., 36.
strong sexual desire, by lack of an adequate partner. Both seem to be instances of the influence of desire on the nature and extent of the specific stimulus (situation), to which the instinctive impulse responds.\textsuperscript{123}

Beginning with this quotation it is possible to reconstruct the causal architecture of Niko’s psychic sensualism. In general, one may say that the birds’ discriminative capacities are treated from a pathological perspective. That is to say, alike to K. Lorenz, N. Tinbergen detected the heuristic value of dysfunctional instinctive acts which allowed him to determine more precisely the underlying physiological causes.\textsuperscript{124} The emphasis of “errors” thus is closely linked with determining the proximate causes. “These aberrations of the sexual impulse have been observed especially in the case of captive birds”, Niko underlines and continues

and it has often been said, that these are “abnormal” and nothing more, and that they consequently are worthless for a real understanding of the psychology of birds. They would only tend to give us a wrong idea of the real nature of birds. I would on the contrary emphasize the importance, which these “abnormal” cases have, especially for psychology, as they show us the working of the inherited instinctive impulses under uncommon circumstances, and reveal in this way characters and features, which remain hidden in normal life.\textsuperscript{125}

Asides the general high esteem of dysfunctional or misdirected sexual impulses, also Tinbergen’s sub-classification in aberrations caused (positively) by relations to humans and dysfunctions caused (negatively) by a lack of adequate objects reveals a causal dimension: While in the former of the two cases the animal selects positively (i.e. “prefers”) an only seemingly adequate object, in the latter case the bird neither chooses nor prefers an inadequate object yet is forced by its own nervous condition and the momentary circumstances to “be content with” an inadequate object. Especially the latter, that is, tautological, case operates with a concept of causality which might be called “mechanical” and which Tinbergen wanted to see applied to Phalaropes only. It has great similarity with K. Lorenz’s concept of vacuum activity: In case of overwhelming nervous excitation an instinctive action pattern may exhibit without adequate stimulation, so to say, for its own sake. That is to say, the cause is its cause. As we will see more clearly later, the shift which can be observed in Niko’s reasoning on causality since his visit in Greenland affected also his views on orientation. Whereas the capacity of Philanthus to recognize its nest was to be discovered by its faculty to choose correctly between dummy- and real nest now it is the error which promised to provide insight into the animal’s emotional status and its physical causation.

I have argued that the two main publications which originated from observations made during the stay in Greenland can be read as complementary approaches. Insofar Niko’s main study on Snow Buntings may take less the psychological rather than an ecological part of the entire frame. Niko’s choice of Snow Buntings as a scientific object was strategic insofar as these birds were a common passerine species in Angmagssalik and, beyond that, had already attained “a certain reputation”

\textsuperscript{123} Tinbergen, “Field Observations of East Greenland Birds I [1935]”, 37.

\textsuperscript{124} Therefore it takes no wonder that Niko quotes Lorenz’s prototypic examples for misguided social instincts which the latter had explained in his early papers (1927, 1931, and 1932) with the simplicity of underlying schemata. See ibid., 34.

\textsuperscript{125} Ibid., 35–36.
through the studies of M. E. Nicholson and E. Howard. Concentrating on Snow Buntings therefore provided the opportunity to relate Niko’s own views to those of others and thus shape his own scientific standpoint. Niko’s Snow Bunting paper can be read as a comment in particular of E. Howard’s understanding of territory and – even more important – its biological function. Moreover, Niko’s Snow Bunting paper is biased insofar as it introduces two methodological options and marks a deliberate decision: “In outlining our program”, he writes,

we had to choose between two possibilities. We could either make a broad review, a survey, of the whole sequence of events during the entire reproductive cycle, or we could restrict ourselves to a study of a few detailed questions, in order to investigate these more thoroughly. | In our opinion, the present knowledge of these problems requires primarily observations without experimental specialization. In purely observational work, it is absolutely necessary not to disturb the bird; consequently, if we direct our attention to only a few specific problems, we lose much time. It is, therefore, a question of efficiency to maintain as broad a view as possible in order to prevent the unnecessary disregard of valuable facts. Moreover, in questions of territory a restriction as to details is at present not justified until a survey has been made.

As a provisional conclusion, we may therefore say, Niko’s Snow Bunting paper is to be read as a survey of these birds’ territorial behaviours. It stresses the question of the biological function and, beyond that, intends to be a purely observational work under natural conditions of life. The paper’s general overtone thus is quantitative, observational and its descriptive approach leads to an increase of information and complexity. In its core the study consists of two parts both of which are supplemented by a final “Summary”. The first of the two sections differentiates the Snow Bunting’s reproductive cycle in nine particulate periods each of which is marked by a new discriminative feature (II. Description of Behavior during the Breeding Cycle). The second section which is entitled “III. Discussion” picks up several aspects Niko had observed in the Snow Bunting’s breeding cycle and compares his view with the various opinions put forward by others. Thus Niko differentiates between those aspects which are related to the Snow Bunting’s common mating system and those qualities which contribute to the discrimination – either of the other sex or a spatial area. Both discriminations are essential for the notion of territory. In general, we may therefore say Niko’s understanding of territory is closely connected to the reproductive cycle of the bird. To shape N. Tinbergen’s position within the epistemic field of the behaviour sciences, in the following I will concentrate on three questions: At first, what distinguishes Niko’s concept of territory from E. Howard’s more utilitarian understanding? Second, in how far does Niko’s ecological approach provide an alternative to Darwinian approaches of reproduc-

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127 See ibid. The passage is a prototypical example for what I have called “performative coincidence” in the introductory section of my paper: In an introductory section the author provides an alternative only one of which is carried out in the main parts of the account.
128 These phases are namely: “First Period: Males Have Arrived and Are Living in Flocks; Females Still Absent”, “Second Period: Male Has Settled on a Territory; Females Still Absent”, “Third Period: Females Are Present, but Still Unmated”, “Male Has Secured a Mate, Female Still in Pre-oestrum”, “Fifth Period: Coition Occurs”, “Sixth Period: Female Laying”, “Seventh Period: Female Incubating”, “Eighth Period: The Rearing of the Nestlings”, “Ninth Period: Young Have Left the Nest”.

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tive behaviour? Finally, how does the causal architecture of significant epistemic frames look like in Tinbergen’s paper? As can be inferred from the paper’s introduction the fact that others had discussed the behaviour of Snow Buntings before gave Niko a push to conduct his own observations. While Niko’s critique of M. E. Nicholson’s conclusions concentrated upon the question whether Snow Buntings in Greenland display territorial behaviours at all, his relation to E. Howard’s account is more sophisticated insofar as two different conceptions of territory conflict with each other. According to N. Tinbergen, E. Howard had suggested that the general function of territory may be the prevention of overcrowding and therefore be triggered by the scarceness of nesting sites or the scarcity of food resources for the young but not the presence of another female whose choice had been the crucial factor in Darwin’s theory of sexual selection. Niko re-established the reproductive context which – on alternate epistemological grounds – had also been Darwin’s major concern insofar as he linked the notion of territory less to a geographic area rather than a behaviour, namely to what he defined as “spring fighting”. “If we take the reaction as a starting point”, Niko underlines, it must be defined carefully. Darwin speaks of spring fighting; for several reasons I prefer to include all fighting linked with mating. This will be called sexual fighting and in this definition I will include all fighting occurring shortly before and during the formation of sexual bonds. Excluded, therefore, are fights to settle a social hierarchy, fights against predators and against direct food predators. As a special case of fighting against predators the defence of nest and young are to be mentioned. This is to be distinguished from sexual fighting as it has another external releasing situation, another seasonal periodicity, and another connection with the occupied area.

From this quotation we may infer that N. Tinbergen conceived territory within the wider context of reproductive behaviour in general and sexual fighting in particular. The male’s sexual fights thus appear as a special case which is restricted to a certain area and has the “function” to secure the female, while the female Snow Bunting’s fight occurs outside the territory and is primarily directed against other females. Their fight therefore is not meant primarily to defend a territory. The behaviour (the fights in general) therefore can explain the territory but not vice versa. Niko’s definition of territory thus is less spatial rather than behavioural. “Mayr is the only author”, he states,
Niko Tinbergen (1907–1988)

who has given a practicable definition, making as sharp a distinction as possible between true
territory and other instances of occupied space. He gives the following definition: “Territory is
an area occupied by a male of a species which it defends against intrusions of other males of
the same species and in which it makes itself conspicuous” (p. 31). In general this description
applies very well to Howard’s conception of territory. As I pointed out in a former paper
(Tinbergen 1936b) I prefer a more direct definition and propose to define territory as an area that
is defended by a fighting bird against individuals of the same species and sex shortly before and
during the formation of a sexual bond. Using the definition of sexual fighting that was already
given, my definition of territory would be: Whenever sexual fighting is confined to a restricted
area, this area is a territory. Like Mayr, I consider it wrong to include any reference to the
function of territory, as the function may be, and in fact is, so different for different species.135

In sum, we may perceive now the entire epistemic frame of Niko’s understanding
of territory. Its general overtone is both behavioural and sexual and this marks a
shift from Howard’s concept which is more spatial.136 In addition to that, the entire
frame has a sort of chronology, too. Taking and defending a territory, in Niko’s
view, precedes temporally and logically the formation of a pair bond. “The fighting
before and during the formation of sexual bonds”, N. Tinbergen underlines,
“therefore, serves to secure objects or situations which are indispensable for reproduction”.137
And this specific linearity which sets a moment of discontinuity in the
first place and proceeds with a mode of transgression in the second place may also
mark a difference to Darwin’s concept of sexual selection. We remember, Darwin
had understood sexual selection as a partly dysfunctional special case within and
at the fringes of natural selection just in the same way as his gradual model of de-
scent with modification conceived the species as the almost pathological final stage
within a process of gradual speciation. Not only was this final stage marked by an
increasingly deep gap to other competing varieties but also by the occurrence of
species-specific reproductive instincts and sexual preferences. This may eventually
be the reason why N. Tinbergen alleges that Darwin had operated with a “psy-cho-
logical” explanation of pair bonding. In Niko’s view, the fighting males are not
capable to gain insight into the ultimate purpose of their behaviour which he sup-
posed to be the securing of the female. “Darwin’s conclusions cover two fields”, he
says:

first, he thinks that the motive of the fighting males is to secure a female; this, it should be
emphasized, is a psychological conclusion. We are now accustomed, on good grounds, to think
that the motive of the fighting is not to be sought in a certain insight of its end-effect, but that
the psychological status of the bird’s body, together with certain external stimuli, causes it to
show an inborn, instinctive behaviour pattern. Insight into the immediate effect, if present at all,
is certainly insufficient to determine the behavior. | Darwin’s other conclusion applied to the
function of fighting, judged by its effect. He thought he had sufficient proof to conclude that the

135 See Tinbergen, “Field Observations of East Greenland Birds II [1939]”, 68–69. For N. Tinber-
gen’s critique of E. Mayr’s definition of territory in the paper mentioned in the quotation above,
see Tinbergen, “The Function of Sexual Fighting”, 5.
136 Whether this shift is indicated by N. Tinbergen when he speaks of a “direct” definition in
comparison to Mayr’s depends on how we interpret Mayr’s view epistemologically and whether
we follow Niko’s equation of Mayr’s and Howard’s definition.
137 Ibid.
females chose the victorious (which were at the same time the more brightly colored) males, whereby the weaker males would be excluded from reproduction.\textsuperscript{138}

Whether Darwin actually believed that the fighting males can have insight in the ultimate purpose of their behaviour is at least an open question.\textsuperscript{139} However, what distinguishes N. Tinbergen’s from Darwin’s approach to reproductive behaviour is the general thrust of the epistemic schemes underlying each concept. While in Darwin’s model exclusion is the final destination (both from a phylogenetic point of view and with respect of the individuals’ life histories), in Niko’s view, it is the starting point. Most interestingly, however, in both schemes this moment of discontinuity is connected with a notion of potential dysfunctionality. Niko excluded the question of the territory’s function from his definition and Darwin’s model leads to what modern evolutionary biologists call a “runaway-effect”, that is, eventually maladaptive exaggerated morphological structures which may guarantee reproductive success in terms of sexual yet not of natural selection.\textsuperscript{140} That N. Tinbergen began to distinguish explicitly between ultimate and proximate causes in his Snow Bunting paper is obvious.\textsuperscript{141} However, in order to clarify whether his paper expresses already the causal intervention which is characteristic both for the ethological and the neo-Darwinian Synthesis it is important to take into account how both forms of causality are linked with the other dimensions of behaviour. Niko had noticed that in Snow Buntings it is mainly the male which establishes a territory by his sexual fighting and this required recognizing adequate target objects. Thereby, alike to Phalaropes and several other animal species, the male Snow Bunting displayed an indefinite aggressive reaction to intruders in the first place and only after that refined its reaction pattern in accordance with the reaction of the intruder: If it is a male, aggressiveness continues, while a female response leads to courtship behaviours.\textsuperscript{142} Niko’s attempt to explain the phenomenon progresses in several particular steps. He begins with the first, indefinite, part of the reaction and at first

\textsuperscript{138} Tinbergen, “Field Observations of East Greenland Birds II [1939]”, 57–58.

\textsuperscript{139} In an earlier paper of the year 1936 with the title “The Function of Sexual Fighting” Niko underlined that Darwin had wanted to explain the phenomenon of sexual fighting in the first place and had not intended to provide a psychological explanation. Niko states: “It was Darwin who concluded that the fighting of the male birds in spring was ’over the females’, and that a female would choose a strong and victorious male in preference to a weak male to mate with. Doubtless this hypothesis was originally intended to interpret the function of the fighting, not to serve as a psychological interpretation of the motives of the fighting males”. See Tinbergen, “The Function of Sexual Fighting”, 1.


\textsuperscript{141} Here it is sufficient to have a brief glance at the headings “The Causes of Sexual Fighting” vs. “The Functions of Sexual Fighting”.

\textsuperscript{142} Tinbergen, “Field Observations of East Greenland Birds II [1939]”, 47, 51–52.
excludes the possibility that purely physical causes are responsible for the Snow Buntings temporary lack of discriminative potential. In other words, the bird’s reaction must be perceptual. The problem thus must concern the central nervous system. Granted that this proposition holds Niko offers two further explanations: Either the bird reacts actually different and it is just we observers who are not capable to recognize the differences due to our less advanced discriminative power or it is the Snow Bunting which in fact treats all intruders in the same way. The latter type of explanation again is elaborated in detail by further guesses. Although the animal may sense an entire field only a few elements reach the higher nervous system and thus can have an influence upon the reaction. “It has been proved in a number of cases”, Niko writes, “that an animal does not react to the complete receptual field, but only to certain elements in it. Other elements may have no influence, although they can be received by the animal’s sense organs equally well”.

In general, one may say Niko’s model of perception is as selective as any other yet I assume that the process of selective perception in his view is not necessarily linked with any holistic central nervous integration: The initial sensation, he argues, might be holistic, while it is only a few elements which have influence upon the reaction. And this linkage of holism with proximate causality (what E. Crist called “mechanomorph”), on the one hand, and particularism with ultimate causality, on the other, may be a clear indicator that Niko’s Snow Bunting paper rests upon a changed causal architecture. Niko’s explanation of the Snow Bunting’s initial indiscriminate reaction corresponded with K. Lorenz’s results insofar as the latter, too, had described fixed action patterns which consisted of a direct correlation between a very simplified (“prägnant” in Lorenz’s words) sender and a summative IRM (the latter being relevant for the reaction pattern). On the other hand, Lorenz had supplemented this reaction type with an additional stimulus-response correlation whose sender displayed a higher amount of significant qualities, while the receiver was characterized by a greater capacity of holistic integration. N. Tinbergen identified this reaction type as the basis of the Snow Bunting’s later sex-specific reaction towards intruders. “A study of the further course of the male’s display reveals new problems”, N. Tinbergen writes and continues:

The quote reveals, to a certain extent, the double nature of the Snow Bunting’s second reaction. On the one hand, it requires a “different mechanism” which is re-

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143 Ibid., 47–48.
144 Leaving aside the causal dimension this would correspond more with A. Bethe’s model of central nervous “integration”.
145 The exact combination of lock and key seems to be liable to errors which are occurring during the discrimination of the object. In other words, a reduced, and with respect of the amount of qualities limited stimulation may produce a maladaptive situation. For an early account of these errors in N. Tinbergen’s writings see Tinbergen, “The Function of Sexual Fighting”, 4.
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teceptive enough to acquire new sense impressions provided by the stimulus object. On the other hand, the sender (here the associate) must be sufficiently complex to display enough significant stimuli. The causal architecture of the Snow Bunting’s second, sex-specific, reaction becomes evident especially in the chapter with the title “Sex Discrimination” which, in my opinion, refers less to the mechanism of the behaviour in question rather than to the stimulating part. Tinbergen here intends to prove that the ability to choose adequately the other sex is present in Snow Bunting generally even in case this ability is suspended temporarily. And, what is even more relevant for my argumentation, this ability to discriminate the other sex is based upon behavioural rather than on morphological stimulation. “This, however, shows”, N. Tinbergen summarizes his argument,

that sex discrimination is present, and that it depends on the behaviour of the other bird, not on morphological characters. Allen’s experiments consisted of giving to a bird another bird, with morphological characters of one sex and the (induced) behavior characters of the other sex, and as the bird always reacted to the behaviour characters, he apparently “did not discriminate”. In general, in birds as well as in other animals, special movements are of no less importance than morphological characters in sex recognition, and it certainly is an anthropomorphic attitude to presume that only the morphological differences are of any value.147

From this quotation we may infer that Niko’s observation that behaviour stimuli may serve as discriminative qualities equally well as morphological ones becomes relevant only within an epistemic scheme that allows behaviours to be selective. Conversely, that N. Tinbergen insists on a non-anthropomorphic attitude indicates that epistemic modifications especially on the causal level of his argumentation must have occurred. Hence, in sum it can be concluded that Niko’s Snow Bunting study represents a stage in his scientific development which reveals both the heterogeneity of his scientific orientation and a reverse causal architecture. While the former of the two interventions generated in particular the criticism of E. Howard’s spatial conception of territory (and to a certain extent also of Darwin’s “psychological” construction of pair bonds), the transposition on the causal level of argumentation made Niko’s position compatible with those other ethologists had developed since the middle of the 1930s at the latest.148 In my opinion, Niko’s Snow Bunting study also reveals the epistemic tensions between the emerging ethological and the (neo)-Darwinian synthesis. The intellectual life-histories of ethologists share transformations analogous to those researchers which operated within the frames the (neo)-Darwinian synthesis provided – yet it must be kept in mind that – with respect of the epistemic deep structure – the Ethological Synthesis differs from the former. This is why Niko takes offence at Darwin’s “psychological” explanations although both orientations put emphasis on reproduction and, beyond that, link expressions of continuous variability with manifestations of ultimate causality.

147 Tinbergen, “Field Observations of East Greenland Birds II [1939]”, 56.
148 In Niko’s Snow Bunting study we can see already the impact of Lorenz’s Special Phylogeny of Releaser. This is, most likely, due to the fact that the paper was published six years after Niko’s stay in Greenland. For us science historians this implies the danger that we date back too far later theoretical achievements. Niko’s behavioural understanding of territory and sexual fighting, however, seems to be a substratum of the time in which the observations for the paper were carried out.
Niko Tinbergen (1907–1988)

(R3) *Philanthus II–IV*. My analysis of the studies which originated from observations made during his stay in Greenland between 1932 and 1933 and which were published later with some time-delay in 1935 and 1939 reveals that N. Tinbergen’s intellectual life-history parallels the trajectories of other ethologists in so far as the years around 1935 entailed an epistemic transposition on the causal level of reasoning similar and analogous to those which can be observed, for instance, in E. v. Holst’s and K. Lorenz’s development. In order to prove my hypothesis more convincingly I will now pick up Niko’s *Philanthus*-research and ask in how far the supplementary studies of the Digger Wasp’s orientation which were carried out between 1935 and 1938 – that is after his return from Greenland – were affected by the intervention on the level of causation, as well. We remember, Niko had distinguished mainly two types of orientation in his dissertation thesis, the ability to find a previously built nest and the recognition of the prey animal. Both orientation types are now elaborated in more detail. The paper published in 1935 thereby put emphasis on prey hunt, that is, the recognition of the prey, while the two subsequent papers published in 1938 reassessed the homing ability of *Philanthus*. All three papers together build a logical intertextual unity which allocated each paper its characteristic binominal organization. Niko’s reassessment of the digger-wasp’s hunting behaviour thus gains profile from the study’s internal order. Thus he distinguishes at the foremost between dead bees and orientation towards living bees. “Da es sich aber herausstellte”, Niko writes,

daß in den zwei verschiedenen Fällen: das Auffinden der toten Biene und das Auffinden der lebenden Biene, die Sinnesorgane in merkwürdig verschiedener Weise benutzt werden, muß ich die Resultate dieser zwei Versuchsreihen getrennt betrachten.

[Since it turned out that in the two different cases: The finding of the dead bee and the finding of the living bee, the sensory organs are used in curiously different ways, I have to treat the results of these two series of tests separately.] (transl. CL)

The former of the two cases applies when the returning wasp drops erroneously the wasp or an unforeseen incident forces *Philanthus* to put down its prey. The key-question thereby is whether or not the digger-wasps pick up the dead insect again and which senses thereby are involved. The result of Tinbergen’s experiments here was that the digger-wasps do not necessarily accept a bee once dropped and that the decisive factor – if the bee is taken back – must be a direct stimulus originating from the bee itself. This direct stimulation turned out to be primarily olfactory yet involved optical impressions, as well – especially when the object of interest moved or its shape could be distinguished from the background. In the second case to which Niko refers with the same title he also used for the paper

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149 Careful readers will have noticed that the linear order of both field of topics has changed in comparison to Niko’s dissertation thesis. The reason is the specific composition of Niko’s early *Philanthus*-Study. For the complete references of the three follow-up studies see fn. 62, page 68 of my thesis.

150 Tinbergen, “Über die Orientierung des Bienenwolfs II. [1935]”, 700, also 706.

151 Tinbergen here uses the German word “zurückgefunden” which sounds artificial but expresses the spatial thrust of the imagination: back to. See, for instance, ibid., 700.

152 Ibid., 701. That the relevant stimulus must be direct, according to N. Tinbergen, implies also that memory plays only a subordinate role (Ibid., 715).

153 For Niko’s reductive argumentation see here ibid., 702–706.
as a whole, “Bienenjagd”, he differentiates at first between prey hunt in captivity and the hunting behaviour of free living wasps. Only the latter case is the one upon which Tinbergen puts his main emphasis and which he regards suitable to obtain valuable results. So far Niko had explained the digger-wasp’s approaching of the prey-animal primarily with the hunter’s olfactory senses. This view is now replaced by a more sophisticated linear action pattern in course of which both visual and olfactory modes of foraging alternate and interact with each other in a complex manner. “Es erwies sich”, Niko argues,

däß die ganze Fanghandlung in eine Anzahl Teilreaktionen zerlegt werden kann, bei deren jeder das Tier von einem anderen Sinn geleitet wird.

[It turned out that the entire capturing movement can be split into several part-reactions in each of which the animal is guided by another sense.](transl. CL) Thus he maintains that seeking and finding of the prey animal is primarily based upon visual orientation yet contains an initial olfactory check as well (during which, however, the optical disposition, that is, the “optische Einstellung”, as Niko puts it, is maintained). The final approach or contact, on the contrary, is said to be guided by visual orientation. The ultimate sting, however, is guided by olfactory stimulation again. According to N. Tinbergen’s study, visual and olfactory orientation therefore alternate on a regular basis. I think it is beyond doubt that N. Tinbergen systematized the digger wasp’s predatory behaviour by dividing it in several phases corresponding to the prevailing sort of stimulation in each case. However, several non-exclusive forms of organization seem to coexist next to each other. On the one hand, there is a hierarchical order according to which subalternal stages of the entire behavioural pattern can be entered only if the corresponding stimulus pattern is matched: Only if the respective prey object matches the visual image of the bee Philanthus aligns its body into the direction of the bee and performs the olfactory check. Only if this check is positive the visually guided approach occurs. If there is contact another olfactory stimulus must be received so that the subsequent phase of the entire pattern can be entered. This bifurcation anticipates the hierarchical model of instinct N. Tinbergen introduced later in his Study of Instinct. On the other hand, N. Tinbergen apparently thought that two or more stages can be bound together by one common instinctive propensity. The pattern of the entire predatory act thus appears to be divided in two main parts consisting of several subordinated phases being regulated by one orientation type each. In particular, with respect of the initial two stages, that is, the phases which regulate the orientation from remote distance, Niko speculates about a strange psychic inhibition which seems to switch off olfaction nearly exclusively during seeking but activates
the sense of smell as soon as the bee comes within reach.\textsuperscript{160} From a more epistemological point of view this leads to a paradox structure which dissolves as soon as Niko’s account switches from “Schweben” (inhibition of olfaction) to “Stoßen” (disinhibition of olfaction).\textsuperscript{161} Although Niko does not elaborate much on the type of stimulation during close contact we may infer from his earlier PhD-thesis that \emph{Philanthus} checks its prey by other than strictly olfactory means, too. Otherwise it wouldn’t be possible to explain that other insects which had been flavoured with the scent of bees were actually not killed by a sting.\textsuperscript{162} Therefore it can be asked whether the epistemic scheme underlying Niko’s account of the digger-wasp’s low-distance orientation might not dissolve a paradox as well. For instance, the initial approach (i.e. “Stoßen”) itself is said to be guided by visual stimulation yet the act of grasping seems to be triggered by an olfactory impulse. The key-question for me now is how the various orientation types are correlated with concepts of causality. One aspect may be that Niko understands the digger-wasp’s hunting behaviour not so much as acquiring a prey animal through a process which is guided mechanically by chemical contact stimuli (like it was the case eventually in his earlier account). Rather the hunting of the bee now is described as an act of active choice a matter of fact which is corroborated quantitatively.\textsuperscript{163} Correspondingly, we can observe that experiments in captivity turn out to be dysfunctional in so far as they are described to have led to less promising results.\textsuperscript{164} The emphasis on \emph{observations} of freely moving and free living insects thus reveals that Niko began to examine the digger-wasps’ olfactory senses in less rigorously experimentalist ways. In this context, it is of utmost importance to notice that Niko’s examination especially of the wasp’s olfactory orientation does not include vivisectional experiments any more and was not performed under the bell jar. Niko’s study of the digger-wasp’s bee hunting behaviour (published in 1935) thus is quantitative-observational and not quantitative-experimental. This revised causal architecture applies to the paper as a whole but particularly to the five stages of approaching non-captive living bees: Alike to N. Tinbergen’s later hierarchical model of instinct the digger wasp’s predatory act seems to encompass a loose dualism between less and more direct forms of stimulation. Corresponding to Niko’s account of the digger-wasp’s hunting behaviour also his interest in homing revealed some modifications on the deep structure level of his research. In his earlier study N. Tinbergen had come to the conclusion that the ability to recognize a nest is based primarily on optical perception of the landmarks. This result stood at the end of a discrimination procedure which had excluded step by step olfactory from visual cues and then colour from shape. In general, one may say that Niko’s follow-up studies of the Digger Wasp’s homing ability (Parts III. and IV. in the series of papers) – both of which were finally published in 1938 after

\begin{itemize}
\item \textsuperscript{160} Ibid., 716.
\item \textsuperscript{161} That re-activation of the olfactory senses rests upon some kind of disinhibition reveals the end-tautological nature of the reference system in question: Disinhibition implies a sort of double-negative.
\item \textsuperscript{162} Tinbergen, “Über die Orientierung des Bienenwolfs I. [1932]”, 328.
\item \textsuperscript{163} Tinbergen, “Über die Orientierung des Bienenwolfs II. [1935]”, 699.
\item \textsuperscript{164} Ibid., 707.
\end{itemize}
several summers of observation – recapitulated this general methodological thrust yet did so on basis of a much finer discrimination of qualities. Insofar the studies are prototypical examples for what K. Lorenz called “Analyse in breiter Front” and therefore reveals already the incipient signs of the next epistemic shift which went beyond the mere transposition of reference systems that establish the causal dimension of behaviour (see below).

Part III. which is mainly concerned with short-distance orientation begins with a twofold and somewhat unexpected observation: On the one side, Niko points out, that digger-wasps often successfully recognized unexpectedly their nest despite the fact that seemingly essential landmarks had been changed or removed. This suggests Niko says,

> daß außer Orientierung mittels Erinnerungsbilder doch auch noch eine andere, vielleicht auf direkter sinnlicher Verbindung mit dem Nest beruhende Orientierungsart eine Rolle spielen könnte.

[that besides the orientation via memory images there might be involved still another form of orientation which is perhaps based on a direct sensual connection with the nest.][transl. CL]165

On the other hand, however, Niko had experienced that digger-wasps got entirely confused if all landmarks within a radius of one meter around a nest had been moved irregularly. This supported his hypothesis that optical landmarks play an essential role in *Philanthus*’s orientation yet also revealed that the criterion to evaluate respective landmark qualities was not only the wasp’s positive choice but also its perceptual errors.166 In contrast to his earlier study Tinbergen thus put greater emphasis on maladaptive instinctive action patterns. In other words, Niko’s presupposition was that digger-wasps got confused and the question was in which cases orientation succeeded nonetheless and in which cases the expectation was fulfilled and orientation failed. Correspondingly, the methodology changed slightly, too.167 While the observations in his earlier study were grounded on the wasp’s choice between a real nest and a dummy nest, the wasp’s option now was between two dummy nests.168 Thus Niko’s test arrangement from the beginning put emphasis on the parameters of deception and less on correct and adaptive perception. Moreover, N. Tinbergen preferred a higher number of smaller objects to build the circular landmarks for his experiments. According to his view, conditioning then takes longer but the method offers advantages with respect of certain research questions. This shows that Niko not only had recognized the heuristic value of perceptual errors but also intended to work with finer differentiations and a broader data basis.169 In addition, the broader data basis, in Niko’s view, became necessary since the wasps’ decision between one or the other setting wasn’t always entirely definite. A preference thus could be determined only with many trials. The idea of choice now was more obviously linked with the idea of quantification than it was

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166 For the emphasis on confusion see ibid., 292, 293.
167 On the paper’s methodology see ibid., 294–297.
168 The detachment from the original nest apparently also made partly superfluous the control-experiments.
169 The stronger quantitative emphasis in Niko’s methodology is in fact an indicator for a later epistemological stage of his development which began to become effective already in 1938.
the case in Niko’s dissertation thesis. Finally, the presentation of each composition or test setting in reverse location was meant to avoid that wasps developed preferences independent of the landmarks. The intention thereby was that digger-wasps which had been scared-up several times and correspondingly decided for one specific composition lastly reveal a certain fixed preference but this preference ought to be based variably on the tested parameters only. For my argumentative purpose it is not necessary to discuss each natural experiment in detail. Niko step by step compared (a) various spatial patterns of two-dimensional objects (chapter three), (b) two-dimensional with three-dimensional objects (chapter four), and (c) various patterns of three-dimensional objects (chapter five). Furthermore he examined (d) the role of size (chapter six), (e) of brightness-contrast (chapter seven), and (f) the distance between landmarks and nest (chapter eight). Finally, he asked (g) when learning takes place (chapter nine) and, lastly (h), which effect the duration of training might have (chapter ten). The result of Niko’s experiments with deceptive situations ultimately converged into a graded scale of selective preferences that was ranging from clues with stronger to those with weaker releasive value. “Die Weibchen von Philanthus triangulum Fabr. benutzen zur Orientierung auf dem Heimflug einen oder mehrere Komplexe von Wegmarken”, Niko summarizes and continues, Von den vielen in der Umgebung befindlichen Gegenständen sind nicht alle als Wegmarken gleichwertig; es gibt einen arteigenen Vorzug für bestimmte Wegmarken. Es werden vorgezogen: Flach “gegliederte” vor gleichmäßig gefärbten flachen Gegenständen. | Körperliche vor flachen Gegenständen. | Größe vor kleinen Gegenständen. | In der Nähe der Höhle liegende vor weiter weg liegenden gleich großen Gegenständen. | Mit dem Boden stark kontrastierende vor mit dem Boden schwach kontrastierenden Gegenständen. | Beim ersten Ausflug (nach einer Regenperiode) anwesende vor später hinzukommenden Gegenständen. | Das wichtigste Merkmal der körperlichen Gegenstände ist deren Höhe. | Eigenschaften einzelner Elemente des Wegmarkenkomplexes werden nach längerer Dressur besser benutzt als nach kürzerer Dressur; bei längerer Gewöhnung an die Wegmarken tritt eine zunehmende Gliederung des Wahrnehmungsfeldes auf. | Wenn die Wespe mit Hilfe der Dressurmarken die Höhle nicht zu finden vermag, nimmt sie sich plötzlich neue, von der Dressur unabhängige Orientierungsmarken dazu. | [Of the many objects located in the environment not all are equally valuable as landmarks; there is a species-specific preference for certain landmarks. The following are preferred: Flat “structured” before homogeneously coloured flat objects. | Bodily [i.e. three-dimensional]CL over flat objects | Large over small objects. | Objects closer to the next entry over more remote objects. | Objects standing out of the ground over slightly contrastive objects. | Objects present during the first approach (after a rainy period) over objects that have been added later. | The most important characteristic of the bodily objects is their height. | The qualities of single elements of the entire landmark complex will be remembered better after longer enduring conditioning than after shorter conditioning; in case of longer habituation phases the perceptual field becomes increasingly differentiated. | If the wasp is not capable to find the nest with the help of landmark

170 All these tests, that is, the chapters three to ten (particularly the chapters three to nine) build a unity insofar as experiments are numbered by increment beyond the chapter boundaries and experiments take into account more and more parameters so that the settings become increasingly complex. However, there might be an internal differentiation: Thus chapters three to eight refer to spatial parameters, while chapter nine and ten are concerned with time. Chapter three, four and five again refer to the internal patterning of two- or three-dimensional objects, while chapter six, seven and eight seem to take into account various relations between the object and the environment.
In sum, we see clearly now that Niko’s accent on perceptive errors was paralleled by a thematic shift from species-specific action patterns to species-specific preferences, a category which appears to be graded and combined with the notion of choice. Moreover, in contrast to Niko’s earlier study of the digger-wasp’s homing ability we find now a stronger interest in the effect of experience and learning. This eventually corroborated his critique of A. Kühn’s concept of mnemotaxis from an additional perspective. Already Niko’s earlier account of the digger-wasp’s homing ability had contradicted the reflexological fundament of A. Kühn’s mnemotaxis concept insofar as it conceived the underlying performance to integrate heterogeneous sensory data both more psychic and therefore also more plastic. N. Tinbergen now renews this point of critique by pointing out that Philanthus does not memorize one single feature of the experimental setting yet the constellation of the objects as a whole. “Es bleibt noch ein anderes Kriterium, das uns für manche der unter Mnemotaxis angeführten Fälle wesentlich zu sein scheint”, he writes and goes on:

Wir haben gezeigt, daß die Orientierung von Philanthus nicht auf Bewegungen beruht, die in Bezug auf ein einzelnes Objekt gerichtet sind, sondern daß die Bewegungen durch eine ganze Konstellation von Wegmarken gesteuert werden. Das Tier beschreibt eine Bahn, und besucht Stellen, die es in ihrer relativen Lage inmitten einer Wegmarkenkonstellation zu bestimmen vermag.

[There still remains another characteristic of some cases being classified as Mnemotaxis: We have shown that the orientation of Philanthus is not based upon movements which are directed in relation to one single object but that the movements are guided by a whole constellation of landmarks. The animal uses a path and visits locations whose relative position it can determine within the constellation of all landmark clues.] (transl. CL)  

By referring to the homing ability of ants A. Kühn had claimed that the animals do not recognize their nest because they know the environment of a nest within a radius of several meters. This however, seem to be exactly the point of Niko’s Philanthus-study. Moreover, that the digger-wasp’s way home to the nest is not guided by any form of taxis (tropotaxis, telotaxis or menotaxis) or a combination of two or more taxes, according to N. Tinbergen, is suggested by the fact that the retinal image of the environment that Philanthus has to take into consideration during the approach to the nest changes permanently. Furthermore, the paths taken by the wasps to their nests differ from one another significantly so that a simple linear optomotor orientation does not seem to be plausible. Kühn, on the contrary, had suggested that insects find their home by recapitulating more or less identically the single sequences in form of which they memorize the paths during the orientation flight by converting complexes of stimulation into linear associations of engrams. Small directional deviations on their ways home, in Kühn’s view, are compensated by corrective movements which realign (“hineindrehen”) the animals to the ideal path – a mechanism which can be explained physiologically as remedy-

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171 Tinbergen, “Über die Orientierung des Bienenwolfs III. [1938]”, 333, also 314.
172 Ibid., 330.
173 Kühn, Die Orientierung der Tiere im Raum, 57.
174 On Kühn’s understanding of “Mnemotaxis” see in general ibid., 39–59.
ing a previously experienced discrepancy between an ideal (i.e. “engramatic”) and an actual stimulation.\textsuperscript{175} The compensatory movements in turn can become part of the engrams on higher levels of integration guaranteeing the fluency of the homing behaviour. In any case, according to Kühn’s reflexological concept of mnemotaxis, orientation occurs only on previously inscribed paths. The insect’s way back therefore must be a “function” of the path to the object, as Kühn put it, that is, either an identical recapitulation or a reproduction in reverse order.\textsuperscript{176} This however contradicted N. Tinbergen’s observations: If the composition of the landmarks had been changed drastically Philanthus was able to regain its orientation from any arbitrary position. “Zusammenfassen läßt sich über die Bahnen der hier behandelten Wespen sagen”, Niko concludes:

\begin{quote}

[In sum, one may say the following about the paths taken by the treated wasps: The paths themselves are not fixed but variable instead so that they cannot be governed by any intercalation of meno- and telotaxes. The trajectory is not dependent from one single of the four landmark clues only, but only from the constellation as a whole. The position of the animal during a possible transition from the seeking movements to the state of orientedness is highly plastic as to the direction into which the landmark clues are located.]\textsuperscript{(transl. CL)}\textsuperscript{177}
\end{quote}

In sum, we may say that Niko’s critique of A. Kühn’s mnemotaxis concept partly rests upon the emphasis on the plasticity of the action pattern – quite comparable to E. v. Holst’s critique of reflexology. In addition to that, there may be two new aspects as well. A. Kühn himself had given mnemotaxis a special status in comparison to other types of taxes insofar as the information about the guiding marks in case of “mnemic orientation” was acquired and not provided by inborn perceptive patterns.\textsuperscript{178} Yet, if I am not mistaken, the type of orientation Niko had detected in Philanthus was indistinguishable from memory, a psychic capacity which refers to a form or preservation based on higher levels of psychic integration. Moreover, we may speculate a little bit whether the point where the acquisition of information during the entire hunting pattern has shifted in Niko’s later study compared with his earlier account. Thus my impression is that Niko, in his dissertation thesis, had reserved memorizing to the initial orientation flight yet described the recognition of the nest itself (like the entire scheme) in terms of selective perception or choice. Kühn apparently shared the linear order of acquisition in the first place (conversion of stimulation into engrams) and choice in the second place (selective realignment

\begin{flushright}
\textsuperscript{175} Kühn here speaks of a trend to “Homophonie”. See \textit{ibid.}, 44–47, passim. “Mnemic orientation”, in Kühn’s view, therefore is based on establishing a state of equilibrium. In addition, Kühn thought that the choice of direction at one point of the path home would excite the following \textit{(Ibid.}, 45–46). This foreshadowing mechanism clearly reveals the proximity of his approach with other reflex-chain theories. In both cases the reaction takes a paradox position insofar as it is stimulus at the same time.

\textsuperscript{176} \textit{Ibid.}, 53.

\textsuperscript{177} \textit{Tinbergen, “Über die Orientierung des Bienenwolfs III. [1938]”, 333.}

\textsuperscript{178} \textit{See \textit{ibid.}, 330.}
\end{flushright}
with ideal paths) but seems to have conceived the entire scheme more as ruled by experience since all tactic orientation movements in his view are determined by the mechanism of the reflex arc. “Alle taktischen Orientierungsreaktionen vielzelliger Geschöpfe setzen sich aus Reflexen zusammen”, he writes and continues:

Auf eine bestimmte Reizung einer bestimmten Sinnesstelle hin wird durch das Nervensystem eine bestimmte Tätigkeit des Bewegungsapparates ausgelöst. [All tactic orientation reactions of multicellular organisms are compounds of reflexes. As a response to a particular stimulation of a particular sensory position a particular action of the behavioural apparatus is released by the nervous system.](transl. CL) 179

Niko, in his later study, seems to have sympathized with this general causal over-tone but shifted the point of acquisition from the initial orientation flight to homing itself, that is, I think, in Niko’s later paper the act of orientation itself is partly caused by sensations stemming from the landmarks themselves. This is how I read Niko’s initial doubt,

daß außer Orientierung mittels visueller Erinnerungsbilder doch auch noch eine andere, vielleicht auf direkter sinnlicher Verbindung mit dem Nest beruhende Orientierungsart eine Rolle spielen könnte. [that besides orientation through visual memory images an additional kind of orientation might be playing a role which is based on a direct sensory connection with the nest.] (transl. CL) 180

In case I am right and orientation is partly based on data acquired later, one could also ask whether orientation as a whole is not a more relational thing, a process, or the product of an interaction between stored visuals and those acquired ad hoc. If I am not mistaken the character Niko ascribed to the orientation flight might have changed slightly either. While his former study had conceived the process of memorizing the composition of the landmarks as the prevailing aspect yet still standing in service of the overall choice of the right nest, his later study (whose experimental setting only allowed to chose between dummy nests) approaches the orientation flight more from an ecological point of view. This is how I read chapter nine, “Der Zeitpunkt der Dressur; die Funktion des Orientierungsfuges” and chapter ten, “Die Zeitdauer der Dressur, zunehmende Gliederung des Wahrnehmungsfeldes; sprunghafte Änderungen in der Wegmarkenwahl; Merkmalausfall”. 181 Like earlier accounts of the orientation flight, both chapters suggest that the landmarks are memorized during a process in course of which the wasp is actively screening the nest and its environment but, in addition to that, they claim that memorizing landmarks is adjustable relative to a current environment, and beyond that, there is a critical period of time during which memorizing is optimal. Thus, on the one hand, Niko had discovered that recognition after only one orientation flight was more perfect if the environment was new or had changed drastically, for instance, after a longer rainy period. “Es scheint also nach diesen Versuchen, daß wir zu der Annahme berechtigt sind”, Tinbergen summarizes his experiments,

daß die Umstände mit darüber bestimmen, ob bestimmte Gegenstände in der Umgebung der Hölle einen höheren oder einen geringeren Wert als Wegmarken besitzen. Bei erstmaliger

179 Kühn, Die Orientierung der Tiere im Raum, 61.

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Einprägung der Umgebung wird die Kenntnis der relativen Lage der vorhandenen Wegmarken schnell erworben; später hinzukommende, wenn auch auf Grund eigener Form- und Farbenmerkmale “starke” Wegmarken werden langsamer aufgenommen. Es gibt eine kritische Zeit während welcher einer optimale Empfänglichkeit für die Einprägung der Wegmarken besteht.

After these experiments we appear to be entitled to make the assumption that the circumstances decide, too, whether certain objects surrounding the nest have a higher or lower value as landmark clues. In course of the primary memorization of the environment the information of the relative position of the existing landmarks is acquired fast, later added objects, even if they are “strong” ones because of their form or colouration, are acquired more slowly. There is a critical period during which an optimal perceptibility exists for the memorization of the landmark clues.

This quotation shows that N. Tinbergen defined the digger-wasp’s orientation similar to K. Lorenz’s later understanding of imprinting as “Zeitgestalt”. There is a sensible period during which memorizing especially of new landmarks is most effective (with a view of the amount of time which must be invested). Later inscription is possible yet more time consuming and therefore less effective. On the other hand, N. Tinbergen had found out that the digger-wasp’s field of perception changed during the training period itself insofar as later landmarks gradually replaced older ones. If I am not mistaken, Niko argues here that fading of conditioned qualities sets free the Digger Wasp’s spontaneous choice of landmarks, so to say, in accordance with its own rules. These rules can be described in relation to the time passed and possibly encompass both a more detailed differentiation of the field of perception and taking into account entire new objects. “Das Hinzunehmen neuer Marken ist also Folge der Desorientiertheit”, writes Tinbergen and proceeds:

Durch das Vorkommen von Fehlwahlen nach Wiederherstellung der Dressuranordnung wissen wir, daß das Tier nicht Marken nimmt, an die es plötzlich von der gewöhnten Konstellation erinnert, denn dann wären die letzten Fehlwahlen ja verständlich. Das Tier vertraut sich also vollkommen neuen, selbstgewählten, nicht unter Drang (etwa einer vom Versuchsleiter an bestimmte Wegmarken gekoppelten Strafe oder Belohnung) gewählten Wegmarken an.

The inclusion of new landmarks is therefore a consequence of disorientation. Due to the existence of wrong choices after restoring the setting of the conditioning test we know that the animal does not accept clues which it remembers from the familiar constellation because in this case the erroneous choices would be explainable. The animal therefore confines to entirely new, autonomously chosen, and not under pressure (e.g. a certain reward or punishment connected with certain objects by the experimenter) selected landmark clues.

I think, this passage shows that the act of memorizing the landmarks might be a complex system in itself in as much as it has its own inner logical or chronological order. If certain landmarks have been “worn out” because they were identified with the experience of disorientation the animal responds with a surprising reaction: It picks a new clue on its own account, obviously a sort of spontaneous acquisition independent from reward or punishment.

Part IV. tested the hypothesis whether Philanthus has the capacity to find home from unknown areas up to one kilometre away from the nest. It is therefore con-
cerned with long-distance orientation. The epistemic frame underlying both the
tests and the paper itself thus is based upon a distinction between unknown and
known. The experiments with the wasps which had been actively transported to
unfamiliar environments revealed that the animals had to learn the landmarks be-
tween starting point and target area, that is, the information provided by landmark
clues had to be acquired.\textsuperscript{186} Altogether Niko thus was able to answer the question
whether the orientation of the wasps is exclusively or at least partly due to some
kind of advanced homing ability or, on the contrary, the wasps have to learn the path
there and back.\textsuperscript{187} “Wir glauben nach dem oben Gesagten zum Schluß berechtigt
tzu sein”, Niko concludes,

\begin{quote}
\textit{daß bei Philanthus Rückkehr aus unbekanntem Gebiet schwierig ist und unter Umständen
gar nicht gelingt. Eine direkte sinnliche Verbindung mit dem Nest, welche ein dauerndes
Orientiersein auch in unbekanntem Gebiet ermöglicht, besteht nicht oder hat höchstens einen
sehr geringfügigen Einfluß.}
\end{quote}

\textit{[After the above mentioned we feel entitled to draw the conclusion that in Philanthus homing
from unknown territory is difficult and eventually might not be successful at all. A direct sensory
connection with the nest, which enables being permanently oriented also in unknown territory,
does not exist or at least has a minor influence.]\textsuperscript{(transl. CL)188}}

The quotation shows that the results of the tests were mainly negative. The pa-
per as whole therefore has a hypothetico-deductive character. The hypothesis that
Digger Wasps had some kind of orientation mechanism beyond the processing of
landmarks such as, for instance, the usage of polarized sun light (K. v. Frisch’s dis-
covery) could obviously be ruled out. The relation between unknown and known
territory remained interrupted. As a result one may say Niko’s experiments with
Digger Wasps displaced in unknown territory ended with a negative result so that
it can be inferred that the animal is not adapted to this problem. The entire frame
of the third paper thus seems to have a negative overtone: Having proved the learnt
character of the wasp’s orientation contradicted the neo-vitalistic assumption of the
existence of any mystic unknown ability.

It is time now to summarize my analyses of the second stage of N. Tinbergen’s
scientific development. I have examined altogether five studies two of which orig-
inated directly from observations made during Niko’s stay in Greenland, whereas
the other three pick up the two main subjects Niko had already treated with in his
dissertation thesis, namely the digger-wasps hunting behaviour and its ability to
recognize the nest. All five studies reveal – relative to their position in the edifice of
Niko’s reasoning about animal behaviour – the same symptoms of a ground break-
ing causal intervention similar and analogous to the one I have observed in the
intellectual life histories of other researchers who placed their works implicitly or
explicitly in a (neo)-Darwinian context. Thus, one may say Niko’s Phalarope paper
examined the effect the reverse sexual dimorphism had on the wader’s behaviours,
Niko Tinbergen (1907–1988) while his study of snow-buntings carved out an ecological concept of territory. The accounts of the digger-wasp's orientation reveal both an observational experimentalism and a psychic sensualism. It is important to notice that Niko revealed the symptoms of the causal turn already in 1935 at the latest – that is before he met K. Lorenz in person and before both researchers conducted their famous study about the intercalation of taxis and instinct. In contrast to D. R. Röell, who put a great deal of emphasis on K. Lorenz’s impact, I am therefore inclined to connect the epistemic shift underlying his modified causal reasoning with the experiences he made during the year in Greenland. The fact that hunting became real behaviour within his real life may have played a critical role. Moreover, it can be asked whether Niko’s attitude towards his photographing changed in comparison to his youth period. Thus we are informed in H. Kruuk’s biography that Niko’s official task on the expedition was to gather and store ethnographic material and photographs for museums and this must have been a more secondary (though joyful) activity of questionable usefulness for his actual interest. What actually triggered Niko’s interest in dysfunctional behaviours and perception errors is to be examined more carefully still. Finally, the fact that there was a transposition of causal epistemic patterns leads to a more differentiated view of what is usually called N. Tinbergen’s “ecological turn” since the combination between evolutionary variability and adaptation turns out to have been a substantial part of Niko’s research already in the middle of the 1930s at the latest – that is at least in one realm of his personality. As I will explain later his turn to Behavioural Ecology therefore completed a process which had begun earlier.

Building the Synthesis: Ethology 1938–1948

Transition Three. After Niko’s return to Leiden in fall 1933 he took up his job at the Department of Zoology. After completing his studies, van der Klaauw had offered a position as research assistant which also was Niko’s formal status during the time he was carrying out his PhD studies and now could be resumed. His responsibilities included designing a course in behaviour with a special emphasis on experimentation and delivering lectures in comparative anatomy. His own research consisted in giving a shape to the observations he made during his stay in Greenland but also focused on his Philanthus-project which was to be supplemented with two additional in-depth studies based on further field studies carried out between 1934 and 1937. In addition to that, new interests entered his horizon and my task in the following paragraphs will be to find out whether, and if so, when and in what form additional epistemic shifts occurred in Niko’s scientific development. My analysis therefore is not a complete survey of N. Tinbergen’s research after 1933. On the contrary, it aims to focus on the turning points and the transfor-

189 Röell, The World of Instinct, 8–9, 108–145.
191 Ibid., 72–86, here 73.
192 Among these new interests which were mostly also cooperative research projects with his students were the territorial behaviour of the Bitterling, the courtship behaviour of the Smooth Newt, the camouflage of small Stick Caterpillars, the tracks of animals in the sand, or the behaviour of the Grayling. See ibid., 102–105.
Intellectual Life-Histories

formation they entailed on the deep-structure level of his life course. Thereby I will focus on mainly two research fields which are indissolubly linked with Niko’s person. On the one hand, N. Tinbergen continued his research in reproductive and social behaviours and this encompassed both the relations of sex mates and between parents and their offspring (i.e. parental care). The primary research objects chosen to answer Niko’s increasingly sophisticated questions were Sticklebacks, Thrushes and Moths. On the other hand, N. Tinbergen abstracted the methods he had already applied in his orientation studies to a general method of holistic causal analysis. Next to the more theoretical texts Niko’s mechanomorph (E. Crist) approach generated, there is also a new research field which may have originated within this theoretical frame: Niko’s interest in Gulls, with a special emphasis on systematics. While the Stickleback studies were bound to the laboratory, his studies of Gulls were based primarily on field observations. I do not believe, as other science historians seem to do, that the two realms in which N. Tinbergen’s life proceeded necessarily coincide with the lab vs. field dichotomy (not even if we take into consideration the causal intervention I have analyzed in the preceding paragraphs). But I do see that observation and experimenting are two different scientific practices which have causal implications. I therefore suggest to use epistemic schemes as primary unit of abstraction and ask how these patterns become manifest. The technique of correlating the epistemological with the phenomenological level will show that even in textual units antagonistic epistemic schemes (including their representations) can be combined together and that therefore statements whether some piece of research is more observational or more experimental therefore can only be made relative to the location in a text or larger philosophical edifice.

\((R_1)\) N. Tinbergen’s interest in the three-spined Stickleback can be traced back at least to a paper published together with J. J. ter Pelkijk in the first volume of Zeitschrift für Tierpsychologie in 1937. The Stickleback is the primary object of reference in Niko’s methodological manifest An Objectivistic Study of The Innate Behaviour of Animals (1942) and takes “pride of place” (Russell & Russell) in The Study of Instinct (1951).

Another cooperative study with J. v. Iersel had been published shortly before in the first issue of Behaviour in 1948 – the journal Niko founded after his move from Leiden to Oxford in order to make public his approach within the Anglo-American scientific community. According to W. M. S. and C. Russell, alone three of the first nine special issues of Behaviour were related to Stickleback research mainly conducted by Niko’s pupils in Leiden and later in Oxford such as P. Sevenster and D. Morris. A. v. Hippel recently underlined that, since Niko’s pioneering work, the Three-spined Stickleback took an unprecedented career as so-called “model organism” both in Ethology and wider neighbouring fields.
such as Evolutionary Biology, Ecotoxicology, and Developmental Genetics. W. M. S. and Claire Russell went even so far to compare the role the Stickleback played for the growth of scientific Ethology with the one Drosophila melanogaster played in Genetics. “In experimental ethology”, they write, “sticklebacks have played a part comparable to that of the genus Drosophila in genetics, and the three-spined to that of Drosophila melanogaster”. As a provisional hypothesis, we may therefore say that Niko’s and his pupils’ interest in Three-spined Sticklebacks coincided with a period of Ethology’s growth, scientization and institutionalization. In addition, I wonder which epistemic fields of the Ethological Synthesis were mainly covered by the Stickleback research and which are the essential shifts in the overall development? I think I should like to begin with a careful reading of J. ter Pelkwick’s and N. Tinbergen’s cooperative paper Eine reizbiologische Analyse einiger Verhaltensweisen von Gasterosteus aculeatus L. In the introductory part we read that the study was performed in 1936 during a practical course in Ethology. The location is referred to as the Zoological Laboratory of the University of Leiden. We may therefore conclude that we have to do with a laboratory study rather than a field study. The topic of the paper is the reproductive behaviour (“Fortpflanzungsverhalten”) of the Three-spined Stickleback. This can be inferred both from the paper’s introduction and the headlines of the succeeding chapters which describe the stages of the Three-spined Stickleback’s reproductive cycle from the establishment of a territory to the male’s parental care. Insofar we may say Niko’s interest in Stickleback’s continued his studies about the mating behaviours of Common Terns, Red-necked Phalaropes and Snow Buntings. All papers had had in common that they evinced the evolutionary variability and the arbitrary character of the mating systems. Thus Niko revealed the mutuality of the pair bonding in a species with no sexual dimorphism (Common Terns), the inversion of “sex”-specific roles in a mating-system with reverse sexual dimorphism (Phalarope) and the variability of object-related behaviours during courtship in a mating-system with only slight sexual dimorphism (Snow Bunting). The Stickleback unifies several of these aspects and carries on the trend to arbitrariness insofar as the males fight for territories, both sexes display courtship behaviours yet only the male exhibits the behaviours of parental care. From a methodological point of view one may say that Niko initially placed his Stickleback research within K. Lorenz’s research program – the special phylogeny of releasers – insofar as he adopted its core theorem: The correlation between schema and corresponding environmental object (i.e. releaser in a wider sense). “Für eine Analyse von handlungsauslösenden Reizsituationen”, ter Pelkwick and Tinbergen write,


Russell et al., “Stickelbacks and Ethology”, 3.


Ibid., 193.

The titles of the chapters are “I. Die Territorialkämpfe der ♂♂”, “II. Der Nestbau”, “III. Die
verschiedener Verhaltensweisen zeigt, deren jede ihre eigene auslösende Reizsituation verlangt. Besonders reizvoll ist diese Analyse noch dadurch, daß hier so oft der Artgenosse als Reizquelle wirksam ist, und wir somit bei der Erforschung der Schemata die Spezies von zwei Seiten her kennen lernen; es ist ja nicht nur die Beziehung Reizsituation-Handlung, welche uns interessiert, sondern auch die Funktion jener reizaussendenden körperlichen Strukturen, die wir mit Lorenz (1935) allgemein als “Auslöser” bezeichnen.

[For the analysis of stimulus situations releasing action patterns the reproductive behaviour of animals with complex mechanisms of pair formation and parental care is a very suitable scientific object because every animal exhibits always a great number of diverse behaviours each of which requires its own releasive situation. This analysis becomes still more intriguing by the fact that here it is the conspecific which yields the effect by becoming the stimulus situation and we therefore get to know the species from two sides while we are scrutinizing the schemata; certainly it is not only the relation between releasive situation and action pattern which interests us but also the function of those stimulating body structures which we, following Lorenz (1935) commonly call “releaser”.] [transl. CL]

Two aspects seem to be relevant in this quotation. On the one side, Niko picks up Lorenz’s methodological dichotomy between sending apparatus and receptive correlate yet seems to put his emphasis more on the sender and less the physical constitution of the receiver (i.e. the schema). On the other hand, however, within the field of the “handlungsauslösenden Reizsituationen” (situations that stimulate action) Tinbergen apparently was eager to take into account both the morphological structures, that is, Lorenz’s “Auslöser” (in a narrow sense), and corresponding behaviours displayed by the partner. Altogether we might eventually say N. Tinbergen’s and J. ter Pelkijwijk’s paper on reproductive behaviour in Three-spined Stickleback is a piece of complex animal sociology with a primary focus upon the sender-side of the interaction process. A detailed analysis of Eine reizbiologische Analyse could make evident that the order of the study is based upon the distinction between simple releaser (in K. Lorenz’s sense) and more complex releasing situations involving behavioural qualities. For my purpose it is more relevant to find examples for both types of releasing situation which are suitable to evince causal linkages and re-evaluations of epistemic patterns. Both criteria are relevant for determining the adequate place of the study in N. Tinbergen’s scientific development. Thus one may eventually say that the two first chapters, “I. Die Territorialkämpfe der ♂♂” (The territorial fights of the Male) and “II. Der Nestbau” (The Building of the Nest), describe the procedure in course of which both the wider and the narrower area is determined where the nest is to be built. Especially the building of the nest thereby reveals the reductive nature of this process. “Wie bekannt”, J. ter Pelkijwijk and N. Tinbergen write,

fängt das ♂ den Bau an, indem es durch Aufsaugen und Wegtransport von Sand eine Mulde herstellt. Dabei kommt die Bindung an eine bestimmte Stelle erst zustande, nachdem das Sand-
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The radius of the area taken into possession by the male seems to decrease corresponding to the action patterns applied to each range. In particular, the territorial fights seem to be released by concise morphological qualities displayed by male rivals such as their bright red belly (also in combination with threat gestures). This little anecdote is significant for Tinbergen’s reasoning in so far as it reveals that the Stickleback’s territorial behaviour is partly triggered by simplified stimulation patterns and – even more important – this leads to perception errors which provide insights into the animal’s fixed action patterns and their causal grounds. The occupation of an area for the nest is followed by building the nest. Tinbergen here apparently perceived maladaptive behaviours in so far his proband animals were not capable to realize that some material combined both advantageous and disadvantageous qualities. Tinbergen thus infers that the recognition of the material for the nest must be based on a simple schema which is fixed and cannot be modified by learning. As a result, we may conclude that Niko’s and Pelkwijk’s paper reveals a stage of development at which the heuristic value of maladaptive behaviours has been realized. What I have called “causal turn” thus is present in the paper though not very prominently. Especially the ultimate interpretations of causality appear more as movements of a second individual or object distant from the male to or in direction of a third place. A good example may be the behaviours described in chapter “III. Die Balz” (The Courtship). Tinbergen distinguishes here between the meaning of female courtship behaviours for the male and, conversely, the effect of male courtship upon the female. The mating behaviours of both partners surely have the function to prepare the female’s spawning in the nest yet both sexes fulfil their part in different ways. The male exhibits a behaviour pattern which N. Tinbergen, following O. Heinroth, calls “Imponierverhalten”: After the male Stickleback has completed the nest the fish reveals the known two step action pattern. Corresponding to his observations in Phalaropes Niko realized that in a first step the male Stickleback attacks all intruders independent of their sex. In a second step, it reacts in a differentiated manner. If the intruder is a male it is attacked, if a female it is guided to the nest. The former of the two action patterns, Niko concludes, must be based on a poor recognition schema. The behaviours of the female thus have the function to make the male guide his partner to the nest. Its


Ibid., 194–195.


Ibid., 197–198.
releaser must be more sophisticated. “Wie schon die unmittelbare Beobachtung des Normalverhaltens zeigte”, Tinbergen and ter Pelkwijk underline,

ist als Auslöser für die männlichen Handlungen, die das ♀ zum Neste führen, die Bewegungsweise des balzenden ♀ weit wichtiger als das so auffällige Formmerkmal des dicken Bauches. Versuche mit “Marionetten” bestätigen dies in schlagender Weise.

[As the immediate observation of the normal behaviour has revealed the movements of the courting ♀ is much more important for the male response than the conspicuous feature of the big belly. Tests with “dummies” confirmed this convincingly.] 

However, the experiments with marionettes revealed that despite the more particular releasing pattern the male Stickleback could be misled insofar as also dead Minnows and Tenchs trigger the male’s “Führhandlung” if they are presented performing the right courtship movements. We may see now: The more elaborate releaser is connected with the directive behaviour. The releaser which is poor of qualities is linked with a behaviour’s potential dysfunction or its deceivability. Nonetheless, in particular the latter is the source of causal explanations. The female’s behaviour to follow the male to the nest is released by the male’s red belly in combination with additional courtship movements. The male’s behaviour thus has the function to direct the female to the nest. The releaser which originate from the female’s behaviours have the function to make the male guide the female to the nest. The guidance, in Niko’s view, is appropriate since the female usually is not familiar with the area. Further examples for directive behaviours based on complex releasers may be the male’s habit to carry clots of eggs back to the nest in case they exceed a certain size, the behaviour of the male to rebuild the nest depending the developmental stage of the young or its habit to carry back the young to the nest depending on their age. In sum, we may eventually conclude that N. Tinbergen’s and J. ter Pelkwijk’s cooperative study examines both simple potentially dysfunctional and complex directive releasing situations in various stages of the Three-spined Stickleback’s reproductive cycle without establishing definite connections between each releaser and a particular sex. Which releaser is effective depends on the point of time in the reproductive cycle (and the releaser itself). Moreover, in contrast to Niko’s later Stickleback research there is no emphasis on hierarchization of specifically released action patterns. With one exception: Niko states in context of chapter III.a (The Meaning of Female Courtship for the Male) that the male’s fight can switch off its guiding behaviour. Tinbergen and ter Pelkwijk underline:

Bei den Versuchen über die Führhandlung des ♂ machten wir die Erfahrung, daß das Führen vom Kämpfen ausgeschaltet wird, und zwar hat ein intensiver Angriff während mehrerer Minuten eine inhibierende Nachwirkung auf das Führen.

[While observing the guidance movement of the ♂ we made the experience that guiding is switched off by fighting, that is to say, an intensive fight during the first minutes has an inhibiting after effect upon the guidance behaviour.] 

I read the paragraph as a hint for two aspects. On the one side, Tinbergen understands the relation between the male’s potential reactions towards intruders, that is,

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210 Ibid., 199.
211 Ibid., 199, 200.
212 Ibid., 198.
either fight or guiding to the nest, as a sort of trade-off which might be an effect of the amount of nervous energy being available. On the other hand, the quotation implies a hierarchy as well. Fight is able to superimpose the guiding behaviour and therefore gives the latter a paradox status: It exists and is potentially effective but is blocked by initially or previously experienced inhibitive instance. From a more epistemic point of view we may therefore conclude that Eine reizbiologische Analyse contains the effects of Niko’s causal turn but not yet the re-evaluations which are characteristic for Ethology’s more advanced developmental stages: The discontinuous element in the epistemic frames is still the prevailing one. This should change in the following years.

The year 1938 eventually constituted a demarcation line both in Niko’s biography and his scientific development. During July and October he went on a long trip to the United States. According to H. Kruuk, Niko delivered a lecture at Cornell University and met many of the great names in animal behaviour research. At the American Museum of Natural History (AMNH) in New York he came into contact with G. K. Noble and E. Mayr. Noble was interested in the conditioning of behaviour and the role played by hormones. Also he examined the effect of colour stimuli in courtship of Lizards and birds. Despite the fact that Noble’s interests partly overlapped with Niko’s, the latter remained sceptical because he found Noble’s experiments superficial, hasty and messy. Mayr was born in Kempten (Allgäu, Germany) in 1904. He began medical studies in Greifswald in 1923 but soon after transferred his studies to the University of Berlin in order to study Zoology – the field in which he finally obtained his doctoral degree in 1926 at the age of twenty-one. After that, he was employed at the Zoological Museum in Berlin as “lowly museum assistant” – as J. Cain put it – and assigned to the library by W. Arndt, with whom Mayr became good friend. In 1928 his mentor, Erwin Stresemann, played a key role in Mayr’s decision to become zoologist: He promised Mayr to send him on an expedition to the tropics. On Mayr’s early exchange with Stresemann over the Red-crested Pochard – a rare duck species Mayr had observed in Saxony, see Haffer, Ornitology, Evolution, and Philosophy, 22–23. For the circumstances of Mayr’s change to Zoology and his dissertation thesis, see ibid., 23, 32, 35–37.


On further details concerning Mayr’s part in the expedition, see ibid., 48–91.
Mayr returned in 1930 as experienced field man. In the following year he moved to New York. Sanford, patron of the ornithological department at the American Museum of Natural History, had financed the Brewster-Sanford Expedition to South America whose harvest formed the basis of a large collection of sea-birds. Moreover, he had raised the funds for the Whitney South See Expedition, later obtained the funding for purchasing the Rothschild Collection, for building the so-called Whitney Wing of the AMNH and, not least, to employ Mayr permanently at the Museum since 1932. Mayr’s job was to curate these massive acquisitions which he himself had helped to collect. Furthermore, the so-called Whitney-Rothschild Collections became the empirical basis for his systematic, biogeographic and evolutionary studies. With Sanford’s death in 1950 Mayr felt less closely tied with the AMNH and as a consequence, in 1953, he accepted a chair for Zoology at Harvard University where he stayed as professor and emeritus till his death in 2005. Next to his later research foci, history of Biology (since ca. 1970) and philosophy of sciences (since ca. 1980), Mayr’s primary professional interest from the early 1940s, throughout the 1950s to the late 1960s was in various aspects of Evolutionary Biology. Mayr used to describe himself as E. Stresemann’s disciple and an advocate of his school. Stresemann for his own part and the Zoological Museum which he represented in ornithological issues were closely affiliated – both in terms of personal and institutional relationships as well as theoretically – with H. Seebohm’s and E. Hartet’s school of “European Ornithology” (J. Haffer) whose most important residence was W. Rothschild’s private museum in Tring near London. In contrast to many leading ornithologists in Britain and Germany both schools operated with a widely conceived conception of species in their microtaxonomic studies and, beyond that, put much emphasis on biogeographical variation on subspecies level as well as the importance of geographic isolation for the process of species evolution. In other words, H. Seebohm, E. Hartet and E. Stresemann (including his pupils) advocated gradualism insofar as they presumed the existence of living intermediate forms which in their view had to be understood as hybrids (or subspecies in their terminology) and therefore did not constitute an independent species as the adherents of a narrow typological species concept (had) claimed.
From an epistemological point of view, one may eventually say that Mayr as well as his colleagues at the Museum of Natural History in the mid-1920s still stood in a sensualist (and that is since the 19th century a Lamarckian) tradition insofar as they denied the relevance of macromutations for evolutionary change. “During the mid-1920s”, J. Haffer stresses,

all of Mayr’s colleagues at the Museum of Natural History in Berlin were deeply concerned with evolutionary questions and fighting against the saltationist views of the “mutationists” like De Vries, Bateson and Johannsen (as well as R. Goldschmidt and O. Schindewolf during the 1930s) who interpreted evolution through macromutations (saltations). All of these latter scientists were typologists who thought new species originated with major mutations and all of them rejected natural selection [in Darwin’s sense] CL. The Berlin zoologists at the Museum of Natural History studied in detail the phenomenon of geographical variation in animals leading to an emphasis on environmental factors. 224

In other words, Stresemann’s and his pupils’ early view on speciation and geographical variation was both gradualist and environmentalist which also implied rejecting natural selection of which Mayr thought it can eliminate but not create something new. 225 Yet Stresemann, and even to a greater extent, E. Mayr (and B. Rensch) reformed this position by redefining the species as a biological unit and thus paved the way for the synthetic theory of evolution within and beyond the field of ornithology – a process which both scholars also understood as a means for the scientization of ornithology. 226 Thus Mayr, in a first step, met with those geneticists who claimed the combination between gradualism, on the one hand, and the principles of Mendelian genetics on the other. 227 Coming from a more gradualist tradition, this synthesis led to a population genetics (also called New Systematics) which, in addition, put great emphasis on geographical isolation, that is, the notion that under favourable environmental circumstances so-called clines (that is character gradients) can develop into different directions and therefore may establish new taxa. 228 In other words, by working through his material Mayr discovered that the geographical distribution of the specimens – which in the last consequence also mirrors the practice of collecting data – was far more discontinuous in order to be

224 Haffer, Ornithology, Evolution, and Philosophy, 45.
225 Ibid., 48.
226 On this reform see J. Haffer. “Die ‘Stresemannsche Revolution’ in der Ornithologie des frühen 20. Jahrhunderts”. In: Journal für Ornithologie 142.4 (2001), 381–389, and Haffer, Ornithology, Evolution, and Philosophy, 46. Furthermore, after his move to New York, Mayr intended to implement his “scientific ornithology” both within the American Ornithologists’ Union (with its publication organ The Auk) and the Linnaean Society of New York (with its Transactions). On Mayr’s efforts to make Ornithology scientific, see Cain, “Ernst Mayr and the ‘Biology of Birds’”, 118–121, 117–118. That N. Tinbergen’s Snow Bunting paper was published in the Transactions of the Linnaean Society of New York in 1939 eventually must be interpreted with respect of Mayr’s zeal to reform these social groups into scientific communities. Mayr had put valuable criticism to the manuscript and suggested that Tinbergen extended his interest to behaviour genetics. See Haffer, Ornithology, Evolution, and Philosophy, 110, 127.
227 This synthesis had become possible by the geneticists’ discovery that genetic variation could be induced by small mutations (Ibid., 45–46, 120). On Stresemann’s, Mayr’s and Rensch’s reassessment of the doctrines introduced by the Seebohm-Hartet-“School”, see Haffer, “Die Seebohm-Hartet-‘Schule’”, 47–50.
228 For Mayr’s emphasis in “island biogeography” see Haffer, Ornithology, Evolution, and Philosophy, 147, 163.
explained by the subspecies concept only. Mayr thus was forced to operate with additional concepts: The species and what he called “superspecies”. The latter of the two was equivalent to the term “Artenkreis” which was coined by B. Rensch and meant taxonomic entities which developed characters too discrete to be described as subspecies of one single species.\textsuperscript{229} Mayr now speaks of a “compromise” between the extremely modern ornithologists and the conservatives, between the motivation to put together all geographical representatives as one species and the demand for perfect integration.\textsuperscript{230} Furthermore, Mayr’s New Systematics brought in a \textit{holistic} stance insofar as the qualities taken into account for the process of geographical speciation included not only morphological features but also ethological, physiological, biochemical and bioacoustic differences. A second epistemological shift on the way to the Modern Synthesis may consist in Mayr’s (and also B. Rensch’s yet to a lesser degree E. Stresemann’s) consequent rejection of their own earlier strictly Lamarckian view upon the causes of evolution. This implied both discussing the normal process of genic variation within the conceptual frame of natural selection but also set free Mayr’s interest in populations of birds which are often endemic to one island only or at least to a very restricted geographical area. Usually these populations are not only small but mostly genetically extraordinary uniform so that they are not capable to adjust to environmental changes or are easily threatened by the intrusion of more advanced predators.\textsuperscript{231} Finally, Mayr’s scientific orientation was subject to essential epistemic re-evaluations. To put it simply, as soon as the epistemic frame underlying the notion of gradual genic variability in populations gained priority, it became – paradoxically – possible to incorporate means of discontinuous speciation into this framework, so to speak, due to the pressure this conceptual modification applied to higher performative levels of theorizing. More concretely, the more abrupt forms of evolutionary change which accompany allopatric speciation (i.e. speciation through geographic isolation) now can appear as a special case of genic variability in extremely small populations. In contrast to Dobzhansky who interpreted the New Synthesis more mathematically and thus, for instance, came to what he called “scattering of variability”, Mayr’s interpretation was also more related to the biological species concept (BSC).\textsuperscript{232} From an epistemic standpoint we may detect two particulate epistemic schemes in Mayr’s

\textsuperscript{229} See Haffer, \textit{Ornithology, Evolution, and Philosophy}, 148, 153. In Ch. Darwin’s theorizing we find at this point the sentence “returning to Kirby’s view” (Richards, \textit{Darwin and the Emergence of Evolutionary Theories of Mind and Behavior}, 142). I wonder whether the analogous sentence here must read “returning to Kleinschmidt’s view”. The ornithologist O. Kleinschmidt had suggested to describe geographical distribution in terms of “Funktionskreise” – a concept which takes into account extension but in contrast to the Seebohm-Hartet—“School” does so within a typological frame. See Haffer, “Die Seebohm-Hartet—‘Schule’”, 42.

\textsuperscript{230} Haffer, \textit{Ornithology, Evolution, and Philosophy}, 148.

\textsuperscript{231} Most interestingly, Mayr’s scientific interest in small island biota was connected with a claim for their protection, i.e. direct measures of preservation. See ibid., 130–132. The scientific part of it was Mayr’s so-called \textit{equilibrium theory} which described an island fauna as a balance between colonization (immigration) and extinction (output) of individuals and thus came to the conclusion that in prehistoric times (i.e. especially before the arrival of humans) the variety of species on these island biota must have been far richer. Mayr’s theory thus was both “dispersalist” and based on proximate overtones. See ibid., 163–165.

\textsuperscript{232} On Mayr’s biological concept of species, see ibid., 203–222, also 230–232.
biological reassessment of the species: On the one hand, species is defined as a reproductive unity (i.e. an assemblage of populations) which allows inbreeding to the inside even in case of obvious morphological differences (as Stresemann put it) or inbreeding may occur only potentially (as Mayr put it). On the other hand, a species must be reproductively isolated. This means, if geographic isolation is presupposed species members must not interbreed even in case the barriers are removed. In other words, separation must have reached a physical (i.e. genic) level – although Mayr did not conceive the gaps between allopatric species as absolute. Careful readers will have realized that both epistemic schemes operate with paradox in their final stages: A quasi-discontinuity in the first case and a quasi-continuity in the second. Moreover, it is also important to notice that Mayr’s conception of species brings in an essential spatial component, that is, in his view a species is both a genic, a reproductive and an ecological unit.\(^{233}\) Mayr’s epistemic re-evaluations coincided also with his turn to evolutionary theory.\(^{234}\) “By late 1939 and early 1940”, J. Cain tells us, “theoretical discussion of speciation and evolutionary processes were beginning to dominate Mayr’s attention. This represented a constricting of his biological interests, not an expansion of his taxonomic ones”.\(^{235}\) An indicator of his transformation from a purely empirical to an increasingly theoretical biologist most likely can be seen in Mayr’s major work *Systematics and the Origin of Species* – the expanded manuscript of his contribution to the 1941 Jesup Lectures to which he had been invited by L. C. Dunn of Columbia University.\(^{236}\) The book was finally published in 1942 and made the author to one of the co-founders of the Modern Synthetic Theory of Evolution. Its main emphasis was put on the horizontal level of evolution (absent in G. G. Simpson). Its main purpose was the integration of allopatric speciation by developing a set of isolation mechanisms – an aspect which was treated only vaguely by Th. Dobzhansky in his *Genetics and the Origin of Species*. In retrospect Niko writes about E. Mayr’s impact on his research:

*My theoretical interest was kindled by Huxley’s writings; I was engrossed by the discussions of his grebe and his Red-throated Diver papers. Even so, I remained an ignoramus until I met Ernst Mayr (1938), and his Systematics and the Origin of Species gave me a real push. The other influence was really David Lack.*\(^{237}\)

What was actually Mayr’s (and also Lack’s) impact on Niko’s research must be clarified by analyzing the works the latter published after 1938. A direct consequence

\(^{233}\) Here one may eventually see a parallel to what Darwin called “representation” and by which he meant the competition for ecological niches. However, Darwin’s focus was more on vertical evolution.


\(^{236}\) On the importance of *Systematics and the Origin of Species* for Mayr’s own development and also for the self-image established by his own and the recollections of others, see ibid., 112. See also Haffer, *Ornithology, Evolution, and Philosophy*, 194–199.

\(^{237}\) Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3156, E 2, letter N. Tinbergen to R. Burkhardt (05/05/1979).
of Niko’s trip to America was that he gained “a large boost of confidence in the research of himself and his group” – as H. Kruuk puts it. In comparing his research with the views of others he had realized the value of his own studies. As it turned out he was capable to counter the criticism of others and comment their views on a well informed basis. Moreover, Niko was considered for a couple of upcoming positions in the United States. Thus, he was offered to become head of the department of ornithology which was about to be established at the University of Wisconsin. Alternatively he was asked to become the head of a newly founded animal behaviour field station in Albany. As a result, Niko’s Leiden superior, H. Boschma, reacted and offered Niko a position as lecturer at his Zoological Department which Niko finally accepted. In addition to that, Niko was appointed editor of the (Dutch) Journal for Professional Biologists in 1940. The main target audience of the journal which had been edited before by the vitalist psychologist J. A. Bierens de Haan was the group of Dutch Biology teachers and Niko saw the opportunity to popularize his field amongst the younger generations of biologists. In general, one may eventually say that this upgrading of Niko’s position and his research went hand in hand with essential re-evaluations of theorems within those epistemic patterns that were subsequently “ruling” his scientific accounts for the following two decades. What was first is difficult to determine. Quite obvious seems to me that the intellectual life courses of the ethologists I have examined so far but have excluded from my thesis were compatible with the Modern Synthesis of Evolution insofar as the Ethological Synthesis originated complementarily and, even more important, did so in a series of analogous epistemic shifts: And also Niko’s revalued self-esteem went hand in hand with epistemic re-evaluations and this occurred in parallel both to Darwin’s theorizing one time layer below and its neo-Darwinian reassessment. That Niko came into contact with E. Mayr exactly at this point of his and Mayr’s scientific development is not an accident. In the following paragraphs, I would like to make evident this coincidence in N. Tinbergen’s works. A study which, in my opinion, represents N. Tinbergen’s scientific development in the late 1930s quite well is Über die auslösenden und die richtunggebenden Reizsitationen der Sperrbewegung von jungen Drosseln – the results of a cooperative research project Niko had carried out between 1935 and 1937 together with D. J. Kuenen. In short, like K. Lorenz in his Companion-study and in his further reasoning on releaser, N. Tinbergen and D. Kuenen presupposed a correlation between

238 For the immediate effects of Niko’s trip to the USA, see Kruuk, Niko’s Nature, 102.
239 See ibid., 100.
240 That E. Mayr must not be reduced to “Mayr the evolutionary biologist” is underlined by J. Cain. See Cain, “Ernst Mayr and the ‘Biology of Birds’”, 112.
241 N. Tinbergen et al. “Über die auslösenden und die richtunggebenden Reizsituationen der Sperrbewegung von jungen Drosseln (Turdus m. merula L. und T. e. ericetorum Turton)”. In: Zeitschrift für Tierpsychologie 3.1 (1939), especially 38–39 for the time period during which the experiments were conducted. A thorough analysis of Tinbergen’s study of the begging behaviour in young Herring Gulls which made use of a similar experimental setting recently revealed that Tinbergen reinterpreted the results of the original study over the years and from publication to publication in which he used the study. Tinbergen, C. ten Cate argues, has more and more detached from the original data in his later descriptions of the original study without repeating the experiments with more unbiased experimental designs. See Cate, “Niko Tinbergen and the Red Patch”, 785–794, especially 792. There are in principle two explanations: Either
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releasing schemata and corresponding objects and / or behaviours which triggered an action pattern but in contrast to the former directed their attention more to the qualities of the releaser themselves. Their question thereby was which features the shape of the parent bird must have in order to release the spread-open behaviour of the offspring in optimal ways. In order to answer the question Kuenen and Tinbergen restricted their focus on one single action pattern, the birds’ fodder begging, and on two species, namely Thrushes (Drosseln) and Blackbirds (Amseln). From a methodological point of view they mainly applied dummy tests within a laboratory environment in which the accurate observation under controlled circumstances was guaranteed. In addition to that, both researchers performed control experiments with free-living Blackbirds and Thrushes which confirmed the basic results of the lab observations. The experimental testing of the releasive parameters of the young birds’ fodder begging behaviour revealed that the behaviour in question was based upon a proper innate releasing mechanism (IRM) which consisted both of a releasive and a directive component. “Es war unsere ursprüngliche Absicht”, N. Tinbergen writes,

242 Für die betreffenden Qualitäten siehe Tinbergen et al., “Über die auslösenden und die richtunggebenden Reizsituationen”, 38, 56.
243 Ibid., 58.
244 For the methodological approach of the paper see ibid., 39–40.
245 Ibid., 56.
246 For the sub-differentiation of both the releasive and the directive constituent see ibid., 56–57. From a strictly epistemological point of view it can be asked at this point whether both part constituents of the IRM are not based on different epistemic grounds. This would lead to a highly arbitrary conception of both the mechanical and the optical areas of stimulation!

Both constituents of the overall schema, that is, the releasive and the directive scheme, for their part again encompassed both a mechanical and an optical mode of orientation but the transition from early mechanical to later optical orientation occurred earlier in the releasive constituent. Moreover, according to Tinbergen, the optimal releasive situations are different in both types of schematism both with
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respect of the mechanical and the optical area of stimulation. The schemata in question therefore turned out to be adjustable during maturation but were mostly not subject to any learning process. “Wir fassen zusammen”, Niko summarizes,


[We summarize: 1. The releasing and directing schemata of the spread-open behaviour we found in both species of Thrush are really innate. 2. Many of the perceptible variations in the responsiveness of the food begging in singing birds do not correspond with learning processes, which affect the schema being related to the food begging behaviour, but instead must be addressed either as appearances of maturation or as learning processes of a different kind.]

In sum, Kuenen’s and Tinbergen’s study seems to take into account the multiple and variable character of the innate releasing mechanism especially with respect of their referent objects. While the schema itself seems to become more complicated by being able to acquire additional data (gravitational plus optical stimulation), the group of referents (optimal parent schemes) seems to decrease during maturation which N. Tinbergen conceived not only as refinement of an action pattern (“Bewegungsform”) but also of the correlation between stimulus and response (“Reiz-Reaktionskoppelung”). Altogether Tinbergen’s and Kuenen’s paper modified Lorenz’s Special Phylogeny of Releaser in several respects: On the one hand, they questioned Lorenz’s exclusive emphasis on degeneration by pointing out that also refinement occurs during maturation and here leads to more discrete food recognition. On the other hand, they not only put emphasis on the objectively observable behaviours but also, within this field, found a more quantitative approach to examine the many-facetedness of Lorenz’s “prägnant” releaser – a trend which continued in the following years. If we compare, for instance, the inner dynamics A. Seitz had ascribed to the innate releasing mechanisms in form of his rule of stimulus summation with N. Tinbergen’s and D. Kuenen’s emphasis on maturation we may eventually recognize the epistemic shift which has taken place from one model to the other: While Seitz’s model had taken into account the inner energetic constitution of an IRM, later models such as W. Schleidt’s principle of selective habituation or N. Tinbergen’s and D. Kuenen’s variation through maturation took more into account the multiple characters and the variability of the IRM over time. The linear and chronological moment therefore seems to be upgraded as well as the scientific practice of recursively applied bifurcation itself might be an indicator for an upgraded quantitative moment – at least if it is thought together with the act of differentiation. In conclusion, I am therefore inclined to say that Über die auslösenden und

247 Tinbergen et al., “Über die auslösenden und die richtunggebenden Reizsituationen”, 59.
248 For the various aspects in Niko’s understanding of maturation see ibid., 45.
Niko Tinbergen (1907–1988)

die richtunggebenden Reizsituationen documents how the epistemic re-evaluations which can be observed in Niko’s theorizing since ca. 1938 finally affected his understanding of the IRM. His slightly later paper Die Ethologie als Hilfswissenschaft der Ökologie (1940), from an even more generalizing point of view, seems to ask which role the examination of an animal’s releasive mechanisms and their modifiability by learning may have within a common frame of ecological research. It reads:


[The preference or rejection of a particular prey object also cannot be clarified without thorough ethological investigation. It applies to every species of Bird that their behaviours to grab food respond only to very few stimulating situations; there exists a very definite association between perception and response which we, in Uexküll’s and Lorenz’s terms, call “the schema”. The most important characteristic of the schema here is not that the reaction is connected with the perception of the prey object at all but, instead, that many parts of the perceptive field are not connected with the reaction. This schema is as inborn as is the response itself. In most, if not all, species of Bird this innate schema of the food response is modified by learning processes. The schema which is modified by learning is the factor which we are interested in from our ecological perspective.][transl. CL]

From this quotation it can be inferred that “Ökologie” serves N. Tinbergen as a wider concept or frame which includes the study of the releasive mechanisms and their correlation with corresponding situations yet also takes into account the modifiability of the “Schema” by learning – a transition which K. Lorenz in the cultural pathology he put forward at around the same time tended to interpret in terms of “degeneration” and “cultural decay”. Speaking of “Ethology” as an “auxiliary science” for Ecology implies the hierarchical prevalence of the ecological moment which here is connected with the schemata’s modifiability through learning.

Another piece of cooperate research work Niko performed together with some of his pupils makes evident even more that his so-called “turn to Ecology” proceeded in two steps one of which already occurred at the end of the 1930s. Die Balz des Samtfalters (1942) perpetuates N. Tinbergen’s interest in releaser but in contrast to earlier accounts which emphasized secondary, more complex forms of social interaction now places the analysis of a “prägnant” releasing situation within the framework of courtship behaviours. Moreover, in contrast to N. Tinbergen’s and D. Kuenen’s study on Thrushes and Blackbirds the focus of the present releaser-study now seems to be less upon laboratory observations rather than on natural

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experimentalizing. The Grayling Butterfly (Samtfalter) thereby turned out to be a promising research object.\(^{252}\) One of the reasons why the Grayling is an appropriate research object is because its most conspicuous behaviour appears to be prone to errors. “Gleich vom Anfang an richteten wir unsere Aufmerksamkeit auf die Aufgabe, einmal ein ‘angeborenes auslösendes Schema’ genau zu untersuchen”, Niko and his coauthors point out and continue:

Die Möglichkeit hierzu bot die auffallendste Reaktion des Samtfalters: das begattungslustige \(♂ \) fliegt auf ein vorüberkommendes \(♀ \) los. Wir sahen nämlich schon gleich am Anfang unserer Beobachtungen, daß die \(♂♂ \) nicht nur vorüberfliegende \(♀♀ \), sondern auch viele andere Tiere und Gegenstände anfliegen, und schlossen daraus, daß dieser Anfliegereaktion wohl ein sehr merkmalarmes Schema zugeordnet sein müßte. Die experimentelle Untersuchung der Frage, inwieweit diese Reaktion mit einer Reflexbewegung zu vergleichen wäre, erwies sich bald als aussichtsreich, und so stellten wir anfänglich unsere Arbeit vorwiegend hierauf ein. \(^{253}\) Später erweiterten wir unsere Aufgabe dahin, die ganze Balz zu beschreiben und an manchen Stellen zu analysieren.

\[ \text{Right from the beginning we directed out attention towards the task to examine for once an “innate releasing Schema” carefully. The possibility was provided by the most blatant response of the Grayling Butterfly: the } \(♂ \), \text{ in the mood for mating, flies into the direction of a } \(♀ \text{ which is passing by. We saw right from the start of our observations that } \(♂♂ \text{ not only approach passing } \(♀♀ \text{ but also many other animals and objects and concluded from this that the approach response must be correlated with a schema that is very poor of qualities. The experimental examination of the question, in how far this reaction could be compared with a reflex movement, soon turned out to be promising and, as a result, we adjusted our research primarily to this question at the beginning. } \text{ Later we extended our mission by describing the entire courtship ceremony whereby we were entering in detailed analysis at certain points.}} \]^{\text{transl. CL}}

This introductory quote shows quite well the structure of the paper’s core area: A more observational and descriptive part (III. Beschreibung des Verhaltens) is supplemented by a causal analysis of the entire courtship (IV. Die Analyse der Balz). The latter section, as we are informed, again consists in a detailed description of the “Anfliegereaktion” (approach flight response) of the male, on the one hand, and an examination of the function of the so-called “Duftfeld” (scent area), on the other.\(^{254}\) Both core chapters are framed with a summary (V. Zusammenfassung) and two introductory chapters which outline the topic and the research question, on the one hand (I. Einleitung und Fragestellung), and an analysis of the butterfly’s specific cryptic colouration (II. Färbung), on the other.\(^{255}\) Altogether, the entire organization of knowledge thus resembles the scheme H. Spencer had called *Special Synthesis* in his *Principles of Psychology* (1855) yet reveals also the particular Darwinian modifications. That means, like N. Tinbergen’s earlier paper about Thrushes and Blackbirds, *Die Balz des Samtfalters* evolves a theme by supplementing an introductory with an empirical part. The latter of which is also the prevailing section. For the sake of clarity I suggest the following illustration (Fig. 2.1). For my argumentative purpose it is important to realize that a scientific prose which structures the presented knowledge by differentiation at the foremost generates tri-
adic epistemic schemes. These patterns again are predestined research objects for examining the re-evaluations which seemed to mark the theoretical founding of Classical Ethology. Therefore, I suggest to go into detail at some promising points of the paper. My first anchor is related to Niko’s reasoning upon the Grayling’s camouflage colouration (chapter II. Coloration) which refers to a morphological rather than a behavioural character. From Gestalt theory we are familiar with the distinction between figure and ground which served Gestalt psychologists to illustrate the abrupt cognitive process we use to describe as “aha-experience” in our colloquial language. On closer inspection, the entire process refers to a transition from a state of mind where figure and ground are undistinguished into a state of mind where both phenomena appear separated and the figure stands out. The transition per definitionem is abrupt and thus discontinuous by itself. The notion of camouflage colouration, however, seems to undermine the clear cut scheme of perception underling the differentiation between figure and ground insofar as the underlying disruptive heuristic process is disturbed. And from an epistemic point of view one may eventually argue that the reason for this disturbance lies in the fact that the notion of indistinguishability (the essence of cryptic colouration) superimposes the disruption which is necessary to perceive the Gestalt of a figure. The result is a para-

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256 See to this the methodology part, section c), page 23, in the introduction of my thesis.
257 Ibid., 183–185.
dox epistemic frame: An object which exists independent from its environment yet may not be perceived as such because it is camouflaged. Further we may conclude:

That the notion of continuity has the power to superimpose the frame from beneath may lie in its upgraded epistemic value. As a reversal conclusion, then one may say that the reason for a topic such as cryptic colouration was popping up at all at a certain point of an intellectual life-history may be that a corresponding epistemic re-evaluation had occurred before which made it possible to think a figure like that in the first place. This is, in my opinion, the epistemological background of Niko’s reasoning about the Grayling’s camouflage. N. Tinbergen himself interprets the modified epistemic scheme underlying the entire theme of procrypsis in terms of its causal analysis and this includes both a detailed description of the body features and a consideration of the causes why the features contribute to the animal’s protection. “Sowohl die allgemeine Graufärbung”, Niko and his coauthors write, 


[Both the general grey colouration and the fine and course camouflage effect (Somatolysis) being evoked by the broken lines contribute to make the animal practically invisible for the human eye upon sandy ground, brownish moss, dried leaves as well as on the bark of a tree (Fig. 2). The behaviour fits to this cryptic colouration in many perspectives. In the state of rest the medianly upwardly folded up wings coincide as such that only their camouflaged parts are visible. The camouflage pattern, too, expands gradually over those parts of the forewing which is visible in a resting animal (see Fig. 1, 2). Furthermore, except during foraging and courting, the animal either moves very fast or not at all. Therefore it drops out of our visual field as soon it settles down somewhere. Many cryptically coloured grasshoppers reveal a similar kind of motion which is to be interpreted surely as cryptic adaptation. That the abrupt sitting still after rapid movements has really an effect for some predators which are searching prey with their eyes is shown by observations made by Lorenz (1927), whose jackdaws became repeatedly attracted by jumping grasshoppers but were not able to trace them once more after the leap. About the effect of cryptic colouration in Eumenis, however, there are existing no observations.][transl. CL]258

Second example. Chapter three (“III. Beschreibung des Verhaltens”) and four (“IV. Die Analyse der Balz”) together built an analytical scheme which, however, maintains the character of a life story, as well. Thus it is mainly chapter three which provides a broad and detailed description of the Grayling’s life cycle and, in doing

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so, gives a survey of the animal’s behaviour repertoire.\footnote{In the following, ibid., 185–198.} To this repertoire belong the sex-specific modalities of procreation (specificity of breeding places, earlier hatching of males), the various strategies in foraging (orientation by scent vs. optical orientation including sub-classification), the less or more drastic motions the Grayling displays during its sun-bathing and, finally, the reproductive behaviours of the butterfly including its courtship ceremony (quivering, fanning and antenna spinning, bowing and clasping) and the laying of the eggs. Altogether the account of the entire life cycle is primarily descriptive and places the behaviour in a linear and cyclic order (so to say, from the egg to the egg). Thus, from a methodological point of view chapter four (‘IV. Die Analyse der Balz’) establishes an interruption in comparison to the preceding one:\footnote{For chapter IV, see ibid., 198–225.} It appears strictly analytical insofar as it concentrates on one single behaviour of the overall life cycle mentioned before (namely the Grayling’s courtship) and, beyond that, treats this behaviour by applying an experimental discrimination procedure in order to find out the prevailing releasive features which establish the sexual bondage both from the side of the male (female releaser) and the side of the female (male releaser). My attention now is directed towards the relation between both chapters (III. and IV.). Certainly, they apply different methodological strategies and insofar they are disconnected. But, on the other hand, singling out “courtship” from the entire life cycle is incomplete insofar as the descriptive chapter three ends with the reproductive behaviours and chapter four, in stressing courtship, thus only perpetuates the linear order with other methodological means. As a result, both core chapters of Die Balz des Samtfalters thus reveal a paradox frame since the causal analysis of the Grayling’s courtship still appears embedded into the life cycle of the animal. The ecological stance, so to say, drowns out the causal analysis which therefore gains a prevailing ecological direction. And from an epistemological standpoint this can be interpreted as a result of upgrading the ecological and evolutionary aspects of behaviour research. Third example for a paradox holistic frame. Chapter four (‘IV. Die Analyse der Balz’) as a whole is analytical by itself, too. It asks in the first place which qualities make the female attractive to the male (‘IV. a. Die Anfliegereaktion des ‚♂‘’) and elaborates on the causes of the female’s readiness to mate in the second place (‘IV. b. Die Funktion des Duftfeldes’). While the former of the two subchapters concentrates on optical orientation of the male, the latter subchapter puts emphasis on the olfactory orientation of the female. The upgrading of the environmentalist aspect in chapter IV. a. becomes manifest in N. Tinbergen’s reassessment of the reflexological concept of “response” which may also be seen in the title of the subchapter. Niko and his co-workers had discovered that the Grayling male’s approach-flight response did not reveal all characteristic features of a spontaneous behaviour since it did not go off in vacuo and, beyond that, required necessarily an external trigger. “Wie gesagt, bewegt ein zu einem ‡ hinfliegendes ‖ sich in unverkennbarer Weise” he states and proceeds:

Die Flügelbewegungen sind hastiger, die Fluggeschwindigkeit ist größer und die zurückgelegte Bahn ist gerader als bei den anderen Handlungen, in welche Fliegen eingeschaltet ist, wie
The specific status of the behaviour thus had to be clarified. In *Die Balz des Samt-falters* Niko and his co-authors thus proceed in two steps. At first, they make clear that the male’s approach-flight behaviour is *not* a typical reflex action yet is based on central coordination. On the one hand, this could be seen in the fact that a male Grayling initially not only approaches females but, erroneously, also other males of the same species and, beyond that, specimens of other butterfly species. And although the entire reaction pattern can refine over time it is this liability to error which makes Niko and his co-workers conclude that the releasive mechanism underlying the behaviour may be simple. On the other hand, Niko’s experiments with free-living and captivated animals revealed that only a few of the qualities which were emitted by the releasing object and which can be potentially taken into account by the sensory capacities of the Grayling male, actually played a relevant role in the butterfly’s reaction-specific releasive schema. Amongst the qualities tested with dummies (Attrappenversuche) neither patterning, nor colouration, nor the shape of the dummy turned out to be discriminative.\(^{262}\) Only the size of the respective releasive object, its distance and the mode of its motion spring out in the releasive mechanism’s constitution. Furthermore, the experiments conducted by Niko and his co-authors revealed that the relevant features can substitute each other within the releasive mechanism. “Wir können also getrost auf Allgemeingültigkeit des Satzes schließen”, N. Tinbergen and his co-workers underline,

> [...] (transl. CL)\(^{261}\)

That means also, the Grayling Butterfly’s perception is spatial.\(^{264}\) Hence increasing size may compensate decreasing proximity and vice versa – yet in a manner N. Tinbergen was not able to detect fully.\(^{265}\) Both the fact that the number of possible sensory qualities becomes reduced by “psychic” means and the summative corre-latedness of the qualities subsumed in the reaction-specific releasing mechanism

\(^{261}\) Tinbergen et al., “Die Balz des Samt-falters”, 199. For the intention to compare the observed behaviour with a reflex action see also the introductory part *ibid.*, 183.

\(^{262}\) For the testing of the single parameters see, *ibid.*, 201–211, 225–226.

\(^{263}\) *Ibid.*, 212. For the summative character of the features see also, *ibid.*, 214–217.


\(^{265}\) See to this E. v. Holst’s later attempt to explain the Gestalt psychological principle of “Größenkonstanz” by his reafference principle.
brought Niko to the conclusion that the physiological entities being responsible for the qualities in question must be centrally coordinated. Niko therefore concludes: The releasive mechanism underlying the Grayling male’s approach-flight response is not based on a simple linear reflex arc nor on a combination of reflexes yet consists of an action pattern which is coordinated by the central regions of the nervous system. At the end of the paragraph in which he made an attempt proved the action-specific waning of the behaviour in question as a further indicator for its centrally coordinated character N. Tinbergen and his coauthors conclude:

As a result, the sexual approaching movement would not be a “pure reaction”. Instead there may be involved also inner, more or less specific factors, although they apparently never obtain any autocracy which is why we have never observed any vacuum response.

The paradox that the releasive mechanism in question is centrally coordinated although no vacuum reactions could be observed and, beyond that, an external stimulus is necessarily required triggered the second step in Niko’s argumentation, that is, the reassessment of the meaning of the response concept. In order to do that Niko and his coauthors, in the first place, draw the final conclusions of their experiments with respect of the entire nervous circuit’s physical constitution and thus came to the conclusion that the type of reaction they had observed cannot be identified with a pure reflex. “Die Koordination dieser ‘Merkmale’ ist rein summativ”, N. Tinbergen and his coauthors write in a concluding remark and proceed,

In the second place, rejecting the reflex as an adequate model led towards a process in course of which the concept of “reaction” is defined ultimately more positively. This “definition” is open and seems to keep being bound – so to say recursively –

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266 I speak of “psychic means” since the reduced perception of the Grayling is not a result of its limited sensory capacities. For instance, the Grayling isn’t colour-blind yet colour does not play a role in the releasive mechanism of the approach-flight!

267 Ibid., 213–214.

268 Ibid., 225. To illustrate the difference between reflex and reaction N. Tinbergen makes use of an illustration in Die Balz des Samtfalters he will also use in his paper An Objectivistic Study of the Innate Behaviour of Animals which I will analyze below. For the illustration see Fig. 2.3, page 130.
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the critique of the reflex-concept. Reflexologists so far had conceived a “reaction” or “response” as single reflex arcs or more complex combinations of reflex arcs. Niko questioned this understanding vehemently and from this critique we can infer, though in rather indirect ways, the qualities he intended to ascribe to a concept of “reaction” so that it fits to the type of behaviour he had observed in the Grayling’s approach-flight. The form of motion (Bewegungsform) should be a complex co-ordination rather than a simple contraction. The optimal releasive situation should be more like a Gestalt rather than a solely quantifiable stimulus. And, finally, a reaction requires a collecting and coordinating centre which connects the incoming with the outgoing parts of the nervous system in a complex, non-unilineal and holistic way.

From an epistemological point of view, one may eventually say that a model of the nervous circuit which is based on concentration in its afferent and extrapolation in its efferent leg was not a new idea since ethologists had changed the causal architecture in their modelling of the nervous system. What makes N. Tinbergen’s model characteristic for the advanced stage of scientific development he had entered since the late 1930s are the finer nuances. Thus both the fact that the type of reaction he was confronted with in the Grayling’s approach-flight did not occur in vacuo and that he tended to understand holistic integration in terms of summation seem to indicate a loss of epistemic value in those parts of his model which represented the more spontaneous constituents of the nervous system and which used to be the preferred target objects of ethological causal analysis. On the contrary, both that the approach-flight required an external trigger and Niko’s insistence on the complexity of the “Handlungsform”, indicate the great importance N. Tinbergen ascribed to those parts of his model which functioned as interfaces with the environment. To understand the topography of Niko’s conception of the nervous circuit it is of interest which of its regions he reckoned the domain of causal analysis. “Wir wissen”, he states,

daß an einer Reaktion drei Organsysteme unmittelbar beteiligt sind: Rezeptor, Nervensystem und Effektor. Wir sehen die Bewegungsweise, d.h. das Endergebnis der Wirksamkeit der Effekten. Unsere Analyse gibt uns weiter einige Einsicht in den Prozeß, der ganz am Anfang des Geschehens steht, der Reizung. Alles was sich zwischen Reizung und Bewegung abspielt, d.h. alle verwickelten Prozesse, die im Nervensystem vor sich gehen, sind uns verborgen. Das Endziel der ethologischen Kausalanalyse ist das Verstehen dieser ganzen Kette von Prozessen als ein kausales Geschehen.

[We know that there are involved three organic systems in a reaction. Receptor, nervous system and effector. We see the behaviour, that is, the final result of the effector’s effective activity. Our analysis provides some further insight into the process which is standing right at the beginning of the entire action, the excitation. Everything that happens in-between excitation and reaction, that is, the complex processes which happen inside the nervous system, are hidden from us. The final objective of the ethological causal analysis is to understand the entire chain of processes as a causal event.]271

The critical information of this quotation is, in my opinion, that it is the central

269 For Niko’s rejection of both traditional conceptions of reflex, see Tinbergen et al., “Die Balz des Samtalters”, 220.

270 For instance, in form of K. Lorenz’s “relativ ganzheitsunabhängigen Bausteinen”.

271 Ibid., 217–218.
parts of the entire nervous circuit which Niko defines as the domain of causal analysis, while the peripheral parts appear accessible by observation. In addition to that, Niko’s conception of the overall nervous system as black-box ascribes a great amount of “heuristic uncertainty” to the central parts of the nervous system whose primary concern allegedly used to be the reduction of complexity – quite independent whether this reductive concentration of information is thought erroneous or functional. In other words, the epistemic shift Niko’s reasoning underwent since ca. 1938 generated a revised physiological model of the nervous circuit which somewhat rated higher the “physical weight” of both the peripheral in comparison to the central parts and the motoric leg in comparison to the circuit’s afferent pathways. If I had to reconstruct Niko’s model of the nervous circuit graphically I would suggest the following roughly simplified illustration (Fig. 2.2).²⁷²

![Fig. 2.2](image)

N. Tinbergen’s Black-Box Model of the Nervous System

Altogether, Nikos’ intention apparently was to meet the reflexologists’ claim for a universalistic reflex concept with his own model of reaction or response. More than its strictly physiological counterpart Niko’s model put more emphasis on the division of labour between the receptoric and effectorial parts of the entire chain and, beyond that, envisaged the impact of the periphery as more overwhelming. To it put in more casual terms: To me it seems as if the complexity which used to be the domain of the peripheral sensory parts of the nervous circuit somewhat spills over into the central parts so that the reduction there turned out to be less drastic, complete or more “soft”. The fact that these parts are ascribed as the dark and unknown parts of the model confirm this view. In conclusion, it may be therefore assumed

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²⁷² *EP* stands for “efferent peripheral”, *AP* for “afferent peripheral”, *ac* for “afferent central” and *ec* for “efferent central” parts of the nervous system. The capitalization of the letters represents the epistemic value of the systemic position in the overall model. The “afferent leg” stands for the receptorpy part of the model, the “efferent leg” addresses the motoric part of the model. The relation between both parts is irreducible to a certain extent. The central parts are the domain of causal analysis, the peripheral parts represent the interfaces of the organism’s interaction with the outer world. Only the modes of this interaction are accessible through observation. The fact that Tinbergen distinguishes between an afferent and an efferent leg of the circuit entails that there are existing two separate types of nervous centre, too. For this dualism of the “collecting” and the “re-dispatching” (i.e. motoric) centre, see N. Tinbergen. “Physiologische Instinktforschung”. In: *Experientia* 4.4 (1948), 128.
that the epistemic re-evaluations in question opened Niko’s eyes not only for the cryptic colouration of animals but also for a sort of reaction which is characterized both by is summative coordination and the adaptiveness to arbitrary stimulation. If my readers could take for granted my reconstruction of N. Tinbergen’s understanding of a “collecting and re-dispatching” centre this would immediately raise the question where we have to locate the IRM in Niko’s model of the nervous circuit. Most likely this question cannot be answered definitely. I am inclined to solve this problem by placing the IRM in relatively lower areas of the more centralized parts of the afferent leg of the circuit.273 On the contrary, the highest levels of integration could be reserved for the more advanced releasing mechanisms which are based on gestalt-sensations.274 The efferent leg of the model and in particular its peripheral section then would represent the visible parts of the action patterns. An action pattern with highly elaborated motor co-ordinations would, for instance, be K. Lorenz’s “Auslöser”, that is, the signal movements or, following N. Tinbergen’s inclination to take into account the more complex nature of the key stimuli, the “optimal releasing situation” and their concatenations. Chapter IV. b. (Die Funktion des Duftfeldes) finalizes Niko’s analytical engagement to isolate the crucial set of stimulation being responsible for the Grayling’s sexual pairing.275 The emphasis in this chapter switches from the male to the female which provides the stimuli for the male’s response. Chapters IV. a. and IV. b. are therefore correlated and the question is raised whether the latter of the two chapters is not to be read as an attempt to determine more precisely which releasive situations might correspond with the different constituents in the male’s IRM, namely the more spontaneous and releasive component, on the one hand, and the adaptive need of an external trigger, on the other. The scent area thereby refers (paradoxically) to a morphological structure located on the wing of the male Grayling Butterfly which is capable to extract and spread chemical stimuli which, thus was Niko’s hypothesis, make the male attractive for the female and, beyond that, increases the readiness of the female to mate.276 Asides a very detailed description of the organ itself and its function during courtship, the way Niko took into account the meaning of the scent area was based on a physical experiment insofar as he neutralized the organ in order to determine its biological sense. Thus Niko sealed

273 According to N. Tinbergen’s later account in The Study of Instinct, at least the process of heterogeneous summation, which is said to be an integral part of the IRM, takes place at the fringes of the nervous centre(s) or – at the very least – “before the impulses reach the motor centre”, as Niko puts it. See N. Tinbergen. The Study of Instinct. Oxford: Clarendon Press, 1951, 81.

274 Over time, ethologist have distinguished various types of releasing mechanism (RM): The innate releasing mechanisms (IRM) are the ones which respond to simple and concise sign stimuli. They integrate incoming stimuli in a stereotypic often summative way. So-called IRMEs are innate releasing mechanisms which have been modified by experiences. So-called acquired releasing mechanisms (ARM) can be modified by learning. All RMs thus vary in grade and type of modifiability. For the definitions see Schleidt, “Die historische Entwicklung”, especially 716–721. The implication therefore eventually would be: The more receptive a releasing mechanism is the more central its mechanism of coordination. A summative mechanism thus would operate on a relatively lower level of integration than an acquired releasing mechanism.


276 The scent area is marked by a black coloured edge on the wings of the upper left butterfly of “Abb. 1”. See ibid., 184.
the scent area with “Lackfarbe” in one group of male animals and treated another area of the wing in the same way in another group of male specimens which served as a control group. Then he compared the reactions of the female specimens to both the de-scented and the non-de-scented animals and found out that copulation rates with males having intact scent areas were significantly higher. The extirpation experiment had proved the sexual function of the scent area. Again the epistemic re-evaluation seemed to have an effect – this time upon the extirpation experiment insofar as the experimental exclusion of a character was applied in service of the attempt to evince the probability of the scent areas’ effectiveness. As a result, of the causal reconfiguration which occurred in course of establishing the Ethological Synthesis, Ethologists more and more were inclined to take into account the dysfunctional behaviours particularly in their taxonomic studies. These behaviours usually were made evident in so-called deprivation experiments. Niko and his co-workers seem to have questioned the exclusive connection between the analytical method of deprivation, on the one hand, and the tendency to focus on dysfunctional behaviours, on the other. Despite the fact that Niko’s way of taking into account the biological meaning of the male Grayling Butterfly’s scent area in the last consequence is based on a deprivation as well, the question of function, nonetheless, seemed to have an overwhelming influence on Niko’s understanding of the female’s receptiveness. The overtone of the epistemic scheme underlying Niko’s deprivation experiments is therefore paradox: In all, it is proximate (experimental intervention) but somewhat superimposed by the initial and guiding idea of ultimate causation (here of adaptiveness). The same applies to the sexes of the proband animals: Although chapter IV. b. seems to focus on the receptiveness of the females for the male’s scents, the effect of the latter, although it is to be thought logically primary, seems to be prevailing or overwhelming.

To sum up my reading of Die Balz des Samtfalters, one may say that it is particularly the more analytical areas of the whole knowledge organization which make evident the effects of the re-evaluation of epistemic schemes which was characteristic for Niko’s and other ethologists’ theorizing since the end of the 1930s. The revised interaction between figure and ground which becomes evident in N. Tinbergen’s interest in cryptic colouration, the embedding of his causal analysis of the Grayling’s courtship within a life cycle study, the redefinition of central coordination as summation, the reassessment of the reflexological response concept and, finally, the use of neutralizing experiments for questions related to the function of the behaviours – all these aspects reveal modified epistemic hierarchies. In addition to that, Niko’s assessment of the Grayling’s courtship behaviour turns out as another example in which recursively applied bifurcation led to a more modified concept (here the IRM) in as much as Tinbergen and his co-workers supplemented the spontaneous constituent of the IRM with a theorem referring to the adaptive responsiveness of the mechanism which, in terms of Niko’s reasoning in complementary realms, was to say that Lorenz’s releaser might address a form of ad hoc physical excitation as well.

My methodological concept of scientific orientation implies that the scientific position of a researcher at a given point of time in his life is not necessarily a uni-
form entity. In so far it is legitimate to ask whether the epistemic re-evaluation Niko’s theorizing on animal behaviour revealed since about 1938 also affected those epistemic schemes which had been covered so far by his studies on orientation and homing. One of the most appropriate historical sources to clarify this hypothesis may be *An Objectivistic Study of the Innate Behaviour of Animals* – a theoretical inventory of ethological research up to the year 1942 when the text was published.  

From a strictly epistemological point of view, N. Tinbergen’s understanding of *causal analysis* resembles – at least to a certain extent – the reductive schemes that can be found in H. Spencer’s *Special Analysis*, W. James’ pragmatist approach to nervous centralization or K. Lorenz’s Gestalt theoretical interpretation of instinctive action patterns. However, there are crucial differences as well. Therefore, it seems advisable to have a closer look at the discrimination process which is implied in ethological causal analysis in the first place. After that, I will analyze more detailed those additional modifications which make Niko’s interpretation of causal analysis specific. The reductive scheme underlying Niko’s conception of causal analysis becomes manifest on various different occasions in *An Objectivistic Study*. One of these contexts is chapter two “The description of specific behaviour patterns” where Niko formulates three methodological rules (“demands”) to be observed in every causal analysis. These are: (a) The claim for an increasingly broad basis of information, (b) the consideration of the entire behavioural repertoire of an animal and, finally, (c) the demand for comparing the behaviour of various different species. The first of the three demands refers to the empirical data basis at the outset of the analytical process. According to N. Tinbergen’s account, this data is descriptive and its scope is a *function* of the current state of analysis: The more an analysis proceeds the more refinement of the initial description is requested. The second demand puts emphasis onto the necessity of taking into account the whole animal. It avoids undue scientific controversies which may originate when researchers make isolated aspects of the entire behaviour repertoire the sole basis for their conclusions and therefore produce too early generalizations. The final demand underlines the importance of comparing the behaviour patterns of a large number of animal species. In Niko’s view, comparison prevents from undue generalization and enhances “the establishment of general rules preparatory to analysis”. It is therefore pitted against reflexological and behaviourist theories of central nervous integration which had applied the question for the causes exclusively to linear types of response and less, as ethologists claim, to more complex networks of mutual innervation. Moreover, the centrally coordinated behaviours ethologists take into account by their species-specific com-

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278 Ibid., 43.
279 Ibid., 43–45.
280 Ibid., 45.
281 Ibid., 45–49.
282 As an example of a “more or less sterile controversy” of this kind N. Tinbergen mentions here the one between K. v. Frisch and C. v. Hess about the question whether or not bees can discriminate colours (Ibid.).
283 Ibid., 45.
comparisons generate homologies of behaviours which, for their part, may serve for
taxonomic concerns. Behaviour thus becomes an object of systematics which de-
mands both the method of comparison and the right material (i.e. the stereotyped
 coordinations in K. Lorenz’s sense). The second and third demand thus operate
with forms of holistic concepts. But the claim for comparison thereby takes a meta-
tatus since it encompasses and multiplies the entire analytical course. Moreover, in
Niko’s view, this course has a direction insofar as it proceeds from the whole to
the part. The whole thereby seems to stand for a continuum of undifferentiated
information, while the part refers to the final stage of each analysis – the confirmed
information. In order to illustrate this process more detailed it seems advisable to
discuss chapter three, “The causal analysis of innate behaviour”, not only because
it is dedicated to causal analysis explicitly, but also it puts on stage the discrimina-
tive procedure on a performative level of the account. Its general motivation may
be described as the claim to isolate – N. Tinbergen also says “to dissect” – the
static constituents of an animal’s behaviour repertoire. On an abstract level the
chapter therefore operates with the distinction of variable and invariable we are
already familiar with from K. Lorenz’s concept of instinct-conditioning intercala-
tion. Yet Niko’s account goes beyond Lorenz’s insofar as it applies the dichotomy
in the following only to one side – the static part of the dichotomy. If this proce-
dure is repeated several times the result will be a recursive heuristic model which
on various levels generates ever finer distinctions. “The process of digging into the
complicated phenomena constituting ‘behaviour’”, in Niko’s view this means, “of
breaking it up into smaller and even smaller units, and of finally recognising the
whole as a special case of coordination of such simple units, naturally has to be car-
ried on until the next lower plane of phenomena is reached”. If applied to his own
textual analysis, on level one (“III. a. Introductory”), we may detect the distinction
between the whole and the part as the prevailing heuristic scheme of Niko’s argu-
mentation. “Therefore”, he argues, “this first step in causal analysis will result
in a splitting up of the behaviour as a whole into its components, each component
being characterised by its own particular causal conditions”. On level two (“III.
b. Internal and external causal factors”) the dichotomy between external and less
or more purely endogenous forms of stimulation is pushed forward. The relation
between internal and external factors thereby is conceived as “compensatory”.
That means both parameters are thought complementary: Strong external factors in
combination with weak internal ones may lead to the same response as weak exter-
nal stimulation in combination with a vigorous internal impulse. The sum total of

284 N. Tinbergen writes: “Like homologisation in Morphology, ethological homologisation leads to
classification and systematics”. See ibid., 48.
285 Ibid., 49.
286 For Niko’s use of the terms “dissect” or “dissection”, see ibid., 44.
287 Ibid.
288 Ibid., 49–50.
289 Ibid., 50.
290 In fact the subchapter in question reveals a procedure of exclusion. Step by step, N. Tinbergen
discriminates purely external, hormonal, and proprioceptive factors only to carve out central
nervous excitation as the one parameter his further analysis will rest upon. “The work of von
Holst (1936)”, Niko concludes, “does not leave the least doubt as to the existence of springs of
impulses within the central nervous system itself”. See ibid., 50–54, 53 for the quote.
nervous energy involved seems to remain constant – a confirmation of the law of the conservation of energy. On level three (“III. c. The hierarchy of special causal factors”) the dichotomy between the ever more sophisticated hierarchy of moods, on the one hand, and the instinctive action pattern itself, on the other, structures the argumentation:291 Some factors may not release simple reactions directly yet serve as an impulse which transfers the animal into a state making it ready for a number of various different activities. In this case N. Tinbergen says the animal is brought into a “mood”, e.g. a reproductive mood which encompasses a whole system of preparatory ritual behaviours. In particular, N. Tinbergen’s own studies of the ‘Three-spined Stickleback’’s courtship ritual and G. P. Baerends’ application of a tree-like model for the hierarchical relations existing between drives and their sub-drives here serve as a broad basis of reference data. Moreover, Niko insists that each species has its own system of functional behaviours so that, contrary to W. McDougall’s intention, no all-encompassing generalization seems possible. Level four (“III. d. Striving and satisfaction”) refers to the structure of simple instinctive action patterns and therefore recapitulates K. Lorenz’s distinction between appetite (the directive moment) and final action (the end of an action pattern providing satisfaction, even it goes of in vacuo).292 The appetite thereby seems to have a stronger functional potential since it directs the instinctive action pattern to its end and, beyond that, lets appear the entire action pattern “directive” as well. “Whenever an animal employs different means to attain one and the same goal” – Niko writes –

we have to do with purposive or directive behaviour. Our implication of a “goal” is based on the fact that the animal continues its searching until the goal is reached, unless the animal gets exhausted. The attainment of the goal is an event which marks the end of the variable purposive behaviour and causes the stereotyped activity to go off. The behaviour as a whole, therefore, comprising the directive elements preceding the stereotyped movements, appears to be directive.293

The strong emphasis of the purposiveness of an instinctive action pattern as a whole which ought to be subject of causal analysis in the first place creates a paradox epistemic constellation. The fact, that this paradox affects primarily the entire frame, however, seems to be an indicator that the epistemic value of the ultimate expressions of causality might have changed in comparison to earlier accounts of K. Lorenz and W. Craig. Another indicator pointing into the same direction may be that N. Tinbergen, following his pupil G. P. Baerends, takes into account not only the appetences which lead to a consummatory act but also those appetences releasing additional secondary appetences so that the concept of appetite is multiplied similar to the hierarchization of moods. “Appetitive behaviour, therefore”, N. Tinbergen concludes, “may belong to a secondary drive as well as to a major drive, and the same considerations that led to the assumption of a hierarchic system of drives, apply to the appetitive behaviour as well”.294 Level five of Niko’s analytical procedure (“III. e. The analysis of the stereotyped movements”) enters into the structure of the final action by putting into the foreground the question whether the stereotyped ac-

292 Ibid., 59–62.
293 Ibid., 59–60.
294 Ibid., 61.
tion patterns are just “a special combination or coordination of muscle contractions of a simpler kind” (the physiologist’s standpoint) or, on the contrary, a “rather new, hitherto unknown type of contraction” (the psychologist’s view).\(^{295}\) Niko’s own stance combines both extreme positions not only in the sense of an intermediate orientation but also by prevailing one side each on the various levels of the part of his scientific paradigm which underlies his understanding of causal analysis, that is, spontaneity with respect of variability and proximate causality with respect of causal reasoning. This leads to the specific ethological model of the nervous circuit which reduces complexity in direction of the centre of the nervous system (afferent part of the circuit) and presumes amplification as to the paths leading from the centre to the periphery (efferent part). Especially the afferent arc of the nervous circuit thereby seems to be the primary subject of causal analysis. Thus Niko points out that the releasing system of central coordinations by no means appears as entirely uniform entity yet may encompass a chain of several preparatory reactions preceding the final act or accompanying it, as it was the case in N. Tinbergen’s and K. Lorenz’s study about the intercalation of taxis and instinct in the egg-rolling movement of the Greylag Goose.\(^{296}\) Moreover, in Tinbergen’s view, it is the “Erbkoordination” which is connected with a specific (psychic) “releasive mechanism” which filters and bundles up those stimulation which is relevant for exhibiting the reaction.\(^{297}\) The holistic character of this integration again is the argument for Tinbergen to claim that instinctive action patterns are not based on combinations of reflexes. “To sum up our knowledge about the ‘Erbkoordination’, that is, the simplest unit of behaviour arrived at by our method of breaking behaviour up into successively linked elements”, Niko summarizes and continues:

The stimulus cannot be characterised as a certain amount of energy, but is a complex, an organised whole, of “Merkmale” or recognition marks. These recognition marks can mutually compensate each other. Somewhere in the central system, therefore, their influence must be brought together, must be collected into one channel. Yet another fact points to this very same conclusion: if one factor or another is left out, the result is a weakening of the response as a whole, and not the omission of certain parts of the reaction, each connected with its own releasive factor. This proves that we have to do, not with bundles of nerve fibres each connecting a part of the receptorial field with a part of the muscle fibres, but with a central station that collects the impulses and redispaches them as a whole. This dispatch, again, is not a very simple bundle of impulses, but as we have seen, a coordinated system, resulting, not in one muscle contraction, but in a complex of coordinated contractions.\(^{298}\)

In order to illustrate the differences between his centralized and the unilinear (reflexological) model of the nervous circuit, N. Tinbergen introduces two graphics.

\(^{295}\) Ibid., 62–77, here 62.
\(^{296}\) Ibid., 65–66. It is of some interest that N. Tinbergen in contrast to K. Lorenz seems to conceive both behavioural constituents, that is, the taxis, on the one hand, and the “Erbkoordination”, on the other, not as entirely discontinuous – eventually a further indicator for the upgraded epistemic status of the continuous forms of variability. For Lorenz’s study of the Greylag Goose’s habit to roll back eggs to the nest which he had examined together with N. Tinbergen in 1937 see K. Lorenz. “Taxis und Instinkthandlung in der Eirollbewegung der Graugans”. In: Idem. Über tierisches und menschliches Verhalten. Aus dem Werdegang der Verhaltenslehre. Gesammelte Abhandlungen. Vol. 1. (Piper paperback). München: Piper, 1965 [1938], 343–379.
\(^{298}\) Ibid., 71–72.
I have added an epistemologically reinterpreted version of N. Tinbergen’s illustrations in my thesis (see the following Fig. 2.3) in order to make more comprehensive the connection between Tinbergen’s illustrations and my own reconstruction of his understanding of the nervous circuit (as outlined in Fig. 2.2, page 123 of my thesis). I suggest to interpret both figures as “input-output models” with their own chronological order. That is, according to Tinbergen’s understanding, the nervous circuit in both behaviour models starts with the receptors and ends with the effectors, the muscles and their activity. Yet, while in figure A the incoming fibres do not bundle up in one single instance and the central parts of the nervous system thus must remain multiple, in figure B – the model favoured by Tinbergen – central nervous integration appears as holistic process. The domain of causal analysis thereby seems to be primarily the receptory part of the circuit. Furthermore, both peripheral ends of the model branch in multiple paths which may also stand for the diversity of sensory impacts. In sum, we may say that Niko’s exclusion procedure also summarizes the scientific development of Ethology, that is, the various stages of discrimination which finally determine a specific scientific object: The web-like nervous structure of the “Erbkoordination”. It therefore is no surprise that Niko ends chapter three with a general remark about the relation between psychology and physiology and how he himself positions his causal analysis (including its characteristic scientific object) within the field of the behaviour sciences – eventually

Fig. 2.3

Nervous Circuit of the “Erbkoordination” (epistemologically reinterpreted version of N. Tinbergen’s illustration). N. Tinbergen describes the receptive part of the circuit concretely as “reception” (A) and “configurational reception with ‘reception marks’” (B). The efferent leg of the circuit is conceived in terms of “muscle contractions”. In case of figure B Tinbergen speaks of “coordinated muscle contractions”.

299 For Tinbergen’s original illustration see Tinbergen, “An Objective Study”, 71.
also the topic of the entire paper (“III. f. Some interrelationships between causal chains”). The scheme of the entire analysis therefore is reductive and based on recursive differentiation of primarily one side of the dichotomy. What does it make characteristic for the stage of Niko’s scientific development he reached since the late 1930s are two aspects. On the one hand, there is the reverse causal architecture which is characteristic both for neo-Darwinians and ethologists. For instance, the descriptions initial to each causal analysis are functional (i.e observational) whilst the final stage of their analysis idealiter consists in reconstructing the causal web underlying the stereotyped behaviours.300 “In the following”, Niko introduces his account on causal analysis,

I will try to give a schematical review of the general method of analysis of the innate behaviour patterns, taking behaviour as a whole as a starting point and then digging down into the causal structure of its constituting components. The “Leitmotiv” for this study will simply be the consistent application of the question “Why does the animal behave as it does?” or, to put the same question in sharper terms: “What are the causes of its movements”?301

Moreover, as we have seen, the appetences are directive as well, while the consummatory acts may be non-functional insofar as they can go off in vacuo or, at least, in inappropriate situations.302 In any case, they stand for a sensual quality which makes the organism experience satisfaction. In addition to that, N. Tinbergen underlines that it is the taxis which is directed not the “Erbkoordination”.303 One the other hand, however, there is also a fundamental turnover of epistemic hierarchies. Several aspects seem to make evident the latter aspect. At first, the fact that causal analysis is a recursive process reveals the repetitive nature and therefore the prevalence of a quantitative nuance. And, most interestingly, it seems to be the recursive or repetitive nature of Tinbergen’s differentiation which allowed Ethology to integrate the numerous themes and theorems into one single heuristic entity. In other words, Tinbergen’s recursive understanding of causal analysis made an essential contribution to the establishment of the Ethological Synthesis at the end of the 1930s and it would be of great interest to find out whether these re-evaluations of epistemic reference systems can be made evident in epistemic communities other than the one I am examining right now. Second, the same applies to N. Tinbergen’s strong emphasis of the descriptive data basis to be generated at the beginning of each analytical procedure. In Niko’s view the initial descriptive part of causal analysis must even become more refined (i.e. particulate) the deeper the analysis proceeds. Third, the relatively high weight Niko ascribes to the hierarchization of instincts fulfil this program on a deeper lying level and so does the multiplication of appetences or of the action chains preceding the so-called “Erbkoordination”. And, last but not least, the placement of causal analysis within the order or the entire text reveals that in Niko’s understanding causal analysis is part of the empirical research which is logically independent from the final conclusions to be drawn. Re-evaluations do not only affect the level of “variability” but also the causal dimension of behaviour. Thus it is rather obvious that although the entire frame of

300 On Niko’s use of the web-metaphor, see ibid., 50.
301 Ibid., 49–50.
302 See to K. Lorenz’s “Leerlaufreaktion”, ibid., 64–65.
303 Ibid., 72.
Niko’s text is coined by the theme of “proximate causes”, N. Tinbergen’s conception of causal analysis not only encompasses the question of function but, beyond that, puts a special emphasis upon it insofar as Tinbergen defines function in terms of evolutionary fitness. “Generally”, he says, therefore, any effect of a life-process, contributing to the preservation and the promotion of the species, will be called its function. This concept, therefore, is about identical with such concepts as “biological value”, “meaning”, “objective end”, etc. terms which are very often quite loosely applied.\footnote{Tinbergen, “An Objectivistic Study”, 84.}

The paradox status the causal architecture of the entire scheme therefore takes becomes evident also in the fact that adaptation overwhelms causation but the organism is neither aware of the effect of its behaviours nor is the function actually governing the animal’s activities.\footnote{Ibid.} Adaptation thus seems to superimpose the entire causal analysis from a subordinate position. A further indicator pointing into the same direction is that, according to N. Tinbergen’s account, many phenomena of life are secured by more than one mechanism so that dropouts may be of disadvantage yet not deadly.\footnote{Ibid., 85–86.} Moreover, signals, in Niko’s view, do not only have the function to release (trigger or cause) but also to guide a corresponding action or bring a companion into a certain mood.\footnote{Ibid., 88–89.} The entire action pattern thus turns out to be less rigid, eventually more dependent on repeated stimulation and, as it seems the case in incipient movements and substitute activities, more emancipated from the overall drive.\footnote{Ibid., 89–91.} Altogether the re-evaluation of epistemic patterns thus seems to generate a new research field: The signal movements. These movements very often rest upon older instinctive structures yet are transformed into something new by re-organization and succeeding ritualization. Insofar they are variable invariants. (\(R_1\)) My primary focus upon the more conservative levels of scientific change suggests that the epistemic development which led to the founding of Classical Ethology reached a provisional zenith already at the end of the 1930s. The following period until the end of the 1950s was primarily characterized by the consolidation of the newly founded discipline. As a result, sciences historians are confronted with the phenomenon that the fundamental convictions remained more or less constant over a longer period of ca. twenty years although the protagonists were subject to essential biographical, societal and political changes. The following paragraphs are therefore more concerned with the question how the expressions of the scientific position N. Tinbergen had noticeably adopted since his visit of the United States changed over the years. The year 1942 thereby surely takes a prominent position in Niko’s biography – in a negative sense.\footnote{For the biographical details see, Kruuk, Niko’s Nature, 114–128.} After the National Socialists had occupied the Netherlands in 1940 they made efforts to implement both their doctrines and their political practices in the annexed territories. As a result of their increasingly restrictive policy, in 1942 Jewish employees of Dutch Universities were forbidden to pursue their profession. A group of professors and lecturers amongst
Niko Tinbergen (1907–1988)

whom was also N. Tinbergen protested and, as a result of their reaction, the university was shut down. After several acts of resistance 460 Dutchmen who used to be part of public life and presumed to be sympathizers of the resistance movement were arrested and taken as hostages, threatened to be shot if the acts of sabotage didn’t stop. Tinbergen who covered the position of a university lecturer at that time, was picked up on the 9th of September and brought to Beekvliet, a prison camp some 100 kilometres away from Leiden. Although the hostages of the camp were not entirely deprived from any intellectual activity his internment is the main reason why N. Tinbergen’s research activities were restricted to a certain extent till his release after two years at the end of the year 1944. However, despite all restrictions he was able to write a small book of 184 pages which, later in 1946, was published in a semi-popular science series under the title “Introduction to Animal Sociology” (Inleiding tot de diersociologie).  

Next to Introduction to Animal Sociology Niko wrote also some small books for his children in which he took a child’s perspective and described the world as he imagined it to be from behind the barbed wire, that is, idealized, seen through a child’s eye, and “as he felt his children wanted to see it” – as H. Kruuk put it. Klieuw tells the story of a Herring Gull’s life cycle. The young Gull hatches, grows up on a Dutch beach where it builds a nest and rears young by itself. Thereby the bird is watched by a certain Mr. Tinbergen from a hide. The story therefore has the character of a fable, an impression which becomes even stronger by the fact that Niko named Klieuw’s chicks after his own children (Jaap, Toos, and Dik). The inner structure of the plot thus is remarkable: It begins with the Gull’s growth and ends with its own procreation. Both poles of the tale are connected by a third position, the observer, whose relationship to Klieuw is somewhat tautological insofar as Klieuw also stands for Mr. Tinbergen. The entire scheme seems to coincide with Niko’s actual situation. What his growing kids could relate to is only a story substitute of their father. This relationship is physically interrupted due to Niko’s internment. But the logic of the story also seems to be that the disconnection both parts of the family are subject to is incomplete – one may eventually say – due to the overwhelming (i.e. also overwhelming the observer N. Tinbergen) power of a child’s fantasy, its desires and also the “naive” language to express all this. I think it is not too far-fetched to say that it is this superposition which makes the observer position a paradox construction, that is, a fully rational human being with a childish way to see the things. The Tale of John Stickle (Het verhaal van Jan Stekel) is an illustrated life-history of the Stickleback and was published later in 1952 as a picture book for children between seven and eleven years. The other booklets Niko wrote while he was imprisoned in St. Michielsgestel remained unpublished such as History of the Drew Drop, The Old Oak Beam or The Sand Book the latter of which Niko had written for his daughter Catrina on the occasion of her birthday. Although


311 Kruuk, Niko’s Nature, 120.


the information we can draw from the accounts Niko produced between 1942 and 1944 are limited we may eventually infer that the specific way of ordering things and putting them into a relation with each other did not change fundamentally in comparison to his scientific texts written before his internment. More likely is, that Niko’s popular book on animal sociology, on the one hand, and his children stories, on the other, can be read as translations of the re-evaluated epistemic schemes into the respective medium – a matter of fact which does not diminishes their emotional value.

\((R_2)\) War-time experiences had a substantial effect on N. Tinbergen’s personality – in particular, however, on the way how he re-evaluated the relationships to other members of his scientific communities especially those who were implicated with the NS-regime.\(^{314}\) At the foremost this affected the relationship to his friend K. Lorenz (and also O. Koehler) but also the German science scene in general from which Niko detached more and more in the years after the war although the personal wounds healed to a certain extent. While K. Lorenz in his later autobiographical account emphasized the triumph of their friendship, we know now that Niko sensed the relationship to his German colleagues much more ambiguously.\(^{315}\) And the reason why these tensions did not lead to an immediate fundamental epistemic re-orientation may be – at least in my opinion – that the re-evaluated epistemic construction of Classical Ethology itself in one essential part provided a scheme to grasp the situation adequately: Applied to ethnologists’ mutual relationship that is, an interruption which is overwhelmed by sympathetic emotions. In other words, I presume that the epistemic deep-structure which partly generated the foundation of Classical Ethology also provided the epistemic practices to “handle the situation”\(^{316}\).

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\(^{316}\) Science historians usually tend to mark the (self-imposed) international *isolation* of German researchers before and after the Second World War which, according to their view, could be surpassed not before the end of the 1950s. For instance, see U. Wegenroth. “Die Flucht in den Käfig: Wissenschafts- und Innovationskultur in Deutschland 1900-1960”. In: R. Bruch et al., eds. *Wissenschaften und Wissenschaftspolitik. Bestandsaufnahme und Formationen, Brüche und Kontinuitäten im Deutschland des 20. Stuttgart: Steiner, 2002*, especially, 53–54, 55. The community of ethologists does not fully fit into this scheme. Other examples to prove the opposite may be E. Stresemann’s early contacts to British and American Museums, E. Mayr’s career, as well J. Huxley’s and J. B. S. Haldane’s early contact to K. Lorenz soon after 1945 and the attempt to win the latter for a position in Britain. The peculiar thing thereby is that several of these scientists belonged to the group of scholars which established the Modern Synthesis of Evolution or were ethologists. For a historical reconstruction of the correspondences related to the attempt to win K. Lorenz for a position in Britain see Chavot, “Histoire de l’ethologie”, 234–253 and with a more elaborate view upon the motives of those interested persons Chavot, *Elements d’Histoire de l’Ethologie en France*, 1–2. The “international dimension” of the so-called Modern Synthesis has been particularly stressed by T. Junker et al. “Einleitung”. In: Idem, ed. *Die Entstehung der Synthetischen Theorie in Deutschland. Beiträge zur Geschichte der Evolutionsbiologie 1930-1950*. (Verhandlungen zur Geschichte und Theorie der Biologie 2). Berlin: VWB – Verlag für Wissenschaft und Bildung, 1999, 10–11.
Next to the demand to cope with the war-time impressions stood the intention to re-build a normal life.\textsuperscript{317} This included Niko’s own research and teaching activities but also the ways to spread the results of ethological research attained so far both by himself and by others. Furthermore, it is no surprise that N. Tinbergen interpreted “doing normal research” primarily in terms of cultivating social relationships. H. Kruuk mentions in his biography that Niko’s social interpretation of research, to a certain extent, was at the expenses of his family relationships.\textsuperscript{318} Moreover, Niko exhausted himself with more and even more work. Both aspects together made him take over the editorship of \textit{Ardea}, the national scientific bird journal, and of \textit{De Levende Natuur}, a popular monthly magazine, which had been edited by J. Thijssen who had died in the so-called “hunger winter” of 1944 / 1945. In addition to that, in 1947, N. Tinbergen founded an international journal for ethological research he simply termed “\textit{Behaviour}”.\textsuperscript{319} \textit{Behaviour} was edited in English language and was meant to replace (at least to supplement) O. Koehler’s and K. Lorenz’s \textit{Zeitschrift für Tierpsychologie} which had been suspended in the years between 1944 and 1948. Although several researchers refused to join the editorial board (J. Huxley and D. Lack), Niko finally managed to establish a veritable group of editors consisting of the Fin P. Palmgren, the Swiss H. Hediger, W. H. Thorpe from Cambridge, the Americans H. Carpenter and F. A. Beach, as well as O. Koehler who had made a new start at the University of Freiburg in Baden.\textsuperscript{320} When N. Tinbergen left Leiden in order to move to Oxford in 1949 his pupil G. P. Baerends became the managing editor of the journal which he continued to be for almost forty years. During that time \textit{Behaviour} became the leading international journal in the field of animal behaviour studies. As a provisional result, one may eventually say that the way Niko rose Ethology from its ashes was marked by deeper lying convictions which guided also his own epistemic practices. To this convictions belonged at the foremost the intention to build an international scientific community of ethologists. These researchers should be able to cooperate, communicate and spread their results in an adequate publication organ. And finally, Niko celebrated self-exhaustive hard work to achieve his objectives. His popularity as researcher and teacher raised the interest of other universities – the University of Groningen offered a chair in Zoology in 1946 and so did the University of Cairo.\textsuperscript{321} As a result, his home University reacted and Niko was appointed full Professor for Experimental Zoology in 1947 – with a generous budget, two research assistants, a caretaker for his animals, a secretary, a cleaner and a technician. It is quite interesting that Niko, soon after his


\textsuperscript{318} See ibid., 130.

\textsuperscript{319} Niko’s motives to establish a new journal for animal behaviour studies (problems with re-establishing the German \textit{ZfT} and the need of an \textit{international} journal) can be inferred from letters he wrote to G. Kramer and D. Lack. See MPG-Archives, \textsc{III. HA, Rep. 77}, file 1, letter N. Tinbergen to G. Kramer (16/06/1946) and Edward Grey Institute, Alexander Library, University of Oxford [quoted as: EGI Alex. Lib.]. David Lack Papers [quoted as: D. Lack Papers], XIX. Correspondence, file 403, letter N. Tinbergen to D. Lack (11/10/1945).

\textsuperscript{320} The question of potential editors is discussed in letters N. Tinbergen exchanged with D. Lack and W. H. Thorpe. See ibid., XIX. Correspondence, file 403, letter N. Tinbergen to D. Lack (19/11/1945) and ibid., XIX. Correspondence, file 403, letter W. H. Thorpe \textsuperscript{[?]CL} to N. Tinbergen (01/12/1945).

\textsuperscript{321} Niko declined but suggested G. P. Baerends for the post in Groningen who accepted.
appointment, took efforts to decrease the exam load for the students and suggested a smaller lecturing program. This benefited the lecturers but also should give the students more time to read enough by themselves. In other words, education, in Niko’s view, should become more effective and proceed more from the bottom to the top and less vice versa. The internationalization of his discipline, popularizing knowledge and the establishing of a less doctrinaire education system thus were the leitmotifs of N. Tinbergen’s own scientific practices shortly after 1945. In conclusion, I think N. Tinbergen’s life-history in the early post-war period may serve as a good example to prove my hypothesis that epistemic dispositions may not only rule the cognitive output of a researcher, for instance the way she or he orders and presents knowledge, but also affects a researcher’s own behaviours. In this special case of N. Tinbergen’s life-history we may even go so far and say that science and life built a unity. On the one hand, Niko both experienced a substantial break in the relation to his German colleagues and felt overwhelming sympathetic emotions especially for his friend K. Lorenz. On the other hand, he was about to realize the vision of an expanding, international, and cooperative branch of animal behaviour research. In both cases epistemic practices characteristic for Niko’s scientific orientation created the environment in which his research (and life) took place. What about his research? So far I have analyzed N. Tinbergen’s writings through several phases of his life-history and I did that along two major lines: One train of research put a great deal of emphasis upon the reproductive behaviours and thereby mainly contributed to what K. Lorenz called “special phylogeny of releaser”. The other line started with Niko’s interest in orientation and finally culminated in the recursive theoretical model of causal analysis he had introduced in *An Objectivistic Study of the Innate Behaviour of Animals*. That was in 1942. In the following paragraphs I will show that N. Tinbergen resumed both lines of ethological research after the Second World War. In particular, I will ask for the specific expressions both parts of the Ethological Synthesis took between 1944 and 1949, Niko’s post-war years at Leiden University.

(R1) Cooperative research projects with students 1944–1948. According to Hans Kruuk, Niko did not spark off new empirical research projects for himself during that period but tended to perform the projects in cooperation with his students including the undergraduates.\(^{322}\) In this scientific practice we may see a strong continuity since cooperating with his pupils was typical for Niko’s research already before his internment.\(^{323}\) “I think it is one of the enjoyable trends in our work”, Niko writes to D. Lack in April 1946,

that we are not only digging deeper but at the same time bring up again with ecology, endocrinology, neurophysiology. Our stickleback work has been in full swing again and still is. It is amazing how many new things can be discovered each new season by very simple, if only consistent, methods!\(^{324}\)

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\(^{323}\) His research projects on Sticklebacks with J. ter Pelkwijk and on Thrushes with D. J. Kuenen prove this, not to mention the paper about the Grayling’s courtship.

\(^{324}\) EGI Alex. Lib., D. Lack Papers, XIX. Correspondence, file 403, letter N. Tinbergen to D. Lack (21/04/1946).
Moreover, the special emphasis on releasive situations perpetuated in the immediate postwar years although the questions were headed into different directions such as the functions of camouflage, the supernatural stimuli, or the role a single type of stimulus played within a behaviour complex of a species. Furthermore, several of the topics Niko raised with (and in) his students and which later developed into extended research fields began “small” either in the summer camps at Hulshurst and Terscheling or within the university labs. In any case, they were practical research work intending to increase knowledge or answer a question by gathering arguments. Finally, many of these projects were concerned with natural selection and less the proximate causes of behaviour. “Many of the ideas were Niko’s”, H. Kruuk underlines and adds, “it all had very little to do with the theoretical aspects of causation of behaviour, but everything with natural selection”. Some few examples may serve to reveal the tenor of these cooperative studies. For instance, in a project he carried out together with Albert (Ab.) C. Perdeck, N. Tinbergen triggered the question which releaser might be responsible for the begging behaviour of young Herring Gulls. Like others the study commenced in a camp for undergraduate studies with Niko’s own “enthusiastic involvement”, as H. Kruuk puts it, but then was left to one of his students. When the adult Herring Gull enters the nest the chicks begin to peck at the bill tips of the parent bird. This makes the adult regurgitate predigested food, the primary food source of their offspring during the first few days. Niko’s question was what characters actually triggered the pecking response. His interest thereby focused on a red spot on the lower mandible of the adult’s otherwise yellow bill which apparently played a key role in the chicks releasive mechanism. In an earlier study published in 1937 the German ornithologist F. Goethe had reported that the chicks responded to various red objects such as cherries, red rubber soles of beach shoes and so forth. “Goethe’s observations indicate”, Niko writes, “that here might be a good opportunity to study innate responsiveness to external stimuli”. That was to say, the red spot functioned as a “sign stimulus” (Schlüsselreiz) in K. Lorenz’s sense which implied that the instinctive act could be released by only a few “prägnant” characters – a matter of fact which made the releasive pattern liable to errors yet at the same time – so to speak as a necessary heuristic precondition – provided the opportunity for experiments with dummies. Niko’s and Ab Perdeck’s project thus commenced with the hypothesis that the red patch functioned as a sign stimulus but soon broadened its perspective to all other possible releasive characters. “Therefore”, N. Tinbergen and Ab Perdeck underline, when after the war field work became possible again, we decided to attempt a systematic analysis

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328 For a description of the chick’s begging behaviour, see Tinbergen et al., “On the Stimulus Situation”, 1-2.
329 Ibid., 2.
of the part played by the red patch. In the course of our work, we extended our study to a general survey of all stimuli releasing the begging behaviour of the chick.\footnote{Tinbergen et al., “On the Stimulus Situation”, 3.}

It is hardly possible to express more precisely the epistemic thrust of Niko’s cooperate empirical projects of the immediate postwar era: Most of them began simple but continuously raised wider and more complex issues. From a methodological point of view, the study primarily operated with dummy tests and a broad inductive basis. The tests themselves had an experimental character insofar as they marked an intervention into the normal cyclus of parental care but, on the other hand, they were conducted in the open and left the animal intact as a whole.\footnote{Ibid., 5.} According to N. Tinbergen and Ab Perdeck, the experiments were of two different kinds: If the releasing value of two or more dummies should be compared the dummies were presented in succession. Two difficulties thereby had to be surpassed: On the one hand, the chicks – if tested several times in succession – revealed a “drop of responsiveness”. This, most likely, was due to the fact that the releasive mechanism was coordinated by the central nervous system and thus was subject to central nervous fatigue. As a consequence, the test results could be compared adequately only if they were evaluated relative to the number of the trial. On the other hand, testing innate responsiveness was disturbed by the learning ability of the chicks. “As will be shown below”, Perdeck and Tinbergen argue, “the chicks soon became negatively conditioned to the models used. The result was a lasting drop in responsiveness toward the dummies used”.\footnote{Ibid.} To prevent this process of “negative conditioning” which Niko tended to identify as holding\footnote{Ibid., 6.} both experimenters presented each dummy equally often so that no selective preferences could be established.\footnote{Ibid., 7.} If the directive influence of certain features was to be tested N. Tinbergen and Ab Perdeck applied the choice method, that is:

Two models, or one model with two parts that were to be put in competition, were presented at the same time and the number of pecks aimed at each of them was counted. In this experiment, it was of course not necessary to keep to the 30 second period, and we carried such a choice test on as long as feasible, that is, until the number of reactions fell of appreciably.\footnote{Ibid.}

From my epistemological standpoint it is important to mention that although the choice experiments were based on comparisons between alternative characters a prevailing tendency to quantify is noticeable in the overall experimental setting. Moreover, Niko mentions that chicks which were put back into the nest after the testings were eagerly adopted by the parent birds even in case the chicks were not their own offspring. This leads to the conclusion that choice in Herring Gulls is not necessarily a selective behaviour.\footnote{Ibid.} As usual the manifold results of the project were presented in a differentiated manner. Experiments with variously coloured spots on dummy bills revealed that red was preferred over other colours such as black but the shape of the spot also functioned as releaser due to the contrast effect.
it produced. Further experiments with graded contrasts confirmed the hypothesis that more contrasty dummies released more pecking. Additional experiments varying the background colour (i.e. the colour of the beak) showed that yellow, the natural colour, did not attain more responses. The conspicuous preference of red suggested “that the red patch acts through its colour as such”. Comparisons between purely red bills and the “standard model” revealed the superiority of the latter. Further experiments with different head colours showed that dummies in natural colours were not superior over other head colours which created a visible contrast to the colour of the beak but beat grey and yellow. In addition, supernatural stimuli, that is, more contrastive dummies than those occurring in nature, proved to be a stronger stimulant than the normal patch. With a view of the shape of the models the tests made clear that the form of the head played a role in the chicks’ recognition but coloured patch outweighed the character “form” by far. If different head-shapes were compared with each other the normal form beat the “cock’s head” and the latter again prevailed over the egg-shaped model, so that a clear hierarchy of shape preferences could be established. The fact that neither the shape nor the colour of the head played a dominant role in the chick’s recognition prompted further experiments with models that consisted of bills only versus models with head plus bill. “The results suggests”, N. Tinbergen and Ab Perdeck underline, “that the head, though not entirely irrelevant, yet has very little influence indeed”. Further examinations of the visual field of the newly born chicks made clear that not the peripheral receptors or their incomplete development were responsible for the neglect of the character “head shape” rather than the innate releasing mechanism (IRM) in the central nervous system itself. In other words, whether a stimulus releases an action pattern or not turned out to be a matter of central coordination. This hypothesis was confirmed by additional experiments with dummies whose colour patch was located at abnormal places. The farther the coloured spot was away from the bill tip the higher the number of misdirected pecks. The bill tip therefore turned out to be the centre of interest. The interruption between the shape of the bill and the one of the head thereby played no decisive role in the Herring Gull chick’s IRM. Experiments with varying bill shapes (length and thickness) suggested a superiority of very long and thin beaks. Bills pointing downward were preferred over bill models presented in horizontal position. The optimal distance between bill and ground was about 5cm. In any case, the bill tip needed to be well below of the chick’s eye level. “Relative lowness” thus turned out to play an

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336 Ibid., 7–8.
337 Ibid., 8–9.
338 Ibid., 10.
339 Ibid., 10–12.
341 Ibid., 13–14.
342 Ibid., 14–15.
343 Ibid., 16–17.
344 Ibid., 17.
345 Ibid., 18–19.
346 Ibid., 22, 24.
348 Ibid., 26–29.
essential part – next to nearness as further experiments proved.\textsuperscript{349} Moreover, both the slight head movements of the parent bird and its food call proved to be of considerable releasing influence.\textsuperscript{350} Most interestingly, N. Tinbergen and his pupil did not regard three-dimensionality as a critical characteristic of the models.\textsuperscript{351} Some control experiments, finally examined whether actually \textit{all relevant} characteristics were detected and, beyond that, whether the found qualities were in fact the \textit{essential} ones. Thus a provisionally optimal model including the crucial characters (red, contrast, thinness) was compared both with a real dead one as well as with a supernatural dummy.\textsuperscript{352} Lastly, the young chicks apparently were able to discriminate between bills carrying food and those which did not.\textsuperscript{353} I have recapitulated the course of the experiments in some detail as they are presented in the publication because I wanted to make evident their reductive character. A huge range of possible parameters is tested in order to single out the relevant ones, that is, those which play an essential role in the innate releasing mechanism of the young Herring Gull chick. The entire program of experimenting thus appears as a veritable example for Niko’s understanding of \textit{causal analysis} which here appears as a subordinate constituent of a textual composition whose own frame is not analytical. One of the characteristic features of the procedure thereby is the recursive repetition of comparison both with respect of one single experimental setting and the entire number of experiments, as well. A rather interesting thought is mentioned by N. Tinbergen and Ab Perdeck in their concluding remarks (Discussion and Summary). They recapitulate the relevant parameters of the Herring Gull chick’s innate releasing mechanism such as 1) moving, 2) a very definite shape, 3) “lowness”, 4) “nearness”, 5) pointing down, 6) a red patch at the tip, characterized by colour and by contrast, and finally 7) something protruding outside the bill’s outline (e.g. food). Yet after that, they claim that all stimuli may function both as a directive and a releasive stimulus. The strict discreteness between taxis and instinct which had been the tenor of N. Tinbergen’s and K. Lorenz’s study of the Greylag Goose’s egg-rolling behaviour thus seems to be questioned in the current paper. “Therefore”, they conclude, although we know that the head of the parent gull both releases the pecking of the chick, and directs it towards the bill tip, and that, therefore, it provides stimuli acting upon two different mechanisms, \textit{viz.} a “fixed pattern” (\textit{Erbkoordination}, Lorenz 1938) and a taxis component or rudder mechanism, we have no means of distinguishing the two mechanisms by their IRMs, which seem to be identical. In this respect our object is different from the egg-rolling movement of the Grey Lag Goose (Lorenz & Tinbergen 1938) and the gapping movement of nestling thrushes (Tinbergen & Kuenen 1939).\textsuperscript{354}

Niko’s “criticism” especially against his and Lorenz’s earlier study has epistemological implications. The causal analysis of a releasing mechanism does not stand alone for its own sake within Niko’s more ecological cooperative studies. And this re-framing apparently re-evaluates also the notion of discreteness which had been

\textsuperscript{349} For the relevance of the distance see, Tinbergen et al., \textit{“On the Stimulus Situation”}, 29–30.
\textsuperscript{350} Ibid., 30–31, 31–32.
\textsuperscript{351} On the model’s solidity, see ibid., 32.
\textsuperscript{352} Ibid., 32–33, 33–35.
\textsuperscript{353} Ibid., 35–36.
\textsuperscript{354} Ibid., 37–38.
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underlying the strict differentiation between taxis and instinct. Moreover, in comparison to the earlier studies concerned with releasive mechanisms, Tinbergen and Perdeck, here seem to take into account the potential waning of an animal’s responsiveness and, correspondingly, the development of selective preferences. Needless to say that the overall composition of On the Stimulus Situation Releasing the Begging Response in the Newly Hatched Herring Gull Chick – if thought through in detail – follows the more or less typical scheme of N. Tinbergen’s more ecological works he published in the immediate postwar era: “Introductory” and “Methods” prepare the empirical sections of the study which for their part consist of causal analysis (“Results”), on the one hand, and an open discussion (“Discussion and Summary” in this order and not vice versa), on the other.

A second example for Niko’s practice to get interested his pupils for one of his research projects is Jan van Iersel. In 1946 Niko made Jan his senior assistant and later, after Niko’s move to Oxford, it was v. Iersel who succeeded on his teacher’s chair at the University of Leiden. According to H. Kruuk, Jan was gifted with “an excellent analytical mind” and had “original ideas in designing experiments”.355

His primary interest was in Sticklebacks and N. Tinbergen apparently was glad to find someone who continued his and J. ter Pelkwick’s research – the latter of whom had died in 1942 during a fight with Japanese soldiers in the Pacific Ocean. In 1946, shortly after his appointment, N. Tinbergen and J. v. Iersel together published a paper on displacement activities in the Three-spined Stickleback.356 It was not Niko’s first encounter with the hierarchization of conflicting behaviours since the study he had carried out with J. ter Pelkwick had already touched the problematic, though not in detail. Also the current study was not the first explicit treatment of displacement activities: There exists a paper which N. Tinbergen had published earlier in 1940 under the title “Die Übersprungsbewegung” in the German Zeitschrift für Tierpsychologie.357 Nor was the underlying phenomenon entirely unknown at that point of time. Several other researchers including A. Kortlandt, A. L. Rand, C. R. Carpenter, F. B. Kirkman, G. F. Makkink and J. Huxley, had at least observed that animals, under certain conditions, perform “irrelevant” behaviours.358 Especially A. Kortlandt’s and N. Tinbergen’s earlier analyses, however, had shown that “such irrelevant movements occur when the animal is under the influence of a powerful urge, but at the same time is in some way prevented from expressing this urge in the appropriate way” – as Niko put it later.359 The nervous energy of the suppressed action pattern then is not suspended but “sparks over” from one drive to another. The imagination underlying the German term “Übersprungsbewegung” thereby is that nervous energy somehow “jumps over” into the pathways of the substitute behaviour. At the beginning of his paper of the year 1940 Niko mentions that his first encounter with displacement reactions was in spring 1933 when he observed

358 For the list of researchers and their terminology see Tinbergen et al., “‘Displacement Reactions’ [1947]”, 56.
359 Ibid.
the territorial fights of Snow Buntings. So why, one may ask, was there a delay of ca. seven years until he began to systematically treat displacement reactions? My personal opinion about that is that displacement reactions in contrast to vacuum activities – which apparently were replaced by the former as the prototypical behaviour pattern of ethological research – operate with another re-evaluated epistemic scheme: Both reaction types presuppose a combination between a suboptimal external stimulus, on the one hand, and a super-optimal internal stimulation, on the other (including the possibility of antagonistic inhibition). In both cases the inner drive is disrupted from the adequate external stimulus. But in case of displacement activities this disruption appears somewhat less absolute (as does disinhibition): “Meiner Meinung nach”, N. Tinbergen writes,

komen die vielen als Balzkomponenten erscheinenden Übersprungsbewegungen dadurch zustande, daß ein innerer Drang zu einer Handlungsphase infolge des Ausbleibens der notwenigen äußeren Reizung sich nicht Luft machen kann und nun als Übersprungsbewegung überläuft. | Dieser innere Drang besteht während der ganzen Fortpflanzungsperiode, kommt aber relativ selten als “Leerlaufreaktion” zum Durchbruch, weil die adäquate Reizung meistens schon auftritt, bevor die innere Stauung ein objektloses Abreagieren verursacht.

[According to my opinion, the manifold displacement reactions, which occur as components of courtship, originate due to the fact that an inner urge for an action sequence cannot exhibit because the outer stimulation is absent and therefore boils over as displacement reaction. | This inner drive exists during the entire mating period but relatively rarely breaks through as “vacuum response” because the adequate stimulation mostly already crops up before the inner congestion causes an exhibition without object.] [transl. CL]

From a more epistemological point of view, displacement reactions therefore reveal a highly paradox frame or constellation: They are affected, at least to a certain extent, by external stimuli from which they are deprived. J. v. Iersel’s and N. Tinbergen’s contribution to the entire problematic was to take the physical analysis of displacement activities as a starting point for further leading questions concerning the evolution of behaviour – especially ritualized social signal movements. From a more epistemological point of view the project thus intended to solve the paradox how a seemingly dysfunctional action pattern may change into a functional signal in course of evolution by what N. Tinbergen and his fellow author called “ritualization”.

The order in which the knowledge is presented in the paper mirrors this epistemic scheme. Thus we find four less or more definite propositions, “a sketchy

Ibid., 18.
N. Tinbergen picked up the concept of “ritualization” from J. Huxley’s classic Great Crested Grebe and Red-throated Diver papers. For the references see fn. 57, page 67 of my thesis. In the latter of the two papers, according to Tinbergen’s own statement, Huxley had already anticipated that displacement reactions can be the “raw material of releasers”. See WRC-RU Fondr. Lib., MS 50, box 14, file 1, letter N. Tinbergen to J. Huxley (17/02/1940), ibid., box 19, file 13, letter N. Tinbergen to J. Huxley (09/11/1951) and ibid., box 19, file 13, letter N. Tinbergen to J. Huxley (13/11/1951). And, indeed, some passages in J. Huxley’s Red-throated Diver papers allow this conclusion. See Huxley, “Courtship Activities in the Red-throated Diver”, 277, 279–280 and with more emphasis upon the derived character of the signal movements Huxley, “The Courtship of the Red-throated Diver”, 48. Niko, in his classical ethological period, also thought that the different course a displacement reaction can take during ritualization might be not only caused by the “direct” pressures but also the somewhat arbitrary mechanism of the displacement reaction itself. See WRC-RU Fondr. Lib., MS 50, box 26, file 5, letter N. Tinbergen to J. Huxley
review of the work thus fare done”, as Tinbergen and v. Iersel put it, introducing the author’s own empirical work.\footnote{363} These propositions include both a nomenclatural statement, that is, the authors’ decision to use the phrase “displacement reaction” to refer to the “irrelevant” movements in question, and some reflections concerning the circumstances under which displacement reactions become conspicuous.\footnote{364}

Either a conflicting drive is aroused which blocks the actual drive or the releasive situation is somewhat flawed, that is to say, a crucial releasive trigger usually provided by a social counterpart is lacking or an external stimulus, after having activated the drive, suddenly stops. In all three cases substitute activities are triggered. In addition to that, we find an explanation of the “path-architecture” of the displacement activities. A behaviour which may function as displacement reaction can be triggered either in the normal way, in this case N. Tinbergen and J. v. Iersel speak of “autochthonous” excitation, or the behaviour is the result of displacement. In the latter case the authors speak of an “allochthonous” impulse.\footnote{365} As a result, we may infer that in case of displacement reactions two nervous pathways may lead to more or less the same response. Finally, J. v. Iersel and N. Tinbergen mention three explicit conclusions to be drawn from the research so far carried out on displacement reaction. “Comparative study of displacement reactions has further led to the following, partly tentative, conclusions”, they write and proceed:

1. The form of the displacement reaction is characteristic of each species. For instance, every male starling preens when its fighting drive is obstructed; a cock or a male skylark always makes pecking movements under the same conditions; a pigeon always preens when the mating urge is frustrated, and so on. This is based on the fact that the displacement reactions are innate. A species may have a number of different displacement reactions, each belonging to a special situation.  
2. In some cases, displacement reactions have a secondary function, serving as a social signal for releasing special responses in other individuals of the same species. Displacement reactions initiated by the fighting drive often have threat function, those by mating drive may have the power to release sexual responses in the partner.  
3. Those displacement reactions which do have releaser function seem to differ from such as have no communicative function by what has been called ritualisation. Instead of being identical, or very nearly so, with the autochthonous example, they differ from it by showing superimposed movements which actually serve to make the movement more conspicuous. Thus a displacement reaction with threat function may display special weapons or bright colours.\footnote{366}

What follows is a recapitulation of the empirical part of the project which in marked positions refers back to the propositions made in the “sketchy review” before. The presentation of the data is consequent insofar as it intends to provide both corrections of A. Kortlandt’s and N. Tinbergen’s own earlier papers and, in addition to

(13/06/1958). In a later stage of his scientific development he put more emphasis upon the fact that one and the same behaviour can be ritualized and non-ritualized. See \textit{ibid.}, box 34, file 4, letter N. Tinbergen to J. Huxley (02/04/1963). On the other hand, Niko, in contrast to J. Huxley, wanted to restrict the concept of “ritualization” to the function of communication only. This can be inferred from a letter discussing the details for a conference on the theme. See \textit{ibid.}, box 37, file 2, letter N. Tinbergen to J. Huxley (27/08/1964).\footnote{363}

\textit{Tinbergen et al., “Displacement Reactions’ [1947]”}.\footnote{364}

\textit{Ibid.}, 56–57.\footnote{365}

\textit{From N. Tinbergen’s earlier paper we can deduce that he adopted the distinction between autochthonous and allochthonous excitation from A. Kortlandt’s study on displacements reactions in cormorants. See Tinbergen, “Die Übersprungbewegung [1940]”, 2.}\footnote{366}

\textit{Tinbergen et al., “Displacement Reactions’ [1947]”, 57–58.}
that, makes available further information to substantiate the hypothesis that signal movements are modified displacement reactions. At first, J. v. Iersel and N. Tinbergen thus explain how the male Stickleback reacts if its fighting drive is obstructed experimentally. If the territories of two male Sticklebacks meet vehement fights often commence at the boundary lines. In these fights, Tinbergen and v. Iersel state, actual fighting is interrupted by threatening. “A threatening male”, N. Tinbergen and his junior author state, stands in vertical position, head pointing downward, and making the movements of picking something up from the bottom [...]. This movement which experiments with dummies have shown to function as a threat, intimidating other males, is, in origin, a displacement activity, and can be experimentally aroused by obstructing the fighting drive (Tinbergen, 1940).

This description of the male Stickleback’s threatening now is supplemented by two corrections of statements Niko made in his former study (mentioned in the quotation) and which refer more to the origin of the displacement behaviour in question. At first, while Niko in his paper of the year 1940 claimed that threatening is displacement feeding, he now insists that the origin of the behaviour must be digging. Second, in contrast to his and A. Kortlandt’s general conclusion that displacement activities is never performed as complete as its autochthonous counterpart he now claims that in some cases the difference between normal and displacement reaction may vanish. “These observations show”, Tinbergen and v. Iersel point out, not only that the threatening movements must be interpreted as displacement digging instead of as displacement feeding, but also that Kortlandt’s and Tinbergen’s general conclusion that a displacement reaction is never as complete as its autochthonous example, does not hold good absolutely. When the obstructed urge is exceptionally strong, the resulting displacement reaction may become complete and practically identical with its example. The only difference is that the displacement reaction, in this case, is performed in a very “nervous” (hasty or jerky, intensive and emphasising) way.

The idea that “example” and derived behaviour may coincide with each other seems to be a very important element in the following argumentation of the study. This argumentation proceeds in two steps. At first, Niko and his fellow author isolate a typical displacement activity which reveals less or no differences in comparison to the original behaviour (subchapter: “Obstruction of the mating drive”). After that, a comparison between displacement threatening and displacement fanning finally is aimed at making conspicuous the relevance of the displacement reactions for understanding the evolution of behaviour. When a male has finished its nest it reacts positively against each pregnant female arriving at its territory. As N. Tinbergen and J. ter Pelkewijk had revealed already earlier in their study of the Stickleback’s courtship behaviour the final part of the entire reproductive cycle thus is introduced by the male’s “zig-zag dance” which is meant to stimulate the female to approach the male. The female’s reaction in turn is the signal for the male to guide its partner

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367 For an outline of this empirical part see Tinbergen et al., “‘Displacement Reactions’ [1947]”, 58.  
368 Ibid.  
370 For the earlier formulation see here ibid., 12, 21, 29–30.  
371 Tinbergen et al., “‘Displacement Reactions’ [1947]”, 60.
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to the nest. If the reaction of the female is not exhibited and she does not follow at once the entire reaction chain is interrupted and the mating drive of the male is discharged in three different possible displacement reactions, namely “pushing” its snout into the roof of the nest, ventilating the fins as if “fanning” the eggs and, finally, “gluing” the constituents of the nest with a particular secretion secreted by his kidneys. “Thus there is a definite connection”, Niko and Jan conclude, “between digging and the fighting drive on the one hand, whereas pushing, fanning and gluing are outlets for the obstructed mating drive”.

In the following part of the argumentation Niko and Jan single out one of the displacement reactions just mentioned, fanning, and compare it with displacement digging (subchapter “Comparison of displacement digging and displacement fanning”). The criterion of the comparison thereby is the question in how far “example” (i.e. the original movement) and the derived action resemble each other. The result of the comparison is that in case of threatening the derived action is far more elaborate than the original movement whereas in case of fanning hardly any difference can be detected.

Moreover, the fact that displacement fanning in contrast to displacement digging apparently had no signal function at all for the respective partner of social interaction led N. Tinbergen and J. v. Iersel to the conclusion that there is a correlation between the advancement of the displacement reaction, on the one hand, and its communicative function, on the other hand. “Now, in spite of all attempts, we never found any evidence pointing to the signal function of these displacement reactions [i.e. fanning, gluing, and pushing],” Niko and Jan concluded, it does not seem to make the slightest difference to a female whether the male shows displacement pushing, fanning or gluing, or omits them. The gluing does have a stimulating influence on the male himself, for a male that is not quite ready to lead a willing female nearly always leads her quite readily immediately after gluing; but we never had any indication of an influence on the female. | These observations, therefore, are striking proof of the correlation between ritualisation and signal function. Displacement reactions with signal function are ritualised, those without signal function are not. | We are of opinion that this correlation is not accidental and that there can be little doubt that ritualisation is the outcome of adaptation of the displacement reaction to its secondary function, viz. that of a signal or releaser.

The transformation process from a simple displacement reaction to a more complex social signal thereby is exactly what is meant when both authors speak of “ritualisation”. In conclusion, one may say that N. Tinbergen’s and J. v. Iersel’s study of displacement reactions is characterized by the intention to extend the strictly causal and physiological approach with further leading questions concerning the phylogenetic development of behaviours with a communicative function. This tendency to progressively add and extend may be identified as the epistemic deep structure of single concepts such as “ritualization”, of the essential argumentative parts of the study or the paper as a whole. In other words, the paper as a whole both “says” and “performs” ritualization. All examples of cooperate studies I have mentioned reveal that the tendency to develop something did not only affect the inner order of scientific publications. Nor add they up in the intertextual relations which some-
times turned out to be of significance. In the special case of Niko’s joint research works farther biographical contexts must be taken into account, for instance, Niko’s practice to get his students interested for research projects he sparked off but then were transferred to one of his pupils and there not rarely developed into a veritable field of ethological research. With a view of the cooperative research projects Niko carried out together with pupils between 1945 and 1948 whose inner organization is based on exceeding a primary idea, this means that the scheme of the practice with which Niko used to socialize his pupils and the structure of the final product of this act of socialization, that is, the composition of the theses, coincided with each other.\footnote{As I will show, it is exactly this coincidence which Niko’s later critical pupils undermined. Hence, form the epistemological standpoint, it is the tautological relation within the epistemic reference system that was underlying Niko’s practices of academic socialization which changed its character over time.} One of the most prominent examples here is J. v. Iersel’s devotion to Sticklebacks. After all it was his talent to refine his master’s initial idea which stood at the beginning of sixty years of intensified Stickleback research at the University of Leiden during which not only Niko’s pupils became involved but also the pupils of his pupils such as P. Sevenster who finally succeeded on J. v. Iersel’s chair. Niko himself, after he had left the Sticklebacks to Jan, never carried out own projects on Sticklebacks but supervised, for instance, D. Morris’ dissertation thesis which examined the reproductive behaviour of the Ten-spined Stickleback, as well as Ph. Guiton’s, F. Hall’s and B. Tugendhat’s dissertation theses which were all concerned with various aspects of reproductive or courtship behaviour in Three-spined Sticklebacks. Furthermore, the Stickleback perpetuated to take a prominent position both in Niko’s theoretical and popular accounts.

Altogether, I am inclined to argue that Niko’s cooperative research since ca. 1937/1938 mainly took place within the epistemic framework K. Lorenz had provided in his “special phylogeny of releaser”. This frame presumed that inner schemata can be correlated with observable responses.\footnote{In a later letter to J. Huxley, N. Tinbergen put great emphasis upon this distinction and complained that even some of his colleagues neglected it. See WRC-RU Fondr. Lib., MS 50, box 34, file 4, letter N. Tinbergen to J. Huxley (02/04/1963).} In contrast to G. Kramer who replaced the system as a whole by another alternative one, Niko developed Lorenz’s edifice further in as much as he “opened” further sub- and sub-sub-distinctions within this system especially as to the systemic positions covered by the IRM and their corresponding observable action patterns. As to how the inner constitution of the IRMs changed over time, we can observe a historical development in Niko’s empirical cooperative studies.\footnote{Answering R. W. Burkhardt’s request Niko later provided some more details about the origin of and his contribution to early ethologists’ understanding of the IRMs. See Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3156, E 2, letter N. Tinbergen to R. Burkhardt (06/06/1979).} In “Eine reizbiologische Analyse” (together with J. ter Pelk-wijk) we find the idea that signal movements, beyond Lorenz’s simplified releaser (in a narrow sense), may be more complex as soon as more intricate encounters between the sexes were at stake. In this study Tinbergen focused primarily on the observable behaviours. Later studies made the correlation between stimulating situation and receptory apparatus their theme. Thus “Über die auslösenden und die richtunggebenden Reizsituationen” (together with D. J. Kuenen) operated with an
intrinsic bifurcation of the IRM in a releasive and a directive constituent. In “Die Balz des Samtfalters” (together with B. J. D. Meeuse, L. K. Boerema and W. W. Varossieau) there is the idea that the innate releasing mechanisms next to (or within?) their endogenous component must include some kind of systemic position which is open for direct ad hoc stimulation. After the war, in “On the Stimulus Situation Releasing the Begging Response” (written together with Ab Perdeck) Niko seemed to have modified and/or elaborated his former conception of the IRM as combination of a releasive and a directive component and tended to argue in favour of what German ethologists later should call “selective habituation”, a general waning of responsiveness not being identical with the transformation of the IRMs by conditioning. Niko’s reactivation of his already earlier conception of “displacement reaction”, finally, paved the way for his later systematic studies since the idea of behaviours jumping over into another behavioural bout was both apt to suspend former more rigid conceptions of fixed action patterns and could be defined as the phylogenetic starting point of adaptive signal movements which obtained their secondary communicative function in a process of ritualization. With a view of their receptory correlate, the observation that autochthonous and derived (i.e. allochthonous) actions in fact may be qualitatively more or less identical supported Niko’s reasoning in nervous pathways that was underlying his conception of displacement reaction. Lastly, Niko’s conception of displacement reaction allowed to integrate the already earlier formulated idea that a corresponding releasing mechanism must be adjusted for direct stimulation which was considered to be combined with the respective endogenous potential in a sort of trade-off. Altogether the focus therefore shifted from simple to complex innate releasing schemata and with a view of the ritualization process eventually also embraced some kind of abstraction or detachment from the original releasing mechanism. In conclusion, I am therefore inclined to argue that in Niko’s cooperative projects Lorenz’s former Special Phylogeny of Releaser step by step developed into an overall approach for the study of the phylogenetic development of signal movements, that is, in other words, an integrated phylogenetic understanding of animal communication. My impression thereby is that N. Tinbergen’s handbook *The Study of Instinct* (published in 1951) partly mirrors the major shifts leading to this integrated view in the organization of its text. Insofar Niko’s book can be interpreted as a provisional peak of his synthetic endeavour. As I will show below this thesis may hold good if one keeps in mind that *The Study of Instinct* is mainly analytical and therefore tends to emphasize the receptive correlates of the visible behaviours.

(R2) *Theoretical accounts 1944–1948*. Besides the projects Niko carried out in cooperation with his students there is a different type of approach to ethological research which stood irreducible next to the former in the period between 1944 and 1949 (and after). “In his own observations and experiments of the late 1940s”, H. Kruuk underlines,

Niko was still mostly concerned with “releasing stimuli”, that is, aspects of the environment in the broadest sense to which animals reacted with specific behaviour patterns (for example the red spot on a bill, the super-normal egg). But his more theoretical interest in the entire

378 That is to say, some kind of functional intercalation.
organization of behaviour was almost separate from this, and it made considerable strides since his 1942 “Objectivistic Study”.\(^{379}\)

The manifestations of Niko’s “more theoretical interest in the entire organization of behaviour” surely was driven by the motivation to bring order into the accumulated data. Moreover, these accounts apparently also originated in a different manner. While the cooperative projects often commenced in undergraduate student camps, Niko’s theoretical accounts not rarely were the result of the lectures he delivered in Europe and especially abroad. Therefore it would be a great mistake to think that ethological theorizing in case of N. Tinbergen was exclusively based on contemplation. By no means. It is not an accident that several of the most important theoretical outlines written by neo-Darwinian researchers (e.g. Th. Dobzhansky, E. Mayr) and, as we will see, also by N. Tinbergen, had their origin in oral lectures which were delivered before a wider academic audience and were only later on transformed into the written language of a handbook. If we look very carefully, we may again detect the disposition of an epistemic practice behind all this which was primarily motivated by the urge to reduce complexity but at the same time had to face the irritations which resulted from the increased mental activity which was reckoned a necessary precondition for determining the correct theoretical anchor. We came across such a paradox constellation already before in N. Tinbergen’s biography: Surely after the war he felt like distancing from his German colleagues but, on the other side, it was exactly the experiences he made during the war which made him receptive for overwhelming emotions – including sympathetic emotions.\(^{380}\) When we have to analyze the origin of the theoretical conceptions of the newly founded discipline Niko represented we are confronted with a similar paradoxon located right at the heart of the problem, the author’s self. Thus it is important to keep in mind that Niko’s lecturing between 1944 and 1949 was combined with (or superimposed by) extensive and therefore also exhaustive travelling.\(^{381}\) To repeat my point: On the one hand, travelling contributed much to broaden the range of opinions on basis of which Niko was able to profile his own views but, on the other hand, the increased mental and spatial motility disturbed the initial urge to anchor Ethology theoretically. In a letter to D. Lack after ending his lecturing tour to Switzerland Niko writes, for instance: “I was very tired after returning from Switzerland, where I had just as stimulating a time as in England. Rather too many stimuli in a short time I guess, but now I am ruminating my spiritual food”,\(^{382}\) And my hypothesis is that the bifurcated epistemological architecture of Ethology in some essential parts matched this ambivalent constellation perfectly well so that, again, so to say via the detour, a harmony between science and life was able to suggest itself.

In spring 1946, D. Lack had visited Leiden for a few days and when he returned to Britain Niko accompanied him.\(^{383}\) D. Lack lived in Oxford and it was at his

379 For the coexistence of both realms see also Kruuk, Niko’s Nature, 144–145, here 144.
380 See to this ibid., 128.
381 For Niko’s restlessness, see ibid., 143–144, 149.
382 EGI Alex. Lib., D. Lack Papers, XIX. Correspondence, file 403, letter N. Tinbergen to D. Lack (31/03/1946).
383 Lack had been invited by Niko in January 1946 to deliver a presentation during “a symposium on ecological problems” Niko organized. See ibid., XIX. Correspondence, file 403, letter N.
place where Niko met M. Southern and Ch. Elton, two of the founders of British Ecology. In Cambridge N. Tinbergen was introduced to W. H. Thorpe and J. Gray, in London he met J. Huxley. His visit to Britain let Niko realize that the field of Behaviour Research suffered from a lack of scientific exchange which encouraged him in his plans to found an international scientific journal. In late autumn 1946, N. Tinbergen was already on his way abroad. E. Mayr whom Niko had contacted soon after the end of the war had organized a three-month lecturing tour across the United States and Canada.\textsuperscript{384} Thus Niko delivered a presentation before the Wilson Ornithological Club in Nebraska which was later published in the club’s bulletin under the title “Social Releaser and the Experimental Method Required for Their Study”.\textsuperscript{385} In addition to that, he lectured at the universities of Chicago, Wisconsin and Alberta. On his way across California he visited Caltech and Berkely. Niko’s lecturing marathon finally ended with six lectures at Columbia University and some additional presentations at the American Museum of Natural History (AMNH) in January and February 1947. Especially, the highly prestigious Columbia lectures stimulated his mind and later became the basis for the book Niko became most famous for, \textit{The Study of Instinct}. E. Mayr had prompted N. Tinbergen to put the lectures into a printable form and Niko had finished the manuscript at the turn to the year 1949, but the book was published not before 1951 due to delays caused by the publisher.\textsuperscript{386} One year after his Columbia lectures, in January 1948, N. Tinbergen was on the move again, this time for a tour across Switzerland. At the University of Zurich he delivered a series of four guest lectures. A summary of these presentations was later published in the Swiss science journal \textit{Experientia} under the title “Physiologische Instinktforschung”.\textsuperscript{387} At the end of the year 1948, Niko was about to organize another trip to Britain for a series of three lectures in London and a couple of additional ones in Oxford, Cambridge, Edinburgh and Aberdeen. Due to a minor nervous breakdown the trip which had been planned for early 1949 had to be cancelled. In February 1949 Niko in fact travelled to England in order to discuss a job opportunity at the University of Oxford. And soon after, in July 1949, he followed W. H. Thorpe’s invitation to present a paper at a symposium the latter had organized on behalf of the British Society for Experimental Biology (SEB). The so-
called “Cambridge-Conference” entered the history books because it was both the first personal get-together with the German colleagues after the Second World War and the starting point of the so-called International Ethological Conferences which till nowadays take place in a biennial rhythm. Niko’s contribution to the symposium treated the hierarchical order of the physical mechanisms underlying instinctive action patterns and was published in the proceedings of the conference in 1950. In sum, Niko’s lecturing trips between 1944 and 1949 generated altogether three theoretical papers and his book, *The Study of Instinct*. “Niko’s main products of these years”, H. Kruuk underlines in his biography,

were first and foremost his book, *The Study of Instinct*, and three papers that mostly contained material which was also presented in the book. Significantly, all of these, the papers and the book, were based on and expanded from lectures he gave abroad. It was the preparation for a talk or a series of lectures that set Niko thinking and assembling his facts, which he then used for a publication. This may be one reason for Niko’s assertive style when he was writing: he was not just putting together a scientific structure and argument on paper; rather, there was a sea of faces in the front of him, and he was on trial. When reading his papers one can almost hear him: “There is no doubt that…”, “certainly …”, “this can mean but one thing…”.

My impression is that the specific circumstances under which Niko’s theoretical foundations of Ethology originated reveal a practical scheme: Theorizing implies the reduction of complexity which is a necessary result of accumulating data and this process should be fixed in an abstract and written language. In case of N. Tinbergen’s theoretical texts the interruption which is usually implied in any abstraction apparently is superimposed by stylistic techniques perpetuating the connection to the audience which is characteristic for an oral presentation. In so far the epistemic practices underlying Niko’s theoretical accounts are eventually not that different from the ones we may find in his *Klieuw*. The following analysis of N. Tinbergen’s theoretical accounts takes this observation as a starting point and examines in how far the epistemic pattern underlying N. Tinbergen’s understanding of causal analysis shapes also his theoretical accounts. In doing so I concentrate on *The Study of Instinct* but will have referred to the theoretical papers where it was necessary and elucidative. According to N. Tinbergen, *The Study of Instinct*, though “incomplete and unsatisfactory in many respects” is the “first attempt at a synthetic treatment” of entire research field. And since it is often the way researchers organize their knowledge which reveals their moves within the epistemic space provided by a scientific community one may ask with just what this order is like in *The Study of Instinct*. What becomes evident already at a first glance is that the scientific practice of systematizing manifests itself primarily in recursive differentiations. “My presentation has a dual aim”, N. Tinbergen begins and continues:

First it is intended to call attention of Anglo-American workers to research done on the European continent. Almost all of this work has been published in the German language, and much of it

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Niko Tinbergen (1907–1988)

has not penetrated into English and American Science. By presenting a review of this work in the English language I hope to contribute to international co-operation in the science of animal behaviour. Second, this book is an attempt at an organization of the ethological problems into a coherent whole. This applies especially to the problems of the causes underlying instinctive behaviour. These problems are dealt with in Chapters I to V inclusive, in which a systematic treatment is attempted. My principal aims in this part have been: (1) to elucidate the hierarchical nature of the system of causal relations, and to stress the paramount importance of recognizing the different levels of integration; and (2) to bring ethology into contact with neurophysiology. Chapters VI, VII, and VIII, dealing respectively with, ontogeny, adaptiveness, and evolution, should not be considered attempts at such a systematic treatment. I added them after considerable hesitation. The fragmentary and more or less unbalanced nature of these chapters, while due in part to my own shortcomings, are also due to the unsatisfactory state of these more or less neglected fields in our science. My main motive for including these chapters has been the hope that by doing so I could contribute towards a more harmonious development of ethology as a whole.391

Already on basis of this brief overview we may infer not only that N. Tinbergen intended to present his knowledge in a highly differentiated way, if we look carefully enough we may also detect the specific schemes underlying this differentiations, in other words, how he constructed the distinctions.392 If we take for granted that the overall “root” is determined by the motivation to present the science of Ethology as a whole, N. Tinbergen’s intention to communicate the achievements of the German speaking scientific culture of the pre-war period into the Anglo-American scientific community is an act of transgression. It is mentioned in the first place. The organization of ethological problems “into a coherent whole” is mentioned in the second place and it is this part which is primarily related to the causal analysis of the mechanisms underlying instinctive action patterns. It is exactly this combination of holism and emphasis of proximate causation which made E. Crist postulate a “mechanomorph” research attitude in Classical Ethology.393 It is not quite clear how bifurcation proceeds within this holistic frame. For certain is that the chapters I to V establish a major contribution to the causal analysis. Moreover, with respect of these five main chapters Niko again mentions a twofold emphasis: To determine the hierarchical order of causal relations, on the one hand, and the enhancement of scientific exchange between ethologists and physiologists, on the other. The latter of the two motivations again implies the transgression of a boundary between scientific disciplines and therefore refers back to Niko’s function as a mediator between the continental European and the Anglo-American research communities. Since the motivation to generate order here is mentioned in the first place, one may infer, that the argumentative thrust underlying chapters I to V is counterdirectional in comparison to the overall argumentative direction. Moreover, like it was the case in N. Tinbergen’s *An Objectivistic Study* the examination of the various levels of integration, in a narrower sense, is placed within an empirical frame. The question now is where to place the supplementary chapters VI, VII, and VIII within this whole tree of ideas. Surely, there are different possibilities but I am inclined to interpret Niko’s

391 Ibid., Preface, v.
392 It is therefore not sufficient to determine the simple fact of differentiatedness. A more elaborate methodology is required.
393 See also Tinbergen, “Physiologische Instinktforschung”, 121.
treatment of ontogeny, adaptiveness and evolution as essential part within and not beside his “attempt at an organization of the ethological problems into a coherent whole”. One of the indicators which support my interpretation is the fact that Niko defines the relation between these and the preceding five main chapters as somewhat disconnected. Niko writes: “I added them after considerable hesitation”. As a consequence, Niko’s reasoning on both ontogenetic and phylogenetic development would be an integral part of his overall causal analytical approach. What contradicts my interpretation to a certain degree is N. Tinbergen’s statement that these parts “should not be considered attempts at such a systematic treatment”, because in my interpretation it is especially Niko’s reasoning on “evolution” which could potentially provide a major contribution to systematic integration. With a view on the inside of this frame one may say that Niko’s treatment of ontogenetic growth surely takes a meta- or exclusive status in comparison to chapter VII (adaptiveness) and VIII (evolution) since the latter two traditionally refer to phylogenetic development. As a result I am inclined to suggest the following scheme to illustrate the higher “levels” of Niko’s system of knowledge in *The Study of Instinct* (Fig. 2.4). Each part thereby covers a particular field of behaviour research and on basis of

![Fig. 2.4](image)

N. Tinbergen, *The Study of Instinct* (1951), Organization of the Book

this knowledge it is quite obvious that how N. Tinbergen constructs one single field is dependent from the overall scheme. In other words, *where* a certain topic, field or

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394 That the study of evolution, according to N. Tinbergen, is an essential part of causal analysis is stated explicitly. See Tinbergen, *The Study of Instinct*, 2. The same holds for the question of adaptiveness. See *ibid.*, 151–152.
area of research appears in the overall scheme determines the set of parameters by which it is primarily approached. It is therefore worthwhile to dig a little bit more into the details and ask how each part of this tree of epistemic schemes is elaborated. My impressions thereby is that chapters one to four belong together whilst chapter five, “An Attempt at a Synthesis”, intends to fulfil N. Tinbergen’s previous promise to enhance the cooperation between ethologists and physiologists.\footnote{Like Niko’s reasoning on ontogenetic growth his attempt to formulate a synthesis thus would have an exempt status in each epistemic complex.} If this attempt is “synthetic” one may, at least tentatively, infer that the chapters one to four might be “analytical”. Moreover within this unit, chapter one, “Ethology: The Objective Study of Behaviour”, seems to take a somewhat exempt position since it provides a general survey of the new research branch of behaviour study and, beyond that, apparently anticipates structurally Tinbergen’s entire train of thought being related with the physiology of behaviour (chapter I-V).\footnote{This coincidence is suggested by the fact that both chapter one and the section which consists of chapter one to five end with some considerations concerning the relationship between Ethology and other zoological research branches (I.4) or particularly Ethology and Physiology (chapter “V. An Attempt at a Synthesis”). In general, the title of chapter one alludes to Niko’s former paper “An Objectivistic Study of the Innate Behaviour of Animals” of the year 1942. Yet in contrast to the former account, Tinbergen now emphasizes the new discipline’s name (“Ethology”), brings in a stronger functional nuance by speaking of “objective” instead of “objectivistic” study, shifts his attention from innate behaviour to behaviour in general and, finally, dropped the special focus on animal behaviour.} As a result, chapter two (“Behaviour as a Reaction to External Stimuli”), three (“The Internal Factors Responsible for the ‘Spontaneity’ of Behaviour”) and four (“Further Consideration of the External Stimuli”) seem to build an analytical unit which partly summarizes Tinbergen’s elaborated view of the frame his friend K. Lorenz had provided with his Special Phylogeny of Releaser yet, beyond that, also establishes the analytical bottom for the “Synthesis” outlined in chapter five. In order to prove the manifold structural coincidences in \textit{The Study of Instinct} which successively enlighten the entire order of the book it would be necessary to read meticulously chapter by chapter. The applied methodology thereby surely must commence tentatively from the top since the upper levels of Niko’s tree of ideas allow – at least to a certain extent – to build hypothetical conjectures about the inner constitution of the lower level regions. These hypotheses, in turn, can be tested only if the resolution of the entire repetitive partitioning analysis (RPA) is increased and the constituents in question are evolved inductively. Only on basis of these collections of more descriptive data it seems legitimate to draw resilient and reliable conclusions concerning the epistemic constitution of the respective textual account or a combination of accounts. However to give the account of my thesis a more straightforward character I shall summarize my readings in a comprehensive overview (see table 2.1) which briefly lists the single chapters of \textit{The Study of Instinct} and the alleged epistemic scheme applied in each section. In a subsequent step I shall go into more detail in those sections of the book which later, in the 1950s and 1960s, gained meaning either because N. Tinbergen built up a research program upon his respective foundations or the main concepts standing out of a single section became subject of epistemological re-modification. The parts I shall confine myself to are the ones N. Tinbergen
Table 2.1 N. Tinbergen, *The Study of Instinct* (1951), Alleged Epistemological Framing of Single Chapters

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<thead>
<tr>
<th>Chapter</th>
<th>Title</th>
<th>Causal Analysis?</th>
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<tr>
<td>I</td>
<td>Ethology: The Objective Study of Behaviour</td>
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<td>II</td>
<td>Behaviour as a Reaction to External Stimuli</td>
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<tr>
<td>III</td>
<td>The Internal Factors Responsible for the ‘Spontaneity’ of Behaviour</td>
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<tr>
<td>IV</td>
<td>Further Consideration of the External Stimuli</td>
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<tr>
<td>V</td>
<td>An Attempt at a Synthesis</td>
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<tr>
<td>VI</td>
<td>The Development of Behaviour in the Individual</td>
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<tr>
<td>VII</td>
<td>The Adaptiveness of Behaviour</td>
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</tr>
<tr>
<td>VIII</td>
<td>The Evolution of Behaviour</td>
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later related to the “Four Whys” of biological inquiry and which turn out to be outlined already in *The Study of Instinct* as systematized thoughts about causation (mainly chapter V), ontogeny (chapter VI), adaptiveness (chapter VII) and evolution (chapter VIII).

Chapter five, “An Attempt at a Synthesis”, eventually is the core of *The Study of Instinct*. It reveals N. Tinbergen’s intention to formulate a synthesis between Ethology and Physiology and thus takes part in the broader synthetic movement taking place within the biological sciences in the decades before and after the Second World War. I think the entire chapter can be read as a longer argument for this overall objective. Moreover, I believe the inner logic of Tinbergen’s argumentation is encoded in the order of the chapter. Thus, one may eventually say, that chapter five, in general, both states shortcomings of ethological research and makes suggestions how to overcome these deficits. This thesis may hold both with respect of the relationship which is established between the introductory section (“Recapitulation”) and the remaining more prospective subsections of Tinbergen’s synthesis, on the one hand, and the attempt to overcome the disciplinary shortcomings which result from a rigid division of labour between Ethology and Physiology, on the other hand. Especially the latter of the two moves seems to coincide with the overall intention of the chapter. Thus N. Tinbergen begins with a sophisticated causal analysis of the problematic, the rigid separation of the two related disciplines. This analysis, in turn, proceeds in two distinct steps. At first, Tinbergen tackles the prob-
lematic that concepts such as “reaction”, “motor response”, “behaviour pattern”, or “movement” embrace a wide range of less and more complex behaviours (see sub-chapter bearing the title “Differences in Degree of Complexity of ‘Reactions’”).

In a second step, Tinbergen seems to explain the separation of the disciplines by claiming that Ethology and Physiology respond to this challenge of imprecise terms and varying grades of behavioural complexity with two different albeit complementary and mutually related forms of systematization: Although ethologists were able to resolve the mere realization of hierarchical organization in fixed action patterns (see subsection “Hierarchical Organization”) by applying further leading conjectures based upon the dualism of appetitive behaviour and consummatory act they had adopted from W. Craig in a modified version, in Niko’s view, some ethologists (e.g. G. P. Baerends) tend to direct their attention primarily to the upper levels of integration, that is the more central regions of their hierarchical models, which, in Niko’s understanding, are characterized by behaviours that are initially and fundamentally guided by the more plastic appetitive behaviours (subsection “Appetitive Behaviour and Consummatory Act”).

Physiologists such as A. P. Weiss, W. R. Hess and E. v. Holst – albeit with a stronger emphasis upon the physical correlates in the brain – have developed models with various levels of behavioural integration, too, yet, contrary to ethologists, they concentrated on lower, that is, irritable levels and, as a result, were prompted to ignore the research area of ethologists. This can be inferred from the fact that the subsection with the title “Neurophysiological Facts” proceeds from “The Relatively Higher Levels” (“Instinct and instincts”, “Displacement activities”) to “The Lower Levels” of integration and, within this frame, to Tinbergen’s account of “P. Weiss’s Concept of Nervous Hierarchy” into which the entire subsection on Physiology finally culminates and which turns out to be the blueprint of Tinbergen’s own hierarchical model. “The concept of a hierarchical organization of the nervous system”, N. Tinbergen writes,

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400 Most interestingly, the mentioned examples (swimming of the eel, swimming movement of Labrus, the Sticklebacks ventilating of eggs, a gallinaceous chick’s reaction to a predator, and the Stickleback’s reproductive behaviour) are arranged upon a scale from simple to complex. See ibid., 102.

401 For earlier and more rudimentary attempts to evince hierarchical organization see ibid., 102–104, especially Fig. 89. For the distinction between appetite and consummatory act see ibid., 104–107, especially 105. For the roots of this dichotomy in W. Craig’s research see W. Craig. “Appetites and Aversions as Constituents of Instincts”. In: Biological Bulletin 34.2 (1918), especially 91–93. Tinbergen’s usage of the dichotomy was mediated by K. Lorenz’s primary reception. Whereas Craig had described the instinctive action pattern as a whole as combination of appetite and final act, Lorenz insisted to reserve the term “Instinkthandlung” exclusively for what Craig had called “consummatory act”. See K. Lorenz. “Über die Bildung des Instinktbegriffs”. In: Die Naturwissenschaften 25.19/21 (1937), 290, 294–295, 311, 326. This reductive gesture required to redefine the combination as a whole. N. Tinbergen, by contrast, preferred the wider concept and this is most likely one of the reasons why it was he and not so much Lorenz who integrated the various theorems into one hierarchical concept of “instinct”. For Tinbergen’s systemic definition of “instinct” see particularly Tinbergen, The Study of Instinct, 111–112. For a defence of this concept against D. Lack’s criticism see EGI Alex. Lib., D. Lack Papers, XIX. Correspondence, file 403, letter N. Tinbergen to D. Lack (02/11/1945).


403 When N. Tinbergen refers to “P. Weiss” in his publications he means Alfred Paul Weiss (1898–1989), an Austrian-American physiologist who made major contributions to morphogenesis, ontogenetic development and neurobiology by adopting a system theoretical standpoint which,
is, of course, not new. And it is especially interesting to see how ethological study has led to the recognition of the hierarchical structure of innate behaviour quite independently of the conclusions drawn by neurophysiologists. Now the ethologist has been considering higher levels of integration than the neurophysiologist. As a result, a combined picture of neurophysiological and ethological facts shows more levels than those recognized by neurophysiologists. Weiss (1941a) enumerates the following levels from the lowest upward: 1. The level of the individual motor unit. 2. All the motor units belonging to one muscle. 3. Co-ordinated functions of muscle complexes relating to a single joint. 4. Co-ordinated movements of a limb as a whole. 5. Co-ordinated movements of a number of locomotor organs resulting in locomotion. 6. “The highest level common to all animals”, the movements of “the animal as a whole”. (Weiss, 1941a, p 23) The levels 3, 4, and 5 are those studied by von Holst in his work on co-ordination in fishes. As will be clear, level 6 in Weiss’s scheme really consists of a number of levels, in fact all the levels from the “fixed pattern” up. It is interesting that Weiss’s classification stops just here, because it is just at this level that one type of co-ordination changes into another type. But it will be clear that the hierarchical principle is the basis of the organization of these higher levels too. Here again is an illustration of the fundamental identity of the neurophysiological and the ethological approach. The only difference between them is a difference in level of integration.404

I have quoted this passage as a whole because it reveals that N. Tinbergen made out a deficit in A. P. Weiss’ hierarchy of instincts: The upper levels remain underdeveloped and, in Niko’s view, this seems to be the place where the ethologists’ expertise comes in, namely, by proving that what Weiss termed “level 6” reveals some inherent differentiation, too. Insofar it is no surprise that N. Tinbergen interprets his own model as extension of A. P. Weiss’ scheme. Moreover, for my argumentative purpose it is thereby of some interest that A. P. Weiss’ model, and in accordance with that also Niko’s description of it, proceeds from the bottom to the top – a matter of fact that seems to run against the overall thrust of the subsection. Insofar one may say that Niko’s understanding of a synthesis between Ethology and Neurophysiology was nourished by the idea that the heuristic thrusts of both disciplines, that is, the top-down view of ethological reasoning, on the one hand, and the bottom-up view of neurophysiology, on the other, can meet somewhere in the middle, provided that both disciplines think within one and the same physiological model.405 Altogether, Niko’s reception of A. P. Weiss’ model of hierarchical organization is therefore aimed at creating a fusion between Ethology and Physiology: Ethology should cover the fields Physiology spared out and vice versa. Beyond that, both

amongst others, led him to believe that growth of basic neural patterns was to be explained with self-differentiation rather than with learning mechanisms. For more details concerning his life and research see J. Overton. “Paul Alfred Weiss, 1898-1989”. In: Biographical Memoirs of the National Academy of Sciences 72 (1997), 373–386. Expressions of Weiss’ holism, which attracted N. Tinbergen, can be found in P. A. Weiss. “Self-Differentiation of Basic Patterns of Coordination”. In: Comparative Psychology Monographs 17.4 (1941), 1–96 and P. A. Weiss. “Autonomous versus Reflexogenous Activity of the Central Nervous System”. In: Proceedings of the American Philosophical Society 84.1 (1941), 53–64. However, I think, it can be discussed whether P. A. Weiss actually shared the move to the strictly causal analytical framework that has been put forward by early ethologists. This threatened the scientific community of physiologists to break up into clans – a development which Weiss observed with sorrow. See P. A. Weiss. “The Place of Physiology in the Biological Sciences”. In: Federation Proceedings 6.3 (1947), 523–525.

404 Tinbergen, The Study of Instinct, 121–122.
405 See also ibid., 205–206.
disciplines should take into account what they have ignored by realizing the results of the respective complementary area of research. As to N. Tinbergen’s scientific development this led to an integrative model he introduces in two graphics and a concrete application of the illustrated model in the concluding subsection of chapter five. I have inserted an epistemologically reinterpreted fusion of both of Niko’s illustrations in my thesis, particularly, in order to light up the, in the last instance, triadic nature of his model (Fig. 2.5). However, I will not recapitulate the author’s application of the model to the reproductive cycle of the Three-spined Stickleback with which the chapter ends. Instead I will summarize briefly the main features of Tinbergen’s model. At first, Tinbergen’s model is hierarchical insofar as it must be read from the top to the bottom. More general “moods” (e.g. the reproductive mood in spring) precipitate in subordinate centres on various lower levels. Each centre thereby seems to “digest” various types of both internal and external stimuli. Second, with a view upon the nervous centres three different types must be distinguished. Whereas the root – and eventually also the lower regions – of the scheme illustrating the fixed action pattern appear to be rather unspecific, the intermediate nodes are more specified: Intermediate centres receive their motivational impulses from various different sources (i.e. the superordinated centres, hormones, external and internal motivational impulses) and nervous energy cannot flow unrestrictedly from upper to lower centres since this stream is controlled by the so-called innate releasing mechanisms (IRM) which function as “blocks” (more precisely as “removers” of inhibitors) that are preventing the continuous discharge. The very highest centre, by contrast, has no block. If there was, the organism would have no chance to exhibit the nervous impulses at all and a neurosis would be the necessary consequence. Moreover, single intermediate centres or clusters of centres are guided by appetitive behaviours which, in Niko’s view, are controlled by their superordinated centre from which they also receive the major share of their motivational energy. The lower levels of integration, by contrast, lack both the additional parameter “appetitive behaviour” and, if I read Niko’s model correctly, also the inhibitive blocks. Furthermore, the upper centres are loaded mainly by the impulses coming from superordinated centres and their own endogenously produced potential. The lower the level the more decisive becomes the impact provided by external stimulation. “In general it seems”, he underlines, “that the lower we go, the more pronounced the influence of external releasing stimuli becomes”.

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406 Ibid., 122–127.
408 For this hierarchical nuance of N. Tinbergen’s instinct model see also his systemic re-definition of the concept of “instinct” Tinbergen, *The Study of Instinct*, 111–112 and Beer, “Ethology [1/2]”, 176–177.
410 Ibid.
411 According to N. Tinbergen, the latter source of motivation is not certain but he considers this possibility probable. See ibid.
412 Ibid.
413 Ibid.
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Fig. 2.5

N. Tinbergen’s Hierarchy of Instincts (epistemologically reinterpreted version)
Third, also the character of the mutual interaction between the centres of one level seems to alter the more the action pattern approaches the lower levels. While on higher levels inhibition between the nervous centres prevails (symbolized by the arrows between the centres in the graphic), it is especially the levels below the consummatory act which allow the rhythmic coordination of forces by simultaneously activating more than one centre (level 4-7 in Fig. 2.5). The bipartite character of the model as a whole still reveals the twofold origin of Niko’s model in both ethological and physiological theorizing, yet, it also seems to apply the dualistic mode of causal analytical reasoning, which Tinbergen applies to every level of integration and maybe also to each centre, to the scheme as a whole. These coincidences can be interpreted as performative reinforcement of the prevailing analytical epistemic pattern underlying Niko’s scheme. Finally, Tinbergen’s model is reductive inasmuch as it reduces the amount of behavioural options as it proceeds downward through the model. However, this reductive character also appears to be somewhat disturbed since Tinbergen presupposes a unified source of motivational force which, at least theoretically, can spread from level to level into ever finer pathways. Insofar Niko’s model proceeds not only from complex to simple but, implicitly, also the other way round. Next to the recursive character of the differentiations, I interpret this observation as a symptom for the paradox overtone of the causal analytical epistemic scheme underlying Tinbergen’s hierarchical model as a whole.

The attempts of researchers to formulate models can be discussed under various aspects by us science historians. One of these perspectives surely is the validity of a model, that is, the question whether it matches with the empirical data, either in a more analogical or a more direct way. In this case, a model will always be a provisional attempt to reduce complexity and Niko was fully aware of this matter of fact. “It should again be emphasized”, he concludes the chapter, “that these diagrams represent no more than a working hypothesis of a type that helps to put our thoughts in order”. On the other hand, however, models eventually can be interpreted as encrypted epistemic schemes not to say that the habit to make use of models at all eventually is already an epistemic practice based on particular dispositives. In case of Niko’s model of hierarchical organization it is most likely the recursive logic of bifurcation, the top-down view, and the increasing receptivity to external stimulation on the lower levels which let the entire model appear as manifestation of the analytical pattern encoded in each of its parts. Insofar Niko’s model turns out to be a highly sophisticated expression of the mechanomorph attitude which characterized the more theoretical accounts of his classical ethological period after the Second World War. With a view of the current fifth chapter of his book, “An Attempt at a Synthesis”, however, one has to say that the practice of formulating models attains its heuristic function only within a continuous process of testing and re-testing. In sum, therefore it is especially the second part of chapter five which reveals a deconstructive gesture: In a first step, Niko wants to meet the complexity of the actual responses with a fused research program that is consisting both of ethological and physiological constituents. In a second step, his hierarchical model, which is the
result of this fusion, is translated back into the realm of physiological processes. It is this attempt to transgress a boundary which structures the chapter as a whole – the boundary between Ethology and Physiology, between an abstract model and the physical reality of brain functions, and between the recapitulation of former results and the formulation of a future research program. The overall composition of the fifth major section of Niko’s book therefore is less analytic rather than synthetic as its title indicates and this general tenor can only be understood adequately if both the composition of the entire treatise and the place of the current chapter within this edifice are taken into account.

Chapter six, “The Development of Behaviour in the Individual”, reflects on the ontogeny of behaviour, that is, the question how, and on what physical basis, the behaviour repertoire alters during individual growth. The headings of the single subsections, “The Growth of Innate Patterns”, “The Maturation of Innate Motor Patterns”, and “Learning Processes”, in my opinion, already suggest a provisional hypothesis about the inner composition of the chapter: The former two sections which are said to be concerned with “innate motor patterns” seem to build a unit since they treat the same phenomenon (viz. innate motor patterns) from two different angles that is “growth” and “maturation”. The third section which is concerned with learning processes establishes a realm of its own. It refers to a mode of change in the individual which is based upon personal experiences. The linear order of both main themes, the innate and the learnt, that is, nature and nurture, eventually implies that learning, in Niko’s view, can only be treated adequately if underlying innate dispositions are taken into account in the first place. “Further”, he writes in the introductory part of the chapter,

although this book is concerned with innate behaviour, learning processes cannot be ignored entirely. The main reason for this is that all learning effects a change in the innate functions; learning, therefore, is a phenomenon of ontogenetic growth of behaviour superimposed on the innate patterns and their mechanisms. Now although it is a continuation of the growth of innate patterns, many learning processes occur so early in the developmental history of the individual that they often precede the completion of innate patterns. Another and more important reason for including learning in this chapter is the fact that there is a close relationship between innate equipment and learning processes; in that learning is often predetermined by the innate constitution. Many animals inherit predispositions to learn special things, and these dispositions to learn therefore belong to the innate equipment.

The quotation illustrates quite well the perspective under which Niko integrates learning in his book about innate behaviour. Innate dispositions often precede learning processes (chrono-)logically. But even the dispositions themselves, and that is a paradox, are sometimes interwoven with learning before they are complete. In other words, within an epistemological frame which is concerned primarily with individual variability and progressive growth the references to innate dispositions take a paradox position. More concretely it has to be asked what distinguishes innate “growth” from innate “maturation”? N. Tinbergen apparently differentiates between “growth of neural motor patterns” and “the problem of seasonal maturation”.

My hypothesis is supported also by the way Niko introduces learning. See Tinbergen, The Study of Instinct, 142.

Ibid., 128.
of the reproductive patterns”.[418] The former apparently treats processes of growth relative to the individual’s life which is understood as an overall continuum, while the latter takes discrete annual reproductive cycles as a reference point. Growth processes correlated with particular lifespans for their part are treated from different angles by N. Tinbergen.[419] From a point of view which primarily takes into account the body structure being involved, organismic growth may result from developmental processes commencing both from the periphery (development of effectors and receptors) and the central parts of the nervous system (CNS). According to Tinbergen, the special cases of hormonal impacts and the effects of peripheral “conditioning” should be distinguished from the modifications of the nervous system in a wider sense. Taking a standpoint which is interested more in the developmental process itself, there are mainly two basic mechanisms of individual growth, namely the process of self-differentiation of a diffuse whole into autonomous partial structures, on the one hand, and the principle of additive growth, on the other. Although Niko is careful with general conclusions he thinks it might be possible that additive growth is more likely on higher levels of integration. In general, the structures for the consummatory acts seem to develop in the first place, in Niko’s view, while those for the appetitive behaviours take form in later stages. Insofar one may say that Niko’s account on ontogenetic growth inverts the top-down view of his causal analysis. His account of the seasonal processes of maturation does not follow this scheme.[420] It is a causal analysis because it wants to find out what the reasons are for the seasonal changes in both behaviour and structure. And it is hypothetical either because Niko presupposes that no growth of the nervous mechanisms is responsible for the arousal of the annually reoccurring reproductive patterns. “One indication is the fact”, N. Tinbergen argues instead,

From this and other indicators Niko concludes that the nervous mechanisms are present the whole year, while the fluctuations in autochthonous sexual behaviour are a matter of hormonal fluctuations (first distinction). All further subordinate levels of, for instance, the Stickleback’s reproductive behaviour, must be questioned for the relative impact of external stimuli, on the one hand, and endocrine and nervous influences, on the other. And although N. Tinbergen insists upon the great plasticity of possible mechanisms of maturation from level to level, he finally seems to suggest a general principle as well. “So far as I know”, he says,

that the reproductive patterns can be activated out of season by administration of sex hormones, and, as Lashley has pointed out (1938), these reactions seem(s) to be too quick to be accounted for by a trophic influence of the sex hormones on nerve cells.[421]

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maturation of this type is a phenomenon of general occurrence. With the increase of motivation, the elements of a behaviour sequence develop in the order in which they are eventually performed; appetitive behaviour appears first, and the acts which complete the behaviour appear last. Each element appears first in the low intensity, and the order of the increase of intensity follows

[418] Ibid., 137.
[419] In the following ibid., 128–137.
[420] Ibid., 137–142.
[421] Ibid., 137.
In case the quotation could be read as such that the outlined principles apply in fact to maturation in general, growth and maturation would not only differ with respect of the time frame taken into account and the greater importance of the hormonal factor in maturation but also in the epistemic scheme which apparently structures Niko’s heuristic thrust in both cases: While growth of behavioural constituents obviously implies that they occur in reverse order, the elements of those behaviours which underlie annual rhythms develop in the order in which they are eventually performed, as N. Tinbergen puts it. If Niko’s understanding of growth and maturation in *The Study of Instinct* actually proved to be valid must be clarified. In any case, his account reveals his own motivation to systematize the information he had at his disposal around 1948 even into the lowest levels of his tree of ideas. The same can be legitimately said about Niko’s account on “Learning Processes” as well. The particular paradigm in which Niko discusses learning as such is directed both against behaviouristic theories of learning and their subjectivist counterparts: The former rejection is achieved by a stronger emphasis on the question what animals actually learn under natural conditions of life, the latter by stressing the anti-introspective and objective attitude underlying Niko’s interest in learning. “Also, it might be useful to approach learning phenomena from a more naturalistic standpoint than is usually done and to ask”, he writes,

not what can an animal learn, but what does it actually learn under natural conditions? It is extremely difficult to give an exact objective definition of learning. This is due to several circumstances. First, the term comprises a great variety of phenomena. Second, since man has to learn much during individual life, and since most of his learning processes are known to him by introspection, man tends to approach the problems of learning from the subjective side than he does when studying unconditioned behaviour. For our purpose it will do to use the following provisional definition: learning is a central nervous process causing more or less lasting changes in the innate behavioural mechanisms under the influence of the outer world.

In sum, Niko’s understanding of learning is both functional and objectivistic. To put it simply, one may eventually say that he approaches learning concretely from two different angles. On the one hand, he apparently wants to introduce a valuable set of parameters with which learning can be detected and separated from other forms of ontogenetic variability. All these parameters, I think, must be read as if they were presented as the various levels of a recursive causal analytical procedure. That is to say, if changes in the execution of the motor response itself or a corresponding releasive mechanism are observed growth and maturation must be excluded in a first step. To avoid misinterpretations further steps need to clarify whether the behaviour modifications are not a result of “sympathetic induction” and “imitation” rather than learning strictu sensu. What Niko calls “acquisition of skills” is based on growth and not learning either. In order to determine what is innate and what is learnt Niko suggests to raise the animals in isolation either by depriving the

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422 Tinbergen, *The Study of Instinct*, 141.
423 Ibid., 142–150.
424 Ibid., 142–143.
animal from certain stimuli or by deliberately changing the environmental conditions. Finally, individual variability might be an indicator for learning yet the fact that a behaviour occurs in all individuals of a group does not necessarily allow the conclusion that the behaviour in question is “entirely innate” since all individual can be subject to the same environmental conditions. All the aspects mentioned above are meant to prevent the experimenter from making methodological and conceptual mistakes since students of behaviour seem to be liable to take non-learnt for learnt (fallacy of too wide a concept of “learning”) and actually learnt for non-learnt (fallacy of deprivation). The heuristic thrust in this section of the chapter therefore is reductive or exclusive. Niko’s second approach to learned behaviour consists of mentioning several examples proving his hypothesis that innate dispositions rule learning processes at least to a certain extent, or more precisely, that learning process can only modify innate predispositions. All examples also serve to make concrete the provisional definition I have quoted above. Therefore it takes no wonder that Niko at first intends to prove that there actually are innate dispositions of learning. His argument is that animals learn some things more readily than others. Learning which is based on such prefixed dispositions is called “localized learning” which apparently also implies that learning here consists of memorizing the spatial relations between objects (e.g. in the homing ability of *Philanthus*).

Further experiments with Herring Gulls proved that conditioning can be related not only to landmarks but to quite different objects or constellations and that it is an innate disposition which directs the conditioning to special parts of the receptive field, as N. Tinbergen puts it. In this case N. Tinbergen speaks of “preferential learning”. Finally, the fact that special liabilities to learn are not only related to objects and spatial constellations but also to critical periods (e.g. in imprinting), according to N. Tinbergen, is another indicator that learning is supported by innate dispositions. To sum up Niko’s argumentation, there are three different aspects proving the existence of innate learning dispositions, namely dispositions related to landmarks, to a wider range of spatial objects and constellations and, finally, dispositions related to particular linear sequences in time.

Chapter seven, “The Adaptiveness of Behaviour”, is the penultimate one which I will examine for its inner differentiatedness. I tend to interpret this section in connection with the last chapter of Niko’s book which is concerned with “Evolution” since both sections are related primarily to phylogenetic development. In short, the chapter consists of three sections, an “Introduction” and two subsections which are concerned with particular behaviours and the changing scopes of beneficiaries these behaviours are related to. These two subchapters are called “Activities of Direct Advantage to the Individual” and “Activities of Advantage to the Group”.

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425 Ibid., 144–145.
426 For the term “localized learning”, see ibid., 145.
427 Ibid., 149.
428 This would explain the way N. Tinbergen sometimes reduces the four areas of causal analysis (in the wider sense he used the concept in the preface of his book) to three, viz. (1) the problem of causation (here including ontogeny), (2) the problem of adaptiveness, and (3) the problem of evolution (e.g. at the beginning of chapter eight. Ibid., 185). The message would eventually be that (2) and (3) treat discrete aspects of phylogeny, while all chapters subsumed in (1), i.e. chapter I to VI, refer to individual development.
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Needless to say that the latter two sections build a unit since both of them ask for the adaptive value of particular behaviours. At first, Niko insists that modern biologists need to take into account both types of causal reasoning, that is, both ultimate and proximate causality. “A peculiar narrowness of modern human thinking is indicated by the fact”, N. Tinbergen says,

that relatively few biologists seem to be willing to give their attention to both the causes and the effects of observed life processes. Many confine themselves to the study of the causes “underlying” the observed phenomena, as do the majority of physiologist, while others prefer to study the way in which life processes contribute to the maintenance of life, as do most ecologists.

In a second step, he marks the differences of both kinds of causal reasoning. The “both and” vanishes into a “versus”. “Now although I want to argue the necessity of studying both causation and adaptiveness”, Niko writes,

I want to stress at the same time that it is of the utmost importance to distinguish clearly between the causal factors underlying the behaviour of the individual and the biological significance of behaviour. [...] When, however, the fundamental difference between these latter “factors” (ultimate factors, Baker, 1932) and the causal factors at work in the mechanisms of the individual (proximate factors, Baker, 1932) is not clearly recognized, this terminology, derived from two widely different fields of zoology, may lead to a revival of the confusion that was prevalent in the period of old-fashioned teleology, when, in the study of the living animals’ functions, actual causal factors and the biological end were indiscriminately considered to be effective (“proximate”) causal factors. In this chapter the adaptiveness of behaviour will be discussed according to this point of view.

The distinction between both types of causality defines the particular approach in the following subsections both as a whole (emphasis on adaptiveness) and in each single part (emphasis on either concept of causality each). That Niko speaks of “direct” advantages for the individual in the title of subchapter VII.2 therefore is not an accident and eventually indicates that the behaviours discussed under this heading provide an immediate (i.e. proximate) selective advantage for the individual. Their status thus marks a sort of paradox: Feeding and escaping imply disadvantageous side effects but they are still of advantage as the title indicates. The more proximate overtone seems also to determine how Niko differentiates on the lower levels. Here the behaviours of feeding are compared with those of escape.

Niko also speaks of need to distinguish between “individual” and “social elements” in each instinct. See also Tinbergen, *The Study of Instinct*, 157.

Ibid., 151–159.

Ibid., 151.

Ibid., 152. Despite the emphasis upon the ultimate forms of causality, N. Tinbergen is fully aware that this is only half of the truth. Behaviours might be virtually maladaptive (vacuum activities, or displacement reactions), convergent evolution must be distinguished from divergent phyletic development, and adaptiveness is closely related to a particular environmental situation which leads to ecological trade-offs (e.g. conspicuousness vs. vulnerability to predators). (Ibid., 153–154). Adaptiveness in the special case of behaviour encompasses mainly three aspects in Niko’s view. The selective sensitivity to specific situations, the ability to perform directive movements, and finally, the highly specialized nervous mechanisms which make fit together releasive situation and response (Ibid., 156–157).

This is once more a pretty nice example for what I called performative cross-referencing.
Both behaviours are related to nourishment but approach the phenomenon that animals eat each other from two different angles, namely from the side of the predator (feeding) and the one of the prey (escape). Moreover, both behaviours seem to be dysfunctional at least to a certain extent and with a varying degree since both the predator and the prey must invest something when they behave either as a feeding or a fleeing animal. Niko discusses feeding more under the aspect of selective food preferences, while successful escape seems dependent on highly differentiated releasive mechanisms and their adequate connection with the right motor pattern. Reactive strategies therefore can range between fleeing, on the one side, and the freezing of a camouflaged object, on the other. Yet, from a nowadays perspective, a behavioural ecologist would eventually argue that in both cases, feeding and escape, the energy balance is not fully positive since the investment can be high. The activities being of advantage for the group, by contrast, are treated from a truly functional perspective. In general, Niko maintains that the behaviours beneficial for the group are more complicated than those serving the individual. Two of the three behaviours more extensively discussed under this heading are related to courtship and / or sexual behaviours, namely “Mating” and “Fighting”. The discussion of mating encompasses both the question by which means the male attracts the female and the fact that copulation must be guided by synchronized behaviours. Fighting, by contrast, is an antagonistic behaviour. According to N. Tinbergen, it is usually subordinate to the reproductive instinct. Very often sexual fights occur between individuals of the same species and sex. The adaptiveness of intraspecific sexual fighting is ambivalent: Though harmful for a specific individual, he argues, it definitely is advantageous for the species as a whole. “It has become clear”, Niko underlines, that the survival value of sexual fighting is to be found in the fact that it divides certain objects, which are indispensable for reproduction, among as many males as possible. These objects are different for different species, as the following examples will show.

One of these objects is the territory, sometimes it is just a single type of object which is necessary for reproduction (e.g. a mussel in bitterlings or the carrion in carrion-beetles). The most likely object of sexual fighting, however, is the acquisition of a sexual partner. In Niko’s view, this includes both to come into contact with the partner and to prevent disturbance by other individuals. From an epistemological point

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434 If the advantages for the individual are called “direct” one may eventually infer via implicature – that is a form of common sense inference – that the advantages for the group are more “indirect”. N. Tinbergen treats the concepts “self-maintenance”, “biological significance”, “adaptiveness”, “directiveness”, “purposiveness”, “survival value”, “ecological functions”, etc. more or less as synonyms, at least as closely related concepts: “They are all intended to indicate the fact that the mechanisms and / or structures considered contribute to the maintenance of the organism”. See ibid., 151.


436 Ibid., 175–182.

437 Niko here argues for a principle evolutionary biologists usually call “group selection”. Whether the target of selection is the group, the individual or even – as especially the sociobiologists should claim – a single gene is a question that challenged evolutionary theorizing from the very beginning especially, however, in the second half of the 20th century.

438 Ibid., 176.
of view, sexual fighting has an ambivalent overtone. On the one hand, most fighting consists of threatening or bluff. Insofar these fights are unreal. Yet, on the other hand, the comment fighting fulfills the function to prevent the competitor from reproduction just as a dead competitor does. Niko, thus speaks of a compromise which takes into account the fact that fighting is both advantageous and disadvantageous. “The compromise that has developed”, he writes, “is to have releasers that intimidate without causing damage. This is why sexual fighting is often accompanied by an elaborate display of ‘gladiatorial vestments’”. 439 We see how Niko’s applies an analytical heuristic scheme in his discussion of sexual fighting that explores deeper and deeper lying levels of aspects. As such both the account of mating and fighting belong together and precede, at least in the chronology of the reproductive cycle, the behaviour which Niko discusses last, the “Care of Offspring”. 440 N. Tinbergen discusses parental care primarily by questioning how the system of mutual interaction is guided by adequate releasers. Insofar he can distinguish between the side of the receiver and the one of the sender. Readers with some biological previous knowledge will also have recognized that Niko’s arrangement of the behaviours in question corresponds with an increase in the adaptive value. Parental care thus would be the most effective investment of a biological organism. Sexual fighting including the development of the exaggerated morphological structures which often accompanies the fights for territories and females, in this view, would tend to be more maladaptive. 441 Readers may also understand much better now why the truly functional behaviours can be described in terms of “indirect” causality. The advantage results from an organism’s investment into the future of the population (which implies a prospective not retrospective view). And the criterion of selective value is the population number, that is, both quantitative and qualitative progression. However, I would like to stress that N. Tinbergen approaches “adaptiveness” in the The Study of Instinct primarily in more communication theoretical terms. Adaptiveness thus turns out to be a word for the grade how releaser and IRM fit together. “Summarizing this paragraph on social releasers”, he writes, it will be clear that although their function has been experimentally proven in relatively few cases, we can safely conclude that they are adaptations serving to promote co-operation between the individuals of a conspecific community for the benefit of the group. It is a striking fact that all social releasers studied seem to be beautifully adapted to activating an IRM, for a social releaser is always specialized in such a way as to send out stimuli that have characteristics of sign stimuli. They are always relatively simple and at the same time conspicuous. This is why Lorenz considers the social releasers as adaptations to the IRM. 442

Although the benefit of the group and its reproductive success stands in the background of Niko’s reasoning on adaptiveness, he does not instrumentalize population genetics to measure this reproductive success. It should be for the sociobiologists to make the major discoveries related to this set of question. Altogether, one may therefore say that Niko’s account of adaptiveness remains within his overall causal and

439 Tinbergen, The Study of Instinct, 177.
440 Ibid., 182–184.
441 The background of this discussion certainly is the paradox status under which evolutionary biologists from Darwin till nowadays must describe the phenomena related to sexual selection.
442 Ibid., 183–184.
analytical frame. Moreover, Tinbergen’s understanding of “adaptiveness” seems to be influenced by neo-Darwinism since it puts the population right in the centre of its conjectures. In *The Study of Instinct* this leads to a less or more drastic separation of Tinbergen’s theorizing on adaptiveness and evolution of behaviour. I think, Niko’s shift into the “comparative mode” in the 1950s also went hand in hand with the development of an inclusive and multistage methodological model for the understanding of animal speciation as a whole. As I will show below, this model put the heuristic machineries of classical taxonomy at the very beginning (i.e. raising and isolating homological behaviours) but then extended this perspective with a deconstructive gesture by asking for the effects of behaviour in evolution (function of behaviour), on the one hand, and raising the question for the evolutionary mechanisms acting upon the phylogenetic development of behaviour (i.e. causes of behaviour), on the other. Especially the former of the two gestures thereby was about to become subject of reinterpretation since the, in the last consequence, more population genetic accent was abandoned in favour of a stronger emphasis of the synchronism of *adaptive radiation*, on the one hand, and *ritualization*, on the other. In a final step, Tinbergen then used to resolve both preceding moves into a more advanced understanding of divergent evolution. As can be inferred from the following paragraphs of my thesis, in *The Study of Instinct* the constituents of this model are already present yet seem to be spread in a more or less illogical form over the account – with one exception: If my proposed order of the account is correct Tinbergen was inclined to read the question of adaptiveness as a momentum of evolutionary study and this frame turned out to be the prevailing characteristic of his endeavour with systematics in the 1950s.

Chapter eight, “The Evolution of Behaviour”, is complementary to N. Tinbergen’s account of “Adaptiveness” insofar as both final sections of his book are concerned with phylogenetic variability. If Niko’s book must be read as an expression of causal analysis, evolution marks the central problematic. Next to the placement of “Evolution” in his book the entire theme of phyletic variability gains its value also in relation to morphology, the major object of Evolutionary Biology so far, from which the study of the evolution of behaviour is to be derived. Yet in doing so, evolutionary biologists meet several particular difficulties which must be surpassed in the first place: The study of behaviour is both more complex and more time consuming. Moreover, it is more difficult to determine the innate in behaviour. Niko concludes that both factors contributed to the “relatively backward position of ethology” within the field of evolutionary research and that there are more, even more remote, “intrinsic restrictions” whose removal is not in the ethologists’ own power and thus cannot be compensated just by intensifying research. In one sentence, the introductory part of the final chapter states that the evolutionary study of behaviour still is in its infancy and proposes several hypothesis why this is so. At first, in contrast to palaeontology, the study of behavioural evolution cannot work with fossils because behaviour simply does not fossilize and fossils do not behave. Second, embryology, like palaeontology, is of no great use for the student of the evolution

443 Ibid., 185–210.
444 Ibid., 186.
of behaviour since E. Haeckel’s so-called “biogenetic law” (ontogeny recapitulates phylogeny) is even more problematic in the field of behaviour than it already is in morphology. Typology, the comparative study of homological morphological characters, by contrast, is more promising to be applicable to behaviour, in Niko’s view, since every “family tree” which was reconstructed with behaviours must necessarily coincide with one based on morphological data. In so far the typology of morphological characters serves as a corrective for the results attained by studies in the evolution of behaviour. In the last consequence any study of the phylogenetic variability of behaviour must take into account the hereditary character of the behaviours in question and thus must rely on genetics. The backward position of Evolutionary Ethology, in Niko’s opinion, to a large extent is a result of the fact that geneticists mainly relied on morphological characters, while ethologists had no interest in genetics. In conclusion, one may say, Niko’s problem analysis is a causal analysis whose motivation is to distil those results generated by other sciences which promise to be of value for a study of the evolution of behaviour. Niko’s approach thus turns out to be eclectic on basis of a broad synthetic interdisciplinary survey. Next to the more methodological presumptions we also find mentioned a whole bunch of empirical and observational data proving that behaviour can be a promising scientific object for the study of evolution. According to N. Tinbergen, useful observational data can only be obtained by obeying some essential principles of systematic research. “The Establishment of Homologies” thus claims not only the observation of hereditary behaviours. It is also a plea to focus on characters sharing the same grade of complexity. The units of examination therefore should neither be too small nor too large. This rule, in Niko’s view, can be legitimately transferred from morphology to behaviour without loosing its validity. As well, it can be precipitated from several morphological instances revealing the necessity to distinguish between convergent and truly homologous qualities. “Now this is a significant fact”, N. Tinbergen summarizes,

> Purely descriptive study of the above type leads us to conclude that behaviour elements of the type of scraping and quivering are those that can be most easily homologized. It is remarkable that these are exactly the elements which physiological analysis has led us to consider as genetically determined, intrinsically co-ordinated units, the “fixed patterns”. Although comparative study is still in its infancy, the scattered data we possess all point to the conclusion that homologization will have the best chances when fixed patterns are singled out as the units to be homologized. They play the same part as “organs” in comparative anatomy.

From this quotation we may infer that N. Tinbergen’s overall intention in this current subsection of his treatise is to translate the insights of morphological systematics to the evolutionary study of behaviour. Within the field of relevant behaviours the “Homologization of Social Releaser” apparently was particularly promising to N. Tinbergen. “As a special example of evolutionary study of behaviour elements

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446 Ibid., 188.
447 Ibid., 189.
448 To this see mainly the subchapter with the title “Facts Bearing on the Descriptive Study of the Evolution of Behaviour”, ibid., 189–195.
449 Ibid., 189.
450 Ibid., 191.
Niko Tinbergen (1907–1988)

based entirely on the method of comparison”, he says, “I choose the study of social releasers, because they are examples of relatively rapid evolution”.\textsuperscript{451} We see, as soon as the focus of evolutionary research changes from pure systematics (evolutionary statics) to the modes of variability (evolutionary dynamics) another criterion next to the possibility to homologize pops up: “relatively rapid evolution”. In Niko’s view, many social releasers appear to have taken their origin as displacement reactions which have acquired survival value by becoming “ritualized”, that is, by becoming “adaptively refashioned according to the needs of a social releaser: simplicity, conspicuousness, and specificity [...][CL]”.\textsuperscript{452} From a science historian’s point of view we may keep in mind that with the emphasis on ritualization the focus shifts from pure homologization towards a wider interest in the modes of evolutionary change. This more extensive view, however seems to encompass a thorough systematic examination including the physical structure of social releaser and their rudiments (e.g. the mechanism underlying the displacement reactions) as well as a comparative study of ritualized movements in several different species. Finally, N. Tinbergen suggests comparative studies of larger units which are not based on homologies and intend to infer the “the general trends of evolution within larger groups without having made a detailed typological behaviour study”, as he puts it.\textsuperscript{453} To summarize Niko’s account of the facts proving that behaviour is a valid object for evolutionary research, one may say, that ethologists apparently intended to make useful the valuable insights attained by morphological systematists but also wanted to gradually extend their narrow focus on pure typology. Especially the latter aspect at first (and paradoxically) led to a type of study which made use of an evolutionary process (viz. ritualization) for systematics. In a second step, however, Niko develops a rudimentary program for an Evolutionary Ethology which outlines phylogenetic trends by taking into account the transformation of single behaviours only. With this move the first section of the chapter ends. The second part of the chapter is less related to the question how to generate useful observational data and under which methodological circumstances this seems possible. Rather it enters the question of evolutionary mechanisms and finally culminates in a brief outline of the perspectives of an ethological study of man. The question what causes phylogenetic variability thereby is approached from two different angles. On the one hand, Niko asks for “The Mechanism of the Evolution of Behaviour”, that is, what are the causal factors of phylogenetic change in behaviour.\textsuperscript{454} His intention thereby is to test the applicability of genetic theories in the field of behaviour research. Niko’s understanding of these genetical mechanisms of phylogenetic variability surely is influenced by the Modern Evolutionary Synthesis but he seems to remain his own interpretation. “Present-day theories of evolution”, he points out, consider mutations in the widest sense as the basis of all heritable change. The variability due to mutational change may show directiveness of various types, adaptive as well as non-adaptive. Adaptiveness is brought about by selection. Speciation, or the divergent evolution of populations originally belonging to one species, starts with geographical expansion of the species’ range to

\begin{flushright}
\textsuperscript{451} Ibid.
\textsuperscript{452} Ibid., 192.
\textsuperscript{453} Ibid., 193.
\textsuperscript{454} Ibid., 195–201.
\end{flushright}
such a degree that two or more populations of one species become reproductively isolated. The various populations thus isolated are usually slightly different in genetical make-up right from the beginning. This difference, together with the environmental differences leading to different selection pressure, account for divergent evolution of the populations which ultimately results, via the formation of geographical races, in the origin of new species, genera, and even families. Whether this “micro-evolutionary” process is at the bottom of all evolutionary divergence, even of those often called macro-evolutionary, is a matter of disagreement. It is certain, however, that the causes of evolution can only be studied in micro-evolutionary processes.\footnote{Tinbergen, *The Study of Instinct*, 195.}

The quotation reveals that N. Tinbergen interprets the Evolutionary Synthesis in a wider sense (following E. Mayr, Th. Dobzhansky, and S. Wright), that is, he is prepared to take into account both the gradual genic variability which is the product of mutation and selection and the process of speciation through geographic isolation. Moreover, alike to the Ethological Synthesis in neo-Darwinian theorizing gradual variability is connected with adaptiveness though on slightly different epistemic grounds. Whether Niko interprets both realms of the neo-Darwinian Synthesis epistemologically correct, is not entirely clear – his own interpretation both of mutation and speciation, however, seems to follow the ethological scheme. Thus he argues in the first place, that mutations might affect behaviours insofar as innate behaviour elements are no different from morphological characters. Both are the product of physiological structure which in turn is dependent on the organism’s genetic constitution. As an example Niko mentions K. Herter’s study of temperature preferences in white domestic mice.\footnote{Niko’s account of mutation thus consists of two steps: An inferences from phenotype to genotype, on the one hand, and a supplementary example, on the other. And this is the ethological way of treating gradual variability which is counterdirectional in comparison to the neo-Darwinian way.}

In the second place, Niko asks in as much the evolution of behaviour is affected by speciation processes. In Niko’s view, speciation is more a synchronous rather than a diachronous evolutionary process. The ethological study of subspecies and closely related species therefore seems promising to examine the evolution of behaviour “in the making”, as he puts it.\footnote{Ibid., 196.} In concrete, N. Tinbergen discusses mainly three aspects of speciation, namely “Subspecific differences” (e.g. habitat and temperature preferences, as well as more elaborate differences in migrant and breeding behaviours), “Specific differences” (especially social releasers and “fixed patterns” in general), and “Sympatric speciation” (viz. speciation without geographical isolation through sudden change of habitat and succeeding variation of secondary preferences such as mating etc.). All three aspects of speciation are supplemented by some critical remarks on “McDougall’s Work on Lamarckism”. W. McDougall (partly together with J. B. Rhine) had made an attempt to prove that the learning curves of rats could be improved over several generations in spite of McDougall’s method of counter-selection (choice of proband animals with worst learning records for further breeding). “In order to rule out the possibility of involuntary selection in picking out the individuals to be used for breeding”, McDougall’s experiments are described by N. Tinbergen,

McDougall selected the individuals with the worst learning records for breeding. Improvement of learning capacity was found in the offspring in spite of this counter-selection. This seemed
to be the first successful attempt to prove the possibility of Lamarckian evolution in behaviour study.\(^{458}\)

According to N. Tinbergen’s account, the results of McDougall’s experiments have been refuted by other researches who repeated his tests and came to different results. I interpret Tinbergen’s criticism of W. McDougall’s experiments as the attempt to defend his own, more holistic (i.e. systematic) view upon evolution against potential attacks by defining the various forms of adaptive speciation as a necessary prerequisite for subsequent systematic conjectures. I have argued that Niko approached the question which mechanisms cause phylogenetic variability in behaviour from two different angles in *The Study of Instinct*. On the one side, he examined the mechanisms changing the behaviours. On the other side, however, N. Tinbergen totally inverts his perspective and asks which role behaviour played in the process of evolution itself.\(^{459}\) The subsection with the title “The Part Played by Behaviour in the Causation of Evolution” thus in a first step is aimed at proving that behaviour contributes to the survival of a distinct species and therefore is effective during the process of isolation. For instance, according to N. Tinbergen specific aspects of courtship behaviour (synchronization, releasing and directing sexual responses in the mate) play the role of an *isolation mechanism* preventing the interbreeding of species. In a second step, N. Tinbergen elaborates on the role played by behaviour during *selection*. More concretely behaviour has a twofold function in selection: Intraspecifically and interspecifically.

Intraspecifically, mating, fighting, care of the young, reactions of the young to parents may all be selective towards individual members of the species. Interspecifically, predators may select their prey, and in general, competition affects behaviour as well as other adaptive characters.\(^{460}\) In other words, selection embraces behaviours yet the scope of the beneficiaries may change insofar as the unit of selection can be both the individual and the group as a whole. As a result, the debate of selection in the field of behaviour does not change the categories with which evolutionary biologists used to approach the complex phenomenon of selection. This might be one of the reason why in the second half of the 20th century the study of phylogenetic variability received major impulses especially from the field of behaviour research. The examples Niko uses to demonstrate intraspecific variability are mainly examples of sexual selection. Evolutionary biologists tend to resolve the paradoxon that the characters underlying sexual selection usually tend to hypertrophy by pointing out that these qualities, despite their partly dysfunctional character, function as signals for the animal’s fitness. N. Tinbergen’s ethological way to solve this paradox slightly differs from this approach. In his view, sexual characters are mainly social releasers and as such have a proper communicative function. “It is a striking fact”, he argues,

that some of the classical examples of hypertely, such as the enormous antlers of *Megaceros hibernicus*, the giant deer, and the canines of *Smilodon*, the sabretoothed tiger, are organs of a type that would be supposed to be social releasers by the present-day ethologist. We have seen in Chapter VII that releasers, though they may serves various ends, have in common that they

\(^{458}\) Ibid., 200.
\(^{459}\) See in the following ibid., 201–205.
\(^{460}\) Ibid., 203.
all have selective value as means of facilitating social co-operation. Our present knowledge of social releasers justifies the belief that hypertely may, much more often than is generally believed, concern social releasers rather than functionless structures of “luxuries”.461

N. Tinbergen’s examples for interspecific selection are mainly concerned with the competitive relationship between predator and prey. Thereby it is especially the prey animal which makes use of various forms of non-disruptive and disruptive cryptic colouration. In conclusion, one may say that the various roles behaviour plays in the process of evolution supplements Niko’s examination in how far evolutionary mechanisms cause the variability of behaviour. Both major subchapters therefore approach the relationship between behaviour and evolution from complementary sides. They are complemented by some remarks concerning “The Ethological Study of Man”.462 Alike to other ethologists such as E. v. Holst and K. Lorenz, Tinbergen insists that there is no fundamental barrier between animal and man in their accessibility for objective methods of behaviour research. On the lower levels humans resemble other animals in the ways how nervous impulses originate and how they are transmitted in the nervous system. Moreover, there is great conformity in simple coordinations such as reflexes and rhythmic motor patterns (e.g. the patterns of locomotion). Instinctive behaviour in man, according to Niko’s account, has been examined under various aspects: Motor pattern, internal factors (motivation), and external factors (sensory stimuli).463 While the first of the three aspects has been discussed already under the heading “The Lower Levels”, the question of motivation and man’s responsiveness to sign stimuli apparently are treated in the subsection bearing the title “Instincts”. The arrangement of the information provided by N. Tinbergen once more is significant. Altogether his brief outline of Human Ethology thus operates within a causal analytical frame that finally leads to the conclusion that specific human behaviours are based upon innate organization: The motoric part of the nervous circuit is separated from its receptoric side. In the latter case the question of motivation is treated separately from the particular constitution of the innate releasing mechanisms (IRM) and the existence of displacement reactions in man.

Concluding, I am tempted to ask which role the study of evolution played in N. Tinbergen’s research in the first and second decade after the Second World War and, beyond that, which parts of his outline in The Study of Instinct played a major role. As to the former of the two questions, one may say with foresight to the following sections of my thesis, that evolution became Tinbergen’s primary field to elaborate and defend the causal analytical scheme which built a major share of the identity of incipient scientific Ethology. Insofar, I am tempted to argue, that Niko’s analytical approach reveals a shift from Physiology to Evolution – especially after D. S. Lehrmann had formulated his famous criticism of Ethology. Thus I think, science historians have partly neglected that Tinbergen’s engagement with evolution had primarily an apologetic function in the 1950s. However, as I will show below, Tinbergen’s theorizing in systematics hardly went beyond the question in how far the

461 Tinbergen, The Study of Instinct, 204.
463 Ibid., 208.
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The notion of “adaptive radiation through ritualization” can be made fruitful for systematic enquiries. At least this implied a holistic perspective upon the living organism as a unit for selection which ruled out the possibility that selective forces primarily act on isolated characteristics of a living organism including the design of its nervous system. N. Tinbergen, at least in the early decades after the war, apparently did not elaborate the ambitious program of an “Evolutionary Ethology” he sketched in The Study Of Instinct. This thesis particularly applies to the study of Man. It is now time to summarize my reading of The Study of Instinct. Although N. Tinbergen’s book took its origin in oral presentations, the succeeding revision finally generated a highly differentiated (hierarchical) organization of parts and subparts. As a result, one may say that it is mainly the model of causal analysis which N. Tinbergen consequently spelt out from the book’s “root” even to the finest differentiations on the lower level of his “tree of ethological knowledge”. The differentiated order of the book has several implications: At first, there is the possibility to read the structure of The Study of Instinct from simple to complex. As such the book documents the growth of ethological knowledge, its increasing differentiation and, finally, the phenomenon that the location the author assigns to a particular topic determines the way how it is treated and therefore also the result. Second, reading the structure of the book into the opposite direction which means to reduce its complexity one more and more becomes sensitive for the cross-references especially from lower to higher levels. Moreover, descriptive scientific practices such as positioning the picture of a threatening Stickleback at the beginning of the book suddenly become significant. However, it is one of the presumptions of my dissertation thesis that the process of reducing complexity reaches a boundary at a certain point and that, as a result, complementary epistemic complexes coexist next to each other. This can be proved impressively by the fact that Niko’s cooperate empirical studies stand next to his theoretical papers more or less independently despite the fact that both realms are interwoven with each other in manifold ways.464 I have examined both realms of N. Tinbergen’s intellectual life-history through several chronological phases before and after the Second World War. One of the results so far thereby is that the period from ca. 1938 to 1951 and, as will be shown, even farther till 1959 reveals conspicuously few changes on the deep-structure level of scientific change. It is the period of Classical Ethology in which analysis and synthesis supplemented each other in various different manifestations. In Niko’s life-history the phases before his internment (1938–1942), during his captivity (1942–1944), as well as the time in Leiden before his move to Oxford (1944–1949) therefore reveal much continuity despite all the biographical turbulences. This is a clear indicator that not environment per se rather than its subjective sensation is the key parameter of scientific transformation. The kind of interaction between a researcher and his / her environment thereby might be an indicator for the subjective mode of processing individual experiences in each case. My task in the following paragraphs will be to show that Niko’s early years in Oxford perpetuated this continuity in another environment until, nearing the end of the 1950s, another drastic epistemic shift can be made evident.

464 Mostly by the fact that certain areas of research typical for one realm can reappear in the other –
“Drifting” to Functional Ethology
The Disciplining of the “Tinbergians” (1948–1959)

Although N. Tinbergen was highly successful in Leiden he decided to leave for Oxford in 1949. His motivations to give up a full professorship to accept a job as demonstrator which ranked even below the level of a lecturer and, beyond that, meant serious financial constraints for a family with five children, naturally have been subject of discussion both amongst colleagues and science historians. According to his own later autobiographical account, the primary motivation to leave Leiden was to propagate his science of Ethology within the Anglo-American scientific community. In addition to that, there must have been a general feeling of unease with his Dutch surroundings inside Niko in the immediate post-war years. And this general dissatisfaction apparently flared up in several different contexts, such as his disappointed hopes for a more liberal Dutch society, his resentments against those who had collaborated with the Germans, or his growing discontent with the sources of his inspiration which so far had been rooted mainly in the contacts with his German and Dutch colleagues. Moreover, his professorship included a heavy teaching load and additional administrative responsibilities which prevented Niko from doing what he really wanted. According to H. Kruuk, who has, amongst others, carefully studied the correspondences with E. Mayr and Bierens de Haan, Niko first toyed with the idea to move abroad in 1945. Since then the topic cropped up at regular intervals in his letters to his close colleagues. In summer 1948 D. Lack, who had been in contact with Tinbergen since October 1945 at the latest, made a visit at Niko’s summer camp in Hulshurst – with him a letter from Alister Hardy in which the latter offered Niko a job in his department. After some considerations with Lies, his wife, and his brother Luuk, and this always at a significant position.

Kruuk, *Niko’s Nature*, 151–157. For the financial constraints the family had to face see ibid., 163, 200.


For Niko’s early correspondence with D. Lack after the Second World War see EGI Alex. Lib., D. Lack Papers, XIX. Correspondence, file 403, letter C. van der Klaauw to D. Lack (18/07/1946). See also ibid., XIX. Correspondence, file 403, letter N. Tinbergen to D. Lack (27/06/1946) and ibid., XIX. Correspondence, file 403, letter C. van der Klaauw to D. Lack (28/03/1947).

For Niko’s mentor, C. van der Klaauw, had taken much effort to promote him but in return demanded much help and, according to H. Kruuk, Niko “found it very difficult to refuse this, especially since van der Klaauw was also an invalid [...]”. See ibid., 153. On the other hand, v. der Klaauw did not seem to be an obstacle in the professional careers of either Niko or Luuk. This impression seems to be confirmed indirectly in some of the letters D. Lack exchanged with his Dutch colleagues soon after the war. For instance, Lack was interested to get Niko’s younger brother, Luuk, to Oxford for a longer period of time – an idea both Niko and van der Klaauw supported yet Luuk seemed to decline. “I have tried all I could”, van der Klaauw writes to Lack, “but he and Dr. Voûte are of the opinion that it is much better for his work that he does not go to Oxford for such a long time already in the beginning of the new job he has now. No doubt Mr. Tinbergen will have written about this question to you extensively”. See EGI Alex. Lib., D. Lack Papers, XIX. Correspondence, file 403, letter C. van der Klaauw to D. Lack (18/07/1946). See also ibid., XIX. Correspondence, file 403, letter N. Tinbergen to D. Lack (27/06/1946) and ibid., XIX. Correspondence, file 403, letter C. van der Klaauw to D. Lack (28/03/1947).

Niko met A. Hardy for final negotiations in February 1949 and lastly accepted the offered position at Oxford University. A. Hardy had promised to upgrade Niko’s position into a lectureship as soon as possible which was fulfilled by the time Niko started at Oxford. Furthermore, Niko would get an additional fellowship and he was allowed to bring one of his assistants from Leiden for one year. The university provided some work space and promised to obtain additional equipment. At the foremost, however, Niko was guaranteed that he could do as much fieldwork as he liked. Despite all these concessions Niko’s restart in England happened on a far less prestigious position than he had covered in Leiden. And it took another eleven years until N. Tinbergen was promoted to “Reader” in 1960 and further five years until he was nominated full professor in 1966. The reasons for this delay are not fully clear. What certainly played a role, however, was the fact that Niko’s research orientations, which in a wider sense either were part of the neo-Darwinian Synthesis or one of its derivatives, did not fully coincide with one of the great university traditions in England – neither the more experimentalist (e.g. Cambridge) nor the classical utilitarian (Oxford). That N. Tinbergen felt partly uncomfortable with forms and rituals of British academia is evident. Nor developed a continuous cooperation with the central figures of British Ecology, D. Lack and Ch. Elton, whose research facilities, that is, the Edward Grey Institute of Field Ornithology (EGI), on the one side, and the Bureau of Animal Populations (BAP), on the other, were both located in Oxford – a matter of fact which had been originally an important aspect why Niko was attracted by Oxford. Also the Association for the Study of Animal Behaviour (ASAB) whose president Niko was between 1954 and 1957 finally turned out to be an environment in which he felt uncomfortable either. For J. B. S. Haldane, one of the most active figures of the ASAB in the 1950s, Niko

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472 P. Chavot in his thesis has put great emphasis upon the division of labour that existed between both Universities in the fields related to Zoology and, according to his view, was renewed through the reception of K. Lorenz’s founding program. See Chavot, “Histoire de l’ethologie”, 208–213, 214–219, 229–230, and 277–316, in particular, however, 211. Yet, my epistemological analyses show that the older Cartesian field and the concrete places where scientific orientations became manifest in actual research centres could not absorb the positions covered by the Extended Synthesis and its own derivatives in the mid-twentieth century. When I speak of “drifting ethologists” three movements have to be taken into consideration: Backwards, sidewards, and polarization. Chavot’s inference that N. Tinbergen’s move to Ecology occurred on basis of an utilitarian motivation (Ibid., 314–315) therefore raises false conclusions though it is not quite false if Chavot’s statement is referred to the level of causality and this dimension of the utilitarian orientations only. As a result, when we aim to relate representatives of the various different classical research traditions such as W. H. Thorpe (Cambridge) or E. Howard (Oxford) to Tinbergen’s research we have to face more encounters across structurally deviating epistemic communities rather than inside one and the same epistemic community.


474 On Niko’s relationships with other scientists of animal behaviour in Britain see ibid., 194–197.

475 P. Chavot has reconstructed the early history of the Institute for the Study of Animal Behaviour (ISAB) and the structural reform activities leading to the ASAB. He is more prone than Kruuk to emphasize the positive role the institute played for the growth of Ethology. See Chavot, “Histoire de l’ethologie”, 174–187, 203–206, 226–229.
even felt great antipathy. All these facts seem to be an indicator that Niko’s research position was far less integrated in British academia than it was in Leiden. How uprisings, growth and social manifestation of the neo-Darwinian epistemic community especially in the second half of the 20th century changed the institutional and academic landscape in Germany, the Netherlands, the United States, yet particularly in Britain therefore would be of great interest for me.

Despite Niko’s urge to break with his Leiden history there is apparently a great continuity on the deep-structure level of his scientific development. As I intend to show in the following, the epistemological foundation of Classical Ethology on basis of two complementary epistemic realms did not change substantially in the years between 1949 and ca. 1959. And this hypothesis holds both for the analytical and the synthetic epistemic framework both of which N. Tinbergen had already applied in the years before and after the Second World War – with quite different scientific outputs. G. Beale applied the distinction between two basic areas of research in his study of the “Tinbergians” by re-activating R. E. Kohler’s lab-field distinction.

On closer inspection, however, and independently whether Beale had in mind what I have called “realms” when he used the dichotomy as a methodological tool, I think the antinomy lab vs. field, even if it is applied in its deconstructed form (“bringing the field into the lab”, “natural experimentalism”), which, by the way, might be also a natural consequence of the transpositions that occurred on the causal level of the orientation after 1933, does not fully work out – especially, when it comes to grasp the more abstract paradigmatic entities of Niko’s scientific orientation as a whole. A brief glance at the sample of studies I have examined so far reveals that what I have called Niko’s “cooperate studies” encompasses both laboratory works (e.g. the Stickleback research performed together with J. ter Pelkwijk and later J. van Iersel) and projects carried out in the wild or at least in semi-natural environments such as L. de Ruiter’s project on countershading in caterpillars. Conversely, in those of Niko’s papers which operated with a causal analytical heuristic scheme we may find exactly the proximate interpretation of causality which used to be the epistemic basis for the experimentation in the lab. And this linkage can be found in some of his field studies (e.g. his later Philanthus papers), in Niko’s works on stimulus discrimination and orientation, as well as in his more theoretical accounts which had their origin in oral presentations – an epistemic practice which is not covered by the lab vs. field distinction at all (at least not without further additional assumptions). I therefore once more suggest to have a closer look on the epistemic deep structures of both realms and ask for their concrete expressions in each situation (both practical and theoretical). This approach promises to be more integrative, allows to take into account the more and the less conservative historical transformation processes and thus also generates the correct lines of continuity.

In a later letter to M. Welch, Niko mentions that there even had been some kind of campaign against him which, according to his account, was based on rumours and the accusation that he had to leave the Netherlands because he was allegedly involved with the Nazi regime. Niko was deeply hurt since he doubtless belonged to the victims of National Socialism. See Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3146, D 45, letter N. Tinbergen to M. Welch (02/12/1982).

Both realms which seem to stand irreducible next to each other in N. Tinbergen’s scientific development most likely shaped not only his science but also his life. Therefore they must be interpreted eventually as fields of dispositives structuring his scientific practices, the modes of perceiving his cultural environment as well as his everyday behaviours. Although a detailed study of these correlations would require a huge amount of rather detailed biographical information and thus seems difficult to be translated into reality, a few hints can already be given.\(^{478}\) Thus there is some evidence that Niko almost notoriously tended to charge the conversations with his pupils by giving them a scientific function. This also implied a tendency to be over-serious – a matter of fact which at the same time eventually was the source of his strong commitment both to his work and his pupils. On the other hand, we know that N. Tinbergen tended to reduce his interests, a matter of fact, which some people who knew him well even interpreted as single-mindedness. But it was exactly this train of his personality which was the precondition for his capability to abstract and therefore the source of his academic brilliance as well as his sense of humour and his sharp-wittedness. Niko had a vision of his science and life and thus felt an obligation to society which sometimes even reached the state of guilt feelings. “The man who arrived in Oxford”, H. Kruuk writes, “was a charming, brilliant naturalist with a vision for a science, but to those who knew him well, he was also a man with a burden”.\(^{479}\) Maybe, it is not quite false to read the various different efforts N. Tinbergen made to make use of his science either as teacher and “ambassador” of an international scientific community or, later, as admonisher who was concerned about the human predicament and, nearing the end of his career, as missionary on behalf of the misrepresented autistic children as attempts to meet this burden. I tend to interpret Niko’s sense of duty like he conceived instinctive action patterns, that is as some kind of want which renews itself permanently and therefore can only be given a direction. Moreover, his burden apparently could only be alleviated if the amount of effort was increased. In Niko’s later years these efforts increased drastically and even reached the level of self-exhaustion.

One of the scientific practices which had already proved to be useful during Niko’s Leiden period was revived in his new research environment, namely the habit to work in cooperation with his students. Soon after his arrival a group of students, which gave itself the revealing name the “Hard Core”, gathered around the maestro and began to fill the bony grid of Niko’s animal behaviour science with flesh.\(^{480}\) With the help of P. B. Medawar, a late Nobel laureate and great admirer of Niko’s work, the latter managed to obtain several student and assistant fellowships from the British charity and the Nuffield Foundation which allowed him to bind the most intelligent students.\(^{481}\) The early members of the “Hard Core” were mostly PhD-students, such as M. Moynihan, M. Cullen, M. Bastock, Ph. Guiton, D. Blest, F. Hall, R. White (later Weidmann), A. Manning (soon M. Bastock’s husband),

\(^{478}\) See for the following Kruuk, *Niko’s Nature*, 161–162.

\(^{479}\) Ibid., 162.

\(^{480}\) See ibid., 164–173.

\(^{481}\) A brief account of Medawar’s life and research is provided by N. A. Mitchison. “Peter Brian Medawar. 28 February 1915 – 2 October 1987”. In: *Biographical Memoirs of Fellows of the Royal Society* 35 (1990), 282–301.
D. Morris and L. de Ruiter who followed Niko from Leiden to complete his dissertation thesis on “counter-shading” camouflage caterpillars. In addition to the PhD-students, two graduated post-doc researchers linked themselves with the group namely U. Weidmann and E. Sager (later Cullen) who had met N. Tinbergen during his lecture trip to Switzerland. E. Sager’s project on the Kittiwakes of the Farn Islands eventually cannot be underestimated as to its impact on Niko’s later full turn to Behavioural Ecology. Most of the “Hard Core” members made important contributions to their research field and later very often became highly influential members of their scientific community although they headed sometimes into quite different directions. According to H. Kruuk, all of them were highly dedicated and endowed with “an extraordinary ethos of enthusiasm”. Moreover, Niko encouraged them to support each other and created an atmosphere of mutual interest and entirely free sharing of information. Although he, like he did before in Leiden, was the one who often sparked off a project with his initiating idea it was the members of the group who actually were supervising each other’s projects. Most likely the informal weekly get-togethers at Niko’s house have supported this cooperative climate to a large extent. Finally, Niko did not interpret his work group in a restricted sense. It was also open for students who were writing a PhD thesis with another advisor. One of these associated group members was R. A. Hinde who worked on a project on great tits under D. Lack. Also B. Russell who was examining the hormones of Xenopus under A. E. Needham had attached himself with the “Hard Core”, not to mention L. de Ruiter who finally submitted his thesis at the University of Groningen under G. P. Baerends. All these behaviours of Niko’s contributed to institutionalize his view of Ethology and it’s quite obvious to me that his practices thereby were expressions of deeper lying epistemic principles. There are styles of scientific thought and research though, like in N. Tinbergen’s case, restricted to the local research centres (Leiden, Oxford) he shaped with his talent and which he chose to translate his visions fruitfully into reality. This reality, in turn, had a reverse impact upon his own science and life. The more empirical projects which originated during N. Tinbergen’s early Oxford years to a large extent were field studies but also included particular research questions that could only be answered in the lab of the zoological institute. Moreover, they were not restricted to one particular “model organism” (R. Ankeny et al.) or “emblematic animal” (T. Munz) since a broad range of animals (Herring Gulls, Black-headed Gulls, Sticklebacks (three- and ten-spined), Caterpillars, Drosophila Fruit Flies, Kittiwakes, Arctic Terns, Moths, Bumblebees etc.) were chosen as adequate and promising scientific objects. All these provisional observations raise the simple question if, and if so, how all these projects can be interpreted as expressions of one common “spirit” asides the practices which accompanied the process of their production.

(\textit{R}_1) However, on basis of this enduring continuity in N. Tinbergen’s epistemic practices, the discontinuities stand out even more. While Niko himself was closely involved in his student projects between 1938 and 1942 / 1948 and mostly appeared

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\textsuperscript{483} See Kruuk, \textit{Niko’s Nature}, 164.
Niko Tinbergen (1907–1988)

as coauthor of the publications, now, since his move to Oxford, he put into practice a clear-cut division of labour: The realm of empirical research was outsourced and left to the PhD students he now began to advise in larger numbers, while his own writings were more theoretical and had the character of reviews. Niko did not perform own empirical studies by himself. He mainly accompanied the projects of his PhD students by giving critical advise, by producing lots of film material and by reflecting theoretically the results of his work group. “Throughout the 1950s”, H. Kruuk writes,

Niko rarely got his hands dirty with research for himself, and he was personally much less involved, with any one project that was his own, than he had been before. There were no more field trips to study some bird or a problem himself; he became a supervisor, actively participating in fieldwork by several of his students and post-docs, but not holding the reins. He was looking over shoulders, commenting on and absorbing what he saw.484

By withdrawing from own empirical research and restricting one’s own activity to accompanying his student projects in the field and reviewing them later, Niko created two complementary heuristic realms or machineries which were tightly interlocked with each other. While it was mostly his idea, the research of another scholar or, in later years, also the thesis of a previous PhD student which started off a project that was left to the student after this initiating, often critical, moment, Niko’s own reviews applied a complementary epistemic scheme: They picked up the empirical results obtained by his students and supplemented or, more precisely, framed and re-framed them with own theoretical reflections. In doing so, Niko’s reviews, while one or more of his PhD students often appeared as coauthors, created a highly sophisticated and almost perfect mechanism to confront his renegade students with his own vision of Ethology. Hence, Tinbergen’s reviews can be interpreted rightly as a means of academic disciplining. The transformation this mutual and crosswise intertwining underwent in the 1950s is most likely one of the keys to the understanding of Tinbergen’s later turn to Ecology. I’d like to reconstruct this transformation process in the following two subsections of my thesis which are bearing the titles “The Disciplining of the Tinbergians” and “Turning Student(s) of Ecology”. The former of the two chapters, in a first step, asks in how far the works of Tinbergen’s first generation of PhD students at Oxford University turned into a major challenge for their maestro’s classical outline of Ethology. In a second step, I will examine how N. Tinbergen responded to this challenge up to the year 1959. In doing so, I will focus on his theoretical works which, in my opinion, articulate impressively the “re-boundarying work” with which he re-framed the works of his pupils. In the subsequent section I change my own perspective and begin with an analysis of how N. Tinbergen finally responded to the criticism that had been pent up in his work group in course of the 1950s. In a second step, then I will ask how his second generation of PhD students, that is, the younger cohort of students, who has been receiving its academic socialization already within the new framework, finally responded to Niko’s late turn to Functional Ethology. Since I am primarily interested in Niko’s own life-history, I will focus on his part and will only provide condensed reports of the results that could be gathered while reading carefully the

484 Ibid., 189.
theses written by members of N. Tinbergen’s first and second generation of pupils. To measure out the structural impact the theses of Niko’s first generation of doctorate students finally exerted upon his own theorizing it seems necessary to have once more a brief look at the reference system I have put forward in my introduction (Fig. 1.1, page 43). The results I have obtained so far show that N. Tinbergen helped establishing the classical Ethological Synthesis by merging together two divergent sets of frameworks to one heterogeneous scientific orientation which subsequently became subject of at least two further reconfigurations (i.e. causal transposition and re-evaluation of part-theorems). This outline has been established in principle already at the end of the 1930s and since then persisted over turbulent times till the late 1950s.  

Tinbergen’s turn to Behavioural and Human Ecology now, at least at first sight, consists of another secondary process of combining two epistemic frameworks. One of these frameworks is the one which so far had been covered by his and his pupils’ empirical works and which can be called in G. Beale’s words “Tinbergian Practice”. The other set of reference systems comes from the neo-Darwinian Synthesis and appears in Niko’s later ecological papers as a more handicap theoretical framework. If we look at this final transition in Niko’s life merely from his theoretical side (“Tinbergian Theorizing”) we may explain this process as replacement of his former causal analytical (or mechanomorph) convictions by a framework that, too, allowed reduction yet more on basis of quantitative observations and a special emphasis on ultimate causation. In this realm Niko’s late transition appears as a rather abrupt event that can be dated between 1959 and 1962, the date of publishing his final report of his Gull systematics and the appearance of his first paper on egg shell removal in Gulls.  

For us historians this finding is not satisfactory because we would like to know the finer gradations of this transformation process. In other words, what is needed is a micro-history of N. Tinbergen’s late turn to Functional Ethology. I consider it possible to approach this problematic if we take into account an additional aspect: The, in the widest sense, handicap theoretical reference system Tinbergen finally adopted in his ecological papers since 1962 somewhat coexisted next to his causal analytical framework already before – so to speak – as “sidelined knowledge” or, as I’d like to put it, as “non-knowledge”. And the key question is how this non-knowledge was represented not so much in Niko’s own writings rather than the works of his PhD students he advised. Moreover, my analysis of several

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485 I therefore partly disagree with R. Sá-Nogueira Saraiva’s thesis that ethologists dropped the study of adaptedness after 1945 in favour of physiological and evolutionary explanations. For his position see Sá-Nogueira Saraiva, “Classic Ethology Reappraised”, 89, 103. In fact, Ethology’s double configuration as a combination of a causal analytical framework, on the one hand, and the study of functional organism-environment relations, on the other, was emerging since the mid-1930s and was only partly suspended since the late 1950s by those ethologists who, alike to N. Tinbergen, were drifting to functional approaches.

486 Both papers will be discussed further below.

487 A sort of background information: A recent study on “cultures of non-knowledge” (Nichtwissenskulturen) distinguishes three types of communities depending on their gradually differing openness for experience, i.e. a controlled culture of non-knowledge, a complexity-oriented culture of non-knowledge and, finally, an experience oriented culture of non-knowledge. See S. Böschen et al. “Entscheidungen unter Bedingungen pluraler Nichtwissenskulturen”. In: R. Mayntz et al., eds. Wissensproduktion und Wissenstransfer. Wissen im Spannungsfeld von Wissenschaft, Politik und Öffentlichkeit. Bielefeld: Transkript-Verlag, 2008, 203–205.
life courses showed that the kind of frameworks that are bound together in one scientific orientation exerts a sort of “repercussion effect” on how the two reference systems of one orientation are constituted – so to speak – to the inside. In concrete, late Tinbergian Practice differs from early Tinbergian Practice in so far as the final result of Niko’s routine of academic socialization, that is, the dissertation theses of his pupils, became gradually adjusted to the new ecological complement which finally replaced Niko’s causal analytical reference system in 1962. Or, if we prefer the reverse conclusion: Their thesis prepared Niko’s turn by gradually adopting the ecological reference system – a process which seemed to put the maestro under considerable pressure to act finally and therefore might be called also a process of “reverse socialization” or “reverse disciplining”. The epistemological “constitution” of the dissertation theses Niko’s pupils have written between 1950 and 1959 thus can eventually function as finer indicator for the overall transformation process.

In order to test this hypothesis it was necessary to clarify in the first place who belonged to this group of people and whose works I wanted to take into account. Certainly, there is the narrow core of Niko’s own PhD students. In this case we can presume a close relationship between advisor and student as well as among the peers themselves. We may also presume that Niko’s pupils had chosen the “Maestro” as an advisor because they were attracted by his works and attitudes as a teacher. However, as I have already mentioned above, Niko has defined the criteria of belonging to his research group more widely so that students who were supervised by other professors could take part as well. R. A. Hinde, for instance, therefore must be counted to Niko’s research group. In addition to that, there were at least two junior researchers who had written their PhDs with other professors and after that came to Oxford as postdoctoral fellows. To this group of “pupils” belonged E. Cullen and U. Weidmann. The table does not include the works of undergraduates or graduates below doctorate student level since I am primarily interested in the dissertation theses as the type of historical source text which is connected most with Niko’s practice of academic socialization. The theses of the “Tinbergians” (G. Beale) were often published as supplementary volumes of *Behaviour*, the journal Niko had founded in 1947 (e.g. R. A. Hinde, D. Morris, M. Moynihan). Some of his PhD-students, however, preferred to publish their results in the shorter form of journal articles (e.g. M. Bastock, E. Cullen, A. Manning) and in this case preferably also in a journal other than *Behaviour*. The results of some theses were eventually not published at all (e.g. R. Weidmann, M. F. Hall, and Ph. Guiton). The criterion for composing my sample was that the respective dissertation thesis has been published (or in M. Cullen’s case has been accessible otherwise) and that the project was undoubtedly related to the period between 1951 and 1960.

The former of the two criteria excluded the R. Weidmann’s, M. F. Hall’s, and Ph. Guiton’s projects, while the latter ruled out L. de Ruiter’s study since he had begun his project on countershading in caterpillars already in Leiden and finally submitted his thesis in Groningen under the formal supervision of G. P. Baerends. All I have listed Niko’s first generation of pupils in Appendix A of my thesis, table A.1. However, it is possible to read a pupil’s later works as a sort of control experiment which is apt to evince Niko’s impact, so to say, “ex negativo”. For his project see Kruuk, *Niko’s Nature*, 137–138 and Burkhardt, *Patterns of Behavior*, 380.
other studies belonged to my sample and have been examined. The reason why I wanted to concentrate upon the follow-up publications was because they were the final products of a multistage review process. If there was any impact of Niko’s and a teacher’s influence can be made evident in an academic qualification thesis then these publications may eventually (though not necessarily) be an appropriate source.

While I was examining systematically the theses of the before mentioned junior researchers I was applying the following research questions: At first, I certainly wanted to know: Do the works of Niko’s pupils reveal the forms of epistemic deviation (viz. transposition on the level of causation, and epistemic re-evaluations) which are typical both for the Ethological and the neo-Darwinian Synthesis? Second, what is the epistemic pattern according to which the text is organized in each case? The question of order eventually reveals the extent of scientific socialization which acts through epistemic placement. Closely connected with this question is a third one: Are there any deviating fields of research which have been omitted or excluded but are likely to have gained more importance later in the lives of Niko’s PhD students (negative forms of representing non-knowledge)? Fourth, are there particular areas within the compositions of the texts (also themes, thematic-complexes, etc.) where the future turn to Functional Ethology was about to be on its way (positive forms of representing non-knowledge)? How do pupils refer to the theorems put forward by their “Maestro” or peers that have adopted them? Finally, do the texts contain any information how N. Tinbergen reacted to the results generated by his pupils? The last question includes the notion that a researcher’s reaction towards the ideas of another can be reflexive. In other words, they can be second order reactions from the type “I comment on your comment of my propositions”. A speech act of this type would reveal not only something about the attitude of the primary speaker but also (the critical) position the secondary speaker takes relative to the presumptions made by the explicit author. Aspect two, three and four can be summarized under the more general question in how far, and if so, in which form sidelined non-knowledge has been represented in the dissertation theses or major research works of Niko’s first cohort of pupils. This question was my primary emphasis.

My case study was leading to the following results. As far as I can see, all of the examined texts show the two epistemic characteristics which are typical for both the ethological and the neo-Darwinian Synthesis, namely the causal intervention and the re-evaluation of theorems within the reference systems.\footnote{R. A. Hinde’s life course seems to be a special case since he, after having completed his dissertation thesis on Great Tits under D. Lack’s supervision, moved to Cambridge in order to become the head of a small ornithological field station where he stayed for the rest of his career. Maybe, it is not quite false to say that Hinde was and still is a representative of the more experimentalist Cambridge tradition. On R. A. Hinde’s life and career see his autobiographical account R. A. Hinde. “Ethology in Relation to Other Disciplines”. In: D. Dewsbury, ed., \textit{Leaders in the Study of Animal Behavior. Autobiographical Perspectives}. Lewisburg (PA): Bucknell University Press, 1985, 193–203. See in addition Kruuk, \textit{Niko’s Nature}, 184–185, and Burkhardt, \textit{Patterns of Behavior}, 381–382.} On the contrary, with some exceptions, I was not able to trace significant signs of academic disciplining \textit{within} the theses themselves or any signs of secondary responses to possible acts of disciplining. This suggests that N. Tinbergen granted his PhD students a large amount of academic freedom within their theses but also that his disciplining was most likely more predominantly existent in his theorizing.\footnote{Some information concerning Weidmann’s biography can be drawn from his brief autobiographical notes in U. Weidmann. “Uli Weidmann”. In: W. Schleidt, ed., \textit{Der Kreis um Konrad Lorenz, Ideen, Hypothesen, Ansichten}. Festschrift anläßlich des 85. Geburtstages von Konrad Lorenz am 7. 11. 1988. Berlin et al.: Parey, 1988, 168–169, and also from Niko’s semi-autobiographical and semi-popular account “Curious Naturalists” which appeared in German language under the title “Wo die Bienenwölfe jagen”. See Tinbergen, \textit{Wo die Bienenwölfe jagen}, 138, 150. See also Burkhardt, \textit{Patterns of Behavior}, 376, 379–380, 413–415, Kruuk, \textit{Niko’s Nature}, 166–167, 188, 199, 209, 295, 335, and 341.} The question how much critical potential the theses and research works of Niko’s early pupils developed by representing the epistemic realm Niko had sidelined was leading to a more differentiated result which I should like to illustrate in another graphic (Fig. 2.6). The illustration must be read bottom-up and shows the three lines of development which seem to be involved in the early development to Ecology. These lines are Niko’s own theorizing marked by a more abrupt turn (Tinbergian Theorizing), Ethology’s empirical realm which is covered by Niko’s practice of academic supervision and the works of his pupils (Tinbergian Practice) and, finally, the epistemic framework Tinbergen ultimately adopted but before 1962 had more the status of side-lined non-knowledge. Depending on how early Tinbergians were related to this realm there can be distinguished four different reaction types and / or stages of incipient criticism. At first, there were those pupils who felt comfortable with the complementary and heterogeneous construction of Classical Ethology. U. Weidmann, I think, is the most significant representative of this group.\footnote{N. Tinbergen’s theoretical accounts are therefore the more adequate source to answer this question. For more detailed information concerning this question see especially my later readings of Niko’s papers with the titles “The Comparative Study of Species-Specific Behavior”, and “Bauplan-Ethologische Beobachtungen an Möwen”. The former of the two is written together with R. A. Hinde. The latter can also be read as a critical appreciation of E. Cullen’s work on Kittiwakes. See pages 213–221, and 221–228 of my dissertation thesis.} His career eventually stands for the completion of the heterogeneous scientific paradigm of Classical Ethology. Besides those who favoured the status-quo, there were those who signalled a wish for change but formulated potential criticism \textit{within} the framework provided by Classical Ethology. Most interestingly, from the epistemological
Fig. 2.6

Tinbergian Practice and Theorizing in the 1950s. “TTth1” stands for Niko’s early ethological theorizing in terms of causal analysis. “TTth2” refers to the behavioural ecological theoretical framework. “TPr” represents the realm of “Tinbergian Practice”, that is, the sphere within which Niko used to place empirical ethological research.

From this point of view, this form of criticism consisted of the crosswise replacement of the epistemic schemes underlying central scientific theorems while keeping the signifiers themselves intact. For instance, A. D. Blest – as can eventually inferred from a paper he had written in cooperation with M. Bastock, disagreed with Niko’s hierarchical system of instincts and, instead suggested alternative more open and relational model which both authors regarded more adjusted to the phenomena they observed. The crucial question, however, seems to be whether this alternative model was an expression of a proper epistemic alternative or just a reinterpretation of one of the epistemic schemes which were already established and accepted within the double framework of Classical Ethology. I am inclined to argue for the latter interpretation but would like to leave open the question at this point.

496 One indicator might be that M. Bastock’s and D. Blest’s cooperative work was published in Behaviour in 1958 and, beyond that, is composed in a way which is structurally identical with the two papers of A. D. Blest which I discuss here. Another aspect which seems to substantiate my view is the description both authors give of their alternative model (Ibid., 270–273, 275–276). From this account we can infer that Bastock’s and Blest’s attempt to reduce complexity
the other hand, A. D. Blest questioned the epistemic logic underlying Niko’s concept of ritualization which was based on the idea that seemingly dysfunctional displacement reactions gained adaptive value (i.e. communicative significance) in a gradual process of refunctionalization.\footnote{497} According to Blest, the displays could not always be traced back to their origin so that he preferred a more discontinuous framework for his explanations of the origin of the displays.\footnote{498} Nor did he presume that the final displays are more functional.\footnote{499} I think a similar crosswise reconfiguration of ethological core concepts can be detected also in M. Cullen’s thesis. For instance, Cullen seems to have replaced Niko’s concept of territory which in his view was based on two components, namely site attachment and aggressiveness, by an alternative multiple, multistage and behavioural model.\footnote{500} According to his view, establishing a territory might include the initial defence of a particular restricted space but could also be an act of mere social interaction (independent from a site) and, beyond that, might also include parental care, an aspect Niko had excluded from his definition of the “territory” concept. Cullen’s understanding of “ritualization”, by contrast seemed to favour more K. Lorenz’s conception which had stressed the motivational independence of the later developmental stages, that is, both their emancipation and their fixation. Changes in a behaviour’s organization (i.e. the re-arrangement of the elements in an action pattern), the halting of a movement at a certain stage, or the modification of a behaviour’s motivation (i.e. its causation), are all \textit{qualitative} and more discontinuous forms of variation and less the small gradual shifts Niko associated with ritualization because he was interested in ritualization as a means to explain the adaptive radiation and the phylogenetic development of behaviour.\footnote{501} In the life-histories of this group of “anarchist” pupils to which I count especially A. D. Blest and J. M. Cullen, there can be found also signs of interests not represented in Niko’s empirical realm but only in a more or less disjunct form of representation. And it is probable that these interests re-entered the lives of these students at a later stage. For instance, in his later autobiographical accounts, A. D. Blest considered himself much more as a pupil of P. B. Medawar and less of N. Tinbergen.\footnote{502} His affiliation with Ethology ended when he left academia in 1968. In 1974 he returned and henceforth developed mainly two
new research interests, namely the taxonomy of New Zealand Spiders and (later) the functional anatomy of the principal eyes of jumping spiders. From biographical accounts of M. Cullen’s life it can be eventually deduced that he, particularly in the earlier stages of his career, was leading a double life between Mike Cullen the field observer and Mike Cullen the mathematician who was interested in quantitative modelling of animal behaviour. And, like it was the case in A. D. Blest’s biography, it cannot be excluded that this excluded component became represented in his postdoctoral research: After completing his PhD, Mike’s focus shifted from the field to the lab and another species, the Pilchard, whose schooling behaviour he tried to grasp by applying more sophisticated models and techniques than were required in his dissertation thesis. I am inclined to interpret the enormous informal impact Cullen developed upon Niko’s work group with his specific combination of mathematical skill and unusual self-exhausting unselfishness which many biographers underlined in their accounts as a consequence of his double-status in the work group. The fact that system immanent critique articulated itself in form of crosswise re-conceptualization did not decide per se which path the life-histories in question actually took. More careful examinations of D. Blest’s and J. M. Cullen’s life courses are therefore desirable.

The doctoral theses of R. A. Hinde, M. Moynihan, D. Morris and – eventually less explicitly – A. Manning most likely represent a more advanced stage of deviation from the classical ethological framework since this group of young researchers had begun to translate sidelined non-knowledge positively into alternative scientific concepts some of which should later become more refined within the framework provided by Behavioural Ecology. On this stage of incipient criticism, sidelined ideas therefore appeared both more explicitly outside the realm of empirical ethological research and within the realm of Tinbergian Practice – in form of more or less consequent re-conceptualization or re-framing of basic ethological ideas. Most of these attacks were directed against the various circumscriptions of Niko’s causal analytical reasoning such as his hierarchical system of drives but also his later systematic interpretation of evolutionary research which used the idea of ritualization to reconstruct phyletic trees and therefore, in the last consequence, as means for taxonomic reduction. For instance, although R. A. Hinde’s study on Great Tits reveals that he had adopted many core theorems of N. Tinbergen’s ethological research such as the concept of “displacement reaction”, the notion of ambiguous sources of motiva-

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504 G. Beale has put special emphasis upon Cullen’s post-doctorate research. See Beale, “Tinbergian Practice, Themes and Variations”, 128–134, and 282.


tion underlying some behaviours such as “fighting”,507 the distinction between taxis and instinct,508 the interplay of appetite and consummatory act or the threshold economy of drives in general,509 in some of Hinde’s conceptual references, however, we can detect the harbingers of his future critique: Thus, he seemed more critical about the ability to establish homologies of display behaviours since, in his view, these behaviours might also be the product of habitat-specific habituation.510 Also, Hinde adopted Niko’s concept of “Sexual Fighting” but changed it to “Reproductive Fighting” which, as a matter of fact, was leading to a more inclusive view upon the defence reactions taking place in the reproductive cycle and possibly also included the protection of the young.511 In addition, like N. Tinbergen, R. A. Hinde operates with the notion of a hierarchical system of motivational forces. However, in slight deviation to the concept of his master, he suggested that one and the same motor pattern could be triggered by the impulse of several quite different nervous centres.512 We remember eventually that N. Tinbergen’s hierarchical model of instincts had distinguished between inhibitive and cooperative levels of integration.513 Hinde’s suggestion shows his inclination to extend the “reign” of interacting centres to some higher levels. From an epistemological standpoint, this trend must lead to a more variable system and, in the last consequence, to a redefinition of what I’ve called the “overtone” of the entire reference system: Discreteness (here both the discreteness of nervous centres and of separate levels in a model) was about to be replaced by continuity and interaction. Hinde’s intellectual life-history shows that he pushed on and elaborated his criticism further.514 However, a more detailed study would have to clarify whether Hinde’s criticism was fully coincident with the one put forward by other early Tinbergians since his life path eventually differed from theirs. Alike to R. A. Hinde, also D. Morris made extensive use of concepts he had adopted from N. Tinbergen’s writings or were common sense within the scientific community of ethologists. To this semantic repertoire belonged the concept of “territory”;515 “territorial” or “sexual fighting”,516 the concepts of “threat gesture” and “threat code”,517 “displacement reaction” and “ritualization”,518 “appetence” and “consummatory act”,519 the idea of antagonistic motivation as well as the equilib-

507 Ibid., 78.
508 Ibid., 157.
509 Ibid., 145.
510 Ibid., 113.
511 See ibid., 71–87, 87–89.
512 Ibid., 154–158.
513 See page 159 of my thesis.
515 Morris, “Reproductive Behaviour”, 26, 30.
516 Ibid., 13.
517 Ibid., 19, 48.
518 Ibid., 46–48, 109, 111–112.
519 Ibid., 104.
rrium economy of stimulus accumulation and threshold lifting. Under the surface, however, we might also detect the latent criticism that is implied in his research. Thus one may say that his so-called “intersecting gradient hypothesis” (a model to explain the energetic economy of fixed action patterns), his “F-A diagrams” (a model to explain “drive conflicts” whereby “F” stands for “flee”, “A” for “attack”) and his replacement of J. v. Iersel’s concept of “spine fighting” by his own term “roundabout fighting” still stayed within the framework of classical ethological reduction or modelling although they already demanded a more of quantification and thus were able to take into account a more complex world. However, some aspects in his work imply more substantial criticism: Like R. A. Hinde, D. Morris’ felt uncomfortable with Niko’s attempt to explain a great variety of action patterns with one single principle. Their main objection was that Niko’s model operated with an illegitimate generalization. Although Morris did not question the heuristic value of Niko’s model as a whole, the modifications he suggested nonetheless were far-reaching enough to shake Niko’s analytical frame. What were these modifications and why did they exceed the epistemological foundations of Classical Ethology? Morris had observed that some action patterns such as “Collecting”, “Boring”, “Fanning”, “Mending”, “Insertion Gluing” and “Retrieving” can co-vary not only with one but with several different phases of the reproductive cycle. That is, the frequency of their occurrence in course of the time line can reveal not only one but more than one quantitative peak. As a result, it became difficult to subsume these multifunctional behaviours to one single motivational sub-centre as Niko’s model had presupposed. “Summing up the above”, Morris concludes, it is clear that is it far from easy to state that this action is a nesting act and belongs to the “nesting sub-centre”, or that that action is parental and belongs to the “parental sub-centre”.

In other words, D. Morris’ observation of multifunctional behaviours questioned, at least to a certain extent, the notion of rigid centralization as a whole. A less centralized form of reducing complexity was demanded. Morris’ solution to the problem was to treat behaviours such as collecting, boring, and fanning as discrete units (which is per se an atomistic stance) whose frequencies could be measured quantitatively relative to the time line and therefore also relative to each other. In doing so, it could be made evident that certain behaviours were statistically correlated and therefore must build a nervous centre together. Yet these units were to be determined by statistics and less aprioristically. With a view of the reproductive cycle of Pygosteus he therefore coins the concept “CBF”-unit which means that “Collecting” (C), “Boring” (B), and “Fanning” (F) build a complex which is activated as a whole. Altogether D. Morris’ conceptual modification thus implies a more polycentric model of causation. And although D. Morris tended to restrict his idea to the level of the “sub-centres” it, nonetheless, had the potential to overthrow Niko’s

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520 Morris, “Reproductive Behaviour”, 33, 43, 100.
521 For these three areas of conceptualization see ibid., 95–98, 48–51, 18.
522 See ibid., 98.
523 On his general approval see ibid., 138.
524 See ibid., 139.
idea of “hierarchization” altogether. There is another field which faced potentially consequences through D. Morris’ thesis. The reason for this is the fact that he did not only interpret his de-centralized model in terms of central nervous organization but also in terms of phylogenetic development and systematics. The fact that D. Morris published his thesis (or a shortened report of it) four years after having submitted it provided the opportunity to react to the signals sent out by his readers in general and his teacher in particular. Morris’ phylogenetic conclusions thus can be read as reciprocal comment of N. Tinbergen’s attempt to maintain his causal analytical interests by transferring the model from the field of central nervous organization (where he had to face serious objections) to the area of systematics. In other words, in making systematic a theme at this distinct location of his thesis D. Morris tended to translate his decentralized view into the field of systematics, as well. How is that? The fact that fanning reveals a statistical peak before the actual parental phase, Morris speaks of “pre-parental fanning”, is explained with an admittedly tentative theory of his. Hypothetically Morris was assuming an increasing divergence of pre-parental and parental-fanning. In his view sexual behaviour extended to later stages of the reproductive cycle and there led to a gradually increasing functional differentiation of those behaviours which had been originally associated with care-of-offspring behaviour. In other words, pre-parental fanning may be the product of an adaptive speciation in the later stages of the cycle and not the dysfunctional initial part of a ritualization process which had been one of Niko’s favoured approaches to explain those transformation processes whose understanding, in turn, surely helped to generate the broader data basis being necessary to derive a valid picture of the taxonomic system in question. In a concluding remark D. Morris therefore points out:

If the concept of CBF unit is valid, it makes it impossible to consider pre-parental fanning in Pygosteus as displacement fanning. (This is certainly in line with all other indications in this species.) I suggest that the evolutionary explanation of this is that sexual behaviour has appeared later and later in the reproductive cycle and has wedged itself in, so to speak between the earlier and later stages of behaviour associated with care of the offspring. It is plausible that eggs were once laid in dense clumps of weeds, where the male protected them from enemies. Later the male probably strengthened the host clump himself, eventually covering the eggs with a rough nest. Although this is undoubtedly improved their protection, it must have increased their aeration requirements. Thus, building and ventilating (CBF) probably became intensified together in evolution. But selection may have favoured those males which began to build before they possessed eggs. (We have seen that it is more difficult to build a nest around eggs than it is to make a nest before acquiring eggs.) In this way, the care-of-offspring behaviour became partially separated into two phases – pre-parental and parental. This partial separation would explain many of the present difficulties. Although I shall comparing Pygosteus and Gasterosteus below, it may be said at this stage that this separation seems to have gone further in the latter species. (In birds, the separation of nesting from parental behaviour is much more distinctly marked.) It must be borne in mind that the above evolutionary remarks and suggestions are extremely hypothetical, and must be regarded as highly tentative. Something of the kind is necessary, however, to emphasize the fact that nesting and parental behaviour patterns are far from distinct from one another in Pygosteus, and to stress that it is therefore dangerous to talk of any of their component actions as occurring as displacement activities, without very special confirmative evidence. When a bird regularly wipes its beak during courtship, the action of beak-wiping is so distinct from any sexual activity, that there is little danger in calling it a displacement activity,
but when *Pygosteus* performs fanning during the pre-parental phase, it is very dangerous to this displacement fanning, simply because no eggs are yet present. Summarising, it may be said that, in the case of *Pygosteus*, it is not helpful to speak of a nesting centre or a nesting drive, or of a parental centre or a parental drive. Rather, it is better to consider separately each response which is functionally concerned with the care of offspring. This avoids a number of difficulties which arise of one attempts to fit all the results into a rigid hierarchy system.\(^{525}\)

I have quoted the whole passage because I think it shows impressively that D. Morris’ critique was based upon deeper lying epistemological objections against the causal analytical scheme which partly prevailed in Classical Ethology – objections which precipitated in several discrete though closely interrelated areas of his research. The multiple occurrence of fanning in the reproductive cycle of the Ten-spined Stickleback brought him to question Niko’s fully centralized hierarchy system. The fact that nesting and parental behaviour were “far from distinct from one another” contradicted a substantial precondition of the concept of “displacement reaction”: The *disruption* between the conflicting primary behaviours and their “sublimatory” secondary substitute which seems a necessary consequence of a model operating with the notion of “sparking over”. In D. Morris’ view nesting and parental behaviour are distinct though closely interrelated parts of one and the same complex centre. As a consequence an alternative phylogenetic explanatory model had to be found. If I am not mistaken and if I am not misreading the quotation above the solution D. Morris suggested for the difficulties he had observed was a model for phylogenetic variability which presupposes adapted differentiation on later stages and as such, at least from a more epistemological standpoint, seems to resemble the inherent “logic” we know from *sympatric speciation*: The accumulation of adaptive differences.\(^{526}\)

For me it is quite exciting to observe that the invention of building a nest in Morris’ account bears a nuance of dysfunctionality since the nest must have reduced the supply with fresh water and therefore generated the need for fanning in the second place. Besides the more or less far reaching forms of

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525 Morris, “Reproductive Behaviour”, 140–141.
526 D. Morris’ alternative model of phylogenetic change implied that – if the adaptive separation of pre-parental and parental fanning was taken as the primary criterion – the Ten-spined Stickleback was actually the phylogenetically younger and more adapted species, while the Three-spined version turned out to be the more rudimentary form. Most interestingly, this exactly was the proposition Niko was attacking in one of his “disciplining” studies being concerned with the defensive behaviour system of both species. See R. D. Hoogland et al. “The Spines of Sticklebacks (Gasterosteus and Pygosteus) as Means of Defence against Predators (Perca and Esox)”. In: *Behaviour* 10.3/4 (1956–1957), 205–236. Within the group of sticklebacks the species with the fewer and more elaborate spines (*Gasterosteus*) turned out to have an advantage in comparison to *Pygosteus*. As soon as the results were interpreted on the grounds of evolutionary theory the species-specific anti-predator devices turned out to be correlated with particular behaviours (mainly of the reproductive system) as well (For the correlation with behaviours see ibid., 233–235). Thus Niko claimed that the Three-spined Stickleback differed from its Ten-spined colleague in its boldness, its tendency to choose more open habitats, the more elaborate habit of females of wandering and schooling in spring and, finally, which again is a more morphological aspect, the animal’s obviously more pronounced colouration. As a result, Niko inferred that although both systems of growth, that is, the protective-morphological system, on the one hand, and the reproductive-behavioural, on the other, must have developed independently in the course of evolution, they nonetheless turned out to be closely intertwined with each other: The emergence of more striking protective devices resulted in a sort of “liberation” of the behavioural system of growth. In Niko’s model of evolutionary change, the
critical reconfiguration of basic concepts within Morris’ thesis, the treatise is also of utmost value for my argumentative purpose because it contains information about sidelined themes which Morris regarded worthy to be addressed in later research. Among these subjects are the avoidance of intraspecific aggression through the establishment of social hierarchies, the question of individual recognition and the effect of experience upon the interaction of stimulus and response in general. For me it is quite exciting to read in D. Morris’ autobiography how his research interests in the aftermath of his PhD shifted into a direction which allowed him to represent the previously sidelined aspects. One of these new areas of research was the social behaviour in finches. Another was the function of social hierarchies in reproductive behaviour – a theme in which Morris saw a link between his earlier research and his later interest in human behaviour. In his interest in supernatural stimuli which had also raised his attention we may eventually see the reappeal of a classical dilemma with which already Darwin had struggled: How can excessively conspicuous morphological and behavioural structures have an (advantageous) biological function despite the fact that they might be maladaptive at least at first sight. The fact that he picked up “the paradox of natural selection” (C.L.) reveals also that Morris’ attitude towards ethological theory had changed in comparison to his early admiration of K. Lorenz’s partly speculative views. In this context, it seems to be a quite significant detail that Morris describes the scientific achievements of his later Oxford years as accidental by-products and the effect of pure chance.

M. Moynihan’s thesis on reproductive behaviour in the Black-headed Gull reveals a similar ambiguity: On the one hand, there are many cross-references to Niko’s works and other members of the work group which show that M. Moynihan applied in his own research many ethological key concepts such as a general understanding of endogenous motivation (vacuum activity, threshold economy), the possibility of ambiguous motivation, a concept of “ritualization”, of “displacement reaction” or “appeasement gesture”. On the other hand, however, his methodology shows conceptual reconfiguration. For instance, Moynihan distinguished between “pairing territories” and “incubation territories” so that his understanding of the concept of “territory” seems to be as wide as R. A. Hinde’s. Moreover, he had developed his own idea of “motivation” by distinguishing it from the, in his view, development of a more striking defence mechanism (in concrete the reduction of the number of spines) was leading to a secondary effect of liberating the behavioural system which let appear the Three-spined form as the younger and more adapted animal. Niko’s model of adaptive liberation thus was standing against Morris’ model of adaptive splitting. From this detail we may conclude that Niko’s intention actually was to maintain and defend his own – that is the classical ethological – epistemological framework. The dates of both publications show that Morris’ study was published later so that it can be read as a response to the one which originated under Niko’s auspices.

See ibid., 104, 109.
Ibid., e.g. 24.
Ibid., 31, 73.
Ibid., 44, 68, 115.
Ibid., 70.
Ibid., 121–122.
narrower concept of “drive”. In contrast to the more rigid drives, he argues, motivation stands for “combinations or mixtures of other motivations” and this, too, might indicate a system with multiple centres.\textsuperscript{535} Readers should also be alert when Moynihan speaks about “the nature of ritualization”.\textsuperscript{536} It is quite interesting to observe that Moynihan at this point did not simply adopt Niko’s concept who had defined “ritualization” as a process in course of which a primarily dysfunctional or decontextualized action pattern gains biological meaning as a symbol of communication. Moynihan’s approach to the theme is a critique of K. Lorenz’s concept. In the view of the latter, K. Lorenz had interpreted ritualization more as a process of emancipation in course of which the behaviour in question becomes more and more detached from the original conflict situation in which it had appeared in the first place. Moynihan’s observations of his Gulls apparently contradicted this view. “Lorenz states”, he says,

that displacement activities, as they gradually become ritualized, lose connection with the conflict situation in which they originally appeared. Such originally displacement movements must then, he implies, acquire some internal independent motivation of their own. The obviously ritualized Choking of the Black-headed Gull, the larger part of which must have originated as a displacement activity, does not seem to agree with this scheme. | Choking certainly remains in a conflict situation; and there is no reason to believe that this is not its original conflict situation. [...]\textsuperscript{537} It is quite true, of course, that Choking can no longer be called allochthonous (employing Kortlandt’s 1940 terminology). Choking has diverged from its original example(s), and is evidently no longer a pure displacement “outlet”. Choking must be autochthonous. But ... the acquisition of an autochthonous motivation is not necessarily the acquisition of some independent internal drive specific to the ritualized movement alone. Choking is still motivated by a combination of attack and escape, and these attack and escape drives do not appear to be qualitatively different from those motivating other threat patterns and conflict situations.\textsuperscript{537}

In other words, the concept of ritualization Moynihan inferred from his own observations, alike to Lorenz’s view, assumes a process in course of which a new motivational state emerges yet, in contrast to Lorenz, Moynihan also presumes that the original ambivalent motivational state perpetuates. On the other hand, despite their greater continuity in terms of motivation the phenomenological appearances seem to differ more drastically than the mere idea of ritualization seems to allow: “Although”, Moynihan writes,

these displays can thus be regarded as “conservative” in motivation, they are undoubtedly changing in one respect. Like the displays cited by Lorenz, these behaviour patterns have become, or are becoming, new “Erbkoordination”, (fixed motor patterns).\textsuperscript{538}

In general, both options discussed by Moynihan at this point of his thesis seem to contradict Niko’s concept from an epistemological point of view because the general heuristic overtone of the frames apparently deviates from the one underlying Tinbergen’s concept: Something qualitatively new emerges during ritualization yet not (as Lorenz had assumed) on basis of an entirely new motivational situation that has been detached more or less completely from its original nervous

\textsuperscript{535} Moynihan, “Some Aspects of Reproductive Behavior”, 19–21.
\textsuperscript{536} Ibid., 73–74.
\textsuperscript{537} Ibid.
\textsuperscript{538} Ibid., 74.
context.\textsuperscript{539} On closer inspection, Moynihan’s concept of ritualization, thus also implies a fundamental critique of N. Tinbergen’s concept – a move which, from the epistemological standpoint, required even more conceptual investment than his re-conceptualization of “territory” and eventually also of “motivation”. There are also some sections in Moynihan’s thesis which seem to refer to latent knowledge. Thus, like in D. Morris’ thesis, we find the statement that the Black-headed Gull is a species whose reproductive system is based on territorial behaviours and less upon the establishment of social hierarchies regulating the access of the males to their female partners.\textsuperscript{540} In so far one may say that the choice of the species, which eventually is also the point where we may see the effect of Niko’s supervision, excluded \textit{per definitionem} a certain set of research questions which potentially could reappear at a later date. Another aspect which is explicitly excluded in Moynihan’s thesis is the entire field of Breeding Biology.\textsuperscript{541} Whether this restriction has deeper lying epistemological reasons is an open question. However, on basis of N. G. Smith’s brief biographical account we may safely infer that it was especially Moynihan’s later paper on the appearance and replacement of displays and his book on cephalopod communication which should be read as a highly original comment of his Oxford years and the several unanswered questions raised during that period.\textsuperscript{542} This seems to indicate that his later research put forward a model to explain the origin and development of displays that eventually deviated both from Niko’s and Lorenz’s focus on ritualization.

A. Manning’s thesis which was concerned with the foraging behaviour of Bumble-Bees is a fascinating document in the history of the behaviour sciences because it attacked K. Lorenz’s “special phylogeny of releaser” and, in my opinion, reinterpreted it in a more ecological framework by claiming that the insect’s adaptation is guided by some kind of law of parsimony. “Once bees have found a good crop”, Manning underlines,

\begin{quote}

it is clear that their behaviour is most flexible, and they can adapt themselves to any peculiarities of the plant concerned. Thus they rapidly become conditioned to the general form of Hound’s-tongue, because its flowers are of little use in guiding them, although it is likely that such a resort will be necessary with only very view of the plants upon which they feed. Conversely, bees will not learn any more than is necessary. When the flowers are conspicuous enough, as with Foxglove, they rely entirely upon them and learn nothing of the plant’s general form.
\end{quote}

Adaptation thus seems to encompass a twofold tendency: While the range of objects becomes wider in a process of becoming independent of direct stimulation,

\textsuperscript{539} Other pupils of Niko’s seem to have shared this idea of gradually shifting motivational states. For instance, D. Morris, made the attempt to explain “ritualization” as a process in course of which the intensity level of a behaviour pattern becomes more and more fixed. See D. Morris. “‘Typical Intensity’ and Its Relation to the Problem of Ritualisation”. In: \textit{Behaviour} 11.1 (1957), 1, 7, 10.

\textsuperscript{540} Moynihan, “Some Aspects of Reproductive Behavior”, 118, 192.

\textsuperscript{541} Ibid., 1.


\textsuperscript{543} Manning, “Some Aspects of the Foraging Behaviour of Bumble-Bees”, 198. In K. Lorenz’s view the transformation of the IRM via conditioning was conceived strictly negative as “degeneration” because the decrease of the complexity of the perceptive schemata was described exclusively in terms of “Ausfall” (fall out) and the “loss of” qualities. Lorenz’s theory of “degeneration”, in turn, had been one of D. S. Lehrman’s points of criticism in 1953. In so far, A. Manning’s
the constitution of the corresponding releasive mechanisms seems to change in an analogous manner: The process of conditioning which A. Manning used as an explanation of this process not only includes the capacity to acquire and memorize previously made experiences but also encompasses a process of abstraction. Manning here seems to recapitulate K. Lorenz’s hypothesis that an animal’s releasive mechanisms mirror approximately the constitution of the outer world. Thus he states:

The cases describe in this paper show how, since bees will adapt their foraging behaviour to meet any requirements of the particular crop, a plant may assume a considerable degree of “control” in the evolutionary relationship between itself and the bees which pollinate it.544

To grasp the novelty of Manning’s thesis correctly it would be necessary, however, to describe more carefully this process of abstraction, that is, the side of the releasive mechanisms, as well as the way the realm of the sender and the one of the receiver are related to each other. Is this process of abstraction a more discontinuous act such as, for instance, the concept of “gestalt perception” implies or have we to do more with a continuous process being mediated by a more rudimentary form of individual variability which is guided by the leading “principle” of behaving economically? My impression is, that A. Manning at this point re-introduces the so-called “rule of parsimony” which was first formulated by C. L. Morgan in his Introduction to Comparative Psychology (1894) but then was also adopted by some behaviourist theoreticians and later, in a modified form, also by ecologists.545 If A. Manning was about to relocate Lorenz’s environmental theory into a more reductive functional framework it would be another striking example how Niko’s pupils modified core concepts while leaving behind Classical Ethology. However, Manning’s re-framing of K. Lorenz’s Special Phylogeny of Releaser seems to based on an alternative reading of the manner how Lorenz’s model is to be interpreted within the concept of the nervous circuit. When I write “alternative reading” this is meant to say “alternative to the reading implicitly favoured by N. Tinbergen”. And this structural discrepancy, I think, is the deeper lying epistemological reason why Niko’s later research on autism established a sort of break with his pupils despite ecological view could also be interpreted as a reaction towards this critique. That Lehrman’s critique influenced Manning’s life-history can be read in his autobiography. See A. Manning, “The Ontogeny of an Ethologist”. In: D. Dewsbury, ed. Leaders in the Study of Animal Behavior. Autobiographical Perspectives. Lewisburg (PA): Bucknell University Press, 1985, 291–292. Manning, “Some Aspects of the Foraging Behaviour of Bumble-Bees”, 199.

544 For Morgan’s canon and its impact on Behavioural Ecology see F. Cézilly, “A History of Behavioural Ecology”. In: É. Danchin et al., eds. Behavioural Ecology. An Evolutionary Perspective on Behaviour. Oxford: Oxford University Press, 2008, 12–13. From the epistemological point of view, Morgan’s canon implied a scale of psycho-physical performances and claimed that it was “unwarranted to refer to higher psychological structures (such as intention or will) when simple systems of the reflex or tropism type could adequately account for the behaviour observed” (Ibid., 12). However, I see at least one difference between Morgan’s law of parsimony and A. Manning’s latent principle to behave economically. While Morgan’s rule is more of a warning directed towards the observer, in Manning’s view the perspective of the object prevails. It is therefore less anthropocentric. Moreover, in Morgan’s perspective negating higher psychological structures is meant to be of advantage for the experimenter, while the causal architecture applied in Manning’s concept presupposes adaptation yet in its final stage thinks a moment of foreign control.
the fact that he developed a homogeneous ecological scientific orientation by himself.

All examples of conceptual reconfiguration I have mentioned so far affected single and subaltern frames within the argumentative edifices of the dissertation theses in question. This changes in the final stage of deviation I have outlined in my illustration above (Fig. 2.6). It is represented by the research works of two women, M. Bastock and E. Cullen. They were “renegades” in so far as in their works conceptual criticism – most likely triggered by the deviating character of their scientific objects – reached a level of coherence that was capable to shape the entire organization in which they presented the results of their works. In short: In Cullen’s and Bastock’s works, the representation of side-lined knowledge reached a paradigmatic level. Remarkably, these studies were primarily not published in Behaviour, the journal Niko had founded to spread Ethology in the Anglo-American world. E. Cullen’s study on adaptations in the Kittiwake’s cliffnesting behaviour appeared in Ibis, the journal of the British Ornithologists Union. If I am not mistaken, the results of M. Bastock’s PhD thesis were published in mainly two shorter papers which eventually must be read together. One of them, the one she published together with her later husband A. Manning, was a more descriptive study mainly concerned with the courtship display of Drosophila melanogaster. It appeared in Behaviour in 1955 which, I think, is a significant information in itself. The other paper, eventually the primary publication of her thesis’ results, appeared in Evolution. Evolution was the publication organ of the Society for the Study of Evolution which had been founded by several so-called “architects” of the Modern Synthesis in 1946 with G. G. Simpson as the society’s first president and E. Mayr as its secretary and, I think, this information might be significant, too. According to V. B. Smocovitis, the journal Evolution was meant to “[...] serve as ‘one voice’ not only for the new scientific society in the United States but also for an international audience of evolutionists”. And it


548 See Smocovitis, Unifying Biology [1996], 64. For the journal’s objectives see also Smocovitis, “Organizing Evolution”, 279–280.
was this general tenor to unify, to gradually reduce complexity or to bring order into chaos which was matching with Bastock’s research attitude: In short, M. Bastock’s thesis may be read as sophisticated train of subsequent arguments making more and more plausible that one gene can be correlated with a definable behavioural expression. This heuristic technique is based on gradual, probabilistic and quantitative reduction and thus deviates as a whole from the causal analytical framework of classical ethological methodology.  

Alike to the theses of other Tinburgians Bastock had adopted the specialist terminology being cultivated in Ethology, in general, and by Niko in particular. The earlier of the two papers thus seems to contain more references to the concepts of Niko’s ethological research. Thus we find the remark that the behavioural element of “orientation” shares some of the characteristics of appetitive behaviour. In general, the fact that M. Bastock translated the behaviour sequences into a threshold model of fluctuating motivation reveals the impact of the ethological concepts which were common knowledge in Niko’s work group. The same applies to her use of the concepts of antagonistic drives, displacement reaction and ritualization, and appeasement gestures. However, there are also some key concepts of Bastock’s research in which she seemed to exceed the Tinbergian framework. To this scope of theorems surely belongs her model of motivation underlying the courtship patterns of *Drosophila melanogaster* she and Manning had been studying. Thus she rejected both the idea that fruit fly’s courtship could be adequately described as a fixed linear sequence and a model according to which

549 Contrary to M. Cobb’s thesis who claimed that Bastock’s thesis “heralded the beginning of a shift towards the kind of reductionist, causal explanations of behaviour that are commonplace today”, my opinion is that more likely it was the move away from Ethology’s “mechanomorph” orientation which provided the basis for Bastock’s findings. For Cobb’s thesis see Cobb, “A Gene Mutation Which Changed Animal Behaviour”, 163. If I am not mistaken, M. Cobb also explains the fact that Bastock’s work did not receive the attention it should have deserved with the closeness of her study to Niko’s research and the implicated consequences. Three major causes are mentioned: First, the rising criticism in Ethology soon let appear outdated the theoretical framework of Bastock’s thesis (Ibid., 167). Second, the more holistic approach cultivated by N. Tinbergen and his pupils made her thesis unattractive especially for the newly arising Neurogenetics which favoured a “single-gene approach” that allegedly had turned out to be more productive (Ibid.). And finally, Niko’s appreciation of genetics was light-hearted. In contrast to Bastock herself who was primarily interest in actual phenotypic expressions of genes and Mayr who had focused on sexual isolation Niko saw in genetics eventually merely a potential tool for his comparative behaviour studies. For Niko’s ambiguous relation to Bastock’s research see ibid., 167–168. For the three different approaches of Mayr, Tinbergen and Bastock to Drosophila genetics see ibid., 164. I think, it’s just the other way round: Bastock’s research was a pioneering venture in a sense that it left behind Classical Ethology in a movement M. Weber in his structural history of the Modern Synthesis called “the return of the phenotype”. See Weber, *Die Architektur der Synthese*, 147–160. The fact that Bastock’s work was not appreciated in a way it would have deserved was more due to the fact that she was several years ahead of her time. Most interestingly, Niko, as far as I know, left a share of the prize money he received for his nomination with the Nobel Prize in 1973 to Bastock – a gesture of late appreciation. Bastock died in 1982 because of cancer.


554 Ibid., 106.
The action patterns in question were to be interpreted as a chain of mutual responses (N. Tinbergen’s reaction-based model). By contrast, in Bastock’s and Manning’s view, the courtship pattern of *Drosophila melanogaster* is neither strictly fixed nor are the changes in the behaviour pattern of the male directly correlated with actions of the courted object. According to Bastock and Manning, all three behaviour elements which turned out to be constitutive elements of the fruit fly’s mating behaviour superimpose but / and do not replace each other. They are nourished from a common source of nervous excitation but differ in their releasing threshold. It reads:

Thirdly, one might imagine the elements to be internally linked only in so far as they receive common excitation, the centres controlling them each having different thresholds for firing. Thus orientation would occur at low excitation, and vibration and licking at successively higher levels. Such a simple arrangement is supported by the fact that each successive element is superimposed upon those preceeding it and does not replace them. In this explanation of the pattern of courtship, the changes from one element to another are due simply to fluctuations in the general level of excitation, and there are no specific stimuli required for the release of separate elements. In other words, all the stimuli suggested in the two previous explanations are imagined to control the pattern of courtship, but in a general rather than a specific way. Proprioceptive stimuli will fluctuate according to the activity of the male, and the stimuli from the female will vary both with her behaviour and her distance. The total excitation at any given time from all these, and other causes, (e.g. “internal factors”, see p. 92), will determine which elements are present in the courtship, and the average level of excitation during a courtship sequence will determine their relative proportions. | It seemed worthwhile to investigate further this third possibility. We decided to examine the relationship between the three elements in more detail and to compare the frequency of their occurrence with some independent measure of sexual excitation.556

The quotation, I think, provides a good impression how Bastock and Manning intended to replace Tinbergen’s hierarchical system of discrete nervous centres. According to their model, there was no such thing as fully discrete centres but only one common source of excitation whereby the question which behaviour is exhibited at each point of the entire sequence appears to be a matter of the intensity level only, that is, a mere quantitative entity. This, however, presupposed the existence of some kind of thresholds which Bastock and Manning not only correlated with particular behaviours but also used to explain the species-specific differences between the courtship action patterns of *Drosophila melanogaster*, on the one hand, and *simulans*, on the other.557 From the epistemological standpoint we may therefore argue that Bastock’s and Manning’s model of motivation is based on a gradualist reference system and therefore less a topographical understanding of the nervous system. The variety of intra- and inter-specific behavioural expressions seems to be explained by a uniform source of excitation which, so to speak, superimposes (“suffuses”, W. James) a notion of constraint, or more concretely, various levels of threshold (also conceivable as drive conflicts). On basis of this general model of motivation the core topic of Bastock’s thesis becomes fairly comprehensive: She intended to demonstrate that the reduced reproductive success of the male yellow

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555 For a discussion of the various models see *ibid.*, 87–88.
mutant of *Drosophila melanogaster* was due to the decreased stimulating effect of these males upon the wild females during courtship.\footnote{558} In other words, the courtship behaviours of the male mutants was not sufficiently stimulating to exceed the threshold of the female’s adequate response.\footnote{559} The handicapped males thus turned out to be of utmost heuristic value in as much as they proved the dependency of the female’s response from a certain intensity level of excitation and, as a reverse conclusion, that if the modified female response was due to a change in the male’s behaviour pattern and if the behavioural modification of the male, in turn, was due to one single mutation only, that ultimately one gene mutation could be correlated with a particular modification of the fruit fly’s courtship display. After refuting possible objections, a genetic variance could be correlated with behavioural phenotypical variance. Bastock’s general excitation hypothesis seemed to receive further support by comparing the differences of the behavioural fluctuations between wild type and mutant during courtship with the differences of the fluctuations that could be observed during and outside the reproductive periods. Thus, the effect of the mutant could be identified as a general decrease in the intensity level of the behaviours and not as a behaviour- or bout-specific effect.\footnote{560} This result supported the overall intensity-based model of motivation and hence contributed to Bastock’s turn.\footnote{561} The question whether M. Bastock’s work included passages referring to sidelined ideas is difficult to answer. In 1959 she married A. Manning and together they soon moved to Edinburgh where Manning had obtained a position as assistant lecturer.\footnote{562} At first, she continued working on courtship and published a major monograph upon the theme in 1967.\footnote{563} Later on she also studied child development and aggressive behaviour. This may indicate that her later research interests were already represented in her thesis to a large extent, at least, in so far as they were related to courtship in animals. A more thorough study of her life-history, including the later stages thus would be of great interest.

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Niko delivered at the University of Basel where she received her academic education. She completed her dissertation thesis on peacock tails under the Swiss zoologist A. Portmann and, finally, arrived at Oxford in 1952. Niko put her on the Farne Islands for her field studies together with M. Cullen who became her husband in 1954. Her five-year study on Kittiwakes (german: Dreizehenmöwe, Latin: *Rissa Tridactyla*), a rather eccentric subspecies in the family of the Gulls, is usually said to have had tremendous impact on the further course of Ethology. Kruuk speaks of an “all-time-classic”, P. E. Griffiths of “ground breaking studies”, and in R. W. Burkhardt’s view her “discoveries played a critical role in Tinbergen’s sense of metamorphosis in the mid-1950s”. Niko himself had underlined how much he had learnt from his student and in his later autobiography even went so far to connect his turn to Behavioural Ecology with E. Cullen’s studies. “With hindsight”, he writes,

I am amazed (and also slightly embarrassed) to realize how long it had taken us to develop this approach, but at the same time I feel that, however far modern “behavioural ecology” has evolved since Esther Cullen’s rightly famous kittiwake work, we have laid at least one of the foundation stones of this fascination and flourishing “growing point” of ethology.

I have argued that one “foundation stone” of Behavioural Ecology, in the last consequence, was already laid in the mid-1930s when Ethology took the shape of a heterogeneous scientific orientation and subsequently adopted the modern causal ar-

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564 See Kruuk, *Niko’s Nature*, 129.
565 Ibid., 169. The thesis was later published as: E. Sager. “Morphologische Analyse der Musterbildung beim Pfauenrad” [Morphological Analysis of the Peacock’s Tail]. Inauguraldissertation zur Erlangung der philosophischen Doktorwürde vorgelegt der Philosophisch-Naturwissenschaftlichen Fakultät der Universität Basel”. In: *Revue Suisse de Zoologie* 62.2 (1955), 25–127. It was accepted by the faculty in February 1953. According to the “Curriculum Vitae” which is added at the end of her thesis, Sager had already spent the summer of 1951 in Oxford “um in mein zukünftiges Arbeitsgebiet eingeführt zu werden” (to get familiar with my future area of work), as she put it. Moreover, I think, the title “Morphologische Analyse” (morphological analysis) disguises the fact that Sager’s thesis went beyond in so far as she asked for the contribution a morphological analysis could make to answering the question “welcher Art die über elementare Funktionen hinausgehende Wirkung der äusseren Gestalt sein kann” [of which kind the appearance’s effect, which exceeds the basic functions, can be] (transl. CL) (Ibid., here 27, but also 105–107, 115–116). In other words, Sager’s research question put its fingers upon the paradox of Ch. Darwin’s theory of natural selection. The thesis’ introduction reveals that Sager was familiar with *The Descent of Man* (Ibid., 25). For A. Portmann’s so-called “Tier-Gestalt-Lehre” which apparently is the scientific context of E. Sager’s PhD thesis see M. Ritter. “Die Biologie Adolf Portmanns in zeitgeschichtlichem Kontext”. In: *Basler Zeitschrift für Geschichte und Altertumskunde* 100 (2000), especially 228–236. In how far Sager’s research matches the epistemic outline of Portmann’s “new Biology” must be clarified more thoroughly. According to M. Ritter, the neo-Darwinian Stresemann School partly distanced itself from Portmann’s teaching after the Second World War (Ibid., 249).
chitecture. The crucial question however is in how far E. Cullen’s study contributed to make an additional second shift which was necessary to build the epistemic foundation of Behavioural Ecology as we know it today. And why was her study so predestined to mark the epistemic changes in question? My hypothesis is that the partly widely deviating behaviours of her scientific object must have had an effect upon the constitution of Ethology’s scientific paradigm as soon as they precipitated into the organization of knowledge. My analysis of Niko’s “re-boundarying work” will show later that this was not a necessity and that N. Tinbergen mostly was sensitive enough to present the discoveries of his pupils so that they went conform with the scientific paradigm of Classical Ethology as he wanted to represent it at least until 1959.\footnote{Niko’s accounts of M. Bastock’s project we find in his letters to E. Mayr are one example of his practice of “re-framing”. See Cobb, “A Gene Mutation Which Changed Animal Behaviour”, 167 and Beale, “Tinbergian Practice, Themes and Variations”, 127–128, with some interesting quotations from a letter of Niko’s written to E. Mayr in March 1956. His theoretical comments on his pupils’ Gull research might be another example of the practices Niko applied to shape his discipline (see below).} One reason why E. Cullen was able to introduce a paradigmatic shift might be that her study was financed primarily by the “Janggen-Pöhn-Stiftung” a foundation which has its headquarters in St. Gallen (Switzerland).\footnote{See Cullen, “Adaptations in the Kittiwake to Cliff-Nesting”, Acknowledgements, 301. The Nuffield Foundation which had provided the major share of the financial resources with which N. Tinbergen financed his “gull program” is said to have provided only a part of the equipment.} The more-of financial independence could have but need not have precipitated in a more-of intellectual independence as well. In Niko’s semi-autobiographic monograph, Curious Naturalists, we read that E. Cullen “fell in love” with Kittiwakes and that Niko perfectly agreed.\footnote{See Tinbergen, Wo die Bienenwölfe jagen, 140.} This scheme corresponds with Niko’s self-view but need not necessarily be the only possible interpretation. Also possible, and indeed even more likely, might be a narrative scheme which takes into account that E. Cullen “fell in love” with Kittiwakes yet increasingly deviated from Niko’s views. Another reason could be that E. Cullen belonged to the older representatives of Niko’s first generation of pupils and, moreover, had already received a PhD degree in Switzerland under the supervision of A. Portmann. Her pioneering research on adaptive behaviours in the Kittiwake is therefore not only the product of influences Cullen adopted after her PhD. In fact, I think, the epistemic reference system within which Cullen placed her study is much more compatible with A. Portmann’s than with Niko’s conception of Biology. The fact that M. Bastock and E. Cullen represented the reference system Niko had excluded in their works even in the way they organized their findings must have led to stronger forms of ambivalence than it was the case with other students. Several, partly performative gestures which can be traced in Cullen’s paper can be interpreted as a reaction to this circumstance. While Niko had encouraged his PhD students to reproduce his practice of academic socialization, that is, the habit to supplement an initial critical reception of the works of others with the student’s own further leading contribution, once more within the theses themselves, Cullen was keen to emphasis that her research was meant to be an additional contribution of Niko’s Gull program. In the paper’s introduction it reads for instance: “In 1952 I undertook a study of the breeding behaviour of 

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the Kittiwake *Rissa tridactyla* in order to extend the scope of studies of various

574 Moreover, the way E. Cullen referred to Niko’s and other Tinbergians’ work marks an exceptional characteristic of her Kittiwake paper: Asides the canonical reference to Niko’s Gull program (introduction) and the acknowledgement of his assistance, references to his work mostly have the character of a scientific exchange about simple observations and seem to involve less the adoption of methodological concepts. 575 But even referring to simple observations seems to imply potential criticism: Because of the excentric taxonomic position of the Kittiwake these references also often have a potentially critical tenor since scientific concepts function as abstractions of the observed behavioural data and deviating data thus reversely develops a pressure upon the used concepts. In the summary of her study Cullen presented a table with altogether eight special categories in which the Kittiwake’s reproductive behaviour deviated from the one of other ground-nesting Gulls. 576 In all these cases the argumentation was of the type: The behaviour of groundnesters (Niko’s domain) is ... while the behaviour of the cliff-nesting Kittiwake (Cullen’s subject) is ...! Furthermore, E. Cullen’s references to the works of other members of the research group have a more informal character. This becomes evident in the proportion of references which include the attribute “drawn from personal communication”. 577 The more informal style of E. Cullen’s way of interacting with other fellows and researchers, I think, can be interpreted as an expression of her scientific orientation, maybe a trait of her personality, but possibly also a gesture to avoid an open scientific controversy. Correspondingly, the use of methodological concepts characteristic for Niko’s research and more frequently used by other Tinbergians appears to be comparatively limited: Thus Cullen adopted Niko’s understanding of “appeasement gesture” and “displacement reaction”. 578 The notion of ambiguous drives which in the works of other Tinbergians took a more prominent position appears only very rarely and implicitly in Cullen’s paper. 579 If I am not mistaken the word “ritualization” turns up not once. Asides the mere observational deviations Cullen was pressed to state because of the excentric taxonomic status of her scientific object, Cullen’s paper, I think, includes lots of critical theoretical potential which mostly remains unspoken and thus requires a more of interpretation in order to be made evident. One of the concepts being endangered by re-conceptualization was Niko’s understanding of “territory”. In Niko’s view territorialization functioned as an initial phase in the reproductive cycle of the animals yet itself was conceived as the final exclusive stage in a longer action pattern. In other words, a spatially exclusive gesture precedes subsequent mating behaviour. This sequel apparently contradicted Cullen’s obser-

575 See ibid., 277 (fighting in Herring Gulls), 279 (attack releasing function of the beak), 280 (no food-fights in young ground-nesting Gulls), 285 (retrieving of young groundnesters fallen out of the nest), 287 (adult wariness at the nest), 288 (detering predators), 293 (keeping the nest clean), 295 (recognition of the young).
576 Ibid., 299–300.
578 For instance, “Choking” is introduced as displacement nest-building (Ibid., 283) and the turning away of the head in young Kittiwakes as appeasement gesture (Ibid., 280–282).
579 See ibid., 278.
vations in Kittiwakes. “In the Kittiwake the males occupy their nesting territories, i.e. their nesting ledges, as soon as they arrive at their nesting cliffs from the winter quarters”, Cullen writes and proceeds:

They advertise themselves there with a special display which attracts females to them and it is on the nesting ledges that the pairs form. Unmated ground-nesting gulls usually do not seem to go straight to their breeding territories after they arrive in the nesting area, but may spend the first few days either on neutral ground, the so-called “clubs” (Tinbergen 1953) or “pre-” or “pairing-territories” (Tinbergen & Moynihan 1952, Moynihan 1955). Here as a rule the pairs form and only later do they seem to occupy the actual breeding territories. In some species pairs may form outside the breeding season (Drost 1952) or perhaps even away from the breeding grounds (Moynihan, personal communication).

Scientific prose in contrast to fictional text requires a match between concept and referent and this requirement becomes evident in Niko’s concept of territory in that the normal temporal order – Cullen writes “as a rule the pairs form and only later do they seem to occupy the actual breeding territories” – precipitates in a causal analytical narrative scheme which was typical for classical ethologists. If the linear order changes, as is the case with pair formation in Kittiwakes, the narrative scheme must shift in an analogous manner. In the last consequence the outcome may be a modified concept of causal analysis. This is exactly the point where behaviour becomes science. What applies to the concept of “territory” may hold for the concept of “motivation” as well: For instance, the Kittiwake, in contrast to ground-breeding Gulls, has developed more sophisticated nest-building habits which include jerking and trampling, the building of deeper cups, collective gathering of nest material and, finally, the habit of stealing. Collective collecting, however required a kind of synchronization which turned out to be irregular and rhythmically interrupted. This again raised the question of stimulation and E. Cullen’s answer was that it was less a group immanent mechanism of mutual stimulation but a common reaction to an arbitrary trigger, namely rain, which released the reaction. That the building outbreaks were correlated with the occurrence of rain then could be formulated as a strong provisional hypothesis which could be tested by statistics. “This synchronization is very remarkable and unusual for a gull colony and might have the function of insuring that a bird finds companions on the collecting grounds”, she explains and continues:

It might be brought about by a strong mutual stimulation to build or by a certain stimulus to which the birds respond simultaneously, or by a combination of both. While I have no evidence for or against the first possibility there is some evidence supporting the second. From my observations in the first two seasons I found that most of the big building outbreaks occurred during or after rain. In 1955 I noted weather and building activities in a colony of about fifty nests during five days, each divided into four roughly equal periods, at the height of the nest-building phase. In ten of thirteen periods without rain there was little or no building (i.e. building at not more than three nests) and in three there was a lot (i.e. building at four nests and mostly more), whereas in all seven periods with rain a lot of building was recorded. Although these figures are small they show that rain is correlated with the building activity in a Kittiwake colony (P<1%). Apart from the function of the rain-stimulus in synchronizing the birds’ building, collecting

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This quotation is elucidating in many respects: It reveals that quantification is the second step to confirm a hypothesis in the affirmative which had been formulated before. The quotation shows also, that the aspect of synchronization is discussed in terms of causation since E. Cullen asked for the nature of the stimulus which triggers the building outbreaks. It is also possible to read this quantitatively substantiated model of motivation as an alternative to the beginning chrono-biological research other Tinbergsians (e.g. J. M. Cullen, U. Weidmann) were about to begin since the mid-1950s. E. Cullen’s approach seemingly was less to mark the distinction between extrinsic and intrinsic factors of motivation in order to evince an endogenous substratum but, conversely, to exclude the endogenous factor in order to evince a *commonly experienced environmental factor* (i.e. rain). Her model of motivation (i.e. causation) thus is less determined by the interplay between the accumulation of nervous energy, on the one hand, and disinhibition, on the other, but, more likely, by shifting nervous intensities and simple “threshold transgression”. Significantly she speaks of “building-outbreaks” and this implies that an inner motivational threshold may be passed by a phylogenetically fixed and somewhat overwhelming adaptive program which allows to respond on fully arbitrarily occurring albeit advantageous environmental circumstances, in other words, an adaptive mechanism which allows an outer factor to become a trigger. The reason why E. Cullen did not make use of Niko’s ritualization concept eventually lies in the fact that her Kittiwake observations raised a different understanding of phylogenetic transformation altogether. In Niko’s view, progressive phylogenetic variation was closely linked with the process of ritualization in course of which meaningless gestures (e.g. the product of displacement reactions) gained biological meaning as communication symbols. Cullen’s observations challenged this framework. For instance, in how far can the turning away of the head in young Kittiwakes – despite its symbolic meaning – be called “derived activity” in N. Tinbergen’s sense if the secondary developmental step is so disruptive that it is difficult to trace the original form. Furthermore, Cullen’s understanding of phylogenetic change did not only allow grasping more disruptive forms of modification but also functional drop-outs of previously fully adaptive behaviours (from the animals behavioural setup) as a result of the expansion into a particular niche (i.e. cliff-nesting). For instance, the fact that the nests of Kittiwakes are protected much better allowed *Rissa Tridactyla* to drop several protective habits such as distracting or attacking predators, defaecating outside the nest or carrying away the egg shells for camouflage reasons. Lastly, I

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581 Ibid., 286–287.
582 Asides the mentioned example the chapter on “Clutch-Size” as a whole mirrors this scheme: A primary hypothesis which is drawn from D. Lack’s famous research (i.e. there is a correlation between clutch-size and amount of food-supply) is tested in a second step by own quantitative tests. See ibid., 289–293, especially 289. The same scheme, I think, also applies to the chapter on “Flying Movements in the Young” in which an initial thesis is elaborated in a second step (ibid., 294).
583 Quite analogously Darwin’s problem was to trace a continuous line of ancestral forms because earlier forms could have been extinct. This notion led to his understanding of phylogenetic development as a process of “representation”, as he put it. The epistemic parallel is significant.
have put forward the hypothesis that in M. Bastock’s and E. Cullen’s theses the criticism of the ethological reductions favoured by their teacher generation reached a paradigmatic level. The criterion for this proposition is the alternative form of knowledge organization. Contrary to the inner logic of E. Cullen’s introductory statement that her thesis is meant to be read as an extension of the scope of Niko’s Gull program, the order of both her and Bastock’s papers is gradually reductive. Bastock intended to reduce several behavioural appearances of the fruit fly’s courtship to one gene mutation. E. Cullen aimed to reduce a whole series of adapted behaviours to one circumstance, the fact that Kittiwakes are cliff-nesting birds. Insofar, one may even say Bastock’s and Cullen’s theses resembled the tenor of many Behaviourist studies to reduce many behavioural phenomena to one or a few principles of association or conditioning!\textsuperscript{584} This reductive overtone pervaded even into the order of Cullen’s Kittiwake study. In general, one can describe this order eventually as the ordered interplay of two complementary heuristic schemes. Either a proposition or hypothesis is set forth in the first place and the subsequently presented data or arguments are meant to reinforce it or, on the other hand, a huge variety of data is to be reduced to one single conclusion. Cullen’s paper, on the uppermost level, applies the latter of the two possibilities, while the inner part of the argument seems structured in accordance with the former of the two principles. The entire argument then goes like this: If in a huge amount of cases x (cliff-nesting) entails y (the adaptive behaviour) then it is allowed to conclude approximatively that y can be traced back to x.\textsuperscript{585} In this argumentation the middle-part thereby plays a crucial role. It lists altogether nine types of behaviour. At first sight, these behaviours are arranged in the linear temporal order of the Kittiwake’s reproductive cycle. However, on closer inspection they test each time anew the overall hypothesis: In how far is the behaviour in question a secondary consequence of the primary cliff-nesting habit? In so far these sections have in common that they test analytically the scope of a primary behaviour’s effectiveness. Beyond that, their arrangement is characterized by an inner (hierarchical) order which is guided by clear differentiation. Thus we find a treatment of agonistic behaviours in the first place (“Fighting Methods and Related Behaviour”).\textsuperscript{586} The rest is reproductive behaviour in a narrow sense. Within this group of behaviours the strictly sexual behaviours can be distinguished from those behaviours which refer to the care of the young. Within the former group Cullen apparently again differentiates between pre-copulatory behaviours and copulation itself (“Advertising Display of the Male”, “Copulation”).\textsuperscript{587} In the latter group three behaviours refer to the period before the young hatch (“Nest-Building”, “Concealment and Defence of the Brood”, and “Clutch-Size”), while the succeeding three sections deal with behaviours displayed after the Kittiwake chicks have

\textsuperscript{584} In addition to that, certain other parallels can be made evident between Behaviorism and Behavioural Ecology such as the tendency to apply parsimonious explanations or the use of experimental devices for testing predictions of so-called optimal foraging models. See Cézilly, “A History of Behavioural Ecology”, 13. However, readers should keep in mind that both scientific orientations are not fully “homologous” because of their deviating causal architecture!

\textsuperscript{585} The latter of the two propositions paraphrases the logical structure of the title: “Adaptations in the Kittiwake to Cliff-Nesting”.


\textsuperscript{587} Ibid., 282–284, 284.
Within the latter group, I think, there is again a differentiation between behaviours exhibited by the parents (“Feeding Young”) and those primarily displayed by the young themselves (“Flying Movements in the Young”, “Recognition of the Young”). The section with the heading “Recognition of Young” therefore takes a paradox position since it includes both the recognition of the chicks by their parents and of the young (as well as the parents) by the young. “Feeding Young” possibly refers to the activity of both the parents and the young. The former “give food” (genitivus objectivus), while the latter take it (genitivus subjectivus). Both activities therefore can be also read as metaphorical circumscriptions for either ultimate or proximate causation. If I was to illustrate the overall order of *Adaptations in the Kittiwake* it would look like the following graphic (Fig. 2.7).

The figure reveals that the structure of the parts is determined by the whole and vice versa. Moreover, it shows that a final conclusion is reached only approximatively, in the way of a mathematical limes equation. Classical ethological reduction which was mostly based on the gestalt theorem is replaced by a form of quantitative, argumentative, approximative, and lastly end-paradox reduction.

In contrast to other Tinbergians and similarly to M. Bastock, E. Cullen was less inclined to sideline information which contradicted classical theorems. In other words, in her paper those aspects which should later become more popular in Behavioural Ecology already reached a level of textual manifestation. Cullen’s biography tells us that her path somewhat drifted away from research at the end of the 1950s, partly for family reasons, and partly because “she felt that she was not aggressive enough for a research career” – as H. Kruuk has put it. After completing her research on Kittiwakes Cullen conducted some observations on Sticklebacks for Niko but she never published again. And this is the more astounding since Esther informs the reader in *Adaptations in the Kittiwake to Cliff-Nesting* that she intended to complement her paper with an additional “more detailed account of other aspects of the behaviour of the species”. However, aside a joint study published together with Mike Cullen on the pecking response in young Kittiwakes and Black-headed Gull chicks this account – as far as I know – obviously never appeared. In other words, E. Cullen’s research engagement ended in a more or less obvious break with academia and I am inclined to interpret the gestures of researchers as significant messages – quite independent of the contingencies of their lives which certainly cannot be neglected as such. According to J. Krebs and R. Dawkins, Mike and Esther Cullen separated after their move to Australia where Mike had obtained a chair for Zoology. Later in the 1990s, E. Cullen appears again as (co-) author of some primary school books for children bearing the title “Animal Shelter” and “Spiders” but she apparently ended her academic career with her Kittiwake study.

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588 For the former three sections see ibid., 284–287, 287–289, 289–293.
592 Whether sex and / or gender turned out to be a disadvantageous factor in the academic life-histories of the “Tinbergians” is an interesting further leading research question. One can partly get the impression, since neither M. Bastock, nor E. Cullen, nor R. Weidmann attained
To sum up my case study on Niko’s first generation of PhD students at Oxford, I’d like to point out the following aspects: Most members of the first generation of Niko’s pupils have in common that they had received a biological education before they joined his work group. This matter of fact substantiates my hypothesis that in some cases only a part of a disciple’s “disposition” could be represented in Niko’s empirical realm of ethological research so that the life histories in question apparently have developed an affection towards these blind spots. From a more abstract point of view, there seem to be mainly two types of patterns of life-history being affected by the way Niko socialized his students within the heterogeneous scientific paradigm of Classical Ethology: Either their biography reveals a tendency to complement Ethology’s classical framework (e.g. U. Weidmann) or the upcoming generation of researchers tended towards a more functional interpretation of Ethology which did not necessarily culminate into a strictly ecological research agenda since interpretations of the newly developed scientific orientation within more physiological contexts turned out to be a realistic option as well. In the latter of the two groups we can observe different stages how sidelined knowledge was represented, either as negative statements pointing to the outside of the reference system or in form of conceptual alternatives of varying “formative power”. On the other hand, it was Niko’s habit to commit his students (at least in their role as authors of their theses) to the realm of “Tinbergian Practice” (G. Beale) which, so to say, as a reverse conclusion, allowed students of quite different epistemological backgrounds to participate in his work group. Eventually this was one of the main reasons for N. Tinbergen’s enormous success as teacher. Altogether a micro-history of N. Tinbergen’s first generation of pupils thus can eventually show that the classical ethological reductions the founding fathers of Ethology had introduced now, in the 1950s, more and more became the object of severe criticism, both from the outside of the ethological community and, as my analysis shows, from the inside of the work group itself. The crucial question now is how N. Tinbergen responded to this challenge. My readings of the theses written by several early Tinbergians suggest that the place where this response has taken place most likely was the realm of Niko’s theorizing and not so much the theses of his pupils. (R3) So far I can see mainly two forms how N. Tinbergen responded to the criticism which was articulated both outside the community of ethologists and, what might even be more important, within his own research group. A first response

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594 A whole wave of criticism questioning ethological theory from outside the ethological scientific community was triggered by D. S. Lehrman’s famous critique of K. Lorenz’s papers being concerned with domestication syndromes. See D. S. Lehrman. “A Critique of Konrad Lorenz’s Theory of Instinctive Behaviour”. In: Quarterly Review of Biology 28.4 (1953), 337–363. The famous controversy following Lehrman’s critique has been analyzed in detail by R. W. Burkhardt and others so that it need not be retold once more. On D. S. Lehrman and his critique see Kruuk, Niko’s Nature, 177–184, Burkhardt, Patterns of Behavior, 9, 210, 366–369, 383–407, Hart, “The Ethical Responsible Conduct of Science”, 286–287 and also P. Chavot’s thoughts about the relationship between Ethology and Comparative Psychology in general, Chavot, “Histoire de l’ethologie”, 122–139.
might be seen in Tinbergen’s choice of experimental animals. As we have seen, the theses of his pupils in the 1950s were mainly concerned with (reproductive) behaviour in the Stickleback (D. Morris, Ph. Guiton, M. F. Hall and B. Tugendhat), or birds (R. A. Hinde and M. Cullen) – an here increasingly with various species of Gulls (M. Moynihan, U. Weidmann, R. Weidmann and E. Cullen). All these animals have in common that they are more or less territorial animals. That is, the males’ access to females and therefore also the reproductive success in general is connected with the establishment and defence of a (spatial) territory and not, as it is the case, for instance, with most mammals via complex social hierarchies. D. Morris’ life course shows relatively clearly, I think, that both forms of social organization amongst animals could be interpreted on basis of competing epistemic frameworks. While the emphasis upon territorial forms of social organization in the last consequence was spatial and therefore supported the classical ethological interpretation or (social) order, a model of reproductive behaviour that is based on shifting social hierarchies seems to imply a more plastic and behavioural idea of social organization. As a result, one may eventually say that Niko’s restriction to territorial animals implied a self-commitment to the classical ethological scientific orientation. Moreover, if we compare the proportions Niko had dedicated to either the organization of the central nervous system or the area of evolution in his *Study of Instinct* with his research interests in the 1950s we clearly see a shift from an emphasis upon behavioural physiological themes to evolutionary systematics, without – and this is of utmost importance – abandoning the *causal analytical* fundament that was underlying both areas of biological inquiry. “Niko was by now getting into comparative mode”, H. Kruuk writes, “and he wanted people to start studying other species of gull”.

I am inclined to interpret Niko’s partial shift from Physiology to Systematics as a sort of *defence reaction* for the sake of the maintenance of the paradigm that constituted his still young scientific discipline. M. Bastock’s and, even more, E. Cullen’s theses created a challenge so severe to Niko’s commitment to mechanomorphism because they extended the form of criticism that was seething already before in his research group into the field (viz. systematics) to which Niko had drawn back. In other words, M. Bastock’s and E. Cullen’s theses threatened Niko’s biotope, niche or sanctuary. Next to this more thematic forms of Niko’s response there is a second more structural mode of handling the growing challenges. Niko’s theoretical papers and reviews used to pick up the results his pupils put forward in their theses. And he did so by commenting these works in a rather sublime way. This process of framing or re-framing I intended to grasp with the catchphrase “re-boundarying work” is the subject in the following paragraphs of my dissertation thesis. N. Tinbergen’s theorizing in the 1950s encompassed a summary of his stu-

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596 I think, it can be shown that this defence of the classical ethological notion of causal analysis also implied maintaining a certain kind of self-centred subjectivism which denied the possibility to synthesize subjective data of self and other. This can be inferred primarily from archive material. See to this Niko’s letter to J. Huxley who apparently made this claim, WRC-RU Fondr. Lib., MS 50, box 28, file 1, letter N. Tinbergen to J. Huxley (21/01/1959). For Huxley’s more objectivistic and continuous view upon the relation of body and mind see *ibid.*, box 28, file 1, letter J. Huxley to N. Tinbergen (17/01/1959).
Niko Tinbergen (1907–1988)

dents’ lab studies on Sticklebacks, a general paper on appeasement gestures, and a theoretical paper on taxonomy and evolution jointly written with R. A. Hinde. Furthermore, we find a paper that was concerned with his comparative phylogeny of the Gull species and can also be read as response to E. Cullen’s findings in the Kittiwake. Finally, there is a concluding research report of his and his pupils’ research on Gulls that was published in 1959 and which most likely has to be read as a turning point in Niko’s life course. From these wider sample of texts I pick out only those which promise to be a fruitful source for my research question, that is, how N. Tinbergen responded to the output of his other world.

Ethologists, especially in the so-called “classical” period of their science, had some difficulties in connecting their research branch with evolutionary theory. The roots of this problematic lies partly in the fact that Ethology as a synthetic construction stands more or less codominant next to the Modern Synthesis of Evolution, with which it shared both the date of its historical origin and the heterogeneous constitution yet not the structure of the overall epistemological paradigm itself. The second origin of these difficulties are the result of the fact that ethological theorizing in the period E. Crist had termed “mechanomorph” tended to holistic explanations. As a consequence, theorizing about the evolution of behaviour between ca. 1938 and 1959 used to have a systematic nuance or overtone which per definitionem was interested in classifying the living world and less (but also) in reconstructing the gradual transformation of the organisms over time – a tension which can be observed within the narrow frame of the Synthetic Theory of Evolution itself. N. Tinbergen’s paper Behaviour, Systematics, and Natural Selection which was published in the year of the hundredth anniversary of the publication of Ch. Darwin’s The Origin of the Species in 1959 most likely must be read both as an attempt to meet these difficulties and a document of their manifestation. My hypothesis is that Niko’s strategy was twofold: On the one hand, he operated with a concept of gradual variability (including the notion of variation through selective pressures) which seemed compatible with the epistemic frame of Ethology. On the other hand, however, it must be asked in how far Niko’s gradualism still was a means of taxonomic purposes. Both strategies, I think, can be made evident in a concluding remark of the paper which I would like to put at the beginning of my analysis. “However, when the real aim of comparative studies is not to classify”, he writes and proceeds but when classification is merely a means towards an understanding of the evolutionary history.

597 For the context of this study see fn. 526, page 190 of my thesis.
then there is no question of an annoying or confusing dispute; what emerges as positive gain is a better description of how and why species have diverged the way they have.603

On the one hand, the notion to differentiate organisms is re-framed within a wider concept of “understanding evolutionary history”, as Niko puts it here, but on the other hand, we find re-established – so to speak on a higher level of epistemic framing – a very strong emphasis on the process of branching, that is, the “the how and why [exactly in this order] CL species have diverged the way they have”. As a provisional conclusion, I am therefore inclined to argue that Niko’s phylogenetic interpretation of behavioural data in the last consequence served the analysis of the divergences and that means the entire enterprise was subject to a modified conception of systematics. In the following paragraphs I aim to clarify both aspects. We can understand Niko’s conception of “Phylogenetic Interpretation of Behaviour Data” only if we take into account that it is profiled as a “more of” of what he calls “The Taxonomic Use of Behaviour Characters”. While the museum taxonomist puts a stronger emphasis on the momentum of discontinuity, either because he tends to choose a few characteristic features and exclude others or because he infers too quickly from different characters to different species, the ethologist is more inclined to reconstruct the entire gradual development of a taxonomic group over time.604 According to Niko, the primary intention of his phylogenetic approach is to interpret synchronous differences as diachronic development of the entire system. And this transformationist stance again has several implications. One of them is that phylogenetic development can only be interpreted in terms of mutation and selection if qualitative differences are reassessed as accumulations of quantitative changes even in case the quantitative changes are conceived as more complex than simple gradual shifts. “It is therefore essential”, Niko underlines, to attempt to reduce the “qualitative” differences to accumulations of “quantitative” changes. Often a formal analysis of the complex differences can pave the way for this. Thus many differences in the waving movements of Uca species are combinations of changes in amplitude, in direction, and in speed of the single components of the total movement (Crane 1957) [...]. Of course, such a formal analysis should ultimately be accompanied by a physiological analysis in order to establish beyond doubt that what appears to be a quantitative shift really is not a misleadingly simple effect of a more complex inner reconstruction, but a comparison of the scale of differences caused by single mutations with those observed between more or less closely related forms strongly suggests that our interpretation must be correct in principle, and that “qualitative” differences are merely more complex than the basic small quantitative steps.605

Asides the reinterpretation of discontinuous through gradual variability the emphasis on evolutionary history also implies not to prefer any character in disfavour of another and this seems also to affect the esteem of behavioural in comparison to morphological data. “The taxonomist”, Niko says, is continually tempted, particularly in difficult groups, to rely for classification on one or a few characters of a large complex to the exclusion of the others. This temptation is particularly strong when a new category of characters is brought into play. Mayr has, I think, convincingly argued (1942) that there are no a priori reasons why one type of character should be more

603 Tinbergen, “Behavior, Systematics, and Natural Selection”, 328.
604 Ibid., 321, 328.
605 Ibid., 323.
reliable than another, and although the taxonomist does a great amount of “weighing”, morphological, physiological and behavioural characters have to be given equal weight for classificatory purposes. They also have to be used in conjunction. Behavioural characters are useful to the taxonomist not because they are more reliable for classification, but because they add to the total number of characters that can be used. Their addition may be helpful in separating species that are morphologically extremely similar, such as the digger wasps *Ammophila campestris* and *A. adriaansei* (Adriannse 1947), or they may be of use in uniting species that have radiated morphologically; thus pigeons and sand grouse (Pteroclidae) are remarkably constant in the way they drink, viz. by pumping. Yet this alone would not justify the view that they must be related; the behavioural character merely adds strength to the morphological evidence.\(^{606}\)

We see, the quantitative view on phylogenetic change goes hand in hand with both a gradualist stance and a tendency to *extent* the inductive basis of taxonomic research. Finally, Niko’s vision of phylogenetic study also encompasses a “relational” stance. In his view, it is primarily the adapted features which are “systems” of interrelated components. “Critical studies of survival value”, he underlines in a concluding remark,

applied to total behaviour patterns, are needed to assess the effects of selection. Where this has been done, either by studying convergence or by comparing divergent related species, it has been found that many “characters” are interrelated components of adapted systems. These systems are complexes of morphological, physiological and ethological features.\(^{607}\)

According to this statement, it is not the isolated character which Niko is primarily interested in but the complex of mutually and functionally correlated features of various different kinds. If the hereditary constitution of an organism is the product of adaptation and this product, at least in Niko’s “atomistic” view, needs to be interpreted as complex conglomerate of physically based functions it is not too far-fetched to suppose that the selective pressures which led to the expression of each character are interrelated as well. In the subchapter with the conclusive heading “Interaction of selection pressures” N. Tinbergen aims to prove this hypothesis by citing examples for various types of both antagonistic and non-antagonistic selection pressures. In detail these forms of functional interaction are: Selective pressures shaping one feature only, selective pressures on quite different social behaviours (spacing out vs. mating behaviours), and selective pressures leading to conflicts between those behaviours favouring the survival of the individual vs. behaviours in service of the group or between sustainable and non-sustainable behaviours. Selective pressures of different kind, finally, favour unambiguity, distinctness of symbolic actions, or the optimality of the interaction between sender and the responsiveness of a receiver. Other selection pressures, according to N. Tinbergen’s account, must be interpreted as a side effect of a primary functional system and thus come close (without being identical) to what Darwin once called correlation of growth. As a result one may eventually say that Niko’s project of phylogenetic study is based upon a systemic view which in a second step is made concrete in terms of functional relations and interrelated selective pressures.

The second part of my argument, namely that Niko, despite his high esteem of evolutionary theory (including the principles of mutation and selection), does not give

\(^{606}\) Ibid., 321.

\(^{607}\) Ibid., 328, also 325–326.
up his primary focus upon divergences, is much more difficult to prove. One aspect which points into that direction surely is his explicitly articulated interest in “how and why species have diverged in the way they have”. Another aspect might be that the fact that Nico placed phylogenetic study within a causal analytical frame also implies a certain scepticism especially against selection – so to say as a heuristic principle. Thus, in his view, the actual evidence of the effectiveness of selection is scarce. “Apart from small mutational steps and extremely fragmentary evidence on the effect of selection”, he states in a concluding remark, “no direct evidence about evolutionary change in time is available, and the argument is based on the assumption that differences between related contemporary forms, and similarities between non-related contemporary forms, reflect changes in time”. 608 And this seems to be more an epistemic presumption rather than a result of factual evidence. “[...][L] the ethologist’s high regard for the influence of selection”, he therefore concludes somewhat diplomatically, “is due to his characteristics rather than to those of the material”. 609 As a result, I am inclined to conclude that N. Tinbergen, despite his verbal support of the primary principles of gradual variability, maintains a certain scepticism against their full applicability: In contrast to later behavioural ecologists he thus seems to keep being a systematist by heart, though in a modified form. Another indicator for the alleged fact that theorizing in causal analytical terms, in the last consequence, generated tensions with both the core theorems of the Modern Synthesis and his own model of phylogenetic variability might also be Niko’s special emphasis on the “indirect effects of selection pressure”. 610 The fact that there exist “numerous relationships between the various functional systems of an animal”, in his view, is the reason why many characters of living organisms are products of indirect selection pressures. And this view allows us to draw some conclusions on Niko’s understanding of the phylogenetic system as a whole. Thus my impression is that Niko’s understanding of adaptedness is not primarily drawn from the notion that origin and development of a character can be the result of a “direct” (still non-Lamarckian) interaction with the environmental conditions of life. The phylogenetic system as a whole, in Niko’s account, to a large extent draws its own dynamic from inner interrelations of functional components, just as, for instance, proprioceptive stimuli are quasi environmental stimuli insofar as they originate from the periphery yet not outside of the system as a whole. Niko’s notion of the phylogenetic system thus turns out to be that of an “only-partly-open system”. And this moment of discontinuity in the presuppositions of Niko’s core concepts in Behaviour, Systematics, and Natural Selection is one of the reasons why I tend to interpret the paper as a whole as a manifestation of his causal analytical theorizing. Finally, there is a very strong argument for this view. It is the composition of the paper. Altogether, Niko’s account on evolution is written rather dense, full of parataxes and highly sophisticated in its organization (at least on closer inspection). The key to understanding the way Niko organized his knowledge eventually lies in the conviction to include equally all sections (including “Summary” and “References”) as well as the fact that Niko at least at two important positions inserted comments which haven’t got

609 Ibid., 329.
610 Ibid., 328.
the status of a subchapter and are connected with the overall headline directly but have the important function to profile the following subchapters on the same level as discrete units. Without going into detail especially on the lower levels of differentiation I’d like to suggest the following illustration (Fig. 2.8). The figure, I think,

![Diagram of the paper structure](image)

**Fig. 2.8**

N. Tinbergen, *Behaviour, Systematics, and Natural Selection* (1959), Upper Levels of the Epistemic Scheme

reveals quite impressively that the order of the paper resembles much the one of the other theoretical papers.

Since ca. 1953 the American Psychological Association and the Society for the Study of Evolution had undertaken more and more joint efforts to link evolutionary theory with the study of behaviour. The outcome was two conferences held in 1955 (New York) and 1956 (Princeton, New Jersey). To the participants of the latter – amongst many others such as F. Beach, D. Griffin, H. Harlow, E. Mayr and B. Rensch, to mention only a few – also belonged N. Tinbergen and R. A. Hinde whose joint presentation finally was published under the title “The Comparative
Study of Species-Specific Behavior” in the proceedings of the conference. Eventually it is not quite false to say that R. Hinde was and still is a representative of the more experimentalist Cambridge tradition. He had graduated in Cambridge but soon after moved to Oxford to become D. Lack’s research assistant. After N. Tinbergen had arrived in England, Hinde – although his dissertation thesis on Great Tits was formally supervised by D. Lack – attached himself with Niko’s research group. Robert’s close contact to Niko and his pupils had a considerable impact on his early research in the 1950s. After receiving his doctorate in 1950, however, W. H. Thorpe offered Hinde to become the head of a small ornithological field station in Madingley and so he moved back to Cambridge again where he stayed for the rest of his career. According to H. Kruuk, he was a brilliant analyst and theoretician, interested especially in quantifying behaviour, and those were qualities that Niko lacked and which he greatly admired. Robert did most of his research initially with captive birds (chaffinches and canaries), and later with monkeys and children. He later developed his own school in Cambridge, and, however well they got on, he clearly did not want a role under Niko.

Nor was R. Hinde fully convinced by ethological theory which he considered too simplistic in many respects. Thus he thoroughly rejected the idea of innate “drives” as “a unit that energizes and directs behaviour”, as H. Kruuk puts it, and openly questioned the heuristic value of K. Lorenz’s so-called “psycho-hydraulic model”. Altogether, R. Hinde thus more and more turned out to be a serious critic of the weak points in ethological theory and we can assume that his criticism also had deeper lying epistemological reasons. If we compare with each other, for instance, the various points of critique he articulated later in his voluminous review Animal Behaviour – a book he originally intended to write together with N. Tinbergen – one gets the impression of someone who did simply not fully share the (naive) holistic stance which, at least from a historical and epistemological point of view, had led to the emancipation of Ethology from Physiology the latter of which he himself regarded as an essential part of behaviour study. That there was – despite all personal respect – an increasing threat of epistemic tension may be the...


See ibid., 185.

For the information that Niko and Robert originally had planned to write the book together, see Hinde, Das Verhalten der Tiere, Preface of the First Edition 1966, 15, and Kruuk, Niko’s Nature, 248–249. See for instance R. A. Hinde’s careful scepticism against scientific models or his critical attitude towards any conceptions of “drive” Hinde, Das Verhalten der Tiere, 25–26, 225–234. Moreover, Hinde eventually interpreted the reductive mechanisms of the central parts of the nervous system more as a means of generating the pathways “between” stimulus and reaction and not as the nervous basis of a permanent state of endogenous excitation (Ibid., 318–325). Spontaneity thus apparently is defined more in terms of (or part of) a “trade-off” between the impulses provided by external forms of stimulation and the internal factors of motivation (Ibid., 354–366). In general, the concept he seems to prefer is “reactivity”, less “spontaneity”. I am inclined to interpret Hinde’s focus on plasticity during ontogeny and his interest in the evolution of the more complex phenomena of behaviour along the same lines. According to H.
background of Niko’s and Hinde’s joint paper on evolution and I tend to interpret it as Niko’s attempt to place Hinde’s views adequately in his scientific edifice. *The Comparative Study of Species-Specific Behavior* therefore can be read as another manifestation of Niko’s disciplinary theorizing. With a view of the paper’s content one may say that it was exactly the holistic stance of Classical Ethology which gave Niko’s theorizing on evolution a more or less strictly systematic nuance. In other words, “evolution” in N. Tinbergen’s understanding meant reconstructing phylogenetic dependencies within a relatively small group of closely related species which, in the ideal case, were monophyletic but on the other hand revealed enough plasticity in relevant qualities to infer the actual course of evolution. Insofar Niko’s approach to evolution was different from Darwin’s whose reasoning on behaviour was not exclusively but mainly connected with the question of sympatric speciation. Nor ascribed Niko a prevailing role to those additional questions which in his own approach had the function to reconstruct the course of evolution. Causation and function thus primarily served as concepts to illustrate the transmutability of the behaviours and therefore also the increase of complexity. But Niko’s prevailing interest still was the reduction of the complexity which used to be regarded as a consequence of the phenomena themselves. The concept which was affiliated with this urge was *comparison* since the comparisons allowed to establish homologies and these homologies, in turn, allowed to group the species in question according the rule: The more common the feature the older and more original it is. The critique D. S. Lehrman had sparked off in 1953 with his paper did not, as the story is often told, lead to Niko’s pure acceptance. We may observe a more defensive reaction as well, at least in the 1950s. Thus Niko stressed that the primary question was not whether or not a certain behaviour was innate or not, or which components of the entire behavioural sequence were more resistant to environmental impacts than others. According to his view, the vital aspect was that *species-specific differences* must be able to be treated as expressions of hereditary dispositions. This shift from ontogeny (which was the primary field of Lehrman’s critique) to phylogeny allowed to leave behind the tiresome debate on nature or nurture by reserving a field (i.e. phylogenetic divergence) for one of the core narratives of Ethology (i.e. the analogy between organs and behaviours and the heredity of behaviour) where it hardly could be denied. As a result, I think, it is legitimate to read N. Tinbergen’s and R. A. Hinde’s joint paper as a manifestation of the causal-analytical scheme which was

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616 N. Tinbergen certainly was aware that his approach to evolution therefore was deemed to play a more marginal role within the entire field of evolutionary study: “All this work”, he writes in a concluding remark, “provides the necessary basis for an attack on the ultimate problem of the dynamics of behavior evolution. Comparative study itself cannot contribute directly to the solution of this problem, but as a phase of research it is indispensable; it alone can supply us with a formulation of the problems to be solved” (Tinbergen et al., “The Comparative Study of Species-Specific Behavior”, 265).

617 Ibid., 255.
characteristic for Niko’s more theoretical publications during the period between ca. 1938 and 1959. Besides the explicit emphasis of the comparative method, the species as primary entity of examination, and the – in the last consequence – binding systematic interest it is again the order of the paper which provides us with a more objective indicator for Niko’s scientific orientation in the late 1950s. Although other forms of knowledge organization may be possible as well, I tend to see a bipartite overall structure consisting of an introductory section, on the one hand, and a main part, on the other. The introductory sections used to function as a sort of “appetence” in Niko’s theoretical accounts. In a very literal sense of the word they lead towards the core of the argumentation. In detail the introduction of *The Comparative Study* consists of reflections on “Aims” and “Methods”, on the one side, and some additional suggestions concerning the adequate choice of the most promising research objects (subchapter “Selection of Characters for Study”). As can simply be inferred from the headlines of the subsections the term “aims” refers to the purposes of the study, and “methods” to its theoretical basis, while the talk of “selection” again indicates that the subsection in question is composed within a frame ruled by the notion of ultimate causality. This order is planned deliberately. Even if we go further into detail and have a look at the level of concrete content, the epistemic frames (as defined in each title) are spelt out consequently. Thus Niko suggests two principal options for an evolutionary study of behaviour. Either the focus is upon the question in how far behaviour is the product of evolution or, conversely, one can ask which role behaviour played in the course of evolution. In a second step, Niko makes a choice: The former of the two possibilities should be the one followed in his and Hinde’s paper. “These two interrelated problems – the influence of evolutionary processes on behavior and of behavior on evolution – comprise a large field about which little is yet known”, he writes and proceeds:

> This chapter [the entire volume organizes the authors’ contributions in chapters] is concerned mainly with the first, namely how behaviour changes in evolution. It is also confined primarily to behavior which is more or less characteristic of the species, and thus discusses only one aspect of the whole problem.

The practices of making a distinction in the first place and a choice in the second characterizes the epistemic scheme of the part of the introductory section referring to the “Aims” of the paper. A similarly controlled application of epistemic practices can be made evident in the subchapter on methodology, as well. Here there are altogether three optically divided paragraphs. While the first section introduces the *comparative method* as a solution to a number of difficulties related to the specific object “behaviour” (lack of paleontological data and ontogenetic evidence), the succeeding two sections seem to be more problem oriented and that means both with respect of the methodology’s concrete application and the specific needs for further clarification raised by the application of the method itself. In all

618 See for all three subsections Tinbergen et al., “The Comparative Study of Species-Specific Behavior”, 251, 251–253, and 253–255 respectively.
619 Ibid., 251.
620 Ibid., 251–253.
621 The former of the two aspects is solved by introducing a heuristic procedure consisting of several distinct steps such as (1) recognition of interspecific similarities, (2) inference of the common
the section on methodology thus can be read as principal reflections to find a solid basis for treating a very specific scientific object within the field of systematics. The topic “selecting the adequate scientific object” is treated similarly deliberately by N. Tinbergen and his coauthor. At the very first glance, several aspects seemed to be relevant for both authors such as the correct size of the units of investigation, the reasons why fixed action patterns and their physical correlate turned out to be the traditional object of ethological taxonomy, the need to take into account the ontogenetic plasticity of behaviour in particular the one which is caused by effects of learning, D. S. Lehrman’s critique which proved the danger to underestimate learning to be a real one, but also the need to avoid overestimating the effect of learning, the insistence on species-specific differences, and finally, the statement that these differences may include dispositions to learning. On closer inspection, I am inclined to read this subsection as a brief epistemological history of Ethology: The initial question which behavioural entities are the right ones for systematic study at first led to a narrow focus on so-called fixed action patterns. The evidence provided by Lehrman, the fallacy to ignore the effect of learning and the mistake to overestimate learning, turned out to be serious problems which to overcome had a liberating effect on ethological theorizing. As a result Niko’s focus shifted from innate behaviours towards the innateness of species-specific differences. Beyond that he even integrated the aspect of learning by claiming that these differences can include dispositions to learning. Altogether we are therefore most likely confronted with a transgression scheme. The core parts of the paper, by contrast, seem to operate with an analytical scheme of knowledge organization. They encompass two major subsections both of which are related to the use of behaviours for taxonomic purposes. At the beginning of the second major chapter it reads:

To exemplify the use of these methods in comparative work we will now consider some of the conclusions reached about the evolution of the threat and courtship displays of birds. Courtship behavior has been much used in comparative studies because of the relatively stereotyped postures involved and the extent of interspecific diversity.622

The passage is of great interest for my reading because it regulates the organization of the information presented. Thus we may infer that the remaining main sections of the paper provide a critical discussion of results already attained. Then we are informed about the primary field of research in which these results had been attained (courtship behaviours) and also the reasons why this “theme” had turned out to be that promising: Courtship behaviours are “relatively stereotyped”, on the one hand, and they reveal a sufficiently large “extent of interspecific diversity”. The former of the two aspects is covered in the chapter with the title “The Evolution of

origin, (3) recognition of slight differences which allow to determine the developmental stage of each quality relative to any other, (4) formulating hypotheses about the origin of each behaviour and marking the differences between present and past forms, and finally, (5) generating a tentative reconstruction of a behaviour’s course of evolution – so to say – as the final result of a comparative study. The latter of the two major aspects refers to the need of further examination. It raises the Why-question: Why did the course of evolution occur in the way it actually did: This includes both asking for the survival value of the adaptive changes and the need to assess the systemic interdependencies of the functional relations.

622 Ibid., 255–256.
Courtship and Threat Displays in Birds" which is the second major section of the paper. The latter theme is treated in the succeeding section being entitled "The Extent of Interspecies Differences in Behaviour". The remaining subsections are more abstract and encompass specific reflections concerning the applicability of the method and a conclusion. As a result, I suggest the following figure to illustrate the overall pattern of knowledge organization (Fig. 2.9).

![Fig. 2.9](image-url)


In the remaining paragraphs of my analysis I shall go a little bit more into the details of each section because in the last consequence it is the micro-architecture of the account in each case which suggests (though not determines) the macro-relations in-between them. Addressing the stereotypic side of display movements, in N. Tinbergen’s and R. Hinde’s view apparently includes the following aspects: At first, a preliminary causal analysis shows that courtship behaviours rest upon a similar ambivalent motivational structure as any other display movement yet are more complex insofar as next to flight not only attack but also sexual attraction influences the nervous economy of the behaviours. What is species-specific, in R. Hinde’s and N. Tinbergen’s view, is the fine equilibrium of the relative intensities with which

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624 Ibid., 261–263.
625 For the former of the two sections see the chapter with the title “The Use of Characters of Behavior in Systematics” (Ibid., 263–265). The concluding remarks are simply called “Conclusion” and, by the way, not “Summary” which would have implied another epistemic connotation. See Ibid., 265.
each tendency articulates itself. “The species differences in display”, they conclude, “thus lie primarily in the relative intensities of components”. A closer look upon the evolutionary origin reveals that there are mainly three types of behaviour (intention movements, displacement activities, and redirection activities) which must be identified as sources of display movements. These stereotypes stood at the beginning of a transformation process which rested upon both the mechanisms of genic variability and the effects of mutual interaction and thus generated the forms as we can observe them nowadays. If the perspective is turned upside down and the focus does not lie upon the origin but the progressive development of these displays, three modes or principles of transformation can be observed, namely the development of conspicuous structures, the variation of the behaviour’s schemata itself (including exaggeration of single components, changes in absolute and relative thresholds and changes in the inner coordination), and finally, the emancipation of a behaviour pattern from its original motivational context. Finally, an extended analysis of their biological significance reveals that displays movements have two major functions namely fighting and courtship (treated in this order). The general assessment of the display’s major functions then culminates in a more abstract discussion about the general effectiveness of natural selection upon the behaviours in question. The tenor of N. Tinbergen’s and R. A. Hinde’s statement at this point is that the overwhelming power ascribed to natural selection by evolutionary biologists needs to be restricted insofar as system-immanent secondary effects of progressive adaptation may occur as well. Both authors conclude:

As Lorenz has pointed out, all these functions require that the display should be effective in eliciting responses in other individuals. This has led to progressive adaptation for signaling. Apart from this, divergence between species is enhanced by the need for maintaining reproductive isolation. This does not mean, however, that selection acting through the disadvantageous consequences of hybrid pairings is the only cause of evolutionary divergence in displays. Since the various characters of an animal are developmentally, causally, and also functionally interrelated, selection for change in any one character will have repercussions on many others. Thus not all differences in displays are necessarily the product of selection for divergence in the displays themselves (see below; Hinde, 1955; Mayr et al., 1956; Cullen, in press).

The quotation shows the ambiguous attitude ethologists must have had towards purely selectionist approaches. On the one hand, they accepted the effectiveness of selective pressures especially within the field of animal communication. On the other hand, however, they claim the existence of a sort of system-immanent and correlated type of phylogenetic development. From the epistemological standpoint, one may eventually say that all four subsections of the chapter, “Preliminary Causal Analysis of the Displays”, “The Evolutionary Origin of Display Movements”, “Elaboration of Display Movements in Evolution” and “The Function of Display”, have in common that they are typical expressions of Niko’s causal analytical scheme of theorizing. They are primarily related to the static of behaviour,
they emphasize the proximate causes (i.e. motivation) and they are reductive in a sense of “digging down” to the origin of the behaviours. In detail the subsections in question elaborate this scheme partly by operating with antagonistic overtones. The chapter with the title “The Extent of Interspecies Differences in Behavior” is less concerned with those aspects of the display behaviours which are indispensable for establishing true homologies. By contrast, it refers more to those factors which are relevant in reconstructing the actual course of evolution. From the epistemological standpoint this chapter must contain (and begin with) veritable paradox since only those “plastic” factors are relevant for systematic analysis which are not only heritable but also rest upon true homologies. The chapter thus can be read as R. Hinde’s and N. Tinbergen’s attempt to “sound out” the boundary where the necessary precondition of “being the product of divergence” ends. Therefore it is quite expectable that the first part of the chapter refers to divergent evolution and the presumptions being connected with this concept, while the later propositions address the a major source of disturbance in systematic study: Convergent evolution. The notion of divergent evolution implies a proportionality between the grade of relatedness and the extent of similarity, as well as the adaptiveness of the modifications – implies further a focus upon the early stereotypic parts of the courtship displays because they mark the discrete factors in geographical isolation, and finally includes the idea that behaviour and structure develop as a systemic whole – only to mention a few aspects discussed within the context of divergent evolution. As to the possible convergences I read N. Tinbergen’s and R. Hinde’s account partly as a warning: Any process of divergent evolution is automatically accompanied with a certain degree of convergence simply because speciation is habitat-specific which means that the survival value of a certain feature is distinctive. Asides the authors’ warning they mention also the types of features which seem particularly liable to become objects of convergent evolution. These are in particular the cryptic structures but also the conspicuous characters which have specific communicative functions in their display movements. Altogether, one may say that the “extent of interspecies differences” is wider than the narrow core of pure homologies. This to show apparently is the latent function of the chapter. In comparison to the preceding major sections the chapter with the title “The Use of Characters of Behavior in Systematics” is less descriptive rather than a part of the critical reflections at the end. The chapter claims at first that behaviour characters can be applied successfully for taxonomic purposes but also formulates some requirements which should be observed. These requirements include the choice of promising characters and the avoidance of convergent features. Furthermore, the chapter opens the reader’s mind for the fact that it is more difficult to disentangle systematic interdependencies in the field of behaviour than in morphology. However, as the results of E. Cullen’s research prove, it is possible to group secondary adaptive effects around a primary core of behaviours. Especially the latter two aspects make N. Tinbergen infer that the use of behavioural characters for systematics and the particular difficulties which are raised by the method force the student of systematics to take a broad

629 Eventually N. Tinbergen interpreted E. Cullen’s thesis as a proof of his hypothesis that the evolution of behaviour follows immanent principles. And it is an interesting question whether she herself saw it that way, too.

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approach. “Many of the difficulties involved in the use of behavioural characters in systematics can be avoided by a broad approach”, Hinde and Tinbergen conclude and proceed: “the importance of a knowledge of the natural history of the animal and of the causation and function of the behavior cannot be overemphasised” 630 In sum, the chapter apparently wants to stress the difficulties yet also offers ways of solution. Insofar it is based upon a typical extension scheme. The final conclusion both finalizes the overall scheme and coincides with it.

To summarize my analysis of N. Tinbergen’s and R. A. Hinde’s cooperative paper The Comparative Study of Species-Specific Behavior, I would like to mention the two major aspects my analysis aimed to carve out. First, I think it is correct to interpret the paper as a manifestation of Niko’s abstract and analytical theorizing. To make behaviour a part of evolutionary study thus primarily appears as a problem of systematics. This can be made evident in Niko’s and Robert’s explicit use of heuristic core concepts. One of the most convincing examples for Classical Ethology’s liability to taxonomic research, in my opinion, is Niko’s theory of “correlation of growth”. Second, my analysis also included the view upon the more performative modes of knowledge organization. If my reading was correct it would prove that Niko spelt out his model of causal analysis in a highly differentiated narrative scheme within which the higher levels have an impact upon even the lowest levels and the specific composition of the details at least suggest what the root of the entire scheme will be. My personal opinion is, that the fact that the paper is the product of joint work had a considerable effect upon the final result insofar as many sequences seem to be epistemologically ambivalent. In other words, on closer inspection the words are often chosen in a way that allows to infer different underlying schemes. This might be interpreted as “portents” of Niko’s own epistemic reorientation at the end of the 1950s. In any case, it is an indicator for a very intense cooperation between researchers with possibly deviating basic convictions.

The next smaller theoretical paper I would like to discuss was part of a so-called “Festschrift” for C. van der Klaauw which was published on the occasion of his sixty-fifth birthday in 1958. 631 Niko’s contribution was written in German language and had the title “Bauplan-Ethologische Beobachtungen an Möwen”. Van der Klaauw was comparative anatomist by heart and this may be the reason why the paper has an anatomical connotation as well. Furthermore, he used to have a profound interest in the history and philosophy of the sciences as well as Theoretical Biology. One of his merits in this field was to develop a system of the biological sciences. This system included also more peripheral research branches such as

631 Cornelis Jakob van der Klaauw was born in 1893, studied Biology in Leiden where he also obtained the degree of a doctor of science in 1922. In 1931 he became lecturer in Zoology and in 1934 professor and head of the Zoological Laboratory. Van der Klaauw is quite relevant for the history of Ethology since he had organized the so-called “Leiden Symposium on Instinct” where K. Lorenz and T. Tinbergen met for the first time in persona. Moreover, N. Tinbergen formally was van der Klaauw’s research assistant since 1933, a position which he resumed after his return from Greenland. He was also the one who had appointed Niko lecturer in 1939 and promoted him to professor of Experimental Zoology in 1947. For van der Klaauw’s career see H. Boschma. “A Concise Review of the Scientific Activities of C. J. van der Klaauw”. In: Archives Néerlandaises de Zoologie 13.Supplément 1 (1958), 5–9, as well as page 59 of my dissertation thesis.
ecology but it was also hierarchical insofar it favoured the classical branches over their more peripheral correspondents. As we have seen, Niko perpetuated this holistic practice of including divergent information or positions in his own theoretical papers. Moreover, he placed his own research work within the tradition of the Leiden School of Comparative Anatomy. At the beginning of his contribution for the “Festschrift” he writes:

> De Leidener Schule der vergleichenden Anatomie, die seit des zweiten Weltkrieges unter Führung Van der Klaauws erneut aufgeblüht ist, kennzeichnet sich u. A. durch die Betonung der Architektonik des Tieres. Ein Interesse in Funktion und Ökologie führte dazu, die funktionell bedingten, wechselseitigen Beziehungen zwischen einzelnen Organen zu studieren, mit anderen Worten “Bauplan-Morphologie” statt bloß “Organ-Morphologie” zu treiben. | Under the influence of this point of view, my co-workers at the University of Oxford and I myself have been thinking about this idea of a body-plan for several years. Some of our results appear to me as if they were useful as constituents of a “Body-plan Ethology”.

In other words, Niko saw his comparative Gull research as a derivative of the school his mentor had established in Leiden in the years before the Second World War and the question which I would like to answer in the following is why this view was possible and legitimate.

Alike to most of the other works on Gulls published either by Niko himself or his Oxford pupils, *Bauplan-Ethologische Beobachtungen an Möwen* must be read as a manifestation of his systematic research program. That is to say, Niko’s primary research interest was a classical one, namely how to use behaviours to classify the species within a likewise small taxonomic group. In order to reach this objective Niko suggests a rather sophisticated methodological model in *Bauplan-Ethologische Beobachtungen*. “Die auf möglichst breiter Front vorgenommenen vergleichenden Untersuchungen erfolgen in drei Stufen”, he claims:


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[The comparative studies which are to be carried out on a basis as broad as possible proceed in three steps: At first, the behavioural inventory of each single species belonging to this group is to be described carefully. Second, the differences between the species are to be determined. Third, these behavioural differences are made object of a diagnosis in the light of neo-Darwinism. Step by step it turns out that, firstly, all Gulls (as expected) resemble each other in their behaviour as they do in their morphological structure. Secondly, that there are very many constant differences between the species; thirdly, that many of these differences can be identified as adaptive (in other words, that these recent differences between the species need to be understood as the result of “adaptive radiation”); and finally, that there are existing connections between the species-specific behavioural characteristics of one species, or to put it the other way round, that there were happening reconstructions of the whole animal during the adaptive radiation. However, we did not only want to ascertain that there were reconfigurations during the branching of the species but also how they can be understood functionally in their details.]

The quotation is part of the paper’s introduction and establishes a correlation between three methodological steps and the corresponding results which are, somewhat atypical for Niko’s usual writing habits, anticipated partly already at the beginning of the paper. The correlation itself profiles more precisely the methodological stage model. The first of the three steps seems to be the one which is most common. Describing precisely the behavioural inventory of a species eventually is the one step which is common sense among most behaviour researchers. Moreover, Niko here has in mind all those behaviours which are common to all species of Gulls. Not so the behavioural qualities he intends to explore on the second stage of his model. Here it is the species-specific variations he is primarily interested in, that is, those small deviations which allow the reconstruction of the course of evolution. The “last” stage of his methodological model which he circumscribes as the “examination” of these species-specific differences within “the light of NeoDarwinism” apparently encompasses two aspects which must be separated from each other from the epistemological point of view. On the one hand, Niko insists on noticing that the species-specific variations are adaptive, that is, they are correlated with a particular habitat so that the systematic tree also mirrors a geographic radiation or distribution. On the other hand, however, he puts great emphasis upon the fact that the species-specific behavioural characters are interrelated within the genetic setup of a species. In other words, in Niko’s view, evolution does not primarily operate upon an isolated character but upon the whole network of functional relations. This is why he speaks of “ganzeitungliche Umkonstruktionen” (very literally: “holistic reconstructions”). “Was sich also im Laufe der Evolution geändert hat”, N. Tinbergen writes later,

ist ein Riesenkomplex von miteinander verknüpften Einzelheiten; das ganze Tier hat sich geändert. Natürlich ist das für denjenigen, der von der Wirkung der natürlichen Auslese überzeugt ist, im Prinzip selbstverständlich: Selektion merzt ja Tiere oder sogar Familien aus, nicht aber isolierte Teile.

[What has been changed in course of the evolution is a huge complex of interrelated particulars; the whole animal has changed. Certainly, this principle is self-evident for those who are convinced of the potency of natural selection: In fact, selection wipes out animals and even families but not isolated parts.]
For the time being, I will not enter into the discussion that sparked off in the second half of the 20th century about the question which “units” are the ones evolution is actually acting upon. For my purpose it is sufficient to notice that Niko’s view on evolution is not only systematic but also systemic. In other words, what makes his approach to taxonomy special is that he places the questions of species-specific variation and adaptiveness within a wider frame that is primarily interested in examining the complex network of functional relations. Now we may eventually understand that Niko’s construction of the line of tradition between his and his mentor’s work operates with an inference *per analogiam*:\(^\text{635}\) Just as J. C. van der Klaauw integrated an “interest in function and ecology” which led him to study the “functionally determined mutual relations between the organs” and thus came to what Niko called “Bauplan-Morphologie” instead of a mere “Organ-Morphology”, he himself was about to integrate the question of adaptive variation just to come to a systemic view of the genetically determined make-up of a species’ behavioural repertoire. “Wenn man von den arterhaltenden Funktionen der behandelten Verhaltenszüge keine Ahnung hätte”, he writes,

\[\text{If one had no idea about the species preserving function of the treated behavioural traits or, if one was interested in functions, yet not in the mutual relatedness of these singular functions, then, this would create only a list of single particularities instead of a body-plan Ethological Synthesis.}^{\text{transl. CL}}\]\(^\text{636}\)

It is not necessary to reconstruct the order of the entire paper in this case like I did in some of my other readings of Niko’s works. For my purpose it is sufficient to realize that the announcement to proceed in three methodological stages in combination with these three steps makes four discrete units which coincide with the paper’s organization in four major numbered sections: The announcement then coincides with the paper’s introduction, the description of the behavioural inventory corresponds with chapter “II.”, the assessment of the species-specific differences happens in chapter “III.” and the discussion of both the adaptiveness and the interrelatedness of the species-specific differences is reserved for the concluding section (i.e. chapter “IV.”) of the paper. I suggest the following illustration to exemplify the three (implicitly four) steps of N. Tinbergen’s argumentation while the numbering of the chapters does not coincide with the methodological step (Fig. 2.10). The visual translation of the inner order of the paper shows its hidden message: Niko’s gesture to frame his pupils attempt to venture into neo-Darwinian regions by claiming that only the body plan of the animal as a whole can become object of selection coincides – so to speak – *per analogiam* with his teacher’s former move to integrate Ecology and other peripheral sciences into his concept of comparative anatomy. N. Tinbergen’s “re-boundarying work” here therefore may have a twofold function: To maintain the bonds of tradition to his own teacher but also to integrate the provocative findings of his pupils into his causal analytical framework.

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\(^{\text{635}}\) Eventually more precisely: “Per homologiam”.  
\(^{\text{636}}\) Tinbergen, “Bauplan-Ethologische Beobachtungen an Möwen”, 381.
N. Tinbergen’s paper *Bauplan-Ethologische Beobachtungen an Möwen* (1958) therefore was not only meant to place his systematic research interest within the holistic tradition of his mentor’s school of Comparative Anatomy but it is eventually also one of the most explicit attempts to place the results of E. Cullen’s research work within his own scientific edifice. Esther met Niko during his lecture trip to Switzerland in January 1948. After that she came to Oxford as a post-doc and began a research project on Kittiwakes which she carried out on the Farn Islands. Her study was exceptional in several respects since she not only described the species-specific characteristics of the Kittiwakes (stage two of Niko’s model) but also went a step further by correlating the birds’ specific behaviours with their particular habitat (stage three of Niko’s model). The Kittiwake (*Rissa tridactyla*, German: “Dreizehenmöwe”) differs from many other Gull species insofar as they are cliff-breeding birds and Cullen was able to show that many of the Kittiwake’s reproductive behaviours can be interpreted as secondary adaptations of their primary habitat selection. Niko dedicated most of the third chapter of his paper to E. Cullen’s study and also developed his own systemic point of view on basis of a “latent critical appreciation” of Cullen’s work. Thus Niko at first repeats the main argument of Cullen’s study as he saw it. “Ihre Hauptschlußfolgerung sei hier vorweggenommen”, he writes in the introductory part of chapter three:

für das Verständnis der vielen typischen *Rissa*-Züge ist die Tatsache, daß die Art als einzige auf sehr schmalen Sims sen auf steilsten Felswänden brütet, von hervorragender Bedeutung. Diese arteigene Wahl des Nistplatzes ist ohne Zweifel eine Form der Verteidigung gegen Raubfeinde: die Brut der Dreizehenmöwe ist tatsächlich, wie Dr. Cullen zeigt, für Raubfeinde.
(sogar für Großmöwen) praktisch unerreichbar. Viele Verhaltensmerkmale, und auch manche morphologische Eigenschaften, stehen nun offensichtlich hiermit im Zusammenhang. Ich wähle aus Dr. Cullen’s langer Liste einige besonders ansprechende Merkmale.

[I should like to mention her primary conclusion already at this point: For the understanding of the many traits being characteristic for Rissa the fact that this species is the only one which is breeding on the narrow ledges of steep cliffs is of utmost importance. This species-specific choice of the nesting site without doubt is a defence reaction against predators: The offspring of Kittiwake is in fact, as Dr. Cullen shows, practically unreachable for predators. Many behavioural characteristics, and also some morphological qualities, are obviously connected with his habit. I choose some extraordinary comprehensive qualities from Dr. Cullen’s long list.] (transl. CL)

What follows is a recapitulation of altogether eight secondary behaviours specific for the Kittiwakes and one further additional paragraph with further characters which Niko just wanted to enumerate.638 What is important for my argumentation is that Niko presents the results of E. Cullen’s study following a specific epistemic scheme which mirrors his view upon the data itself. There is a primary choice of habitat, a fact of “hervorragender Bedeutung”, which entails, so to say as derivatives, a whole bunch of secondary morphological and behavioural characters (see the quotation above). Eight strictly distinguished characteristics of the Kittiwakes are supplemented by a paragraph with a whole bunch of morphological and behavioural characters which are not discussed in detail but seem to be treated as consequences of a primary disposition as well. Finally, the peculiar, habitat-dependent, behaviours of the Kittiwake are reduced to a genetic origin or heritable differences. “Viele dieser Unterschiede”, Niko infers,

sind nicht direkt von der Umgebung, sondern genetisch bedingt. Für manche ist dieses durch Versuche bzw. durch Dänische Beobachtungen in einer auf flachem Boden brütenden Kolonie bewiesen (Salomonsen 1941); für andere ist es auf Grund vergleichender Beobachtungen wenigstens sehr wahrscheinlich. Wir planen aber systematische Austauschversuche zur genaueren Prüfung dieser Frage.

638 These species-specific character are in detail (1) the Kittiwake’s tameness, (2) the peculiarities of their nest building habits, (3) the lack of protective colouration in the young, and (4) the inhibition of the chicks’ local movements which prevents them from falling off the cliffs. Moreover, the Kittiwakes reveal several peculiarities in their expressive movements which may root in the impact of their habitat as well. Thus they (5) do not use the “Upright Position” as a threat gesture, (6) they do not make use of “Cheering” (Jauchzen) for their singing, (7) they use “Thrusting Upwards” (“Nach-Oben-Stößeln”) and not “Facing-Away” (“Wegsehen”) as appeasement gesture during courtship, and finally (8) in Kittiwakes even the young apply “Facing Away” when they are attacked. All these gestures, in Niko’s view, are secondary modifications of primary stereotypes. If the latter, as a consequence of the particular habitat choice is different, also the process of ritualization must have taken another course. In addition to that, also the following behaviours are connected with the habitat choice of the Kittiwakes: For instance, Kittiwakes are not as keen as other Gull species to camouflage their nest by avoiding to mark the nest edge with their faeces or by carrying away the bright egg shells. Moreover, the clutch size of the Kittiwake is relatively smaller because a high number of offspring would increase the danger to fall of the nest. Fighting strategies include throwing the offender off the cliffs, the female lies during copulation, Kittiwakes tend to steal nest material from other birds so that parents watch over their nests even before their young hatch. Due to shortage of space, the parents do not need a special call or gesture to lure their young and vice versa. In contrast to other birds which breed in colonies, there is no individual recognition of the young. Specific postures prevent the offspring from falling off and their claws are stronger than usual. See ibid., 374–379.
Many of these differences are not determined directly by the environment but genetically. For some of them this has been confirmed by experiments or, respectively, by Danish observations of a colony breeding on flat grounds (Salomonsen 1941); for others it is at least rather likely on basis of comparative observations. However, we are planning also systematic exchange experiments in order to examine this question more thoroughly.\[^{639}\]

In Niko’s three-stage model, the assessment of species-specific differences functions as a precondition for the treatment of these differences in “the light of Neo-darwinism”, as he puts it. Insofar one may say, E. Cullen’s descriptive work as a whole also introduces and prepares N. Tinbergen’s critical reflections in terms of evolutionary theory in *Bauplan-Ethologische Beobachtungen*. Within this theoretical part we meet the same procedure again. E Cullen’s proofs of the adaptedness of the Kittiwake’s peculiarities introduce, prepare and are the empirical basis of Niko’s systemic view. Nearing the end of the final chapter it reads:


[The body-plan ethological micro-analysis that has been carried out by Dr. Cullen, finally, also shows very nicely how some qualities have been developing under positive selective pressure, while others have been receding as a consequence of waning pressures. The building of the nest platform is a new acquisition, whereas the loss of the chicks’ protective colouration, or the loss of the removal of the egg shells, probably must be counted to the second category. | However, we are far away from being able to explain all differences between *Rissa* and the other Gulls. Why, for instance, should *Rissa*’s beak be yellow? Why does this species have another wing pattern than other Gulls? Why is the voice different? Certainly, it can be that some differences between *Rissa* and the other Gulls have nothing to do with any variation in their adaptiveness. Cullen’s work, however, urges us to be careful at this point. Its primary value is eventually lying in the fact that it is leading us away from any naïve negativism and, instead, is directing us towards positive research within this and other groups. I believe that, while doing this, a holistic attitude, a view upon the connections between the things, will be immensely fruitful – as long as this inspection is based on analysis.]\[^{640}\]

From this quotation we may eventually infer that N. Tinbergen wanted to supplement the mere focus upon the adaptiveness of the species-specific variations with a more holistic stance that takes into account the immanent systemic (and therefore potentially non-functional) causes of evolutionary divergence. And this specific practice of (recursive) supplementation can be observed on several stages –
especially, however, on stage two and three of his model. Thus the mere description of species-specific variation needs to be supplemented with an examination of these differences in the “light of Neodarwinism”. The entire frame as a whole, which consists of observation, assessment of differences, and assessment of adaptiveness of heritable variability, then, as it seems, is once more supplemented with a holistic and systemic perspective. In sum, one may therefore say that N. Tinbergen operates with a stage model of systematic research which is guided but does not coincide with the composition of the paper. The places where and the manner how E. Cullen’s study and its results are mentioned reveal that Niko apparently felt that Esther’s “positive Forschung” (positive research) should be complemented with a more holistic attitude (“ganzheitliche Einstellung”) so that the entire scientific edifice still could be rendered compatible with the epistemic ground-plan (Bauplan) of Classical Ethology. Moreover, I think that this implied a process of academic socialization, as well.  

Scientific differentiation allows placing the results of others so that a researcher’s own paradigm can be maintained and this process is textual in the very first place. As such N. Tinbergen seems to have integrated the results of his pupils as an empirical basis for his own theoretical conclusions. In this practice he behaved quite analogous to his mentor C. J. van der Kleuauw in whose tradition he placed his own research. In turn N. Tinbergen’s conclusions very often were the starting point of his pupils’ own scientific works so that it is allowed to characterize Ethology’s classical epistemic setup a highly liable for processes of crosswise scientific exchange.

*Comparative Studies of Behaviour of Gulls (Laridae): A Progress Report* has been called the most important paper N. Tinbergen published during his early years in Oxford. It was published in 1959 and marks the climax in Niko’s affiliation with the mechanomorph research attitude which now had been an essential part of an classical ethologists’ self-understanding. In comparison to Niko’s earlier physiological modelling, his phylogenetic interest in display behaviours of various species of Gull shifted the thematic focus of causal analysis from the hierarchical organization of the nervous system to the phyletic order of a specific group within the animal kingdom. In so far one may eventually speak of a thematic reinterpretation or translation of a fully developed epistemic scheme within or into a “new” context. When I type “new” between quotation marks I indicate that Niko’s turn to comparative phylogeny of behaviour coincided with K. Lorenz’s earlier attempt of the year 1941 to use the more conservative behaviour patterns of *Anatinae* for taxonomic

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641 In addition to that, I believe, that N. Tinbergen has misrepresented the epistemic order of E. Cullen’s study. Cullen had reduced adaptations to a one particular habitat condition. Niko derives adaptations from the particular habitat. This also implies a distortion of the epistemic ground plan underlying the neo-Darwinism Niko refers to.

642 From a linguistic point of view the term “Bauplan-Ethologie” seems to be the formation of a new word by analogy to “Bauplan-Morphology”.

643 Kruuk, *Niko’s Nature*, 189–190. Some more details concerning Niko’s thoughts about this paper during the writing up period can be inferred from a letter to J. Huxley. See WRC-RU Fondr. Lib., *MS 50*, box 27, file 2, letter N. Tinbergen to J. Huxley (10/08/1958).

644 The basic idea of reductive causal analysis guiding the text, however, seems to be remained intact. This can be concluded eventually from D. S. Lehrman’s criticism of Niko’s unitary drive model. See Bod. Lib., *N. Tinbergen Papers*, Ms.Eng. c. 3157, E 29, letter D. S. Lehrman to N. Tinbergen (22/04/1960).
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objects. In relation to Niko’s research interests after 1959 *Comparative Studies of the Behaviour of Gulls* can be interpreted as the last paper which operated within a strictly causal analytical frame. “And finally”, H. Kruuk remarks, the paper marked something of a turning-point in his scientific career. He subtitled it “A progress report”, but with it he ended his personal involvement in studies of displays and likewise his interest in the analysis of causes of behaviour, in the internal states of animals that produce displays. After he had published the comparative gull paper, he focused on biological effects of behaviour rather than on causes, and he restricted his personal research interest to other, non-display types of behaviour.

There is something more in the subtitle of the paper: From an epistemological point of view, it indicates a paradox. The paper as a whole summarizes and brings into an order the amount of data which had been generated by the projects he had supervised in the preceding years. Yet, the paper’s subtitle can also be read as if it is the empirical studies performed by his students which have a significance far beyond the current state of research as documented in Niko’s retrospective account. In sum, I am inclined to put forward the hypothesis that in 1959 this paradox form of self-description was applied for the last time since, as soon as the innovation generated by Niko’s students fully overwhelmed his own standpoint, a corresponding epistemic frame needed to be found which was capable to represent the situation adequately. From a perspective like that N. Tinbergen’s turn to Behavioural Ecology would have to be interpreted more as a form of “reverse socialization”. For the moment, however, I would like to stick with Niko’s Gull study and ask in how far the paradox tension implied in the ethologists’ understanding of causal analysis precipitated in the way Niko presented his knowledge.

To assess correctly the meaning of the topics Niko elaborates upon in each relevant section of his progress report it seems wise to reconstruct the paper’s organization provisionally in the first place. This provisional picture, then, allows to make some further leading conjectures as to how the overall order might precipitate into certain micro-areas of the account. In a second step these constructive hypotheses can be tested by cautiously reading the most promising part sections so that I will be finally able to obtain a more profound understanding of the overall study.


In concrete Niko’s progress report is divided into eight chapters bearing the titles “I. Introduction”, “II. An Attempt at a Rationale of the Taxonomic and Evolutionary Approach”, “III.
introductory section of the paper, readers find a short paragraph in which Niko provides a rough overview of the paper. He writes: “The present paper attempts to give a summary of the results so far obtained, with a discussion of some problems of function, of motivation, of some evolutionary aspects, and of methods of study.” What can be inferred from the quotation with safety is the bifurcated structure of the entire paper in a “summary” and “discussion” whereby the latter of the two parts, again, encompasses a discussion of several aspects related to function, motivation (here eventually another word for “causation”), evolution and methodology.

If we try to connect Tinbergen’s brief outline with the chapter titles we find in the table of contents, it stands out that there is no one-to-one correlation so that we may have to guess, at least to a certain extent, which chapter belongs to what major section. The “summary” thus seems to consist of the chapters two (“An Attempt at a Rationale of the Taxonomic and Evolutionary Approach”) and three (“Description of the Agonistic and Pair Formation Displays”), while the chapters four (“Functions of the Displays”), five (“Causation”), six (“The Origin of the Displays”) and seven (“Some Evolutionary Aspects”) cover the discussion. How the arrangement of the chapters beyond their differentiation in “summary” and “discussion” actually looks like cannot be said with complete certainty. There is more than one possibility, especially, as to the question what reference system guides the introduction and how to place the units which build the main section of the paper (i.e. chapters IV–VII). However, another short passage at the beginning of the paper in which N. Tinbergen names retrospectively the aims of his research program on Gulls seems to tackle this question indirectly. “The aims of our study were”, Tinbergen says,

First, a description of the behaviour of as many species as possible; second, as complete a coverage as possible of the entire behaviour pattern of each species; and third, analyses of the functions, the causation and the origin of the displays, with the ultimate aim of understanding how they could have originated and diverged in the course of speciation.

The vital question is whether N. Tinbergen intended to mirror the inner logic of this processing in his paper and its organization. If so, Tinbergen’s “discussion” as a whole would be arrangeable in form of a multistage model of systematic reasoning in which two initial “aims”, namely the assessment of “function” and “causation”, turn out to be supplemented by a phylogenetic reconstruction of the displays so that, lastly, both the narrower and the wider aims can culminate into the ultimate problematic: The evolution of the behaviour machinery. I suggest the following illustration for the supposed order of the paper (Fig. 2.11). The figure suggests that Niko’s “summary” of the results of his and his pupils’ research on Gulls encompasses mainly two connected aspects, that is, some kind of

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649 Ibid., 2.
650 Ibid., 1.
651 Needless to say that the multistage model of systematic reasoning Tinbergen seems to have applied in his “Progress Report” is obviously structurally analogous to the one he had elaborated in “Bauplan-Ethologische Beobachtungen”. See Fig. 2.10, page 225 of my thesis.
methodological introduction, on the one hand, and the description of two kinds of behaviours, on the other. These behaviours are described as “Agonistic” and “Pair Formation Displays”. The “discussion”, step by step, seems to embrace both questions of causation and development. On closer inspection, chapter four, “Functions of the Displays”, thereby provides an ordered listing of the display behaviours by assessing their communicative function. Chapter five, “Causation” provides means for a motivation analysis of the displays. Chapter six, “The Origin of the Displays”, seems to reinterpret former considerations concerning the adaptiveness of behaviour by suggesting concepts (ritualization, derived activities, adaptive radiation) for the phylogenetic reconstruction of the display movements. “Some Evo-
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olutionary Aspects” (chapter seven), finally, includes conjectures concerning the question in how far phylogenetic development affected the “behaviour machinery”. Taking into consideration the epistemological outline of each section and the paper as a whole, one may eventually say that, no matter how we arrange the overall composition of Niko’s progress report, the core of the paper consisting of a “summary” and a subsequent “discussion” establishes the scheme of a causal analysis since the manifold observed data is reduced and made subject to a critical problem oriented reassessment. Especially the epistemological outline of chapter four and five cannot be determined with certainty. The reading I suggest aims to avoid “counter-intuitive” interpretations so that the emphasis of “function” (ultimate causation) corresponds with synthetic reasoning while the notion of “causation”, in accordance with classical ethological mechanomorphism, usually coincides with a reductive and analytical heuristic procedure. N. Tinbergen’s account of the “origin” of the displays operates with a synthetic scheme while chapter seven, as it is to be expected, once again reduces complexity. I have summarized the supposed epistemological framing of each section in another table (see Table 2.2).

Table 2.2 N. Tinbergen, *Comparative Studies of the Behaviour of Gulls* (1959), Alleged Epistemological Framing of Single Chapters

<table>
<thead>
<tr>
<th>Chapter</th>
<th>Title</th>
<th>Causal Analysis?</th>
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<tr>
<td>I</td>
<td>Introduction</td>
<td>-</td>
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<tr>
<td>II</td>
<td>An Attempt at a Rationale of the Taxonomic and Evolutionary Approach</td>
<td>+</td>
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<tr>
<td>III</td>
<td>Description of the Agonistic and the Pairformation Displays</td>
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<td>IV</td>
<td>Functions of the Displays</td>
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<td>V</td>
<td>Causation</td>
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<tr>
<td>VI</td>
<td>The Origin of the Displays</td>
<td>-</td>
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<tr>
<td>VII</td>
<td>Some Evolutionary Aspects</td>
<td>+</td>
</tr>
<tr>
<td>VIII</td>
<td>Summary</td>
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In the following it shall be asked in how far can a careful reading of those sections Tinbergen framed with the term “discussion”, to which I shall restrict myself, support my alleged reconstruction of the paper’s overall organization? Chapter four, “Functions of Display”, in my opinion consists of two parts. While Niko provides the reader with some introductory preliminaries at the beginning of the chapter, the latter parts introduce a more detailed specification of the display movements relative to their function. The former of the two sections thereby proceeds according to a known scheme. Initial considerations concerning the respective scientific object are complemented with an account of the applied methodology. As to the specific character of the scientific object, that is the function of the display movements, N. Tinbergen marks certain difficulties:652 In contrast to so-called

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maintenance behaviours the biological meaning of display movements used to be obscure. Yet, ethologists such as K. Lorenz were able to remove this obstacles by suggesting that display movements primarily function as releaser. “However, mainly through the work of K. Lorenz (1935) and others”, he underlines, “it is now clear that the overall function of displays is that of ‘releasers’ (Lorenz) or signalling devices, and as such they are a distinct class of effector organs, functioning in inter-individual relationships”.\footnote{Ibid.} In other words, the biological meaning of displays is to enable social communication. From an epistemological point of view, the theme “communication” thus combines the ultimate cause of “increased fitness through communication” with a supra-individual entity of investigation, namely the community or the population. Tinbergen’s reasoning concerning an appropriate methodology, again, proceeds in two discrete steps.\footnote{Ibid., 23–24.} At first, he ascertains that Gulls turned out to be inappropriate animals for experiments with dummies. This type of test thus had to be replaced with what Tinbergen calls “‘natural’ experiments”. “However”, Niko says, the study of unplanned, or “natural” experiments has enabled us to make fair guesses as to the functions of most of the gulls’ displays, and have led to some hypotheses which seem worth checking. While such natural experiments do not as a rule provide information about the part of the total display which is effective (e.g. whether sound, movement, posture, or colour is the main agent) they do, if observed with care and with an eye for possible flaws and for “natural controls”, and if repeated often enough, tell us a great deal about the functions of the displays as wholes. All the same, the conclusions drawn in this section must be regarded as tentative.\footnote{Ibid., 23.}

In a second step, Tinbergen seems to collect evidence for the legitimacy of this methodological decision, either by quoting literally from field observations or by pointing the reader to more specific publications of some of his pupils.\footnote{For some example of quoted observation protocols, see ibid., 23–24.} The final paragraphs of the chapter seem to be dedicated to the functions of the display movements themselves.\footnote{Ibid., 24–29.} According to N. Tinbergen, the listed postures are exhibited by the Gulls in agonistic (i.e. $\sigma^-$-$\sigma^-$ encounters) and sex-related situations ($\varPhi^-$-$\sigma^-$ encounters). For my epistemological purpose it is of utmost importance that Tinbergen thereby distinguishes between “distance-increasing” (“Group I”) and “distance-decreasing” (“Group II”) gestures.\footnote{The former of the two groups is also called “Spacing-out” by N. Tinbergen and encompasses “Aggressive Upright”, the “Oblique-cum-Lang-Call”, the “Forward”, “Jabbing”, the “Mew Call”, “Choking”, and “Pecking-into-the-Ground”. See ibid., 24. In the second group Tinbergen places “The Hunched”, “Head Tossing”, “Facing Away”, and “Upward Choking”. See ibid., 27.} This suggests that the biological meaning of the display movements, that is their communicative function, actually consists of distance regulation. The overall criterion of their arrangement is approach and withdrawal.\footnote{Needless to say that from a more epistemological standpoint “approach” represents an ultimate, “withdrawal” a proximate form of causation.} For my argumentative purpose it is not necessary to go into further detail. It is sufficient to notice that Tinbergen’s primary distinction between distance-increasing and distance-decreasing gestures is further evolved by apply-
ing additional binary oppositions such as responsiveness to a relatively “narrow” vs. a “wider” scope of situations, relatively “more defensive” vs. “less defensive” displays, or postures with “milder” or “more drastic” effects. For instance, with a view upon the threat displays Tinbergen writes in a concluding remark:

Thus my suggestion is, that there might be an advantage in having five different threat displays. One is used as a long-distance threat (and song, see below); then there is one aggressive and one defensive display effective with accidental intruders and near-intruders respectively; and one aggressive and one defensive display effective with determined intruders and near-intruders. Yet this can not be the whole story; apart from the discrepancy pointed out in the Kittiwake [Kittiwakes have no “Long Call”] the Mew Call does not seem to fit in a clearly defined pigeonhole, nor is the function of each display exactly the same in all species. Clearly more purposeful and systematic investigations of the functions are required.660

The fact that N. Tinbergen does not spell out each “branch” of the tree he unfolds cannot obscure the common principle the author makes use of: Tinbergen develops an increasingly complex matrix of finely scaled behaviours. What thereby appears as N. Tinbergen’s terminological refinement at first sight has its reasons in the real world: According to N. Tinbergen, each posture is adapted to a limited set of frequently recurring situations so that their refinement contributes to disambiguation.661 The development of this matrix thus proceeds from simple to complex. And although especially the second part of the chapter which is concerned with the functions of the postures themselves reveals structural peculiarities (viz. a more exclusive summary at the end), the organization both of the core of this second part and of section four as a whole seems to recapitulate this general synthetic thrust since in case of the former textual entity the account proceeds from “distance-increasing” to “distance-reducing” and in case of the entire section the line of argumentation evolves from abstract (i.e. the preliminaries) to concrete (i.e. the description of the functions).

Chapter five, “Causation”, is the one in which N. Tinbergen discusses “aims and methods of analysis of the motivation of the displays” – as he puts it in the concluding remarks of his research report.662 At the beginning of the section there is another statement which provides some kind of outlook. “In this chapter”, Tinbergen underlines, “I shall discuss some concepts and some methods used, and some of the results so far obtained”.663 The scientific practice of “discussing” in N. Tinbergen’s writings indicates an analytical heuristic thrust. The key words “concepts”, “methods”, and “results” name the major themes of chapter five.664 Moreover the syntactic structure of the quotation above suggests that we, eventually, have to read the paragraphs dedicated to “concepts” and “methods” as a unit while the “results” seem to build an additional entity. The introductory section of the paper, which is not mentioned in the quote, and the explicitly mentioned sections are finally framed by a concluding part at the end of the chapter.665 Can the inner composition of each

661 Ibid., 24–25.
662 See ibid., 65.
663 Ibid., 29.
664 That this major themes correspond with actual textual sequences can be confirmed. See to this ibid., 29–30, 30–35, and 35–43, respectively.
665 For this concluding paragraphs see ibid., 43–44.
part section substantiate the supposed arrangement of the chapter and thus confirm my hypothesis that N. Tinbergen’s treatment of “Causation” in 1959 still follows the traditional causal analytical reference system?

In fact, Tinbergen’s account on concepts proceeds in three connected steps. A terminological extension (a) is used to formulate a methodological claim, namely to take into consideration the multiple motivational roots of display movements (b), and this “multiple motivation hypothesis” then is declared a more common phenomenon (c).

Ad a): For his motivation analysis Tinbergen introduces two concepts, namely, “motivation” and “tendency”. 666 Both terms have in common that they refer to the internal state of an animal inasmuch as this state can be deduced from overt movements. Yet, both concepts approach the hierarchical system of centres, which N. Tinbergen still seems to presuppose, at different levels. Whereas “motivation” implies the idea of an undivided motivational force arising from a particular situation, the “tendencies” refer to “component motivations” or “sub-systems” of the entire motivational complex. “To indicate the complex conditions which make a bird attack, escape or mate”, Tinbergen states, we need a term of the same type as “motivation”, but applying to one of these single systems only. In order to avoid the word “drive” which is ambiguous because it has been used in different senses, I use the word “tendency” (Hinde, 1955; Tinbergen, 1955). While this word again is nothing but a shorthand description of the state of an animal as indicated by the movement it makes, it is needed to describe the total motivation of an animal at any given moment in terms of simultaneous arousal of two or more tendencies in the above sense; and this intended as a first step in the causal analysis of displays.667

Ad b): The quotation already includes the second step of Tinbergen’s train of thought: The causal analysis of display movement, even before separating external from internal stimulation, must begin with “splitting up the total motivation in two or three component motivations, each of which is unitary in the above sense and thus comparable as regards degree of complexity with feeding, etc.”. 668 The sub-systems Tinbergen thinks relevant in his analysis of the display behaviours are mainly three: Attack, escape, and sexual behaviour. 669 Altogether, Tinbergen thus seems to profile the displays as a sort of behaviour with multiple, simultaneously excitable motivational sources against behaviours with unitary motivation to which Tinbergen seems to count the maintenance behaviours. Display movements and particularly their motivation analysis thus match perfectly well the inclination of classical ethologists to operate with soft of loose reductions of complexity. Ad c): However, N. Tinbergen does not want to confine his claim for a analysis of multiple motivation to displays only. Rather, in their nervous constitution he is seeing a prototypical example for other types of behaviour and, as a result, the display behaviours can be analysed within the frame of this wider problematic. 670 Altogether, N. Tinbergen’s reasoning on methodological concepts therefore seems to end with and, as a whole, seems to proceed like the sort of synthesis we are already

666 Ibid., 29
667 Ibid., 29–30.
668 Ibid., 29.
669 Ibid.
670 Ibid., 30.
acquainted with from *The Study of Instinct*: The ultimate extension of one concept with another or the transfer of one theme into a wider area of research. The introduced methods themselves are of a threefold kind: (a) The postures in question can be interpreted as combinations of constituents being part of various “recognisable motor patterns”. On basis of the correlation with overt movements the source of motivation is to be inferred. To put it in Darwin’s words, Niko’s methodology here consists in establishing a correlation between a sequence of a motor pattern, the expression (or its constituents), and an underlying emotion. (b) The second method consists of taking so-called “time scores” which means that an experimenter records carefully which overt behaviour patterns alternate in quick succession with the display in question. The underlying presumption thereby is that animals do not easily switch their motivational state so that behaviours linked with each other through rhythmic alteration most likely belong to one and the same source of motivation. If I am not mistaken the inference here is made from the frequency of a behaviour’s relative occurrence to the (relative) intensities of both tendencies. (c) The third method proposed by Niko consists of comparing “the external situations which evoke ‘pure’ attack and ‘pure’ escape with the situations which evoke threat displays”. The method apparently makes use of the fact that displays are often situation dependent: The owner of a territory reacts with pure attack when spotting an intruder within his territory but reacts with escape when he meets the same intruder in his own territory. The threat displays, however, usually occur in the boundary zones where the situation is intermediate between both extremes. The heuristic thrust thus proceeds from the either-or to the both-and. And although N. Tinbergen does not make entirely clear at this point what the effect of this method lastly may be, I think it is the attempt to verify the hypothesis that a certain ambiguous motivation may be expressed in each of the extreme reactions or intermediately. N. Tinbergen finishes his account of methods by underlining that the results of all three methods when applied independently tend to point into the same direction. This can be interpreted as a common overtone of all three methods. After having elaborated upon methodological options, N. Tinbergen is continuing his account on causation by entering into a closer examination of three types of displays, the agonistic displays, the appeasement gestures and, finally, the displays related to pair formation. Thus the core sections of chapter five proceed from the abstract (aims and methods, concepts and methods) to the concrete. As a result, Tinbergen’s account of relevant displays is less guided by the urge to classify states of motivation or define discrete motivational centres corresponding to particular behavioural expressions rather than by the question what the behavioural effect of their simultaneous arousal might be, as Niko puts in the quote above. Again, from the epistemological standpoint the question is less the content of the provided information itself rather than the manner of its presentation. A brief glance back to Tinbergen’s functional matrix of display behaviours outlined in the previous chapter suggests two things: Firstly, in comparison to the much more complex matrix of behaviours the current focus upon agonistic, appeasement, and courtship postures

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671 Tinbergen, “Comparative Studies of the Behaviour of Gulls”, 30–35. In addition, they are meant to be applied in the field.
672 Ibid., 34.
Niko Tinbergen (1907–1988)

turns out to be an abridged albeit structurally representative reduction. Secondly, the narrative of the preceding section suggests that it is the appeasement gestures and the courtship behaviours together that build a unit because contrary to the agonistic behaviours the former are described as “distance-reducing”. According to N. Tinbergen they belong to “Group II”. This is eventually supported by the idea that postures of pair formation are often secondary derivatives of hostile encounters between males. “Briefly this theory states”, he writes, “that courtship originated as, and often still is, the outcome of a conflict between sexual attraction and agonistic tendencies”. And finally, appeasement gestures are often (though not exclusively) part of the courtship ceremony. At this point I am wondering what the corresponding states of motivation might look like in each case? The primary characteristic of the agonistic behaviours displayed amongst hostile males thereby seems to be a conflict between the tendencies of attack and escape. Which behaviour prevails is dependent on what tendency is able to override the other. Moreover, N. Tinbergen here puts great emphasis on the notion that finest nuances in the displays may be correlated with corresponding states of motivation. The appeasement gestures differ in general from the threat postures in that aggression is not the primary component in their motivation and that fear might be involved. “It seems”, N. Tinbergen clarifies the motivation state underlying appeasement gestures, “that they are the outcome of a conflict between escape and a tendency to approach or to stay put, but the difference with the treat postures is that this latter tendency need not (though it can) be aggression”. The courtship behaviours seem to encompass both a sexual tendency (i.e. to mate) and some agonistic tendency while attack (expression of aggression) and escape (expression of fear) are themselves in conflict. Moreover, sooner or later the sexual overrides the agonistic tendency. N. Tinbergen’s account of single gestures thus seems to proceed from distance-increasing to distance-decreasing postures while the states of motivation seem to change correspondingly. To put it in my own words, I’d say: The more distance-reducing a posture becomes the more “framed” seems the original agonistic tendency to be a moment of attraction. In other words, the potential conflict of escape and attack is superimposed, though not overridden, by a liability to be attracted.

The chapter on causation finally ends with a concluding paragraph. This paragraph contains both a reassessment of the pros and cons of the applied methodology, the field observations, and the claim for a shift from the field to the lab in the future. “Yet it becomes clear”, Niko concludes, that amplification by laboratory tests is required; now that the problems are seen a little more clearly such tests are possible and promising. The most suitable experimental method seems to be control rather than to assess the unitary behaviour tendencies separately and to create conflicts between them so as to check and work out conclusions based on interpretations of the type

673 See ibid., 39, also 43. For the differences between the strictly agonistic and the courtship displays see ibid., 42.
674 See ibid., 35.
675 For the continuous relation between motivational tendency and overt movement see ibid., 36.
676 See ibid., 37.
677 See ibid., 40–41.
This quote reveals that N. Tinbergen’s understanding of motivation analysis starts with field work yet in the last consequence is headed towards the lab where deliberate experiments were meant to check the interpretations gathered in the field. And it is apparently this heuristic thrust which he regards promising even for the future. Summing up the epistemological patterns of each part section one can confirm that the overall heuristic thrust of chapter five is analytical inasmuch as preliminary remarks concerning concepts and methods are confronted with concrete results and this encounter is reflected critically in a concluding comment. Comparing the mode of analysis N. Tinbergen used to apply in the immediate years before and after the war with the one proposed in his Gull research one might detect both similarities and differences. On the one side, like it was the case in Niko’s hierarchical model of instincts, the problem of causation is still addressed in analytical terms. However, while analysis in The Study of Instinct, An Objectivistic Study or Physiologische Instinktforschung was more or less identical with recursive partitioning in the tautological element of the reference system, the main field of refinement now seems to lie in the paradox element. As a result, one may eventually speak of two different “interpretations” or “modes” of causal analysis: One encircles a problem while the other narrows it down. From a more epistemological point of view, maybe this can be interpreted as a more advanced stage in the process of re-evaluation.

Chapter six, “The Origin of the Displays”, raises the question how the displays have developed in course of evolution. Thereby N. Tinbergen obviously provides a reinterpretation of his earlier reasoning on the role adaptiveness played in the course of evolution. While in The Study of Instinct reasoning on adaptiveness was influenced by a neo-Darwinian understanding of selection and therefore put great emphasis on various entities of beneficiaries (i.e. the units selection acts upon), adaptiveness now is re-conceived in strictly ethological terms as a means of animal communication. Asking the question for the origin of the displays therefore implies a reconstruction of the evolutionary process which is leading to more and more finely nuanced communication signals. One of the driving moments, that is in the last consequence the ultimate cause, thereby seems to be the need for disambiguation. I believe, that this general thrust from simple to complex again is mirrored in the organization of the chapter’s narrative. Thus a brief glance at the composition of the chapter reveals a dual scheme which provides the reader with some introductory preliminaries and a main part consisting of a basic classification of the displays’ components, on the one hand, and a detailed phylogenetic reconstruction of a whole bunch of var-

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Tinbergen, “Comparative Studies of the Behaviour of Gulls”, 43. I think it worth a while to consider how Niko addresses the aspect of causation in his later text On Aims and Methods in comparison to this present account from an epistemological standpoint. That is to ask, in how far changes the placement of the two settings and their corresponding practices in the overall account and what effect might this produce upon the treatment of the theme within the eventually modified reference system.
ious different displays, on the other hand. In other words, Niko’s account of the evolutionary dynamics underlying the phylogenetic development of the displays in *Comparative Studies of the Behaviour of Gulls* proceeds from a systematic mode of reasoning to a study of specialities. This synthetic scheme applies both to chapter six as a whole and, particularly, to its second part where “discussion” is followed by concrete exemplification. “I will first discuss some elements which are found in more than one posture”, Tinbergen writes in an overview of his account in the introductory section of the paper, “and then proceed to deal with the displays. The sequence will be the same as in preceding chapters”. According to N. Tinbergen’s introductory notes, both his own motivational analysis of the displays and the works of other ethologists suggest that displays must be understood as derived activities of more or less obscure original behaviours. If the roots are obvious, the display behaviours appear clearly as compositions of other, partly antagonistic tendencies from which they are derived. In other cases, however, the origin of displays is less obvious because a complex process of ritualization has transformed the roots of the behaviours in question so much that they cannot be determined that easily. This process of ritualization, in Niko’s view, can be reconstructed in two different ways: “Comparison of a given display in a number of closely related species”, he writes, “allows one to arrange these species according to the degree of the derived movement to its supposed origin”. In addition to this taxonomic argument, N. Tinbergen claims that the more ritualized – and that means “the less easily recognisable movements” – are “functionally better suited than the others to the task of providing strong, conspicuous and unmistakable stimuli”. Adjustment to the needs of communication thus seems to be the main driving force in the displays’ evolution. “These two considerations”, N. Tinbergen consequently concludes, suggest that divergence and evolution of displays are the result of a secondary adaptation to a new function of derived movements. As such there is a close parallel between them and, for instance, the secondary adaptation of the first pereiopod in many crayfish, originally a locomotor organ mainly, to the new function of catching and crushing prey, to which it has become adapted, for instance in the Lobster.

Next to his notes related to the peculiarities of the displays and the ways these difficulties can be overcome methodologically Tinbergen’s introduction also contains some kind of review and, as the quotation above shows, a short overview. The former of the two parts mentions two known main sources of display behaviours, namely, so-called “autochthonous” movements (i.e. movements directly evoked by a situation), on the one hand, and so-called “displacement activities” (i.e. movements that appear to be irrelevant or functionally out of the context), on the other. Summing up the introductory account of particular difficulties related to the scientific object in question, of appropriate methods and possible phylogenetic sources of display behaviours, one may say that N. Tinbergen related his own reasoning

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679 Ibid., 45.
680 Ibid.
681 Ibid., 44.
682 Ibid., 45.
683 Ibid.
684 Ibid.
about the origins of the displays directly to the current state of knowledge which the author must have conceived as “limited” so that his own results can be interpreted as additional supplementary information or, at least, as secondary derivative of what was already known.

Niko’s own contribution to the problematic does not only include a detailed assessment of single displays but also a more abstract “discussion” of the constituents common to many or all displays. “Elements common to more than one posture”, Niko writes, “can be classified in fixed components and orientation components”. In general, Niko’s move to isolate behaviour elements “common to more than one posture” may be interpreted as an attempt to reduce complexity. The epistemic practice by which he aims to achieve this objective apparently is explicit differentiation (viz. classification). How can both poles of this classification, the fixed components, on the one hand, and the orientation movements, on the other, be determined more precisely from a more epistemological standpoint?

Most likely it is the epistemological connotations connected with the movements which have suggested their relative position in Niko’s account: Thus the fixed components are distinguished in “bill pointing” (pointing up indicates a more of aggression and vice versa) and “lifting of the carpal joints” (lifting up indicates increased aggression-escape conflict). Both types of behaviours seem to operate mainly in the vertical plane. The orientation components, by contrast, are separated in those operating in the vertical and those being exhibited in the horizontal plane. In the latter case, again, Tinbergen describes both more offensive (head and bill pointed to the opponent) and more defensive gestures (turning head and bill away). The avoidance tendencies are elaborated in more detail. As to Niko’s account of the “full displays” one may say that the reader here is confronted with a detailed enumeration of various different displays. The order of their arrangement thereby seems to be guided by the questions in how far the displays are based on ritualization, how obscure their origin is, and also in how far direct orientation is actually involved in comparison to the more static nervous tendencies. An interesting question thereby is whether N. Tinbergen thought that a more of orientedness, that is, the intercalation of more orientation movements, simultaneously indicates a more of ritualization or the other way round. In the summary of the chapter Tinbergen writes:

The origin of the displays (chapter VI) is varied. Some have clearly arisen as preparatory or intention movements of the patterns directly aroused by the situation (“autochthonous” movements); of these, some are redirected to inanimate objects. Others are derived from movements belonging to functional patterns not directly aroused by the situation (“displacement activities”); their various origins are discussed, and it is shown that they are second components

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685 Tinbergen, “Comparative Studies of the Behaviour of Gulls”, 45.
686 Of course Niko’s distinction here reminds us to K. Lorenz’s theory of intercalation which had structured explicitly the paper about the egg-rolling movement of the Greylag Goose. In comparison to this former study, however, Niko’s interpretation of the underlying epistemic deep structure now seems to have changed altogether.
687 Ibid., 45–46.
688 Ibid., 46.
689 Ibid., 46–47.
690 These are the “Upright”, the “Oblique”, the “Forward”, “Choking”, “Upward Choking”, the “Mew Call”, “Pecking-into-the-Ground”, the “Hunched”, “Head Tossing”, and “Facing Away”. See ibid., 47–59.
of a dual movement, of which the first component is “autochthonous” in the above sense and facilitates the displacement activity.\textsuperscript{691}

In other words, the heuristic pattern with which N. Tinbergen aims to assess the phylogenetic origin of the display movements is based upon a binary opposition of patterns that are “directly aroused by the situation” and the ones that are “not directly aroused by the situation”. In doing so, the latter of the two constituents seems to repeat the primary distinction in itself so that one can infer that the more complex displays repeat or reveal the phylogenetic process as a whole. Moreover the adverbs “directly” and “not directly” as well as the description of the origin of the more complex displays as “functional patterns” has implications in terms of causality. In more complex displays the original component is dysfunctional and therefore associated with proximate causation, and so are the causal connotations of the origins of the simple displays. Both the derivatives within the framework of the more complex displays and the more complex displays in relation to their more rudimentary counterparts are more adapted since their communicative potential increases. With this refinement of the signal function of the displays the grade of orientedness towards the conspecific individual eventually increases, too. As a result, N. Tinbergen’s reasoning about the origins of the displays re-conceptualizes the classical ethological intercalation of a guiding and an endogenous component both by re-framing the underlying epistemic scheme and by inverting the inner sequence of this scheme. In so far Tinbergen’s reasoning on displays and their origins can be interpreted as a sort of secondary derivative of the classical ethological understanding of fixed action patterns. In other words, Tinbergen repeats the epistemological scheme underlying the idea of “ritualization” on a performative level of his account, both more structurally in form of the organization of the narrative and in content, namely, by relating less complex with more complex original moments of origination.

Chapter seven, “Some Evolutionary Aspects”, refers mainly to the problematics involved in systematics. It encompasses altogether four different approaches each of which seems to have its own inherent logic. These approaches are in detail: The diagnosis that there are interspecific similarities, the assessment of intra- and interspecific differences, the problematic of convergences with other species and, finally, the question in how far the “behavioural machinery” was affected by phylogenetic change.\textsuperscript{692} The combined organization of all four subsections shapes the overall frame in which N. Tinbergen aims to discuss evolutionary change and which can be read as a multistage heuristic scheme serving one purpose, namely, to raise a proper inductive basis for the establishment of a well founded systematic order of the various different Gull species. “In chapter VII”, Tinbergen underlines in the summary of the paper, “some ultimate causes of evolutionary change are discussed, and a preliminary functional classification of alleged changes in displays is presented”.\textsuperscript{693} More precisely, Tinbergen understands the final subsection of chapter seven as tentative attempt to classify modes of evolutionary change in display behaviours

\textsuperscript{691} Ibid., 66.
\textsuperscript{692} For each section see ibid., 54–55, 55–60, 60–62, and 62–65 respectively.
\textsuperscript{693} Ibid., 66.
“according to the changes in underlying causal organisation which must have been involved”. 694 The closer examination of various kinds of ultimate causes thereby is sharing a common objective since they all in their own way help to carve out the relevant types of variability. Yet, on closer inspection, elaborating on ultimate causation also seems to serve different purposes depending on the level of Tinbergen’s analytic procedure. Subsection two bearing the title “Intra- and interspecific differences” thus seems to substantiate the general thesis that all recent species of Gull share one common phylogenetic origin (as outlined in subsection one) by introducing four different selective pressures which act in service of the divergence. 695 “The evidence therefore suggests”, Tinbergen summarizes in a concluding remark, that, while many displays have undergone specialisation in the direction of their improvement as signals per se, resulting in increased conspicuousness, their divergence in evolution seems to be adaptive in three other respects as well: there must have been pressure towards intraspecific unambiguity, pressure directly favouring interspecific unambiguity and indirect pressure through other behaviour, either displays or non-displays. | This analysis of the adaptive character of divergence now allows us to “strip” species of many of the effects of adaptive radiation and thus, by way of final check, compare the “cores” of what must be assumed to be older characters. As argued in chapter II, these cores should be more similar than the total complex of characters if the species have descended from a common ancestor. This is actually so in the gulls. [...]CL “peeling off” the obviously adaptive differences strengthens still more the conclusion, already drawn from a mere description of taxonomic characters, that the gulls must be a monophyletic group and that the displays which were given a common name are actually the same. 696

From my epistemological point of view one may explain Tinbergen’s attempt to interpret adaptive variability in service of his monophyletism as a retrospective reduction of a nurture-component to a nature-component the latter of which also provides the entire frame for this enclosure. The phenomenon of convergent evolution, by contrast, seems to disturb the systematist’s concern since the adaptation to environmental conditions here leads to similarities of characters in biological taxa that did not descend directly from one common ancestor (e.g. fins and torpedo like torso in both fish and whales). 697 According to N. Tinbergen’s account, convergent features are a potential source of fallacy since the systematist might be deceived to misinterpret convergent as divergent qualities. 698 Raising taxonomically relevant data thus requires to peel off all convergent features. Next to this exclusive gesture there is another line of thought in Tinbergen’s account which, so to speak, on a higher analytical level is apt to make fruitful the phenomenon of convergent evolution for the author’s overall analytic purpose. The reason why many non-monophyletic groups of organisms develop the same or at least rather similar characters, Tinbergen argues, is because their potential to develop adaptive variability is restricted or underlying constraints. 699 If this is so, one is inclined to infer, then an organism’s inherent machinery generating heritable variability must have a more

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695 For a detailed analysis of these four selective pressures see ibid., 56–59. For the monophyletism of the Gulls see ibid., 55.
696 Ibid., 59–60.
697 Ibid., 60–61.
698 Ibid., 60.
699 See ibid., 62.
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systemic character. In other words, Tinbergen uses the phenomenon of convergent evolution to substantiate indirectly his thesis that only the organism as a whole is subject to selection and less each of its single characters. From my epistemological point of view, one may therefore conclude again that in N. Tinbergen’s account a nurture-component is retrospectively re-framed by its opposite to which it is reduced. In other words, Tinbergen resolves paradoxa and uses the emerging sense effects for his argumentation. Only if the systematist has enough indicators that he / she has to do with a monophyletic group, furthermore, only if the examination of adaptive pressures substantiates this monophyletism by evincing the adaptiveness of the divergences and, finally, only if all disturbing convergences are excluded, the systematist is allowed to evolve his systematic order. Especially the phenomenon of convergent evolution thus seems to direct the ethologist’s attention towards the organism’s “behaviour machinery”. Having a brief glance at Tinbergen’s systematics of the changes that may have taken place during the evolution of the displays one may eventually say that the author interprets the notion of “evolutionary change” as a process more or less identical with “ritualization”. Analogous to the idea that displays are derived activities Tinbergen also seems to presuppose that the psycho-physical correlate of the display movements underwent some kind of transformation process. To grasp this process he implicitly distinguishes “lower” from “higher” levels of integration and within both categories eventually again “qualitative” from “quantitative” (viz. “gradual”) variation. As a result, the altogether seven forms of transformation suggested by N. Tinbergen will make more sense when the reader distinguishes between quantitative changes on lower levels (1. increase of responsiveness; 2. purely quantitative shifts), qualitative changes on lower levels (3. increase of amplitude; 4. rhythmic repetition), qualitative changes on higher levels (5. combination of elementary displays into one and fixation of sequences; 6. changes of underlying motivation) and, finally, quantitative changes on higher levels of integration (7. increase of decrease of speed). I am particularly interested in Tinbergen’s account of the motivational changes since here the process of ritualization or, more precisely, the psycho-physical correlate of this process becomes particularly clear. “It seems possible”, Tinbergen writes, that many pair formation displays, while originally motivated by sexual attraction mixed with aggression and fear, may have become incorporated more firmly in the sexual pattern and lost part of the original agonistic motivation. This may be so even in those cases where signs of overt aggression and escape are still observable in the meeting ceremony. I read this quotation as if the more of adaptive (i.e. communicative) refinement of the postures during the process of ritualization, at least in Tinbergen’s account of the courtship displays, is correlated with a re-framing of the original agonistic tendencies with more advanced sexual ones.

Concluding my reading of chapter seven, one may fairly claim that Tinbergen’s attempt to establish a classification of evolutionary changes on basis of the underlying causal organization is rooted in the classical ethological understanding of causal analysis. On various levels of the analytic discourse nurture is reduced to

700 See ibid., 62–64.
701 Ibid., 64.
or incorporated by nature and this basic gesture appears both on the level of content (e.g. the reconfiguration of motivations during ritualization) and on the more performative level of Tinbergen’s account which particularly mirrors in the organization of the author’s line of argument. Looking over the organization of the entire paper I am inclined to see in it a manifestation of a causal analytical structure, too. The paper therefore stands in the tradition of Niko’s more theoretical papers and books. However, in comparison to former analytic, that is primarily systematic and comparative, accounts, Comparative Studies of the Behaviour of Gulls includes also some specialities: At first, in comparison to Niko’s early outline of the “Four Whys” in The Study of Instinct his Progress Report does not contain any thoughts about ontogeny.702 Instead, we find a more elaborate functional matrix of the displays in chapter four. Furthermore, in course of the 1950s, N. Tinbergen and his research group have developed a purely ethological understanding of “adaptiveness” by emphasizing the aspect of animal communication and its refinement during evolution through ritualization. Second, the main areas of biological enquiry now appear to be arranged in a hierarchical analytical discourse. Thereby it is primarily the inductive basis of subsequent reductions which is subject of further elaboration. I am inclined to interpret this matter of fact as a consequence of the increased criticism Niko was confronted with both inside and outside his research group and which he was challenged to reintegrate in his theoretical accounts. I have argued that this “shift of focus” finally led to another, in comparison to The Study of Instinct slightly modified, model of causal analysis. Finally, while in former studies behavioural systematics mostly added up in the twofold logic of finding the monophyletic origin of a respective taxonomic group, on the one hand, and reconstructing the actual course of evolution by tracing the adaptive radiation of particular functional characters (mostly having a value as signal), Niko now puts much more emphasis upon the disturbing role the phenomena of convergent evolution might play in this heuristic program. And, apart from the fact that thinking about convergent evolution brought back on the agenda the “behaviour machinery”, it apparently seemed much more complicate to peel off all those characteristics which were not of use for a taxonomic analysis before the core of relevant features could be isolated than to switch the reference system altogether and ask for the qualities which were standing out in a purely adaptive framework because they seemingly established a handicap for the organism in question. Choosing the latter of the two options coincided with Niko’s turn to Ecology and we can only guess whether or not Tinbergen felt that his model of causal analysis was no longer defensible.703 In other words, I think

702 For the exclusion of ontogeny see Tinbergen, “Comparative Studies of the Behaviour of Gulls”, 4, especially 29.

703 I think it would be an interesting further leading research question whether not only the positive results obtained by Niko’s students but also their potential failure increased Niko’s inclination of changing his theoretical approach. For instance, I think it can be asked justly whether the taxonomic order M. Cullen suggested in his thesis on basis of his behavioural studies actually was correct. Questioning the taxonomic value of behaviours, as Niko explicitly did in his Progress Report (Ibid., 60), meant to question one of the founding pillars of Classical Ethology. And, most interestingly, as we will see, G. Kramer was rather sceptical about the hypothesis put forward by classical ethologists that behavioural qualities might be useful as reliable taxonomic characters.
that the ethological model of causal analysis was of advantage when ethologists wanted to integrate otherwise separated theorems into one uniform model or when N. Tinbergen felt the need to reintegrate challenging results in his disciplinary accounts. Yet, I believe, that the scientific quarrels Ethology faced in the 1950s had deeper lying epistemological reasons inasmuch as a model of analysis based upon an end-tautological epistemic reference system is \textit{per definitionem} not capable to bring the analytical process to an ultimate end.\footnote{M. Vicedo’s reconstruction of the criticism pitted against Ethology mainly in the field of ontogeny substantiates my view. See Vicedo, \textit{The Nature & Nurture of Love}, particularly chapter four.} Maybe, the modified model Tinbergen developed in the 1950s can be interpreted as a response to this problematic, yet, it was not able to solve it. At the end of the 1950s the displays turned out to be not more conservative and hence not more appropriate for taxonomic studies than other behaviours as well as they had begun to reveal a liability to become subject of convergent evolution.

At this point I’d like to conclude by discussing a general methodological problematic. In the last consequence my method of treating textual manifestations as expressions of deeper lying epistemological configurations relative in time requires a technique how to reduce the complexity of the manifestations. In short, my technique consists of proving that behaviour scientists, while composing their publications, not only differentiated highly sensitively but also \textit{obeyed particular orientation-specific rules of differentiation}. The problematic thereby seems to be that such a rule of differentiation can only be confirmed if \textit{all} or “nearly all” branches of the entire “tree of theorems and propositions” a scientific publication is built upon is worked through or examined. And, for the time being, I see no other technique to achieve this objective other than careful reading and description. But I am fully aware that it might be extraordinary difficult to reconstruct a publication’s tree of ideas on basis of such a description. Better and more comprehensive forms of presentation are therefore required. To sum up, the classical ethological models of knowledge organization, independent whether causal analytical techniques had been applied while examining the organization of the nervous system or as a methodological framework for systematics, became more and more object of severe criticism. This criticism has been put forward both by researchers outside the ethological community (e.g. D. S. Lehrman, T. C. Schneirla) and within N. Tinbergen’s own research group. My micro-analysis of the qualification theses with which Tinbergen’s first cohort of PhD students finalized their academic education under the their “Maestro’s” guidance reveals the various different epistemic forms and stages of this criticism. Moreover, an analysis of Niko’s theoretical accounts turned out to be an apt tool to make evident how he responded to this challenge: Both the choice of a field of biological research in which the mechanomorphisms of Classical Ethology could be perpetuated and the choice of a corresponding scientific object that fitted to this research can be interpreted as defence reactions N. Tinbergen applied in order to meet the rising criticism. Moreover, I was able to show, that both forms of selection were accompanied by a sophisticated “re-boundarying technique” with which N. Tinbergen was able to integrate the results of his pupils within the heuristic framework he wanted to maintain and which he identified with his still young
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scientific discipline. Between 1959 and 1962 at the latest N. Tinbergen’s scientific orientation changed drastically in as much as his own theorizing followed the general direction the works of his pupils had traced out (without fully adopting their position). In doing so, Tinbergen became one of the pioneers of a new functional line of ethological research that was about to become concrete not only in Behavioural Ecology, as it is often claimed implicitly or explicitly, but also in new forms of Functional Anatomy and Physiology and, as Niko’s own life course reveals, in a fairly fascinating conception of Human Ecology. The institutionalization of this functional line of behaviour study, which was branching out of the classical framework long before Niko’s final move, is subject of the following two subchapters of my dissertation thesis.

Turning Student(s) of Ecology (1959–1974)

Transition Four. (R2) I have dedicated a considerable amount of investment to reconstruct N. Tinbergen’s scientific development between 1938 and 1959. Although his life-history went through several stages and drastically changing environments (Leiden, Hostage Camp, University of Leiden, Oxford) the two main realms of his scientific orientation did not change on a deep structure level. This does certainly not mean that there has not been any change at all. By no means. However, the shifts I was able to make evident, for instance his reinterpretation of the causal analytical frame in terms of evolutionary systematics, have the character of a phenomenological reinterpretation rather than a modification of underlying epistemological paradigms. This matter of fact changed nearing the end of the 1950s. The following parts of my dissertation thesis thus intend to find out when and how this break occurred in his life-course. I thereby presume that the mode by which N. Tinbergen himself left behind the convictions of the founding period of Ethology was not identical with the mode his pupils apparently made the same move. While some of Niko’s pupils apparently merged together divergent realms of biological research in a period of their life-histories following their previous academic socialization, just in the same way the generation of their teachers had before them, Niko’s “turn” to Functional Ethology occurred fairly late in life and, I think, we also have to presume other motivational factors. Moreover, science historians most likely have not made sufficiently clear so far that N. Tinbergen’s functional understanding of Ethology went through different phases and, in doing so, became manifest in different concrete manifestations. While his theorizing between 1962 and ca. 1972 was mainly concerned with themes that should later become even more prominent in Behavioural Ecology, his late engagement with early childhood autism and the so-called “Alexander technique”, in my opinion, should be interpreted as pioneering endeavours into the field of Human Ecology, a matter of fact historians seem to have neglected so far. The reason for this “blind spot” in the history of Ethology are twofold: On the one side, it seems that those science historians who made an attempt to reconstruct N. Tinbergen’s life and research felt affiliated more with his purely behavioural ecological works and therefore seemed to push into the background Niko’s engagement with childhood autism which absorbed his
Another reason might be, that Niko’s research in childhood autism needed to be corrected in some aspects from a crudely scientific standpoint and thus did not match the critical verdict of some of Niko’s pupils who had in mind his long list of scientific merits. However, the more I became engaged with N. Tinbergen’s research on autism the more I was convinced that some of the corrections the specialists in the field lodged against Niko and Elisabeth Tinbergen’s writings, require some correction by themselves from a nowadays point of view! I think, whether or not the statements made by a researcher at a certain point in the development of his discipline or his life later turned out to be outdated or even obsolete certainly cannot be the criterion whether these statements may or may not enter a historical account. The key question to me is which epistemological reference system Niko’s late research provided, how the respective framework could generate viable results in case of one interpretation and why another produced seemingly erroneous answers. I am inclined to argue that an epistemological reference system cannot be “wrong” per se. As to Niko’s aetiology of childhood autism as well as his suggestions for the cure of the autism disorder syndrome, I am inclined to argue that his distinction between genetic dispositions and secondary “psychogenic” or “functional” causes anticipated, from a more epistemological standpoint, what we, from nowadays perspective, might address as the difference between genetic and epigenetic causes of the autism disorder syndrome. As I will show in the subsequent subsection it was only in the very recent past that some of Niko’s claims could be verified by geneticists being concerned with mental disorders. From this perspective it is not justified any more to blend out the Tinbergens’ research on autism. It is to be discussed seriously from our current state of knowledge and it should be asked in how far Niko’s ecological fundament provided a fruitful breeding ground for later discoveries and what the reasons are for the fact that Niko’s interpretation of this fundament in some cases prevented deeper insights, while in other cases it was even liable to mistakes. I therefore suggest to distinguish two main periods in N. Tinbergen’s commitment to Functional Ethology: The phase between ca. 1958 and N. Tinbergen’s retirement in 1973, on the one hand, and his late research which was mainly dedicated to Human Ecology, on the other. The former of the two periods will be treated in this subchapter of my thesis. Thereby I will proceed in two steps: At first, I shall discuss how N. Tinbergen’s theorizing switched from his earlier mechanomorphism to his later commitment with ecological inquiries. What are the themes Niko raised and in how far did he anticipate basic lines of behavioural ecological research which later should become prototypical topics of this new incipient area of biological research? In a second step, I should like to return once more to the realm Niko reserved for educating stu-
dents. At the end of the 1950s and the early 1960s a new and younger generation of pupils arrived at Oxford which had received its academic education already within the new scientific paradigm Niko had institutionalized with his formal turn to Functional Ethology. The crucial question thereby is how this new, second generation of pupils responded to N. Tinbergen’s turn. As I will show in a brief outlook at the end of this subsection of my thesis, the later cohort eventually revealed the same dualistic reaction pattern as the previous cohort – albeit under drastically modified new circumstances.

I have argued that Niko’s first generation of pupils at Oxford University prepared the move away from Classical Ethology. However, in formulating their alternatives to the causal analytical framework within which N. Tinbergen reintegrated the empirical work of his students as an inductive basis for his systematic research program they did not (and could not) reach any level beyond the textual organization of knowledge. Therefore the question can be raised when the final stage of “institutionalization” occurred and, since the establishment of a modified research program cannot be thought without the one who holds the chair, this question is more or less equal to the one when Niko himself adopted the new line of thought which apparently had grown more and more within and outside his work group. Furthermore, what triggered his final move? And finally, if Niko’s path away from Classical Ethology did not fully coincide with the one taken by his pupils, although the target destination was finally identical, the question is how Niko’s own move can be characterized from the epistemological point of view. It is therefore necessary, I think, to elaborate upon N. Tinbergen’s theoretical transformation process before I ask again how the works of his second generation of pupils related themselves to the new scientific paradigm. “After he had published the comparative gull paper”, H. Kruuk writes about Niko’s metamorphosis, “he focused on biological effects of behaviour rather than on causes, and he restricted his personal research interest to other, non-display types of behaviour”.706 So far I have distinguished between Niko “the advisor” and N. Tinbergen “the creator” or even “the defender” of his discipline. Within the second realm Tinbergen’s accounts had more the character of theoretical contemplations. Without being based on any own research project these accounts were meant to summarize and discuss the output of other ethologists and particularly his pupils. In 1959 this situation changed. Niko ended his abstinence in doing own research which had lasted more than ten years and started at least two different projects during the 1960s. These projects were his own or he was at least involved more directly. As a provisional result, we may therefore say that the overtone of N. Tinbergen’s theorizing changed after 1959 in as much as theoretical statements were formulated on basis of own practical research. Niko’s projects were his so-called “eggshell removal study” which also provided the basis for his famous paper On Aims and Methods (1963) and a second study he conducted together with two post-docs, M. Impekoven and D. Franck. I will discuss briefly the published results of both projects including On Aims and Methods, the paper many regard as N. Tinbergen’s most important theoretical achievement, ever. The former of the two projects lasted three years and involved a number of assistants

706 Kruuk, Niko’s Nature, 190, also 213.
and volunteers, according to H. Kruuk, mostly non-British post-docs from South Africa, Poland, and Switzerland, as well as students from Holland and France who were doing the work for their degrees. As a provisional result, we may therefore conclude that N. Tinbergen’s ethological theorizing since 1959 not only attained a more empirical but also a more cooperative character. Moreover, Tinbergen relied on younger foreign students he apparently did not supervise in a narrow sense of the word, while his own PhD students worked parallel on their own projects. “All of us”, H. Kruuk remembers, “worked alongside the PhD students who were doing their own projects”. H. Kruuk’s recollections are a strong indicator that N. Tinbergen changed the epistemic practices with which he socialized his disciples: While the placement of their works in the 1950s occurred mostly abstract in form of joint publications or his critical comments, the strategy changed in the 1960s insofar as he began to recruited new pupils earlier in their career and through practical work. “Just now my main concern is the continuation of our Animal Behaviour Research Unit”, Niko outlines his plans in a letter to J. Huxley and continues: the ten-years’ (very generous) Nuffield support will expire soon. Prospects for something really wonderful are bright, and a more permanent and better staffed research unit seems in the bag now, but to start this will cost time and will require my presence here for quite a while. Also, my main concern is and will remain, not my own private research, but the education of really good young people. This is not a matter of good doctors’ theses alone, but rather one of delivering people who will do well later.

As a result, the crosswise exchange between the two realms I have carved out as Niko’s characteristic way to interpret the scientific paradigm provided by his discipline now obtained a more personal quality, too. Together with the epistemic practices the epistemic framework of the discipline (at least how Niko now saw it) itself changed: The heterogeneous constitution which had characterized Classical Ethology over the past twenty years now was replaced by a homogeneous scientific orientation which adopted those realms his previous generation of pupils had to sideline: Now, as it appears, both Tinbergian Practice and Tinbergian Theorizing turned out to have a more practical nuance. Moreover, as it appears, Niko not only adjusted his theorizing but also his behaviours. I was always wondering why it was exactly the so-called “eggshell removal project” which became the model study for Niko’s ecological turn. The answer I found for myself is that the study can be read not only as the product of any empirical work but also as a symbolic gesture which was directed backwards to Niko’s early cooperation with K. Lorenz in their joint

707 Ibid., 211. H. Kruuk who became later Niko’s biographer was one of these helpers. Later he continued his research in his own PhD project on Black-headed Gulls.
708 Ibid.
710 Maybe, it isn’t an accident that Niko intended to re-establish scientific cooperations both with R. A. Hinde, with whom he planned to write a handbook of Ethology, and with D. Morris. Morris had become famous (and rich) with his book The Naked Ape which was published in 1967 and which Niko found so inspiring that he encouraged Morris to return to his institute. The cooperation, however, waned leaving Niko’s expectations somewhat unfulfilled. See Kruuk, Niko’s Nature, 245–247. Niko’s planned cooperation with R. A. Hinde finally did not work out due to Niko’s overload with work and Hinde wrote the book ultimately on his own. It was published in 1966 under the title “Animal Behaviour” (Ibid., 248–249).
study of the Greylag Goose’s egg-rolling movement. Lorenz had written contact with N. Tinbergen since 1935 and a year later both researchers met each other for the first time in person in Leiden where C. J. van der Klaauw had organized a small symposium on instinct.\footnote{That N. Tinbergen corresponded with K. Lorenz since 1935 and also received his articles is mentioned in Röell, The World of Instinct, 111. For the so-called “Leiden ‘instinct’ symposium” see ibid., Burkhardt, Patterns of Behavior, 199–205, and Kruuk, Niko’s Nature, 93. See also Lorenz’s later report to O. Heinroth, O. Koenig, ed. Oskar Heinroth / Konrad Lorenz. Wozu hat das Vieh aber einen Schnabel? Briefe aus der frühen Verhaltensforschung 1930-1940. Mit Beiträgen von Katharina Heinroth, Amélie Koehler, Niko Tinbergen und Wolfgang Wickler. (Serie Piper 975). München: Piper, 1988, letter K. Lorenz to O. Heinroth (05/01/1937). Lorenz’s contribution to the colloquium taking place on the 28th of November 1936 was later published in Folia Biotheoretica. See K. Lorenz. “Über den Begriff der Instinkthandlung”. In: Folia Biotheoretica, Serie B 2 (1937), 17–50.} According to N. Tinbergen, both researchers “clicked” at once and decided to meet again in the following year in Altenberg for common ethological research.\footnote{N. Tinbergen. “Biography of Nikolaas Tinbergen”. In: The Nobel Foundation, ed. Nobel Lectures in Physiology or Medicine 1971-1980. London et al.: World Scientific Publishing, 1992 [1973], 111, and Tinbergen, “Aus der Kinderstube der Ethologie”, 309. See also the previous version of Niko’s contribution to the Festschrift published on the occasion of K. Lorenz’s 85th birthday, Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3156, E 16A, ms. “Für K. Lorenz’s Festschrift” (ca. 1988) and WRC-RU Fondr. Lib., MS 50, box 34, file 1, letter N. Tinbergen to J. Huxley (23/01/1963). That Niko interpreted his research attitude complementary to the one of Lorenz can be deduced from ibid., box 21, file 1, letter N. Tinbergen to J. Huxley (18/02/1953). Lorenz, “Taxis und Instinkthandlung [1938]”.} The result of this collaborate effort amongst others was the famous study on the egg-rolling movement of the Greylag Goose.\footnote{See to this also a rather challenging letter of Niko’s to his friend K. Lorenz in which he questions} Both ethologists had observed that Geese, whose egg had been put outside their nest, take this egg under their beak and roll it back into their nest. Thereby two distinct components, Tinbergen and Lorenz called “taxis” and “instinct”, worked together insofar as the instinctive constituent was responsible for the proximal movement of the egg from the outside to the inside, while the function of the taxis constituent, which in contrast to the instinct was supposed to be more plastic, was to correct and stabilize the movement in the horizontal plane. The study became legendary not the least because it provided an elucidating imagery not only for the division of labour between two researchers but also for the modified causal architecture which placed Ethology within the wider Darwinian context. The movement of the egg from the outside to the inside of the nest not only reduces a distance and therefore is a “reductive gesture” it also symbolizes the notion of “proximate” or direct causation which turned out to be the cornerstone of analytical theorizing of classical ethologists in the following twenty years in various different kinds of expressions: The egg is rolled from the outside to the inside of the nest. Therefore it appears to be a statement which goes beyond the mere scientific observation that Niko’s “eggshell removal study” does not deal with the egg as a whole but with its scattered parts, the pieces of the egg shell, and, furthermore, the behaviour consists of carrying the shells away from the nest and not a movement from the outside to the inside. Niko’s eggshell removal project therefore also indicated a sort of break with Classical Ethology by bringing in both a more atomistic (also systemic and relational) nuance and the notion of ultimate causality.\footnote{One of the reasons N. Tinbergen put...}
forward explicitly to explain his move was that he had observed a tendency in Ethology to overemphasize the study of proximate causes in ontogeny while neglecting the question of adaptiveness.\textsuperscript{715} His move therefore can be also interpreted as the attempt to counteract an imbalance.

The results of N. Tinbergen’s egg shell removal project were published in three papers one larger and two shorter ones. The former of them was published in Behaviour, the latter two in Bird Study and British Birds respectively.\textsuperscript{716} When I analyze these texts in the following I will apply methodological categories similar to the ones I have used in my readings of the works published by Niko’s first generation of pupils at Oxford. With these categories I intended to determine more precisely the “locations” and the “movements” of these works within the epistemic space of the ethological scientific community. In concrete I asked for the order of the presentation, whether or not Darwin’s epistemic interferences have been adopted, whether there are any signs of non-knowledge, and how the author refers to other scientific works (formal vs. informal, critical vs. affirmative, reference on concept vs. simple observation, etc.). Furthermore I have tried to find traces of re-
In addition to these five research questions I would like to put emphasis upon one further aspect which I have neglected so far. If the reference systems in question are to be read not only as cognitive frames but also as behavioural dispositions or patterns of epistemic practices they might be paralleled within a wider range of practices – practices that are connected with the dissemination of knowledge or the reproductive dynamics inside an epistemic community. For instance, maybe Niko’s break with Classical Ethology itself was schematic to a certain extend since he left behind gradually the common epistemological foundation until he finally marked the break. For the time being, I would like to use this category as a lose experimental tool to make my reader and myself sensitive for any kinds of gestural parallels.

The question of knowledge organization, though partly difficult to answer, is vital for my argumentation: The order especially of textual manifestations turned out to be a firm identifier for a researcher’s position within his epistemic community. If we try to determine these orders this is most likely always a process of reduction of complexity which is liable to errors. It is certainly not a new idea that classifications can be multiple and ambiguous – and this applies both to the primary process of scientization yet even more to the reconstruction of the output of this process. Hence, my own style in reconstructing the way in which a researcher organized her or his knowledge intends to be both more argumentative and observational. Moreover, one may ask when this reduction ends. Does it end by determining the essential parts within one and the same paper and their mutual relationships? Do I have to take into account intertextual relationships, as well, or still even wider biographical contexts? My answer to this question is, that we have to decide from case to case what is relevant. I for myself decided to proceed gradually to the core of a scientific orientation and stop when I felt that additional contexts, even if treated in detail, would not alter the epistemic disposition my “analysis” aimed to carve out. This habit is inspired from the mathematical notion of limes which implies that reductions can (only) be “quasi-complete”. My experience so far is that a particular scientific position often precipitates very clearly within a scientific publication which is a strong argument for not ignoring the heuristic value of scientific publications. The dissertation projects N. Tinbergen supervised build a different case since they gain their signal function in Niko’s life course only if we take into consideration the specific scientific practices of academic socialization he applied while advising the theses. In case of Niko’s “egg shell removal study” we are confronted most likely with an intertextuality phenomenon just as it was the case in his early Philanthus papers or the two studies concerned with “Field Observations of East Greenland Birds”.

Within this entire complex Egg Shell Removal by the Black-headed Gull which was

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717 If we define reciprocity narrow, that is, as explicit comment of a comment, the results are poor. This does not exclude the existence of any mutual scientific exchange. The crucial factor here simply seems to be the time span between submission and publication. If N. Tinbergen quoted the works of his pupils the references have in general a more reciprocal character.

718 This question tackles the very severe problematic whether or not a researcher’s movement in his community can be reduced to what I have called “reference system” or “epistemic scheme”. Although I do see parallels in the life paths of different researchers – e.g. eventually Darwin’s and Einstein’s – I cannot answer this question but the autobiographies written by researchers would be the genre of historical source to answer it.
Niko Tinbergen (1907–1988)

published in *Behaviour* in 1962 seems to be the most important text. Whether its order actually is representative for the entire complex is a question that should be discussed with caution. As a provisional hypothesis, one may eventually say that Niko’s turn to Behavioural Ecology also may have modified the structure of his narrations. Especially what formerly appeared as expressions of his causal analytical reasoning now shifted towards a new paradigm: Watching and Wondering. The new scheme differed from its predecessor not so much in its general heuristic thrust, careful observation (watching) should still precede more analytical scientific experimentation (wondering). However, the overtone of the entire heuristic frame changed in so far as the practice of asking questions prevailed. And this implied that heuristic certainty, even more than it was the case before, could be obtained only in form of a provisional truth – in form of so-called “plateau phases”. We can understand the turn N. Tinbergen’s intellectual life-history took in the 1960s adequately only if we are prepared to take into account that these plateau phases provided only temporarily (heuristic) rest before they were resolved by further questioning. I would go even so far as to say that not only the framework of Niko’s research followed this scheme but also his general behaviour such as his habit of raising new projects and burying them after a while, or his treatment of other people – not to mention the way how he was affected by his (endogenous) depressions. During the 1960s Niko’s depressive periods became more frequent and partly drastically affected his life and work. Although Niko thought to be healed several times and the reasons were said to be found, the actual physical causes eventually could never be determined with complete certainty. This matter of fact resulted also in a great deal of suspiciousness Niko directed against his physicians and the psychiatric profession in general. *Egg Shell Removal by the Black-Headed Gull*, I think, reveals the epistemic scheme Niko later declared the motto of his autobiography by coining the phrase “Watching and Wondering”. A concluding section which consists of both a “Discussion” and a “Summary” is preceded by a main part which as a whole has a more empirical and descriptive character. Two questions can be asked: First, do the three papers on egg shell removal behaviour build an intertextual unit. That the papers are partly numbered points into that direction. Second, does the new framework reveal the repercussions that are typical in a homogeneous scientific orientation in comparison to a heterogeneous one?

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719 In Niko’s correspondence with J. Huxley the study is first mentions in April 1960. See WRC-RU Fondr. Lib., MS 50, box 29, file 4, letter N. Tinbergen to J. Huxley (19 [?]CL/04/1960).

720 “Watching and Wondering” also became the title of Niko’s late autobiography.

721 Niko’s deliberately chosen methodological uncertainty is also one of the criteria in which his later accounts on Man differ from Lorenz’s and Morris’. Tinbergen’s presupposed that Man does not know Man.

722 Although the various kinds of cooperation with R. A. Hinde (handbook of Ethology), D. Morris (Ethology and humanity), and H. Falkus (“Signals for Survival”) were terminated already in the initial stage, did not fulfil the expectations of both sides or were ended immediately after completion for quite different reasons we, nonetheless, may see a pattern in Niko’s behaviour: His engagements were or could be only of a temporary character. See Kruuk, *Niko’s Nature*, 248–249, 229–235, 245–247.

723 Two questions can be asked: First, do the three papers on egg shell removal behaviour build an intertextual unit. That the papers are partly numbered points into that direction. Second, does the new framework reveal the repercussions that are typical in a homogeneous scientific orientation in comparison to a heterogeneous one?

724 For both concluding sections see Tinbergen et al., “Egg Shell Removal, I.”, 111–115 and 115, respectively.
Problems”.\textsuperscript{725} It is difficult to decide whether this introductory section as a whole is “functional” because it aims to direct the attention of the reader towards the main parts of the paper which altogether have the character of an experimental study, or, conversely, the introductory sections as a whole are meant to state a sensed problem that is to be examined empirically in the second place. Which scheme actually applies can only be inferred from the epistemic outline of the part constituents that build both major entities. For instance, from the fact that the twenty three experiments, Niko and his coauthors explicitly numbered as such, “all” appear, without any exception, within chapter three (“The Survival Value of Egg Shell Removal”) and four (“The Stimuli Eliciting Egg Shell Removal”) it can eventually be inferred that we have to do with a form of differentiation in a quantitative frame.\textsuperscript{726} Experiments mentioned later are not numbered. Both chapters therefore seem to build a unit which, as a whole, is supplemented by two further chapters which have more the character of further leading inferences and observations.\textsuperscript{727} The supplementary sections of the paper’s experimental part are concerned with “Changes in Responsiveness in Time” (chapter five) and “The Lack of Promptness of the Response” (chapter six).\textsuperscript{728} Both chapters seem to be concerned with responsiveness and less the stimulation. It is also important to mention that chapter three and four have alternating causal implications. While in “The Survival Value of Egg Shell Removal” the Black-headed Gull’s anti-predator system (or defence system) is approached from the side of the predator (or hunter) by proving that its reactiveness towards the prey object (the newly hatched Gull chicks) is determined by the visibility of the nest (which increases as soon as the eggs are broken and the brighter inside of the eggs becomes conspicuous and decreases when the shells are removed), the succeeding section changes the perspective: It intends to determine those parameters which release the Black-headed Gull’s behaviour to remove the visible broken egg shells from their nest – the behaviour with which they increase the grade of their nests’ camouflage. As a whole the Black-headed Gull’s protective behaviour therefore can be interpreted as an adaptive responses to the selective pressure exhibited by the predators’ own visual capacities. In sum, I therefore would like to suggest the following figure to illustrate the order of the paper (Fig. 2.12).

On closer inspection we might detect some of the characteristics of the new narrative scheme which apparently coincided with N. Tinbergen’s ecological turn. One of the aspects that strikes me is that the role played by the main parts including their location eventually is another. While in former studies the main sections built a unity with the concluding ones insofar as they provided the raw material for the final conclusions, they now appear to be more the provisional solution of a problematic introduced by the introductory parts – a logic which apparently does not coincide on the highest level of the paper’s organization (e.g. by taking into ac-

\textsuperscript{725} See Tinbergen et al., “Egg Shell Removal, I”, 74–75 and 75–76, respectively.

\textsuperscript{726} See \textit{ibid.}, 77–85, and 85–105.

\textsuperscript{727} That section three and four build a unit is also indicated by the fact that the experiments mentioned in these parts are numbered continuously beyond the chapter boundary: Experiment 1–7 is placed in chapter three whereas 8–23 is part of chapter four. The idea that a continuous moment exceeds the interruption caused by a chapter break resembles the scheme of classical analysis, at this point.

\textsuperscript{728} \textit{Ibid.}, 105–109, 109–111.
Fig. 2.12

count the relationship between main and concluding parts). Moreover, the rather canonical supplementary parts which used to be added to the introductions and very often were termed “Material and Methods” (or vice versa pending on the overall composition) now obtained a new headline: “Statement of the Problems”. It signals that the section in question functions as the apex of the entire introductory complex where the problematic tapers to its point. With a view of the inside of this specific section it can be said that Niko amplifies a basic problematic, the question of the behaviour’s survival value, by developing quite a number of competing possibilities. In a second step, these possibilities are reduced to one: Black-headed Gulls might carry away egg shells because their conspicuousness reveals or “betrays” their camouflage. In a concluding remark it reads:

These observations combined suggest that neither the avoidance of injury, nor of parasitic infection, nor of interference with brooding are the main functions of egg shell removal – if this were so, then the Kittiwake as the most nidicolous species of gull would not lack the response. The most likely function seemed to be the maintenance of the camouflage of the brood – neither Kittiwake nor Sandwich Tern can be said to go in for camouflage to the extent of the other gulls and terns. Thus these observations naturally led to an investigation into the function of the response and to a study of the stimuli eliciting it. In the following we shall deal with the problem of survival value first.

Finally, also the concluding sections seem to have obtained another slightly modified tenor: While in earlier publications concluding sections tended to bring the result to the point, we now face a more paradox constellation at the end – including the presence of more opening gestures. The dualism of “Discussion” and “Summary”, if applied in this constellation and sequel, expresses this aspect. In sum, I think, the structure displayed in Egg Shell Removal by the Black-Headed Gull has more resemblance with the organization of E. Cullen’s Kittiwake paper than with Niko’s own theoretical papers written up around 1959 although the composition of both papers might not be identical – as well as the frame represented by the main parts in Niko’s account might not coincide with the overall frame so that we once more face some kind of distorted tautology in a reference system of a homogeneous orientation.

A very important part of my argumentation is the question whether the new epistemic framework within which N. Tinbergen placed his more theoretical accounts reproduced Darwin’s epistemic interferences. This question can only be answered in a differentiated way. On the one hand, it is possible that the epistemic frame N. Tinbergen applied in his first egg shell removal paper deviated from the one I’ve called “Darwin’s paradox” in a sense that the starting point of his reasoning on adaptation was more to reconstruct wide adaptive radiations and less the act of sympatric speciation. On the other hand, however, Niko’s conceptions which later should be identified as the beginnings of Behavioural Ecology did not fall back

\[^{729}\] This observation entails that the combination of the realms does have a repercussion effect upon their inner organization.

\[^{730}\] Tinbergen et al., “Egg Shell Removal, I.”, 76, 77. In contrast to earlier forms of reduction of complexity, one may eventually say, that the new mode enumerates more explicitly non-valid and valid options. It is a typical heuristic gesture found very often in textbooks of Behavioural Ecology.
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into a genuine Lamarckian or neo-Lamarckian orientation just in the same way as Ch. Darwin did not go behind his achievements in his *Origin* particularly when composing his accounts on “Geological Succession”, “Bio-Geography I” and “Bio-Geography II”. The most comprehensive indicator for this matter of fact is Niko’s emphasis upon the “survival value” of the behaviours. “In the many species which carry the egg shell away”, Tinbergen writes, “the response, occurring as it does just after hatching, when the young birds need warmth and protection from predators, must be supposed to have considerable survival value”.731 The quoted passage clearly shows that N. Tinbergen anticipated what later ecologists called “handicap theory”, that is, the idea that the grade of disadvantage a behaviour implies might be of heuristic value in so far as it might be a measure for the selective pressure which is exerted on the respective animal.732 The scope of adapted behaviours thereby did not solely encompass the symbolic movements (*viz.* the displays) like in his previous accounts but, like E. Cullen had suggested, all those behaviours which can be related to particular environmental niches. The more we may be surprised that N. Tinbergen, despite the fact that he paid tribute to Esther and Mike Cullen’s studies, nonetheless sidelined their works to a certain degree.733 The simple fact that neither Kittiwakes nor Sandwich terns carry away egg shells left both authors only the chance to contribute on a more methodological level but made impossible a more direct form of cooperation.734 This function was taken over by younger generations of pupils, especially C. Beer and, less prominently, G. Manley. Beer had worked on “Incubation and Nest-building by the Black-headed Gull” and submitted his thesis in 1960. It is this treatise to which N. Tinbergen repeatedly refers in *Egg Shell Removal*.735 For instance, according to N. Tinbergen, it was C. Beer’s observation that some shells were not carried away but used for nest-building instead, which gave Niko the impulse to perform a set of experiments to clarify the exact shape of the shells that were misinterpreted by the Black-headed Gulls. He writes:

731 Ibid., 74. The fact that the adaptiveness of the behaviour reveals itself particularly when the behaviour prevails although the strategy has also disadvantageous consequences shows the end-paradox construction of the underlying scheme!


733 For his acknowledgement see Tinbergen et al., “Egg Shell Removal, I”, 74, 111. It would be an intriguing further leading research question what the reasons for this partial exclusion might be. As a provisional hypothesis, I’d say that the choice of scientific objects played a crucial role (Gulls do carry away egg shells, Kittiwakes don’t). Moreover, the forms of knowledge organization in the papers, though sharing the same overtone, differ and the question is whether this yielded secondary content-related effects. Finally, I think, Niko’s pupils eventually both reinterpreted differently Lorenz’s former correlation between releasing situation and receptory apparatus and, in combination with this, were presupposing a model of the nervous circuit other than Niko himself was applying in his late ecological studies.

734 That the Kittiwake and the Sandwich Tern do not carry away egg shells is explicitly stated in Niko’s paper. See ibid., 76.

735 See ibid., 76 (carrying away a huge variety of different objects, readiness to show the response at different times of the season), 77 (observation that no fox ever preyed any egg), 85 (great variety of objects can elicit the response), 99 (some shells are used for nest-building due to their similarity with nest material), 103 (normal duration of the incubation period), 105–106 and 108–109 (reference to unpublished material regarding constant responsiveness over the breeding
Experiment 19. | This was done in 1959 with the special aim of investigating how the gulls distinguished between egg shells and nest material. The immediate impetus to this was given by Beer’s observations, illustrated in Fig. 2, which had shown (a) that some objects were similar to objects which the gulls were sometimes seen to carry to their nests while building; and (b) that a bird would sometimes actually alternate between carrying an object to the nest and carrying it away [...].

I think the quotation shows quite impressively that Niko’s research questions were partly directly inspired by the results obtained by his pupils, here C. Beer. On closer inspection several of the major problems addressed by N. Tinbergen and his coauthors can be interpreted as “response” to theses formulated by C. Beer. Thus Niko’s extensive discrimination experiments to clarify the relevant stimuli emanated by the objects carried away and their relative releasive value seems to respond to Beer’s statement that a huge variety of objects is carried away. Niko’s interest in the annual rhythmicity of the Black-headed Gull’s responsiveness seems to pick up Beer’s hypothesis that the Gull’s readiness remains more or less constant. As a result, one may eventually conclude that C. Beer’s thesis and its results inspired N. Tinbergen’s own interests so that it necessarily must be taken into account – so to speak – as a background text of N. Tinbergen’s egg shell removal study. Given the fact that Niko eventually also gave the reverse impulse for C. Beer’s thesis, either directly or more indirectly, we may infer that his references to Beer’s study have a more reciprocal character. Another aspect which is worthwhile to be clarified at this point is whether Niko referred to theorems and concepts put forward by himself in papers written before 1959. This leads, I think, to a rather exciting observation. I have already underlined that Niko proved the adaptedness of Black-headed Gull’s egg shell removal by the observation that the Gulls perform the activity despite the possibility that their behaviour also has negative effects for the young which need to be left alone and unprotected during the time of the adult birds’ absence. The paradox of natural selection is made productive here in a more heuristic sense – just as E. Cullen did before Niko when she proved the adaptiveness of the more risky habit to breed on cliffs in the Kittiwake. Niko goes a step beyond and claims that the manifold and complex process of behavioural adaptation, in the last consequence, may lead towards antagonistic adaptive pressures, severe conflicts of selective pressures, or even a whole system of competing strategies within one and the same species. From the epistemological standpoint I am inclined to argue that N. Tinbergen’s systemic view which previously had appeared wide season), 112 (data regarding the synchronisation of the breeding calendar), 115 (again removal of wide scope of objects).


That Beer’s study gave an impulse can eventually also be inferred from a letter to J. Huxley. See WRC-RU Fondr. Lib., MS 50, box 26, file 5, letter N. Tinbergen to J. Huxley (13/06/1958).

Without being able to make my thoughts fully comprehensible, I believe that Niko’s starting point for his ecological reductions was much wider in comparison to E. Cullen’s and M. Bastock’s who aimed to reduce behavioural peculiarities to one environmental condition or one mutation only. I am inclined to explain this nuance with the possibility that in Niko’s ecological reference system the tautological relation was non-coincident. That means, the starting point of Niko’s reasoning on adaptiveness – and here he maintained Ethology’s empirical tradition – was wide since he was still interested in adaptive radiation and manifold behavioural phenomena so that the initial impulse contradicted somewhat the overall tenor of the frame.
in various different forms of expression such as his hierarchical system of drives, in his concept of displacement reaction or lately in his interpretation of a species’ phylogenetic development as a system with its own inner dynamics, here reappears in a still more complex form: What he now postulates is a system of partly antagonistic selective forces – a notion which should turn out to be path-breaking for the further history of Behavioural Ecology. In a longer passage nearing the end of the part termed “Discussion” and which I would like to quote as a whole it reads:

Thus the picture that emerges is one of great complexity and beautiful adaptedness. It has further become clear that at least some of the different means of defence are not fully compatible with each other, and that the total system has the character of a compromise between various, in part directly conflicting demands. These conflicts are of different types. First, the safety requirements of the parents may differ from those of the brood. Thus the parent endangers itself by attacking predators. This is suggested by the fact that Foxes succeed in killing large numbers of adults in the colony. Though we have never seen a Fox killing an adult, their tracks in the sand cannot be misinterpreted. Often they kill many more birds than they eat. Some of these birds were “egg-bound” females (Manley, 1958), but in 1960, when we sexed 32 gulls killed by Foxes we found that 21 of these were males. Many of these gulls have their tails torn off and / or their legs broken. We believe that a Fox sometimes kills such birds by jumping at them when they “swoop”. All this suggests that a certain balance between the tendency to attack a Fox and the tendency to flee from it is selected for. | The conflict between “egoistic” and “altruistic” behaviour is also very obvious in the time when the winter preference for wide, open spaces changes into the preference for the breeding habitat which, as we have just seen, is dangerous to the adults. The switch towards the breeding habitat selection is not sudden; there is a long period in which the birds show that they are afraid of it; even when, after long hesitation, they settle in the colony, there are frequent “dreads” when the birds suddenly fly off in panic; these dreads gradually subside (see also Tinbergen 1953 and Cullen, 1956). Towards the end of the breeding season the adults begin to desert the colony in the evening to roost on the beach, leaving the chicks at the mercy of nocturnal predators. | Second, there are conflicts between two “altruistic” modes of defence, each of which has its advantages. Crowding, advantageous because it allows social attacks which are effective against Crows, has to compromise with spacing-out which also benefits the broods. | Finally there may be conflicts between the optimal ways of dealing with different predators. Herring Gulls and Crows might be prevented entirely from taking eggs and chicks if the gulls stayed on the nests, but this would expose them to the Foxes. While Herring Gulls and Crows exert pressure towards quick egg shell removal, neighbouring gulls exert an opposite pressure; the timing of the response is a compromise. | We cannot claim to have done more than demonstrate that egg shell disposal is a component of a larger system, nor are we forgetting that much in our functional interpretation requires further confirmation. It seems likely however that a more detailed study of all the elements of anti-predator systems of this and other species, and of the ways they are functionally interrelated, would throw light on the manifold ways in which natural selection has contributed towards interspecific diversity.739

For science historians who are only a bit familiar with the history of Behavioural Ecology the quotation above is exciting because it reveals how N. Tinbergen laid the foundation for future research. Thus we find anticipated several of the key topics which, later in the 1960s and 1970s, should become the figureheads of the new research branch such as the notion of conflicting behavioural strategies, altruism, the notion of trade-offs and the development of so-called “optimality models”.740

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For my argumentation it is vital to keep in mind that these topics were generated by re-framing an older epistemic scheme and its renewed reinterpretation. If my hypothesis was correct that all three papers on the Black-headed Gull’s egg shell removal build a unit only together, it would be likely that we are confronted with alternating schemes of composition at least in one of the two studies which supplemented the main paper as discussed above. This hypothesis, I think, can be warranted. The paper with the title “Egg Shell Removal by the Black-Headed Gull (Larus ridibundus L.) II. The Effects of Experience on the Response to Colour” which was published in *Bird Study* in the same year reveals another general heuristic thrust. It is a typical follow-up study. Already during earlier experiments Niko and his collaborators have noticed that Gulls, which hadn’t laid own eggs and whose nest therefore were filled with dummy eggs of abnormal colours, after that preferred exactly the same colours when it came to carrying away the egg shells. This matter of fact suggested that some kind of effect resulting from previous experience might be responsible for the Gulls modified colour preferences. “A pilot test, in which the response to black and khaki models was tested in birds which had been prevented from laying any eggs that season and had been sitting instead on black eggs”, Tinbergen writes,

showed that such gulls responded more to black models than control gulls who had been incubating their own, khaki-coloured eggs. It was decided to investigate this with larger numbers of gulls and with green eggs as well, and also to examine whether this increased response was due to a learning process or to the birds carrying objects of a colour which at the moment of the test matched the colour of its eggs. In addition, we decided to use these same birds to investigate the effect of this type of experience on egg rolling, or retrieving.\(^\text{741}\)

The overall composition most likely mirrors the amplifying character of the paper on several levels of the entire organization. Thus the introductory section (consisting of the “Introduction” and a brief chapter on “Methods”) is supplemented by a part which covers the main empirical “Results”.\(^\text{742}\) The complex as a whole is rounded off by a brief “Summary” (which, by the way, is not called “Conclusion”).\(^\text{743}\) The internal argumentative structure of each part reveals the highly reflected way in which Niko presented his ideas and, beyond that, substantiates the overall order. Thus it does not seem to be an accident that the introduction recapitulates the results of the main paper and only after that derives its own research question. It is not an arbitrary fact that Niko’s account on his methodology provides a description of his procedure before he discusses potential “flaws”. Moreover, it appears to be Niko’s deliberate practice that the section called “Results” has a more argumentative character and, beyond that, directs the attention of the reader into two different sets of test, namely the experiments related to the Gulls’ egg shell disposal, on the one hand, and the retrieving of the egg, on the other – in exactly this linear order. The tests were simple. They consisted in replacing the Gulls’ normal clutch with dummy eggs of different colours. After a certain period of time their responsiveness to egg shells of varying colours was tested. The results revealed a

\(^{741}\) Tinbergen et al., “Egg Shell Removal, II.”, 123.
\(^{742}\) See *ibid.*, 123, 124–126, 126–129.
\(^{743}\) See *ibid.*, 129–130.
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statistically relevant correlation between the colour of the incubated eggs and the preferences during carrying away. In order to make obvious the effect of experience a second experiment was performed in course of which the eggs of the clutch were replaced shortly before tests with dummies of a different colour were carried out. This time the birds did not show any significant preferences so that Niko felt entitled to draw the reverse conclusion that some effect of experience plays a role in the Black-headed Gull’s colour preferences. Both types of test were applied to the egg rolling behaviour of the Gulls as well. The outcome substantiated the previous results: The Gull’s preference for the colour of the “adopted” egg stemmed from experiences made during incubation and not, Niko’s competing hypothesis, some sort of ad-hoc comparison or perceptive colour match established immediately before the test. Nonetheless, N. Tinbergen and his coauthors hesitated to ascribe the effect to a process of conditioning. In their view, the fact that immature Gulls confronted with eggs or egg shells before any egg was laid nonetheless showed the normal response, demonstrated that this response could not be entirely acquired. Nor could the natural preference for white and the weak scores obtained with green shell dummies (one of the results of the main paper) be explained by this learning. Like the main paper Niko’s study of the Black-headed Gull’s colour preferences maintained the epistemic advancements which generated the Ethological Synthesis. For instance, the fact that mainly two behaviour patterns with opposite causal implications (i.e. carrying away vs. retrieving) were used for the tests and the results are narrated in the given order signals that Niko left the obtained causal architecture intact. Moreover, distribution of paradox and tautological conceptual relations within the epistemic frames may be like expected. For instance, the fact that the research question was derived from Niko’s earlier study seems to superimpose also the independent status of both papers. As if the results of the current study somewhat “shadowed back” upon its origin. The remark that further more detailed studies are required to decide of which nature the effect of experience actually is, by contrast, marks a sort of desideratum or omission – a gap to be filled later. That the study is a follow-up of the main paper also shapes the way how it refers to other Tinbergian studies. Thus there are quite a number of quotes which indicate that “Egg Shell Removal, I.” functions as a background text. Some relations are established to C. Beer’s and U. Weidmann’s Gull studies yet nothing more. Even his own papers from the past which had heavily drawn from discrimination and choice experiments and which were, from a methodological point of view, not that different to Niko’s egg shell removal studies didn’t make it into the new framework which was mainly guided by the question of the behaviours’ survival value. The references explicitly established in the current study therefore also have both a more self-referential and a more exclusive character in a sense that they point into the future not the past. With some caution one may therefore also conclude that the epistemic scheme applied in Niko’s theoretical account in the last consequence led towards a more self-enclosed understanding of his research which, so to speak, as a side effect rendered

\[ \text{Ibid., 129, 130.} \]

\[ \text{Those who like counting might interest that “Egg shell Removal, I.” is by far the most frequently quoted text in the paper.} \]

\[ \text{See ibid., 124.} \]
the research of his pupils a more and more autonomous area. The crosswise stimulation between Tinbergenian Practice and Tinbergenian Theory which had characterized the 1950s took another shape in the 1960s insofar as two fields, which became increasingly complex each in their own way, coexisted next to each other.

The second follow-up study which was published also in 1962 in British Birds under the title “How do Black-headed Gulls distinguish between Eggs and Egg-Shells” recapitulates, with some exceptions, the epistemic scheme underlying “Egg Shell Removal, II”. One of these exceptions is that there are only three major sections – “Introduction”, “Method”, and “Summary and Conclusion” – while the core of the results is placed under the heading “Method”. This is quite unusual and makes the reader reflect the results provided from a more theoretical point of view just as the text as a whole obtains the status of a message that goes beyond the mere result. Moreover, the scheme leaves no doubt that N. Tinbergen polarized his accounts by applying recursively binary differentiations to his material. Finally, the gesture includes a message: Every result is only a beginning (i.e. part of an introduction) – which, indeed, is a rather “reflexological” move. The notion of “polarization” also precipitates in the title which refers to the Black-headed Gull’s ability to discriminate between egg and egg shell. Maybe, I go too far but I also hear an additional latent question which concerns the history of the discipline: How can Niko’s egg shell removal studies be related to the older retrieval studies, that is, how can new Ethology be related to old Ethology? And the answer implies a paradox: Despite the obvious break the new set of questions can establish a connection. This, too, implies another question: How does the notion of discriminative experiment have to be modified conceptually so that it is compatible with the new ecological framework? Or to put it the other way round: Can discriminative experiments, if applied within an ecological framework, can make fruitful the achievements of Classical Ethology inside the new scientific paradigm? Maybe, that’s the question which superimposes the entire text as a whole from a methodological perspective. The modified conception of discriminative experiment which Niko develops in this paper deviates from earlier outlines in mainly two aspects. At first, the heuristic frame within which an animal’s ability to make choices is tested is another. While in former studies preference tests were applied in order to explore the psycho-physical mechanisms in the central regions of the nervous circuit, the question is now how relevant the capacity in question is for the survival of the species. In the introduction it reads:

The first study, while not allowing us to list all characteristics of the situation which elicits egg-shell removal, showed that birds distinguish between egg-shell and nest material by at least four characteristics: in fact, the egg-shell is distinguished by being three-dimensional, rounded, less oblong than nest material, and partly white. The present paper deals with the question of how gulls distinguish between egg-shells and eggs. Failure to do so would naturally endanger the brood, and we have actually never observed a gull removing its eggs or chicks.

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Please keep in mind that meta hodos literally means “the way to and beyond”.

The eggs stands for the whole, the shells for its parts, in this linear order.

Ibid., 120.
Failure would decrease the number of offspring and therefore endanger the survival of the species. As a reversal conclusion one may therefore presume that the capacity to distinguish between egg and egg shells must have a survival value. The quotation also reveals a second characteristic of Niko’s modified understanding of discrimination experiment. While former tests used to begin with a wide range of possible factors determining the receptory apparatus of the experimental animal of which the irrelevant ones were to be eliminated step by step until the relevant parameters and their causal organization were left over, the heuristic procedure now has changed: Niko and his collaborators began with a more or less clearly defined alternative of two complementary behaviours each of which was released by its own set of stimuli.\(^{751}\) The subsequent experiments must be read as an attempt to refine the parameter in question by amplifying and grading them. The tests were simple: N. Tinbergen and his associates presented various kinds of models, one at a time, and observed the reaction from a hide. The reaction patterns were also refined by splitting the two main reaction types, retrieving and removal, in four sub-categories each, “Intention-rolling”, “Rolling”, “Lifting”, and “Nibbling”, on the one hand, and “Intention-carrying”, “Carrying”, “Poking” and “Ignoring”, on the other.\(^{752}\) The scores were counted and evaluated in accordance with commonly accepted statistical principles. In concrete Niko and his coauthors tested mainly three types of parameters in three experiments to which they refer as “Experiment A”, “Experiment B”, and “Experiment C”, respectively.\(^{753}\) These parameters might be circumscribed as the “grade of intactness of the egg” (which implies how much “white” the egg shows), the “extent of the egg’s filling and consequently its weight”, and finally the “nature of the egg’s rim and the grade of its ‘raggedy’”. The ultimately presented results refer to three main categories of research question: The nature of the stimuli, the nature of the Black-headed Gulls’ reaction chain and the query whether the Gull’s capacity to discriminate is the product of nature or nurture. In a concluding remark Niko and his coauthors write:

The egg-shell elicits removal because it differs from the intact egg in the following characteristics: it shows a thin edge; this edge is serrated; and it shows white. The “decision” to remove it is already taken before the bird can have checked the weight. Neither the interruption of its outline nor its hollowness could be shown to contribute to removal, though both seem to exert an inhibiting influence on rolling. | In addition, it was shown that egg-shell removal is a chain of acts: nibbling is elicited by visual stimuli; during nibbling the weight is checked and, if it does not grossly exceed that of a real shell, the object is carried; if it equals the weight of an egg or a chick, the chain is broken off. This prevents chicks from being carried away when they have hatched but not yet left the shell; whether other safeguards exist as well we cannot say. | Most of the population in which these responses were studied must have had previous breeding experience. Very little can be said, therefore, about the extent to which the responses are innate or could be consequence of conditioning. Three one-year-old birds, which were tested with

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\(^{751}\) Ibid., 121–122. For Niko’s general claim to combine the study of function with thorough experiments of “all possible attributes of animals” see WRC-RU Fondr. Lib., MS 50, box 38, file 5, letter N. Tinbergen to J. Huxley (20/03/1965).

\(^{752}\) For the applied methodological practices see Tinbergen et al., “How Do Black-headed Gulls Distinguish Between Eggs and Egg-Shells?” 122–123.

\(^{753}\) Ibid., 123–124, 124–126, 126–128.
eggs and shells when they had not yet laid at all, rolled in an egg and removed a shell in a way indistinguishable from experienced birds (Tinbergen, Kruuk and Paillette 1962). In sum, one may say, that How do Black-headed Gulls distinguish between eggs and egg-shells? introduces a new concept of discrimination experiment on basis of an alternative epistemic pattern. This pattern reveals itself both in some parts of the paper and the composition as a whole. The scheme generated a sort of “anti-hypothetico-deductive” approach to choice experiments by presupposing alternative behaviours, in a first step, and testing amplified and graded nuances of the parameters determining the releasive situation, in a second. It also produced another focus upon the obtained results. This is difficult to describe. I think, that both the “black-box” model of the nervous apparatus examined by Classical Ethologists and the nature of the “decision” Niko sketches in the current study have paradox “overtones” or to put it with K. Lorenz must be spelt with small letters. Why? The classical ethological program to reduce the complexity of the central nervous system by determining its hierarchical organization reached its own boundary just in the same way as N. Tinbergen hesitates to describe the Gulls’ capacity to make a “decision” to any form of higher mental ability. This is most likely the reason why he puts the term in quotation marks. There is no deliberate act of choice – nonetheless there is the articulation of a preference. The way how both epistemic frames differ from each other seems to lie in the nature of the paradox. While causal analysis in classical ethological understanding construes the paradox through the “beginning of the scheme”, Niko’s advanced concept established it from the end since the choice now appears to be the product of a phylogenetic program acquired in course of a process which is guided by selective adaptation. In other words, decision making contributes to the animal’s survival value which has always guided its formation. The effect determines the cause. This specific construction of the underlying epistemic scheme both on the level of the behaviours’ variability and their causation is also a strong indicator for my thesis that the ecological framework as a whole maintained the epistemic achievements which had led to the biological syntheses of the 1930s. Another example might be Niko’s interpretation of the reactions exhibited by the Black-headed Gulls. The term he uses is “chain of acts” and as such it resembles, at least to a certain extent, the terminology of the reflexologists. Niko’s “chain of acts” has in common with the notion of “chain reflex” that each response within the chain acts as a stimulus for the next partial reaction but on closer inspection there are at least two aspects in which both concepts fundamentally disagree. The behaviourist or reflexological model of action chain appears to be relatively more static and determined by its fixed end, while Tinbergen’s “chain of acts” turns out to be liable to break-offs. Moreover, the interpretation in terms of causation is quite different as well since the interruption of the chain is said to have a protective function despite the fact that incomplete behaviours seem to bear the stigma of being dysfunctional. Finally, Niko’s treatment of the question whether the


755 As I will show in the second life-history I will examine Niko’s new procedure of discrimination might resemble what G. Kramer called “differential diagnosis”.

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Gull’s capacity can be ascribed to nature or nurture reveals his caution insofar the question is left open – so to speak – in form of a hypothetical alternative which can be tested in a further study: Some experience must be involved. However, both the non-deliberate quality of the “decision” and the fact that inexperienced one-year-old Gulls can perform the action chains in question speaks for an innate program. From a science historian’s perspective I am inclined to say that N. Tinbergen here anticipates indirectly what ecologists later might have called an “open adaptive phylogenetic program” a notion which includes, for example, all kinds of play. The “quasi-reflexological” model which N. Tinbergen implicitly also applied to the scientific process as a whole supports my view that as soon as he had replaced his older causal analytical stance of ethological theorizing the interaction of the two “epistemic worlds” in which his research had taken place so far lost their mutual contact – at least to a certain extent. This is to say, the simple logic of crosswise exchange, historians might associate with the concept of “histoire croissee” namely that the output of one system can function as the input of the other and vice versa, does not hold any more within the scientific orientation underlying Niko’s Functional Ethology. Mutual entanglement in the strict sense therefore turns out to be a transitional historical phenomenon in itself. When H. Kruuk underlines that the projects started by pupils of Niko’s during the 1960s more and more went independent, this might also have deeper lying epistemological reasons independent or next to the more “arbitrary” circumstances of N. Tinbergen’s life-history such as his age, his work load, the increasing growth of the discipline which made it difficult to keep up with its rapid development, not to mention his suffering from depression. That Niko’s theoretical world began to be self–enclosed – at least on a strictly scientific level (or stage) – can be seen in the detail that the references in How Black-headed Gulls distinguish between eggs and egg-shell? mention only three titles two of which were his own papers on egg shell removal behaviour. The epistemological and methodological culmination as displayed by Niko’s three Gull studies and their intertextual relationship therefore eventually also affected those practices which guided N. Tinbergen’s perception of the works of others including his own pupils. However, the, in the last consequence, also more retrospective perspective provided the opportunity to think up a model of choice experiment which – albeit qualitatively different from its predecessors – proved to be compatible with the new ecological framework and, beyond that, opened the field for a new line of research: Open behavioural programs. N. Tinbergen’s study of the egg shell disposal in Black-headed Gulls culminated in methodological questions and they, in turn, raised the question of the “epistemological constitution” of the ethological discipline as a whole. With Niko’s turn to a research program which was primarily related to the question of survival value the older convention that defined Ethology as a biological branch of behaviour research in the “no-man’s-land” in-between the more vitalist scientific orientations, on the one hand, and reflexology and Behaviorism, on the other, proved to be in-

756 For the way how behaviour ecologists developed and applied game theory see Cézilly, “A History of Behavioural Ecology”, 23.

sufficient and the new placement therefore needed to be renegotiated. Further “epistemological investment” was required to place the new line of research into the framework of the increasingly growing ethological discipline. Science historians who were concerned with the history of Ethology genuinely agree in that, first of all, it was N. Tinbergen who made an attempt to meet this challenge, while his life-long companion, K. Lorenz, tended to defend the classical constitution of his discipline. On Aims and Methods of Ethology, the text for which Niko became famous for, must be read as his answer to the epistemic splitting of his discipline. The paper appeared first in the German Zeitschrift für Tierpsychologie in 1963 and was dedicated to K. Lorenz at the occasion of his 60th birthday. Its title and the dualism of concepts it suggests rests upon the same epistemic grounds as the title of his later autobiography: “Watching and Wondering”. Both phrases are condensed formulas of Tinbergen’s late research attitude. They combine the gathering of data with subsequent “reduction” of complexity in a non-analytical (i.e. non-exclusive) manner which is signalled by the “and” in-between the two signal words in each title. Within the paper itself the double nature of the frame becomes evident at several distinct locations, for instance, in Tinbergen’s dual ap-


759 Some of Lorenz’s late statements even reveal a feeling of being betrayed. See to this Lorenz, Vergleichende Verhaltensforschung [1978], 20. That K. Lorenz who used to have a profound interest in philosophy and historical epistemology did not make a more advanced and less reactionary attempt to explain the inner dynamics of his discipline, to me, still is the “mystery of mysteries” in his life-history. This question (which is a “Why”-question) should be examined more carefully! For Lorenz’s inclination to preserve the epistemic status quo see Chavot, “Histoire de l’ethologie”, 30.

760 See N. Tinbergen. “On Aims and Methods of Ethology”. In: Zeitschrift für Tierpsychologie 20.4 (1963), 410. And also see Niko’s later comments on his own text including his re-definition of “Ethology” as the biological study of behaviour, Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3156, E 2, letter N. Tinbergen to R. Burkhardt (16/06/1982).


762 This attitude can be shaped more precisely by taking into account Niko’s correspondence with E. Mayr discussing On Aims and Methods. See Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3156, E 17, letter E. Mayr to N. Tinbergen (06/06/1963). Mayr seemed to have criticized Niko’s understanding of learning as too wide. In addition, he recommended to emphasis stronger the heuristic value of the method of “observation”. In addition, he corrected Tinbergen by claiming the greatest peak of the opposition against the idea of natural selection was reached in early Mendelians, particularly Bateson and De Vries.
Niko Tinbergen (1907–1988)

proach to formulate the two main objectives of the paper in a first step and then, in a second move, to supplement these “aims” with an additional legitimation – the causes for Niko’s engagement. “In this paper I wish to attempt an evaluation of the present scope of our science and, in addition, to try and formulate what exactly it is that makes us consider Lorenz ‘the father of modern Ethology’”, Niko says and continues,

Such an attempt seems to me worthwhile for several reasons: there is no consistent “public image” of Ethology among outsiders; and worse: ethologists themselves differ widely in their opinions of what their science is about. I have heard Ethology characterised as the study of releasers, as the science of imprinting, as the science of innate behaviour; some say it is the activities of animal lovers; still others see it as the study of animals in their natural surroundings. It just is a fact that we are still very far from being a unified science, from having a clear conception of the aims of study, of the methods employed and of the relevance of the methods to the aims. Yet for the future development of Ethology it seems to me important to continue our attempts to clarify our thinking, particularly about the nature of the questions we are trying to answer. When in these pages I venture once more to bring this subject up for discussion, I do this in full awareness of the fact that our thinking is still in a state of flux and that many of my close colleagues may disagree with what I am going to say. However, I believe that, if we do not continue to give thought to the problem of our overall aims, our field will be in danger of either splitting up into seemingly unrelated sub-sciences, or of becoming an isolated “ism”. I also believe that I can honour Konrad Lorenz in no better way than by continuing this kind of “soul-searching”. I have not hesitated to give personal views even at the risk of being considered rash or provocative.763

In quoting this longer introductory passage at the outset of On Aims and Methods I would like to stress the recursive logic of Niko’s way of presenting his argument. The double aim of giving an overview of the discipline’s current scope and of giving a “Why” for K. Lorenz’s status as a “father of modern Ethology” is supplemented with a secondary “Why” on a higher level of argumentation with which Tinbergen gives a legitimation (i.e. a cause) for his double attempt. The internal logic of the argument thus repeats recursively so that “lower parts” coincide with structurally identical parts in the “upper regions” of the scheme and vice versa. The former step increases the latter reduces complexity. A very simplified illustration of the structure underlying the quotation above would be the following graphic (Fig. 2.13).

![Fig. 2.13](image-url)

Fig. 2.13

N. Tinbergen, On Aims and Methods (1963), Introductory Argumentation

Please keep in mind that the terms I have chosen to illustrate the recursive dynamic of N. Tinbergen’s introductory argumentation, the “And” and the “why”, refer to different dimensions of behaviour. Some of us may have already realized that the introduction’s structural pattern eventually coincides with the composition of the

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paper as a whole. Thereby, however, it must be kept in mind that the main “activity” of the account takes place in the middle part of the above scheme and coincides – so to speak – with what I have called “why”¹. From a semantic standpoint, in this part N. Tinbergen defines the epistemological scope (in a Spencerian sense) of his discipline, not so much in an exclusive form but with a future perspective, that is, how he wants his discipline to be. It encompasses six major topics, “Ethology as a branch of Biology”, “Observation and Description”, “Causation”, “Survival value”, “Ontogeny” and, finally, “Evolution”.⁶⁴ If we would like to understand the inner argumentative relationships existing between these parts we must have a brief glance at the chapter with the title “Ethology a branch of Biology”. It outlines the raw state of the order, so to say, by defining the grid of the ethological research process (or better: research program). It starts with a provisional definition of “Ethology” and complements this definition with a what N. Tinbergen means by it. All further exemplification can be read as a sort of recursively differentiated tree of epistemic practices. “In the course of thirty years devoted to ethological studies I have become increasingly convinced that the fairest characterization of Ethology is ‘the biological study of behaviour’”, Niko writes and proceeds:

By this I mean that the science is characterised by an observable phenomenon (behaviour, or movement), and by a type of approach, a method of study (the biological method). The first means that the starting point of our work has been and remains inductive, for which description of observable phenomena is required. The biological method is characterised by the general scientific method, and in addition by the kind of questions we ask, which are the same throughout Biology and some of which are peculiar to it. Huxley likes to speak of “the three major problems of Biology”: that of causation, that of survival value, and that of Evolution – to which I should like to add a forth, that of ontogeny. There is, of course, overlap between the fields covered by these questions, yet I believe with Huxley that it is useful both to distinguish between them and to insist that a comprehensive, coherent science of Ethology has to give equal attention to each of them and to their integration. My thesis will be that the great contribution Konrad Lorenz has made to Ethology, and thus to Biology and Psychology, is that he made us realise this close affinity between Ethology and the rest of Biology; that he has made us apply “biological thinking” to a phenomenon to which it had hitherto not been consistently applied as was desirable.⁶⁵

For the sake of brevity I would like to translate this passage into a visual form of representation. I think the major propositions can be arranged in the following tree structure (Fig. 2.14).

Niko’s heuristic move now obviously is to establish a canon of epistemic practices which in his view characterizes “the biological study of behaviour”. This canon consists of mainly two “branches of his tree”, namely the claim to begin with the description of observational phenomena (which is the first pre-analytical step I called “A”), on the one hand, and to apply his four “Whys” (the last step in Niko’s branching account, I called “B”). It can also be discussed whether it is not this dual composition which Niko identifies as K. Lorenz’s contribution and “major breakthrough”.⁶⁶ This would mean that Lorenz, in Niko’s view, defined the theoretical foundation of Ethology, that is, what he used to call “Analyse in breiter Front”, in

⁶⁵ Ibid., 411.
⁶⁶ Ibid.
accordance with his understanding of instinctive behaviour – that is as a sort of intercalation between appetence (the beginning) and consummatory act (the end). And it is eventually a crucial aspect of Niko’s move that he agrees with Lorenz in the general heuristic thrust ethological explanations should take, namely from inductive observation to the treatment of specific problems, quite independent of the fact that Tinbergen had begun both to re-frame and to redefine the two epistemic practices in question. The further composition of the paper mirrors the division of labour Niko wanted to see applied in his science:767 While section three “Obser-

767 When I use the word “mirrors” I refer to what I have earlier called “performative coincidence” by which I mean that structurally equal parts within a text may be projected upon each other. That our brain is capable to detect these parallels is a precondition for both the increase and the reduction of complexity – pending on the mode of the projection.
“Observation and Description” refers to the inductive side of ethological research, part four, five, six and seven address the four problems of Biology. In sum, thus I am inclined to illustrate the overall composition of the paper as follows in Fig. 2.15. The overall composition of the paper and the framework within which the entire account is located also entails that Niko more or less exclusively addressed the “reductive side” of K. Lorenz’s research program and therefore tended to neglect, for instance, his Special Phylogeny of Releaser, at least on the “upper levels” of his theorizing. The linkage of observation and description, on the one hand, and the problem of causation with the notion of reductive analysis, on the other, however reveals that both scholars shared the epistemic cornerstones of both the Modern Synthesis (MS) and the Ethological Synthesis. Yet, despite all the verbal emphases of K. Lorenz’s contributions, the paper, so to speak, under the mere phenomenological surface contained no less than a veritable subversion of the ground plan upon all ethological theorizing was planted until that point. This move was not only directed against Lorenz’s reductions but also against Niko’s earlier conception of the four “Whys”, for instance, in *The Study of Instinct*. In order to grasp how substantial the latent criticism formulated in *On Aims and Methods* actually was it is necessary to have a brief glance upon how N. Tinbergen re-conceptualized the meanings under the mere signifiers “Causation”, “Survival value” (the former adaptedness), “Ontogeny” and “Evolution” in comparison to his own earlier understanding.

Thus N. Tinbergen’s earlier conceptions of proximate causation were paradox at the beginning and tautological at the end because they usually inferred from the effect to the cause. This directionality changed now – a matter of fact which becomes evident only indirectly on a more abstract level in Niko’s chapter on “Causation”. It proceeds in two steps insofar as Niko, at first, mentions three aspects of causation which he has drawn from Lorenz’s works. These aspects are only mentioned in a brief overview at first. In a second step, he intends to “elaborate these points to some extent.” The reverse order of the causal inference becomes evident if we take into account that Niko’s first step is based upon an act of reception and the causal implication of this epistemic practice, while the second step marks the *effect* Lorenz’s “points” have had. In other words, Niko’s modified treatment of proximate causation infers from the cause to the effect. There are several concrete examples which substantiate my view. For instance, Tinbergen claims:

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768 The graphical illustration I have chosen is eventually not the only one possible. What I have called “First Part” can eventually be re-written or re-painted by applying another rule of differentiation, namely the one which had guided Lorenz’s Special Phylogeny of Releaser. That both readings can overlap is eventually the key to the paper’s hidden message. Structurally it consists of a non-coincident tautology at the beginning of the reference system. The message then is: Lorenz’s special phylogeny can be integrated in a theoretical ecological framework but only if this theoretical framework leaves behind the former mechanomorphism. On closer inspection this structural ambiguity is highly sophisticated!

769 Tinbergen, “On Aims and Methods”, 413. These points are (1) Lorenz’s early analogy between organ and behaviour, (2) the observation that behaviour is a more complex phenomenon than assumed which “applied equally to the sensory, the motor and the central nervous processes involved” (Ibid.), and lastly (3) the observation that initiation, coordination and cessation of behaviour might be less controlled by external rather than internal factors. I will not explain the way N. Tinbergen modifies the epistemic deep structure of each theme, while elaborating upon it since this would lead me too far away from my question which is the causal dimension of
On Aims and Methods of Ethology (1963)

[Final Part]

Summary

Conclusion

Evolution

Ontogeny

4 Problems of Biology

Variability

Ontogeny

Survival Value

Causation

Observation and Description

Ethology as a Branch of Biology

Introduction

First Part

Main Part

[That means ...]

4 Problems of Biology

Causation

Fig. 2.15

N. Tinbergen, *On Aims and Methods of Ethology* (1963), Order of the Paper
The treatment of behaviour patterns as organs has not merely removed obstacles to analysis, it has also positively facilitated causal analysis, for it led to the realisation that each animal is endowed with a strictly limited, albeit hugely complex, behaviour machinery which (if stripped of variations due to differences in environment during ontogeny, and of immediate effects of fluctuating environment) is surprisingly constant throughout a species of population. This awareness of the repeatability of behaviour has stimulated causal analysis of an ever-increasing number of properties discovered to be species-specific rather than endlessly variable.\textsuperscript{770}

The quotation is illuminating because it says a twofold capacity of the analogy between organ and behaviour. On the one hand, it is said to have “removed obstacles to analysis” (a sort of inhibition of inhibition). On the other hand, the “the repeatability of behaviours” of a certain type has carved out the species-specific (i.e. uniform) character of these behaviours – so to say as a quantitative indicator. The latter aspect involved a paradox since the many (repetitions) is reduced to the one (the species-specific form) on a higher level. The former of the two aspects deals with an issue being harmful for causal analysis (even in case it is removed) the latter is explicitly associated with a positive effect (“positively facilitated”, “has stimulated causal analysis”). The examples show a redirected causal reference system. A similar mechanism might have been applied to the concept of “Survival value”. We remember, N. Tinbergen’s reasoning on adaptedness so far was bound to a peculiar theme, namely animal communication and the process in course of which seemingly dysfunctional actions obtained a biological meaning in as much they became communicative symbols in service of the “greater good” of an animal population. Ritualization therefore stood for a phylogenetic transformation process from the dysfunctional to the functional.\textsuperscript{771} This linear order now changed and in doing so a new set of phenomena entered the naturalist’s horizon: The seemingly dysfunctional derivatives of otherwise quite adequate behaviours turned out to be a paradox indicator for their survival value. One of the most impressive examples for this type of behaviour is Niko’s account of “rocking”. Some insects which usually maintain their camouflage by freezing their movements in case of danger skip this strategy in favour of a widely conspicuous rocking movement which, at first sight, blows their camouflage. Niko’s argumentation now aims to put forward a “despite” by claiming that this movement is adaptive although the opposite might be supposed. “Heinroth (1909) already suggested”, N. Tinbergen claims, that the rocking movements of Phyllium might well be harmless because predators might recognise them as passive movements of a leaf slightly moved in the wind. It seems to me quite possible that many young birds actually do learn that certain types of movements are passive, and not indicative of animal prey, and that it might not only be harmless for certain cryptic animals to perform these movements but that it might be definitely beneficial to them because it might ensure that a predator sees them and concludes that they are just vegetable matter. A motionless cryptic animal “hopes to be overlooked”; a rocking cryptic animal makes sure that it is seen and ignored – which means survival.\textsuperscript{772}

\textsuperscript{770} Tinbergen, “On Aims and Methods”, 414.
\textsuperscript{771} Here is the place where Niko mentions Lorenz’s study of releaser. See ibid., 417.
\textsuperscript{772} Ibid., 420–421. Another example may be the Black-headed Gull’s egg shell removal behaviour which is not only of advantage because the Gulls leave the young alone and unprotected while they are carrying away egg shells. See ibid., 422.
From a more methodological standpoint the paradox position the study of survival value takes is mirrored by the fact that, in Tinbergen’s view, it can be examined with precise experimentation – and all that within a framework of studying function which used to be stigmatized as non-scientific “guesswork” or even as “armchair science”.\textsuperscript{773} In sum, one may eventually say that a modified scheme of functional study is applied in both a more concrete and a more methodological context. In both cases advantage is opposed to disadvantage, while the latter is supposed to turn out as only seemingly negative. This order deviates from earlier conceptions of adaptedness: What formerly appeared as a study of adaptedness because its objective was to reconstruct the communicative value of gradual inter- and intraspecific differences in display behaviours now takes another course because it is headed towards experimental testing. These tests take a paradox position within the entire frame of functional study because, according to Niko, the student of survival value, on the one hand, looks “forward in time” but, on the other, (and unlike the physiologist but in accordance with his own understanding of studying causation) determines the cause and tries to traces the effect. This is how I read the following passage which is difficult to understand unless we realize that Niko circumscribes different constituents of the framework in which he placed the study of functions and quasi-functions. It reads:

Our study always starts from an observable aspect of a life process – in the present case, behaviour. The study of causation is the study of preceding events which can be shown to contribute to the occurrence of the behaviour. In this study of cause-effect relationships the observable is the effect and the causes are sought. But life processes also have effects, and the student of survival value tries to find out whether any effect of the observed process contributes to survival if so how survival is promoted and whether it is promoted better by the observed process than by slightly different processes. It is clear that he too studies cause-effect relationships, but in his study the observable is the cause and he tries to trace effects. Both types of worker are therefore investigating cause-effect relationships, and the only difference is that the physiologist looks back in time, whereas the student of survival value, so-to-speak, looks “forward in time”; he follows events after the observable process has occurred. The crux is that both are concerned with a flow of events which can be observed repeatedly, and which thus, unlike the unique events of past evolution, can be subject to observation and experiment as often one wished.\textsuperscript{774}

The paragraph remains ambiguous (and it is meant to be like this) for it is uncertain which kind of study of causation Niko has in mind when he marks the contrast between the student of “causation” and the student of “survival value”. Is it his own modified, a classical reflexological or another concept of proximate causation which he seems to ascribe to the “physiologist”. We can only state that this concept involves the notion that past events can have observable effects on present behaviour and that, although the concept ultimately works with repeatedly observable events, it nonetheless seeks the causes behind these effects. The student of sur-

\textsuperscript{773} For the depreciatory attitude with which zoologists used to meet the study of function see \textit{ibid.}, 418, 421. Niko himself makes a difference between the effect of natural selection which, in his view, can only be traced indirectly and “survival value” which “is just as much open to experimental inquiry as is the causation of behaviour or any other life process” (\textit{ibid.}, 418). Later on in the text “survival value” is made a subject of discussion once more as the paradox indicator to study the effect of natural selection. See \textit{ibid.}, 423.

\textsuperscript{774} \textit{Ibid.}, 418.
vival value, by contrast, seeks to trace the adaptive value of a behaviour within and behind the results of her or his experiments. In other words, in his late theoretical account Niko adopted a more Darwinian concept of adaptedness which contradicted both the one he had applied in his own ritualization studies and the one underlying classical ethological reduction. In the former case the crux lies into the directionality in the latter case in the overtone of the underlying epistemic pattern. Or to put in another way: There are at least three paths leading towards Niko’s understanding of “survival value”, (1) the direct adoption of the Darwinian or neo-Darwinian equivalent, (2) the transformation of his own earlier concept of adaptedness, or (3) the transformation of the causal architecture underlying Lorenz’s physiological reductions. It might be possible that Niko uses option (2) and (3) next to each other in his chapter on “Survival value” – less option (1) which would be more the way applied by his pupils. A fourth reference point would be his own modified understanding of causation. I am inclined to say that this reference is also present because N. Tinbergen insists that the study of causes should differ from the study of effect in the linear order of the epistemic practices being involved. He says:

The fact that we tend to distinguish so sharply between the study of causes and the study of effects is due to what one could call an accident of human perception. We happen to observe behaviour more readily than survival, and that is why we start at what really is an arbitrary point in the flow of events. If we would agree to take survival as the starting point of our inquiry, our problem would just be that of causation; we would ask: “How does the animal – an unstable, ‘improbable’ system – manage to survive?” Both fields would fuse into one: the study of causation of survival. Indeed, logically, survival should be the starting point of our studies. However, since we cannot ignore the fact that behaviour rather than survival is the thing we observe directly, we have, for practical reasons, to start there. But this being so, we have to study both causation and effects.

Next to the analysis of N. Tinbergen’s explicit statements we can also try to assess the more performative mode of knowledge organization within the chapter in order to get an impression of the system of causal concepts. Thus I think it is no accident that Niko describes his understanding of “Survival value” in the first place before he enters into the reception history of the concept. The latter aspect again seems to be subdivided in an account of the reasons why the concept was rejected, on the one side, and several positive examples for studies which adopted the concept, on the other. Ontogeny was one of the themes N. Tinbergen had integrated only rather reluctantly in The Study of Instinct. Now its status seems to have changed. Moreover, the view upon the topic is also a new one: In The Study of Instinct both the overall composition of the treatise and the location where the topic “Development of Behaviour in the Individual” was placed within the entire edifice determined the

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776 The examples for a positive adoption of the concept include E. Cullen’s study of cliffnesting in Kittiwakes and N. Tinbergen’s own paper on egg shell removal in Black-headed Gulls. See ibid., 422.
777 For those who like counting “Ontogeny” and “Causation” take each ca. 23.5% of the amount of pages invested to elaborate on all “four problems of Biology”. The account on “Survival value” covers ca. 38.2% and “Evolution” ca. 14.8% of the pages. If it was legitimate to take the number of invested pages as an indicator for the author’s esteem we would be allowed to conclude that Niko rated the study of ontogeny as highly as the study of causation.
way it was treated. For Niko ontogenetic variability was a phenomenon related to an organism’s plasticity but also thought that any sort of learning can always be superimposed upon innate disposition only. The order of chapter six in The Study of Instinct mirrored this view since Niko started with phenomena of growth and then elaborated upon maturation before he finally entered into the learning theme. In other words, he proceeded from nature to nurture. Thereby it was primarily the nature part classical ethologists sought to sift out through analytical reduction – a practice which, in turn, generated the so-called “Kaspar-Hauser” or “deprivation” experiments. Niko’s criticism in On Aims and Methods is primarily directed against this practice to claim “innateness” for those behaviours which were fully displayed after the organism in question had been deprived from several or many possible external influences. Within this analytical frame innate, in Niko’s view, can only mean independence of the tested parameter and therefore would always have the character of an argumentum ex negativo which leaves open the possibility of additional untested influences. The term “innate”, in his view, thus proved to be inadequate because it is “suggesting a positive statement where merely a negative statement would be in order”. “And I submit”, Niko continues, that most statements about “innateness” of behaviour are based on the elimination of one or some out of several, perhaps many, possible influences. I am again criticising myself just as much as others, for I am now convinced that I have helped to perpetuate the confusion. If we raise male Sticklebacks in isolation from fellow members of its own species, subject them as adults to tests with dummies, and find (E. Cullen 1961) that they attack red dummies just as selectively as do normal males, we are entitled to say that exposure to red males cannot be responsible for the development of this selectiveness of response. We cannot, however, say anything about the problem whether or not interaction with the environment during “practising” has influenced the form of their fighting movements. When Grohmann (1939) showed that the incomplete flying movements which young pigeons make while growing up (and which might be interpreted as providing “practice”) did not influence their flying skill (birds that were prevented from flapping on the nest flew as well as controls on their first attempt), he eliminated a different form of interaction with the environment than Cullen did with Sticklebacks. It is not helpful and even wrong to apply to both behaviour patterns the term “innate”, because in each case only one out of various environmental effects was excluded, and these were different in each case. The conclusion can only be formulated correctly in negative terms, in describing which environmental aspect was shown not to be influential. There is, in addition, another reason for not applying the term “innate” to the fighting behaviour of the Kaspar Hauser Sticklebacks. Knoll (1953) has shown that the rods of tadpoles raised in darkness do not function properly; exposure to light is required to allow them to become fully functional. We have no information about this problem in Sticklebacks, and this means that, in the absence of evidence with respect to either rods or cones in Sticklebacks, we must allow for the possibility that light – an environmental property – is required for the proper “programming” of part of the Stickleback’s behaviour machinery. This brings me to another point which I consider important: the term “innate” whether applied to characters, or to differences, or to potentialities, or to developmental processes, is not the opposite of “learnt”; it is the opposite of “environment-induced”. These few considerations seem to me sufficient to conclude that the application of the adjective “innate” to behaviour characters, and to do this on the basis of eliminations of different kinds is heuristically harmful. If I were to elaborate this further I should have to cross swords with my friend Konrad Lorenz himself – both a pleasure and a serious task requiring the

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778 For the details please see pages 160–163 of my thesis. 779 Ibid., 424.
most thorough preparation – but this is not the occasion to indulge in swordplay, and I prefer to
continue with my sketch of the procedure which seems to me more fruitful.\textsuperscript{780}

I have quoted this longer passage because it reveals that Niko’s criticism of the
deprivation experiments was a substantial one which was directed against the epistemological reference system as a whole within which classical ethologists had
sought to carve out what they thought to be “innate”. From a heuristic point of
view the crux seems to lie within the fact that the primordial distinction between
the (eliminated) “learnt” and the (allegedly) “innate” can be recursively repeated
on the side of the innate as often as one likes. The innate – and already W. James
was aware of this fact – therefore will always have the character of another distinc-
tion. Within a system like that the innate can only be determined approximately
or in form of a negative statement. If so, what was N. Tinbergen’s conceptual al-
ternative for the study of ontogeny in \textit{On Aims and Methods}? According to his
account, the “phenomenon” of ontogeny means “change of behaviour machinery
during development” which is not to be fused with the “change of behaviour dur-
ing development”.\textsuperscript{781} In order to examine the changes in the machinery he suggests
a heuristic procedure which is not unlikely to the one we already met in his ac-
count on “Survival value”. Observation comes first then analysis. “It seems to me”,
he writes, “that if we return to a description of the phenomenon and the formul-
ation of relatively simple questions, our course is laid out clearly”.\textsuperscript{782} One of these
simple questions seems to be: What has been brought about the changes in the be-
haviour machinery? Or how are these changes controlled?\textsuperscript{783} In order to answer this
question Niko suggests to proceed in several steps. In a first one a student of on-
togeny has to distinguish between externally induced and internal influences during
development.\textsuperscript{784} External agents are determined by manipulating environmental pa-
rameters during development and subsequently watching the effects. If influences
turn out to be ineffective this would be a first indicator for internal control. The
“ultimate demonstration of internal control”, however, “must come from direct in-
terference with internal events”.\textsuperscript{785} This general procedure then must be applied
repeatedly on several levels of integration.\textsuperscript{786} “This general procedure, when ap-
plied at various levels of integration – the complex patterns, single acts, and even
smaller components of the total behaviour machinery –”, Niko underlines,

\begin{itemize}
\item seems to me much more fruitful than either basing a conclusion about innateness on elimination
\item of part of the environmental properties, or proceeding on the assumption that all adaptedness
\item of behaviour is acquired through interaction with the environment. It has been pointed out
\item repeatedly (see Pringle 1951, Lorenz 1961) that there are two methods of “programming” the
\item individual: the evolutionary trial-and-error-interaction with the environment which results in the
\item specialisations of the genetic instructions, and the ontogenetic interaction between the individual
\end{itemize}

\textsuperscript{781} Ibid., 424.
\textsuperscript{782} Ibid., 425.
\textsuperscript{783} See ibid., 426, similarly 424.
\textsuperscript{784} External and internal thereby seems to be defined primarily in causal terms: External means
\item externally controlled!
\textsuperscript{785} Ibid., 426.
\textsuperscript{786} If differentiation between externally and internally controlled characters of growth was the first
\item step then repeated application on various levels of integration seems to be the second.
and its environment – which, incidentally, takes the form of trial and error only where evolution has not given precise direction to the ontogenetic process.  

If I read this quoted text correctly, N. Tinbergen rejects a view which determines phylogeny and ontogeny as the two constituents of an intercalation which is guided by the trial-and-error principle and, in the last consequence, renders ontogenetic development the “negative rest” not being fully affected by the principles of phylogenetic development. Niko’s model of ontogeny, by contrast, seems to be more like a graded stage model in which each level of integration reserves locations which are receptive enough that external factors can intervene and act upon them. From his discussion of W. H. Thorpe’s studies of song learning in singing birds we may eventually also infer that this external control, in Niko’s view, may only act upon the basis of already existing selective preferences. This view is mediated by the notion that organic growth primarily consists of establishing physical relations and that external influences can only modify but not “invent” these pre-existing connections. In a third step, aside observation and asking the question of control on various different levels of integration, N. Tinbergen seems to have in mind also a concluding third step for his model of ontogenetic study: For the various different types of ontogenetic control the question of survival value must be asked separately. The question “What for” also provides the opportunity to connect the study of ontogeny with the study of survival value and a function oriented examination of the individual’s life-history. In sum, one may say that the trilogy of “Growth”, “Maturation” and “Learning” which served as the cornerstones of ontogenetic research in the *Study of Instinct* now is replaced by a more comprehensive and practical instruction how to approach individual development. This model includes observation, asks how the development of the individual is controlled on various different levels of integration and, finally, aims to examine the survival value of each factor. Niko’s model for ontogenetic study thus may operate upon the same epistemic ground plan as his understanding of biological research in general. From a structural point of view we therefore have to do with another example of performative coincidence. 

The study of “Evolution” played a marginal role in *The Study of Instinct*. Yet, during the 1950s evolutionary systematics turned out as N. Tinbergen’s primary area of causal analytical theorizing – and not the hierarchization of neuronal mechanisms, as we could have expected from the prevalence of the nervous system in *The Study of Instinct*. I have interpreted this move as an evasive gesture and response to the increasing criticism of the oversimplifications put forward by classical ethologists. The epistemic reference system of Tinbergen’s systematic program remained identical in comparison to his previous reductions which also allowed to maintain
the unity of the discipline. However, criticism from within and outside his work group renewed itself within the new field and thus proved to be of a more substantial kind. Ultimately it was the area of evolutionary systematics in which some of Niko’s pupils formulated a veritable alternative framework which Tinbergen apparently finally adopted. How did he interpret and refine this reference system in *On Aims and Methods* and against which older conceptions was the new paradigm profiled? In Tinbergen’s opinion evolutionary study has two major aims: “the elucidation of the course evolution must be assumed to have taken, and the unravelling of its dynamics”. According to Tinbergen’s account the former of the two objectives is pursued mainly through comparison of groups of closely related species. The method of the behavioural systematist here is very similar to the one of the taxonomist: “we judge affinity”, Niko explains,

by the criterion of preponderance of shared characters, particularly of those which we consider non-convergent. Once we have hardened the conclusion, often already reached by the taxonomists, that a certain group must be monophyletic, we judge the degree of evolutionary divergence by the degree of dissimilarity of those characters that must be considered highly environment-resistant ontogenetically – we try to exclude from our material such differences as are the direct phenotypic consequence of different environments, such as an individually acquired darkening of external coloration under the immediate influence of a moist environment (which of course, is very different from differences in ability to respond to the environment).

As a provisional result, one may claim that Niko’s understanding of evolutionary “static” consists of a twofold heuristic gesture: In a first step, the behavioural systematist determines the monophyletic origin of his sample (which is a reduction). In a subsequent step he aims to judge the “degree of evolutionary difference”. In any case, behaviour systematics here appears to be a derivative of morphological taxonomy since the clusters obtained on basis of behavioural characters had mostly confirmed and only rarely overthrown the achievements of the taxonomists. If we compare the model of systematic research which Niko introduced at this point of *On Aims and Methods* with the one applied in his review papers before 1959 we will immediately see the difference. While his earlier attempts used adaptive radiation as an indicator for slight gradual deviations in display behaviours not only for its own sake but also in order to get a more accurate picture of the systematic order (which Niko lately also conceived as a system of organic forces with its own inner dynamic), he now begins with the reduction and proceeds with determining the finer differentiation. Again I am therefore inclined to say he inverted the heuristic thrust of his epistemic practices. This idea is being substantiated by the fact that the reconstruction of the evolutionary course is supplemented by the “unravelling of its dynamics” by which Niko means “the study of the influence of selection on behaviour evolution”. Again the task in question is tackled in two ways: “One is the study of survival value of species-specific characters”, he argues, “the other is
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the direct application of a controlled selection pressure and its results over a series of generations”. As a provisional result, one may say that alike to Tinbergen’s model of ontogenetic study his phylogenetic research program consists of a number of dichotomously arranged epistemic practices: Determining the monophyletic origin of a sample and judging grades of evolutionary divergence should help the behavioural systematist to determine the allegedly course of evolution – the study of the impact possibly exerted by selective pressures aims to reconstruct the actual evolutionary dynamics. Especially the final stage of the heuristic course, that is, the experimentation with controlled selection pressure, reveals the end-paradox constitution of the entire framework: The organism’s survival value under artificially controlled circumstances is meant to generate heuristic repercussions (in a sense of a reverse inference) upon the selective pressures exerted under normal conditions of life. This stance contradicted both the strictly systematic interest of the previous studies and the attempt to approach adaptedness by merely observing adaptive radiation. To sum up my reading of On Aims and Methods, one may say that N. Tinbergen, despite his verbal adherence to the works of his friend K. Lorenz, consequently straightened out all four major areas of biological research (including their prototypical theoretical concepts) according to the epistemic framework of his newly adopted scientific orientation. How he organized his knowledge, what he omitted, the way he maintained the achievements of neo-Darwinism, and how he transformed key concepts in comparison to his own and his companion’s earlier theoretical statements – all these aspects reveal that Niko’s move away from classical ethological theorems was wholehearted and consequent. However, I still have to look for any information in In Aims and Methods concerning the question how Niko intended to connect his conceptual alternative with the paradigm of Classical Ethology. His late theoretical account is more a manifest of his new scientific orientation rather than a reader’s manual how to understand the dynamics in his scientific community. What we can say is that Niko profiles “Ethology” as “the biological study of behaviour” which seems to encompass both the realms with which K. Lorenz introduced “biological thinking” to the study of behaviour and implicitly (at the foremost via the organization of the text) also his new deviating view. However, some passages in On Aims and Methods can also be read as an attempt to find another word for the division of labour which had characterized the heterogeneous constitution of Classical Ethology. “These briefly mentioned samples do indicate, I believe”, Niko says,

how analyses of behaviour mechanisms which were initiated in the earlier ethological studies are moving towards a fusion with the field conventionally covered by Neurophysiology and Physiological Psychology. As far as the study of causation of behaviour is concerned the boundaries between these fields are disappearing, and we are moving fast towards a Physiology of Behaviour, ranging from behaviour of the individual and even supra-individual societies all the way down to Molecular Biology. There ought to be one name for this field. This should not be Ethology, for on the one hand Ethology has a wider scope, since it is concerned with

795 Ibid.
796 Please keep in mind that I have distinguished between “Tinbergian Theory” and “Tinbergian Practice” and that my conclusion only refers to the former of the two realms, while the latter will be examined later!
other problems as well; on the other hand, ethologists cannot claim the entire field of Behaviour Physiology as their domain, for they have traditionally worked on the higher levels of integration, in fact almost entirely on the intact animal. The only acceptable name for this part of the Biology of Behaviour would be “Physiology of Behaviour”, and this name should be understood to include the study of causation on animal movement with respect to all levels of integration.

And later on it reads:

It is through Lorenz’s interest in survival value that he appealed so strongly naturalists, to people who saw the whole animal in action in its natural surroundings, and who could not help seeing that every animal has to cope in numerous ways with a hostile, or at least unco-operative environment. Incidentally, just because Lorenz’s work has revived interest in the study of survival value, and because this is an aspect of Ethology which may well fertilise other fields of Biology (where survival value studies are being neglected) I think it is regrettable that his fine new Institute has been named “Institut für Verhaltensphysiologie” – its field of research extends far beyond Physiology.

Both quotations show that N. Tinbergen wanted to reserve the terms “Ethology”, “Physiology of Behaviour”, and “Biology of Behaviour” for certain areas or parts of behaviour study. Some passages in this quotes sound like the founding document of new institute in Seewiesen which was meant to establish a cooperation between Lorenz’s holism and E. v. Holst’s later Functional Physiology. For historical reasons Tinbergen apparently saw the Physiology of Behaviour more represented in the realm of the synthesis covered by Lorenz’s holism, whereas he identified the complementary part with Lorenz’s Special Phylogeny of Releaser, in his view “an aspect of Ethology” being concerned with matters of survival value. This raises the question whether the realm Niko dedicated to his theoretical outline of Behavioural Ecology was interpreted as another aspect of Ethology and, beyond that, whether he considered the “Physiology of Behaviour” to be a part of Ethology, too. What can be confirmed is that N. Tinbergen had a wide understanding of his discipline but he eventually also tended to interpret Ethology as the study of adaptiveness whereby the term “Biology of Behaviour” served as the even wider integrative concept. He writes:

I have tried in this paper to give a sketch of what I believe modern Ethology is about. I have perhaps given Ethology a wider scope than most practising ethologists would do, but if one reviews the various types of investigations carried out by people usually called ethologists, one is forced to conclude that the scope is in fact as wide as I have indicated.

And shortly after N. Tinbergen adds:

Finally, I should like to touch briefly on a matter of terminology. It will be clear that I have used the word “Ethology” for a vast complex of sciences, part of which already have names, such as certain branches of Psychology and Physiology. This, of course, does not mean that I want

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[798] Ibid., 417.
[799] At this point it seems necessary to take into consideration the date of Niko’s publication, 1963. After E. v. Holst’s death in 1962 the MPI for Behavioural Physiology was facing a structural reform in course of which the original two departments were redefined as four. And it is likely that K. Lorenz’s “Zickzackweg auf dem Grat der Wahrheit” (E. Oeser) – in course of this reform – once more made a U-turn which might have led to a reassessment of his hypothetical realism, that is, the one constituent Niko called an “aspect of Ethology”.
[800] Ibid., 430.
to claim the name Ethology for this whole science, for this would be falsifying its history; the term really applies to the activities of a small group of biologists. What I have been at pains to develop is the thesis that we are witnessing the fusing of many sciences, all concerned with one or another aspect of behaviour, into one coherent science, for which the only correct name is “Biology of behaviour”. Of course this fusion is not the work of one man, nor of the small group called ethologists. It is the outcome of a widespread tendency to apply a more coherent biological approach, which has expressed itself in what may well have been quite independent developments within sciences such as Psychology and Neurophysiology. Among zoologists and naturalists, it is Lorenz who has contributed most to this development, and who has more than any other single person influenced these sister disciplines in this particular way.\textsuperscript{801}

If I have understood correctly, Niko’s wide understanding of Ethology encompasses mainly two realms. On the one hand, we might interpret his special approach to behaviour by asking the four questions in a way he has outlined it in \textit{On Aims and Methods} as one essential part of the ethological study of behaviour. On the other hand, one is inclined to say, Lorenz’s very early engagement in the study of adapt- edness in Niko’s account appears to be an essential aspect of Ethology as well, whereas what he calls “Physiology of Behaviour” does not seem to be part of Ethology yet of the wider concept of “Biology of Behaviour”. As a provisional result, one may therefore say that Niko developed a special view upon the epistemic dynamic which led towards and away from the synthesis established in the 1930s. And it can be asked whether the historical account Niko gave in order to assess the transformation process of his discipline cannot be read as an expression of his late scientific orientation.\textsuperscript{802} From the epistemological point of view, Tinbergen’s “move away” from Classical Ethology consisted of a process in course of which traditional concepts (i.e. “Causation”, “Survival value”, “Ontogeny”, and “Evolution”) were \textit{re-founded} in a sense that their underlying epistemic reference systems were replaced by alternative ones. Hence, Tinbergen’s move cannot be described adequately without taking into account the more conservative levels of scientific change. However, what seems a merely “structural” effect in fact turns out to have veritable phenomenological repercussions. This phenoepistemological side of scientific and cultural change should be examined more thoroughly. What can be said so far is that scientific prose does not and cannot negotiate pure abstract reference systems. Science deals with concrete forms of hypostasis. These must be compatible with their underlying reference systems and therefore may or may not function as their phenomenological interpretation or manifestation.\textsuperscript{803} Changing a concept’s “deep-structure”, I suppose, may also have a sense effect since the equilibrium of tautological and paradox semantic relationships which establish a reference system gets into motion and as a result generates modified sense effects. For instance, the notion that something may deviate from a norm and this deviation – on a higher

\textsuperscript{801} Ibid.

\textsuperscript{802} In a sense that the Classical Synthesis originated in an act of replacing Behaviour Physiology by a Physiology of Behaviour in combination with Lorenz’s early ecological studies. The move away from this amalgam can be read as maintenance of Lorenz’s realm while the Physiology of Behaviour needed to be replaced once more with Niko’s ecological study of the Four Whys.

\textsuperscript{803} For instance, the widely discussed phenomenon of Darwin’s delay in formulating his theory of mind and behaviour might be symptom of the claim that an anticipated epistemic pattern needs to find its concrete match. The choice of so-called model organisms or typical experimental animals might be another.
level of argumentation – is supposed to confirm the norm opened the door to various new fields of research which are mostly anticipated though not elaborated in Niko’s theoretical accounts written after 1958. To these fields of inquiry belong the existence of antagonistic behavioural strategies and the experimental testing of their adaptive value, and the notion of non-deliberate choice which opened the door to game theory. The paradox conception of individual development drew attention to the effect of drop-out phenomena and the notion of experimentalization within the scope of functional study made it possible to think about testing directly selective pressures. These examples show clearly that Niko’s move did not only lead straightly towards Behavioural Ecology as is often supposed. His move must be interpreted as epistemic re-orientation which possibly entailed repercussions in various kinds of newly emerging research fields such as Neurogenetics and Neurophysiology as well. In conclusion, my readings of N. Tinbergen’s theoretical accounts written after 1959 should have demonstrated so far how the realm of his theorizing changed from a causal analytical reductive to a quantitative approximative reductive model and how the new framework was interpreted concretely so that a new set of ecological inquiries could emerge.

The last project I would like to discuss is N. Tinbergen’s joint study with M. Impekoven and D. Franck on “Spacing out”. According to H. Kruuk it was Niko’s last experiment in the field. Later he concentrated on filming and advising the projects of his students without being involved directly by himself. M. Impekoven and D. Franck were two post-docs who had come from Switzerland and Germany to join Niko’s research group. The project, however, was mostly inspired by Niko’s own previous studies and the work of his co-workers (L. de Ruiter and I. Patterson) in “connection with certain data in the literature”, as he puts it in the paper. The central hypothesis of the study is that “certain predators exert a pressure on individuals even of well-camouflaged prey species to live well spaced-out”. Animals protect themselves from being preyed by disturbing the visual orientation of the predator through camouflage colours. These morphological characters are mostly accompanied by corresponding behaviours (such as freezing). Niko and his co-workers believed that spacing-out is one of the behavioural correlates of camouflage in a sense that their survival value increases the more loosely the aggregation they live in is organized. Moreover, if I have understood correctly, Tinbergen and his co-workers established a correlation between the interindividual distances, on the one hand, and the predator’s visual capacities and their foraging range, on the other: The more the distance from animal to animal exceeds the “distance from which predators usually detect them directly”, the more protected is each single

804 From this perspective the life-history of those Tinbergians whose path did not lead into Behaviour Ecology, such as D. Blest’s, deserve more of us science historians’ attention.
807 For D. Franck’s life and research see Franck, Eine Wissenschaft im Aufbruch, 52–55. M. Impekoven’s life path seemed to drift somewhat away from academia. Her life-history still needs to be clarified.
809 Ibid.
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individual. From these short remarks we can already infer why “spacing-out” fitted in Niko’s ecological research agenda: Behaviour researchers used to treat animal aggregations (including their social structure and / or modes of communication) as if they guaranteed per se the adaptedness of the group by providing a more of fitness, for instance, through common defensive strategies. Niko and his co-workers inverted this perspective by pointing out the paradox that interindividual isolation might be of advantage as well. Furthermore, the topic reveals rather impressively that “spacing-out” might include a compromise between conflicting behavioural strategies, namely the advantages provided by a social group and the advantage of the protective effect entailed by interindividual isolation. The fact that spacing-out strategies prevail despite their partly negative side effects reveals that the advantages must outweigh the disadvantages – a matter of fact which in turn can be interpreted as a confirmation or even a measure for the normal selective pressure which is exerted by the predators. Without naming it directly the study thus anticipates one of the characteristic topics of Behavioural Ecology namely the conflict between altruistic and egoistic strategies of behaviour. The setting of the tests was quite simple. Wild Carrion Crows (Corvus corone L.) were used as predators – painted camouflaged Hens’ eggs as prey objects. The question was whether predators once they had found a camouflaged object were more successful in preying similar objects when the population of these items is more densely organized rather than at lower densities. In order to answer this question N. Tinbergen and his co-workers tested the responsiveness of the Crows in several “egg fields” of varying density. Thereby one egg functioned as “sample egg” which was meant to attract the predator. One advantage of the chosen experimental animal was that the Crows’ motivation to forage did not wane after having eaten their fill since all further eggs were taken away and buried. When recording the predators’ response Niko and his co-workers distinguished between the number of taken eggs, the time interval between abandoning one egg and finding the next, the period of time the Crows continued searching the place after the last egg was found and, finally, the total time spent at each plot. The “Results” presented in the paper are arranged in accordance with these four categories.

In general, they substantiated Niko’s initial hypothesis that crowding is penalized: In scattered egg fields relatively less eggs were taken, the searching time per egg increased which, conversely, means that the reward rate per time for crowded eggs is higher than for scattered eggs. Further, Crows spent more time in a scattered field before they finally gave up which Niko interpreted as an indicator for that lower rates of found eggs cannot be explained with a loss of motivation. Lastly, the total time spent at each plot was higher when the inter-egg distance was higher. The lower mortality rates in case of scattered prey objects thus cannot be the result of a lower effort. Despite the fact that the results of the experiments supported Niko’s initial presumptions his “Discussion” of the

810 Ibid.
811 If the disadvantages taken into account could be measured this quantity could be interpreted as a measure of the selective pressure. The ambiguity of the phrase “spacing-out” expresses this connection because it can be read both as transitive and intransitive verb.
812 For the methodology see ibid., 309–313.
813 See ibid., 313–316.
results and their implication is characterized by cautiousness.\textsuperscript{814} It is therefore of some interest that the epistemic practice of “discussing results” now, in contrast to earlier applications, tended to involve more questioning. One of Niko’s questions thereby was whether penalizing crowding actually was the decisive predator pressure for “spacing-out” and whether or not different forms of camouflage and camouflage behaviour might compensate each other. If we take together what information is provided in each section and how this is done we might be well entitled to say that Niko’s paper on “Spacing-out” is organized in the expected way. Moreover, the emphasis on survival value which is guiding the experiments reveals the compatibility of the paper with the neo-Darwinian framework not only because of its causal architecture and the typical distribution of paradox and tautological conceptual relations but also, more directly, because of picking up what I have called the paradox of the concept of adaptedness. That the paper was triggered mostly by Niko’s own previous studies seems to support my hypothesis that Tinbergen Theory became a more self-enclosed undertaking during the 1960s. However, especially in the discussion part we can find a tendency to open the horizon of further leading research questions. This is also the place where Niko’s paper refers to some works of his pupils (I. Patterson, H. Kruuk, R. A. Hinde). If I was to evaluate the paper from a science historian’s perspective I’d intuitively say it is on the verge to something new. Niko has taken into account that selective pressures might interact with each other in a more complex manner but does not develop a tool to determine them. This task remained to be fulfilled by more advanced ecological methods.\textsuperscript{(R\textsubscript{1,2})} So far my line of argument encompasses three steps. I have examined the forms of criticism which developed in N. Tinbergen’s research group in course of the 1950s and how the works of his pupils challenged his classical ethological convictions. In a second step, I examined his “re-boundarying” to exemplify the technique with which he responded to these challenges up to the year 1959. After that, I made an attempt to trace N. Tinbergen’s “turn to Functional Ethology” and show how he institutionalized the new scientific paradigm within his scientific community by translating his four main areas of research (causation, adaptiveness, ontogeny and evolution) into the new framework. In the following I’d like to return once more to the realm Tinbergen had reserved for the empirical work and the education of his PhD students. My central question thereby is how the later generation of PhD students who joined Niko’s Animal Behaviour Research Group (ABRG) since the end of the 1950s and therefore received its academic education already \textit{within} the new scientific paradigm responded to this new outline of behaviour study.\textsuperscript{815} In first approximation to the question we seem to be confronted with a

\textsuperscript{814} See Tinbergen et al., “An Experiment on Spacing-Out”, 316–317.

\textsuperscript{815} G. Beale concedes a continuity between earlier and later Tinbergians and across the lab-field divide in the commitment to study natural (i.e. innate) behaviour (Beale, “Tinbergen Practice, Themes and Variations”, 199–200, 257). Moreover, he underlines the existence of a general “methodological pluralism over the course of the school” (Ibid., 201–202). However, he also traces a trend to more “specificity of study” (Ibid., 200, 257) and a trend away from purely observational studies, “in favour of much more interventionist and experimental studies” which, if I have understood correctly, especially applies to the lab studies (Ibid., 200–201, 257–258). The field works, in his view, also reveal a tendency to offer adaptional explanations of behaviour. See \textit{ibid.}, 256–257.

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paradox. N. Tinbergen had interpreted the heterogeneous constitution of Classical Ethology so that theory (“TTh” in Fig. 2.6) and practice (“TPr” in Fig. 2.6) could mutually inspire each other. The output of one realm could possibly function as the input of the other and vice versa. This structural setting might be one of the reasons for the intense formal and informal mutual reception which had characterized both Niko’s theoretical accounts and the works of his doctorate students during the 1950s. However, as soon as Niko had adopted the position which had become more and more popular in his research group (“Representation of non-knowledge” in Fig. 2.6) the cooperative framework somewhat broke up – as I believe – for epistemological reasons. At least the interaction between “Tinbergian Theory” and “Tinbergian Practice” obtained another quality which still remains to be examined more carefully. This is at least my first impression after I have examined Niko’s late theoretical statements. On the one hand, we can infer from Niko’s egg shell removal project that he eventually changed slightly his strategy of recruiting young zoologists by integrating younger students on pre-doctorate level in his own ecological research endeavour. H. Kruuk is one of these students who began to work with Niko as undergraduate and then continued with a PhD project. On the other hand, as a result and in return, Niko’s student projects seemed to get their own dynamics in several respects: There was eventually a stronger trend to more collective and informal supervision which was supported by M. Cullen and the role he played within the research group. In addition to that, student projects began to stimulate student projects. While the initial act of “suggesting” a topic for a project in the 1950s seemed to be related more closely to Niko’s own writings, for instance by providing a limited number of experimental animals from which a PhD candidate could choose one, the starting point of the later projects very often was a thesis written by a member of the previous cohort. And this sophisticated strategy of scientific socialization applied both to graduate and undergraduate students. “Nico carried the principle of the Oxford tutorial to a quirky extreme”, R. Dawkins writes in his autobiographical recollections,

Where other tutors gave out a reading list that covered the topic, Niko would hand me nothing more than an unpublished doctoral thesis by one of his graduate students. I was to write an essay around the thesis, criticize it, go into the library to sleuth down its bibliography, and plan future research to carry it further. In effect, my undergraduate task was to play at being a doctoral examiner for a week, and then again the following week with a different thesis.

Another more advanced form of this scheme to “carry” something “further” from the known to the unknown was to entrust someone with a topic who had already

816 My view is corroborated by H. Kruuk’s observations. According to his opinion, N. Tinbergen ran out of ideas in course of the 1960s. See Kruuk, *Niko’s Nature*, 224–225, 232, 244, 247.


818 That early Tinbergian Practice of thesis supervision consisted of “giving” pupils both the material and the idea can be inferred from a letter Tinbergen wrote to J. Huxley. See WRC-RU Fondr. Lib., MS 50, box 26, file 5, letter N. Tinbergen to J. Huxley (14/07/1958). Eventually Niko has been criticized for this practice. One argument seemed to be that he himself was loosing contact to personal research while working together with his students. For Niko’s intention to provide his PhDs with an intensive training in the field see also *Ibid.*, box 21, file 1, letter N. Tinbergen to J. Huxley (18/02/1953).

819 Dawkins, “Growing Up in Ethology”, 194. Similarly Stamp Dawkins, “King Solomon’s Herring
participated in Niko’s own egg shell removal project as research assistant (e.g. H. Kruuk’s project). The more common scheme in the early 1960s, however, must have been the thesis-by-thesis socialization which eventually more and more created a self-enclosed cosmos of peer-to-peer tutoring. H. Kruuk writes, for instance, None of this detracted from the lively science scene in the group, which revolved around Mike but was established by Niko. There was still a lot happening, but then gradually, in the second half of the 1960s, things began to peter out somewhat. Just as in the study areas in Ravenglass and Walney, Niko’s fund of ideas began to run out: his preoccupation with filming took him somewhat away from science, and he was plagued by health problems. Several years later, around 1969 when Niko was 60 years old, Oxford ethology really went through the doldrums, as Niko himself remarked. He was aware that there was a lack of guiding spirit. It showed in the nature of student projects, which had little of the originality that marked his earlier studies: they tended to expand on previous ones.

Maybe, Kruuk’s account follows here to much the epistemic scheme of his own scientific preoccupations but the statement, nonetheless, reveals that the realm I termed “Tinberian Practice” including the inner sociology of the work group and the interaction between the members of the group and N. Tinbergen changed in course of the 1960s. To answer this question would require a more extensive research project. In comparison to that, the question I’d like to answer in the following is of limited nature. How did Niko’s second generation of pupils respond to the new functional framework? To answer this question the same methodological questions can be applied as in my examination of the previous cohort: What is the epistemic outline of the dissertation thesis? Are there any fields of sidelined knowledge and, if so, how are these fields related to the later life-course of a student in question? What can the cross-references tell us about the mutual interaction between advisor and student or within the peer group?

According to N. Tinbergen’s own words, nearing the end of his academic career in 1968, he had produced 35 “doctors” so far in his life. Of these 35 projects two have been carried out while Niko was still professor in Leiden (G. P. Baerends and J. v. Iersel) and ca. eleven belong to the first cohort. Pending on how Niko

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820 *Gull’s World*, 170.

In this context, it is important that Niko’s pupils established a “slave system”, that is, PhD students were assisted by undergraduates or unpaid volunteers while carrying out their research. What might sound like a play with social hierarchies in fact had eventually an important function in the process of academic socialization since the youngsters from time to time developed their own research interests while assisting their elders. For some brief remarks concerning this system of “slaves” see Dawkins, “Growing Up in Ethology”, 199 and J. Delius in his interview with the Hessian Broadcasting Cooperation, K.-H. Wellmann. *Wissenswert – Niko Tinbergen: Ein Leben für die Verhaltensforschung. Gespräch mit Juan D. Delius*. Hessischer Rundfunk, Hörfunk-Bildungsprogramm, Sendung vom 13.04.2007, Manuskript 07 – 025. Frankfurt a. Main: Hessischer Rundfunk, 2007, 6–7. According to Delius the “slaves” had also a function during the observation process: The observer could only enter his observation tent without irritating the Gulls too much by deceiving the animals. Two students approached the tent, one of them stayed and took his position, while the other left again. According to Delius, the Gulls did not recognize whether one or two persons left so that they immediately calmed down and the observation of their “normal” behaviour could begin.

821 Kruuk, *Niko’s Nature*, 244.

822 Ibid., 242.

823 See table A.1, page 694 of my dissertation thesis. These eleven people do not include the post-
calculated the amount of his “doctors”, his second generation of PhD students must encompass around 22 projects plus the ones he supervised between 1968, the date of his statement, and his retirement in 1974. The list I was able to compile includes 23 names and projects.\footnote{I have listed the members of N. Tinbergen’s second generation of pupils in table A.2 of my thesis.} This means that the list might be almost yet not fully complete. Moreover, it does not include those members of the ABRG who received their PhDs under J. M. Cullen’s supervision such as J. Krebs, L. Partridge, F. Huntingford, K. Wilz and J. N. M. Smith. In case of S. Neill I am not certain but the topic of his thesis, “camouflage and shoaling in fish”, seems to be closer to Cullen’s than to Tinbegen’s interest. T. R. Halliday was initially accepted as a student by Niko but then it was decided that it would be better if M. Cullen took over supervision. As a result I have not included him in my sample. At a first glance the contents of the table show a number of details which are worthwhile to be mentioned.

First of all, there is both continuity and discontinuity as to the experimental animals. On the one side, students of Niko’s still focused primarily on birds (mostly Gulls) and insects. Nearing the end of his academic career, however, Niko also advised projects related to mammals, viz. the Tree-shrew (R. D. Martin’s study), the African Elephant (I. Douglas-Hamilton’s project) and the Orang-Utan (J. R. Mackinnon’s thesis). Most interestingly, two of these three theses, in contrast to all other theses submitted before, explicitly bear the word “ecology” in the title. In some cases theses even have the character of a follow-up study or, at least, they refer back to a previous study via the choice of a characteristic scientific object. Thus Dick Brown’s and Stella Crossley’s theses picked up M. Bastock’s interest in courtship behaviour of Drosophila. N. Blurton-Jones worked with Great Tits as did R. A. Hinde in the early 1950s and H. McLannahan’s experimental animal was the Kittiwake – the species that had initiated E. Cullen’s pioneering results. M. H. Robinson’s and H. Croze’s projects stand in the tradition of L. de Ruiter’s study via the topic “camouflage” and “anti-predator behaviour”. On the other side, the choice of experimental animals in the 1960s also marks a break with the research of the previous decade. For instance, there is hardly any dissertation project on Stickleback behaviour, in particular, or Fish, in general. R. N. Liley’s project at the beginning of the 1960s as well as Mike Cullen’s post-doctoral research on schooling in Pilchards and Esther Cullen’s transient engagement with Sticklebacks therefore seem to be research interests running against the common trend.

Second, one of the unifying characteristics of many first generation projects had been the emphasis on reproductive behaviour. This can be interpreted as a result of the fact that Niko approached the question of adaptedness primarily through the lens of “animal display” (especially in courtship behaviour). His interest in reproductive behaviours seems to have perpetuated in the 1960s (see. C. Beer’s, I. Patterson’s, B. Nelson’s, S. Crossley’s and R. G. B. Brown’s projects) but it was complemented by a variety of additional topics which were related to other adapted behaviours such as defence and camouflage (G. Manley’s, H. Kruuk’s, N. Blurton-Jones’, M. H. Robinson’s, and H. Croze’s thesis), housebuilding (M. H. Hansell’s...
work), various aspects of feeding (M. Stamp Dawkins’), M. Norton-Griffiths’ and L. Shaffer’s projects), and social behaviour (J. Galusha’s study). N. Burton-Jones (motivation), R. D. Martin (taxonomy), H. McLannahan (ontogeny), R. Dawkins (ontogeny) and eventually also L. Shaffer (ontogeny ?) seem to have had in mind Niko’s four “Why’s” while formulating the titles of their theses or of the publications related to them.

Third, already a brief superficial glance at the life-histories of each single researcher reveals that the topic of the respective dissertation projects – with some exceptions such as R. Dawkins (who skipped the chicks) or Dick Brown (who dropped the flies) – often laid the foundation for a life-long interest which resulted in further supplementary studies or pervaded into related research fields (especially St. Crossley, M. H. Hansell, M. H. Robinson, M. Stamp Dawkins, and I. Douglas-Hamilton). This means that Niko’s second generation of PhD students – again with some exceptions – eventually tended to continue the research interests that has been founded in their PhDs.

Fourth, within the group of Niko’s second generation of PhD students there is a preponderance of men. Only three women (out of the twenty-three pupils I was able to track), viz. St. Crossley, H. McLannahan and M. Dawkins, received doctorate degrees under Niko in the 1960s and early 1970s, but, in contrast to the female doctors of the previous cohort, most of them made career within academia: Marian Dawkins later succeeded on Niko’s chair at Oxford University, St. Crossley obtained positions as lecturer and later professor of Psychology at Monash University (Australia), and H. McLannahan covered several lecturer and senior lecturer positions, for instance, in Health Studies at the Open University (Oxford, UK).

Fifth, corresponding to the widening of the research foci Niko’s pupils published the results of their theses in several publication organs other than *Behaviour*, which has been Niko’s “domestic” journal for several years. If I have counted correctly only ca. 29% (6 of 21) of the studies published in the 1960s and early 1970s appeared in *Behaviour* compared to ca. 71% (5 of 7) in the previous cohort. Moreover, my impression is that the scheme to publish the study as a whole or at least an abridged version of it (often as supplement issue of *Behaviour*) was replaced by the habit to publish the results in form of one, two or more brief journal articles. This matter of fact can eventually be interpreted as an adjustment to the publishing habits commonly accepted in the natural sciences but it might also be seen as an expression of the less holistic research attitude advocated by some of Niko’s later students. Insofar the publishing habits might be a scientific practice guided by epistemic dispositions as well.

Finally, according to H. Kruuk, Niko had obtained a larger funding from the British

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826 In order to guarantee comparability, in the first cohort of Oxford PhD students, I have not taken into account the (most likely) unpublished theses (R. Weidmann, Ph. Guiton, M. F. Hall), papers resulting from post-doc projects (E. Cullen, U. Weidmann) and from projects formally supervised by others (R. A. Hinde, L. de Ruiter). As to the second cohort, I interpreted “unpublished” strictly as “publication or related publication not traceable” so that I calculated with 21 published theses in the second and 7 in the first cohort.

827 R. Liley’s and H. Kruuk’s study on “Reproductive Isolation in some Sympatric Species of Fishes” and “Predators and Anti-predator behaviour of the Black-headed Gull” seem to be an obvious exception to this rule.
Nature Conservancy at the beginning of the 1960s “through the help of the very eminent Max Nicholson”, as he puts it, and therefore found himself in the comfortable position of being capable to cover the expenses of all fieldwork, the salaries of M. Cullen, a secretary, a Land-Rover, and various other expenses. The financial support started in the early 1960s and lasted until Niko’s retirement in 1974. An additional grant provided by the US Air-Force increased his financial possibilities and sparked off an additional more electro-physiological project with Gulls. On the basis of this knowledge, any exceptions of this common funding structure would eventually be significant.

On basis of this introductory information I have picked five dissertation projects which I have examined more carefully. Thus I chose C. Beer’s project on “Incubation and Nest-Building in the Black-headed Gull” because he was one of the first who represented a younger generation of students in Niko’s group. Moreover, C. Beer’s Gull study and especially his latent doubts in the Black-headed Gull’s capacity of visual discrimination had a certain initiating effect on Niko’s egg shell removal study. H. Kruuk’s thesis on “Predators and Anti-Predator Behaviour of the Black-Headed Gull” is of interest because he was “socialized” already within Niko’s ABRG but was concerned with the same scientific object as Beer was, namely the Gulls. His work thus may be examined as a later approach to the Black-headed Gull, so to say, as a comparison. In J. Delius’ project on Skylark behaviour I was interested because his life course eventually took another path which was partly leading away from Functional Ethology. Finally, I chose J. R. Mackinnon’s thesis with the title “The Behaviour and Ecology of the Orang-Utan” because he carried out his project late in Niko’s career and it is one of the theses bearing explicitly the term “Ecology” in the title.

The result of my sample study can be summarized as follows. At first, the scientific practice N. Tinbergen applied while initiating a PhD project remained more or less the same. That is to say, students were encouraged to extend the results of a previous study after they had received it critically in the first place. In other words, the epistemic realm within which Niko placed the act of educating PhD students remained more or less unaltered. However, all examined theses show that the final result of this process, the theses themselves, followed the new ecological scheme Niko had outlined in On Aims and Methods. Second, a careful reading of the follow-up publications that were based upon the dissertation projects – my primary focus

828 See Kruuk, Niko’s Nature, 243.
829 For the research grants Tinbergen was able to raise in the early 1960s see WRC-RU Fondr. Lib., MS 50, box 31, file 1, letter N. Tinbergen to J. Huxley (27/01/1961).
830 The project was carried out by two former PhD students, Dick Brown (who had switched from Drosophila to Gulls for his post-doc) and Juan Delius, and began in 1961. After four years the project was terminated due to its lack of feasibility. In contrast to E. v. Holst who had obtained valuable results in domestic chicks by applying the method of brain stimulation, Gulls simply turned out to be an inadequate scientific object for the project. Moreover, some of the results simply contradicted Niko’s view of the nervous system. See Kruuk, Niko’s Nature, 243–244. Whether the failed brain stimulation project encouraged N. Tinbergen to set his primary focus upon Behavioural Ecology should be examined more carefully.
831 If my information is correct C. Beer was born in 1933. In comparison to that many members of the first cohort were born almost a decade earlier, such as R. A. Hinde (born in 1923), E. Cullen (born in 1924), U. Weidmann (born in 1925) and M. Bastock (born in 1925).
like in my case study of the earlier cohort – shows that Niko’s students perpetuated the structural characteristics which had been leading to the establishment of both the neo-Darwinian and the Ethological Synthesis, namely the reversed causal architecture and the re-evaluation of theorems within the reference systems. The continuation of these characteristics guaranteed the institutionalization of the new functional orientation which therefore was able to grow to a veritable conceptual alternative in comparison to older behaviourist and neo-Lamarckian scientific orientations. The question which function the PhD theses had within the life courses of each of Niko’s pupils must be answered in a more differentiated way.

C. Beer’s study was concerned with the behaviours of the Black-headed Gull’s reproductive cycle and their motivational causes. The results were published in five separate journal articles in Behaviour between 1961 and 1965. I think the general tenor of C. Beer’s dissertation thesis was to proof the effectiveness of a “wider” uniform motivational factor including the endocrine system which is guiding more than one behaviour of the reproductive cycle. This implied the idea that the tendency for the behaviours which can be observed in the later stages of the breeding cycle grow gradually and that therefore the readiness to perform the action pattern in question is directly proportional to the time span between the measure point and the point of time this behaviour is revealed. The closer the distance the higher the readiness, the wider the more wanes the tendency. In his thesis, Beer implicitly proposed this factor in a first step and intended to make this factor evident approximatively (in the sense of a mathematical limes construction) in a second. In order to obtain this objective he applied a certain kind analysis which proceeded in reverse chronological order. That is to say he began with the high point of the Black-headed Gull’s breeding cycle, the incubation (paper I), and then moved backwards in time by treating the laying period (paper II) and the pre-laying period (paper III), each time “measuring out” in how far the source of motivation ruling the ultimate behaviour can be made evident statistically in each previous stage of the breeding cycle. Altogether the composition of the thesis as a whole and its central idea, a motivation system which is not organized in discrete centres, therefore can be interpreted as a manifestation of the new functional orientation. However, the turn


834 In proposing a gradualist perspective, C. Beer contradicted R. Weidmann’s results. See Beer, “Incubation and Nest Building Behaviour III.”, 64.

835 To put in H. Spencer’s words, C. Beer approached the “unknown”.

836 The fourth paper apparently does not continue the reverse time-line but the internal account of the paper continues the notion of reverse chronological order by comparing “Nest-Building” in the “Incubation Period” with its correspondent in the earlier stage, the “Laying Period”. The fifth paper of the series has a meta-status in some ways. At first, it was published after a gap of
to functional Ethology in case of C. Beer’s intellectual life-history did not lead to a
behavioural ecological standpoint in a narrow sense but opened the door to a new
line of questioning: The effect of hormones and the endocrine system in general.\textsuperscript{837}
In this context, we may also place the further leading questions Beer postponed in
his thesis, namely the proximate causes of the so-called brood-patches.\textsuperscript{838} Brood-
patches are featherless places on the underside (i.e. the ventral side) of the birds’
torso which, though eventually disadvantageous for the parent bird, have the func-
tion to transmit more body heat to the eggs of the clutch. Beer is inclined to argue
that the Gulls loose their feathers even before the laying of the egg and this would
mean that the loss of feathers had no mechanical but hormonal reasons. In pointing
to the potential fruitfulness of this topic C. Beer therefore also expresses his in-
cipient interest in endocrinological research which most likely was also one of the
reasons why he felt attracted to D. S. Lehrman’s institute at Rutgers University. Af-
ter completion his thesis on “Incubation and Nest-Building of Gulls” he returned to
New Zealand for a few years where he had already obtained his BA and MA degree.
In 1968 he came back to Oxford after having been appointed lecturer in N. Tinber-
gen’s research group but soon moved on to Rutgers University in Newark (United
States) where he intended to work with D. S. Lehrman.\textsuperscript{839} However, Lehrman died
relatively soon after in 1972 and Beer was the one to succeed him as professor. Ac-
cording to H. Kruuk, Beer continued Niko’s research tradition and retained both his
interest in fieldwork and the affiliation to the scientific object of his PhD, the Gulls.
However, in contrast to Tinbergen, Beer was also a more philosophical mind “be-
coming decreasingly obsessed with quantification”\textsuperscript{840}. Moreover, in some ways
alike to M. Stamp Dawkins, he became strongly involved with Cognitive Ethology
whereby “animal intentionality” turned out as his primary focus of research. Beer’s
later research therefore in some way seemed to get closer to the origins of Etho-
logy than his dissertation thesis would let us suspect since his PhD thesis still more
adhered to the trend away from the roots. One of the indicators for this general
tenor, especially in the publications of the years 1961 and 1962, was Beer’s doubts
whether the Gulls were furnished with the capacity of visual discrimination early
ethologists had ascribed to this species of animals. If I have read correctly, there is
a trend in Beer’s Gull papers to take into account more the non-visual, in particular,
tactile forms of sensation.\textsuperscript{841} In proofing that C. Beer eventually rejected discrimi-
nation experiments unjustified Niko played back the ball in his egg shell removal

\textsuperscript{837} For Beer’s attempts to take into account the effects of the hormone system see, for instance, Beer,
“Incubation and Nest Building Behaviour IV.”, 171, and Beer, “Incubation and Nest Building
\textsuperscript{838} See for instance, Beer, “Incubation and Nest Building Behaviour II.”, 295, Beer, “Incubation and
\textsuperscript{839} For the details of his appointment at the University of Oxford see also Dawkins, “Growing Up
in Ethology”, 203.
\textsuperscript{840} H. Kruuk here quotes literally from an interview with C. Beer of the year 2000. See Kruuk,
\textsuperscript{841} See Beer, “Incubation and Nest Building Behaviour I.”, 85–86, also 87.
study by revealing that the youngsters might be endangered by the same fallacy they had criticized in the works of their teacher generation – namely the unjustified obedience to a particular epistemic framework.

J. Delius’ life-history is one of those which cannot be done justice in a few paragraphs. The undertaking turns out to be the more difficult since hardly any biographical information is available. 842 What I do know is that Delius was born in Essen (Germany) in the year 1936 and therefore belongs to the later cohort of Niko’s pupils who were born between 1933 and ca. 1945. He grew up in Argentina yet studied Biology in Germany at the Universities of Freiburg and Göttingen before he moved to Oxford. 843 There he became Niko’s PhD student. His project was concerned with the reproductive cycle in Skylarks. He submitted his thesis in 1961. The main results were published later in 1963 in the German journal Zeitschrift für Tierpsychologie (ZfT) under the title “Das Verhalten der Feldlerche” (The Behaviour of the Skylark). 844 That the study is dedicated to the German ornithologist G. Kramer is a sign that Delius must have known him. 845 Whether Kramer’s tragic death in 1959 was one of the reasons why Delius came to Oxford to join N. Tinbergen’s ABRG is something I can only speculate about. The coincidence of the dates seems to suggest that both events might be connected with each other. Other facts contradict this hypothesis clearly: Thus we can infer from Delius’ account that ringing and observation of the birds already had begun in summer 1958 at the latest, that is, before Kramer’s accident. 846 A matter of fact is that J. Delius already knew N. Tinbergen since they had met in 1957 during a conference in Freiburg. 847 Delius, as a student, had to assist N. Tinbergen by putting the colour slides for his presentation into the slide projector and after the lecture Niko told Delius that he was in search of “slaves”, that is, unpaid assistants for his PhD students. From this little anecdote we can infer that Delius was integrated in Niko’s research group already before he started his own PhD project. Delius’ thesis was actually supervised by N. Tinbergen yet it was not submitted at Oxford University but at


843 The date of J. Delius’ move is not entirely clear. In the cv attached to the original of his dissertation thesis it reads: “In den letzten 3 Jahren hielt ich mich 18 Monate in England an der University of Oxford auf, wo unter Leitung von Dr. N. Tinbergen die vorliegende Arbeit entstand” [In the last three years I spent 18 months in England at the University of Oxford where under Dr. N. Tinbergen’s supervision this thesis took shape[transl. CL]. The thesis is dated to the year 1961 so that I guessed that J. Delius had taken up his work at Oxford in 1958 at the latest. J. D. Delius. “Das Verhalten der Feldlerche”. In: Zeitschrift für Tierpsychologie 20.3 (1963), 297–348.

844 For the dedication see ibid., 297. On G. Kramer’s biography see the following section of my thesis.

845 Ibid., 299.

846 In an interview with the Hessian Broadcasting Corporation J. Delius tells how he first met N. Tinbergen. See Wellmann, Wissenswert. 6. The International Ethological Conference of the year 1957 was held in Freiburg so that I presume the mentioned “congress” eventually was the International Ethological Conference.

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the University of Göttingen. After earning his PhD, J. Delius stayed in Oxford as Senior Research Assistant and, together with R. G. B. Brown, was involved in a project on brain stimulation in Gulls which had been funded by the U.S. Air Force Office of Scientific Research but – as I have mentioned above – did not yield the desired results and suffered from the fact that the initially intended personal cooperation between R. G. B. Brown (who was supposed to deliver the field data) and J. Delius (who was to examine the Gulls in the lab) apparently did not work out either. G. Beale interpreted these experiments as a sort of anticlimax to the non-experimentalist ethos of the early Tinbergians and the “idea that ethologists don’t cut up the animals they studied”. The crucial point, I think, is another: J. Delius experiments with brain stimulation in Gulls had its precursor already in the classical period of Ethology namely in E. v. Holst’s and U. v. Saint Paul’s brain stimulation studies with domestic chicks. These studies were “functional” as well in a sense that Holst was interested in what he called “Wirkungsgefüge der Triebe” (effective system of drives). Moreover, Holst was keen to compare the results he obtained in the laboratory with behavioural observations that had been made with chicks living under normal circumstances. However, the setting of both stimulation projects differed in their presupposed epistemic reference system. While Holst’s experiments intended to make behave domestic chicks just as if they were acting under natural circumstances and thus demonstrated that the boundary between technology and the living organism could be transgressed, the experimental setting at Oxford placed a completely wild animal into an artificial or semi-artificial environment and, beyond that, apparently intended to demonstrate the ongoing effectiveness of a functional system of locatable action patterns. Maybe it is false to presume Niko’s initial impulse to begin the brain stimulation project as an attempt to confirm his classical views. The date of the beginning of the experiments in 1961 and the choice of the experimental animal (Herring and Lesser Black-headed Gulls) eventually suggest that he intended to raise another research area within the new functional paradigm besides and in close connection with the more ecological emphasis he had laid with his egg shell removal project. In other words, J. Delius’ brain stimulation project eventually does not mark the breaking point G. Beale has read into it – at least from the structural point of view. The comparison of C. Beer’s and J. Delius’ intellectual life-history seems to suggest that a “turn” actually did occur in their lives but that it was more connected with a later integration of cognitive ethological aspects and, maybe, also with a reinterpretation of the classical ethological framework. And my question would more be how the partly failed stim-

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851 He obtained this data mostly from the Upper Bavarian amateur scientist E. Baeumer.
ulation experiments contributed to this move. Delius left Oxford in 1967. From then on the traces of his life-history become somewhat hazy. He taught Animal Behaviour as a Lecturer at the University of Durham (1967–1974) and as Professor at the University of Bochum in Germany (1974–1987). He has been Visiting Professor at the Universities of California, Mexico, Buenos Aires and Barcelona. Finally, Delius was appointed Professor of Experimental Psychology at the University of Konstanz in the southern part of Germany – a position he covered till his retirement in or around the year 2004. After his PhD, J. Delius continued publishing on various aspects of the behaviour of Skylarks for another few years but, beginning with the brain stimulation project, his research interests seemed to move away from his original scientific object into more neuroethological inquiries. In addition to that, he became involved in at least two further areas of research, namely the processes of cultural evolution and the “biopsychological foundations of cognitive processes in animal and man”. This rough overview of J. Delius’ life course may already suffice to see that his engagement with Skylarks was a transitional period which was to be supplemented or even replaced by further themes. The turn to cultural evolution (paralleled in R. Dawkins’ shifting interests) as well as the incorporation of cognitive aspects into Ethology (paralleled in C. Beer’s and M. Stamp Dawkins’ biography) suggest that J. Delius eventually belonged to the group of Niko’s pupils who were socialized within the paradigm of Functional Ethology but then moved away from this scientific orientation. One of the driving factors of this move most likely was a deep-rooted latent interest in the processes of human and animal cognition which, in Delius’ case, for instance became manifest in his interest in spatial learning. In reading the works related to J. Delius’ PhD project I should ask therefore when this incipient new tendency came into prominence and in which concrete forms it became manifest.

J. Delius’ dissertation thesis examined the reproductive cycle in Skylarks. He submitted his thesis in 1961 at the University of Göttingen yet the project itself was...

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852 The Gulls did not behave “naturally” despite the fact that they were treated in an artificial environment – they behaved “artificially”, at least in different ways than expected. And the question is why this is possible at all.

853 G. Beale has put emphasis upon Delius’ “vivisectionist turn”, as he put it. See Beale, “Tinbergen Practice, Themes and Variations”, 192–199.

854 See for a short notice Pawlik et al., The International Handbook of Psychology, xvii. For a summary of J. Delius’ view upon cultural evolution see J. D. Delius. “The Nature of Culture”. In: M. Dawkins et al., eds. The Tinbergen Legacy. London et al.: Chapman and Hall, 1991, 75–99. The epistemic reference system within which Delius placed his theory of cultural evolution should be examined more carefully and be compared with R. Dawkins’. Only a few remarks: Cultural evolution and its replicators, the so-called “memes” (originally R. Dawkins), are treated from a naturalistic point of view: “The nature of culture”. Genetic and cultural evolution are thought as widely independent reproductive systems. Within this framework the activity of cultural replicators causes heuristic paradoxa: As memes are thought to have a physical correlate in the brain genes must (at least indirectly) shape their existence. Conversely, memes are capable to channel genic evolution. Alike to K. Lorenz’s and also N. Tinbergen’s view cultural and biological evolution bear a fundamental asymmetry in as much as cultural evolution runs at a faster pace. This aspect is interpreted as potential danger to the human condition and according to the authors requires acts of deliberate correction. J. Delius approaches cultural evolution through the lens of various kinds of symbiotic systems, preferably antagonistic, that is, parasitical ones. This leads to the notion of a more or less mechanical and dualistic view on parasite-host interaction.
Niko Tinbergen (1907–1988) carried out in Oxford. The main results were published later in 1963 in the German journal *Zeitschrift für Tierpsychologie* (ZfT) under the title “Das Verhalten der Feldlerche” (The Behaviour of the Skylark). As to the organization of the paper, one may eventually say, the account of the reproductive cycle in the Skylark resembles much E. Cullen’s thesis but does not quote it. The project was completely based on field work, that is, the data it provides has been raised primarily by the method of observation. In case J. Delius’ observations included his direct intervention, for instance in case of egg rolling experiments, we find a typical trait of ethological studies: The intervention causes a dysfunctional behaviour and this matter of fact is made productive from a heuristic point of view. Classical ethologists such as K. Lorenz often saw their hypothesis that instincts were at work confirmed when animals performed the action pattern in question without adequate stimulation, out of context or other dysfunctional manners. Delius’ treatment of the skylarks’ habit to move back eggs – like geese they complete the movement even without an egg – confirm the causal architecture which is typical for ethological reasoning. Another example is that Skylarks breed wooden dummy eggs. Some of the results obtained during his study of Skylarks are not included in “Das Verhalten der Feldlerche”: The presented results are described as “Teilergebnis” (first results, part-result) and the reader’s attention is directed towards two further papers which are said to be in press or in preparation. These papers are related to the “Populationsdynamik” (population dynamics), on the one hand, and the non-reproductive behaviour (“das nichtreproduktive Verhalten”) of the Skylarks, on the other. If we have a look at the papers J. Delius published on Skylark behaviour in the aftermath of his PhD we find both a paper with the title “A Population Study of Skylarks” and at least one further article being concerned with other than reproductive behaviours. For my argumentative purpose it would be of great interest to describe precisely how these two supplementary studies are related to each other (if so) and to the primary text. Both of them are sidelined in relation to the main study yet nonetheless Delius saw all three publications as a series. “A Population Study of Skylarks” thereby allows more than one structural interpretations. One of them is to read it as the attempt to determine the positive and negative determinants of reproductive success. Thereby the account of the breeding cycle appears to be inverted in a sense that J. Delius implicitly asks for the proportion of all offspring which finally reaches a state to reproduce itself. A reading like that would presume a more reductive organization in the core parts of the paper. A *Stochastic Analysis of the Maintenance Behaviour* describes itself as one paper in a “series dealing with the behaviour and

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855 Delius, “Das Verhalten der Feldlerche [1963]”.
856 Delius says he has altogether spent fifteen months in the field. See ibid., 297.
857 On these tests see ibid., 327.
858 See ibid., 330.
859 See ibid., 297.
862 I think it significant that in the main paper the notion of territorialization appears at the beginning, as a precondition of the formation of the pair, while in the population study it appears at the end, as another means to check the access to reproduction.

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ecology of the Skylark” and, in doing so, formulates a twofold scientific objective: On the one hand, the paper intends to describe a behaviour seemingly irrelevant in the reproductive context – the maintenance behaviour which, though not defined theoretically, among others seems to encompass a number of comfort movements such as preening, bodyshake, wing stretching and so forth. On the other hand, however, the study aims to introduce an “analytical procedure” from which Delius says it promises to be “useful for behavioural studies”. The double-nature of description and stochastic analysis determines the organization of the study: As a whole it provides both a profound overview of a number of commonly accepted methods of quantitative description and adds to this canon one further Delius calls “random event series analysis”. “One of the contributions ethology has made to the study of animal behaviour”, Delius points out, has been to stress the necessity of extensive and accurate descriptions of behaviour as premises to explanations of behaviour. This has led to a search for more precise descriptive frameworks starting with the simple qualitative descriptions of early ethologists, followed by the sequence diagrams (e.g., Hinde, 1954) which were then formalized to transition matrices (e.g., Andrew, 1966) and supplemented by frequency correlation matrices (e.g., Stokes, 1962) and ending in the detailed descriptive study of Nelson (1964) combining all these techniques while adding interval distributions to them. The present study attempts to add to this list yet other formats: correlation functions and as derivations from them, frequency response functions. If I am not mistaken J. Delius himself had adopted the new methodology mainly from neurophysiologists who had conceived the organism as a black box and on basis of this notion correlated input with output frequencies. Correlations based on random inputs then had been translated in more advanced mathematical functions which Delius in his study transferred from the original context, the input-output correlations, to the side of the output alone, that is, the observable animal behaviour. According to Delius, random event series analysis have the advantage that the applied functions provide a “more of” additional information and – if I have understood correctly – a certain independence from the factor “time” which had determined the previously applied methods of description to a very large extent. Moreover, on basis of the results obtained in this way it could be easily distinguished whether the action patterns in question were based on rhythmical processes or exhibited in essentially random fashion. Taken both supplementary studies together, I think, they can be read as different interpretations of the new functional orientation in as much as they either addressed the ecological factors of reproductive success or applied stochastic methods to the description of overt behaviour. Under the surface, however, both texts contain theorems which seem to be compatible with the classical framework of Ethology such as the more exclusive

863 Delius, “A Stochastic Analysis”, 137.
864 Instead the behaviours in question are approached in a more prototypical way. See the chapter “Behaviour Description”, ibid., 144–148. I think all these behaviours have in common that they are related to the homoeostatic systems or equilibria of the body and thus imply also an epistemic reference system which is capable to compensate irritations.
865 Ibid., 172.
866 For the focus on overt behaviour see ibid., 173.
867 See ibid., 172.
868 Ibid., 175.
Niko Tinbergen (1907–1988)

view upon the young individual Skylark’s chances to participate in reproduction, the conception of the animal as a system or the replacement of Niko’s system of drives by a stochastic model that allowed to determine the extent of correlation between coordinating “centres” empirically. Both supplementary studies – and my impression is the population study even more than the account on stochastic analysis – therefore seem to indicate that Delius addressed themes that had been criticized before and now were waiting to be reinterpreted on basis of a more advanced theoretical basis. Can this hypothesis be made more plausible in the main paper, that is, in the way how J. Delius referred to ideas and concepts which had been characteristic for Niko’s and other Tinbergians’ research? In J. Delius’ thesis we do not find the extent of critical discussion that took place within the theses of other early Tinbergians. Cross-references to methodological concepts applied either by Niko himself or by one of his former PhD students are of two different types. On the one hand, there are those which seem to be more compatible with the new functional paradigm. For instance, when treating the shifting intensities of singing, Delius operates with the extended model of motivation C. Beer had suggested before and which included the affects of the endocrine system. On the other hand, however, J. Delius relied on some concepts which belong more into the repertoire of Classical Ethology such as Niko’s understanding of territory (as a combination of the bonding to a particular area and hostile behaviour to conspecifics), M. Moynihan’s concept of “redirected activities” or his “dual-drive theory” which Delius adopted in a slightly modified form in order to explain the agonistic behaviour of Skylarks. All these concepts are related to, or imply a notion of motivation conflict which, in turn, seems to suggest that underlying nervous centres are thought in discrete forms. With a view of J. Delius’ life-history it would be of interest to clarify whether this situation was more the result of a “not yet” or “not any more”, or even a mixture of both of it. The publication date of the paper (1963), that is, after Niko had made public his egg shell removal work, and the fact that Delius must have worked already at the new brain stimulation project at that point of time suggest that the use of the classical concept ran against the convictions of the new functional paradigm and thus may eventually also be read as the result of the reciprocal interaction between N. Tinbergen and his pupils. Next to the fact that J. Delius apparently was partly reluctant to abandon the conceptual achievements of Ethology’s classical period, both the choice of the publication organ, the German ZfT and the language of the article (i.e. German) might be taken as a symbolic gesture.

In order to round off my reading of the major part of J. Delius’ thesis I should also have a brief look at J. Delius’ post-doctoral research project. Among other

869 Perhaps it is also of interest to notice that Delius apparently did not interpret Functional Ethology solely in terms of Behavioural Ecology such as, for instance, H. Kruuk who read the notion of organization in terms of social organization and thus was able to establish a more uniform heuristic framework for his research. In J. Delius’ work we find neurophysiological interests (also related to the question of nervous organization) next to strictly ecological questions such as the one for the factors of reproductive success.


871 For cross-references to Niko’s territory concept see ibid., 302–303. On Moynihan’s “redirected activities” see ibid., 312. For his dual-drive theory see ibid., 310, 343.
things, the brain stimulation experiments in Lesser and Black-headed Gulls apparently led to a reassessment of the so-called “displacement activities”\textsuperscript{872}. Displacement reactions got out of fashion in course of Niko’s functional turn because they required to presume a more or less unitary system of discrete nervous centres: If it could be proved that certain behaviours “spark over” statistically more often into certain displacement patterns than into others there must be a system which regulated the grade of affinity of these centres just in the same way as the idea of a phylogenetic tree represented the varying degrees of genetic relatedness within a systematic group of organisms. Those among Niko’s pupils who did not agree with his unitary system of drives also tended to attack the concept of displacement reaction, for instance, by denying the \textit{exclusive} relationship between autochthonous and allochthonous behaviour.\textsuperscript{873} If I have understood correctly, J. Delius’ account of displacement activities refuses this critique and therefore revises the revision: The results of his brain stimulation experiments apparently did not only show that many action patterns can be elicited from discrete brain loci but also that one arbitrarily chosen behaviour pattern such as for instance “preening” could be elicited statistically more often from certain loci than from others and that therefore some sort of “association” must exist which makes one behaviour more likely to function as displacement reaction than another. In order to substantiate my view I quote a longer passage. “A great variety of responses have been obtained”, J. Delius writes,

but here we will only consider a behavioural syndrome which is characterized by preening and staring down, and more rarely by pecking, yawning, squatting, relaxation (fluffing of plumage, shortening of the neck, general diminution of activity, intermittent closure of eyes) and occasional sleep. We find that several, and sometimes all, these component patterns can often be elicited from single loci with the same stimulation strength, usually less than 50 µamp, either as a result of a single stimulation train or more frequently in the course of several consecutive trains. In Table 1 all 202 loci so far explored have been classified into those which yielded preening and those which did not. Within each class of loci the percentage which yielded the different other components is shown. All the component patterns were associated with electrodes eliciting preening rather than with those which did not, and the association is significant. A similar relationship may also hold for mandibulation, shaking the body and head, wagging the tail and shaking the foot, but because these patterns are also frequent during control periods without stimulation, a decision is difficult. No such association could be detected for some twenty five other various behaviour patterns examined. It is significant that preening positive points clustered in several discrete anatomical areas of the telencephalon and diencephalon and that ten electrodes responsible for more than half the entries in the non-preening class also lay within or close to these areas. There is not sufficient information to decide whether the associations of components are stronger in some areas than in others, although some evidence points in this direction. The conclusion that these diverse behaviour patterns reflect the activation of a more or less unitary system leading to de-arousal, and are not a result of the simultaneous stimulation of contiguous but otherwise unrelated neural systems, is supported by observations on unstimulated normal gulls which suggest a high temporal and sequential association between the component patterns including sleep.\textsuperscript{874} I think the passage shows impressively that the results obtained in J. Delius’ brain


\textsuperscript{873} Please see Beer, “Incubation and Nest Building Behaviour IV”, 167–168.

\textsuperscript{874} Delius, “Displacement Activities and Arousal”, 1259–1260.
stimulation experiments with Gulls tended to support the notion of a more or less unitary system of nervous centres and therefore put forward exactly one of those controversial concepts that had been criticized before by those who intended to replace the classical mechanomorph reference system with a new functional one. My argument therefore is that the path of J. Delius’ life-history was headed towards the scientific orientation functional ethologists had abandoned before. With a view of J. Delius’ and R. G. B. Brown’s post-doc research it is therefore problematic to speak of “failed” experiments. Maybe, the results were just unintended from a functional ethologist’s point of view and sparked off a process in course of which theorems put forward by classical ethologists were reinterpreted on basis of a more advanced state of knowledge.

H. Kruuk, I think, is a typical representative of the new generation of Niko’s PhD students. He was already involved in N. Tinbergen’s egg shell removal study before he concentrated on his own dissertation project on “Predators and Anti-Predator Behaviour in the Black-Headed Gull”. After obtaining his degree, his way at first led away from academia: He moved to East Africa in order to help setting up the Serengeti Research Institute (SRI) in the Tanganyika National Parks. The institute owes its existence to the initiative of the German nature conservationist B. Grzimek and the strategic talent of J. Owen who had originally intended to prevent the local herds of wildbeest, zebra and gazelle from being culled by the Tanganyikan government for local consumption. Thanks to J. Owen, a former Oxford undergraduate student who later became the director of the national park, and his success as “fund-raiser and charmer” (H. Kruuk’s attributes) enough money flowed from Germany, the United States, Canada and elsewhere to build several research buildings, acquire several small planes and employ fifteen and more scientists and many assistants. Over the course of time the SRI became a first class address for ecological research and wildlife management. Between 1964 and 1969 Niko visited H. Kruuk and his wife Jane every year for some weeks and after a couple of visits J. Owen asked Niko to become a member of the institute’s scientific council. According to H. Kruuk, Niko was involved in decision making and research policy of the institute until his interest waned as a result of suffering a series of nervous breakdowns during a series of lectures he had delivered in Nairobi in 1967. Kruuk’s own engagement in East Africa was not only of organizational kind. Eventually as a consequence of the favourable conditions he developed a profound and long-lasting interest in social behaviours and foraging strategies of carnivorous mammals, in particular the spotted hyaenas to which he dedicated an entire monograph. Back in Oxford, Kruuk was put in charge of Niko’s field research group

875  For a brief sketch of his academic course see Kruuk, Niko’s Nature, 342.
876  In a letter to J. Huxley Niko comments on Kruuk’s dissertation thesis which was apparently submitted at Utrecht University. Despite their close cooperation Niko underlined that Kruuk carried out the research for his PhD independently. See WRC-RU Fondr. Lib., MS 50, box 47, file 2, letter N. Tinbergen to J. Huxley (n. d.).
877  For H. Kruuk’s engagement in East Africa and the role N. Tinbergen played in the establishment of the institute see Kruuk, Niko’s Nature, 225–229. For Niko’s support of this work see WRC-RU Fondr. Lib., MS 50, box 38, file 1, letter N. Tinbergen to J. Huxley (13/01/1965).
878  Some additional information concerning Grzimek’s engagement in East Africa can be found in his autobiography. See Grzimek, Auf den Mensch gekommen, 383–430.
and when N. Tinbergen retired he moved on to the Institute of Terrestrial Ecology which was located in the Scottish Highlands. He finally obtained his own chair at the University of Aberdeen where he advanced to one of the pioneers of Behavioural Ecology. “My field of interest stayed mostly with mammals, but moved into behavioural ecology”, he writes, especially social organization and foraging of carnivores. I think that my career was built on my PhD project with Niko, and it resulted in, amongst other things, several books and a score of PhD students (some of whom now have professorships, several books to their name, and many PhD students themselves, people such as David Macdonald and Gus Mills).879

As a provisional hypothesis, we can infer from this quotation that his intellectual life-history did not include further drastic turning points as was the case, for instance, in C. Beer’s or M. Dawkins’ life course. More likely his further interest turned out as a fulfilment of the program outlined very early in his PhD thesis albeit mainly realized with gregarious mammals. It is difficult to make this trend concrete already in his dissertation thesis. However, a few remarks can eventually be made nonetheless. H. Kruuk’s thesis was published as a supplement issue of Behaviour which had been the typical way for Niko’s students in the 1950s to publish their works.880 Moreover, the study was also characteristic in the way it was derived from previous research if we take into account Kruuk’s participation in Niko’s egg shell removal project. On the one hand, Kruuk surely contributed to the results obtained by N. Tinbergen in his project. On the other hand, however, Kruuk carried further Niko’s results in his own dissertation thesis. One of the advancements which Kruuk has introduced in his PhD study and which should become one of the cornerstones of his later ecological studies was that adaptive behaviours need not necessarily be species-specific. On the contrary he claimed that the anti-predator behaviours of the birds can change individually corresponding to the varying circumstances.881 Despite the continuity between his PhD study and Kruuk’s later ecological accounts as to the variability of the individual’s adaptedness there is also a moment of discontinuity which appears to be the result of the chosen scientific object: The Black-headed Gull. Niko’s PhD projects had in common that they approached social (in particular reproductive) behaviour as far as it was concerned with the establishment and maintenance of territories. Partly in contrast to mammals, Gulls are territorial animals which means that acquiring natural resources in the widest sense is mediated by the claimed territories and not so much by any sort of more or less complex social organization. The choice of the scientific object thus somewhat prevented from raising these research questions. Another aspect which pointed into the direction of future research is Kruuk’s mentioning that the predators might improve the effectiveness of their strategies by refining their so-called “searching images” – a question which apparently had already been raised before by Niko’s younger brother, the Dutch ecologist Luuk Tinbergen.882 Kruuk’s use of the concept “search-

881 This point of demarcation is also mentioned in his Tinbergen biography. See Kruuk, *Niko’s Nature*, 227.
882 See Kruuk, “Predators and Anti-Predator Behaviour”, 110. And also Bod. Lib., N. Tinbergen
Niko Tinbergen (1907–1988)

ing image” is of interest because two of Niko’s later PhD students (H. Croze and M. Stamp Dawkins) explicitly made searching images the topic of their theses. Finally, like most other Tinbergians of the second generation Kruuk was sceptical about the centralized and hierarchical models early ethologists had read into the organization of the nervous system but at the beginning of the 1960s a better and fully fledged alternative did not yet exist. As a result, H. Kruuk dealt with this question only tentatively – a gesture which opened another future field of research. These few remarks are sufficient to realize that Kruuk’s (future) interests were placed within and not outside the epistemic paradigm Behavioural Ecology was built upon. Yet, I think his interest in organization translated into the question of social and less of central nervous organization as it was the case, for instance, in C. Beer’s research.

There are some indicators in Kruuk’s thesis which seem to point into that direction. Besides assuming a more plastic motivation system, one of these indicators probably is Kruuk’s reassessment of the Gull’s discriminative ability. Thus some of Kruuk’s experiments tested explicitly the discriminatory ability of the Gulls. For instance, he confronted his proband animals with different models of predator animals (fox, hedgehog, stoat) and was able to show that Gulls are capable to apply various types of attack patterns to each species of enemy. More precisely the response patterns of the Gulls varied in a number of discrete parameters such as the number of attacks, the distance within which the enemy was tolerated (i.e. attack range), the attack-frequency of individual Gulls, the closeness of the attacks, the amount of Gulls in the flock, the distance within which the Gulls flew up or the relative frequency of the so-called tremulous calls relative to the kek calls. If the Gulls are capable to respond in a differentiated way to different predator objects they must possess the adequate (visual) discriminative capacities. However, in an additional remark Kruuk underlines, that it is less the morphological shape which the Gulls recognize rather than the behaviour pattern with which they attack. In epistemological terms this aspect reveals how the notion of discrimination has been re-framed within the ecological paradigm – a matter affect which can also

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883 In particular, ethologists such as R. A. Hinde had observed that the intensity of anti-predator reactions waned over time – a matter of fact whose function, in Kruuk’s view, wasn’t understood at that time. See Kruuk, “Predators and Anti-Predator Behaviour”, 118.

884 See ibid., 121.

885 In so far his results seemed to support N. Tinbergen’s view and not C. Beer’s scepticism.

886 On these discriminative experiments and their results see ibid., 76–82, 84–85, 101. With two exceptions H. Kruuk has adopted M. Moynihan’s conventions of naming the calls of the Gulls. The so-called “Kek-call” (Moynihan’s “alarm-call”) consists of a series of sharp yet not very loud “kek”s which have a distinct staccato quality. Its function is to warn the conspecifics. The so-called “tremulous call” (Moynihan’s “attack-call”) is described as a strident rattling scream, “kak-ak-ak” or “krek-rek-rek-rek-rek”. For Kruuk’s remarks concerning the names of the calls see ibid., 6–7.

887 Predators develop means of counter-adaptation which in turn result in modified and more refined defensive strategies. To take into account these mutual behavioural adaptations required a concept of “recognition” which was more complex than was implied in the concept of simple “releaser” which had been put forward by early ethologists in order to demonstrate the species-specific character of the behaviours in question. For the complexity of the adaptive systems see ibid., 117–118.
be made evident in C. Beer’s treatment of the methodological concept but, I think, in contrast to C. Beer, Kruuk is more prepared to retain the visual discriminative capacities. Moreover, the physical mechanisms of sensation are one of the fields in which H. Kruuk demonstrates inadequacies in the defensive strategies of the Gulls. Yet the potential malfunctions turn out to be the heuristic tool for assessing the survival value of the behaviours, the question how different selective pressures interact with each other – sometimes even antagonistically in form of so-called trade-offs.\(^{888}\) If we ask for signs of reciprocal interaction between H. Kruuk and N. Tinbergen we have to take into account that Kruuk himself participated both in the realm of Tinbergian Theory and Practice. Being socialized academically while being involved in Niko’s egg shell removal project shaped Kruuk’s interest for the question of survival value but his dissertation thesis also went beyond Niko’s inclination to concentrate on species-specific behaviours in taking into account both the complexity and the variability of the adaptive systems. In his later studies, Kruuk left behind territorial animals such as Gulls and focused on social organization in mammals.

The final intellectual life-history I should like examine is J. R. MacKinnon’s. MacKinnon is one of today’s well-known experts on wild-life conservation in Africa, the Far East and China. On the website of the University of Beijing to which MacKinnon was or still is affiliated I found the following summary of his life which I would like to quote. It reads:

John MacKinnon | British, 62 years age. | John is an internationally famous conservation expert and author. He is a grandson of Britain’s first socialist Prime Minister – Ramsay MacDonald; but has spent more than 40 years study and conservation of wildlife in many African and Asian countries. John was the first biologist to complete field studies of all the world’s great apes starting with chimpanzees under supervision of Jane Goodall and then orang-utans under supervision of Nobel Laureate Niko Tinbergen. He subsequently studied gorillas and bonobos as well as the “Lesser” apes – gibbons and siamang. He is author of 17 books and producer of several TV documentaries. He first came to China to work on the WWF Giant Panda project in 1987 and is an expert and author on birds and mammals of China. He has since served for 14 years as co-chair for biodiversity matters to China Council for International Cooperation on Environment and Development (CCICED). John was awarded the prestigious Order of Golden Ark with highest rank of Commander by Prince Bernhard of the Netherlands for his life-time services to conservation. John has a Chinese wife, is fluent in basic Mandarin and currently resides in Beijing working for the large EU-China Biodiversity Programme.\(^{889}\)

The text cannot be exactly dated but it must have been made available online in the early two-thousands.\(^{890}\) Asides the socialist tradition which the text underlines


\(^{890}\) In an interview with the Shanghai Daily of the year 2010 MacKinnon is introduced as 63 years old so that the quoted text may be dated to the year 2009. See E. Fu. “The Real Danger of Mistreating the Environment. [Interview with J. R. MacKinnon]”. In: Shanghai Daily March 28 (2010), I–2. URL: http://www.shanghaidaily.com/article/print.asp?id=432462 (accessed on July 5, 2012).
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and the tendency to speak in superlatives it shows quite impressively at least two aspects which may be of interest for my argumentation. On the one hand, the studies which finally culminated in his PhD turn out to be a more or less distinct episode in J. MacKinnon’s life which is separated from his interests before (study of chimpanzees with J. Goodall) and after (subsequent studies of further species of primates and apes). On the other hand, however, his life-history also shows a long-lasting even life-long dedication to the subject whose foundations were laid early in his graduate student years and, according to his own account, even before he entered university. In addition to the pure scientific account on Orang-Utan behaviour, MacKinnon later published a more popular and semi-autobiographical account about the time he spent in the jungle under the title “In Search of the Red Ape”.\(^{891}\) There we also find some information about the roots of J. MacKinnon’s research interests. “Before going up to university”, he tells us,

> I had the luck to spend a fascinating and instructive year, working with Jane and Hugo van Lawick at the Gombe Stream Reserve in Tanzania. I originally intended to study only insects there but who could resist the excitable chimpanzees and their engaging personalities? It was in Gombe that I learnt the techniques of tracking animals and observing and recording the behaviour of wild primates. When I returned to Oxford I took with me a deep interest in apes.\(^{892}\)

In addition to that, we are informed in his book *In Search of the Red Ape* that his studies on Orang-Utans in Indonesia and Malaysia already had begun before he finished his zoology degree at Oxford University in late 1968 or early 1969.\(^{893}\) This means that J. MacKinnon belongs to the group of PhD students who had received their early academic education at Oxford and that he had shaped his particular research interests already at the end of his predoctoral studies only extending it into his PhD project. Moreover, alike to the life courses of H. Kruuk and I. Douglas-Hamilton, MacKinnon’s path, after earning his PhD, partly drifted away from academia without loosing contact – neither to research nor to the type of field work that had already characterized his studies on Orang-Utan behaviour. In this context, I think, we have to read his cooperation with the Chinese government and the EU. As a provisional hypothesis, we may therefore say that MacKinnon’s PhD studies laid the foundation for his later interests but that his approach to the subject in his later life was both more practically oriented and – somewhat paradox to the ethos of a field naturalist – keen to use his authority in service of protective intervention. In several ways MacKinnon’s project was untypical for Niko’s second generation of PhD students: At first, it was completed rather late in N. Tinbergen’s career in 1972, two years before his retirement in 1974. In addition to that, it is one of two projects which were not concerned with one of the “emblematic” animals that had characterized the work of the ABRG over the years. Niko’s interest in mammals was raised late in his career during his visits in East Africa and then switched rapidly to homo sapiens – either in form of his concerns about the condition of humanity and human kind in general or, more related to his own health condition, in form of his late project on childhood autism. Finally, MacK-


\(^{892}\) Ibid., 18.

\(^{893}\) See ibid., 67.

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innon’s thesis which was submitted under the title “The Behaviour and Ecology of the Orang-Utan, Pongo Pygmaeus, with Relation to the other Apes” and whose main results were published in *Animal Behaviour* two years later in 1974 explicitly pushed into foreground the ecological research tradition Niko had co-founded but in the meantime had grown into a considerable area of research. The questions ecologists asked were related to the adaptiveness of competing strategies of reproductive, foraging, and social behaviours and, from a more epistemological perspective, worked with what I’ve called “Darwin’s paradox”. In other respects, MacKinnon’s study was typical Tinbergian: On the one hand, the mode of the project’s initiation resembles much the epistemic practice N. Tinbergen had applied in earlier projects to build a continuous research tradition. On the other hand, however, like Niko in his late functional papers, MacKinnon had adopted a framework for his account I have abstractly circumscribed as “Darwin’s paradox” in order to make clear both its inner logic and its descent. Both aspects need to be elaborated in more detail. From the brief biographical account quoted above we can infer that MacKinnon’s PhD project commenced – so to speak – in an initial move beyond a previous research interest. This move becomes manifest both in the shift from the Chimps to the Orangs – a fairly mysterious and unknown species at that time – and in the change of the advisor, Niko instead of Jane. In addition to that, it seems that MacKinnon’s shift also had methodological implications: In D. Attenborough’s foreword to *In Search of the Red Ape* we find indicators that J. MacKinnon carried the scientific practice to go into the wild and adopt life and habit of his scientific object to an extraordinary extreme. According to Attenborough, the Orang-Utan is an extraordinary shy primate species and lives either in small groups of two or three individuals, or solitarily. In addition, the ways of its wanderings are fairly unpredictable so that a scientist whose research is dependent on a certain amount of observational data faces the near-impossibility to maintain contact with his object of observation. “John MacKinnon’s solution to this problem had an appalling starkness”, Attenborough writes:

He decided that once he found an individual, he would simply follow it through the forest, sleeping where it slept, moving when it moved. What is more, he would do so for days and

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894 J. MacKinnon published several articles on Orang-Utan behaviour. The paper which seems closest to his PhD, I think, is his 1974 article in *Animal Behaviour* which is why I have taken it as the primary basis for my further analysis. See J. R. MacKinnon. “The Behaviour and Ecology of Wild Orang-Utans (Pongo Pygmaeus)”. In: *Animal Behaviour* 22.1 (1974), 3–74. At the end of the paper we also read the sentence: “This MS was originally accepted as an Animal Behaviour Monograph”. The monograph-like character of the study supports my view that it is most likely the main publication of a series. The comparison of both titles (i.e. of the original thesis and follow-up publication) shows that the comparative focus included in the project slightly shifted from an inter-species comparison (“with relation to other apes”) in the original thesis to a comparison between Bornean and Sumatran populations “in relation to the zoogeography of these two islands”. See ibid., Abstract, 3.


if necessary weeks on end; and he would take with him no more than the minimum rations, a knife and a sheet of plastic under which to sleep.\footnote{898}{D. Attenborough. “Foreword”. In: J. R. MacKinnon. \textit{In Search of the Red Ape}. London: Collins, 1974, 11–12.}

From this quotation we can infer that the scientific practice of observing wild animals reached a new quality in J. MacKinnon’s project in as much the observations were carried out less from a fixed hide but involved the observer’s own permanent motility.\footnote{899}{See MacKinnon, “The Behaviour and Ecology of Wild Orang-Utans”, 10–11, and MacKinnon, \textit{In Search of the Red Ape}, 19.} In this context, it would be of great interest to know whether the fact that J. MacKinnon had changed the advisor for his PhD study can be correlated with his changed attitude to observe animals in the wild. He reports that he, following J. Goodall’s and G. B. Schaller’s successful attempts in habituating wild chimpanzees to the presence of humans, also made such attempts with Orang-Utan specimens yet finally abandoned this strategy at an early stage of the study because too many different animals were found and familiar animals could be encountered only infrequently. As a result, MacKinnon remained “concealed from the animals whenever possible”.\footnote{900}{MacKinnon, “The Behaviour and Ecology of Wild Orang-Utans”, 11, also 21 and 34–35.} It is theoretically possible that the Tinbergian mode of observing wild animals mostly without habituating them to the presence of humans was able to meet more J. MacKinnon’s needs. From his account we can infer that the nature of his scientific object made necessary this readjustment in the first place.\footnote{901}{Ibid., 11.} In addition to that, MacKinnon underlines that contrasting methods such as whether the animals are habituated or not may generate different results. In comparing his findings with those of others (P. S. Rodman and D. A. Horr) MacKinnon claims that deviating results may be the effect of the different geographical, climatic and ecological habitats of the chosen research areas including corresponding effects on population and habits of the animals but they may also be the outcome of deviating methodologies. He writes:

If we accept that orang-utans do have a tendency to remain resident for long periods in suitable areas, e.g. where there is abundant year-round food, but also have a capacity for large-scale movements whenever such behaviour is at a premium, then we can see that such contrasting methods of study are liable to reveal different slants on orang-utans’ behaviour. Use of a habituation method ensures that it is the resident members of the population that will provide most of the data collected, and the researcher is bound to be impressed by the static nature of these animals. If only a small area is investigated, and few individual animals observed, it is not possible to assess how widespread such resident behaviour is in the whole population. By studying more animals in a larger area I was able to get a broader picture of my Segama population but had less information on the resident animals: how extensive were their individual ranges, etc. Our different approaches may well go some way to explaining differences in our findings, but I do not think they go all the way. Rodman and Horr did not see evidence of the seasonal movements that were very apparent in both Segama area A and Segama area B. Also the orang-utans in Rodman’s Kutai area do seem to have had very much smaller ranges than those I have designated as resident in Ulu Segama.\footnote{902}{See ibid., 32. In his autobiographical account the traces of MacKinnon’s initial attempts to apply the method of habituation can be made evident. See MacKinnon, \textit{In Search of the Red Ape}, 38, 40, 45, 49, 62, 75, 117. We are also informed that sometimes direct interventions became...}
The passage, I think, shows impressively that J. MacKinnon’s practice not to habituate but instead to follow his animals was more apt to take into account the dispersion of certain behaviours within a population. With putting emphasis upon non-resident and wandering small groups and sub-groups of Orang-Utan he was also able to see the animals’ adaptedness (and individual adaptability) to their climatic environment as a result of which MacKinnon interpreted their movements. The broader and more divers basis of data then could lead to more elaborate inter- and intraspecific comparisons. Mobility, in his view, turns out to be advantageous for the animals if – due to annual climatic changes – the vegetation (including the amount of food resources) changes correspondingly. “The extreme plasticity of orang-utan ranging behaviour”, MacKinnon underlines, “appears to be highly adaptive for life in a diverse rain-forest flora with such a complexity of fruiting cycles. Similar intra-specific variation is found in other primate species (Jay 1968)”.

My argument now is that MacKinnon’s population thinking was more compatible with, or even generated by, the scientific paradigm provided by Behavioural Ecology rather than by any other scientific orientation. As a result, one may eventually say that, although, as we will see, the impact of direct interaction seemed to wane nearing Niko’s retirement, the deeper lying epistemic convictions of the group nonetheless yielded a certain impact upon the projects. MacKinnon’s initial move therefore had a considerable effect on the way to approach his scientific object. The gesture to develop farther a previous conviction in an act of more or less overt criticism is what Niko expected from all his PhD students at the beginning of their project. The only deviation from this scheme in J. MacKinnon’s case seems to be that the potential criticism was directed neither to one of Niko’s own works nor to a thesis composed previously by one of his PhD students. More likely it addressed a research tradition which was characterized by a more interventionist train in as much as the technique of habituation implied that humans became foreign though partly accepted members of a social group of animals.

I have argued that much of the innovative potential of the new ecological paradigm was drawn from adopting the end-paradox epistemic pattern which had shaped wide parts of Darwin’s argumentation and now was made productive within the

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903 From his autobiographical account we can also infer that J. MacKinnon applied different strategies of observation which depended also on the stage of his project and the familiarity with his subject. Thus there were short trips in the jungle at the beginning which ended with the return to the base camp (Ibid., 36, 42, 44). Later he followed one group for several days (Ibid., 45, 53). Finally, he also applied the strategy to choose a rich feeding ground and wait for the arrival of the Orangs (Ibid., 120, 123).

904 MacKinnon, “The Behaviour and Ecology of Wild Orang-Utans”, 33, similarly 38. I also see a parallel to H. Kruuk’s project in as much as the species-specific focus (eventually more Niko’s point) apparently was more and more replaced by intraspecific comparisons which were more liable to uncover the individual adaptability of the Orang-Utans. Conversely, we might argue that the abandoned focus on interspecific comparisons was picked up in J. MacKinnon’s later ape studies and therefore marks one of the productive omissions I was able to track also in other PhD projects advised by N. Tinbergen. One of his later papers, for instance, is J. R. MacKinnon. “A Comparative Ecology of Asian Apes”. In: Primates 18.4 (1977), 747–772.
framework of Behavioural Ecology by reinterpreting it in many different though structurally similar ways. As we have seen, themes like optimal foraging, play or altruism, from an epistemological standpoint, have in common that they measure out the adaptive value of a seemingly maladaptive behaviour strategy or make at all the conflict of antagonistic strategies the pivotal point of their argumentation. In J. MacKinnon’s thesis we find a rather impressive interpretation of this epistemic outline. Several examples may corroborate my hypothesis. Firstly, MacKinnon’s study is almost exclusively based upon observations in the field. Between June 1968 and November 1971, we are informed at the beginning of his study, he had spent twenty-one months and altogether fifteen hundred hours of fieldwork with studying “wild populations of orang-utans in Borneo and Sumatra”. Next to the study of wild animal, however, we can also find some information in his paper that he compared the behaviours of wild Orang-Utans with the one of captive and semi-captive specimens. The former of the two categories refers to animals kept in zoos which MacKinnon had observed by himself or whose behaviours had been reported to him by zoo keepers. The second type of Orang lived in what MacKinnon calls “rehabilitation centres”, that is, stations in which wild orphans are brought up by foster mothers with the intention to make the animals acquainted with their natural environment and finally release them. Both categories of animals served MacKinnon as objects of comparison but his own observations in the wild prevailed by far. Secondly, N. Tinbergen, in his spacing-out paper of the year 1967, had put the notion of animal association in what would behavioural ecologists nowadays might call a “handicap theoretical” context. That is, he more or less explicitly questioned the adaptive value of the aggregation by asking for the disadvantage the social forms of life might have with respect of the risk to become a predator’s prey object. J. MacKinnon picked up this thread in his dissertation thesis by revealing a trend to “desocialization” in the evolutionary history of the Orang-Utans in Indonesia and Malaysia. In his view, the Orang-Utan populations of Borneo and Sumatra have – each to a different extent – “learned” to live in small groups and sub-groups because these forms of social organization, despite their seemingly maladaptive character, turned out to be more adaptive to the fluctuating vegetation cycles upon which their cropping was depending. In other words, the benefits of the solitary or semi-solitary forms of social organization must have outweighed their disadvantages such as the loss of social protection against predators. It is a specific quality of J. MacKinnon’s thesis that he translated his ecological findings into an evolutionary theory how the various Orang-Utan populations might be re-

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906 On this kind of comparative data see ibid., 13, 39, 46, 50, 55–58, 60, 66 and 70.
907 See ibid., 4–5, 37, 38, 43, 46, 56, 58, 60, 71.
908 What is abandoned, the benefit of social life, thus can be interpreted as a minimum measure (i.e. “handicap”) for the selective pressure favouring solitary feeding.
909 For the concept of “desocialization” see ibid., 66.
910 Ibid., 31, 32, and also 65–67. Analogously he claims that reducing the birth rate within a population may have an advantage which is, both from a biological and an epistemological point of view, a paradox. See ibid., 21.
911 The “value” of these abandoned advantages thus stands for the extent of selective pressure being exhibited in direction of the solitary forms of social organization.
lated to each other. According to his account, since the Pleistocene there must have been a larger and more terrestrial ancestral archetype of today’s Orang-Utan in Java, Indo-China and presumably also in Borneo and Sumatra which descended into various discrete insula populations as soon as the sea level rose and inhibited the gene flow between the populations in questions. In MacKinnon’s view, the rise of the sea level separated first Borneo and Java, then Borneo and Sumatra and lastly Java and Sumatra. See MacKinnon, “The Behaviour and Ecology of Wild Orang-Utans”, 68. In addition to that, we are informed that Sumatra split from the mainland more recently than the Bornean insula and that it might be expected therefore that the Sumatran race would be more similar to the prehistoric form (Ibid., 69). On the existence of a bigger more terrestrial ancestral form see also MacKinnon, In Search of the Red Ape, 212. MacKinnon had observed that large adult male Orang-Utans are forced to live on the ground because of their weight and concluded that the reduction of size in comparison to the ancestral type must have enabled the species to lead the life of a more flexible arboreal ape. See ibid., 55, 72.

According to MacKinnon, both populations are so similar that their status as discrete sub-species is doubtful. Yet nonetheless, there are a number of morphological and especially behavioural differences. For these differences see ibid., 69–71. For the following see ibid., 66–67. For the different climatic circumstances and their effect upon the vegetation (including the greater or lesser extent of temporal and spatial clumping of foods) see ibid., 33. For some more information concerning the climatic cycles on Borneo and their effect see also MacKinnon, In Search of the Red Ape, 56, 59, 69, 118–119, and MacKinnon, “A Comparative Ecology of Asian Apes”, 749–750.

The Orangs of the main land and on Java were extinguished by the early Holocene leaving only the Sumatran and the Bornean populations. According to MacKinnon, both populations are so similar that their status as discrete sub-species is doubtful. Yet nonetheless, there are a number of morphological and especially behavioural differences. The Bornean sub-population was confronted with a more fluctuating vegetation and thus reveals a more advanced stage in the process of desocialization. The Sumatran populations lived closer to the equator where the annual fluctuation of food production is less drastic and as a result the social organization of the Orang population turns out to be closer to the original type. In MacKinnon’s view, the rise of the sea level separated first Borneo and Java, then Borneo and Sumatra and lastly Java and Sumatra. See MacKinnon, “The Behaviour and Ecology of Wild Orang-Utans”, 68. In addition to that, we are informed that Sumatra split from the mainland more recently than the Bornean insula and that it might be expected therefore that the Sumatran race would be more similar to the prehistoric form (Ibid., 69). On the existence of a bigger more terrestrial ancestral form see also MacKinnon, In Search of the Red Ape, 212. MacKinnon had observed that large adult male Orang-Utans are forced to live on the ground because of their weight and concluded that the reduction of size in comparison to the ancestral type must have enabled the species to lead the life of a more flexible arboreal ape. See ibid., 55, 72.

In addition to that, the existence of more and larger predator species (including man) on the Sumatra insula favours the maintenance of the group structure. From this angle it makes sense why J. MacKinnon decided to compare the behaviours in two different main research areas one of which lied in the North of Sumatra, while the other was located in Sabah, in the Malaysian part of Borneo. This brief description may show how the chosen epistemic framework entailed J. MacKinnon’s research interests and how the research questions were translated into his own action. I have added an illustration which shows the two main biogeographical research areas J. MacKinnon had chosen for his dissertation project (Fig. 2.16). One of the structural preconditions of the conflicts between epistemic communities...
as a whole was that the new ecological paradigm did not fall back upon any Lamarckian predecessor and did not coincide with any neo-Lamarckian reinterpretation of the previously mentioned position. In order to achieve this it was mandatory that Behavioural Ecology maintained and reproduced the epistemic interventions Darwin had introduced and the neo-Darwinians had reinterpreted both within the frameworks of population and ecological genetics. In J. MacKinnon’s thesis, alike to all other examined projects carried out by pupils of Niko Tinbergen, the Darwinian causal architecture appears in various different forms of expression. The most obvious sign of this is the connection MacKinnon creates between the plasticity of the behaviour of Orang-Utans and their mobility in space, on the one hand, and their adaptability to varying habitats, on the other.\footnote{See fn. 904, page 306.}

Conversely the captive and semi-captive animals are described partly in terms of dysfunctional behaviour modifications.\footnote{See ibid., 175–179. For instance, under captive conditions Orangs tend to gain more body weight and, in MacKinnon’s view, divert more energy into their sexual activities. MacKinnon made these observations productive for his field studies. For instance, he had observed that wild male Orang-Utans tend to rape their female partners but was able revise his initial view on basis of the additional observation he had obtained with captive animals. The comparison between captive and wild Orangs thus raised the further leading question of the adaptedness of various different antagonistic sexual behaviours.} In one of his later studies we can find an even more comprehensive example of this aspect. In MacKinnon’s view, there is interspecific competition mainly for existing food resources in a geographic area. This competition, however, is reduced, that is, sympatric coexistence of different ape species becomes possible.
if the species in question develop their own foraging strategies which, in MacKinnon’s opinion, usually are correlated with differences in body size. From a heuristic standpoint it is therefore the point when the principle of natural selection is reduced which is made productive for deeper ecological insights. In addition to that, MacKinnon applied the recursive formula for reproductive success that nowadays is typical for both ecological and sociobiological studies: An individual’s fitness, if measured by reproductive success, does not only include the amount of her / his own offspring (with his / her genes) but also the reproductive success of the offspring generation: The amount of her / his children’s children. On a more methodological level of the study, the emphasis on functions and reasoning in terms of ultimate causation becomes manifest in so far as the increase of knowledge which is implied in the scientific practice of description is connected with the concept of “aim”. “The aim of this study”, writes MacKinnon, “was to investigate the behaviour and social organization of the orang utan and attempt to understand these in relation to those ecological factors that affect this species”. Since N. Tinbergen’s On Aims and Methods at the latest, the term “aim” had served as a signal word that the current text unit was to be read in terms ultimate causation. In case of J. MacKinnon’s thesis thinking the notion of adaptedness pervades the entire argumentation. It is also important to note, I think, that the productive treatment of heuristic paradoxes also implicitly generates the legitimation for the research work. According to J. MacKinnon, the Orang-Utan populations of Borneo and Sumatra are threatened by extinction through man. More detailed knowledge about the species and their behaviours might serve their protection even if the examination means another intervention.

My primary research question while reading the dissertation theses of several of N. Tinbergen’s later cohort of pupils was how their theses could be related to the interests they revealed in later periods of their lives. In J. MacKinnon’s life course, I think, we have to seek for early indicators of his engagement as nature conservationist. In this context, it is remarkable that this interest emerges as paradox constellation: The protection of the endangered natural species partly requires its engulfment as scientific object. To put it provocatively, in J. MacKinnon’s life research has handicap theoretical implications. The extent an endangered species becomes subject of scientific assessment might be a measure for the endangerment it has to face. MacKinnon’s thesis anticipates this paradox aspect which later should structure his life both as environmentalist and university teacher.

To sum up my readings of some dissertation theses written by members of N. Tinbergen’s second generation of pupils, one may say that there might be in principle two different patterns of response to his late move to Functional Ethology. Either pupils “stayed” and complemented the scientific orientation within which they were

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925 Ibid. We can infer from J. MacKinnon’s account that on this early stage of his career he believed in the direct effect his research work might have. I’d be curious whether or in how far this attitude to research changed over time.
socialized or they moved away from it by applying various kinds of critical gestures. This scheme, under changing circumstances, eventually applies already to Niko’s first generation of pupils but also to his second. While H. Kruuk and J. MacKinnon, in their theses, laid the foundations for a lifelong commitment with a theme or field interest and their life course more looks like the fulfilment of a previously outlined program, the trajectories of others (C. Beer and J. Delius) reveal more drastic caesuras. It is possible that in Niko’s second generation of pupils there were a number of individuals who repeated the life courses of their teacher generation in as much as their academic socialization spread their research interest over antagonistic scientific orientations so that they were challenged to merge divergent interests in course of their post-doctorate careers. Both C. Beer and J. Delius might belong to this group of researchers since their later life-histories reveal a growing interest in issues of Cognitive Ethology and / or cultural evolution. Richard and Marion Stamp Dawkins eventually shared this tendency in different ways. R. Dawkins belonged to a group of young ethologists who had arrived at Oxford after Niko’s turn. They were being socialized already within the new paradigm yet their further life course, in contrast to convinced ecologists, eventually reveals a tendency back to the epistemic roots of Ethology and the wider context of the Modern Synthesis. If Dawkins headed his autobiographical account “Growing up in Ethology” we are eventually not entirely mistaken to hear the ambiguity which lies in the “growing up within” and the “growing up into”. After earning his PhD he moved to Berkeley where he continued his research on chicks at G. W. Barlow’s institute for another few years. Back in Oxford the interest in decision making perpetuated for another five years and culminated in several papers partly written

926 D. F. Alwin and J. McCammon underlined that there is evidence in support for the cohort replacement model of social change but also for alternative views. See Alwin et al., “Generations, Cohorts, and Social Change”, 44. My approach to combine a model for cyclic transformation with the examination of life-histories eventually provides an explanatory model for the question when we have to expect what response pattern.

927 G. Beale, by contrast, claims: “Both in ethos and in practice then (if not in theoretical object), Dawkins’ experiments were almost as far from the early Tinbergians work as it is possible to conceive”. See Beale, “Tinbergen Practice, Themes and Variations”, 192. From a more epistemological standpoint and with a view of R. Dawkins’ further life course I venture to question this view openly. Please see to this how M. Stamp Dawkins describes her and Richard’s response to the advances of Functional Ethology: “Richard and I responded to these changes in somewhat different ways”, she writes and continues: “He initially turned to the analysis of hierarchical organisation at a behavioural level (Dawkins, R., 1976a) and we did some joint work on decision-making in chicks and flies (Dawkins & Dawkins 1973, 1976), which no-one took much notice of but which I still think had some original ideas. He was then inspired by the advances in evolutionary behaviour and started working on what was eventually to become The Selfish Gene (1976b)”. See Stamp Dawkins, “King Solomon’s Herring Gull’s World”, 173–174. Both intellectual life histories reveal, to a certain extent and each in a different form, a movement back to the “holism” of the early days: Either in form of an interest in hierarchical organization and evolutionary theory, that is, the bigger picture (R. Dawkins), or the integration of the advancements of Cognitive Ethology and the animal welfare movement (M. Stamp Dawkins). The role their stay at Berkeley (1967–1969) played in this move should be examined more carefully because, as we all know, the places of research have their own tradition and reputation!

and published in cooperation with Marian Stamp Dawkins.\textsuperscript{929} Since the mid-1970s, however, his theoretical interest in evolution has beaten its way and finally found its expression in his best seller \textit{The Selfish Gene} which can eventually be read as the part of a new synthetic movement within the biological sciences.\textsuperscript{930} In addition, his engagement in decision making waned and was replaced by a number of projects which mostly involved the use of computer programming and whose tenor apparently was to transgress the boundary between the organism and its behaviour, on the one hand, and human technology, on the other. Both Marian and Richard Dawkins were part of this movement which “in form of their persons” also reached the level of academic institutionalization. After covering a position as University Lecturer in Animal Behaviour for several years, R. Dawkins was appointed Charles Simonyi Professor for the Public Understanding of Science in 1995, a position from which he retired in 2008. Marian Stamp Dawkins completed her PhD on “Searching Images” in Birds in 1970 and finally succeeded on Niko’s chair after D. MacFarland’s retirement. Later on she developed a profound interest in animal welfare. With a view of her growing interest in animal welfare in the 1970s she writes:

Behavioural ecology was getting going, exploring questions about adaptation in the light of the new impetus from game theory and kin selection, and had turned away from questions about development and motivation, which were seen as the concerns of old-fashioned ethology, despite being central to the study of animal welfare. Animal welfare, in other words, was not mainstream animal behaviour. It was marginal, not very exciting and with highly dubious overtones of subjectivity and lack of scientific rigour. It was not a proper subject to be studying.\textsuperscript{931}

As a result, we may eventually conclude that the epistemic communities being concerned with the study of behaviour saw another synthetic movement already in the mid-1970s to which certainly E. O. Wilson’s new Sociobiological Synthesis belonged but also a return to the classical ethological scientific paradigm which was interpreted by new concepts and by partly adopting the achievements of Cognitive Ethology.

\textit{Rehabilitating Autistic Children (1972–1983)}

The final period of N. Tinbergen’s life I would like to discuss is characterized by his late interest in childhood autism. The interest in human behaviour was more or less latently omnipresent from the very beginnings of Ethology but has beaten its way more and more in course of the 1960s and 1970s. O. Heinroth had already transferred the notion of existing species-specific characteristics to humans not to mention Lorenz’s theory that the drop-out of instincts in both animal animals and human animals under the conditions of domestication might cause their “degeneration”.\textsuperscript{932} Although Lorenz abandoned the National Socialist interpretation of his theory after the Second World War, I do not think, he ever revised the un-

\textsuperscript{930} Ibid., 206, 206–212.
\textsuperscript{931} Stamp Dawkins, “King Solomon’s Herring Gull’s World”, 175.
derlying epistemic structure of his argumentation, namely that the reduction of an organism’s instinctive repertoire might entail the increase of the plasticity of its behaviour – regardless of how this more of individual plasticity was to be evaluated. This could be demonstrated in all his later works which were related to the welfare of human civilization such as On Aggression (1963), Civilized Man’s Eight Deadly Sins (1973) or The Waning of the Human (1983).

Niko Tinbergen shared Lorenz’s concerns about the state of human kind, concerns which finally culminated in a manuscript or, more precisely, the drafts for a book which was meant to be titled “Man the Guinea Pig of Evolution” yet remained unpublished altogether. Already Tinbergen’s inaugural lecture delivered during the festivities on the occasion of his nomination to full Professor at the University of Oxford was dedicated to aggression in animal and man – a theme Lorenz had raised at the peak of the Cold War in 1963.

Nine years later, in 1972, Tinbergen once more was concerned with human behaviour at a highly acclaimed location, namely, in his so-called “Croonian Lecture” – a prestigious lecture-award assigned annually by the Royal Society.

Besides Lorenz’s and Tinbergen’s concerns about the human predicament, Ethology, in common, had faced the foundation of a new sub-branch since the early 1970s – Human Ethology – whose main representatives were H.

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Also Lorenz’s model apparently has not become fully obsolete: For instance, the idea that a depersonalization of warfare through guided weapons allowing the killing of others from distance might have a disinhibiting effect upon the aggressive potential in humans is still one of the explanatory models of bellicose aggression pervading public media even nowadays. How this narrative is interlocked with Lorenz’s concerns about the mother-child dyad in his writings and that this parallelism was accepted by U.S. American psychologists in the Cold War period can be inferred from Vicedo, “The Father of Ethology”, 288–290. In other scientific contexts such as the biting inhibition of wolves Lorenz’s Special Phylogeny of Releaser obviously has led to erroneous conclusions. See to this example Sax, “What Is a ‘Jewish Dog’?” 16–17.


Intellectual Life-Histories

Prechtl, P. Leyhausen, I. Eibl-Eibesfeldt and N. Blurton-Jones. D. Morris had become famous with his best seller *The Naked Ape* – a book which Niko at first filled with enthusiasm but more and more let him think about alternative ways how to apply the ethological method to humans. Moreover, since the beginning of the 1950s a number of child psychologists and psychiatrists like J. Bowlby had begun to incorporate ethological methods into their studies and it was the inspiration of their works – both positive and negative – which, in the year 1970, let N. Tinbergen spark off another research project which was related to childhood autism. Somewhat typical for a Tinbergenian project the final impulse came from the outside: In 1970 Corinne and John Hutt, two child psychologists who had become interested in applying the methods of Ethology to the study of mental disorder, sent N. Tinbergen a copy of their latest book *Direct Observation and Measurement of Behavior*. Their work, they explained in the preface of the book, owed a great deal of influence to Niko’s support and encouragement in the early critical stage of their work. Apparently the Hutts had become dissatisfied with the prevalence of experimentalist techniques in their own discipline, that is, the application of highly quantifiable experiments in tightly controlled experimental settings and, as a result, had begun to adopt the observational and descriptive methods of Ethology of which they thought they could provide a degree of precision equally advanced as the one expected of experimental studies. E. A. Tinbergen, Niko’s wife, read and commented the book. She asked Niko to forward her comments to colleagues.
and both Tinbergen and his wife had inserted themselves into a long-standing and acrimonious debate in child psychology. On one side were researchers who had concluded that autism was a lifelong neurodevelopmental disorder with a genetic basis that only responded to intensive behavioural therapy (if it responded to any treatment at all). On the other side were those who still believed that autism was probably caused by conditions in a child’s environment, that is, if it is understood in the context of autism research and treatment in the late 1960s through the early 1980s. He was hardly alone in his understanding of autism as a disorder that was influenced by environmental factors, including parenting style. He corresponded with an international network of scholars and clinicians who were using it as a model for understanding how social interactions could shape children’s emotional development. These researchers drew Tinbergen and his wife into the field and they welcomed their attempts to apply ethological reasoning to explaining the cause of autism. Others in the field, however, dismissed his ideas. It turns out that he and his wife had inserted themselves into a long-standing and acrimonious debate in child psychology.

Niko Tinbergen (1907–1988)

and both Tinbergen and his wife began to elaborate these comments into a paper which they finally sent to a number of experts in the field including J. Bowlby, M. Rutter, L. Wing and F. Hall, a former PhD student of Niko’s who had drifted into child psychology. Although the reactions turned out quite controversial, the Tinbergens felt encouraged to make their views available to a wider public audience. The paper Niko and Elisabeth Tinbergen submitted to Science, however, was declined by the editors and as a result the Tinbergens extended their manuscript into a small book which eventually was published in 1972 under the title “Early Childhood Autism: An Ethological Approach”. The study was the formal beginning of a more than ten-year-long engagement in childhood autism resulting in a considerable amount of correspondence and several further publications including a more extensive book with the title “’Autistic’ Children. New Hope for a Cure” (published in 1983) and the written version of the speech Niko had delivered on the occasion of his award with the Nobel Prize in the year 1973. Science historians have pointed out that friends and colleagues responded with dismay to Niko’s late interest in childhood autism and the results of the project. H. Kruuk even went so far as to say: “All in all, perhaps the Nobel lecture would be best forgotten”. The reception of Niko’s works among professional psychiatrists and child psychologists was highly controversial – in Silverman’s view, a result of the fact that Niko had sided with one party in the already existing scientific dispute over the physical causation of the autistic disorder. “Tinbergen’s work becomes easier to understand and looks far more intellectually rigorous than critics have assumed”, she writes.
**Intellectual Life-Histories**

psychoanalytic interpretation of the disorder was valid, and that children with autism responded to psychoanalytic therapies.  

The quotation calls to our mind that since L. Kanner first described the autistic syndrome in 1943 a veritable controversy had developed as to whether and, if so, in how far the described mental disturbance was due to environmental factors.

And it has been remarked that Niko’s belief in a psychogenic theory of autism must be read in context with his own suffering from (endogenous) depressions and his personal desire for a helpful and effective cure. Another source of N. Tinbergen’s environmentalism surely was the controversy between D. S. Lehrman and the ethological community in the 1950s which for many ethologists had been a mind opener for the nurture aspects of behaviour. Somewhat contrary to the development in Ethology the scientific community of psychiatrists, however, abandoned the notion of psychogenic causation in course of the 1970s as the genetic and / or organic roots of autism were thought to become more and more obvious. From this perspective Niko’s view appears as the “failure” of an aged scientist who left his accustomed field of expertise and - influenced by his own personal needs – voted for the “wrong” side in a scientific controversy. On closer inspection however things appear to be more complex and N. Tinbergen’s own argumentation eventually was more sophisticated than his critiques were prepared to concede. For instance, Niko most likely underestimated the extent of genetic and / or organic causation but he did not neglect it. In “Autistic” Children he underlines:

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949 Silverman, “‘Birdwatching and Baby-Watching’”, 177. For the controversial character of the reception see also Kruuk, Niko’s Nature, 278–279.

950 For L. Kanner’s famous paper see L. Kanner, “Autistic Disturbances of Affective Contact”. In: Nervous Child 2.2 (1943), 217–250. Interestingly, Kanner himself inferred from “the children’s aloneness from the beginning of life” that autists suffered from an “innate inability to form the usual, biologically provided affective contact with people” but he also asked explicitly to what extent disturbed family relationships contributed to the condition of the children. See ibid., especially 248, 250.

951 This view is supported by the fact that N. Tinbergen himself drew a connection between nurture causes and curability. See, for instance, Tinbergen, “Ethology and Stress Diseases [1974]”, 20, 23. The disappointment Niko had experienced in connection with his own depression which appeared to be incurable for many years might also be the reason for the partly aggressive undertone we find in his publications on autism. See to this Kruuk, Niko’s Nature, 276. For an explanation of this aggression see also WRC-RU Fondr. Lib., MS 50, box 45, file 3, letter N. Tinbergen to J. Huxley (ca. 1972).

952 In a later ms. Niko himself said it is ironic that a science like Ethology that has been preoccupied with innate behaviour now needs to argue in favour of nurture. See Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3147, D 64, ms. “An ethological approach to Early Childhood Autism” (02/1979). See also ibid., Ms.Eng. c. 3145, D 26, letter N. Tinbergen to B. Rimland (22/02/1983).

953 H. Kruuk writes: “Recently [which here means ca. 2003] it has been demonstrated that autism is, indeed, an organic problem: it is biochemically detectable as a physical abnormality at birth, not just an affliction environmentally induced by, for example, lack of parental bonding. Evidence has emerged recently that autism may be an autoimmune disease”. See Kruuk, Niko’s Nature, 279. For a more up to date review see M. Fakhoury, “Autistic Spectrum Disorders: A Review of Clinical Features, Theories and Diagnosis”. In: International Journal of Developmental Neuroscience 43 (2015), 70–77.

954 In a recent historical account Niko’s environmentalist views – without mentioning his name – are classified under the rubric “Ideas once held with conviction, which proved to be unfounded”. See S. Wolff, “The History of Autism”. In: European Child & Adolescent Psychiatry 13.4
To recapitulate our views on the extent to which “nature” (genetic predisposition) and “nurture” (influences from the environment) causes a child to become autistic: while we do not deny that there may well be hereditary components in the causation of the autistic derailment, we assert that these components do no more than determine the degree of vulnerability to pressures exerted by the environment. There is of course no either/or to this; what we claim is that environmental autismogenic factors are at the moment being greatly underrated, indeed hardly given any attention. We further suggest, more specifically, that the responsible environmental factors are largely of a social nature. And since they act primarily through sensory inputs that affect the child’s motivational state and through this his behaviour, our interpretation must be classed as being largely “psychogenic” – “organic” (structural) defects seem to us to be of minor importance.

I think, N. Tinbergen’s claim that structural (in his understanding inherited) defects play a minor role amongst the causes of autism is not correct. However, his hypothesis that autistic children have a genetic predisposition for a more of “vulnerability” (i.e. liability to develop autistic symptoms) in fact seems to agree with recent genetic findings. Thus A. Feinstein writes in his late History of Autism:

There have been some exciting recent developments. In February 2008, US researchers identified two separate genetic defects linked to autism, one which directly causes the disorder in about 1% of cases and a second that may play a role in a much larger percentage of patients by increasing their susceptibility to environmental or other genetic influences.

If I understood correctly the former of the two genetic defects is caused by the ad-hoc deletion or duplication of a particular segment of chromosome 16 whereby “ad-hoc” (my circumscription, C.L.) here means that the aberration was found in children with autism but not in their parents, “indicating that it was a spontaneous mutation that occurred at some point after fertilization”. The other defect seems to affect a larger group of subjects and is traced back to a gene called “contactin-associated protein-like 2”, or CNTNAP2, which produces a protein that allows the brain cells to communicate with each other and may eventually dispose children to autism. Furthermore, recent gene sequencing technologies have not only led to a more precise understanding of the sequential order of the human genome but have also revealed the occurrence of so-called “copy-number-variations” (CNV). These spontaneous (or inherited) forms of genetic variability, again, are made responsible for humans’ susceptibility to a number of common diseases and therefore eventually might corroborate N. Tinbergen’s hypothesis of a general “vulnerability” in autistic children. It is of some interest that N. Tinbergen, heavily sensitized and

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According to R. Plomin autism is one of the mental diseases with the highest degree of heritability. See Plomin et al., Gene, Umwelt und Verhalten, 8.


Ibid., 273.

Ibid., 273–274.

Ibid., 274. “Susceptibility” is also discussed as an effect of varied genes encoding neurotransmitter receptors and transporters (SLC6A4) as well as in context of genetically or epigenetically induced reduction of the amount of expressions of genes playing a pivotal role in neuronal migration and prenatal development of neural connections (RELN). See A. M. Persico et al. “Searching for Ways Out of the Autism Maze: Genetic, Epigenetic and Environmental Clues”. In: Trends in Neurosciences 29.7 (2006), 352 and 354–355 respectively.
alert by the controversy with D. S. Lehrman, insisted upon the possibility of non-inherited prenatal forms of causation – a notion which seems to apply at least to one of the genetic defects mentioned by A. Feinstein. Yet it must also be realized that Niko did not fully make the “turn” to what we would nowadays eventually call epigenetic research (in a narrower sense). The task of us science historians, I think, would be to find out why. As a provisional answer, I’d say one of the reasons might be how Tinbergen “resolved” the antagonism of nature vs. nurture. My impression here is that Tinbergen on the one hand claimed there is “no either/or to this” but on the other hand made extensive use of the dichotomy in his own argumentation while – so to speak – leaving each part of the antagonism intact, in a sense of two coexisting heuristic poles. “Both and” can mean a lot: It is quite a difference whether two antagonistic poles coexist in a conjunct disjunction or there is a proper third, a real intersection. To use a picture: It is a difference whether, say, a red and a blue coloured paint spot coexist or there is one lilac, that is to say, one which represents the compound of both colours. Both models can be referred to as “both and” and my argument is that the Tinbergens tended to understand the dichotomy of nature vs. nurture in the sense of a conjunct disjunction and that this view might have prevented him from breaking through to epigenetics. “Non-genetic means, per definition: environmentally induced”, Niko writes in the manuscript for a lecture with the title “Early Childhood Autism seen as the consequence of psychosocial stress, and a new, successful therapy”. However, it is exactly this simplified binary opposition of “genetic” vs. “environment-induced” which does not hold any more from nowadays point of view although we must concede that Niko primarily meant “inherited” when he spoke of “genetic”, that is, more precisely, determined by the genetic information encoded by the genes of the DNA passed onto a human being by both of his or her parents by 50% each. In a recent paper T. Kubota, K. Miyake and T. Hirasawa, distinguish between “de novo mutations in synaptic genes”, “abnormalities of epigenetic control (for example, Rett Syndrome)” and “acquired alterations of epigenetic control induced by various environmental factors” in order to make clear that the autistic syndrome may be caused not only by spontaneous mutation of synaptic genes but also by the (partly environment induced) alteration of their expression. “These findings suggest”, they underline, “that neurodevelopmental disorders such as autism can be caused not only by congenital genetic and epigenetic defects, but also by epigenetic dysregulation in the brain induced by various environmental factors [...]”. If the, or at least one, current trend to explain the autistic syndrome was to combine the rather new research area of epigenetics with the previously obtained achievements of psychological and psychiatric therapies, it seems important to consider the role of environmental factors in the development of autism.

For further information concerning the term “epigenetic” and the field of research it represents see fn. 108, page 41 of my thesis. Sophisticated readers certainly will argue that from a chemical standpoint the compound might consist of particles of each kind and the “one” in fact is a “two”. I’d agree but the difference in view or resolution still remains. Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3147, D 69, ms. “Early Childhood Autism seen as a consequence of psychosocial stress, and a new, successful therapy” (ca. 11/1981). T. Kubota et al. “Epigenetic Understanding of Gene-Environment Interactions in Psychiatric Disorders: A New Concept of Clinical Genetics”. In: Clinical Epigenetics 4.1 (2012), 1–2.
research, that is to say, by a stronger emphasis upon partly environment induced chemical modification of DNA and histone proteins independently of the underlying inherited DNA sequences, Niko’s claim to take into account environmental impacts during early and earliest childhood seems quite legitimate either, since it can and will be asked what effect might have both non-social (e.g. nutrition) and social factors (e.g. stress) upon the process of epigenetic dysregulation of brain functions “at some point after fertilization”, as A. Feinstein put it. And since we now know that epigenetic alterations being virulent in various diseases do not only occur in response to internal or external cues but, beyond that, that they can also be inherited from one generation to another – that is in fulfilment of Lamarck’s “inheritance of acquired characteristics” – the Tinbergens’ claim to take into account the mother-infant system as a whole (with respect of both the diagnosis and the cure of the autistic syndrome) appears to be quite prescient in retrospect.

In sum, one may say that Elisabeth and Niko Tinbergen’s concept of “vulnerability” which they considered the result of genetic (i.e. inherited) effects and / or intrauterine impacts as well as their emphasis on psychic stress with hindsight appear to be quite ahead of their time. This leaves unanswered the question whether their psychogenic explanation of how children become autistic on basis of their disposition applies equally well. N. Tinbergen was fully aware that autism is a highly complex phenomenon with many different symptoms, a high grade of individual

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967 Research on mother-infant bonding is nowadays and integral part of psychiatric and psychological research. See E. Geerts et al. “On the Role of Ethology in Clinical Psychiatry: What do Ontogenetic and Causal Factors Tell Us About Ultimate Explanations of Depression?” In: P. R. Adriaens et al., eds. *Maladapting Minds. Philosophy, Psychiatry, and Evolutionary Theory*. Oxford: Oxford University Press, 2011, 121–122, 131–132. E. Geerts and M. Brüne thus proposed a correlation between early attachment and parental rearing on the one hand and the non-verbal behaviour in adult depressed patients. However, please note that this proposition is meant to refer to depression and not to autism spectrum disorders (ASD). The research question put forward by Geerts and Brüne, however, matches with the Tinbergens’ interest.

968 For the “transgenerational epigenetic inheritance” in general and the effect of stress in particular see Kubota et al., “Epigenetic Understanding”, 5 where also the quotation can be found.
variation in these symptoms and manifold forms of causes some of which remain unknown even today (2015). Under these circumstances he insisted on keeping a heuristic balance which he thought suspended by a biased clinical research elite that – in his view – impeded the children’s curability by presupposing one-sidedly genetic and organic roots of the mental disorder in question. Niko saw his work on childhood autism as a means to re-establish the heuristic balance he considered essential to solve the riddle of autism. And, as I believe, he was fully aware that he, in order to obtain this objective, needed to provide a one-sided view by himself, in a sense of a correction. We will see later on why this imbalance must have had the smack of an “unpleasant cure” or even of something that was “out of the order” by itself but the history of autism shows that Niko’s persistence on methodological balance was legitimate and functional even in case some of the propositions he made needed to be corrected by themselves. In some other aspects Tinbergen anticipated or at least reinforced trends which later became or are about to become common habit, knowledge or at least an accepted research question such as to understand the autistic syndrome as a continuous spectrum ranging from less to more severe affection, his claim for a broader phenotype, the trend to reduce the earliest age of diagnosing autism or the possibility of regression during ontogeny, not to mention his highly elaborated sensitivity for the functioning of constructivist mechanisms in academia.

Recent studies which intended to place Tinbergen’s late project on autism within the history of Ethology have claimed not to forget that N. Tinbergen himself saw his late autism research as continuation of his and his research group’s animal behaviour studies. However, up to now I haven’t read an account that fulfils this request. In particular, science historians haven’t made sufficiently clear so far, if at all, and if so, in how far Niko’s late autism research perpetuated his late turn to Functional Ethology. My analysis of N. Tinbergen’s intellectual life-history shows that the “N. Tinbergen” does not exist, nor is there the one and only ethological methodology which Niko is said to have translated into his autism studies. More concretely, how do we actually know that Niko’s late project in childhood autism does not – from a more structural point of view – return to the classical setting of

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969 For N. Tinbergen’s link between the nature vs. nurture controversy and the question of curability, see Tinbergen, “Ethology and Stress Diseases [1974]”, 20. From a nowadays perspective Niko’s logical connection between genetic and / or organic causation and alleged pessimism or even neglect as to the children’s curability seems at least questionable. He wanted to have exposed a trend within clinical psychiatry towards more basic research and therefore a neglect of cure oriented science which he connected with the psychiatrists’ presumption that autism had genetic / organic causes. On the other hand, scholars nowadays are fully aware that the scientific view upon the phenomenon of autism creates the reality of an autist’s life and that the label an autistic child receives may change the child. See for this awareness of constructive power, Feinstein, A History of Autism, 290. The whole point of Niko’s rebellion against what he perceived as clinical elite was his awareness of this constructivist mechanism: A child whose mental disorder was categorized “incurable” in his view was hardly liable to be cured.

970 For a current discussion of the latter three aspects see ibid., 280–281, 284–285, and 290 respectively. According to A. Feinstein, there is even a current tendency to incorporate the so-called “Asperger’s syndrome” which so far was defined as a separate form of autistic disorder into the autism disorder spectrum. See ibid., 291.

Ethology (comparable to the course some of his later pupils took)? And how do we know that he did not create an entire “new” scientific paradigm comparable to Darwin’s late studies on mind and behaviour? In fact some passages in “Autistic Children” can be read as if Niko had applied another epistemological intervention similar to the one I think it can be detected in Darwin’s The Descent of Man and The Expression of the Emotions. However, I think, a more accurate analysis how his late project is related to his previous works, in particular the ones published after 1963, can reveal in how far and how his autism studies reinterpreted the scientific paradigm his later functional studies were based upon. On the basis of this more detailed knowledge it will be possible to trace more precisely the points of conflicts which had generated the controversy. Altogether my analysis therefore aims to leave behind the oversimplifying focus upon the “nature vs. nurture controversy” which has shaped so far both the historical and the professional reception of Niko’s late autism research, in particular, as it appears, if the authors of these historical accounts argued from a psychiatric point of view (which sometimes can pervade into the field of the history of psychiatry as well). To reconstruct once more Niko’s scientific orientation from his late writings and ask how the underlying reference systems are made concrete (both mental operations can be performed by our brains simultaneously) will therefore be the basis both for determining more precisely the points of conflicts between his and other scientific standpoints and for answering the question if, where and why Niko’s account partly failed to match the empirical reality. This approach entails a couple of secondary questions. At first, as my previous analysis of Niko’s life has shown, he has interpreted the synthetical construction of the ethological paradigm in two discrete realms one of which was filled by the projects of his pupils, while the other was reserved for his own more formative accounts. With Niko’s retirement in 1974 and the abandonment of his teaching responsibilities the mutual intertwinemment between “Tinbergian Theory” and “Tinbergian Practice” witnessed a considerable break and therefore needed to be reinterpreted. As a provisional working hypothesis, I therefore suggest to distinguish methodologically more precisely between those statements of Niko’s which were related to an “aetiology of autism”, the reasoning about the causal factors or the definition of the symptoms of the disorder, on the one hand, and his suggestions concerning an appropriate cure, on the other. In other words, I suggest a methodological differentiation between diagnosis- and cure-related utterances. Second, science historians have drawn our attention to the fact that Niko’s late studies on childhood autism were carried out in close cooperation with his wife. E. A. Tinbergen (“Lies”) had supported her husband over the years of his professional career in the background but beginning with the couple’s commencing interest in childhood autism Lies began to play a more obvious role in his research. Maybe, it is not quite false to say that E. Tinbergen filled the gap Niko’s students had left by taking over the role they had played over the years in his quite sophisticated

H. Kruuk writes: “The Tinbergen husband-wife team made a very attractive combination, with Niko as the experienced behaviourist and Lies as the fanatic children-watcher. Niko himself felt pleased that, after a life-long pursuit of his own interest, now Lies could have a crack of the whip. Lies’ influence was very strong; the study was a joint one, but it was largely Niko lending his abilities to what Lies wanted to do, doing it the way she wanted”. See Kruuk, Niko’s Nature, 275.
system of mutual scientific exchange. Elisabeth Tinbergen’s part therefore must be
determined more carefully in each realm of inquiry. According to H. Kruuk, her
impact was “very strong” and Niko once, in one of his letters, called her “a real ma-
triaxch”.

But on the other hand, we are also informed that Niko was the one who
“wrote it all”.

Finally, science historians have taken for granted (as a self-evident
fact) without further questioning that Niko’s interest in autism fell into the domain
of psychopathology in as much as the concept “autism” refers to a variety of cor-
related mental disorders or malfunctions some (or several) of which are related to
the children’s social behaviours. Again as a provisional hypothesis, I am therefore
inclined to establish a logical connection between Niko’s spacing-out study (and
eventually also J. MacKinnon’s further development of the basic idea underlying
the paper) and his approach to autism. Both studies, certainly each in its own way,
tried to make productive, at least from a heuristic point of view, that in social spe-
cies seemingly anti-social behavioural aberrations in fact do occur which – so to
speak – on a higher level of argumentation turn out to be meaningful in a sense
that the “abnormal” provides deeper insights into the functionality of the “normal”.
Niko’s approach to autism, in this respect, would be another attempt to make pro-
ductive what I have called “Darwin’s paradox” and the dispute with psychiatrists
and child psychologists might turn out to be one between different epistemic com-
unities and the scientific orientations which typically take form in course of the
reproductive dynamics which perpetuates these communities rather than between
different positions within one and the same community. In other words, Niko’s “ad-
venture” into the sphere of psychopathology and the subsequent disputes may be
read as expressions of a far more severe type of scientific encounter whose man-
ners of operations have not been understood so far. Thus it seems wise to read the
sources related to Niko’s late autism research with open eyes and ask for seemingly
atypical forms of scientific interaction. Finally, it has been rightly claimed that espe-
cially Niko and Elisabeth Tinbergen’s suggestions how to cure the autistic disorder
changed over time – even that they developed quite antagonistic stances in course
of the years. Hence, it seems essential to assume that the Tinbergens’ engagement
with childhood autism has a history in itself. Furthermore, it should not only be
asked for the concrete impulses that made them change their views but also in how
far these shifts articulated or corresponded with a shift in the two realms underly-
ing N. Tinbergen’s late scientific orientation. From this perspective N. Tinbergen’s
engagement with early childhood autism would eventually provide excellent oppor-
tunities to reconstruct the micro-architecture of the functional scientific paradigm
and the interaction of its constitutive realms. Altogether I would like to suggest the
following course of historical events: An initial impulse (the reception of Corinne
and John Hutt’s book and E. Tinbergen’s comments) ultimately resulted in a first

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974 See Kruuk, *Niko’s Nature*, 275. This can be confirmed. See Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3146, D 37, N. Tinbergen to H. Hassenstein (10/03/1982), here page 6. For the division of labour in the Tinbergen couple see also ibid., Ms.Eng. c. 3146, D 43, letter N. Tinbergen to M. Welch (07/10/1978). For Niko’s appreciation of his wife’s talent as a child-

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more elaborate publication. This publication, *Early Childhood Autism*, summarizes and exceeds the informal discussion that had preceded before 1972. Its general tenor is to reduce the facts and come to a reliable alternative hypothesis about the causation of the autistic syndrome. The account is therefore diagnosis-oriented. N. Tinbergen’s nomination with the Nobel Prize in 1973 marks a turning point to a certain extent. In his so-called Nobel Lecture, *Ethology and Stress Diseases*, he recapitulates the achievements of the previous years but provides a far-reaching outline of human ecological research including a more cure-oriented perspective upon childhood autism. This preoccupation ultimately culminated into a second major book, “*Autistic*” *Children. New Hope for a Cure*, which was published in 1983 and whose tenor is less to develop a deviating fresh aetiological perspective upon the phenomenon of “autistic disorder” rather than to translate the previously outlined hypothesis concerning the functional causation of the syndrome into direct practical forms and means of therapy. “*Autistic*” *Children* is therefore a cure-oriented statement. Its underlying epistemic thrust (including its composition) therefore differs fundamentally from the account of the year 1972. In the following I will give a brief outline of each of the cornerstones.

(R1) Informal scientific exchange in the forefield of the publications. In his later Nobel Lecture N. Tinbergen underlined that the immediate impulse for his and his wife’s engagement in childhood autism was coming from Corinne and John Hutt’s book *Direct Observation and Measurement of Behavior* which had been published in 1970.975 The Tinbergens found at least two main aspects which made the topic “childhood autism” compatible with Niko’s understanding of Functional Ethology as he had begun to shape it since ca. 1962. On the one hand, the Hutts’ work marked a break with their clinical profession in so far as they opted in favour of observing the children in their natural environment instead of applying the experimentalist practice of testing under controlled artificial conditions.976 On the other hand, the Hutts put forward the idea that the behaviours of autistic children, with exception of gaze aversion, were lying on a continuum with the behaviours exhibited by normal children in situations of emotional discomfort. “These observations and analyses of film records therefore indicate”, they write, “that, apart from aversion from the face, all other components of the social encounters of these autistic children are those shown by normal nonautistic children”.977 Not atypical for a Tinbergian project Niko and Elisabeth Tinbergen’s engagement with childhood autism therefore started with an intensive reception process of a previously published treatise. And quite in agreement with the PhD projects Niko had supervised, this reception included criticism.978 Apparently it was E. Tinbergen who drew Niko’s attention to the observation that the “aversion from the face” the Hutts described as exclusively


976 See Ibid., Direct Observation, 3–4.

977 See ibid., 147. See also Tinbergen, “Ethology and Stress Diseases [1974]”, 21.

978 Most interestingly, we can find also an indicator in J. Hutt’s letter to N. Tinbergen that the Hutts eventually felt a discrepancy between their and Niko’s position. “In a way which you will not entirely appreciate, not only this book, but the whole direction of our work, owes an inestimable debt to you”. See Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3144, D 1, letter J. Hutt to N.
autistic expression is also displayed by normal children, for instance, when they are confronted with a potential threat.\(^{979}\) From a more epistemological standpoint we may therefore infer that the Tinbergen's, from the very beginning of their study of autism, rated higher the notion of continuity between normal and autistic than child psychologists like the Hutts were prepared to do. In addition, from E. Tinbergen's comments we can infer that she tended to explain the children's atypical behaviour as the product of a motivational conflict between the desire for social interaction (or of being "fascinated by the environment") and the anxiety that was accompanying this wish when the children were not familiar with either the object or the person in question and, in addition, momentarily felt a lack of security, for instance, because the parents were absent or their attention was bound otherwise.\(^{980}\) As a result she inferred that these children eventually could be "tamed" by avoiding over-intrusive stimulation and they were playfully given the opportunity to built a relationship of trust and confidence with the strange person or object.\(^{981}\) In other words, the Tinbergen's were inclined to interpret the atypical behaviours of the children (regardless whether they were autistic or not) in terms of an either inherent or acquired pathological insecurity (or motivational imbalance) that was caused by unfamiliar over-intrusive stimuli which in turn made them interrupt the otherwise desired social bonding.\(^{982}\) The Tinbergen's developed their thoughts into a more elaborate paper which they forwarded to a couple of experts and thus made a subject of their informal critique.\(^{983}\) The response was controversial. While F. Hall remarked that many professional therapists applied the non-confrontational methods of cure the Tinbergen's had suggested, M. L. Rutter and L. Wing were more critical about Niko’s and Elisabeth’s venture on psychopathology. Thus Rutter argued that there was only little evidence for the Tinbergen's argument that what they called “temporary autism” and what psychiatrists called “Kanner’s syndrome” were two different points on the same continuum and therefore thought Niko had made a failure not to make a clear differentiation between the two sets of symptoms. Moreover, he was critical about Niko’s biased focus on psychogenic factors: “However the evidence from a number of studies now seems to suggest”, he underlines,

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\(^{979}\) Tinbergen (02/04/1970). C. Silverman, I think, has misrepresented the quotation by dropping the first part of the sentence. See Silverman, “‘Birdwatching and Baby-Watching’”, 178, fn. 4. E. Tinbergen’s comments on the Hutt’s book are included in a letter of Niko’s to the Hutts as a literal quote. See Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3144, D 1, letter N. Tinbergen to C. and J. Hutt (11/04/1970), here page 1, 3.

\(^{980}\) See ibid., Ms.Eng. c. 3144, D 1, letter J. Hutt to N. Tinbergen (02/04/1970), page 2.

\(^{981}\) See ibid., Ms.Eng. c. 3144, D 1, letter J. Hutt to N. Tinbergen (02/04/1970), page 2–3 and also WRC-RU Fondr. Lib., MS 50, box 45, file 3, letter N. Tinbergen to J. Huxley (ca. 1972). It might be of interest that Niko saw the ideal of non-intrusive and playful education realized in the eskimo society he had lived in for one year during his stay in Greenland (1932–1933).

\(^{982}\) Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3144, D 1, letter J. Hutt to N. Tinbergen (02/04/1970), page 3, and in a concluding remark on page 5. It is not difficult to think ahead the underlying argumentation: What appears to be a dysfunctional (since unsocial) behaviour in the first place can be interpreted on a higher level of argumentation as protective and therefore in principal adapted gesture.

\(^{983}\) Among these addressees were J. Bowlby (expert on mother-infant relationships), L. Wing (who became famous for establishing the term “Asperger Syndrome”), M. Rutter (one of the experts on autism in Britain), and F. Hall (a former student of Niko’s).
Niko Tinbergen (1907–1988)

that only rarely is Kanner’s syndrome due to psychogenic factors. That is not to say of course
that the kind of social withdrawal shown by autistic children may not be due to psychogenic
influences, but rather that the whole syndrome in which of course social withdrawal is merely
one part is rarely due to psychogenic factors. Although you emphasise the gaze aversion shown
by autistic children, it is clear from several follow-up studies that the social abnormalities are in
many respects the most transient of the handicaps. The language and cognitive difficulties being
very much more persistent.984

L. Wing who worked in a Social Psychiatry Unit of the Medical Research Coun-
cil at that time articulated similar concerns. She pointed out that “early childhood
autism (as described by Kanner) is a condition with an organic aetiology” which,
on the contrary is absent in cases of social withdrawal due to environmental causes
so that she suggested not to apply the term “autism” for the latter behavioural ab-
normalties.985 Other remarks were related to the question how representative a
symptom gaze aversion (the symptom the Tinbergens had put in the centre of their
focus) actually was in the entire symptomatology of the autism disorder. Instead she
underlined that neurological symptoms such as aphasia, agnosia, apraxia including
visual and perceptual problems were much more central consequences of the con-
dition leading to difficulty in understanding and using both verbal and non-verbal
language. Finally, she conceded that ethological methods could be useful in ex-
amining the ways in which people react to children but apparently did not see how
these methods contribute to either the diagnosis or the cure of the autistic syndrome.
To the contrary, L. Wing clarified that there was no hard evidence in favour of the
theory that parental child rearing practices could made responsible for the mental
disorder of their children (which could be inferred from Niko’s psychogenic stand-
point) and “[...]CL that it is neither sensitive, humane, nor helpful to the children
to resurrect the old fashioned view that their parents have caused their problems
 [...]CL”.986 I think it is important to mention at this point that N. Tinbergen’s inten-
tion was not to blame the parents and make them feel guilty for their children’s
problems. However, Niko, trained as a field ethologist and having examined social
interaction among animals for most of his professional career, insisted that – neither
with respect to the diagnosis nor to the treatment of the autistic syndrome – the child
must be seen as an isolated individual rather than a part within a whole network of
social relationships.987 Yet, this transindividual approach, as a consequence, surely
did imply to ask for the role the children’s social environment played in the gen-
esis of their mental health problems (a matter of fact the Tinbergens later in their
publications justified with the benefit of the children even the intended therapy led

985 For the following see ibid., Ms.Eng. c. 3144, D 1, letter L. Wing to N. Tinbergen (02/09/1970),
and ibid., Ms.Eng. c. 3144, D 1, letter L. Wing to N. Tinbergen (22/09/1970).
986 Ibid., Ms.Eng. c. 3144, D 1, letter L. Wing to N. Tinbergen (02/09/1970).
987 In a ms. of January 1973 Niko in this context mentions the impact Helen Clancy, a therapist from
Brisbane, had upon him in developing his environmentalist view and his conviction to study
the whole mother-child system. See ibid., Ms.Eng. c. 3147, D 52, ms. “Draft About Autism”
(01/1973), here pages 17–18. See also ibid., Ms.Eng. c. 3147, D 55, ms. “Bird Watching and
child watching” (n. d.). For the intention not to blame parents but Niko’s persistence on the
existence of environment-induced “temporary autism” see ibid., Ms.Eng. c. 3144, D 1, letter N.
Tinbergen to L. Wing (04/09/1970) and even more pronounced ibid., Ms.Eng. c. 3144, D 1,
letter N. Tinbergen to L. Wing (02/10/1970).
to unpleasant insights in their parents’ mind and behaviour) but his environmentalist view also involved – as we will see later – a much wider perspective upon the, in Niko’s view, malfunctional development of modern western civilizations. The wider view on human civilization helped to translate Niko’s criticism into a more anonymous sphere of the superindividual systemic dynamics and thus provided the opportunity to maintain his point without blaming a particular group of society. However, it would be false to interpret Niko’s shift to human kind simply as rhetoric strategy. As his unpublished manuscript on *Man* shows, N. Tinbergen seriously shared the concerns of other ethologists about the development of human kind. Moreover, one of Niko’s strategies to legitimate his emphasis of psychogenic causes was to question the exclusive differentiation between “genetically caused” and “environmentally caused”. In a letter to L. Wing he underlines:

> [...] the distinction between “genetically caused” and “environmentally caused” characteristics is simply no longer valid – every single characteristic whether structural or behavioural is both at the same time; we ethologists have initially simply been repeating the mistakes in thinking that for instance experimental embryologists had overcome some 30 years before us. And remember Medawar’s writings and work, for which he just received the Nobel Prize. It would be sad if the more difficult science of psychiatry were to repeat this mistake once more.

From the quotation eventually follows that Tinbergen in turn criticized psychiatrist to connect (in their view) two different symptoms with either nature or nurture, while he himself apparently applied both logic categories for both symptoms (at the same time over-emphasizing one of them). In other words, Niko applied to psychiatry exactly the same point of criticism D. Lehrman had put forward against Ethology in the early 1950s. If both the atypical behaviours of normal children and the behavioural deviations of autistic children shared, in principle, one and the same mode of genesis, that is, they were both the product of a division of labour between nature and nurture, it is – at least from a conceptual point of view – easier to think these phenomena as points on a continuum and not as qualitatively different psycho-pathological categories as L. Wing and M. L. Rutter suggested. To sum up, one may eventually say that the incipient conflict between the Tinbergens and the psychiatric scientific community originated from two main aspects: At first, Niko and Elisabeth Tinbergen were prepared to think a continuum of autistic syndromes which was meant to encompass not only more or less pathological cases but, even more far-reaching, normal and non-normal cases. Second, in any case, the abnormal was conceived more as environment-induced rather than as spontaneous effect of any genetic and / or organic disposition. Both aspects seem to be more or less direct consequences of the particular epistemic constitution shared both by the classical and the functional ethological scientific paradigm. Despite the partly critical discussion, the Tinbergens decided to publish their paper in *Science* but the editors presumably rejected the article which in turn gave the impulse to extend the original draft into a more extensive small book. In sum, one may therefore say that Niko

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988 For this wider context see Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3144, D I, letter N. Tinbergen to L. Wing (02/10/1970). This is where his studies on childhood autism meet with his earlier concerns on human kind.

989 Ibid., Ms.Eng. c. 3144, D I, letter N. Tinbergen to L. Wing (02/10/1970).

and Elisabeth Tinbergen’s engagement with childhood autism was sparked off by
the intensive reception of Corinne and John Hutt’s book. The subsequent process
of criticism and being criticized lastly culminated in a draft for a publication. Its
rejection led towards the extension of the draft into a small book. With writing the
book the activity shifted more to Niko.

*Early Childhood Autism.* The extension of the initial draft for a paper which fi-
nally culminated in *Early Childhood Autism* reveals an epistemic practice which
corresponds perfectly well with the route most of the dissertation theses Niko had
advised over the years had taken. Following G. Beale I have described this epis-
temic practice as “Tinbergian Practice”. However, as we have seen in the analysis
of the theses of Niko’s PhD students the character of these works which used to
stand at the end of this process changed over the years and depending on the over-
all scientific orientation these projects were placed within. In order to determine
the epistemic status Niko and Elisabeth Tinbergen’s first public statement on childhood
autism it is therefore necessary to analyze closely the argumentative scheme of the
book. In the preface of *Early Childhood Autism* the Tinbergens recapitulate the
genesis of their publication. “Our attention”, they write,

> was first called to early childhood autism by Drs. Corinne and John Hutt many years ago. We
> have become gradually aware of the basic correctness of their conviction that autism ought to be
> studied ethologically; and it was when we realised that the evidence pointed clearly to a definite
> hypothesis, and that this hypothesis had so far not been formulated by any worker on autism,
> that we decided that publication of our views should not be postponed any longer.

The quotation not only informs the reader about the genesis of the publication it
also indicates the general *methodological* overtone of the book. Its overall inten-
tion, we are informed shortly later, is to come to a hypothesis about the nature of
autism which in turn might include the possibility for an alternative therapy. In the
introduction it reads:

> This is why, although we shall call attention to a number of facts, both known and unknown,
> our main objective will be a discussion of points of method, and we hope to demonstrate the
> considerable potential of these methods for studies of non-verbal communication in general.
> We shall then present an hypothesis about the nature of autism which, if correct, could lead
> to a better understanding, possibly prevention, and conceivably even to curing of at least a
> proportion of autistic children, namely, those that are not suffering from “organic” or extreme
> genetic damage. As will be seen, we are convinced that this proportion may well be very much
> higher than is assumed by at least some of the specialists who have most recently discussed the
> problems.

As a tentative conclusion one may eventually say that *Early Childhood Autism*
contains a “reductive argumentation” whose intention was to prove an alternative
model of causation (including its practical consequences). In the following I would
like to reveal the pattern of this argumentation. It consists of mainly six propositions

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991 For the complete reference see fn. 945, page 315. A condensed version of the text was published
in the same year in the second volume of *The Animal in Its World*, a collection of selected
works of N. Tinbergen. See N. Tinbergen, “Early Childhood Autism – an Ethological Approach
Allen & Unwin, 1972, 175–199.

992 Tinbergen et al., *Early Childhood Autism*, 5.

993 Ibid.
which more or less coincide with the order provided by the chapters. Furthermore, this order is supported by the inner composition of each section: (1) Observations under natural and semi-natural circumstances show that children when confronted with unfamiliar persons or objects show ambivalent reactions.\(^9\)\(^4\) (2) These reactions can be analytically classified by applying two categories, the qualitative distinction between approach and withdrawal, on the one hand, and, on the other, a couple of supplementary parameters being apt to measure these types of behaviours quantitatively on a graded scale of intensities.\(^9\)\(^5\) (3) Observations show that the symptoms ascribed to Kanner’s syndrome are not only shown by autistic but also by normal children under certain circumstances.\(^9\)\(^6\) The Tinbergens claim:

Our observations so far, not tabulated but nevertheless substantial, not only confirm fully the opinion of the Huts that the negative responses (though even in the visual sphere infinitely much richer than the catchphrase “gaze aversion” might suggest) that are found in autistic children are seen regularly in normal children; they also have convinced us that the observational procedure is still in urgent need of further development. We find this also true of our own animal studies, even with species which we have studied for a lifetime. We must now elaborate our claim (confirmed by the Huts and several other colleagues in personal discussions) that normal children often show, under certain circumstances which we shall describe and interpret below, many other, and not only visual aspects of behaviour usually found in autistic children.\(^9\)\(^7\)

Normal children can therefore be made “temporarily autistic” which – in N. Tinbergen’s view – proves that both types of behavioural deviation lie on one and the same continuum.\(^9\)\(^8\) “Normal” children, in the Tinbergen’s view, differ from “autistic” ones only insofar as they show those deviating behaviours temporarily which have more permanency in autistic children. (4) Studies of courtship behaviours in Gulls revealed that ambivalent behaviours originate from motivational conflicts which, in turn, emerge when antagonistic tendencies such as sexual attraction and anxiety are raised simultaneously.\(^9\)\(^9\) When male Gulls court a potential female partner they raise in them an ambivalent state of motivation since the females are attracted sexually to the males but also tend to withdraw as a response to the male’s aggressive gestures which, in turn, are due to the fact that the females share a couple of qualities with other male rivals. In course of a normal courtship ceremony the conflict between approach and avoidance is resolved mostly by the part of the male applying suitable appeasement gestures to which the female responds and which support the reduction of the female’s anxiousness and help establish contact. The wide range of ambivalent reactions (as exhibited mostly by the female) can be explained by or “reduced to” (this is why that chapter is called “Complexity and Order”) the notion of two antagonistic though interacting motivation systems. The dissolubility of the conflict is explained by the high grade of plasticity of the entire

\(^9\)\(^4\) Tinbergen et al., Early Childhood Autism, chapter II., 12–16, especially 16.
\(^9\)\(^5\) Ibid., chapter III., 17–18. The latter category is related to concepts such as “extent”, “forcefulness”, “speed”, and “duration”. They are treated from three different angles: The form of the behaviour elements, their “sequential association with overt approach and withdrawal”, and their function (Ibid., 17).
\(^9\)\(^6\) Ibid., chapter IV., 18–21.
\(^9\)\(^7\) Ibid., 19.
\(^9\)\(^8\) Ibid., 20–21, also 40.
\(^9\)\(^9\) For the following see ibid., chapter V., 22–26.
motivation system which allows especially the female Gulls to respond adequately. Since the female Gulls react both to the males and to other surrounding environmental circumstances it is not legitimate to treat them as isolated scientific objects. The entire network of social and/or environmental relationships must be taken into account as a whole. (5) With the reservation that children are not motivated sexually the notion of dual motivation can be transferred to infant behaviour. Children confronted with strangers are both curious and anxious. “When we applied them [these methods] to child-stranger encounters in the three situations described at the start”, the Tinbergen’s claim,

we were forced to the conclusion that an encounter between a child and a strange adult creates in the child a state of motivational conflict that is very similar to that described for female Gulls in the pair-formation stage, except that of course in children the approach tendency is not sexually motivated. The children show by their overt behaviour that they are attracted to the stranger, i.e. tend to make eye contact, to approach him or her, and to further engage in social interaction of a variety of types. At the same time they are definitely afraid (the terms “timid”, “shy”, “anxious”, “insecure” etc. are often used loosely, and indicate slightly different complexes of motivational conflict states). This avoidance tendency expresses itself in a rich syndrome of more or less concurrent details of behaviour, such as keeping distance or moving away, avoiding eye contact, various degrees of turning away the head, various degrees of closing the eyes, etc. It is further important to notice that, with different children, the sensory modality which the child “locks out”, “filters out”, or “refuses to admit” can vary: most children avoid primarily visual input, but some reject even auditory or tactile input. We have to stress once more that for our understanding of the child’s state it is of paramount importance to realise that the ‘input’ that is relevant is specific, not general; the relevant inputs are those which specifically stimulate or reduce either the withdrawal system or the approach system. A child that seems “deaf” (i.e. ignores some acoustical social input) may (as we know from detailed experience) be at the same time extremely sensitive to, and attracted by non-social noises such as the faint ticking of a clock, the calling of a bird outside, or sounds that give it information about the activities of another child in a different room. A child that averts its gaze from us may at the same time be highly alert to the visual properties of its toys. It has to be stressed once more that few practices have blocked understanding of the behaviour of these children more than the thoughtless, but unfortunately fashionable use of general terms such as “perceptual malfunctioning”, “quantity of input” and “general arousal”. Those who apply these terms are often not aware that they are discarding and even contradicting a great deal of relevant information, and, because of that, may be drawing wrong conclusions.

Analogous to the courtship ceremony of the Gulls Tinbergen connects the adaptive responsiveness of the (“normal”) children to moment-to-moment fluctuations “within” their motivational system and these shifts, in turn, are traced back to stimuli emanated both within the body and in the outer environment. This is the reason why the children’s responses are characterized by a high degree of individual variability and/or subjectivity. Moreover, the fact that children respond to changes in their environment forbids to treat their behaviours as isolated phenomena. “What we have discussed so far suggests therefore strongly”, the Tinbergen’s underline,

that in order to understand even ‘temporarily autistic’ children referred to above, and perhaps the history of pathologically autistic children as well, it is not sufficient to study merely the behaviour

1000 Ibid., chapter VI., 26–28.
1001 Ibid., 26–27.
1002 Ibid., 27–28.
of these children themselves. It is clear that, even though a genetic factor will undoubtedly
be involved in rendering some children more liable to intimidation than others (see Rutter
1968), the behaviour of the adults in its early environment must be of tremendous importance.
It is therefore imperative that the behaviour of parents of autistic children be studied equally
thoroughly, not only because the mother can herself behave over-intrusively towards a child,
but because she may be a powerful agent in eliciting, and even soliciting such over-intrusive
behaviour in visitors. Surprisingly little evidence of the required quality is available.1003

(6) The dual motivation of children can be tested in experimental situations (i.e. the
“taming” of the child by the experimenter) and is supported by the ways children
react to over-intrusive gazes of fellow infants.1004 Proposition one to six lead to the
conclusion that autistic children suffer from a motivational handicap that prevents
them from resolving motivational conflicts in favour of social interaction, that is, an
environment-induced, anxiety-dominated imbalance of the motivation system.1005

“We submit”, the Tinbergen’s conclude,

that in each encounter with adults every infant is initially in a state of motivational conflict
between social or bonding tendencies, and timidity or fear. In normal children, growing up in a
normal society the conflict is solved, at every encounter, by combination of waning of fear and
elicitation of socially positive responses. If a combination of genetic and early environmental
factors produces an over-timid child, its encounters with adults take longer to swing towards
bonding. But the oversensitivity of fear may, in more extreme cases, prevent the unbalance of
the motivational conflict from being solved at all, and the child enters into a vicious circle, in
which the overactivating of fear becomes progressive. The resulting lowering of its thresholds
leads to fear responses to a greatly widened range of stimuli, which can ultimately include
signals which normally have a bonding effect, such as the adult’s face, and even a friendly smile.
Particularly in a world crowded with strangers the continuously increasing input into the fear
system simultaneously starves the bonding system. This can go so far that even normal parents
fail to establish a bond. The conflict between the two remains, resulting in general arousal
with all its consequences (such as for instance stereotypies), and the failure or even regression
of social developments (such as that of speech). According to this hypothesis the core of the
problem would seem to be found in desperate frustrated attempts at socialisation combined with
constant and intense fear.1006

This ultimate conclusion that the autistic disorder may be caused by an hyper-
aroused fear-system, in turn, serves as the basis of an alternative cure that is aimed
at a stepwise “taming” of the child, that is to say, analogous to the courtship display
of the Gulls, a play of mutual interaction in course of which the therapist perma-
nently monitors the gestures of the child and reacts correspondingly.1007 In doing so
the therapist both avoids irritating the child (e.g. through directly gazing at it) and
encourages the child to establish social contact.1008 In order to understand the argu-
mentation put forward by the Tinbergens adequately and to put it into perspective, I

1003 Tinbergen et al., Early Childhood Autism, 31.
1004 Ibid., chapter VII. and VIII, 28–31, and 32 respectively. The Tinbergen Papers include a letter
from J. T. Flynn, an ophthalmologist from New York, who supported N. Tinbergen’s view that
intrusive gazing might have an intimidating effect. See Bod. Lib., N. Tinbergen Papers, Ms.Eng.
c. 3144, D 8, letter J. T. Flynn to N. Tinbergen (10/07/1974).
1005 See for this chapter IX which is bearing the title “An Hypothesis”, Tinbergen et al., Early
Childhood Autism, 33–36.
1006 Ibid., 34.
1007 Ibid., 34.

The Tinbergen’s believed that drastic methods of treatment such as the application of electro
think, it is necessary to add a few comments. Firstly, it seems vital to keep in mind that the Tinbergen related their suggestions as to diagnosis and cure of the autistic disorder to a specific target group. In doing so they differentiated three main types of “autism” in *Early Childhood Autism*, namely “genetic”, “organic” and what they called “psychogenic” autism. From their account we can infer that the attribute “genetic” was meant to address the cases with *inherited* dispositions for Kanner’s syndrome which were considered difficult to be healed. In doing so and following D. S. Lehrman’s critique thereby they questioned the coincidence of the extensions of the two concepts “innate” (in a sense of “exhibited from birth onwards”) and “inherited” (in a sense of predisposed by gene effects) since they considered possible the existence of prenatal environmental impacts. The attribute “organic”, by contrast defined those cases of autism being caused by non-inherited external factors with recognizable physical effects such as brain damages or the mother’s infection with rubella during pregnancy – a hypothesis N. Tinbergen adopted from secondary literature but later was thoroughly questioned.

With “psychogenic autism” they meant a number of cases which were difficult to separate from temporary motivational imbalances in normal children and whose aetiology, in their view, was environment-induced. According to Niko and Elisabeth Tinbergen, “psychogenic autism” is a stress disease and only as such it is referred to by their theory on the “nature of autism”. The Tinbergen writes:

> Our remarks can best apply to the unknown proportion of children that are neither genetically so strongly predisposed to autism that they will develop the syndrome regardless of their early environment, nor are known to have suffered brain damage, in other words, to psychogenic autists. We are also well aware of the fact that on many occasions cures have been successfully applied to a variety of mental disturbances which seem to have no relation whatsoever with their causation. Nevertheless, we feel that we have the duty to make a few suggestions with regard to early recognition of incipient signs of autistic tendencies, and to treatment that is most likely to reduce the dangers of psychogenic autism.

The conception of autism within the wider context of stress diseases in connection with Niko’s environmentalist view involves not only the families but also the wider social systems which are considered relevant for the development of the children. From the quotation above, I think, it is possible to draw the conclusion that the Tinbergen primarily had in mind cases of, in their view, environment-induced mental disorder and less the cases with inherited disorders. However, we are not informed about the physical correlate of what they called “psychogenic autism” besides the hint that it is caused by a motivational imbalance and the fact that “normal” children are capable to dissolve the underlying conflict because their motivation system is highly flexible and therefore can adjust itself to changing stimuli situations.

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1009 For the differentiation of “genetic”, “organic” and “psychogenic” autism see ibid., 33.
1011 Tinbergen et al., *Early Childhood Autism*, 36.
1012 On Niko’s criticism of the modern urban civilizations see ibid., 34–35.
We can only infer, without having a proof in the text, that the motivation system of autistic children, in Niko’s view, is lacking what he called “moment-to-moment fluctuations”. Second, N. Tinbergen blamed “even the most open-minded workers on autism” of “riding certain ‘hobby horses’” by which he was to say that their research attitude (including their methodology and the results this methodology generated) was biased to a certain extent. In doing so, he drew implicitly a connection between the research tradition within which a particular researcher was standing and the results she or he produced. There is no doubt that this epistemological relativism applies to N. Tinbergen’s own writings as well. Scientific orientations acting within the field of behaviour studies sometimes not only chose so-called “model organisms” but also “model behaviours”. While Niko’s research on social behaviour established a tight connection between the study of displays and particular scientific objects such as the Stickleback or the Gull, later ecology-oriented projects broadened the perspective from signal behaviour (i.e. the exclusive focus on animal communication) to a wider range of adaptive behaviours. However, in course of this process, at least this is my impression, another prototypical behaviour soon turned out to obtain a representative status: The so-called maintenance behaviours which, for instance, include feeding, preening or grooming. As I have already mentioned these behaviours are meant to maintain various kinds of bodily equilibria and as such are part of the homoeostatic systems of living organisms. From the epistemological standpoint maintenance behaviours are structurally different from displays since their origin does not lie in an unusual deviation from a normal state of motivation (e.g. as is the case in the displacement reactions) rather than a temporary re-establishment of a normal state of equilibrium after this equilibrium state has been irritated by impacts or intrusions coming from the outside. I have already pointed out that Niko’s turn to Behavioural Ecology (or Functional Ethology in general) partly included a process in course of which he “re-framed” older concepts (such as the method of discrimination experiment) into the new scientific paradigm. My personal opinion is that Niko and Elisabeth Tinbergen’s studies on childhood autism perpetuated this tendency insofar as they re-conceptualized one of the most essential if not the most essential scientific concept(s) of Ethology’s classical period, the concept of stimulus- and reaction-specific motivation, in terms of a homoeostatic system. The crucial point of Niko’s “theory of autism” was and still is that he defined the motivation system underlying human social behaviours as, in principal, balanced and fluctuating system of antagonistic tendencies which get out of balance when they are confronted with over-intrusive stimulation but can be brought into a state of equilibrium through a discrete act of correction. The autistic disorder, in N. Tinbergen’s view, thus was to be understood as more or less temporarily state of imbalance which could be corrected, in principle, by an adequate cure. Niko’s view of Kanner’s syndrome and the children they were affected by the mental disorder in question was both subjectivist (in a sense that he emphasized the individual variability and the fluctuating character of the underlying motivational states) and mechanical (in a sense that the state of disorder can be changed back

1013 Some more details can be inferred from the illustration the Tinbergens added to their account. See Tinbergen et al., *Early Childhood Autism*, 35, Fig. 10.
1014 Ibid., 33–34.
into the previous state of order through an adequate intervention). The latter aspect becomes evident, for instance, in Niko’s comparison of the autistic disorder with a broken car that can be fixed – or better, whose defect can be avoided at all by applying some behavioural modifications to the driver. Niko’s description of the autistic syndrome as “derailment” points into the same direction because it implies corrigibility. In other words, what E. Crist called “mechanomorph” research attitude and which had been present in ethological theorizing whenever the causal analytical framework was applied now is re-placed as part of or essential constituent within the new functional paradigm and, in doing so, experiences a conceptual modification which makes it compatible with the new framework or the respective parts of it. It is therefore not quite correct to draw a simple connection between Niko’s display studies and his later work on autism since the underlying understanding of motivation has been made subject of a fundamental epistemological shift. The re-placement of Niko’s older concept of motivation – at least to a certain extent – also implied the reassessment of his widely criticized system of discrete drives. Some paragraphs in Early Childhood Autism therefore read as if they were a late rejoinder against his critics. In his view it was essential that overt reactions need to be understood as both situation- and subject-specific expressions which implied a more topographic idea of the nervous system. This is eventually one of the reasons why Niko attacked so fiercely all concepts which conceived motivation solely in terms of “general arousal” or understood the afferent leg of the nervous circuit through the lens of mere quantification. In Early Childhood Autism it reads:

What is important to stress is that it has been shown that, with regard to animals, it is too simplistic to speak of these phenomena in terms of “general arousal” only; what is aroused in many of these situations is a set of relatively specific behaviour systems. The matter is complicated because one of the secondary results of dual arousal of specific systems is probably

1015 For Niko’s emphasis of the subject in a sense that her/his state of motivations including its moment-to-moment fluctuations matter, see ibid., 27–28. What N. Tinbergen here re-activates is the criticism early ethologists put forward against reflexological theories of behaviour, namely that incoming stimuli are filtered while they are conveyed to the central parts of the nervous systems and therefore the causation of behaviour must be thought together with the process of centralization. It would be of great interest to find out whether and how Tinbergen’s late understanding of centralization differed from his earlier model.

1016 See for Niko’s use of the car metaphor in Early Childhood Autism, ibid., 27, 38–39. C. Silverman stumbled at Niko’s “broken-car” metaphoric (Silverman, “’Birdwatching and Baby-Watching’”, 181) but in fact it can only be appreciated adequately if we take into account that it might be an allusion to K. Lorenz’s use of the metaphor. See K. Lorenz, “Induktive und teleologische Psychologie”. In: Idem. Über tierisches und menschliches Verhalten. Aus dem Werdegang der Verhaltenslehre. Gesammelte Abhandlungen. Vol. 1. (Piper paperback). München: Piper, 1965 [1942], 385–386, and K. Lorenz. “Taxis and Instinctive Behaviour Pattern in Egg-Rolling by the Greylag Goose”. In: Idem, ed. Studies in Animal and Human Behaviour. Vol. 1. Cambridge (Mass.): Harvard University Press, 1970 [1938], 356–357, respectively. My opinion is that N. Tinbergen, in reactivating the metaphor, marked the difference between his late homeostatic understanding of motivation and the more centralist-oriented concept that had coined Ethology’s pre-ecological stage: Lorenz’s understanding of causal analysis was headed towards more drastic intervention, while N. Tinbergen’s homeostatic concept is directed towards self-healing – an endogenous nuance which is eventually implied in the idea of “homeostasis”. This is also how we have to read Niko’s appreciation of the “do-it-yourself” mothers (DIY) to whom the Tinbergen’s later publication “Autistic” Children. New Hope for a Cure (1983) is dedicated. I come back later to Niko’s emphasis on self-healing by non-artificial measures.

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an increase in general arousal, but it is important to realise that this is a consequence of the
initial elicitation of specific systems. Consequently, speaking in terms of general arousal only is
discarding part of the available evidence. This is important for the assessment of the value of a
number of physiological measurements that are being made at the exclusion of more relevant
direct measurements of the basic phenomena. Similarly, it is too simplistic, and neither in
accordance with the facts nor fruitful for further research, to describe such conflicts merely in
terms of overall “quantity of input” - in many cases of motivational conflict it is above all the
types of input that count, defined in terms of which behaviour patterns they specifically elicit.1017

Despite Tinbergen’s insistence on the relative specific character of the behaviour
system, I think, it would be incorrect to claim that the model of behaviour organization
which he outlines in the quotation above coincides with his classical system
of drives. It rests upon another reference system since it conceives the elicitation of
specific systems as “primary” and the general level of excitation as “secondary”.
Also Tinbergen claims that the “types of input” should be defined in terms of
their effect – the types of overt behaviour they release.1018 Complementary to re-
conceptualizing the concept of “motivation” we can also make evident a modification
of the scientific practice of observation. While earlier studies were based on
observations made from hides and mostly without any kind of direct intervention,
the situation changed with the study of children. The observer now was directly
involved with the object that was to be observed and thus took a paradox situation
of being both observer and experimenter.1019 In fact the observer found himself
mostly bound in a triangular constellation consisting of the child, the mother and
the observer-experimenter who tried to grasp the gestures of the child as well as the
mother who, in turn, responded to both actors. It is of some interest that it is the
observer-experimenter who takes the ambiguous part within this setting. From the
epistemic view he or she is therefore structurally connected with the (autistic) child,
just as well as the notion of ambiguous placement within a reference system enlight-
ens further Niko’s understanding when he, for instance, claimed a methodological
imbalance in psychiatric methodology. To sum up this line of thought, I’d like to
stress that the hypothesis Niko and his wife put forward to assess the aetiology of
childhood autism (motivational imbalance) eventually implied another, eventually
more homoeostatic, understanding of the nervous circuit (and especially it afferent
part) which deviated both from Niko’s own earlier classical understanding and the
one put forward by several of his pupils criticizing his early reductions. Thirdly,
in building an analogy between the courtship ceremony of the Gulls and the cure
of autistic children which, at least to a certain extent, is mediated by the concept

1017 Tinbergen et al., Early Childhood Autism, 26.
1018 From a historical and structural point of view this model is therefore much more like O. Hein-
roth’s early typology of “Stimmungen” (moods) rather than Niko’s own hierarchical system of
drives outlined, for instance, in The Study of Instinct (1951).
1019 See Niko’s reflections upon the status of the observer ibid., 16, 18–19. That the Tinbergens’
method of observation included a type of experiment that included themselves as “dummies” that
is as observing experimenter can also be inferred from a lecture Niko had written to be delivered
in Santiago de Compostela in April 1982, the so-called “Spanish Lecture”, which finally had
to be cancelled for Niko’s health problems. See Bod. Lib., N. Tinbergen Papers, Ms.Eng. c.
3157, D 70, ms. “A ten years’ study of Early Childhood Autism and a new, successful therapy”
(1982). In Darwinian practice N. Tinbergen must have re-read and corrected the text at a later
date. At the top we find the annotation: “I am now happy with this text N. Dec. 1987”.

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of “taming”, with which the Tinbergens used to describe their approach of therapy playfully, their theory of autism obtains a gender-connotation.\textsuperscript{1020} Since it is the female Gull which is described in terms of motivational conflict and the male which regulated the course of the courtship ceremony with his behaviours the autistic patient is implicitly associated with the female sex (and gender), while the therapist or caregiver is latently supposed to be male.\textsuperscript{1021} From a strictly scientific point of view, however, this gives us a wrong impression of the mental disorder in question since it has been made evident by statistical studies that boys not girls are more liable to be affected by the autistic syndrome.\textsuperscript{1022} That Niko and Elisabeth Tinbergen’s understanding of childhood autism has a gender bias can eventually be explained by the fact that the differentiation between proximate and ultimate causation which also regulates the way they framed the phenomenon can be interpreted in terms of sex- and gender-related concepts. That the causal architecture underlying the argumentation of the Tinbergens was about to produce a wrong impression as soon as it was expressed in terms of sex-related terms shows that the modes of knowledge production work quite well even in case the applied epistemic schemes and their expressions do not match the empirical reality. Niko’s latent misrepresentation, however, shows how virtuously he handled cultural codes and their semantic subtleties: He actually did not only understand his science as a process of scientization (i.e. conceptual representation of empirical phenomena) but also as reproductive dynamics of a (i.e. his) scientific community. In other words, a fictitious account or a “wrong” scientific statement \textit{still} fulfils a function in a sense of maintaining the dynamics or the process of cultural reproduction – and even goes beyond insofar as it makes this dynamics obvious! What is if Niko Tinbergen was aware of this? What about rereading his late works with keeping this idea in mind. This leads me to a fourth aspect. The Tinbergens insisted that their intention was not to put forward oversimplified inferences from animal to human behaviour but, instead, to apply the methodological achievements of scientific ethology to a field in which they thought the methods of observation under non-artificial conditions and the examination of motivation conflicts underlying non-verbal communication could make a contribution.\textsuperscript{1023} Yet, even in case we take for granted the primary methodological motivation of the study it still remains to ask why Niko referred back to the social behaviour of a highly territorial species of animal although especially the newly emerging and rapidly growing branch of Behavioural Ecology had already begun to understand the more complex forms of social organization in higher mammals.

\textsuperscript{1020} See Tinbergen et al., \textit{Early Childhood Autism}, description of the courtship ceremony, 22–26, and 26–27.
\textsuperscript{1021} Just a note: From the six case histories included in “
\textit{Autistic” Children}, Paula, Olga, Susan, Fae, George and Judy, five are girls! See Tinbergen et al., “
\textit{Autistic” Children}, 269–305.
\textsuperscript{1022} Feinstein, \textit{A History of Autism}, 29, 140–141, 175–176, 180, 271.
\textsuperscript{1023} For this dual motivation of the study see the explanatory introduction Tinbergen et al., \textit{Early Childhood Autism}, 9–12, especially 11-12, and also 22. In a ms. for a lecture delivered in 1972 we find a slightly modified version of this argument. Here it reads: “Our exercise is \textit{not} so much adding to factual information – rather: \textit{putting facts in a different context}”. See Bod. Lib., N. Tinbergen Papers, Ms.Eng., c. 3147, D.55, ms. “Autism Colloquium Tavistock Febr. 1972” (02/02/1972), here page 1. Thus the “methodological” transfer turns out to be more a process of “re-contextualization” or epistemic re-framing.
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and even in primates – as J. Mackinnon’s and I. Douglas-Hamilton’s dissertation projects show. “Of the large variety of social interactions in animals studied by ethologists”, the Tinbergen writes,

those most relevant to our present subject concern the process of “bonding” or “socialisation” in animals, in particular that of pair formation in monogamous species, in which a personal bond between male and female is established. Of this category, those species (numerous in at least four or five main classes of vertebrates) in which the reproductive season begins by an upsurge of intraspecific aggressiveness in the male are the most relevant. In most, though not all of these species the male’s aggressiveness is coupled with the development of an attachment to a particular site; these two phenomena together result in the occupation and defence of a breeding territory – incidentally, the concept so often rashly applied to human behaviour. In our discussion it is primarily the method, not the phenomenon itself that will occupy us, and further the aggression aspect rather than the site attachment (even though the latter is not entirely irrelevant). Our description will refer to a group of species to which we have devoted a lifetime of research: the Herring Gull and relatives, and the Black-headed Gull.\footnote{\textit{Ethology and Stress Diseases}. In October 1973, N. Tinbergen received a call from Stockholm to inform him that he had been awarded the Nobel Prize for Physiology and Medicine together with K. Lorenz and K. v. Frisch for their discoveries concerning the organization and elicitation of individual and social behaviour patterns.\footnote{\textit{Early Childhood Autism}, 22. For the methodology transfer see also \textit{ibid.}, 19. For many including N. Tinbergen himself and the people who were involved with him the nomination was a surprise since Biology and Zoology were none of the areas in which scholars can be honoured with the most prestigious of

On basis of this quotation we may argue that Tinbergen’s expertise in Gull behaviour allowed him to infer from the known to the unknown or that the process of re-placing older convictions within the new functional paradigm required to establish a cross-reference to these concepts. However, I think, it is legitimate to ask whether the fact that the Tinbergens chose a territorial animal for their analogy also had a heuristic effect which a mammal species with a complex social organization based on social hierarchies and corresponding behaviours could not have entailed? One aspect which surely mattered was that both in a male Gull courting his female partner and the therapist re-socializing an autistic patient are required to dissolve “rejection” into “social interest” (in a very literal sense), “withdrawal into approach”, or “avoidance” into “social contact”. Insofar one may say the transfer the Tinbergens introduced in \textit{Early Childhood Autism} was less one of methodology rather than of a heuristic basic structure which helped to grasp the phenomenon or, to put it in other words, to read order into complexity. In addition to that, one may eventually say that autistic children express their emotions by translating them into time and space. Non-verbal gestures like turning away the head, gaze avoidance, turning ones back to an object and so forth are primarily spatial expressions of motivational constellations which eventually might be more connected with the regulation of distance rather than the regulation of social hierarchies as could be expected when dealing with adults. The reference to a territorial species of animal thus might be a more appropriate heuristic tool than we might be prepared to concede at first sight.

(R2) Ethology and Stress Diseases. In October 1973, N. Tinbergen received a call from Stockholm to inform him that he had been awarded the Nobel Prize for Physiology and Medicine together with K. Lorenz and K. v. Frisch for their discoveries concerning the organization and elicitation of individual and social behaviour patterns.\footnote{See for the details concerning N. Tinbergen’s nomination, Kruuk, \textit{Niko’s Nature}, 268–273.}
all international awards and – as H. Kruuk argued – the prize usually is granted for unique outstanding single discoveries. According to H. Kruuk, Sir P. B. Medawar who had received the Prize in 1960 for his discovery of acquired immunological tolerance most likely was the one who had recommended the three ethologists for the nomination. Medawar was a friend of Niko’s, had been admiring his work for many years and had supported Niko on “several important occasions”, as H. Kruuk put it.\footnote{1026} Despite the distortions his work had to face in several newspapers and magazines echoing his nomination with the Nobel Prize and the distraction the discussion about his friend’s Nazi past had caused, the honour he had received had also an encouraging effect upon Tinbergen’s belief that Ethology can and should make a contribution to human welfare. This was the overall tenor of N. Tinbergen’s acceptance lecture he delivered during the award ceremony on December 12\textsuperscript{th} 1973. It was later published in Science as “Ethology and Stress Diseases”.\footnote{1027} If we take the perspective of someone who is about to reconstruct N. Tinbergen’s engagement in childhood autism, one may eventually say that, in comparison to Early Childhood Autism N. Tinbergen’s Nobel Lecture, although it is much shorter, provides a more extended view insofar as it places the autism problematic within the wider context of stress diseases together with an account of the so-called “Alexander technique”. Both aspects are put forward as examples for the contribution Ethology could make to Medicine. Ethological research, in turn, could be upgraded as “now being acknowledged as an integral part of the eminently practical field of medicine”.\footnote{1028} The text is not so much of interest because it provided ultimate novelties. However, from a science historian’s point of view it is quite a remarkable document since it presented the knowledge in a way that was atypical in comparison to Niko’s late theoretical accounts and also in comparison to Early Childhood Autism. The core of the later publication consisted of two main topics, “early childhood autism” and the so-called “Alexander technique” each of which were treated in four unmarked subsections. Thus Niko’s account on childhood autism began with alleged “uncertainties” he ascribed to the research of the professionals and a brief account how they (i.e. the Tinbergens) came to study autism (together a sort of introduction).\footnote{1029} After that it continued with a brief account of their view in matters of diagnosis and cure and, finally, ended with a short outline of the main results of their study. An assessment of these results in terms of “what alerts” and “what gives hope” lastly rounds off the account. In so far, the sections on autism recapitulated less their previous study, Early Childhood Autism, rather than the entire course of their engagement that had begun as a more or less private interest but soon extended into the public sphere. F. M. Alexander, born in Tasmania in 1869 and, as Tinbergen put it, “a reciter of dramatic and humorous pieces”, suffered from “serious vocal trouble” and, according to Niko’s account, “came very near to loosing his voice al-

\footnote{1026}{See \textit{ibid.}, 268.}
\footnote{1027}{For the full reference see fn. 946, page 315 of my thesis. H. Kruuk has underlined that Niko’s Nobel Lecture was even more concerned with human kind, its welfare and the contribution Ethology could make than in his inaugural lecture of the year 1968 and his Royal Society Croonian Lecture he had delivered in 1972. See \textit{ibid.}, 273.}
\footnote{1028}{Tinbergen, “Ethology and Stress Diseases [1974]”, 20.}
\footnote{1029}{See \textit{ibid.}, 21–23.}
In a process of self-healing he managed not only to cure himself but, in doing so, developed what we would nowadays eventually call a “physiotherapy”. In short, his therapy was aimed at erasing the misuse of the body and its locomotor system by careful observation and successively manipulating the entire muscle system. According to Tinbergen, it promised improvement in quite a number of sufferings in various fields such as high blood pressure, breathing, depth of sleep, overall cheerfulness and mental alertness, resilience against outside pressures and a couple of other psycho-somatic illnesses. Tinbergen’s account is divided in two parts. With a more empirical approach he describes in a first step F. M. Alexander’s life and history as well as his technique and the documents showing his success before he elaborates upon his own experiences with the therapy which he had been able to gather during a self-experiment. In a second step, he enters into an analysis of the causal mechanisms underlying Alexander’s therapy. In doing so, Tinbergen mentions three areas of physical study (the question of nervous organization, a reassessment of the body-mind boundary, and the reassessment of the muscular system as a web of muscles) to which Alexander’s approach could possibly make a scientific contribution. A final conclusion rounds off the account. Although Niko claims that his “second example of the usefulness of an ethological approach to medicine has quite a different story” he, nonetheless, established a connection between the two examples insofar as both of them demonstrated the usefulness of the kind of open-minded observation he associated with his catchphrase “Watching and Wondering”. Moreover, both examples referred to non-professional or even inexpert, though in Niko’s view, highly promising and trustworthy ways of treatment of what he called “stress diseases”. In addition, in both cases the diseases were conceived as deviations of an originally healthy state of the body. On the other hand, my structural reading shows that both accounts operate with two complementary epistemic schemata: While his treatment of autism understands the “usefulness of the ethological approach” in a sense of making scientific insight productive for a wider public community, Niko’s account of the so-called Alexander technique inverts the perspective and asks how inexpert knowledge can be made productive for scientific enquiries. The former of the two processes is practical, the latter is analytical and my impression is that Niko applied both epistemic schemata more in the way a classical ethologist would have approved of it. Altogether we can read N. Tinbergen’s lecture eventually as the attempt to use his ethological heritage in order to penetrate the boundary between science and public community from both sides and thus to expand the perspective of both social systems. In doing so N. Tinbergen perpetuated also an epistemic tradition which can be traced back to the very early days of Ethology. The Tinbergens remarked in “Autistic” Children that their previous works including the Nobel Lecture “received a curiously, but interestingly, mixed reception”. “The majority of professional students of autism”, they continue,
Other colleagues and friends like M. Zappella remarked that the controversy Niko caused with his interest in childhood autism was led with unusual vehemence – a matter of fact he explained with both the emotional attachment of some of the protagonists in the field (such as Lorna Wing who had an autistic child herself) and the fact that Niko was invading into a field of research that was not his own.\textsuperscript{1034} Can I determine more precisely where exactly the demarcation line between the different positions was? The correspondence on autism in N. Tinbergen’s papers shows that some wrote the Tinbergens because they felt that they needed to defend the method of testing under controlled conditions.\textsuperscript{1035} Another issue where the opinions clashed was Niko’s thesis that there existed no clear cut difference between “normal” and “autistic” children.\textsuperscript{1036} Some correspondents claimed that Elisabeth and Niko Tinbergén’s disregard of the potential heritability was ill founded and contradicted by clinical studies.\textsuperscript{1037} The replies of the Tinbergens in general show that they were convinced that their view – although it represented the position of a minority – was justified and could make a contribution to help the affected children. Moreover, both their replies to critics and the comments they wrote to persons who were “benevolently interested” help to peel off their views more accurately. Thus, in a letter to \textsuperscript{1038} Mason we find more detailed information about their method of observation. Observation in their view means the quantitative assessment of “even the slightest non-verbal expressions” relative to the specific environment the child dwells in the moment of showing the behaviours. This also included the possibility of minor manipulations for the sake of both therapy (“taming procedure”) and diagnosis. The correspondence with J. Richer reveals that putting forward the continuity-hypothesis was not only a strategic move but also an aspect that concerned therapists in their everyday work.\textsuperscript{1039} “You point out”, writes Richer, that one feature of much behaviour is that there are fine gradations between what is taken as one thing and what is taken as another. This has dogged my work on stereotypies, there are many occasions when I would like to say that some behaviour is functionally the same as a stereotype

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\textsuperscript{1033} Tinbergen et al., “Autistic” Children, 2–3, also 214. See also Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3147, D 55, ms. “Confidential” (22/10/1972).
\textsuperscript{1034} For Zappella’s retrospective account see ibid., Ms.Eng. c. 3146, D 47, letter M. Zappella to N. Tinbergen (11/05/1980).
\textsuperscript{1035} Ibid., Ms.Eng. c. 3144, D 3, letter B. and D. L. Bridgeman to N. Tinbergen (22/07/1972 [!]\textsuperscript{CL}), incl. unpubl. ms. for Science.
\textsuperscript{1036} Ibid., Ms.Eng. c. 3144, D 3, letter B. and D. L. Bridgeman to N. Tinbergen (22/07/1972 [!]\textsuperscript{CL}), incl. unpubl. ms. for Science.
\textsuperscript{1037} Ibid., Ms.Eng. c. 3144, D 3, letter B. and D. L. Bridgeman to N. Tinbergen (22/07/1972 [!]\textsuperscript{CL}), incl. unpubl. ms. for Science. J. Newson claimed “that it is far too simple to attribute the syndrome of autistic behaviour to any failure of the parents to react in an ordinary way towards their babies”. See ibid., Ms.Eng. c. 3144, D 5, letter J. Newson to N. Tinbergen (26/03/1973).
\textsuperscript{1038} Ibid., Ms.Eng. c. 3144, D 5, letter N. Tinbergen to [?]\textsuperscript{CL} Mason (11/01/1973).
\textsuperscript{1039} Ibid., Ms.Eng. c. 3144, D 5, letters J. Richer to N. Tinbergen (24/01/1973) and N. Tinbergen to J. Richer (01/02/1973).
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but am held back because it seems to occupy an uneasy position between what even the most conservative would call a stereotypy, and “normal” behaviour.\footnote{Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3144, D 5, letter J. Richer to N. Tinbergen (24/01/1973), page 1. A later letter written by J. Richer shows that he not only shared Niko’s continuity hypothesis but also his environmentalist stance and his thesis that autism was rooted in an emotional defect. See \textit{ibid.}, Ms.Eng. c. 3144, D 10, letter J. Richer to N. Tinbergen (01/01/1975), incl. draft mss. for a film on autistic children and a paper for the \textit{Nature} magazine.}

In Richer’s view the quantitative work forces the observer in decisions which he otherwise “would rather put into abeyance”.\footnote{Ibid., Ms.Eng. c. 3144, D 5, letter J. Richer to N. Tinbergen (24/01/1973), page 1.} Niko’s response clearly reveals that his understanding of a graded scale of behaviours did not exclude internal classifications being based on refined techniques or capabilities, on the one hand, or on the establishment of correlations in time, on the other.\footnote{Ibid., Ms.Eng. c. 3144, D 5, letter N. Tinbergen to J. Richer (01/02/1973).} In other words, therapists were confronted with a need “to bring order into chaos”, as the Tinbergens put it, and it was the ethological expertise which provided the measures. We can infer from Niko’s letter that these measures in the first place consisted of a more “open-mindedly” observational exploration of all the behaviours displayed by an infant and, subsequently, a more intuitive measuring and correlating with specific circumstances. Comments on the nature vs. nurture problematic show that the Tinbergens refused the notion that autism spectrum disorders (ASD) were caused by “purely” heritable factors and therefore at least partly due to a disturbance of the child-adult relationship.\footnote{See \textit{ibid.}, Ms.Eng. c. 3144, D 5, letters N. Tinbergen to J. Richer (11/01/1973), and \textit{ibid.}, Ms.Eng. c. 3144, D 5, N. Tinbergen to J. Newson (29/03/1973), here page 2–3 of the attached ms. See also \textit{ibid.}, Ms.Eng. c. 3144, D 3, letter N. Tinbergen to B. and D. L. Bridgeman (28/07/1974), and \textit{ibid.}, Ms.Eng. c. 3144, D 9, letter N. Tinbergen to B. Børresen (09/12/1974).} In his comments to J. Newson’s manuscript of his paper \textit{Towards a Theory of Infant Learning} N. Tinbergen repeats his claim to understand the mother-infant interaction not only in terms of mutual communication but also as a mutual programming system.\footnote{\textit{Ibid.}, Ms.Eng. c. 3144, D 5, N. Tinbergen to J. Newson (28/03/1973) and N. Tinbergen to J. Newson (29/03/1973), incl. ms. with comments on Newson’s paper “Towards a Theory of Infant Learning”. Newson’s paper was later published under a slightly changed title. See J. Newson. “Towards a Theory of Infant Understanding”. In: \textit{Bulletin of the British Psychological Society} 27 (1974), 251–257.} In doing so, he tapered his approach to the receptive functioning of the mother-child dyad which he conceived as a holistic unit. Newson, by contrast, though in principle sharing the environmentalist approach, tended to widen the perspective beyond the dualism by integrating a broader variety of causal factors including different forms of heredity and cultural transmission.\footnote{See, for instance, \textit{ibid.}, 253–254.} Amongst all criticism published in books or scientific journals L. Wing’s and D. M. Ricks’ paper \textit{The Aetiology of Childhood Autism: A Criticism of the Tinbergens’ Ethological Theory} eventually was one of the severest.\footnote{See L. Wing. “The Aetiology of Childhood Autism: A Criticism of the Tinbergens’ Ethological Theory”. In: \textit{Psychological Medicine} 6.4 (1976), 533–543.} After summarizing the theory put forward by \textit{Early Childhood Autism} and Niko’s Nobel Prize acceptance lecture Wing mainly concentrated on six aspects in which she disagreed and favoured an alternative standpoint. At first, Wing claimed that the concept of motivational conflict may not apply to autistic children in the same way it does
with normal ones. She argued that neither normal children showing behavioural deviations in response to deprivation from their mother nor intellectually retarded children who have suffered from privation in early life show the same behavioural symptoms as autistic children. Second, Wing partly agreed with the Tinbergen's hypothesis that normal children under certain circumstances show autistic symptoms (i.e. social withdrawal) yet claims that no evidence has been put forward to show “that autistic children, in their early lives, have been exposed to more events, such as admission to hospital, which cause disruption of social bonding than comparable groups of normal children or children with other handicaps”. Moreover, in contrast to the theory that autism is due to an anxiety dominated motivation conflict Wing postulated that autistic children suffer from severe impairment of the normal ability to classify and label experiences and to build up a store of ideas in coded (symbolic) form, which can readily be drawn upon to help in understanding the present and planning for the future.

In other words, L. Wing saw the roots of the autistic disorder in the process of cognitive integration and less, as the Tinbergen did, as the loss of the emotional (motivational) plasticity which they considered necessary to restore a motivational equilibrium. In addition, Wing claimed that the symptoms shown by autistic children resemble developmental receptive speech disorders and that autistic behaviour “is closely analogous to the behaviour seen in some congenitally blind and deaf/ blind children, especially those affected by maternal rubella [...] or retro-lental fibroplasia”. Third, Wing suggests that the observation that many autistic children do not show all symptoms right from birth cannot be taken as an argument against a potential hereditary condition. “The autistic syndrome”, she says, “unfolds and changes with the different stages of development from infancy to adult life and to understand the syndrome one must have experience of it in babies, children, adolescents and adults”. Fourth, L. Wing questioned that the parents of autistic children stand out in matters of child-rearing methods or their personalities. Fifth, Wing was sceptical about the Tinbergen's claim that a sizeable number of autistic children can recover particularly when being treated with their non-intrusive therapy. She writes: “There exists nowhere in the literature acceptable proof that any therapy, physical or psychological, has produced a complete cure in children suffering from the syndrome described by Kanner”. In order to understand Wing’s argument correctly it is necessary to keep in mind that she distinguished sharply between “complete recovery to normality”, on the one hand, and “a reduction in secondary behaviour problems and the acquisition of useful skills, leaving the basic impairments unchanged”.

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1047 Ibid., 536–537.
1048 See ibid., 537–538, here 538.
1049 Ibid., 538.
1050 This suggests that both researchers also had a different understanding of the functions of the central parts of the nervous system.
1051 See ibid. This would refer more to the disturbance of the peripheral parts of the nervous system being held responsible for the perception or even sensation of external stimulation.
1052 See ibid., 539.
1053 Ibid.
1054 See ibid.
might be incurable, at least on basis of the current state of knowledge (1976), only refers to the former of the two described effects of treatment. In addition to that, she maintains that the diminution or disappearance of single symptoms such as social withdrawal does not necessarily mean that the child has been “cured” in the narrow sense of the word which does not exclude the possibility that an appropriate training might not have a positive effect in the second wider sense of the term. Finally, L. Wing underlined that there is no hard evidence for the hypothesis put forward by the Tinbergens that autism is either more common than previously assumed or actually on the increase. The epidemiological studies she refers to, in her opinion, show that “there is no evidence of any increase in the prevalence of the typical or near-typical autistic syndrome within the last decade”. Although Wing was prepared to concede that the label “early childhood autism” was to be handled with care and that a wider range of problems may be classified as early childhood autism she rejected the implications of the Tinbergens’ thesis that autism might be in the last consequence a common epidemiological phenomenon. Thus she discarded both the notion that autism is primarily a non-organic phenomenon and that there is no qualitative difference between normal and autistic children. Wing thus took offence at the Tinbergens’ more general practice to approach the phenomenon in question in terms of continuity and her criticism of this practice also mirrored in the accusation the Tinbergens were confusing concepts, for instance, when lumping together “cognitive” and “speech defect” or, as Wing marked, their ambiguous use of the concept of “non-verbal behaviour”. In doing so Wing’s criticism turned into a discussion of scientific standards whose maintenance, in her view, included “precision and clarity of definition, care in selection of the subjects to be studied and of control groups, and detailed attention to methods of measurement and presentation of results”. “Even more breathtaking”, L. Wing writes nearing the end of her paper,

is the Tinbergens’ statement, “we reject as utterly unscientific the remark that ‘the onus of proof is on us’”. The onus of proof may not be on the proposers of any hypothesis but, as Popper maintains (1972), the onus of trying systematically to disprove their hypothesis certainly is, and this duty the Tinbergens appear to have rejected out of hand. The result is that they have given us no reason why we should take their theory seriously, while a study of the relevant literature suggests strongly that it should be discarded.

Asides the fact that L. Wing referred back to the earlier correspondence with the Tinbergens in this quotation, it reveals that she declared the Popperian hypothetico-deductive method a mandatory methodological prerequisite of psychiatric research

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1056 See ibid., 539–540.
1057 Ibid., 540.
1058 Ibid., 540, 541.
1059 See ibid., 541. According to L. Wing, the term “non-verbal” can refer to cognitive processes or methods of communication that are not spoken out loud or may be used to address practical skills that do not require linguistic symbols for their performance. In her view autistic children “are markedly impaired in both vocal and non-vocal symbolic processes, but may be very good indeed at non-verbal (non-symbolic) fitting and assembly tasks” (Ibid.).
1060 Ibid.
1061 Ibid., 542.
as she saw it. However, the functional framework into which the Tinbergen had translated their research on childhood autism was not fully compatible with Popper’s concept. In the controversy with L. Wing we can therefore observe, as Niko Tinbergen quite rightly recognized, a clash of scientific “regimes”, as he put it. On closer inspection, I think, there are at least three main epistemological deviations that can be precipitated from Wing’s six fields of objection. At first, there may be a fundamental difference as to whether the autistic syndrome should be described in terms of continuity or discontinuity. This point of demarcation mirrored in the question whether or not there is a qualitative (organic) difference between normal and autistic children but also in the more methodological question how analytical the applied methods ought to be. Second, the Tinbergen stretched the notion of continuity wider than it was common practice in the field of psychiatric research. This becomes evident, for instance, in L. Wing’s objection against the extreme widening of the label of “autism” she has identified in the Tinbergen’s works although she was prepared to concede herself that more phenomena might be classified as childhood autism than it was done so far. Finally, the epistemic modifications particularly on the level of causality which the ecological orientation had inherited from Classical Ethology have led to an alternative model of the nervous circuit which now clashed with the one applied in clinical psychiatry. In contrast to the Tinbergen, L. Wing’s understanding of the afferent leg of the nervous circuits seemed to be a process of cognitive integration and abstraction primarily mediated by the capacity to speak. Lastly, we can infer from L. Wing’s criticism that the clash of epistemic regimes resulted in a more severe type of scientific conflict in as much as the question of scientific acceptability was asked in general. I consider it a significant gesture in itself that Elisabeth and Niko Tinbergen did not adopt Wing’s practice of refutation and disciplinary exclusion in their rejoinder but, more productively, intended to draw once more the readers’ attention to those aspects of their theory they considered “a potentially fruitful approach to the problems posed by the autistic deviation”. 

The Tinbergen felt misunderstood since they had intended to introduce another perspective. Correspondingly, the disagreement in their view, turned out to be less a “matter of facts per se” rather than as “one of how to look at the problems”. That is they intended to make familiar the scientific community of psychiatrists with an allegedly unfamiliar approach which, in their view, might yield promising results even in case it cannot be reconciled yet with all the facts that are regarded as established. Niko and Elisabeth Tinbergen’s rejoinder therefore more or less consists of the propositions they had put forward in their book without replying overtly to the arguments put forward by L. Wing and D. M. Ricks. Thus they characterize once more the cornerstones of their ethological methodology (plea for more non-intrusive observations, comparison of normal with autistic children, and correlation of observable behaviours with specific environmental conditions) before they, in a second step, elaborate upon three aspects they consider relevant when treating the subject of childhood autism: These main areas of examination are the nature of

1063 Ibid.
1064 Ibid., 549.
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autism, genesis and development of the autistic syndrome and, finally, the question of treatment and prevention. What might stand out in this account in comparison to their earlier publications can be summarized in three paragraphs. At first, there is a less rigorous and exclusive definition of the dichotomies of both nature vs. nurture and organic vs. psychogenic. “With regard to both issues”, the Tinbergen claim, “it is of course not a matter of either-or; of course, organic and psychogenic influences can act together, and the same is of course true of genetic and environmental agents. In neither case are the notions mutually incompatible”. That is to say, in contrast to most of the other works on autism published by the Tinbergen I see here a tendency to enter the intermediate area between the proposed dichotomous terms. Second, and somewhat analogous, we can find a more precise conception of the continuum the Tinbergen presupposed to exist in-between the behaviour of normal and autistic children. The normal behaviours of autists, they claim, resemble the more autistic behaviours of normal children. Asides the fact that this statement reveals the Tinbergen’s intention to deconstruct the boundary between normal and non-normal from both sides the re-conception of the continuum in terms of an area of intersection also allows us to think each pole with individual properties not being shared by its counterpart. In other words, the Tinbergen took seriously L. Wing’s and D. M. Ricks’ objection that neither all deviant bouts of normal children need to be autistic in character nor that all behavioural symptoms displayed by autistic children can be traced (however rudimentarily) in normal ones. Yet on the other hand, the partly revised concept in fact allowed, despite the viability of the objections, to insist upon the possibility of a potential phenomenological coincidence (or better: intersection) of normal and autistic behaviour. The Tinbergen underline:

Our conviction that there is in principle a continuum between the two is based on the fact that autistic bouts of normal but apprehensive children overlap considerably with the more normal bouts of autists. The overlap goes so far that normal children can at times show all the behaviours typical of autists and that, conversely, if a young autist is left alone in his favourite surroundings he can shed many of his peculiarities and behave surprisingly normally. Needless to say that such more normal behaviour does not appear during a visit to the psychiatrist’s clinic.

Finally, I think, the rejoinder of the Tinbergen implicitly also includes some more hints that they might have presumed a more organic form of acquired autistic condition as well. The background eventually was that the Tinbergen objected L. Wing’s dualism of complete and partial recovery which implied that a complete recovery was impossible because the underlying condition was likely to be inherited and thus present (though not always revealed) from birth. The Tinbergen did not question that autistic children might be furnished with an inborn vulnerability but they also claimed that some dispositions of this kind might be acquired while being exposed to unfavourable circumstances and therefore be reversible. They write:

We believe that it is most likely that the continuum will be found to exist in young children but that, as they grow up, they sort themselves out into those who enter into a downward spiral and those who overcome their initial handicap. That the issue is still so controversial is, we think, mainly due to the fact that there are degrees of “oddness” at birth; to the fact that most parents

1066 Ibid., 548.

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do not become aware of signs of abnormal development until the downward spiral is already well on its way, so that they can hardly ever report retrospectively and reliably about the first weeks or months; and also to the fact that clinical psychiatrists see mainly the most advanced, most extreme cases.\footnote{1067}

The Tinbergen's notion of “derailment” resolves the qualitative distinction between partly and completely curability as soon as the notion of “oddness from birth” is made the subject of a continuum itself or, as the Tinbergen here do, explained as a retrospective interpretation put forward by the parents or the psychiatrists from a later state of development of the autistic disorder. In other words, the fact that the Tinbergen in principle leave no period of human development untouched when they argue in favour of a susceptibility for environmental impacts in the last consequence raises the question of prenatal influences upon the unborn child. Metaphorically spoken they push back anti-chronologically the dualism between organic and psychogenic factors and, in doing so, reduce the organic part to an ever smaller minimum – just in a sense mathematicians use to operate with a limes figure. If we want to, we can conceive the independency that modern geneticists claim between purely genetic DNA effects and the epigenetic control of gene expression as the latest interpretation of this heuristic movement. To have realized and introduced this structural heuristic movement within the area of Human Ecology surely is one of the merits of the Tinbergen's work on early childhood autism.

"Autistic" Children. As to the history of Niko and Elisabeth Tinbergen's interest in childhood autism one may eventually say that the Nobel Lecture not only marked the zenith of N. Tinbergen's academic career but also a turning point in his engagement with autism. While the years between 1970 and 1973 / 1974 were mostly dedicated to clarify the roots of the autistic disorder and, in doing so, to come to an alternative hypothesis (viz. the functional causation), in the years following Niko's retirement the focus drifted more and more to the question of cure.\footnote{1068} This shift of attention finally culminated in another book which was published in 1983 under the title “‘Autistic’ Children. New Hope for a Cure”.\footnote{1069} While the Nobel award put N. Tinbergen’s person into the foreground, writing the book was a joint enterprise with his wife Elisabeth.

\footnote{1067} Ibid.
\footnote{1068} In a letter to the Deputy Head of the Milton Ford School in Portsmouth Niko informs the reader about the work process in course of which his late book emerged. Whereas the first part was written while Niko was still a busy professor, the second half which is concerned with the question of cure has been written after his retirement. See Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3145, D 20, letter N. Tinbergen to J. Tierny (05/06/1981).

\footnote{1069} From a letter N. Tinbergen wrote to the Canadian psychologist J. A. Allan we can infer that the final subtitle of the book was suggested by the publisher. Niko’s original title was “‘Autistic’ Children. And How They Might Be Saved”. See ibid., Ms.Eng. c. 3146, D 32, letter N. Tinbergen to J. A. Allan (20/12/1982), and ibid., Ms.Eng. c. 3146, D 45, letter N. Tinbergen to M. Welch (05/10/1982). The correspondence between B. Hassenstein and N. Tinbergen shows that the German publisher of the book sent around the manuscript to experts in the field for evaluation. One of these reviewers was Hassenstein who argued very much in favour of Niko’s treatise but also suggested to make the chapter headlines more pregnant. N. Tinbergen seems to have discarded most of the suggestions which, in my opinion shows, that he felt the headline of a chapter should represent the epistemic order of its content. For instance, Hassenstein suggested for chapter five “Development and Causation of the Autistic Condition” but Niko wanted to keep “What Makes a Child Autistic?” – most likely simply because it should be a question at this
I think the overall epistemic structure of the book can be traced best if we focus upon the notions of “cure”, “recovery” and “healing” which seem to be central in the account. From a logical point of view all these concepts have in common that they represent a process in course of which a state of disorder (?) (i.e. illness or suffering) is transferred into a chronologically secondary state of health. Needless to say that illness in the view of the Tinbergen is associated with the notion of a body’s dysfunctions, whereas the state of health is connoted with “functioning”, “adaptedness” or “fitness”. Finally, the malfunctions of a body eventually might cause its depression or even its decay, while the notion of health – or what I have called the “anthropological level” of behaviour – is connected with the notions of “growth”, “improvement” and “progress”. The key to Niko and Elisabeth Tinbergen’s understanding of “cure” is the question how these two states of mind and / or body are related to each other. The Tinbergens inserted descriptions of their own treatment methods in both of their main publications on autism, *Early Childhood Autism* and “*Autistic*” *Children*, as well as they can be found in their letters. From these accounts we can infer that their technique was based upon a paradox: The patients were to be resocialized but the Tinbergens tried to achieve this objective by “ignoring” the children, for instance, by avoiding eye contact in the early stages of the cure. For instance, in a letter to C. and J. Hutt it reads:

The process of establishing contact is fascinating, and both Niko and I have a kind of standard procedure. Avoid looking at the child, particularly smiling intrusively and above all talking (“and what is your name dear?”). When, as usually happens, the child approaches, keep ignoring it until it touches you. Then don’t look, but just touch its hand with yours. Even that may be too much, but soon this will be accepted. And then you can vary this contact, and even play (say, playfully grab the hand for a moment, laugh with it but without looking at it, etc.) Then one can gradually begin to try and establish eye contact – short at first, just friendly momentary glances. Laugh when it laughs, etc. Then one can look at it, but still not too intensively. Etc.etc. Incidentally, Niko applies the same with dogs, and it is astonishing how many of them come and lay a paw on his knee. And he does not particularly like dogs, did the same, until people asked “why do dogs always try and make friend with you?” And he said: “Because I ignore them”.1070

Another indicator that the entire cure system has a paradox overtone may be that the transition to a state of mental health is not only conceived as a gradual process of improvement since it may include more or less “cataclysmic” events or even moments of setbacks. Finally, I have already mentioned that N. Tinbergen’s late re-conceptualization of the motivational system was mediated by the concept of “maintenance behaviour” and therefore of “homoeostasis”.1071 This idea, per defi-
nitionem, implied a static nuance which, for instance, becomes evident when the mind (including its motivational system) is conceived in terms of an equilibrium system. This idea holds even in case neo-Darwinian theorizing on “homoeostatic systems” involves a more-of dynamics which can be made evident in Niko’s writings, for instance, in that the capability to dissolve motivational conflicts is based upon the notion of “moment-to-moment fluctuations”. It is quite obvious to me that the entire argumentative pattern of “Autistic” Children can be evolved from this basic idea, that is, the epistemic logic underlying the notion of “homoeostasis” which is implied in Niko and Elisabeth Tinbergen’s understanding of “cure” and “mental health”. In short, this “logic” presumes that a homoeostatic system can integrate environmental stimulation by rebalancing the irritation on higher levels. If abstracted onto a more conceptual level we are confronted with heuristic systems that are prepared and capable to cope with expressions of subjective and non-subjective otherness and, in doing so, are capable – so to speak – to immunize themselves against potential irritation such as the criticism put forward by others. Applications of this scheme can be found in the history of ideas in manifold expressions such as R. Descartes’ practice to publish both the objections against his Meditations and his comments of this objections, H. Spencer’s concepts of “canon” and “belief” as well as in some parts of the so-called “vera causa principle” which Darwin had applied to structure his “Origin of Species”. The idea of “testing the scope of a hypothesis’ applicability” is central in “Autistic” Children. Throughout the book”, the Tinbergens underline, “it has been our concern to check the validity of hypotheses – our own as well as those of others – by examining how wide a range their explanatory power covers; for how many known facts they can account”. The notion of testing “the explanatory power” of presupposed hypotheses by asking for “how many facts they can account” most likely is the prevailing epistemic scheme which rules the knowledge organization of the account as a whole but also in several of its integral parts. Thus it is not an accident that the main parts of “Autistic” Children are supplemented by a “Postscript”, that theoretical reasoning on the nature of autism and its recovery is supplemented by sections providing


1073 Please note that these reference systems always include their complementary opposite on subaltern levels of knowledge organization. Their deconstructibility is therefore part of their nature. However, the mere statement of their deconstructibility is not sufficient since it is the topographic distribution which determines the overall epistemic scheme.

1074 The notion of being capable to cope with criticism is mentioned explicitly in the preface of “Autistic” Children. See ibid., 3. In addition to that, there are numerous hints in the letters N. Tinbergen exchanged with friends and colleagues that he was aware to have put forward an unpopular “environmentalist” standpoint in his book that will be criticized therefore. The anticipation of this criticism in the forefield is part of this “homoeostatic” strategy of dealing with irritation coming from the outside. For this anticipation of criticism see Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3145, D 26, letter N. Tinbergen to H. Hemminger (07/01/1983), page 1, ibid., Ms.Eng. c. 3146, D 32, letter N. Tinbergen to J. A. Allan (19/11/1981), ibid., Ms.Eng. c. 3146, D 40, letter N. Tinbergen to J. Prekop (08/11/1982), and very pronouncedly ibid., Ms.Eng. c. 3146, D 41, letter N. Tinbergen to J. Prekop (13/02/1983), here page 3.


1076 The figure also reappears in the notion of refinement the book’s content. See Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3145, D 26, letter N. Tinbergen to H. Hemminger (09/03/1983).
practical proof, that theorizing on autism is combined with “Practical Suggestions to Parents and Caregivers”, that theoretical reflections on condition and cure are questioned for their further leading methodological implications, that theorizing on autism consists of both reflecting the primary condition as well as the question “To What Extent Can Autistic Children Recover”, and that, finally, determining the nature of autism includes both the examination of the autistic condition (being autistic) and the process of becoming autistic, the latter of which clarifies the ontogeny, genesis, or aetiology of the disorder. In sum, it may be presumed that “Autistic” Children originated over a longer period and therefore consists of several more or less independent sections some of which build the core, while others seem to have been added in later stages of the work.1077 This view, at first sight, might contradict the notion of an overall framing. Yet my argument then would be that the idea of testing ever wider ranges of applicability matched perfectly well with the process underlying the book’s genesis.

I would like to point out several aspects which I consider relevant for understanding Niko and Elisabeth Tinbergen’s late work on autism in relation to their previous studies. Thereby I concentrate on those issues which appear to be either more or less elaborated than in the previous publications or which mark a more drastic qualitative deviation in comparison to former accounts.

The method of observation. I have already mentioned that epistemic reference systems are ambiguous inasmuch as they embrace antagonistic part-schemata. In doing so, they generate both tautological and paradox semantic relationships between them and the main frame in question. If we take for granted that Elisabeth and Niko Tinbergen’s leitmotiv in “Autistic” Children was to sound out a the scope of applicability of a hypothesis, those sections which are concerned with the method of observation under natural conditions run across this main frame. Why? The idea of “watching and wondering” the Tinbergens put forward in their late book on childhood autism encompassed not only the claim to gather as many data and as unbiased as possible but also a process of abstraction. “In other words”, the Tinbergens write, we advocate a “descending” analytic procedure; one which begins by scrutinising the behaviour as a whole and which leads gradually to digging deeper and deeper into the details of its causation. In this step-by-step procedure, too large and too hasty “jumping to conclusions” (i.e. to premature hunches) has to be avoided or has at least to be distinguished from the formulation of well founded hypotheses. There is of course nothing wrong with the jumping as such – in fact, it is an essential part of the exercise – but what is wrong is the premature elevation of mere hunches to the status of conclusions, for this closes the mind to further exploration.1078

This gradual and in principal open process of abstraction or, as the Tinbergens used to put it, of bringing order into chaos, however, turns out to be a complex mul-

1077 The Tinbergens inform their readers that they interrupted the writing process several times to observe children. See Tinbergen et al., “Autistic” Children, 3. For some more details concerning the process in course of which the book was written see Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3146, D 41, letter N. Tinbergen to J. Prekop (13/02/1983). This process is described as a transition from oral speech (as applied in presentations) to printed text while more and more adopting the critical feedback of the audience.

1078 See Tinbergen et al., “Autistic” Children, 19. Correspondingly, they claimed with P. B. Medawar to observe normal behaviour in the first place before comparing it with the abnormal. See ibid., 26 and 206.
tistage operation in itself which mostly consists of classifying the data (and also, to a certain extent the interpretation of it) by applying two different independent criteria: The qualitative distinction between approach and withdrawal, on the one hand, and the ordering principle of an “intensity scale” inside each of these realms, on the other. Insofar “Autistic” Children picks up the trail the Tinbergens had blazed in Early Childhood Autism. Yet my impression is that a new extended and more sophisticated perspective made its arrival since we are informed that not all symptomatic behaviours can be classified in either the approach- or the withdrawal-category. “In addition”, the Tinbergens write, “we mentioned a number of movements which could not at first glance be so classified, e.g. ‘nervous’ movements, facial expressions, often co-occurring with mild, tentative forms of both approach and avoidance, or with staying at a ‘safe distance’”. The aspect should not be underestimated since these non-classifiable expressions raised not only the question how to conceptualized them – they also needed to be explained in terms of both their causation and their overt expression. As to the latter aspects, we might eventually say that the notion of motivation conflict itself needed to be supplemented by a concept that went beyond, while the overt behaviours themselves could be conceived more precisely by arranging them on a scale ranging from less to more interruptive. The more differentiated symptomatology also generated the possibility to bring in a long-term perspective including the ontogeny of autistic children. It also revealed the paradox functionality of the behaviours exhibited by autistic children. What appeared to be dysfunctional (i.e. abnormal) at first sight turned out to be perfectly well adapted to the children’s tendency to “cut-off” social relationships. “Although, as we said before, this list of autistic behaviour is not complete”, the Tinbergens underline, we believe that we can claim that our way of trying to discover the origin of such seemingly senseless, often “bizarre” behaviour of autistic children leads to results that do make sense in terms of our hypothesis. There is certainly good reason to predict that further study will show that all autistic behaviour fits in with the idea of the primacy of an anxiety-dominated emotional conflict, which forces the child to make movements of some kind, in particular the types or movements that we know from many animals in similar conditions. The “senselessness” of so much autistic behaviour seems to be due to formalisations of several types, to the overall retardation of autistic children, and in part to the cunning ways in which such children succeed in not inviting social contact, an aim in which they often succeed so very well. In other words, “senseless” or “functionless” behaviour often serves this negative function so well that we adults are literally “conned” into leaving the child alone.

1079 For making use of the phrase “bringing order into chaos” see ibid., 24, 26, 30–34, 67. For the process of abstraction see ibid., 31.
1080 Ibid., 31, and in addition also 28–30 (“Other Behaviours”), 67.
1081 I think it can be discussed whether the more drastic avoidance behaviours the Tinbergens mention, especially what they call “tension postures” fall under this category. See ibid., 67–70 and 87–95.
1082 Ibid., 94–95. The Tinbergen Papers contain quite an exciting letter written by the Swiss primate ethologist H. Kummer in which the author put forward the notion that the so-called “defects” of autistic children might be “secondary adaptations” in situations of extraordinary external demands. If I am not mistaken the concept of “secondary adaptation” can be traced back to A. Portmann, E. Cullen’s Swiss teacher, and the story comes full circle. See Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3145, D 28, letter H. Kummer to N. Tinbergen (23/11/1984). See also ibid., Ms.Eng. c. 3147, D 58, ms. “Motivational conflict and stereotypies in autistic children” (n. d.), here page 1, and 2.
The paradox, that is to say “Darwin’s paradox”, is exactly the point where Elisabeth and Niko Tinbergen’s studies on childhood autism meet with N. Tinbergen’s earlier spacing-out study! To put it in a nut-shell, it is important to keep in mind that the Tinbergen’s placed their research on autism in an adaptationist framework.\textsuperscript{1083} In sum, I think, it is not quite false to say that Elisabeth and N. Tinbergen’s late study on childhood autism operates with a more sophisticated symptomatology of the autism disorder syndrome and that the more differentiated view upon the overt behaviours required a more elaborated model of the motivation system. This leads me to my next point.

**Motivational system.** That the Tinbergen’s insisted that the causes of the behaviours displayed by autistic children should be examined on basis of what they called “input-output approach”, in other words, a “black-box” model, is mentioned explicitly in their “Methodological Comments”.\textsuperscript{1084} However, while taking note of this matter of fact, readers must be aware that the black-box model underlying their account might have changed substantially in comparison to N. Tinbergen’s classical studies.\textsuperscript{1085} Thus, one of the results of my previous analysis of *Early Childhood Autism* was that Niko, like in former days, insisted upon conceiving the afferent leg of the nervous circuit as a unity of more or less discrete nervous operating entities *but*, on the other hand, seemed to have re-conceived the entire process of centralization: While in classical ethological studies it was the periphery of the nervous system which was associated with a huge variety of complexity (resulting from the manifold kinds of stimulation a living organism is confronted with) that needed to be reduced on the upper levels of the system by corresponding receptive mechanisms (which, according to gestalt theoretical considerations might include the possibility to perceptive mistakes), the view now apparently has changed: If we read carefully the respective parts in “Autistic” *Children* we might see that eventually neither the afferent nor the efferent peripheral part of the nervous circuit is affiliated with the extent of complexity these parts were associated within former conceptions of the model (either in form of the complexity originating from both proprioceptive and exteroceptive stimulation or the complex “branching” of the nerve fibres while addressing the peripheral parts of the motoric system). Instead, as the more sophisticated account in “Autistic” *Children* shows, it is the peripheral interface between the organism and its environment which is described more in terms of “uniformity”. Autistic children, in Niko’s view, eventually both perceive and, even more obvious, act in stereotypies.\textsuperscript{1086} Stereotypic behaviours and mannerisms were part of the canon of symptoms L. Kanner had defined to identify between the bouts the autistic syndrome and since then were considered an essential part of any symptomatology including Niko and Elisabeth Tinbergen’s

\textsuperscript{1083} This runs somewhat counter to some late attempts to reassess classical ethological theory for the examination of psychiatric disorders such as depression and thus put it against adaptationist theory. See Geer et al., “On the Role of Ethology in Clinical Psychiatry”, especially 120 and 130–131.

\textsuperscript{1084} See Tinbergen et al., “Autistic” *Children*, 209.

\textsuperscript{1085} For an illustration of the former model see Fig. 2.2.

\textsuperscript{1086} For more detailed information concerning N. Tinbergen’s understanding of “stereotypy” see Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3147, D 58, ms. “Motivational conflict and stereotypies in autistic children” (n. d.). The ms. is addressed to a “you” but it cannot be
Autistic children tend to reveal the same reactions in the similar situations. Furthermore, we are informed that it is part of a normal human being’s adapted constitution that we, in principal, function best when we perform one action at a time. “We need hardly point out”, the Tinbergens argue, that even though Man is somewhat better than animals at doing more than one thing at a time (e.g. we may read a book or make notes while having lunch) this too requires an effort, we function best when we do “one thing at a time” – either eat or concentrate on our work. However, this is not so because different activities are necessarily physically incompatible; many things that could be physically combined are not done at the same time: the mutual suppression of, for instance, feeding and love-making is a matter of central nervous competition between the two systems, not of incompatibility of the movements of the two systems. The rule of “one thing at a time” is not entirely hard and fast – thus we keep breathing during all our activities. But for the behaviours we shall be concerned with, mutual exclusiveness is the general rule.

The quote is of some interest because it might give us some additional hints how the revised black-box model needs to be understood. At first, I think, there is a stronger emphasis on competition in the upper levels of the centralization process which implies, at least to a certain extent, relatedness. In addition to that, we are informed elsewhere that what kind of stimulation is conveyed into the central parts of the nervous system is less a matter of the quality of a specific receptive mechanism or apparatus rather than the effect of major functional systems which – so to speak – calculate the effective stimulation by adding up the stimulation provided by both the internal conditions and the external events. Second, my impression is that the “mutual exclusiveness” which this central system of mutual competition is aimed at and which in pathological cases generates anxiety dominated motivational imbalances, so to speak, in itself provides the opportunity of exceptions. The motivational correlates of the more or less unclassifiable behaviours I have mentioned above, I think, can be located in these regions of the model. In doing this, I think, the Tinbergens brought in a mechanism which resembled Niko’s former “displacement reactions” yet on closer inspection also reveals some essential differences in comparison to the earlier concept. The behaviours which are neither approach nor withdrawal emerge when two motivation systems are aroused simultaneously, so to speak, as a third more or less discrete state of motivation. In contrast to the

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1087 Own definition. Autistic children tend to reveal the same reactions in the similar situations. Furthermore, we are informed that it is part of a normal human being’s adapted constitution that we, in principal, function best when we perform one action at a time. “We need hardly point out”, the Tinbergens argue, that even though Man is somewhat better than animals at doing more than one thing at a time (e.g. we may read a book or make notes while having lunch) this too requires an effort, we function best when we do “one thing at a time” – either eat or concentrate on our work. However, this is not so because different activities are necessarily physically incompatible; many things that could be physically combined are not done at the same time: the mutual suppression of, for instance, feeding and love-making is a matter of central nervous competition between the two systems, not of incompatibility of the movements of the two systems. The rule of “one thing at a time” is not entirely hard and fast – thus we keep breathing during all our activities. But for the behaviours we shall be concerned with, mutual exclusiveness is the general rule.

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1089 For Niko and Elisabeth Tinbergen’s reception and discussion of the various canons and the role the stereotypies play within them see Tinbergen et al., “Autistic” Children, 7–10, especially 9–10. For a later reassessment see ibid., 95–99. The canon of symptoms encompasses: (1) Failure in forming normal social relationships, (2) reluctance to venture out, (3) non-development or regression of speech, (4) frequent performance of stereotypies and mannerisms, (5) avoidance of and resistance against change, (6) overall retardation in combination with islets of above-average performance and, finally, (7) sleeping difficulties.

1087 See ibid., 67–68.

1088 See ibid., 40–41, here 41.

1089 For this modified reassessment of A. Seitz’s original “law of heterogeneous stimulus summation” see ibid., 31–34.

1090 See ibid., 67, also 74. As an extreme example for an overt expression of this kind of motivation
former concept of “displacement reaction” which considered simultaneous arousal of antagonistic motivation systems in the first place and a moment of disinhibition (i.e. the sparking over) in the second, the mechanism here in question starts with a biased motivation conflict whose bias, as it seems, vanishes in the state of its deviation. This “state of deviation”, in turn, seems to be characterized by the over-arousal of the systems. An increase of the general level of arousal therefore seems to be responsible for a type of behaviour that is caused by simultaneous (also non-alternating) excitation of otherwise antagonistic nervous centres and reveals itself in extreme forms of motoric tensions. Altogether we may say that the elaboration of the black-box model and the systematic correlation between input and output thus led towards a better understanding of a wider range of more severe behaviours revealed by autistic children. The idea of crosswise intertwining between observable behaviour and receptory correlate is thereby maintained and we can see now why N. Tinbergen did not “cross swords” with his friend K. Lorenz.

Paradigm of causes. When the Tinbergens ask for the genesis of the autistic disorder during individual development, that is, the question of “becoming” autistic in comparison to the autistic condition (i.e. “being” autistic), they approach the issue from two different angles, that is, the question “what can set off the autistic deviation or derailment in the first place”, on the one hand, and the question “what can cause the further deterioration that is supposed to be the inevitable sequel”, on the other. It is the former of the two realms in which they develop a grid of factors being possibly involved during the genesis of the autism spectrum disorders before they finally come to name a number of concrete causes they consider essential in the aetiology autism. What I have called “grid of factors” in fact encompasses a complete paradigm consisting of three independent dichotomies whereby each constituent of one distinction is considered combinable with any other constituent on each of the remaining levels. These dichotomies are the differentiation between nature and nurture, between organic and non-structural causes, and finally, between central and peripheral causation.

The distinction between nature and nurture thereby refers to what the Tinbergens

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1092 See for the distinction between the two questions ibid., 106.
1093 For this hint see Tinbergen et al., “Autistic” Children, 91. Here it reads: “Research on animals suggested that over-arousal occurs as a consequence of a motivational conflict rather than, as Hutt seemed to suggest for autistic children, as the central cause of the autistic syndrome”.
1095 A ms. of early 1973 that is passed onto us in the Tinbergen papers shows that this more
describe as “genetic predisposition” in contradistinction to the “influences of the environment”. Niko and Elisabeth Tinbergen thereby insist that there is no either / or and suggest to reformulate the question whether Kanner’s syndrome is determined by a genetic disposition or, instead, by environmental factors in a way that takes into account the range of effectiveness ascribed to both sides, that is, “to what extent is autism due to a genetic defect and to what extent to the early environment”, as they put it. In doing so they are prepared to concede that nature is involved in the genesis of childhood autism in as much as autistic children, in their view, reveal inherited differences in their “vulnerability” to become victims of Kanner’s syndrome. With “vulnerability” they mean a general liability to be affected by the syndrome which is said to be correlated usually with a number of additional psychic qualities. “Following some methodological comments”, Niko and Elisabeth Tinbergen write,

we argued that the contribution of heredity is almost certainly far less decisive than it is in the disorders that are known to start with a fault in the chromosomal endowment of the fertilised egg, and that the genetic aspect of the problem is rather one of causing differences between children, of whom certain types are more susceptible, more vulnerable than others. (How to characterise the susceptible children we do not yet know, but there seems to be a correlation between being highly perceptive, socially sensitive and intellectually or artistically gifted and being at risk of falling victim to autismogenic external conditions).

In addition to that, we are elsewhere informed that the “vulnerability” to autism might be the result not only of an inherited disposition but also the effect exerted by intrauterine impacts. However, the Tinbergens ascribe the major share of variability which leads to the deviant behaviours symptomatic for the autistic disorder to nurture-causes. As a consequence much of the argumentative effort taken by the Tinbergens is directed against the advocates of genetic and organic causes including the evidence provided by twin studies. In order understand the Tinbergens’ rejection of inherited causes correctly, I think, it is also necessary to have a elaborated differentiation of antagonistic concepts on independent levels developed soon after the publication of Early Childhood Autism. The only difference might be that the later dichotomy between central and peripheral in this early stage was conceived in terms of “primary” vs. “secondary” causes. See Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3147, D 52, ms. “Draft About Autism” (01/1973), here page 7.

Tinbergen et al., “Autistic” Children, 112. Later on it reads: “Most behaviour is neither completely learned nor completely innate, but develops under the control of both genetic and learned instructions” (Ibid., 149, and similarly 155).

Ibid., 154.


See ibid., 114–116. Some evidence provided by B. Hassenstein seems to have supported Niko’s view that monozygotic twins need not necessarily develop concordant phenotypes presupposed that they are equally liable to become victims of the autistic syndrome. See Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3146, D 36, letter B. Hassenstein to N. Tinbergen (27/05/1980). In a ms. for a lecture written to be read by Tsuneo Taguchi in Japan in November 1981 Niko refers to a twin study which proved that out of eleven monocygotic pairs of twins four were concordant, while seven were discordant. See ibid., Ms.Eng. c. 3147, D 69, ms. “Early Childhood Autism seen as a consequence of psychosocial stress, and a new, successful therapy” (ca. 11/1981). Even in nowadays, twin studies do not provide a coherent picture since both concordance and
closer look which type of genetic variation they had in mind when referring to “ge-
netic” causes. My impression thereby is that they, especially in later stages of their
work, wanted to understand genetic aberration as “fault in the chromosomal endow-
ment of the fertilized egg” or “other kinds of abnormal genetic equipment”. The
autism spectrum disorders certainly are not caused by duplications of entire chro-
mosomes like, for instance, the Langdon-Down-Syndrom. Insofar the Tinbergens
were right. However, the state of knowledge in the genetic sciences of the late 1970s
and the early 1980s was already sufficiently advanced to think about more complex
forms of intra- and inter-chromosomal genetic variability. The neglect of genetics
therefore was more the result of Tinbergens’ own epistemic “regime” rather than
due to a real lack of knowledge. On the other hand, we therefore need to take into
account that Elisabeth and Niko Tinbergen’s approach to autism is a typical exam-
ple for what M. Weber called “the return of the phenotype”. That is, the starting
point of the Tinbergens was the behavoural symptom and less the biochemistry of
the human genome. “Finally, we repeat once more that, in this context too”, they
write nearing the end of their late book,

it is not important whether or not the children concerned were “real” autists; as we have all
the time been at pains to emphasise, we are speaking of children who show “most or all” of
the symptoms we have described in Chapter 2. The reaction we have heard ad nauseam to
our reports on successful treatment, viz. that the children who have recovered cannot have been
“true” autists is in many cases not only at odds with what we know of their pre-treatment
behaviour and with the diagnosis, given in many cases by professionals, but it is, as we have
tried to explain, the natural consequence of taking “ineducability” to be a proven fact instead of
what it is: and inference based on having, so far, failed to rehabilitate the children. The
Tinbergens’ emphasis on symptoms certainly can be read as an expression of a
heuristically unhealthy methodological bias. On the other hand, however, it might
also be read as a mind-opener: It is at least thinkable that similar effects (even ge-
netic effects such as duplication and drop-out of gene sequences or chromosome
shortening) might be the result of quite different causes such as ageing, stress, can-
cer disease, immunological dysfunctions, or even inherited deviations. The Tinber-
gen’s approach therefore was and still is suitable to sensitize readers for potential
interconnections between the various different phenomena.

The second distinction is more difficult to grasp. It is described as opposition of
“structural” and “non-structural” causes. Moreover, it is connected with the dimen-

discordance in monocygotic twins has been proved. See Persico et al., “Searching for Ways Out
of the Autism Maze”, 349 vs. 350 with further leading references. For the fact that twin studies
are still subject of discussion see G. M. Anderson, “Twin Studies in Autism: What Might They
Say About Genetic and Environmental Influences”. In: Journal of Autism and Developmental
Disorders 42.7 (2012), 1526–1527. If I’ve understood correctly, G. M. Anderson’s argument
is that seemingly environment induced phenotypic discordance in monocygotic twins can be
partly due to genetic and epigenetic factors since twinning need not be symmetric as to both
spontaneous mutation after fertilization (e.g. in case of CNV) or inherited epigenetic variation.

See Tinbergen et al., “Autistic” Children, 154, and 115 respectively. See also Bod. Lib., N.
Tinbergen Papers, Ms.Eng. c. 3147, D 70, ms. “A ten years’ study of Early Childhood Autism
and a new, successful therapy” (1982), here pages 6–7.

See Tinbergen et al., “Autistic” Children, 198. For the emphasis of symptoms see also Bod. Lib.,
N. Tinbergen Papers, Ms.Eng. c. 3144, D 5, letter N. Tinbergen to [?]C M. Mason (11/01/1973),
1–2.
Niko Tinbergen (1907–1988)

sion of time insofar as “organic” or “structural” causes are said to be permanent, while non-structural causes are more conceived in terms of temporary disturbances. In addition to that, though not very overt, the dichotomy between structural and non-structural causes also seems to run parallel with the antagonism of proximate vs. ultimate causes. This can be inferred from the fact that the Tinbergens sometimes circumscribe the dichotomy in terms of “organic” vs. “functional”. In addition to that, the temporary disturbances also seem to be conceived as functional disorders. Especially in later sections of the treatise we can get also the impression that when Elisabeth and Niko Tinbergen speak of “psychogenic” causes they intend to refer primarily to this second level of causation and, even more specifically, to the transient malfunctions.\(^{1104}\)

According to Elisabeth and Niko Tinbergen’s opinion, the differentiation between “central” and “peripheral” causes does not coincide with either the nature vs. nurture or the organic vs. functional opposition. It refers to the location in the nervous circuit where the malfunction needs to be placed, that is, the question whether the disturbance is rooted more in the central or more in the peripheral parts of the nervous system. The Tinbergens seem to have integrated this latter opposition into their grid for historical reasons. Many clinical psychiatrists, at least in the view of the Tinbergens, tended to explain Kanner’s syndrome with malfunctions in the periphery of the nervous system that is either with errors occurring in the field of sensory perception (including subsequent cognitive defects) or in terms of disturbances of the motoric control.\(^{1105}\) The Tinbergens, on the contrary, were more liable to locate the malfunctions within the central areas of the nervous circuit – a gesture which partly coincided with the criticism early ethologists had put forward against the reflexologist schools of behaviour study.\(^{1106}\) According to Niko and Elisabeth Tinbergen, the motoric and/or cognitive disturbances were secondary consequences not primary causes of the autistic disorder.\(^{1107}\) As a consequence they postulated that human learning capacities are closely connected with the emotional state of mind. “How exactly”, they write,

the emotional peculiarities of autistic children affect their intellectual development – for that matter how the normal emotional state controls the development of skills and intellect of normal children – we neither intend nor are competent to discuss. What we try to drive home is the fact that and to how great an extent much of our intellectual development is under the control of our emotional state. This is an aspect of child development that does not seem to receive enough attention in the literature, yet it seems to us that it is exactly to this emotional basis of mental growth that the damage is done which leads to autism, and probably to some other developmental aberrations as well, which are usually given other labels.\(^{1108}\)

Moreover, the focus upon the central parts of the nervous system also implied a greater extent of both inter-individual and moment-to-moment variability of the exhibited symptoms.\(^{1109}\) One of the arguments the Tinbergens never tired of mention-

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\(^{1105}\) See for this aspect of the Tinbergen’s reception of psychiatric research ibid., 17–18, 113.

\(^{1106}\) For the emotional character of the disorder see ibid., 73, 97, 167 and 213.

\(^{1107}\) See ibid., 12, 18.

\(^{1108}\) Ibid., 73, and also 92.

\(^{1109}\) For the “subjective” character of autistic behaviour and its variability see ibid., 139, and also
intellectual Life-Histories

ing in defending their position was that a child who does not speak is not necessarily physically unable to speak but momentarily blocked to display the performance in question.1110 As a result, the Tinbergens criticized all methods of treatment which in their view concentrated merely on the peripheral symptoms of the disorder and not the central causes.1111 However, in order to understand the emphasis the Tinbergen's put upon more central nervous mechanisms it is necessary to take into consideration the modifications they had applied to their model of the nervous circuit as a whole. In a concluding remark it reads:

From what we wrote in the preceding chapter, it will be clear that we think of autism as primarily a functional rather than an organic affliction (even though organic aspects may be involved as the consequence of the (psychological) malfunctioning and vice versa) and that we consider it a matter of central, “emotional”, “motivational” rather than peripheral malfunctioning. Although we shall have to return to these two aspects in what follows, our main discussion here will be concentrated on the nature-nurture issue. We shall argue that, although genetics may enter into the picture as having an influence on the vulnerability of children to autism-producing influences, the deviation is very largely due to environmental factors, and although we recognise the possibility of some organic agents such as rubella and “minimal brain damage” (which we consider an otherwise pretty useless term), we ascribe autism mainly to the “psychogenic” influences among these external agents.1112

Altogether one may eventually say that the entire grid or paradigm not only provided a scheme to avoid the sort of confusion the Tinbergens said to have disclosed within the secondary literature they had received but also as to their own earlier account which primarily had operated with the dualism of “genetic” and / or “organic” forms of causation, on the one hand, and what they called “psychogenic” causes, on the other. The heuristic strength of the newly introduced scheme originates primarily from the fact that all three dichotomies are conceived as logically independent in a sense that their constituents turn out to be mutually combinable. Thus Niko and Elisabeth Tinbergen claim that organic causes do not coincide with “innate” or genetic causes since they can be both inherited and acquired.1113 Genetic factors, on the contrary, can be potentially conceived both as organic and non-structural, and so forth.1114 Whether experts arguing from our current state of

1111 See Tinbergen et al., “Autistic” Children, 172. Mere “skill training” and training of “motoric abilities” in their view therefore was mere “symptom treatment”. See Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3147, D 57, ms. “Autistic children – a reply to your request” (Summer 1974), here page 3.
1112 Tinbergen et al., “Autistic” Children, 144.
1113 Ibid., 112.
1114 The Tinbergens take into account this possibility in principal. See ibid., 116. Here it reads: “As long as a purely genetic basis of autism is so unlikely, it is futile to discuss whether, if future research were after all to discover an underlying genetic defect, this would have to be considered to be of an ‘organic’ or a ‘psychogenic’ nature. As we shall see, such a discussion is far from futile when it comes to tracing possible effects of environmental aspects”.

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knowledge would agree with the options the Tinbergs had chosen to place their arguments is another question. The Tinbergs themselves conceded that they, in their earlier publication, overestimated the importance of the psychogenic factors while having underestimated the effectiveness of organic-environmental causes.\footnote{Ibid. For the organic causes see also the subchapter with the title “Consequential Autism” (Ibid., 137).} Thus there is a remarkable tendency in the later stages of their work to take into account the connection between nutrition and mental malfunctioning.\footnote{Ibid., 228. This means that the Tinbergs wanted to take into account a broader range of body systems other than the motivational system. For the relevance of this approach see Woods et al., “Epigenetic Epidemiology of Autism”, 334.} This shift not only becomes evident in their book but also, and even more overtly, in their correspondence with experts such as, for instance, B. Rimland, a clinical ecologist who was working at the Institute for Child Behavior Research in San Diego, California.\footnote{Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3145, D 26, letters N. Tinbergen to B. Rimland (15/01/1983), B. Rimland to N. Tinbergen (10/02/1983), and N. Tinbergen to B. Rimland (22/02/1983).} In a letter to Rimland of February 1983 N. Tinbergen writes:

> It begins to look to us as if with all children both the holding and corrected food must be attempted, and that the effect of these two main attacks may well vary proportionally from one child to another. Although we have mentioned the food aspects in the treatment of autism in our book, we have not given it sufficient emphasis, but we shall certainly do this in our future personal contacts with parents and with other therapists. As an ethologist I have probably been preoccupied with the behavioural aspects and thought too exclusively of psychogenic origins, even though with my own emotional troubles I had, after psychiatric and megavitamin experiences, finally become convinced that the clinical ecologist who tackled the nutritional problems more widely, was the one who could help me most. Never too late to learn.\footnote{Ibid., Ms.Eng. c. 3145, D 26, letter N. Tinbergen to B. Rimland (22/02/1983), here page 1.}

The quotation shows not only that there was a shift towards organic causation in Niko’s reasoning but also that it was motivated by his own medical history. His correspondence with friends and colleagues thus give us a fairly solid insight in how the explanations for his own health problems changed over time: While Niko in earlier letters argued with an hyperactivity of the thyroid gland, in later accounts of his cure he claimed that his own mental disorder was likely to be caused by some kind of chronic hypoglycaemia in combination with secondary food allergies and a lack of certain minerals.\footnote{For the earlier view see, for instance, ibid., Ms.Eng. c. 3146, D 43, letter N. Tinbergen to M. Welch (15/10/1980), ibid., Ms.Eng. c. 3146, D 47, letter N. Tinbergen to M. Zappella (03/06/1980), ibid., Ms.Eng. c. 3147, D 66, letter N. Tinbergen to L. Pauling (26/10/1980). For the later explanation see ibid., Ms.Eng. c. 3146, D 37, N. Tinbergen to H. Hassenstein (10/03/1982), ibid., Ms.Eng. c. 3146, D 37, letter N. Tinbergen to H. and B. Hassenstein (14/01/1983), here pages 2–3, ibid., Ms.Eng. c. 3145, D 26, letter N. Tinbergen to B. Rimland (15/01/1983), here pages 1–2, and ibid., Ms.Eng. c. 3145, D 26, letter N. Tinbergen to B. Rimland (22/02/1983), page 2. See also ibid., Ms.Eng. c. 3146, D 40, letter N. Tinbergen to J. Prekop (08/11/1982), ibid., Ms.Eng. c. 3146, D 45, letter N. Tinbergen to M. Welch (23/08/1982), and ibid., Ms.Eng. c. 3146, D 47, letter N. Tinbergen to M. Zappella (23/09/1982), here page 1. That Niko’s depressions eventually were never healed completely can be inferred from those letters which report set-backs. See, for instance, ibid., Ms.Eng. c. 3146, D 40, here page 1.} Niko’s own medical history had an impact on his view upon the autistic condition insofar as he recognized the effect of nutrition. However, he still marked a difference between his own depression and the autistic syndrome.
insofar he considered psychological factors the primary causes of becoming autistic. Moreover, his stronger emphasis on “organic” factors did not go as far as to ask for the physical correlate of what Niko called “psychogenic” causes. One of the rare occasions Niko elaborated upon this question may be a letter he wrote to J. Prekop in July 1982 to convince her of his view that the autistic syndrome may be due to a primary vulnerability (caused by genetic effects and/or intrauterine impacts) in combination with secondary traumatic experiences. There it reads:

Jetzt[t]\textsuperscript{CL} diese semantisch verwirrende Sache der “Hirnschaden”. Bitte glauben Sie uns, dass wir nie behauptet haben und nie behaupten werden, dass es keine hirngeschädigten Kinder gäbe!!! Wir sagen nur, und werden immer mehr davon uebenutz, dass [...]\textsuperscript{CL} unter den als “autistisch” (und “autistiforme” – bloedssinniges Wort) bezeichneten Kindern [es]\textsuperscript{CL} sehr sehr wenige gibt, die eine \textit{strukturelle} Hirnschädigung haben. Natürlich haben sie alle Hirndysfunktion, denn das Verhalten wird ja bei jedem Menschen (und jedem Tier) vom Gehirn gesteuert. Wir erwähnen in unserem Buch auch “Konsequential” autistische, Kinder, wie die vier Ihrer 37, autistisch geworden sind als sekund[a]\textsuperscript{CL}ere Folge einer wirklichen, strukturellen Gehirnabnormalitaet. [...]\textsuperscript{CL} – Was wir behaupten, ist, kurz gesagt, dass mit dem Gehirn der meisten autistischen Kinder strukturell nichts los sei ausser \textit{moeglicherweise} (aber nicht mehr) [die]\textsuperscript{CL} sekundaere[n]\textsuperscript{CL} strukturellen, chemischen usw. Folgen der ganz starken Traumatisierung[.],\textsuperscript{CL} die von fehlgeschlagener Affiliation mit der Mutter angesetzt worden ist. Dazu kommt dann noch, dass dieses Fehlen oft an erster Stelle vom Baby sozusagen init[i]\textsuperscript{CL}iert wird, naemlich dann wenn es sich entweder um ein abnorm ruhiges (“gutes”) Baby handelt, oder um einen Neonat der unaufhoerlich schreit und nicht aufgenommen werden will. (Das kann teilweise genetisch bedingt sein, teilweise, glauben wir, schon von Erfahrungen wahrend der Geburt oder sogar in utero[)]\textsuperscript{CL}. Wir besprechen diese viele, von uns vermuteten und nicht gut untersuchten, “autismogenen” Aussenfaktoren in Detail in unserem Buch. Also auch unsere These ist durchaus, dass “Autismus”, grosstenteils auf eine “emotional” (“affektive”) Stoerung zurueckgeht. (Wir gebrauchen hierzu das Wort “Motivation” in einfaches Sinne, der “Bereitschaft zu gewissen Verhaltensweisen”. Simplistisch, aber fuer vorlaeufigen Zwecken genug.). [...]\textsuperscript{CL} Sicherheit ueben “keine Hirnschadigung” , kann man natuerlich nur in einer Autopsie erhalten; meine Behauptung ist, dass (es)\textsuperscript{CL} fuer Autismus als Folge einer strukturellen oder chemischen Hirnabweichung einfach keine Evidenz besteht, und dass (ass)\textsuperscript{CL} nicht nur unsere Analyse der Aetiologie, sondern auch die Ergebnisse der modernen (Welch) therapie darauf hinweisen, dass es sich um potenziell normale oder sogar ueberempfindliche und begabte Kinder handelt, die traumatisiert worden sind. Also wir unterscheiden scharf da Diagnostisieren (dass wir selbst nur aufgrund beobachtbarer Verhaltensabnormalitaeten machen) und Deutung (ob strukturelle Hirnschaden oder Traumatisierung oder beide). Das scheint uns unbedingt wesentlich als methodologische Forderung. Die systematische Behandlung dieser Sachen kann aber nicht kurz in einem Brief gegeben werden.

[...Now as to this semantically confusing matter of “brain damage”. Please believe us that we have never claimed and will never claim that there are not existing any brain damaged children!!! We only say, and become more and more convinced, that [...]\textsuperscript{CL} amongst those children named

\textsuperscript{1120} See ibid., Ms.Eng. c. 3145, D 26, letter N. Tinbergen to B. Rimland (15/01/1983), here pages 1–2.
“autistic” (and “autistiforme” – stupid word) there are very very few which have a structural brain damage. Of course they all have brain dysfunctions since the behaviour in any human being (as well as in any animal) is controlled by the brain. We also mention in our book “consequential” autists, children who alike to the four ones in your sample of 37 became autistic as a secondary consequence of a real structural brain abnormality. [...] – What we claim is, in short, that nothing is structurally wrong with the brain of most autistic children except possibly (but nothing more) the secondary, structural, chemical etc. consequences of the very strong traumatism which has been set off by the failed affiliation with the mother. In addition to that, it is often the baby who initiates this failing in the first place, namely if it is either an abnormally quiet (“good”) baby or it is a neonate that is permanently crying and does not want to be picked up. (This can be partly due to a genetic condition, partly, as we believe, due to experiences during birth or even in utero). We discuss these many cases of “autismogene” environmental factors – which we have presupposed though not examined carefully enough – in detail in our book. Therefore, also our hypothesis is that autism is for the most part the result of an “emotional” (“affective”) disturbance. (In doing so we use the word “motivation” in the simple sense of “readiness to perform certain behaviours”. This is simplistic yet for our provisional purpose sufficient.). [...] – Certainty that there is “no brain damage” can, of course, only be obtained in an autopsy; My contention is that there is simply no evidence for autism as a consequence of a structural or chemical abnormality in the brain and that not only our analysis of the aetiology but also the results of modern therapy (Welch) indicate that we have to do with potentially normal or even hypersensitive and gifted children who have been traumatized. Therefore we distinguish sharply between diagnosing (which in turn can be done only on basis of observable behavioural deviations) and interpreting (whether there is a structural brain damage or a traumatism or both). This to us appears to be a vital methodological demand. The systematic treatment of these issues however cannot be achieved in a letter.]

The quotation shows that N. Tinbergen in fact had a physical understanding of what he called “psychogenic” factors or “dysfunctions” of the brain in order to approach the causes of autism since he claimed the heavy traumatic experiences might have “secondary”, “structural” and “chemical” consequences. As a result, we may therefore say that the Tinbergens not only began to take into account environmental organic causes (e.g. nutrition) but also conceived the dichotomy between structural and non-structural causes slightly less rigid. Whether there was a similar shift on the axis that was marked by the antagonism between nature and nurture is an interesting question. At least in some parts of their book, referring on individual genetic differences, general vulnerability plays an important role in the argumentation put forward by the Tinbergens: For instance, critics questioned Niko and Elisabeth Tinbergen’s psychogenic theory of autism by pointing out that, if taken for granted the virulence of psychogenic factors, all children subject to harmful circumstances must have developed the syndrome which, in fact, wasn’t the case. The Tinbergens replied that, like in a major epidemic not all individuals are equally liable to develop the syndrome. The vulnerability, in turn, had been related partly to an inherited disposition. In sum, however, we might say that the Tinbergens underestimated the importance of inherited organic causes. Some factors which turned out to be important seem to lie somewhere in-between the antagonistic poles the Tinber-
gens suggested which raises the question in how far the notion of dualism applies at all to the complexity of the phenomenon. That the Tinbergen's abandoned their dichotomous approach primarily in their discussion of the effective range of nature- and nurture-causes yet not equally consequently on all other levels is something I experience as a severe methodological deficit – just as well as the fact that the suggested classification of causes lacks its empirical bases and therefore has more the character of a projection.

Parallel between ontogeny and phylogeny. Another aspect which to me seems essential for understanding Niko and Elisabeth Tinbergen's late study on autism consists of a structural or epistemic parallel construction between ontogenetic and phylogenetic development. I have already mentioned that it was the refinement of certain parts of the black-box model which allowed the Tinbergen's to take into account a wider range of less but also even more severe autistic behaviours. Most likely it is also this process of recursive differentiation and sub-differentiation which is responsible for the fact that “Autistic” Children in comparison to Early Childhood Autism reveals a more pronounced chronological perspective which found its expression in a stronger emphasis of both ontogenetic and phylogenetic development. As to the normal course of the autistic disease we may say that the Tinbergen's held an ambiguous perspective. “Long-term change”, they claim,

leads either to a certain degree of recovery or (allegedly much more frequently) to a gradual deterioration of the condition, characterised by a steadily increasing degree of retardation, and a set of such severe and deep-rooted handicaps that the patient is doomed to dependence on others for the rest of his life.\textsuperscript{1124}

Moreover, when autistic children grow older their behaviours, the Tinbergen's claim, become more and more stereotypical.\textsuperscript{1125} Severe forms of withdrawal behaviour, such as aggression, are said to develop also at a later date in the life of an autistic child.\textsuperscript{1126} Moreover, the Tinbergen's argue that the differences between “autistic” and “normal” children become increasingly evident in course of their individual development (ontogeny).\textsuperscript{1127} In order to grasp this process the Tinbergen's introduce the concept of “formalisation” that they, as far as I can see, had not used in their earlier publication.\textsuperscript{1128} According to Elisabeth and Nikolaas Tinbergen, the formalization of behaviour in advanced stages of the course of the autistic disorder can

\textsuperscript{1124} See Tinbergen et al., “Autistic” Children, 106. For the long-term effects see also ibid., 82–84.

\textsuperscript{1125} See ibid., 74.

\textsuperscript{1126} See ibid., 73.

\textsuperscript{1127} See ibid., 119.

\textsuperscript{1128} For the concept of formalization see ibid., 58–60, 74, 84, 94–95, 98, 100. In 1976 the Freiburg biologist B. Hassenstein was working on an update of his book “Verhaltensbiologie des Kindes”. On this occasion he wrote N. Tinbergen asking for the latest news in matters of childhood autism. Niko’s reply contained a rather drastic self-critical evaluation of his 1972 publication. Moreover, we are informed about the course his reasoning on the autism problematic has taken. Thus he adds the notion that over-anxiety not only blocks the building of social relationships but also impedes the child’s explorative behaviour. Further, we find the distinction between short-term and long-term effects of the disorder whereby the latter aspect is connected with the notion that an anxiety dominated motivation conflict can become permanent over the years. For the correspondence see Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3146, D 36, letter B. Hassenstein to N. Tinbergen (20/12/1976), and ibid., Ms.Eng. c. 3146, D 36, letter N. Tinbergen to B. Hassenstein (09/01/1977).
include both its “simplification” and its “exaggeration”. In addition to that, the Tinbergen underline that autistic children often suffer in general from an emotional retardation. Therapy, on the contrary, must therefore invert the perspective and apply a process of “deformalization”. To understand the argumentation of the Tinbergen it is also necessary to mark the difference between formalization and what N. Tinbergen in earlier studies had called “ritualization”. Thus ritualization represented a gradual evolutionary process in course of which dysfunctional (or displaced) behaviours obtained a biological function as a communicative signal. This process possibly also included the exaggeration of the behaviours mostly to make particular morphological structures more conspicuous. Formalization, though it refers to an equally gradual process, seems to invert this logic insofar as the process in question started with intact behaviours yet which, the more the process of deterioration advances, seem to loose their functionality. Ontogeny, in the view of Elisabeth and Niko Tinbergen, thus seems to imply a process of gradual deterioration, increased stagnation and decreased “fitness”. I think it has become sufficiently clear how the Tinbergen structured their account of the genesis of the autistic syndrome in the individual.

My argument now is that the Tinbergen’s critical view upon the course of human development shared the epistemic scheme underlying their account on the aetiology of the autistic disorder, so that both contexts could stabilize each other mutually. In their view, human civilization suffered from a “derailment” structurally similar to the one of the autistic or normal child when being exposed to maladaptive environmental circumstances. The more human evolution proceeded the more were humans capable not only to supplement their biological with cultural evolution (i.e. the transfer of acquired cultural traditions from generation to generation) – they also began to shape by themselves the selective pressures which in turn were determining their own future biological development. Yet in Elisabeth and Niko Tinbergen’s view, the capability of taking evolution into one’s own hands had not only

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1130 Ibid.
1131 Ibid., 75.
1132 Ibid., 58.
1133 See fn. 946, page 315 of my thesis.
1134 The parallel can be inferred indirectly from the metaphors being used in the account. For instance, the Tinbergen describe humans as the “Guinea Pigs” of evolution, by which they mean that humans are their own experimental animal in their own created “laboratory of evolution” (Ibid., 142). On the other hand, however, the Tinbergen compared the long-term effects of the autistic disorder with the behavioural modifications animals suffer in long-lasting captivity – a syndrome they call “experimental neurosis” (Ibid., 57). For a description of civilized Man’s estrangement from his original way of living in small family systems see ibid., 147. For this evolutionary perspective on human kind see ibid., 140, 144–148, 148–151, 151–153, especially 152 for the shaping of one’s own selective pressures. Maybe, without mentioning it explicitly the Tinbergen at this point argue in favour of what is usually called the “Baldwin effect”, that is, the idea that human culture might have a secondary effect on their genetic development insofar as culture shapes the parameters of selecting future mutations. In other words, culture might direct biological evolution. For a highly recommendable reassessment of the concept see E. Crispo. “The Baldwin Effect and Genetic Assimilation: Revisiting Two Mechanisms of Evolutionary Change Mediated By Phenotypic Plasticity”. In: Evolution. International Journal of Organic Evolution 61.11 (2007), especially 2470–2472.
positive effects since humans also invented selective pressures which turned out to be harmful.\footnote{1136} Apparently it was the notion of modern highly competitive civilizations including the repercussions the global competition might exert upon the social structure of the communities and their constituents, the families, which the Tinbergen\'s criticized most.\footnote{1137} In particular, the modern education systems which revealed a shift from intuitive, playful and person-oriented learning to what they called “learning by instruction”, in their view, damages the original unity of the families.\footnote{1138} The loss or drop-out of natural social skills, the retardation of parental behaviours and the social estrangement humans face in modern anonymous societies, in turn, appear to be the source of all other factors the Tinbergen\'s called “autismogenic” and which they made responsible for the development of the autistic syndrome in children being vulnerable to the condition.\footnote{1139} “When now”, the Tinbergen\'s write,

in the light of this wider view of “human nature” and the changes in the human condition, we look back at our list of “autismogenic factors” we will see that many of them are, directly or indirectly, related to the deterioration of certain aspects of our social climate. Rather than running through the list once more, we rely on our readers to see this for themselves.\footnote{1140}

That the Tinbergen\'s had quite a physical understanding of the psychic effects which result from social relationships is revealed by the way how they use the term “pollution”. Next to the common usage of the word in terms of “environmental pollution” they also apply the concept in a sense of “psychological pollution”. “In fact”, they underline,

the “autismogenic” factors that we have indicated must be considered as expressions of genuine psychological pollution, which itself is only part of the overall process of disadaptation to which our civilization is subjecting us. While it may well be impossible to undo a number of other aspects of our disadaptation, there is no valid reason and therefore no excuse to accept meekly the traumatisatation of so many of our own children.\footnote{1141}

\footnote{1136} Tinbergen et al., “Autistic” Children, 40. The “harmful” effect apparently originates when the adjustability of Man is exceeded so that a gap emerges between his deeds and the extent of responsibility he is capable to take (Ibid., 150–151).
\footnote{1137} The more of competition, in the opinion of the Tinbergen\'s, leads to a destruction of the playful atmosphere which in their view is necessary for the adequate rearing of the children. See ibid., 256–257.
\footnote{1138} See ibid., 71–72, 136, 147. The Tinbergen\'s reflections on the modern education systems also cast another light upon N. Tinbergen\’s way of socializing his students. I have argued that this mode changed in later generations in a sense that younger students were integrated on earlier stages of their academic education. In this context, I also read the suggestion to follow the Tinbergen\'s and learn practically how they apply the method of “watching and wondering”. See ibid., 23–24.
\footnote{1139} For a list of these “autismogenic” factors see ibid., 121–136. This list includes a number of strictly environmental factors such as the influence of nutrition and environmental pollution, intrainertine prenatal impacts, psychic stress and violence, conditions of birth, mutual programing between child and mother shortly after birth, illness and hospitalization, birth of another sibling shortly after the birth of a child, conditions and change of accommodation, or even multilingual education. Other aspects are more directly related to the social bonding of the children such as early deprivation from the mother, the emotional state of the parents, and divorce or loss of parents. In addition to these “autismogenic” factors see also the Tinbergen\'s intention not to want to blame the parents ibid., 13, 126, 224 and 332.
\footnote{1140} Ibid., 154, and also 167, 214–215, 259–260.
\footnote{1141} Ibid., 140, similarly 153–154.
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In sum, we might eventually say that Niko and Elisabeth Tinbergen’s critical account of human civilization followed the same logic they had traced in the genesis of the autistic syndrome insofar as in both processes developing “mis”- or “disadaptations” coincides with a trend towards a more of unfitness.\textsuperscript{1142} Both developments are described in terms of a maladaptive “deviation” or, more metaphorically, as “derailment”.\textsuperscript{1143} As a result, both ontogenetic and phylogenetic development therefore appear as two different expressions of one and the same narrative epistemical scheme which implies a gradual trend to deterioration. However, in addition to that, we might say that both forms of development are not only construed in parallels but also intertwined with each other since each of the processes addressed in both accounts can be interpreted as the starting point of the other. The spread of psychogenic autism reinforces the derailment of human culture and the maldevelopment of human civilization reinforces the dissemination of the autistic syndrome.\textsuperscript{1144} Altogether the Tinbergens thus seem to have perceived human kind within a sort of vicious circle which to escape required the intervention of a cure.

Avoidance of intrusion. A more pronounced demarcation between Elisabeth and Niko Tinbergen’s later work on autism and their early publication can be made evident in the measures they considered appropriate to cure autistic children. While “cure” in \textit{Early Childhood Autism} primarily meant a process of gradual “taming”, that is, the successive establishment of social relationships between the autistic child and its environment by both avoiding over-intrusive stimulation and by applying encouraging gestures, the modes of treatment suggested in \textit{“Autistic” Children} remarkably imply a significant more of intrusion.\textsuperscript{1145} Critics have pointed to the inconsistency that possibly resulted from this turn in matters of cure.\textsuperscript{1146} “In the 1972 paper and the Nobel lecture”, H. Kruuk writes,

Niko advocated that “anything must be done to avoid over-intimidation” of the autistic child, “watching all the time but acting only when the baby demands it”, acting lovingly to regain the child’s confidence. But some years later their advice on how the mother should be taught was radically altered, and the Tinbergens’ preferred approach became that advocated by Martha Welch, “forced holding” of the (often struggling) patient, in a tight, intimate, and enforced embrace by the mother daily, for half an hour or longer. It was this last treatment that appeared

\textsuperscript{1142} For the Tinbergens’ use of the concept of “fitness” which in biological reasoning closely connected with an organism’s adaptiveness see \textit{ibid.}, 155, 215–216, 228.

\textsuperscript{1143} The metaphor of “derailment” reveals the mechanical way of thinking. It also implies the corrigibility. The metaphor appears many times in the text especially when the Tinbergens describe the course of the autistic disorder. See \textit{ibid.}, 75, 86, 106, 107, 139, 155, 213, 220.

\textsuperscript{1144} Autism in the view of the Tinbergens therefore is a disease of modern civilization which is caused by stress. See \textit{ibid.}, 140. The increase of affected children, in their view, is not only a question of more accurate statistics but also possibly a matter of actual facts. See \textit{ibid.}, 143, and also Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3144, D 15, letter N. Tinbergen to [V. D.]\textsuperscript{CL} Sanua (03/06/1978), here page 2. Recent studies seem to substantiate the hypothesis that autism statistically affects more persons than a purely genetic theory can explain. K. Miyake \textit{et al.} state: “The number of autistic children has been increasing [in]\textsuperscript{CL} recent years in Japan, USA and other countries. This increase cannot be solely attributed to genetic factors, because it is unlikely that the mutation rate has suddenly increased in recent years. Therefore, environmental factors are more likely to be involved in this increase”. See Miyake \textit{et al.}, “Epigenetics in Autism”, 92.

\textsuperscript{1145} For a recapitulation of both non-intrusive methods of cure see Tinbergen \textit{et al.}, \textit{“Autistic” Children}, 71.

\textsuperscript{1146} The Tinbergens themselves have indicated to have partly revised their older views. See \textit{ibid.}, 176.
My approach to historicize helps to resolve what appears to be a contradiction in the first place. The Tinbergen’s, in their later autism study, have not abandoned their conviction that the source of the autism disorder syndrome might be a motivational imbalance. Nor did they give up completely their non-intrusive approach. They had only observed more severe forms of autistic behaviours which, at first sight, appeared to be non-classifiable either in the withdrawal- or the approach-category and they had met this challenge of their theory by refining the afferent central parts of their black-box model. In my opinion, this refinement was primarily based on implementing the notion of “hyper-arousal” which supplemented the notion of motivation conflict in quite a concrete sense, namely in that the Tinbergen’s considered “over-arousal” as the product (i.e. secondary effect) of the motivation conflicts and less as a feature of their central causation. If we can accept that Niko and Elisabeth Tinbergen’s approach to the autism problematic developed over a period of more than ten years, it is only a small step to understand that observing more severe forms of autistic symptoms also required a refinement of the methods of their treatment. In carefully reading “Autistic” Children I could not get rid of the impression that the autistic syndrome in its more severe expressions is also the result of a hierarchical imbalance in as much as the children, according to the Tinbergen’s, manage perfectly well to superimpose (or overwhelm) the social efforts of their reference persons with their own tendency to cut off these social bondings (or the corresponding efforts) – which, by the way, seems to generate quite an ambivalent or paradox psychic constellation in the mother or the therapist. This is, I think, where M. Welch’s therapy of forced holding put itself into position. The

1147 See Kruuk, *Niko’s Nature*, 277. G. Beale, I think, has misrepresented H. Kruuk’s statement that the Tinbergen’s late understanding of cure “had little to do with their ethological study and hypotheses” to a certain extent in referring it to Niko’s studies before his engagement with autism. Kruuk, I think, had primarily (though eventually not exclusively) in mind the Tinbergens’ ethological approach to autism itself. For Beale’s critique see Beale, “*Tinbergian Practice, Themes and Variations*”, 243–244. His claim “that the autism studies do fit better with the rest of Tinbergen’s opus” is justified albeit imprecise because we must clarify to which of the developmental stages in Niko’s intellectual life-history his studies of childhood autism actually “do fit”.

1148 See Tinbergen et al., “*Autistic* Children”, 19–21, 79–82, 231–232.

1149 *Ibid.*, 91. The whole point is where in the model of the black-box the idea of “hyper-arousal” is located. See also Bod. Lib., *N. Tinbergen Papers*, Ms.Eng. c. 3147, D 55, ms. “Early Childhood Autism” (n. d.), here page 2.

1150 For a description of Welch’s therapy see Tinbergen et al., “*Autistic* Children”, 174–179 and also the case history she added to the Tinbergen’s book in “Appendix I”, 324–334. Her contribution to Niko’s book apparently consisted of a paper that had been rejected before. See Bod. Lib., *N. Tinbergen Papers*, Ms.Eng. c. 3146, D 43, letter M. Welch to N. Tinbergen (23/11/1980). For an abridged summary of the Welch-therapy. See *Ibid.*, Ms.Eng. c. 3145, D 21, ms. with the title “How can an autistic child be helped?” (08/1981). A correspondence between N. Tinbergen and an R. W. Zaslow, a psychology professor from San Jose State University (California), in the aftermath of the lecture N. Tinbergen had delivered during the Lindau Nobel Laureate Conference in 1981 shows that Zaslow had applied a similar method of forced holding since ca. 1968 and therefore claimed originality. N. Tinbergen, however, seems to have adopted the method primarily through M. Welch who put more emphasis upon the notion that the mother
Tinbergen did not claim that the therapy of forced holding was their invention—they rather argued that it was M. Welch’s merit to have provided the right answer in a moment when they had got stuck with the notion of motivation conflict. In his so-called “Spanish Lecture” Niko argues:

We began to realise that autism was in essence due to a deep-rooted over-anxiety, and that the syndrome as I have described it consisted mainly of secondary effects of this emotional imbalance, in fact to symptoms, we began to hope that the best cure might well be found, not in symptom treatment such as speech therapy, nor in operant conditioning of the cruder kind such as penalising “mannerisms”, but in reducing the child’s anxiety. And indeed we found that dropping the teaching-by-instruction of skills (the practice in most normal schools) and concentrating instead on “putting the children at ease”, on loving them, on playing with them and on helping them socialise, did lead to quite striking improvements not only in the child’s emotional condition but also in the development of his «their» skills such as the emergence of speaking, of listening, of thinking, and on motor skills of all kinds, without these skills having been specifically taught. But we also found that these improvements went only a limited way; they did not lead to complete recoveries; almost all the children got stuck at a level that was still below the completely normal level. It was at this stage that we were approached by the New York psychiatrist Dr Martha Welch, who had read an earlier publication of ours (which, while on the right track, was still in many respects immature). She had argued, on the basis of considerations quite different from ours, and in a rather more empirical way, that autistic children could recover completely if they were taken back so to speak to “square one” in their development, and made to start their affiliation anew as if they were babies.

In doing so the holding therapy also intended to establish a more healthy hierarchical constellation insofar as it transferred the “ambivalence” back into the child—in a sense of re-establishing the motivational balance that the Tinbergen deemed necessary to resolve motivational conflicts. J. Prekop, for instance writes to a colleague:


For breaking the child’s resistance see Tinbergen et al., “Autistic” Children, 176–177. In addition to that, we are informed in “Autistic” Children that in so-called “hopeless cases” the prospects of curing the child are less promising because the mother reinforces what the Tinbergen called “downward spiral” by her own ambivalent behaviour. See ibid., 194–195. In a letter to H. Hemminger, a former pupil of B. Hassenstein, Niko also adds a psychoanalytical nuance to the holding-therapy: During the holding the child comes up with memories of traumatic experiences. See Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3145, D 26, letter N. Tinbergen to H. Hemminger (09/03/1983), here page 2. The recollection of these experiences can be interpreted as establishing some kind of otherness within the self of the child. Niko’s interest in the mothers as an object of further examination becomes evident in a letter to J. Prekop. See ibid., Ms.Eng. c. 3146, D 40, letter N. Tinbergen to J. Prekop (17/07/1982).
Ich vermute, daß bei jenem autoaggressiven Jungen die richtige Dynamik der jeweiligen Sitzung nicht hergestellt ist. Es sollte sich ja nicht um eine Beruhigung handeln, sondern um eine Herausforderung der autistischen Ambivalenz, die aus folgenden Polen besteht [Furcht vor dem Kontakt etc. vs. Freude am Kontakt etc.] und «in» diesen Polen dem Kinde zum bewußten Erlebnis gemacht werden muss [...].

[I guess that in case of this auto-aggressive boy the right dynamics in each session has not been established. In fact it shouldn’t be [or: it is not about] a calming down but rather the provocation of the autistic ambivalence that consists of the following antagonistic poles [contact anxiousness etc. vs. contact pleasure etc.] and which must be made the child’s conscious experience in these antagonistic poles.] (transl. CL)

In the last consequence this apparently also implied to “break” the children’s resistance (forcefully). That Niko and Elisabeth Tinbergen repeatedly demanded a “need for discipline” can be read also as an expression of the inner logic of M. Welch’s approach. Holding turned out to be a fairly promising therapy not only for autistic children but also for other mental disorders and its application more and more turned into a success story especially in Germany where the course of the events can be reconstructed on basis of the correspondence passed onto us in the Tinbergen Papers. In 1981 N. Tinbergen attended the so-called Nobel Laureate Congress in Lindau. The conference is a get-together of Nobel Laureates of one section (e.g. Medicine) and takes place in triennial rhythm. There Niko delivered a speech with the title “An Effective Therapy for Childhood Autism” which he himself wanted to be seen as a follow-up lecture of the presentation he had delivered three years before in 1978 and which had been concerned with the theory of the autistic condition. In contrast to the earlier speech, the lecture delivered in 1981 (as did the later book) focused upon the aspect of cure. Attracted by the speech and the echo it received in the media a couple that had an autistic son (Robert S.) and was living in the Lindau area approached the Tinbergens during the conference in order to be instructed in the Welch therapy. As far as I can see, it was Elisabeth Tinbergen who together with Helma Hassenstein, wife of the Freiburg Zoology professor B. Hassenstein, visited the family and made the couple familiar with the technique.

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1156 The successful application of the method to a wider range of disorders as well as the dispersal of the method in countries other than Germany can be inferred from the letters J. A. Allan exchanged with N. Tinbergen. See ibid., Ms.Eng. c. 3146, D 32, letter J. A. Allan to N. Tinbergen (15/02/1983), ibid., Ms.Eng. c. 3146, D 32, letter J. A. Allan to N. Tinbergen (04/05/1983), ibid., Ms.Eng. c. 3146, D 32, letter J. A. Allan to N. Tinbergen (05/02/1987).
1157 A draft of the later speech is preserved in the Tinbergen papers. See ibid., Ms.Eng. c. 3147, D 66, ms. “Lindau 1981[,...]. An Effective Therapy for Childhood Autism” (1981). In addition to that, Niko provided a fairly long summary of the talk in a letter to Helen Blohm who had asked for more detailed information about the speech. This summary is helpful for reconstructing the content of Tinbergen’s speech. See ibid., Ms.Eng. c. 3145, D 21, letter N. Tinbergen to H. Blohm (>16/07/1981). The letter has not a date but the date of Blohm’s complementary letter to which Niko replied is notified as “16 July 1981”. So it must be later.
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Stuttgart, was prepared to adopt the method and give it a try with other patients of hers. “Eins von den wenigen englisch herausgegebenen Büchern”, she writes,


[One of the few books edited in English language I read with the help of a dictionary some years ago was in fact your work on autism. Since that time you have become a name for me and I integrate your views in my interpretations of the genesis of autism and in the therapeutic strategies. [...] I have been missing the method of holding like an important line in a crossword puzzle. I presume that the method can be applied quite successfully in cases of autism with affective condition. With autism conditioned also by severe perceptive disorders (like is the case with Robert) the success may be a little smaller but be interpreted as decisive help. In fact the holding may be helpful in other disorders in as much as the child was not able to make this basic experience with his own mother.]

Although J. Prekop appreciated to have a practicable method of cure with holding she did not entirely share N. Tinbergen’s theoretical convictions. This becomes evident in the quotation above and the fact that she made a difference between “affective autism” and autism caused by severe “perceptive disturbances”. In addition to that, I think, it can be made evident in her letters that she never abandoned the possibility that autism might be caused by organic damages in the extreme way Niko did. However, her theoretical resentments did not prevent Prekop from success-

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1161 If I have understood correctly J. Prekop, for instance, argued that autism might be due to an “inborn hypotonia” which prevents the child to adjust to the movements of the mother. See ibid., Ms.Eng. c. 3146, D 38, letter J. Prekop to N. Tinbergen (ca. 11/1981), page 1. See also ibid., Ms.Eng. c. 3146, D 38, letter J. Prekop to N. Tinbergen (ca. 12/1981), ibid., Ms.Eng. c. 3146, D 39, letter J. Prekop to N. Tinbergen (20/06/1982), and the statistics she developed to demonstrate the successfullness of the cure, ibid., Ms.Eng. c. 3146, D 39, letter J. Prekop to N. Tinbergen (10/01/1982). For N. Tinbergen’s objection see ibid., Ms.Eng. c. 3146, D 39, letter N. Tinbergen to J. Prekop (25/06/1982). Prekop’s rejoinder is remarkable: In her view, the success of holding shows that more cases of autism than previously assumed were of the emotional type. However, she was not prepared to neglect the existence of organic autism, Niko’s “rotes Tuch”, as she put it. Some structural damages might be virulent although they will be able to be made evident only with future technologies such as EEG and computer tomography. Moreover, she says the knowledge of structural damage does not necessarily lead to a defeatist attitude as Niko claimed. Instead we may infer that, in Prekop’s view, knowledge of the real causes might be relevant for finding the adequate cure. See ibid., Ms.Eng. c. 3146, D 40, letter J. Prekop to N. Tinbergen (03/07/1982). Niko’s reply is equally sophisticated: He does not neglect the existence of brain damaged children. Yet he claims that there is nothing wrong with the brain of autistic children except the secondary chemical etc. consequences of primary traumatic experiences.
fully applying the holding by adjusting the method individually to each case.\textsuperscript{1162} Moreover, the letters exchanged between J. Prekop and N. Tinbergen between 1981 and ca. 1985 show that Prekop turned out as strategically thinking and highly gifted promoter of the “Welch-Tinbergen Therapy” as she put it. Most likely it was her efforts that finally fostered the acceptance of the approach amongst the professionals in West Germany.\textsuperscript{1163} In countless public speeches, as an administrative member of the German “Bundesvereinigung ‘Hilfe für das autistische Kind’”, as publisher of several progress reports and, finally, in her every day work as therapist and instructor of parents and other therapists she never tired of propagating the promising prospects of the holding therapy.\textsuperscript{1164} Around the year 1983 when the correspondence with N. Tinbergen began to wane due to a brain stroke the latter had suffered,\textsuperscript{1162} For Prekop’s individual adjustment of the method see \textit{ibid.}, Ms.Eng. c. 3146, D 37, letter H. and B. Hassenstein to N. Tinbergen (10/03/1982).

\textsuperscript{1163} This can be deduced from a little episode whose course of events can be reconstructed on basis of the letters exchanged between J. Prekop and N. Tinbergen. After his speech in Lindau the German psychiatrist H. Kehrer has published a critique of Niko’s approach in \textit{Autism}, the journal of the German Society “Hilfe für das autistische Kind”. Niko was outraged because he believed that Kehrer who was thought to have considerable influence in his scientific community had written his critique in basis of mere secondary information. However, he left it to Prekop to reply. Henceforth she made it her own business to “convert” Kehrer in which she finally succeeded, at least partly. According to Prekop’s account, it was her reply to Kehrer in \textit{Autism} which was leading to an increase of interested patients and her election in the “Vorstand der Bundesvereinigung ‘Hilfe für das autistische Kind’”. For H. Kehrer’s criticism see H. Kehrer. “Kindlicher Autismus. Eine Angstneurose (Antwort auf Tinbergen)”. In: \textit{Autismus. Zeitschrift des Bundesverbandes “Autismus Deutschland e.V.”} 12 (1981), 2–3. For J. Prekop’s rejoinder see J. Prekop. “‘Festhalten’. Erste praktische Erfahrungen nach Tinbergen und Welch”. In: \textit{Autismus. Zeitschrift des Bundesverbandes “Autismus Deutschland e.V.”} 13 (1982), 12–15. For additional archives documenting the entire controversy see Bod. Lib., \textit{N. Tinbergen Papers}, Ms.Eng. c. 3146, D 38, letter J. Prekop to N. Tinbergen (ca. 11/1981), page I. \textit{ibid.}, Ms.Eng. c. 3146, D 38, letter N. Tinbergen to J. Prekop (30/11/1981), \textit{ibid.}, Ms.Eng. c. 3146, D 38, letter N. Tinbergen to J. Prekop (29/12/1981), \textit{ibid.}, Ms.Eng. c. 3146, D 39, letter J. Prekop to N. Tinbergen (20/06/1982), and \textit{ibid.}, Ms.Eng. c. 3146, D 47, letter N. Tinbergen to M. Zappella (21/03/1982). For the indicators that H. Kehrer partly revised his attitude towards holding see \textit{ibid.}, Ms.Eng. c. 3146, D 41, telegram J. Prekop to N. Tinbergen (07/02/1983), \textit{ibid.}, Ms.Eng. c. 3146, D 41, letter N. Tinbergen to J. Prekop (13/02/1983), \textit{ibid.}, Ms.Eng. c. 3146, D 41, letter J. Prekop to L. and N. Tinbergen (25/09/1983). As an example for Prekop’s published instructions see J. Prekop, “Anleitung der Therapie durch das Festhalten nach Welch/Tinbergen”, In: \textit{Autismus. Zeitschrift des Bundesverbandes “Autismus Deutschland e.V.”} 15 (1983), 2–8. In addition to that see also a series of papers Prekop

\textsuperscript{1164} Indeed he emphasizes that autism is caused by a primary liability (caused by genetic effects and / or intrauterine impacts) and secondary traumatic experiences causing the affective disturbance. In other words, N. Tinbergen’s claim to distinguish strictly between diagnosis and inference rendered autism primarily a phenogenetic phenomenon. See Bod. Lib., \textit{N. Tinbergen Papers}, Ms.Eng. c. 3146, D 40, letter N. Tinbergen to J. Prekop (09/07/1982). That Niko’s disregard of neurological research resulted also from personal experience can be concluded from a letter he wrote to J. Prekop in November 1982. See \textit{ibid.}, Ms.Eng. c. 3146, D 40, letter N. Tinbergen to J. Prekop (08/11/1982).
Prekop was supervising around fifty therapies and requests had become so numerous that she had to restrict her engagement to the area of Baden-Württemberg.1165 “Es ist ein für mich nicht zu bewältigender Ansturm von allen Ecken!”, she writes the Tinbergens in September 1983.1166 Other advocates of the holding therapy, besides M. Welch, who were corresponding with the Tinbergens on a more or less regular basis, were the Italian psychologist M. Zappella, the Canadian psychologist J. A. Allan, Ph. Elmhirst, a psychologist from New York and former pupil of J. Piaget, the London therapist J. Bayley and Lies Tinbergen’s sister in law, the Dutch therapist Hens Rutten. We can also infer from the letters Niko has written that the Tinbergens would have liked to apply the therapy by themselves.1167 Yet they also realized that their lack of medical education and their age turned out to be a handicap.1168 On the other hand, Niko felt that he was ignored by the clinicians in Britain and this is also the reason why he differentiated very clearly between the acceptance of the cure in Germany and its neglect in Britain.1169 In his view,
Germany turned out to be a forerunner in matters of holding. An aspect science historians have neglected completely so far is the way Niko Tinbergen has pulled the strings together. His letters show that he, despite his age, developed an enormous impact behind the scenes as the one who established contact between the advocates of holding, as booster of mutual scientific exchange, as organizer of several “mini-symposia” at his place in Oxford, as mediator of scientific ideas and medical practices, as “broker” for potential “clients” and, finally, as the one who took care indirectly through his letters that instructing parents and therapists was done correctly.

In a letter to M. Welch, Niko writes:

Now that our book is approaching completion [...] I am thinking of the next steps for us, and one of them is of course to make propaganda for your therapy and to act as a kind of clearing house so that kindred souls can get in touch with each other if they happen to approach us.

N. Tinbergen very much perceived the controversy between him and the psychiatric community in colours of black and white (very much like the type of unresolved conflict he supposed to be the causal origin of autism). There were only allies and foes and he made it his business to form the alliance of the advocates of the holding therapy. Followin the logic of a homeostatic system he therefore anticipated a severe scientific controversy in the forefield of the publication of his book and described this controversy as “medico-political battle.” In a letter to M. Welch from October 1981 N. Tinbergen remarks:

As to a conference: for the time being L. and I are very very busy, we may not even have time for him [Zaslow] in January, but let’s keep this in mind; I too feel that the psychogenic baddies should close ranks relatively soon – “psychogenic baddies of the world – unifie!” will


On this “crusade” see also ibid., Ms.Eng. c. 3146, D 47, letter N. Tinbergen to M. Welch (19/11/1981).


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have 6o [to] be our slogan. I feel that, whatever disagreements and even quarrels we might have or make, the interests of the autistic children and their families must come first! I think it can be discussed how uniform Niko’s alliance actually was. Thus, in course of a few years the cure developed into different varieties depending on therapist and the experiences she / he had collected. One of the points that raised discussion thereby was who should do the holding. Whereas M. Welch and (less explicitly) also J. Prekop considered it more or less mandatory that the mother should perform the holding, R. W. Zaslow, M. Zappella and J. Allan handled the question more flexibly and put forward that in certain cases it might be useful if the father or even the therapist performed the holding therapy. N. Tinbergen, who did recognize Welch’s argument that if the child’s father succeeded in holding more than his partner this might cause additional tension in the mother, tended to argue that M. Welch treated the question (only) seemingly too rigidly.

Another aspect that caused a debate was the question how “forced” the holding was to be. While M. Welch and J. Prekop claimed that the success of the technique was best when the child’s resistance was provoked before it was “broken” in order to let the infant experience the loving bonding to the mother, others had more reservations against this aspect of the therapy. M. Zappella, for instance, seems to have tested a less intrusive and therefore less stressful form of therapy in later years which intended

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1175 Ibid., Ms.Eng. c. 3146, D 44, letter N. Tinbergen to M. Welch (27/10/1981). The self identification as “baddy” can be read many times in N. Tinbergen’s letters.


1177 See Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3146, D 47, letter M. Zappella to N. Tinbergen (15/11/1981), and ibid., Ms.Eng. c. 3146, D 47, letter M. Zappella to N. Tinbergen (12/05/1982). In a later report Zappella speaks only of “the adult” and does not differentiate between mother, father or therapist. See Zappella et al., “Parental Bonding”, 4–6, passim.

1178 Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3146, D 47, letter N. Tinbergen to M. Zappella (16/02/1982). In one of his instruction letters he provided arguments why the mother should do the holding. See ibid., Ms.Eng. c. 3147, D 67, ms. “How can an autistic child be helped?” (08/1981).

1179 However, Prekop also took seriously the concerns of the parents. See ibid., Ms.Eng. c. 3146, D 40, letter J. Prekop to N. Tinbergen (01/08/1982). In addition, we can infer from N. Tinbergen’s letters that Lies’ sister in law and also some of the parents had difficulties with this provocation of rage. For these concerns as well as Tinbergen’s and Prekop’s position see, for instance, ibid., Ms.Eng. c. 3146, D 39, letter N. Tinbergen to J. Prekop (25/06/1982), ibid., Ms.Eng. c. 3146, D 40, letter N. Tinbergen to J. Prekop (09/08/1982), ibid., Ms.Eng. c. 3146, D 40, letter J. Prekop to N. Tinbergen (22/09/1982), ibid., Ms.Eng. c. 3146, D 40, letter J. Prekop to N. Tinbergen (30/10/1982). An account how Prekop proceeded practically can be found in ibid., Ms.Eng. c. 3146, D 41, letter J. Prekop to N. Tinbergen (01/02/1983). According to Zappella’s opinion, holding is most efficient when it raises an intense emotional reaction in the child. See ibid., Ms.Eng. c. 3146, D 47, letter M. Zappella to N. Tinbergen (ca. 10/1981). There is also a long letter written by H. Hassenstein asking N. Tinbergen, amongst others, whether forced holding is equally useful for all types of autism including those being based on severe “cerebral disturbances”. In other words, Helma Hassenstein was concerned whether forced holding might not cause damage if the method was applied to inadequate cases or by uneducated parents. See ibid., Ms.Eng. c. 3146, D 37, letter H. Hassenstein to L. and N. Tinbergen (15/02/1982). In his reply Niko defended his views. See ibid., Ms.Eng. c. 3146, D 37, N. Tinbergen to H. Hassenstein (10/03/1982).
to induce changes in behaviour through “possibly joyful and attractive interaction” and beyond that was meant to address “motivations and relationships rather than discrete behavioral patterns” and therefore was “likely to be more efficient”.\textsuperscript{1180} The letters J. Prekop exchanged with N. Tinbergen also show that she began to use the “resistance behaviour” of the child as a diagnostic tool.\textsuperscript{1181} This might be an indicator that the practice of cure had a feedback effect upon the theoretical assessment of the autistic condition. A third aspect of demarcation, finally, was the question whether the holding was to be supplemented by further additional therapies such as the training of speech or motoric skills in general. While the holding itself was meant to restore the damaged roots of the mother-infant bonding and therefore \textit{per definitionem} a therapy that was aimed at curing the emotional constitution of a patient, skill training more addressed the peripheral parts of the nervous system.\textsuperscript{1182}

While the Tinbergens in their earlier work seemed to put emphasis on restoring the emotional balance, in their later work we can note a more neutral view that also left space for supplementary therapeutic strategies such as skill teaching.\textsuperscript{1183} My impression is that of all advocates of the holding therapy it was primarily M. Zappella who treated these issues most flexibly and therefore was able to synthesize the various different impulses he had obtained while interacting with his colleagues.\textsuperscript{1184} Moreover, he seemed to be more interested in the question how N. Tinbergen’s ethological theory could be made productive in child psychiatry.\textsuperscript{1185} In this context, Zappella appreciated not only Niko’s theoretical input but also that he has established fruitful relationships between researchers. He writes:

I feel that all these exchanges of people with convergent attitudes and interests are very good and allow me a powerful input: and I am very grateful to you who have been organising all this net of relationships between us. In my feelings this contribution on your behalf is a major one as well as the scientific insight that you gave us on these problems.\textsuperscript{1186}

\textsuperscript{1180} Zappella et al., “Parental Bonding”, 10.
\textsuperscript{1181} Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3146, D 40, letter J. Prekop to N. Tinbergen (02/08/1982).
\textsuperscript{1182} That the holding therapy supported Niko’s theory of autism as an emotional damage can be inferred from a letter he wrote to J. Prekop. See \textit{ibid.}, Ms.Eng. c. 3146, D 38, letter N. Tinbergen to J. Prekop (16/09/1981). Another letter to Prekop shows that Niko believed Prekop was, under the influence of the “grossen Piaget”, overrating the training of motoric skills. See \textit{ibid.}, Ms.Eng. c. 3146, D 38, letter N. Tinbergen to J. Prekop (30/11/1981).
\textsuperscript{1183} See \textit{ibid.}, Ms.Eng. c. 3146, D 43, letter N. Tinbergen to M. Welch (07/10/1978), incl. sketchy summary of the core theses of Niko’s book. In a letter to M. Zappella the question of additional measures of therapy is correlated with the child’s age and its stage of development. See \textit{ibid.}, Ms.Eng. c. 3146, D 47, letter N. Tinbergen to M. Zappella (16/02/1982).
\textsuperscript{1184} For instance, the information that Zappella adjusted the method to his practical needs can be found in \textit{ibid.}, Ms.Eng. c. 3146, D 47, letter N. Tinbergen to M. Zappella (01/10/1981). For his criticism of the Welch-method see \textit{ibid.}, Ms.Eng. c. 3146, D 47, letter M. Zappella to N. Tinbergen (15/11/1981). For his more eclectic position see also \textit{ibid.}, Ms.Eng. c. 3146, D 47, letter M. Zappella to N. Tinbergen (13/01/1983).
\textsuperscript{1185} See \textit{ibid.}, Ms.Eng. c. 3146, D 47, letter M. Zappella to N. Tinbergen (07/04/1982). Thus the correspondence between N. Tinbergen and M. Zappella shows that the latter, together with J. Richer and V. D. Sanua, planned to write a comparative cross-cultural study on autism – an idea which Niko appreciated very much. See \textit{ibid.}, Ms.Eng. c. 3146, D 47, letter M. Zappella to N. Tinbergen (25/09/1981), \textit{ibid.}, Ms.Eng. c. 3146, D 47, letter M. Zappella to N. Tinbergen (07/04/1982), and \textit{ibid.}, Ms.Eng. c. 3146, D 47, letter M. Zappella to N. Tinbergen (12/05/1982).
\textsuperscript{1186} \textit{Ibid.}, Ms.Eng. c. 3146, D 47, letter M. Zappella to N. Tinbergen (12/05/1982), here page 2.
In the mid-1980s Zappella felt that adopting ethological theory in combination with the holding might be the key to a whole new paradigm of child psychiatry that might provide a promising therapeutic tool to a wider range of mental disorders including the deviant behaviours of both brain damaged and non-brain damaged children.\footnote{1187} The later letters Zappella sent Niko in the years before the latter’s death in 1988 even show that he had developed a cure for the so-called “Rett-Syndrome” (RTT), a mental disorder that only affected girls (and therefore was likely to be determined genetically to a large extent) and to which holding could not be applied successfully at all.\footnote{1188} Instead, Zappella applied a combination of behavioural therapy and pharmacological treatment and therefore, in a certain way, proved wrong Niko’s refutation of organic and genetic causes. On the other hand, he claimed that it was mainly the ethological concept of motivation conflict that had led to a better understanding of the new disease and therefore to a breakthrough in its curing.\footnote{1189} In conclusion, one may therefore say that both theory and practice of childhood autism were subject to transformation over the years. As to Niko and Elisabeth Tinbergen’s altered view upon the methods of curing I therefore suggest to treat the transformations of their views historically that is relative to time and in context of the other modifications their approach to childhood autism experienced during the period of more than ten years of their engagement with the problematic. These other advancements included a refinement of the black-box model and a stronger emphasis on both ontogenetic and phylogenetic development including their mutual intertwinement.

The wider scope of aetiologies. The final aspect I would like to elaborate in more detail is related to the way how the Tinbergen made use of a wider range of inexpert knowledge in order to substantiate their own arguments.\footnote{1190} The trend to take into account non-scientific and / or non-clinical knowledge can be made evident already in the publication of the year 1972 but it experienced a boost in the following years. In his Nobel Lecture, N. Tinbergen had dissolved the boundary between science and public from both sides. According to Tinberg’s account, inexpert applications of the ethological approach, if adopted in science, can lead to heuristic progress just as translating ethological expertise into the public sphere can contribute to a recovery of human civilization. In “Autistic” Children we can find both argumentative patterns in particular, however, the former of the two. In order to explain my point I need to widen the perspective. Passages in which the Tinber-
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gens criticize professional psychiatrists are many in their late study.1191 There are at least two main points of criticism. It reads:

The more pessimistic views so widely canvassed at the moment (at least in the English-speaking world) are in our opinion biased both by the nature of the research methods applied and by the fact that the children seen by most experts are not a representative sample of the total population of autists.1192

At first, the Tinbergen blame the clinical profession for constructing the incurability of autistic children by making (in their view) erroneous and one-sided methodological presumptions such as over-emphasizing the virulence of genetic and organic causes.1193 In addition to that, they claim that the method of experimental testing handicaps the children so that they are not capable to show their real faculties during a test or examination.1194 Especially the latter argument profiles their own advocated method of “watching and wondering” to be the more appropriate one. The other point of criticism outlined in “Autistic” Children is statistical: The Tinbergens accuse psychiatrists to substantiate their own convictions by concentrating primarily on severe cases.1195 In their view, however, the scope of children fulfilling the symptomatic criteria for Kanner’s syndrome is much wider than psychiatrists are prepared to concede and, beyond that, include mostly cases in which the parents or caregivers succeeded in recovering the child by intuitively applying the “right” treatment.1196 Moreover, according to their opinion, many autistic children are treated in institutions without classifying their mental disorder as “autistic” thus preventing them from a correct treatment.1197 In other words, according to Niko and Elisabeth Tinbergen, the autistic phenomenon is both more widespread and more diversified insofar as it includes not only the “hard” cases but also a larger number of children suffering from what they usually call “psychogenic autism”.1198 To make these cases visible and to represent them in their book thus turns out as an argumentative strategy which seems apt to support several of their main hypotheses: At first, the larger number of children being affected by the autistic syndrome reveals that the phenomenon is more common. Therefore, it is more plausible to interpret the appearance of the syndrome as a negative side-effect of the evolutionary maldevelopment taken by modern western civilizations. Second, given that we follow the argument that the curability of the autistic disease (a word which I don’t like in this context) proves the psychogenic nature of its causation, a more of successful case stories certainly would corroborate their claim for taking into account nurture-causes including the social environment of the children. Finally, the methods which, according to Elisabeth and Niko Tinbergen, had been applied success-

1192 Ibid., 164.
1193 For the Tinbergen’s constructivist criticism see ibid., 9, 17, 76, 164–165.
1194 See ibid., 205.
1195 See ibid., 13, 25.
1196 Ibid., 119–120, 139, 193, 193–194, 196.
1197 Ibid., 136.
1198 The view that there existed a continuous spectrum of autistic disorders upon which normal and autistic children only marked the extreme poles certainly substantiated this hypothesis. For applying the notion of a “continuum” see ibid., 11, 13, 70, 119.
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fully by home-therapists not only coincide with the suggestions they had inferred from their theory of autism, they also correspond with the idealized pre-modern picture the Tinbergens had drawn from the family on basis of their evolutionary theory of human civilization.\textsuperscript{1199} Mentioning successful amateur case histories thus not only supports the Tinbergens’ theory of “psychogenic autism” in particular but, more general, also their wider view upon human kind. Lastly, the notion of intuitive, though educated, “do-it-yourself” treatment also expresses the homoeostatic understanding of “cure” insofar as it implies the notion of endogenous self-healing. The Tinbergens’ suggestions to “cure” human civilization thus did not coincide structurally with the measures put forward, for instance, by K. Lorenz which under other (and wrong) circumstances had helped to legitimate severe eugenic interventions. All three aspects might give us a clue how we need to interpret the Tinbergens’ practice to consult popular accounts written by parents or caregivers, informal reports and case histories or home videos produced by the parents.\textsuperscript{1200} In addition to that, they refer to the correspondence they maintained with non-experts and in which they now claim to find what Niko and Elisabeth Tinbergen commonly call “grass-root agreement” to their theory.\textsuperscript{1201} However, with adopting and making productive inexpert knowledge (including practical knowledge) the question of reliability was raised. In “Autistic” Children the Tinbergens in fact do realize that non-scientific accounts tend to be unreliable because they are often incomplete, loaded with emotions or might be one-sided success stories.\textsuperscript{1202} In their view, all these aspects had contributed to the fact that these accounts were widely neglected by professionals.\textsuperscript{1203} Their reaction to this problem in their book was to claim for universal standards of observation which should be made available to a wider audience of interested non-experts.\textsuperscript{1204} Beyond that, both successful and failed accounts of applied treatments should be published.\textsuperscript{1205} As a result, we may therefore say that widening the basis of used knowledge in their book eventually not only substantiated the arguments of the Tinbergens but also triggered a process of scientization which led to the question how to spread scientific standards.

To sum up my account on N. Tinbergen’s late interest in childhood autism, I’d like to point out several aspects. At first, Niko and Elisabeth Tinbergen’s engagement with autism which had formally begun in 1970 and lasted well into the mid-1980s reveals several more or less discrete stages each of which was characterized by its own interest, scientific practices and schemes of publication. My impression thereby is that the actual course of events was not unlike to the paths Niko’s PhD projects had taken over the years before his retirement: An initial and critical review process allowed them to develop views that went beyond existing doctrines by developing a functional aetiology of the autistic syndrome. Their first book, \textit{Early Childhood Autism}, then resembled most of the works written by members of N.

\textsuperscript{1199} Ibid., 30.
\textsuperscript{1201} Ibid., 3, 210.
\textsuperscript{1202} See ibid., 170.
\textsuperscript{1203} Ibid., 193.
\textsuperscript{1204} Ibid., 170, 179, 196.
\textsuperscript{1205} See ibid., 198.
Tinbergen’s second generation of pupils insofar as it intended to bring order into chaos and develop a sound hypothesis as to the causes and the nature of the autistic syndrome. The Nobel Lecture reveals a widened perspective inasmuch as it recapitulated the Tinbergen’s work on childhood autism and placed the problematic within the wider context of stress diseases. It also marked a sort of turning point since the years after 1974 were more dedicated to translate the previously formulated hypothesis into the direct praxis of curing the children. This shifted interest finally culminated into a second major publication, “Autistic” Children, whose primary intention was to test the previously obtained hypothesis’ scope of applicability. Second, my historical perspective showed that the Tinbergen’s approach to childhood autism was in flux over the years. In particular, a more careful reading of “Autistic” Children revealed how they refined their method of observation, their model of motivation, how they brought in a more developmental perspective (i.e. both onto- and phylogenetic) and, finally, how they made use of inexpert knowledge. Third, despite the fact that Niko and Elisabeth Tinbergen’s one-sided emphasis on environmental forms of causation partly led towards insufficient propositions, their accounts on autism, nonetheless, can be read as pioneering works in Human Ecology. As examples I would like to mention their homoeostatic reinterpretation of the motivational system, their sensitivity for the causes and effects of psychosomatic diseases (in particular stress) as well as their global and evolutionary view upon human civilization. Finally, I do agree with G. Beale that N. Tinbergen’s late studies on childhood autism perpetuated his previous research interest, especially, as I am inclined to say, the studies which he published after his turn to Ecology in 1962. Thus my readings of his works showed that N. Tinbergen did not break with his former convictions but was able to re-place them within the framework of the new scientific paradigm provided by Functional Ethology. This applies to his discrimination experiments just in the same way as to his homoeostatic reinterpretation of motivation and the re-conception and refinement of the black-box model. Other concepts reappeared more in form of a counter model. Thus I would even go so far and claim that formalization is a sort of anti-ritualization, while Niko’s adoption of the notion of “over-arousal” more turns out as a reconfiguration of the former concept of “displacement-reaction”. Lastly, N. Tinbergen’s adoption of the functional framework in his studies on autism was not identical with the one put forward by most of his pupils. The clarification of the exact demarcation line requires more detailed historical studies.

In conclusion, I would like to point out that science historians so far have not taken into account sufficiently how N. Tinbergen in cooperation with his wife Elisabeth has developed further the ecological framework to a science of Human Ecology. Despite the fact that some of his convictions needed to be corrected over the years, the accounts on childhood autism read as rather modern statements – at least if we can abstract the patterns of the heuristic gestures which have led the Tinbergen to their convictions. In some aspects N. Tinbergen seemed to be far ahead of his time. In 2005 M. Rutter published a paper in which he passed through in retrospect the forty years of his research on autism. My impression in reading the paper

1206 See M. Rutter. “Autism Research: Lessons from the Past and Prospects for the Future”. In:
is that the corrections he had to make in course of his career show that at least some of the aspects put forward by the Tinbergen and which have been heavily criticized when they were first published seemed to point into the right direction. I mention only a few obvious aspects. Thus Rutter admits that the serious language impairments which are often part of the autism spectrum disorder in fact turned out to be associated with “serious social deficits”, an idea which was implied in Niko and Elisabeth Tinbergen’s theory of autism from the very beginning simply because the interest in social behaviours was an essential part of the ethological research tradition Niko was standing in. Moreover, we read that severe deprivation eventually may cause behaviour patterns similar to the ones displayed by autists. Quite independent whether the Tinbergen had conceived correctly the physical basis of what they called “psychogenic” factors, deprivation was one of the environmental causes they had made responsible for the development of the disorder in vulnerable children. Finally, from Rutter’s account we can infer that the Tinbergens’ claim to abandon the qualitative distinction between “normal” and “autistic” children experiences some late support, too. “Like everyone else”, Rutter writes, “when I started investigating autism, I assumed that autism necessarily involved a qualitative distinction form normality. That, too, now seems somewhat less certain”. Not “everyone” believed in a qualitative distinction. And again the reason why the Tinbergen, following John and Corinne Hutt, questioned this distinction at a very early stage in the history autism is epistemological insofar as they placed their research on childhood autism in a human ecological framework. In other respects, the phenomenology-oriented program they suggested provided a handicap: The Tinbergen were more interested in the symptomatology of the disorder and its cure rather than the physical (viz. neural) correlates of the causes they had suggested. As a result, we can hardly find any information concerning the physical impact traumatic experiences might have upon the motivational system in humans asides the “secondary”, “structural” and “chemical” consequences Niko mentioned in one of his letters to J. Prekop. My very personal opinion, however, is that the answer to this question is relevant for how we might evaluate N. Tinbergen’s theory of anxiety-dominated motivation conflict. In a recent account E. Geerts and M. Brüne remark:

Animal experiments have shown that the care-giving behaviour of mothers affects hypothalamic gene expression in pups. Variation in maternal care is associated with variation in (the development of) the pups functioning of the hypothalamic-pituitary-andrenocortical axis (HPA axis; for a review see Meaney 2001). The axis represents the biobehavioural stress-response system (e.g. fight-flight, see Korte et al. 2005). The effect of early maternal care on the expression of genes is one example of the epigenetic effects of environmental contingencies. A crucial aspect in the light of natural selection theory is that via epigenesis the same gene can lead to different phenotypical outcomes depending on the way it is activated or deactivated by maternal care. One can hypothesize that the HPA axis is also involved in human support-seeking strategies in medicine.

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1207 See ibid., 247–248. For the relevance of focusing on non-verbal behaviour see also Geerts et al., “On the Role of Ethology in Clinical Psychiatry”, 122.
1209 Ibid. For the need to presuppose “a broader phenotype” see also ibid., 245, 250–251.
I have quoted this passage although it is not related to autism spectrum disorder in a narrow sense because to me it seems to show that there are particular areas in the brain (here the hypothalamus in general and the so-called HPA axis in particular) which regulate ambiguous behaviour tendencies in relatively discrete systems (here fight-flight) and, moreover, that these “areas” are liable to epigenetic modification as a result of environmental impacts (here maternal care). Moreover, neurogeneticists found out in animal experiments that aberrancies in the expression of genes encoding so-called γ-aminobutyric acid (GABA) receptor subunits – GABA is one of the key regulators of excitability in the mammalian central nervous system – may lead to deficits in socialization, seizures and anxiety. From this perspective we may blame N. Tinbergen that he missed to conceive his “psychogenic” factors in terms of (epi-)genetic aberrations yet if we take into account that epigenetic variability – as the quotation above shows – refers to the phenogenetic process of gene expression (and not inherited variability s. s.), that is, in Niko’s terminology a functional and not a “structural” variation, his dualism of (inherited) vulnerability and secondary environment induced deviation was not false at all – at least from a structural point of view. Furthermore, Tinbergen’s claim that there is a genetic disposition both for increased sensitivity and deficient plasticity (i.e. hypo- and hyper-connectivity) seems to be supported by recent epigenetic findings, too. Yet, on the other hand, N. Tinbergen’s restriction of genetic influences to a child’s vulnerability seems insufficient because, as is well known now, there are quite a number of genes which are involved in the structural changes of the CNS (e.g. synapse formation, cell migration, receptor units, etc.) that researchers make responsible for the autism spectrum disorder beyond a mere general vulnerability. The same applies to spontaneous failures in the epigenetic control.

It is time now to summarize my account of N. Tinbergen’s intellectual life-history. On the one hand, also in his development the idiosyncratic epistemic shifts can be made evident that had led to the classical Ethological Synthesis such as the establishment of a heterogeneous scientific orientation, the revisions in the dimension related to his reasoning in terms of causation and, finally, the epistemic re-evaluations that sorted the inner constitution of the core epistemic schemata anew. It could be shown that Niko’s classical ethological period started in the late 1930s and lasted about twenty years until, around 1959, reasoning in terms of function and adaptiveness began to prevail. During this relatively long period of continuity beyond the ruptures brought about by the Second World War and his subsequent move to Oxford we can observe that Niko’s research occurred in mainly two realms I have, partly following G. Beale’s terminology, called “Tinbergian Theory” and “Tinbergian Practice”. It seems to be one of the specialities that Niko’s ethological research program not only encompasses his own abstractions, his reviews and the works in

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which he shaped his discipline but also an increasingly growing realm covered by others and dedicated to practical work. It was this practical realm within which Niko used to place the mostly descriptive projects of his PhD students and, in doing so, established a highly sophisticated system of crosswise scientific exchange. Moreover, my analysis of the place the PhD projects took in the biographies of a number of pupils belonging to the first generation after Niko’s move to Oxford revealed that Niko’s highly sophisticated way of socializing his pupils entailed mainly two types of subsequent life courses: Either students felt comfortable with the scientific paradigm Classical Ethology provided and they stayed within this heterogeneous framework or they more and more distanced themselves from the doctrines provided by the generation of their teachers. To this latter group of students I count D. Morris, M. Moynihan, D. Blest, A. Manning and M. Cullen, yet in particular two women, M. Bastock and E. Cullen. Generally speaking, criticism of Classical Ethology articulated itself primarily in the various different ways Niko’s pupils questioned the diverse manifestation of what E. Crist called “mechanomorph” attitude including Niko’s hierarchical model of instinct but also his later systematic re-interpretation of the causal analytical framework. This criticism affected both the realm of non-knowledge and, in different forms and to varying extent, their practical work which finally culminated in their written theses. Another speciality of N. Tinbergen’s life course surely is that he, beginning with the year 1959, yielded to the pressure that had grown within and outside his research group by translating Classical Ethology into a new functional framework. His egg shell removal study but also his paper on spacing-out are both expressions of this move. Parallel to the establishment of the new theoretical framework the interaction between Tinbergian Theory and Tinbergian Practice seems to have changed qualitatively. The biographies of N. Tinbergen’s second generation of pupils show that they mostly received their undergraduate education at Oxford University so that their academic socialization started at an earlier age. In addition to that, the teacher-pupil instruction more and more changed into a peer-to-peer tutoring system which ascribed growing informal impact to some members of the ABRG. Moreover, I think, it can be confirmed that Niko’s theoretical realm produced repercussions upon the practical work of his PhD students in as much their theses, in contrast to the previous generation of students, applied an alternative form of knowledge organization resembling more Niko’s theoretical account but whose prototype eventually had been E. Cullen’s study on cliff-nesting in Kittiwakes. However, as far as I can see, Niko’s scientific practices with which he used to socialize his students remained more or less the same quite independent whether the projects were lab studies or raised observational data in the field. As in all the years before, N. Tinbergen wanted his stu-

1213 K. Hoffmann, one of G. Kramer’s pupils who spent some time in Oxford and Cambridge in the mid-1950s, emphasized the criticism articulated by M. Cullen, M. Bastock and U. Weidmann. See MPG-Archives, III. HA, Rep. 77, file 14, letter K. Hoffmann to G. Kramer (19/06/1955). I think, my analysis shows that all three pupils are representatives of at least to two different types and stages of criticism.

1214 It might be that this tutoring and self-tutoring system also had a negative side effect: The self-enclosure of the work group. This can eventually inferred from the impressions K. Hoffmann, one of G. Kramer’s pupils, collected during is stay in England. See ibid., file 15, letter K. Hoffmann to G. Kramer (26/08/1956).
dents to begin with a critical gesture (in later years particularly a thorough criticism of a thesis already completed) before students entered into their own particular interests. From several autobiographical accounts written by Niko’s later pupils we can infer that only the former of the two steps included a doctrinaire moment such as, for instance, the choice of the experimental animal. The later stages of the projects used to be free of interferences. Like it was the case among the early Tinbergians, the fact that Niko placed the projects within a practical framework which was characterized mostly by descriptive – in later years increasingly quantitative – ethology, generated two types of subsequent types of life course. Either students that had been socialized within the framework provided by Functional Ethology staid within this scientific orientation while elaborating, completing and reinterpreting especially its theoretical program or they detached themselves from this position. In the latter case, as we can infer especially from R. Dawkins’, M. Stamp-Dawkins’, C. Beer’s and eventually also J. Delius’ life course, this new synthetic move implied a return to the epistemic framework of Classical Ethology which now was reassessed by integrating the results of Cognitive Ethology but also revealed a strong interest in cultural evolution. All life-histories I have examined “around” Niko’s own course thus seem to confirm my hypothesis that scientific development is based upon a reproductive dynamics that can be made evident in the biographies of researchers whose lives cover the turning points which I regard as essential structural moments within this dynamics. Nearing the end of my chapter on N. Tinbergen’s life course I have dedicated a considerable amount of space to his late engagement in childhood autism. One of the reasons why I did that was because I wanted to show that Niko and Elisabeth Tinbergen’s works on autism perpetuated the general heuristic thrust of the functional studies supervised and carried out in the 1960s. Thereby I have argued, for instance, that translating ecological core ideas such as the concept of “maintenance behaviour” into the realm of Human Ecology generated a homoeostatic understanding of motivational system which, in turn, became one, if not the, cornerstone of the Tinbergens’ theory of autism. In general, one may eventually say that the Tinbergens’ engagement with autism which stretched over more than fifteen years from ca. 1970 (the formal beginning of the project) until well into the mid-1980s has a history in itself: A first critical reception of Corinne and John Hutt’s book and the informal scientific exchange in the aftermath thus led to the Tinbergens’ first publication Early Childhood Autism (1972). This short study, which N. Tinbergen himself criticized as “immature” in later years, was in itself theory-oriented and primarily aimed at translating ethological methodology into the realm of child psychiatry. Niko’s so-called Nobel Lecture widened the perspective and tried to evince early childhood autism (together with the bodily malfunctions addressed by the so-called Alexander Technique) as a special form of stress disease. After Niko’s retirement in 1974 the interest of the Tinbergens shifted towards the question of cure. Niko’s letters to friends and colleagues show that at this point he had already written the first, theoretical part of a second book on autism that was finally published in 1983 under the title “Autistic Children. New Hope for a Cure”. Its overall objective was to prove his theory of autism, which he had outlined in his earlier publication and reassessed in the first part of the second book,
by inferring adequate means of therapy and revealing the effectiveness of the latter. My account of Niko and Elisabeth Tinbergen’s engagement with childhood autism was following a twofold objective. On the one hand, I wanted to understand their view as a product of their time that is in connection with the concept of Functional Ethology Niko had begun to shape in the decade before his retirement and the epistemic conflicts that can be predicted when the epistemic schemata underlying the ecological orientation clash with the traditional experimental outline that I presupposed to be characteristic for the psychiatric schools Niko got into conflict with. On the other hand, however, I became more and more fascinated by the idea that Niko and Elisabeth Tinbergen’s psychogenic theory of autism – despite the partly justified criticism it released – might be read with a view of more recent findings in Epigenetics which suggest that environmental factors such as nutrition and even psychosocial factors as stress may have an impact upon the expression of genes “independent” of the underlying DNA. I therefore suggested to read the ‘Tinbergen’s’ attempt to understand human health as homoeostatic equilibrium system that is challenged by both abiotic and biotic disturbances as pioneering work in Human Ecology which, despite the fact that it needed to be corrected here and there, in some aspects seemed to be far ahead of its time.

b) Gustav Kramer (1910–1959)

My thesis put forward the hypothesis that Classical Ethology must be interpreted – both structurally and chronologically – as a co-foundation next to the Modern Synthetic Theory of Evolution and as such has accomplished its major theoretical cornerstones at ca. 1942 at the latest. What we can observe after that is a further refinement of this classical framework on the one hand and, beginning with the late 1950s, a process of branching into different lines on the other. My analysis so far has generated two major results. On the one hand, this process of branching did not lead to an end or fall-down of the classical orientation which continued to flourish in several different research centres, at the foremost, the Max-Planck Institute for Behavioural Physiology that had been founded in 1954 and moved to its new location in Southern Bavaria in 1957. The history of this institute, I think, deserves its own historical study clarifying not only its very beginnings, the circumstances of its foundation and the thrilling story of finding an appropriate location but also the precise transformation process in course of which the institute developed from a two-department structure into an organization with four departments including the epistemological consequences being related to this structural modification. On the other hand, I was able to show in my careful reconstruction of N. Tinbergen’s life-history how Functional Ethology finally branched out of the classical framework and in doing so not only laid the foundations for modern Behavioural Ecology but also, as Niko’s late engagement with autism shows, paved the way for a modern ecological understanding of human kind, welfare and environmentalism. I did not reconstruct the intellectual life-histories in question for their own sake. They need to be read within a wider picture namely the question in how far and how the epistemic community Ch. Darwin had outlined in his Origin of Species became a self-reproducing unit of scientific change in the 20th century. In order
to complete this bigger picture (at least provisionally) it is necessary to reconstruct one further line of behaviour study of which I think it branched out of Classical Ethology simultaneously to Functional Ethology without coinciding with it. Like the phrase “Functional Ethology” was apt to encompass a number of related areas of behavioural research such as Behavioural Ecology, Human Ecology and Functional Anatomy I consider it also possible that its antagonistic counterpart included a wider range of fields of biological and behavioural study such as Cognitive Ethology, the study of animal awareness and welfare, as well as varieties of evolutionary theory beyond the Modern Synthesis. In order to make this path visible I have chosen the life and work of G. Kramer, an ornithologist and evolutionary biologist who was highly appreciated during his life-time by his colleagues but fell into oblivion almost entirely as a consequence of his early tragic death in 1959. Science historians being concerned with the history of Ethology so far have declared Behavioural Ecology the principal heir of Classical Ethology (Kruuk, Burkhardt, Beale) and thereby have almost totally forgotten to mention that the move to Functional Ethology was part of the reproductive dynamics within a wider frame – the epistemic community – and as such accompanied by simultaneous parallel movements such as the increasing interest in animal cognition since the 1970s;1215 When we hear the catch-phrase “Cognitive Ethology” it is usually the names “Donald R. Griffin” and maybe, from a more evolutionary biological perspective, “Stephan J. Gould” which come to our minds.1216 The number of historical studies mentioning Kramer’s life and work, by contrast, is short: Asides an article in Neue Deutsche Biography written by K. Lorenz and some obituaries published after his death in 1959 there is not even a handful of historical studies mentioning his scientific achievements.1217 The neglect of G. Kramer’s work especially amongst science historians, I think, is standing in sharp contrast to the scientific contributions he made to his discipline especially, as we will see soon, in the area of animal orientation.1218 I think I do not

1215 However, see Wuketits, *Die Entdeckung des Verhaltens*, 155–159.


1218 However, for a late appreciation of his work see R. Wiltschko et al. “Avian Navigation: From Historical to Modern Concepts”. In: *Animal Behaviour* 65.2 (2003), 257, 260–262. This paper shows that Kramer’s impact was not only to provide new insights but also a model
break a confidentiality agreement when I mention that it was no other than N. Tinbergen who considered Kramer, next to E. v. Holst, as a potential candidate for the Nobel Prize he finally received himself in 1973 together with K. v. Frisch and his friend and colleague K. Lorenz. In a letter to I. Eibl-Eibesfeldt Niko writes: “Von Frisch is of course a great man, but had Erich von Holst lived, he ought to have had the prize. And what about Gustav Kramer???”.

i) Becoming an Advocate of the Modern Synthesis?

From Berlin to Heidelberg (1930–1934)

Since Kramer’s work is widely unknown nowadays and his personal papers haven’t been taken into account systematically by any historical study so far (as far as I know) it seems wise to proceed with utmost caution when it comes to make any presumptions about the scientific orientations Kramer is likely to have covered in course of his life. However, particularly from E. Stresemann’s obituary there can be inferred two structural moments that seem to be suitable to order the events of Kramer’s life provisionally. On the one hand, Stresemann claims that Kramer’s research took place in two carefully separated realms. In alluding to Goethe’s words Stresemann writes:


[In the breast of the naturalist Gustav Kramer in whose historical view nature turned out to be “an experimental field without experimenter in which all sorts of things happen, emerge, vanish and persist” (30), two souls, though strictly separated, were living peacefully next to]

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that structured the future discussion (Ibid., 261, 268). Insofar we may say his contribution was also epistemological. For more historical background information concerning the themes “orientation” and “navigation” see K. P. Able. “Orientation and Navigation. A Perspective on Fifty Years of Research”. In: Condor 97.2 (1997), 592–604.

each other. The romanticist in him was able to enjoy to the full and sensitively the beauty and the sublimity of nature without interfering with his neighbour, the dissecting researcher of causality. It was this causal analyst who became known to many even then if they had listened to Kramer’s presentation only once or read only one of his studies. Certainly, for himself his reckless atomistic procedure – independent whether it was applied to body structure or behaviours – was not regarded a purpose for its own sake but instead was an essential work process that served a higher objective. When he had revealed the bundle of functional relations his examining intellect again carefully embraced it [the bundle of functional relations] with an intellectual tie to one re-established wholeness which appeared to him even more astounding than it did before. He simply called this “biological thinking”. The other, that is, the directly and sensitively perceiving Gustav Kramer, the cheerful epicure, the impishly smiling philosopher, however, has not chucked himself away haphazardly on anyone. Only in those whom he trusted in every aspect of human nature he confided himself without reserve. He had a fine sense for what is bad and evil. He could not be deceived by any hollow pageant and rated the integrity of someone’s attitude even higher than any of his intellectual achievements. Those who had won him as a friend were blessed for their life. He did not put his sympathy into words but expressed it in action; and in case he intervened he did so from an urge as a result of a strong emotion.\[transl. CL\]

Certainly, this is E. Stresemann’s perception of a, in his view, essential characteristic of Kramer’s yet, nonetheless, it might serve as a provisional hypothesis, while reading Kramer’s works: What we may keep in mind therefore is that Kramer’s life-history covered different realms. However, what Stresemann described as G. Kramer the romanticist “vs.” G. Kramer the atomist might have been subject to transformation like it was the case in the lives of other ethologists. Moreover, a first superficial glance at the scientific studies Kramer published between ca. 1930 and 1959 reveals that he was interested in mainly two different areas of biological research namely Ornithology, on the one hand, and Evolutionary Biology, on the other. It also strikes me that, with some few exceptions, he was apparently concerned with two major groups of experimental animals namely Amphibia (i.e. the African Clawed Frog) and Reptiles (i.e. Lizards), on the one hand, and various species of Birds (e.g. Pigeons, Crows, etc.), on the other. I think it cannot be presupposed per se, and therefore should be treated as an open question that whether both groups of experimental animals necessarily were connected one-to-one with the two major areas of Kramer’s research. Moreover, exceeding Stresemann’s description, I wonder how separated (“säuberlich getrennt”) the realms of Kramer’s personality and research actually were. Next to the more synchronous moment of coexisting realms in Kramer’s personality the existing accounts of his life give us a first impression of its chronological succession or course. Thus at least eight or nine discrete phases can be distinguished which I have summarized in the following table (Table 2.3).\[1221\]

\[1220\] Stresemann, “Gustav Kramer”, 262–263 and similarly K. Lorenz. “Gustav Kramer”. In: Journal für Ornithologie 100.3 (1959), 266. G. Kramer himself once distinguished between different types of researcher, namely the aesthete who does research for its own sake, on the one hand, and the one who is oriented by social purposes and material bondings. See G. Kramer. “Das Bewusstsein des historischen Hintergrundes in der Naturforschung”. In: Pubblicazioni della Stazione Zoologica di Napoli 27 (1955), 58–60.

\[1221\] The information included in the table is mostly drawn from E. Stresemann’s obituary for G. Kramer. See Stresemann, “Gustav Kramer”, 258–263. See also Archives of the Max-Planck-Society, Berlin [quoted as: MPG-Archives]. MPI for Behavioural Physiology [quoted as: II.
**Table 2.3** G. Kramer (1910–1959). The Stations of his Career

<table>
<thead>
<tr>
<th>Year</th>
<th>Institution</th>
<th>Research</th>
<th>Exp. Animal</th>
</tr>
</thead>
<tbody>
<tr>
<td>1928–1932</td>
<td>University Training in Freiburg i. Brsg., Königsberg and Berlin</td>
<td>Various Ornithological Publications</td>
<td>Birds</td>
</tr>
<tr>
<td>1933</td>
<td>University of Berlin; Institute of Prof. R. Hesse</td>
<td>Dissertation Project on Sensory Capacities and Orientation in the Clawed Frog</td>
<td>Clawed Frog</td>
</tr>
<tr>
<td>1933–1934</td>
<td>Work at the KWI for Medical Research, Heidelberg</td>
<td>Gas Exchange Analyses as Indicators for Metabolic Activity</td>
<td>Lizard, Albino Rat</td>
</tr>
<tr>
<td>1934–1936</td>
<td>Research Assistant at the German-Italian Research Station for Marine Biology in Rovigno d’Istria</td>
<td>Metabolism in Coelenterata; Micro-systematic of Italian Lizard populations</td>
<td>Sea Anemone, Octopus, Lizard</td>
</tr>
<tr>
<td>1936–1941</td>
<td>Vice Director of the Department of Physiology at the Zoological Research Station in Naples</td>
<td>Research on Colouration and Locomotion in Cephalopods; Behaviour and Ontogeny of Lizards; Ecological and Population Genetics</td>
<td>Cephalopods, Lizard</td>
</tr>
<tr>
<td>1941–1945</td>
<td>Military Service, Italy</td>
<td>Acting as Interpreter and Laboratory Assistant in a Military Hospital; Bacteriological Research</td>
<td>Bacteria</td>
</tr>
<tr>
<td>1945</td>
<td>Prisoner of War</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1946–1948</td>
<td>Habilitation at the University of Heidelberg; Assistant and “Privat Dozent” at the Zoological Institute headed by E. v. Holst</td>
<td>Further Publications on Italian Lizards; Sun Orientation in Various Species of Migratory Birds</td>
<td>Lizards, Birds</td>
</tr>
<tr>
<td>1948–1959</td>
<td>Director of one of the Departments at the MPI for Marine Biology, Wilhelmshaven</td>
<td>Research on Orientation and Homing in Starlings and Carrier Pigeons; Studies on Allometry in Mammals, Fish, Reptiles, and Birds</td>
<td>Various Species of Birds; Lizard, Whale, Dogfish, Cod, Gull, Crocodile</td>
</tr>
<tr>
<td>1959</td>
<td>Director and own Department in the MPI for Behavioural Physiology; Director of the “Vogelwarte Radolfzell”</td>
<td>Research on Relative Growth and Avian Navigation; Growing Interest in “Bio–climatology”</td>
<td>Birds</td>
</tr>
</tbody>
</table>
The table shows that G. Kramer harboured an interest in the behaviour of birds since his early years as a student in Freiburg, Königsberg and Berlin. However, he seems to have pushed this passion into the background in the years between 1933 and 1948 in favour of more physiological and experimental studies. In 1948 orientation and homing in birds (re-)entered his research agenda and henceforth built one of the major pillars of Kramer’s research without abandoning his other interests. On closer inspection “these other interests” also seem to have undergone a transformations process. What started with Kramer’s dissertation thesis on sensory capacities and orientation behaviour in the Clawed Frog developed partly into purely physiological studies of metabolism in Lizards but seems to have adopted tentatively a behavioural component as well – albeit with a negative result. However, especially the transitional interest in sexual, social and maintenance behaviours finally seemed to culminate into a veritable encounter with Evolutionary Biology including Population Genetics, Systematics and Ecological Genetics as well as the question of speciation. The drafts of Kramer’s lectures on “Ökologische Genetic” (Ecological Genetics) he delivered as “Privatdozent” at the University of Heidelberg in 1946 and 1947 show that he had become a representative of the Modern Synthetic Theory of Evolution and was familiar with the writings of E. Mayr, B. Rensch, S. Wright, G. G. Simpson and other architects.\footnote{See MPG-Archives, III. HA, Rep. 77, box 1, ms. “Ökologische Genetik” (ca. 1946), 48 pages. In addition to that, see Kramer’s scientific exchange with B. Rensch which shows that Kramer was particularly interested in the question of race differentiation and that he acknowledged Rensch’s work. See ibid., file 1, letter B. Rensch to G. Kramer (28/02/1947). His exchange with the American biologist L. R. Dice may be seen in this context as well. See ibid., file 1, letter L. R. Dice to G. Kramer (28/07/1947), ibid., file 3, letter G. Kramer to L. R. Dice (28/08/1947) and ibid., file 3, letter L. R. Dice to G. Kramer (06/09/1947). I think Kramer’s part in establishing the Synthetic Theory of Evolution has not been recognized at all. Th. Junker, for instance, has not mentioned him at all in his book. See Junker, \textit{Die zweite Darwinistische Revolution}.} The beginnings of Kramer’s interest in Evolutionary Biology seem to fall into the time he spent at the International Zoological Research Station in Naples which had become famous for being a melting pot of zoologists from countries all over the world.\footnote{See C. Groeben. “Catalysing Science: The Stazione Zoologica di Napoli as a Place for the Circulation of Scientific Ideas”. In: C. Groeben et al., eds. \textit{Stätten biologischer Forschung / Places of Biological Research. Beiträge zur 12. Jahrestagung der DGGTB in Neapel 2003}. (Verhandlungen zur Geschichte und Theorie der Biologie 11). Berlin: VWB, 2005, especially 53.} The table also brings to our mind the limited availability of archive sources. While the holdings of the Max-Planck Society mostly cover the period after 1945 and therefore document Kramer’s part in the Max-Planck Institutes of Marine Biology (Wilhelmshaven) and later of Behaviour Physiology (Seewiesen), the reconstruction of the earlier stations of his career on mere archive material would require painstakingly finicky work. In particular, the period between 1941 and 1945 when Kramer was serving as soldier in Italy is a dark chapter and raises the question what his research on “bacteria”, that is, the “bakteriologische Untersuchungen” (bacteriological investigations), E.
Stresemann mentions in his obituary was all about.\textsuperscript{1224} A more detailed biography, I think, would have to answer these questions. Since I am mainly concerned with Kramer’s intellectual life-history\textsuperscript{1224} I will begin with the published sources, that is, his research papers, which can provide us science historians with a more or less continuous flow of representations of a person’s scientific development over the years. Before I will enter into an examination of several of Kramer’s key texts I will first put forward a brief statistical analysis of his publications. Thus I have taken as a sample the seventy-six papers E. Stresemann listed at the end of his obituary and classified these studies along two major parameters, the scientific objects Kramer dealt with in the respective paper, on the one hand, and the general theme or area of biological research, on the other.\textsuperscript{1225} As to the former of the two parameters I have chosen categories of experimental animals beyond or above the species level in order to obtain a slightly higher degree of abstraction. Thus I do not distinguish between Pigeons, Lizards, Crocodiles, Dog Fish etc. but use class names such as “Birds”, “Reptiles” and “Fish”. Two rubrics needed to be defined even more general: In some few papers G. Kramer provided more general popular or theoretical reflections on “animal and man” or even more unspecified on “nature” in general. In these cases I exceed the differentiation in animal classes by even wider entities of biological research. The second category refers to the area of biological research. Thus I thought it might be useful to distinguish between “general theoretical or popular reflections”, “the conservation of nature”, “the ontogeny” of animals, Kramer’s “physiological studies on gas exchange and metabolism”, those studies which address more generally the “allegedly cognitive, social, reproductive, protective or predatory behaviour” of an animal and, finally, his studies on evolution, that is, systematics, population and ecological genetics. Within these classes of topics the theme “orientation and homing” takes a special place since it touches the area of sensory physiology but also refers to a special case of “instinctive behaviour” based on central nervous mechanisms which are processing both a number of external environmental stimuli and the impulses provided by the endogenous clock of the animal. The results of my tentative survey are summarized in Fig. 2.17. The graphic illustrates the number of publications and their kind for every year between 1930 and 1961. Each bar is separated in two columns one of which is reserved for the scientific object (brown, red and pink colours) while the other indicates the area of biological research (green and turquoise colours).\textsuperscript{1226} The graph thus is apt to reveal possible correlations between scientific object and research question. It gives

\textsuperscript{1224} See Stresemann, “Gustav Kramer”, 258. More detailed biodata shows that Kramer, since December 1941, had to do military service, first as interpreter in the air force, later as first-aider in a military hospital. See UAH, PA 4639, “Meldebogen auf Grund des Gesetzes zur Befreiung von Nationalsozialismus und Militarismus vom 5. 3. 1946” (03/06/1947). As a provisional result, one may say that his study on bacteria was carried out for medical purposes. See UAH, PA 10014, ms. “Lebenslauf von Dr. Gustav Kramer” (31/08/1946). Further information seems to confirm this view. See State Library, Berlin [quoted as: SBB]. Erwin Stresemann Papers [quoted as: NL 150], file 37, letter G. Kramer to E. Stresemann (24/12/1943), ibid., file 37, letter G. Kramer to E. Stresemann (09/01/1944) and ibid., file 37, letter G. Kramer to E. Stresemann (24/01/1945).

\textsuperscript{1225} For the list see Stresemann, “Gustav Kramer”, 264–266. Please note that this list includes Kramer’s research papers only and not, for instance, his reviews of the works written by others.

\textsuperscript{1226} My usage of colours does not have any political implications!
us the following provisional insights. At first, the distribution of bird studies over time supports my previous impression that G. Kramer returned to ornithological questions in 1948 at the latest when moving to Wilhelmshaven and becoming one of the directors of the newly founded Max-Planck Institute for Marine Biology.\textsuperscript{1227} Second, we can see clearly that the interim period was dedicated to physiological research and later more and more to Evolutionary Biology – an interest which perpetuated beyond 1945/1948 particularly in Kramer’s work on allometry that is the study of changing body proportions during ontogeny and phylogeny. Third, the diagram also shows that the years 1936, 1939, 1942–1945 and 1947 are not represented in any published scientific work.\textsuperscript{1228} The year 1950, by contrast, marks a dramatic increase of publishing activity which henceforth stays on a relatively high level.

Fourth, there is a very strong one-sided correlation between the study of orientation and homing, on the one hand, and the scientific object “Bird”, on the other. This correlation begins with 1948 and means that there exists a high conditional probability for “Bird” presupposed we hold in hand an orientation study. The exception to this rule seems to be the dissertation thesis Kramer had written under the supervision of the Berlin Zoologist R. Hesse and which had dealt with both the “sensory capacities” and the “orientation behaviour” in \textit{Xenopus laevis Daudin}, the so-called “African Clawed Frog” (Krallenfrosch).\textsuperscript{1229} Moreover, the reverse conclusion apparently does not hold. Not every bird-study is an orientation study since Kramer for instance also examined the voice of Raven and Hooded Crow (1930), the behaviour of carrion crow towards friend and foe (1941), as well as the predatory behaviour (1950), the nest-building (1950) and the moult (1950) of Red-backed Shrike. In a logical thinker’s words we therefore might say the proposition “orientation” is a more or less necessary but not sufficient condition for the proposition “bird”.\textsuperscript{1230} Fifth, there is a fairly strong correlation between the choice of reptiles (particularly Lizards) as scientific objects and the study of evolution (in later years particularly

\textsuperscript{1227} An exception seems to be a paper on the behaviour of the Carrion Crow Kramer published in a “Festschrift” dedicated to O. Heinroth in 1941. E. Stresemann dates back Kramer’s return to his ornithological passion to his Heidelberg period. See Stresemann, “Gustav Kramer”, 259.

\textsuperscript{1228} The reasons may be manifold: The year 1936 coincides with Kramer’s move to the Naples Zoological Research Station, the gap between 1942 and 1945 can be explained with wartime commitments and the lack of publications in 1947 might be a result of Kramer’s commitment to his habilitation thesis and his teaching responsibilities. For Kramer’s teaching responsibilities in Heidelberg see SBB, NL 150, file 37, letter G. Kramer to E. Stresemann (08/11/1945) and even more pronounced \textit{ibid.}, file 37, letter G. Kramer to E. Stresemann (12/04/1946), as well as, \textit{ibid.}, file 37, letter G. Kramer to E. Stresemann (11/07/1946). For the time being, I do not see any obvious explanation for the gap around 1938.

\textsuperscript{1229} That R. Hesse functioned as primary advisor next to Carl Zimmer can be inferred from the printed thesis itself. See G. Kramer. “Untersuchungen über die Sinnesleistungen und das Orientierungsverhalten von Xenopus laevis Daud.” In: \textit{Zoollogische Jahrbücher. Abteilung für Allgemeine Zoologie und Physiologie der Tiere} 52 (1933), 628 and the “Lebenslauf” (Curriculum Vitae) at the end, 677. For a short overview of R. Hesse’s life and work see H. Autrum. “Hesse, Richard”. In: Bayerische Akademie der Wissenschaften (Historische Kommission), ed. \textit{Neue Deutsche Biographie}. Vol. 9. Berlin: Duncker & Humblot, 1972, 15. His impact on the emergence of Classical Ethology should be examined more carefully since he was both G. Kramer’s and E. v. Holst’s mentor. Further pupils were H. Autrum and G. Tembrock.

\textsuperscript{1230} “Orientation studies are almost exclusively / only bird-studies. Yet not every bird-study is concerned with orientation. ‘Orientation’ as quality therefore characterizes insufficiently the amount of bird-studies”. I think, it’s also possible to turn things the other way round and argue:

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of allometric relations). Yet there are exceptions to this principle, too. Thus G. Kra-mer used Lizards in his early experimental studies of the physiological mechanisms underlying gas exchange and metabolism in animals. Conversely, the evolutionary biological questioning was not only applied to Lizards but also to other reptiles such as Crocodiles and even other animal classes such as Fish (Dog Fish, Cod-fish), Birds (Gulls) and mammals (Whalebone Whales). This aspect again refers primarily to the allometric studies Kramer conducted often in cooperation with co-workers such as Count Fred v. Medem, Lore Dinnendahl or Gerhard Huhn. Both types of correlation show that researchers in fact do have preferences as to their experimental animal but that any apriori presumption of so-called “model organisms” or “emblematic animals” may be an oversimplification which is simply too coarse – at least in the history of Ethology. Finally, the information included in the bar graph might serve as a basis for establishing a provisional hypothesis concerning the transformation processes taking place in G. Kramer’s development as a scientist. On the one side, we might eventually ask whether Kramer’s early “naive” etholog-ical and ornithological observations (mostly of birds) have not developed into the causal analysis of orientation and homing behaviour that dominated his research in the post-war period. From this point of view, Kramer’s ornithological research surely experienced a process of specialization. In addition, I consider it worthwhile to ask for the continuity between Kramer’s early medical research in Amphibia, Reptiles, Coelenterata and Cephalopods, on the one hand, and his later research on systematics, geographical distribution, speciation, and inheritance of particular qualities in Lizards which were finally leading towards his studies on allometry in Reptilia and in several other than reptile species.1231 Most interestingly, Kramer’s generalizations had the effect that the specific focus on reptiles as scientific objects seems to have disappeared in his allometry studies after 1955. To examine carefully these different strains of knowledge transformation over time and from an episte-

1231 The proposition “bird” is a necessary yet insufficient condition for the proposition “orientation”. That is to say: Only if a study is a bird-study it can be an orientation-study but not every bird-study is an orientation-study (exception here: The Clawed Frog).

1 Consider the study of “allometry” a special area of research within the wider frame of Evolutionary Biology. For a concise introduction see A. W. Shingleton. “Allometry: The Study of Biological Scaling”. In: *Nature Education Knowledge* 1.9 (2010), 2, and J. Gayon. “History of the Concept of Allometry”. In: *American Zoologist* 40.5 (2000), 748–758. According to J. Gayon the concept of “allometry” is used in mainly four contexts: (1) Ontogenetic allometry, which refers to relative growth in individuals, (2) phylogenetic allometry, which refers to constant differential growth ratios in lineages, (3) intraspecific allometry, which refers to adult individuals within a species of a given local population and, finally, (4) interspecific allometry which takes into account relative growth in related though different species. In any case, allometry examines the correlations between changes in the relative dimensions of single body parts, on the one hand, and the changes of an organism’s overall size, on the other (Ibid., 748). The four mentioned understandings of the concept are determined by the type of comparison involved. It will be one of my tasks to find out upon which kinds of allometry Kramer focused and how he shaped the concept. On basis of J. Gayon’s account one may eventually suspect that Kramer’s allometry studies were performed in a period when the concept became quite important “among biologists who were obviously working within the paradigm of the modern synthesis”, such as S. J. Gould who is picked as an example by J. Gayon in his paper (Ibid., 755). Gayon further claims that evolutionary biologists realized after 1945 that “both the term and the equation of allometry were equivocal” (Ibid., 748). For Gould’s interest in relative growth see York et al., *The Science and Humanism of Stephen Jay Gould*, 57–59.
Gustav Kramer (1910–1959)

mological point of view will be my task in the following sections of my PhD thesis. I begin with Kramer’s early intellectual life-history. Like other researches of the same generation who were born in the first decade of the 20th century and have received their academic education in the period between the wars also G. Kramer was showing research interests that were belonging to quite different and partly antagonistic epistemic fields without fully coinciding with one of them. On the one hand, we can therefore find those papers which were standing in O. Heinroth’s tradition and included plain ornithological observations of captive and semi-captive birds. As we will see soon these papers were not dissimilar to the ones K. Lorenz had written in his very early days – both with respect of the chosen topic and their overall epistemic tenor. On the other hand, however, since 1933 at the latest, Kramer also published experimental studies. His dissertation thesis on sensory physiology and orientation in the Clawed Frog most likely was the first manifestation of this kind. With a view of both types of study I have two major questions: At first, I would like to know which realms these studies covered of either the experimentalist or the neo-vitalist orientation both of which were partly addressed by Kramer’s research. And second, like it was the case with N. Tinbergen’s life-history, we can eventually presuppose that the respective double nature of any scientific orientation has repercussions on each of the realms or parts it consists of. It is therefore necessary to have a closer look upon the inner epistemic constitution of each realm that in fact is represented by both types of G. Kramer’s research interests. The former of the two questions therefore also involves the question which realms are not represented in Kramer’s research interests, while the latter aims to clarify the epistemic foundations of those realms that are represented.

I will not analyze Kramer’s early ornithological publications in detail but, instead, will provide a compilation of their key ideas. All these representations have in common that they are extensions of core concepts, themes, scopes or (spatial) areas of research in a very Cartesian sense. Thus, inspired by O. Heinroth’s work, Kramer reasoned about the heuristic value of supplementary observations of semi-captive and trained animals additional to the behaviour studies of wild (captive) animals. The underlying epistemic figure thereby seems to be the existence of a presupposed sphere of influence which is extended without being resolved altogether. “Es braucht kaum darauf hingewiesen zu werden”, Kramer writes in Vom Freifliegen zahmer Vögel,

\[\text{See G. Kramer. “Vom Freifliegen zahmer Vögel”. In: Der Zoologische Garten 3.11/12 (1930), 328–339.}\]
or returns to him on a more or less regular basis. But also the free-flying in itself provides enough interesting aspects from an animal psychological perspective to let appear justified some considerations from this point of view.]

In other words, Kramer construes a setting for observation which is arranged around a fixed spatial centre while the influence of the observer is waning the more the object in question approaches the periphery of the system without getting lost altogether. The maintenance of the observer’s sphere of influence depends upon the (conditioned) behaviour of the bird: Either it keeps close voluntarily or it returns periodically for food, an adequate sleeping place or social contact. The latter notion again is the place where G. Kramer introduces the concept of orientation: The capacity to return to the host requires a corresponding skill. Kramer continues:


The notion of a periodically returning animal requires a behavioural skill which Kramer conceives as “Orientierungsvermögen” (power of orientation, ability to orientate). And it is of some interest to mention that Kramer’s very early understanding of orientation involved the notion that birds may use landmarks. “Wenn oben die Ungegliedertheit der Umgebung als ungünstig bezeichnet wurde”, he underlines, so ist damit die Orientierungsmöglichkeit als weiterer bei Freiflug wichtiger Punkt schon berührt. Orientierungsvermögen kann nur da wirksam sein, wo Anhaltspunkte vorhanden sind, d.h. Glieder des Raumes, die durch ihre Lage im Großraum hervorgehoben sind.

I think, there is resting a certain kind of ambiguity in Kramer’s early conception of orientation: Either the centre of the system is conceived as the host / observer and the plastic part of the system as the freely flying bird whereby the system is held together by the “Machtbereich” (sphere of influence) of the observer. Or, on the other hand, the presupposition which brackets the system is conceived as the ani-

Ibid.
Ibid., 332.
Gustav Kramer (1910–1959)

mal’s primordial instinct (e.g. its unrest of migration, migratory “instinct”, innate biological rhythms, etc.). Then Kramer’s epistemic system could be interpreted as if orientation was the capacity to solve a problem and return to the host who, in this case, more appears as the one who rewards the bird’s performance with food etc. I think the former of the two readings is expressed by the paradox which is represented in the title “Vom Freifliegen zahmer Vögel” (On Free-Flying of Tamed Birds), whereas the latter reading especially applies to those parts of Kramer’s accounts where the returning failed: Like K. Lorenz while conditioning jackdaws on him – the observer-experimenter – Kramer had to struggle with the fact that sometimes the animal’s natural instincts prevailed and the animal got lost, did not return or deceased. Another paper which allows multiple readings of one and the same epistemic scheme seems to be Bewegungsstudien an Vögeln des Berliner Zoologischen Gartens which was published in the German Journal für Ornithology in 1930. Early ethologists such as O. Heinroth but also Ch. O. Whitman and W. Craig were convinced that behavioural systematics could supplement traditional morphological systematics and K. Lorenz event went so far as to claim that fixed action patterns might be able to establish even wider macrosystematic genealogical relationships than had been able to be obtained by taking into account merely morphological characters. In so far one may say that the notion of an animal systematic based on behaviours exceeded the classical program without refuting it altogether. One of the classic examples systematists picked to demonstrate the taxonomic value of behaviours was the scratching behaviour. Thus O. Heinroth, in a presentation before the German Ornithological Society in October 1917, had distinguished between two techniques of scratching behaviour – “vorn herum” (“under the wing”, also “directly”, i.e. lateral of the breast to the head, ) and “hinten herum” (“over the wing”, also “indirectly”, i.e. hind leg behind or over the wing) –, claimed that the respective method was species-specific and therefore could be used as group-specific taxonomic characteristic. Other ornithologists were more sceptical whether the behaviour in question was in fact as group-specific as previously supposed. G. Kramer indeed recognized that behaviours can be used for systematic studies but also took into account possible objections.

1236 See ibid., 332–333.
1237 See G. Kramer. “Bewegungsstudien an Vögeln des Berliner Zoologischen Gartens”. In: Journal für Ornithologie 78.3 (1930), 257–268.
1239 See O. Heinroth. “Deutsche Ornithologische Gesellschaft. Bericht über die Oktobersitzung 1917”. In: Journal für Ornithologie 66.1 (1918), 111–112. The report has been written by O. Heinroth himself so that we may conclude his views are represented authentically.
1240 W. Wickler later summarized the discussion which helps us to understand better Kramer’s move. See W. Wickler. “Über die Stammasgeschichte und den taxonomischen Wert einiger
one hand, he argued that the suggested wider taxonomic relationships might be the result of convergences as well.\textsuperscript{1241} This implies that these characters are individual ecological adaptations of the respective species or group and therefore have less taxonomic value for macrosystematic enquiries. On the other hand, he claimed that even the inter- and intraspecific behavioural deviations could be made fruitful – in particular when these variations turned out to be dysfunctional (since then they are not likely to be functional or ecological adaptations). “Eine Stütze für solche Betrachtungsweise sind denn auch die Fälle, wo derartige Verwendungen des Fußes ’außerhalb der Reihe’ auftreten”, he writes at the end of his analysis of foot-usage in several different species of Birds and continues,

\textit{Porphyrio} führt Nahrungsbrocken mit dem Fuß zum Schnabel, woran bei anderen Rallen gar nicht zu denken ist. Auch innerhalb der Fringilliden kommt Daraufentreten nach Raben-Meisen-Art vor (Kreuzschnäbel, Stieglitz, Zeisig). – Erst recht führt man sich zur Vorsicht veranlaßt, wenn man sieht, wie wenig System man in das Sich-vorn- und -hintenherum-Kratzen bringen kann, wie auch wieder die sich vornherum kratzenden Singvögel zeigen. Von Spechten beschreibt Heinroth, daß sie sich gewöhnlich hinten herum kratzen, gelegentlich aber auch oberflächliche Kratzbewegungen vornherum machen. Bei \textit{Agapornis roseicollis} Vieill. sah ich, wie sich dasselbe Exemplar nicht nur wie gewöhnlich hinten herum, sondern auch, seltener zwar, aber ausgiebig, vornherum kratzte. Bei einer einzigen \textit{Agapornis taranta} Stanl., die ich beobachten konnte, konnte ich nur sehen, wie sie sich vorn herum kratzte. Das Gewöhnliche ist bei dieser Gattung das Hintenherum–Kratzen, aber, wie man sieht, geht es etwas ungeregelt zu. Etwas Derartiges kann wohl nur bei Papageien vorkommen. Es setzt ohnehin in Erstaunen, daß viele von diesen Vögeln gerade bei Kratzen ein so umständlicher Weg im Nervensystem vorgeschrieben ist, wo ihnen doch bei der manngfachen Beweglichkeit von Bein und Fuß der kürzere Weg so nahe liegen sollte. Bei anderen Vögeln ist solch beliebige Kratzweise kaum denkbar. Einer Grauflügelamsel sah ich z.B. zu, wie sie sich buchstäblich bis zur Erschöpfung abquälte, ihr steifes rechtes Bein auf den vorgeschriebenen Wege zum Kopfe zu führen, an dem sie anscheinend starken Juckreiz verspürte. Sie geriet manchmal mit dem Fuß in ihre Achsel und machte da Kratzbewegungen. Nach Tagen und auch heute noch ist sie ebenso weit, kann es vermutlich auch nie lernen, sich vornherum zu kratzen. Nach derselben Richtung weisen ja junge Singvögel, die, noch nicht fest auf den Beinen, beim Versuch, sich artgemäß zu kratzen, das Gleichgewicht verlieren, nie aber versuchen, sich vornherum zu kratzen. [Such a view is even substantiated by those cases where such foot-usage occurs “outside the ordinary”. \textit{Porphyrio} puts food pieces to the bill with the foot which cannot be thought of at all in other rails. Also within the group of Fringillidae \textit{[finches]}\textsuperscript{CL} stepping-on \textit{[the food]}\textsuperscript{CL} occurs in accordance with the technique applied by raven and finch (Crossbills, Goldfinches and Siskins). – One is being made alert even more if one realizes how little system can be brought in the behaviours of over-the-wing- and under-the-wing-scratching which is again demonstrated by those song-birds which scratch over the wing. Heinroth writes about woodpeckers that they commonly scratch over the wing but from time to time perform cursory scratching movements under the wing. In \textit{Agapornis roseicollis} Vieill. I saw how one individual not only scratched over the wing as usual but also, though more rarely yet more extensively, under the wing. In one and the same \textit{Agapornis taranta} Stanl. which I was able to observe I could only see how it scratched under the wing. The usual behaviour in this species is under-the-wing-scratching but as can be seen things are somewhat disorderly. Something like that can only occur with parrots. It amazes us anyway that many of these birds, especially in their scratching behaviour, is dictated such an awkward method by the nervous system, although the shorter way should be

\renewcommand\thefootnote{\fnsymbol{footnote}}
\footnote{Verhaltensweisen der Vögel. Eine methodisch–kritische Erörterung”. In: \textit{Zeitschrift für Tierpsychologie} 18.3 (1961), especially, 323–328.}
\footnote{See Kramer, “Bewegungsstudien an Vögeln”, 266–267.}
more feasible considering the manifold motility of leg and foot. In other birds such an arbitrary technique of scratching is barely conceivable. For example I observed a grey winged Blackbird how it literally struggled to the point of exhaustion with putting the right leg in the prescribed way to the head where it apparently felt a strong itch. Sometimes its leg got caught in the axil where the scratching was performed. After days and even today the bird is as far as before, and can presumably never learn to scratch under the wing. Into the same direction point young song-birds which, not yet stable on their feet, loose their balance when they try to scratch in the prescribed way but never try to scratch under the wing.]

The quotation shows that Kramer suggested another interpretation of the epistemic scheme that had led Heinroth to formulate his program of a behavioural systematics. While Heinroth’s approach had been aimed at making evident one behavioural character in wider groups of species and thus profiled the classification of behaviour as a more macro-systematic tool, Kramer, by contrast, apparently wanted to shape the taxonomy of behaviours as a means for the micro-systematic sub-classifications within larger taxonomic entities and therefore as a supplementum of a functional morphology that, in his account or according to his conception, was primarily focused upon convergences. Both interpretations work upon one and the same epistemic grounds but eventually produce quite antagonistic sets of propositions on the mere phenomenological level. The fact that Kramer supplemented the view of his mentor Heinroth with an antagonistic interpretation of the epistemic pattern it was based upon not only left this scheme intact but also strengthened it in so far as it applied its inner logic – one presumption applicable to many phenomena – to its own use. This form of self-referential immunization of a scientific position is performative by nature and thus goes beyond the level of explicit utterance.

In general, Kramer’s early papers reveal the intention to look behind the scenes and make his reader sensitive for aspects he had not taken into account so far. Thus in one of his early publications he defined the “Vogelwarte Rossitten” (Ornithological Research Station Rossitten), where he had spent the summer semester of the year 1930 as workmate, not only as a place of research but, beyond that, also as an institution for public education. In particular, Kramer informed the reader

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1242 Ibid., 267–268.
1243 If behaviours, even they vary in one and the same individual, turn out to be an inefficient option favoured in comparison of a more effective / adapted one they cannot be interpreted as convergences and thus must be the product of a phylogenetic program. If so, they can be used for systematic purposes – however in a narrower taxonomic unit. That Kramer connects the intraspecific and even interindividual plasticity of the scratching behaviour with the notion of dysfunctionality is, I think, a result of the fact that the new neo-Darwinian causal architecture which generated more a focus on functional micro-variability was not yet established in the year 1930. Therefore I think Kramer’s micro-systematic program might focus on what W. Wickler called “Merkmalskorrelationen” (correlation of qualities) in “Schlüsselgruppen” (key groups) and which might eventually refer to what Darwin called “correlation of growth”, that is, characteristics which developed connected with and thus as a by-product of another trait. See Wickler, “Über die Stammesgeschichte und den taxonomischen Wert”, 331. These qualities, by no means, need to be ecologically or functionally adapted.

1244 See G. Kramer. “Gefangene Vögel der Vogelwarte Rossitten”. In: Der Zoologische Garten 4.1/2 (1931), especially, 39. O. Heinroth functioned as director of the Rossitten Bird Observatory between 1929 and 1936. He was succeeded by E. Schüz. After the Second World War the research station which had been integrated into the Kaiser-Wilhelm Society in 1923 was formally transferred to Radolfzell at Lake Constance. G. Kramer was nominated director of the observatory in 1959 shortly before his tragic death. 1959 was also the year when the institute was
about adequate methods of caging birds which he discussed systematically by developing a sort of range from single large birds (sea eagle), over eagle owls and common ravens to the cages for a variety of collectively kept small birds. A further note underlined the unfavourable conditions being raised by using bodily harmed individuals for observation studies with ringed birds: Only healthy individuals, Kramer argues, show their natural migratory instinct and therefore can serve as adequate objects of observation, whereas inadequately kept individuals might develop deviating abnormal behaviours (in Kramer’s example flying against the normal direction of the migratory route) and thus contaminate the observational data. Another paper made ornithologists familiar with the need to distinguish between low and high flying flocks while observing migrating birds on the Curonian Spit where the Rossitten Bird Observatory (nowadays Biological Station Rybachy) lies. In contrast to lower flying birds, individuals migrating in great height are easily overlooked and apparently do not primarily orientate by using landmarks – a matter of fact which, if neglected, might lead to opposing observations and thus to avoidable controversies. One of the heuristic problems of going to and beyond the limits of perceptibility actually was that the observer, even in case he used binoculars, was able to cover only a certain range beyond which observation could not generate reliable data. All these studies intended to teach the reader by taking into account or anticipating partly unfavourable side effects and insofar have a "homoeostatic" character not dissimilar (though not identical) to the one of N. Tinbergen’s late work on autism: The possibility of causing damage (while keeping animals or ringing birds) or making mistakes (while observing birds) is fed into the system as information in order to avoid the situation it describes.

A special variety of Kramer’s urge to transgress boundaries was his inclination to resolve opposing positions or stances into a state of indistinguishability which he conceived as discrete heuristic sphere lying beyond the mere antagonism and thus opened the mind for aspects not being thought of. To this kind of study I count a very early account upon the compatibility of hunting and conservation of nature. Furthermore, Kramer, for instance, insisted that in contrast to the opinion some ornithologists had put forward, the voice of Carrion and Hooded Crow cannot be distinguished incontestably. In addition, he claimed that K. Lorenz’s distinction

1245 See Kramer, “Gefangene Vögel der Vogelwarte Rossitten”, 39–43, especially, 41, for the possibility to provide inadequate cage constructions for eagles. The account finally ends with non-caged animals.


1248 See ibid., 69–70.


1250 See G. Kramer. “Stimme von Raben- und Nebelkrähe”. In: Ornithologische Monatsberichte
between two landing techniques in birds ("Unterfliegen" and "Rütteln") does not apply in a sense of an either–or. Many birds, he argues, use both methods simultaneously when landing.\textsuperscript{1251} In Allerlei von Paradiesvögeln (1932) we can find a contrast between a great sexual dimorphism and small interspecific differences in this characteristics, a contrast between non-bastards and bastards as well as, finally, a distinction between the more conspicuous male and the more uniform female types.\textsuperscript{1252} G. Kramer treated all this antagonisms as if they were resolvable and in doing so confronted the dualism as a whole with one of its inherent constituents. Eventually one of the most impressive of Kramer’s unmasking gestures was his examination of “Lumpi”, a dog that allegedly possessed higher intellectual capacities such as counting, reading or even calculating.\textsuperscript{1253} Since the beginning of the twentieth century a number of reports on “intelligent” animals had captured both the fields of popular and academic science and led to serious controversies across the mentioned spheres.\textsuperscript{1254} On the one hand, there were quite a number of pet owners but also several representatives of academic research such as H. E. Ziegler, E. Claparède and H. Kraemer who were convinced that mammal animals were endowed with cognitive abilities similar to the ones in us humans. Others, like C. L. Morgan (famous for his canon), E. L. Thorndike and the Berlin psychologist C. Stumpf – while arguing from different scientific positions – aimed to resolve seemingly higher capacities with more down-to-earth explanations before they went down to ascribing cognitive abilities to their scientific objects.\textsuperscript{1255} Thus in a famous study, the Berlin psychologist O. Pfungst succeeded in proving that the so-called “Clever Hans”, a horse that belonged to the retired teacher Wilhelm v. Osten and, according to his owner, was capable of performing intelligent behaviours, in fact was capable of reading the subtle facial and behavioural clues the experimenter had provided unconsciously during the tests.\textsuperscript{1256} Pfungst was member of and driving force within an informal community of scientists called the “Hirnrinde” (literally...
“brain rind”, meaning the “cerebral cortex” in the brain) which existed between 1903 and 1933 and whose intention had been to enhance the scientific exchange between Brain Anatomy, Physiology, Psychology and Biology in matters of behaviour. According to J. Abresch’s and H. E. Lück’s account, identifiable members or persons being associated with the group besides O. Pfungst were K. Goldstein, L. Heck, A. Guttmann, C. Stumpf, H. Liepmann, R. Henneberg, H. Poll, E. M. v. Hornbostel, L. Armbruster, E. Weigl, W. Köhler, E. Schwarz and, most important, O. Heinroth. O. Pfungst died in August 1932 after a longer illness and, according to J. Abresch and H. E. Lück, it was on the occasion of the commemoration ceremony for Pfungst on 16th February 1933 when the “Hirnrinde” had its first and only public appearance. O. Heinroth was among the ones who delivered a speech honouring O. Pfungst. Moreover, Heinroth had observed the “Clever Hans” several times in 1904 and, together with L. Heck, C. Stumpf and O. Pfungst, was part of the expert committee of altogether thirteen persons – the so-called “September-Kommission” – which had been gathered under Stumpf’s initiative to evaluate the “Clever Hans”. Whereas the initial report of the committee seemed to exclude the possibility that W. v. Osten’s horse was able to decipher the experimenter’s latent clues, a later statement of C. Stumpf, dated to December 1904, apparently favoured this explanation. It was this point at which it was left to O. Pfungst, one of C. Stumpf’s pupils, to establish heuristic clarity with his study  


which was finally published in 1907. Kramer’s evaluation of “Lumpi” and the further development of Pfungst’s methodology thus most likely was a result of the mediating role O. Heinroth had played between Kramer’s interests and the work of some members of the “Hirnrinde”, in general, and O. Pfungst’s unveiling results, in particular. Although Kramer in his account of the “Clever Dog from Weimar” underlines that an earlier study published by L. Plate and A. N. Sewertzoff provided the initial impulse for his engagement with “Lumpi”, one may therefore speculate that at least his critical and witty methodology applied while testing the dog was based on Pfungst’s results which Kramer apparently carried further.

It is R. Kressley-Mba’s merit of having pointed to the possibility that O. Pfungst’s study might have a similar structure as R. Virchow’s works leading to the “demystification” of the syphilis disease. See Kressley-Mba, *The History of Animal Psychology in Germany*, 205.

According to his own account, O. Heinroth became acquainted with O. Pfungst in 1914 [?].

Pfungst’s witty criticism G. Kramer had built highly sophisticated transparent cards which showed the dog another symbol or combination of symbols than the experimenter, Ms. S. Hensholdt, the owner of the pet, was able to see. In other words, the setting of the test was as such that the person providing the cards from the perspective of the dog could only communicate “false” information or erroneous cues. Kramer’s “observations” are remarkable because they give us the impression of a shifting and increasingly sophisticated process of experimentation in course of which the initial experimenter (the pet owner) became aware of the deception Kramer had initially installed. Kramer, in turn responded to the changed preconditions by taking over more and more the role of the experimenter and thus needed to leave behind his state of being an uninvolved observer. Although his observations suggested that “Lumpi” was a clue reading animal his study raises the impression of being incomplete not least because of the increased complexity of the communicative situation Kramer’s test had to deal with. Thus Kramer mentions that he was not allowed to perform further tests with the Weimar dog applying re-adjusted methods. As a result he argues with conspicuous caution and marks the need for more extensive studying. In general, however, in his accounts of the clever dog we can feel a great deal of scepticism towards anthropomorphization which, in his view, becomes manifest in the fact that allegedly intelligent animals were tested for genuinely human and less animal-specific forms of perception and intellectual characteristics. “Wie wenig Derartiges mit unseren bisherigen Kenntnissen, nicht nur tierpsychologischen, vereinbar wäre”, he writes,

das darzutun ist hier nicht der Ort, zumal sich davon übergewog aus der Blütezeit der denkenden Tiere vorfindet. Nur auf eins sei in solchem Zusammenhang hingewiesen: Wenn ein Hund fähig ist, die Uhrzeit nach der Taschenuhr abzulesen und kleine Druckschrift, z.B. Visitenkartenumschriften zu lesen, so setzt das nicht nur eine Sehschärfe, sondern auch – wie Lesen überhaupt – eine Formentüchtigkeit voraus, die man am wenigsten einem Makrosmaten zutrauen möchte. Überhaupt muß doch bei den ganzen Sinnesleistungen denkender Tiere auffallen, daß sie sich alle in einer menschlichen, d.h. rein optischen Umwelt bewegen. Sinnesphysiologisch besser, wenn auch intellektpychologisch gleich wenig verständlich wäre es, wenn ein Hund anzeigen könnte, was für ein Braten in Nachbars Küche schmore.

[Here is not the place to demonstrate how less compatible with our knowledge, not only our animal psychological knowledge, such things would be, particularly since enough of it can be found in the prime time of the thinking animals. Only one aspect is to be mentioned in this context: If a dog is capable to read the time from a pocked watch or even small letters from a visiting card this requires not only visual acuity but also – as reading in general – a competence with forms [evtl. the ability to abstract] with which one least may credit a macrosmatic animal [i.e. an animal with highly developed senses to smell]. It must strike us at all that all these

Deutsche Gesellschaft für Säugetierforschung” (German Society for Mammal Research) on 22nd January 1932 Kramer explicitly refers to O. Pfungst’s pioneering work. See Kramer, “Mitteilungen über einen neuen denkenden Hund”, 91.

For the witty criticism in which both researchers obviously resembled each other please compare Stresemann, “Gustav Kramer”, 258 and H. Poll, “Pfungst als Persönlichkeit”. In: R. Henneberg, ed. Oskar Pfungst zum Gedächtnis. Berlin: Goedecke & Gallinek, 1933, 6, respectively. Even still there are further parallels: After his engagement with the “Clever Hans”-problem, O. Pfungst carried out further animal psychological studies with apes, dogs and – even more exciting – with carrier pigeons the latter of which would become one of Kramer’s primary research objects after the Second World War. For O. Pfungst’s experimental animals see Abresch et al., “Der Kluge Hans, Oskar Pfungst und die Hirnrinde”, 85, and the list of Pfungst’s publications.
sensory performances of thinking animals occur in a merely human, that is, purely optical, environment. Sensory physiologically better, though from an intelligence-psychological point of view less comprehensive would be if a dog could indicate which kind of roast is stewing in neighbour’s oven.] (transl. CL)

In sum, we may therefore say that the episode with “clever Lumpi” revealed Kramer’s urge to supplement the anthropomorphisms put forward by both amateur and professional scientists by more parsimonious types of explanation. Moreover, it shows his general interest (though critical) in questions of animal cognition. As we will see later this theme should reappear in the second half of the 1950s under changed epistemological circumstances in Kramer’s extensive controversy with the American parapsychologist J. G. Pratt upon the homing abilities in pigeons.

In connection with this general sceptical overtone we need to understand also Kramer’s intention to grasp the physical correlates of the conspicuous behavioural phenomena in *Beobachtungen und Fragen zur Biologie des Kolkraben*. The paper marks a shift in Kramer’s scientific development because it enters into the question whether behavioural expressions can be correlated with corresponding states of physical excitation. Kramer, again, answers the question by providing antagonistic phenomenological interpretations of a constant scheme one of which is identified with the understanding of motivation K. Lorenz had put forward in his jackdaw paper. On the one hand, it is possible to presume a fixed correlation between a state of motivation and a corresponding expression. As a consequence, if an observer realizes the waning of a particular expression he may conclude that the corresponding excitation may have decreased as well (fixed relation between expression and “meaning”). Thus Lorenz had observed that the jackdaw’s reproductive behaviour underlies an annual cycle which he explained by corresponding changes in the motivation system. G. Kramer, by contrast, put forward the idea that expression and meaning – per definition – might be related to each other in a more discontinuous way. He had observed that the reproductive mood / expressions of a bird can perpetuate beyond the breeding season (in a narrow sense) and argued that an expression can detach itself from its original state of motivation (meaning) and change into an utterance which is articulated for its own sake or the sake of “Selbstnachahmung” (self-imitation), as he put it. In the one model of explanation a fixed expression-emotion correlation leads to quite different forms of expressions over the year, while in the other model a discontinuous correlation between behaviour and state of excitation guarantees that one and the same behaviour can be considered to be occurring all over the year though as expression of changing physical conditions. My argument now is that both models do not operate upon different epistemic foundations but need to be explained as different phenomenological expressions of one and the same epistemic scheme – so to speak as a means of reinforcing the scheme itself on a higher performative level. In one model the “motivation” takes the variable and the behaviour the static systemic position, while in the other “motivation” is considered the static and the behavioural expression the variable moment. As

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a provisional result, we may therefore say that Kramer’s early ornithological and observational studies are quite coherent as to the epistemic deep structure they rest upon. One and the same scheme appears in quite different forms of manifestations and, beyond that, is even applied performatively to its own use. G. Kramer’s very early publications thus give us the impression of an intellectual and highly sceptical young man who considered criticism and its anticipation necessary to immunize the heuristic system which he was a part of and which he conceived as a systemic, even organismic unity. In contrast to the model of causal analysis which later became one of the pillars of Classical Ethology, G. Kramer’s conception of unity was intended to be inclusive and therefore, as a whole, stayed within the framework provided by O. Heinroth’s works. As such it was primarily a means to extend a young researchers horizon in unknown areas without loosing contact to his mentor, his ideas and convictions. However, it should be kept in mind that the way G. Kramer interpreted the framework of his mentor’s research was more sophisticated and eventually revealed a more elaborate interest in micro-systematics.

I have argued that in order to place a scientific orientation correctly it is wise to have a deeper look on the inside of the realms these orientations consist of. In fact, I think that the antagonistic homogeneous scientific orientations which had gained weight among the generation of teachers under which G. Kramer, E. v. Holst, K. Lorenz and contemporaries received their academic education is structurally not as coherent as the term “homogeneous” might suggest. In any case, I think, that both the polarization of the scientific orientations as a whole as well as their specific dualistic constitution (to the inside) might be responsible for the repercussions we can observe in each realm of a scientific orientation. As to Kramer’s early works the question of possible repercussions can only be answered for the realm they represent and not for those parts of the orientation which remained silent. In order to answer the question I will mostly elaborate on how Kramer shaped the introductory parts of his accounts. Although I believe that beginnings do not necessarily represent the order of the whole – epistemic schemata can be both tautological and paradox in their beginning – the particular structural preconditions of Kramer’s early works let this focus appear to be an adequate one. In other words, if there are repercussions of accompanying epistemic realms within a particular scientific orientation, they are likely to become manifest mostly in the initial sections. While I was reading Kramer’s early papers I stumbled several times over passages in which he applied a more reductive analytical mode of narration which, considering the overall tenor of the publications, appeared as foreign bodies within the argumentative network his papers introduced. These restrictive and reductive gestures can appear in slightly different varieties. For instance, there are opening gestures which include – relatively unspectacular for scientific texts – a thematic restriction like the one I have quoted in fn. 1267, page 401: “Here is not the place [...]\(^{\text{CL}}\). At the beginning of Beobachtungen und Fragen zur Biologie des Kolkraben it reads:

[I am not about to publish the collected observations haphazardly and in doing so report things which better experts of wild ravens than I am have obtained while wearing down their shoes. Instead, from a limited amount of angles, there should be made some considerations which to obtain was supported by observations made with captive ravens, especially a pair in the Zoological Garden of Berlin.](transl. CL)1269

With a view on the Rossitten Observatory he says:

Bei der Geldknappheit, die sich bei unserem Institut ganz besonders bemerkbar macht, kann auch in dieser Hinsicht nicht das Angestrebte voll erreicht werden; zwar möchte man weniger darauf bedacht sein, mehr Arten oder Individuen zu halten, als vielmehr das Vorhandene in einer für Tier und Beschauer günstigeren Weise darzubieten.

[Considering the restricted financial resources which make themselves felt particularly in our institute, also in this respect the desired cannot be reached completely; Although one would like to be less eager to keep many species or individuals [anyways] one [now under the given circumstances] the more prefers presenting the existing [stock] in manners more favourable for both the visitors and the animals.](transl. CL)1270

I think the compilation of short quotes reveals the pattern: The many is rejected in favour of the few or the one and this restricted entity is associated with the notion of a better functioning. Other papers operate with pronounced repudiations of opinions or hypotheses put forward by others. This applies in particular to Stimme von Raben- und Nebelkrähe (1930) and Über den klugen Weimarer Hund (1931).1271

With a view of the latter paper, the choice of a critical opening gesture might also explain why O. Pfungst’s pioneering work is not mentioned and used to legitimize the endeavour although this would have been also a plausible possibility to begin with. Furthermore, in Beobachtungen und Fragen zur Biologie des Kolkraben (1932) we find an explicit dismissal of an alternative epistemic practice, namely the accumulation of data. Kramer writes:


[It is not the purpose of the following to compile an all-encompassing survey [lit. “sum”] of observations about the behaviours of some birds but I should like to emphasize some few characteristic traits mainly from comparative perspectives. In particular, certain movements will be taken into account which are usually applied by some species of Birds during foraging or ripping the prey object to pieces.](transl. CL)1272

A speciality of Kramer’s writings, finally, is a certain subtlety as to the usage of connotations associated with spatial or, more concretely, geographical relations. For instance, in Zug in großer Höhe (1931) we are informed that the normal migratory direction taken by the birds on their annual trip from north-east to south-west

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1270 See Kramer, “Gefangene Vögel der Vogelwarte Rossitten”, 39. The second sentence of the German quotation is awkward and I have translated in a way it can make sense. However, it includes my interpretation.
is deflected by the geographic position and the shape of the eastern shores of the Curonian Lagoon where Kramer had chosen a lookout. Moreover, Kramer argues that the deflection of the migratory course causes a congestion of migrating birds which is responsible for the annually reappearing masses of birds at this particular geographic location. I have added a graphic to illustrate the situation from which G. Kramer’s observations originated (Fig. 2.18).

My opinion is that Kramer presents this information in a particular way and at a distinct position in the introductory part of the text so that the respective section expresses the wished epistemic form: From a geographical point of view, which here means also quite concrete the place of his observatory, the event of migration therefore appears as deviation from the normal course and within this deviation, again, we are confronted with a jamming or condensation of a huge amount of birds which usually take the described route. In sum, I am inclined to argue that all the mentioned opening gestures operate with reductions of more or less metaphorical kind and, beyond that, the placement of these gestures is not arbitrary. My readings

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1273 Kramer, “Zug in großer Höhe”, 69. The position of his lookout is defined as between Juwendt and Nemonien.

1274 The figure includes a contemporary photography taken by a satellite. It is therefore not a political or historical map but may be closer to the bird’s eye perspective. The graphic is actually taken from wikipedia and has been modified for my purpose. See http://en.wikipedia.org/wiki/Curonian_Spit.
of G. Kramer’s later publications should reveal in how far this sort of epistemic practice is a specific characteristic of his early works. His dissertation thesis reveals another quality. Not only did it emerge in another scientific environment and was linked to the work of another mentor, R. Hesse, it is a genuine experimental study. It picks up J. v. Uexküll’s notion that a living organism’s perceived environment is dependent from its sensory capacities which, in turn, vary from species to species. The objective of Kramer’s dissertation thesis was to reconstruct the particular environment of the African Clawed Frog. “Ziel dieser Arbeit ist”, Kramer writes,


The objective of this study is to examine some parts of the Clawed Frog’s sensory world. In doing so we would like to be put in the position to build up a picture of the treated species’ environment (in v. Uexküll’s sense). It is the phylogenetic position in connection with the ecological character of Xenopus which let appear this task extraordinary interesting. The obtained picture of the environment will challenge to make comparisons with other Phaneroglossa, on the one hand, and evaluations with a view of the ecological milieu, on the other.

The quotation reveals the general overtone of Kramer’s study: The particular data obtained in a number of sensory physiological experiments is to be synthesized in a general “picture” of the Clawed Frog’s specific environment which, in turn, provides the basis for concluding comparisons with other species of frog (viz. other Phaneroglossa, that is, frogs with a conspicuous tongue) but also its place within the frog’s particular milieu. In other words, Kramer’s thesis was meant to place a particular species of frog both within its phylogenetic and its ecological system. The overall tenor of the thesis therefore suggests that we have to do with a heuristic procedure that might be called “General Synthesis” in H. Spencer’s sense and operates with a mathematical limes logic. That is to say, the empirical main parts are headed towards a result that has been projected from the very beginning and with which the particular results now are meant to coincide. I think this gesture of coincidence is formulated explicitly in one of the thesis’ later sections which is termed “Rückblick” and which, I think, refers back to one of the later sections of the empirical part of the thesis in a way that both sections operate with a “synthetic” heuristic procedure. “Außer dem Abschnitt über das Suchen”, Kramer writes there,

der synthetisch gehalten war, setzte sich die Darstellung aus Einzeluntersuchungen zusammen, deren jede für sich bestand, ohne Beziehungen zu anderen aufzuweisen. Hier noch ein paar Worte zum Ganzen.

1275 In one of CVs Kramer mentions that the choice of the topic “Untersuchungen über die Sinnesleistungen und das Orientierungsverhalten von Xenopus laevis” was his own choice. Moreover, Kramer seems to have dropped an alternative topic before after only a few weeks. The topic of this brief endeavour was “Zweibeiniges Springen bei Säugern” and is said to have been based on mutual “agreement”, too. See UAH, PA 10014, ms. “Lebenslauf von Dr. Gustav Kramer” (31/08/1946).

1276 Kramer, “Untersuchungen über die Sinnesleistungen”, 630.
[Except the section about the searching behaviour which was treated synthetically, the account [i.e. the thesis as whole] CL was composed in singular studies each of which existed independently without being connected to others. Here some few words as to the whole. ]

The quotation shows that G. Kramer conceived his dissertation thesis mostly as a more atomistic compilation of singular experimental studies but pulled the threads together in the final part to obtain the intended “picture”. We also need to take into account that Kramer describes this procedure of summarizing abstraction as “synthetic” whereby only two singular chapters are explicitly affiliated with this attribute, namely the sections with the title “Suchen” (Searching) and “Rückblick” (Recapitulation). The explicit information G. Kramer gives us about the order or composition of his thesis are not many enough to derive one single pattern of knowledge organization. As a result, we have to deal with a certain extent of uncertainty or, to put it optimistically, interpretative liberty. The scheme I have made the basis of my following argumentation is the following (Fig. 2.19). It is a binominal order not only because every outline can eventually be described in that way but also because I am convinced that behaviour researchers thought in these schemes. Only if one proposition is ascribed to one branch, and one branch only, it obtains its specific identifiable sense (comparable to a mathematical probability and / or semantic value) and this increase in precision surely was conceived as an essential part of a discipline’s scientization. Also, the scheme I suggest includes more structural information than is mentioned explicitly in the text since it is based on additional latent structural information. Thus I am very sure that the main section of Kramer’s argumentation distinguishes between “behaviour” (here of the animal as a whole) and “sensory capacities, to be examined experimentally”. Each of these main constituents again seems to have its inner organization. Thus in his “Preliminary Remarks Concerning Behaviour”, G. Kramer’s account proceeds from the periphery to the centre of the nervous system since the motility of the Clawed Frog’s extremities are described in the first place before and the author enters into the peculiarities of motivation in a second step. It is not an accident that the movement of the forelimbs is examined in the first place and that of the hind legs in the second, and so forth. The part which refers to Kramer’s experiments is the core of the study. The information is arranged in several sections differentiated by senses. Thus we find treated mainly four areas of sensory perception, the optical senses, the mechanical senses, scent and taste and, finally, the light-receptiveness of the frog’s skin. Each of these parts, in turn, has its own inner composition. Thus Kramer, while examining the optical senses, differentiates between the frog’s visual capacities above and under the surface of the water and comes to the conclusion that Xenopus has poor eye sight in either media since its eye is hyperopic under water and myopic in the air. The account on the mechanical senses is concerned with the Clawed Frog’s predatory behaviour and the two specific types of receptor

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1277 See Kramer, “Untersuchungen über die Sinnesleistungen”, 674.
1278 See ibid., 630–631, 631.
1280 Both forms of visual dysfunction have their own epistemic connotation: While shortsightedness (myopia) reduces the visual field, longsightedness (hyperopia) exceeds it beyond the optimal point.
G. Kramer, Examinations of the Sensory Faculties and the Orientation Behaviour of Xenopus laevis Daud. (1933), Knowledge Organization
which are involved while approaching the prey object. These senses are namely the lateral line organ, on the one hand, and the tactile sense of the whole skin, on the other. They are described at first from an anatomical perspective. After that, their particular sensory “role” is outlined experimentally.\textsuperscript{1281} An additional supplementary section clarifies the spatial function of each of the mentioned mechanic senses. It discusses the spatial function of the tactile sense after direct touch, the spatial perception of the lateral line organ and, finally, the tactile sense’s ability to localize far remote objects. The order of the account therefore proceeds from close to remote stimulation. Moreover, the heuristic procedure in the subsection on spatial function is often analytical since hypotheses are presumed in the first place that are tested (and mostly refuted) in a following step.\textsuperscript{1282} Kramer’s main result here is that the farther away the source of stimulation is located the more receptors may be involved and consequently a more of coordination may be required.\textsuperscript{1283} That is to say that in case of the lateral line organ and even more in case of the localization of remote objects by the skin (which is a function independent of the response to direct touch) the receptors in question provide many qualitatively different impulses that are strictly independent of each other and therefore need to be coordinated in the central parts of the nervous system in order to obtain one directive information.\textsuperscript{1284} “Es besteht also die Notwendigkeit zur Annahme”, Kramer argues,

\begin{quote}
\begin{center}
daß mehrere Lokalzeichen zu Komponenten einer gemeinsamen Resultante werden, die zentral als eine sekundäre Lokalqualität aufgebaut wird.
\end{center}
\end{quote}

[As a result, there exists the necessity to presume that several local signs become constituents of a common resultant which is built up as secondary location-specific information.]\textsuperscript{(transl. CL)1285}

And in case of long-distance orientation it reads:

\begin{quote}
\begin{center}
Das Verhalten [der Haut]\textsuperscript{CL} auf entfernte Reizung ist also sehr wohl zu unterscheiden von der Reaktion auf direkte Berührung. Die Reizquelle wird in die Ferne verlegt, wenn auch wirklich genaue Richtungseinstellung und besonders kräftiges Drauflosschwimmen vermißt werden. \end{center}
\end{quote}

Dieses Fernverlegen ist ebenso bemerkenswert wie die Tatsache, daß überhaupt reagiert wird. Im Falle ferner Reizung spricht ja eine große Menge von Receptoren auf einmal an, was gar nicht im Sinne der eigentlich adäquaten Berührungsreizung ist. Wir stellen auch hier die Fähigkeit fest, aus der Art der Reizverteilung sekundäre Lokalwerte aufzubauen.

[The response [of the skin]\textsuperscript{CL} to remote stimulation therefore is to be differentiated indeed from the reaction to direct touch. The source of stimulation is projected into the distance even if there is a lack of precise directive adjustment and, in particular, there is no vigorous straight forward swimming. | This projection into distance is as remarkable as the fact that there is a reaction at all. Thus, in case of remote stimulation a great amount of receptors respond at simultaneously which is not in agreement with the original adequate tactile stimulation. We realize also here

\textsuperscript{1281} Thus the side line organ responds mainly to shock waves in the water, while the skin responds to both direct and more indirect impulses.
\textsuperscript{1282} For instance, Kramer discusses O. Koehler’s hypothesis that the principle of orientation applied by the lateral line organ of the Clawed Frog is the \textit{tropotaxis} and refutes this idea. See Kramer, “Untersuchungen über die Sinnesleistungen”, 651, 653. He discusses whether the impulses received by the peripheral sensory organs might be more information rich (i.e. include information about the direction of the object) than previously assumed and refutes this possibility. See \textit{ibid.}, 654–656. Other examples of exclusive heuristic procedures could be added.
\textsuperscript{1283} \textit{Ibid.}, 654.
\textsuperscript{1284} \textit{Ibid.}, 653, 654, 658.
\textsuperscript{1285} \textit{Ibid.}, 656.
The section on taste and scent is organized in a dualistic way, too. It clarifies the potential receptiveness for chemical stimulation, that is, taste and scent, in the first place. Thereby Kramer reveals that taste is less involved in the frog’s response to prey than scent which seems to apply more to remote and less to direct stimulation because he was able to detect taste organs in the frog’s mouth. In a second step, he answers the question what kind of mechanism is underlying the searching behaviour which is stimulated by the chemical sense. The observed behaviours of blindfolded individuals showed that prey objects are found faster than mere random searching would allow so that finding by mere chance could be excluded. Instead the Clawed Frog seems to respond to differences in the concentration of odorous substance within the water basin by trial and error. That is, areas with lower concentration are avoided in favour of areas with dense ones. The behaviour is therefore “reductive” in a sense that it must direct the experimental animal to a centre in course of a recursively applied discrimination procedure. Finally, G. Kramer shows that the light-receptiveness of the frog’s skin is responsible for its avoidance of light (negative phototaxis), that the respective stimulus is calculated as sum-total of particular stimulation and that *Xenopus* does not respond to ultraviolet light. In this context, it is noteworthy that Kramer thought about a law of heterogeneous summation several years before A. Seitz’s published his papers. Core-idea of the concept is that one response requires a certain intensity of stimulation capable of exceeding the action-specific threshold and, furthermore, that the amount of stimulation may be gathered from different sources. Lastly, Kramer invalidates the objection that the frog’s light-response in fact might be a light-heat response. In sum, one may say each of the discussed sections seems to have its own inner organization which supports the overall tenor of the paper in each detail. Furthermore, on closer inspection, G. Kramer seems to have ordered the four sections about the senses eventually not only “from the face to the periphery” but also according to the criterion of sensitiveness. While the optical senses are described as coarse, the skin, on the other side of the scale, seems to react highly sensitively. These inner principles of organization are not named as such on any meta-level of the account, they are simply performed or applied, and thus remain in the performative sphere. To take them into account requires a high extent of sophistication both of the one who analyzes a scientific publication in this way as well of the one who reads the analysis. Nevertheless, I think, to take into account this additional information is legitimate and eventually supports my hypothesis that Kramer organized his knowledge in a highly reflected and sophisticated way which was apt to support the overall limes-structure of his study on all levels of its composition – even the finest peripheral ones. Due to its overall limes-structure G. Kramer’s treatise

1286 Ibid., 659.
1287 Ibid., 661, 664.
1288 Ibid., 665.
1289 Ibid., 668 and 675.
1290 Ibid., 670–671.
1291 Ibid., 671–673, 673–674.
therefore is not a survey, a mere accumulation of data or the elaboration of a basic criticism which was characteristic for many theses written by Niko Tinbergen’s first generation of pupils (not taken into account the changed causal architecture).

However, the suspected order also reveals the peculiarities of the homogeneous scientific orientations. Thus there is great deal of structural variety below the surface. This can be proved very easily by comparing two reductive sequences. For instance, if we take the two final parts of the thesis which tie together the diverse information obtained in the empirical main sections and a more reductive sequence in the main part of the thesis, say the section with the title “Preliminary Remarks Concerning Behaviour” we see the difference immediately. Thus the final sections provide us with a condensed recapitulation in the first place: Please remember that Kramer himself had introduced the section with the title “Rückblick” in terms of “wholeness” and “abstraction”. The recapitulation, finally, is supplemented with a summary (“Zusammenfassung”). Thereby the summery, as is tradition in biological reasoning, consists of a brief enumeration of the main results and therefore has to be read as a more detailed elaboration of the recapitulation, the central result. The final parts thus proceed from the general to the special. Not so in the reductive sections in the main parts. They proceed from the special to the central aspect which can be seen in Kramer’s account on behaviour where the narrative account is correlated with the process of centralization in the nervous system. As a result of this structural arbitrariness I am inclined to interpret Kramer’s dissertation thesis as a more or less classical experimental study. In other words, unlike E. v. Holst’s dissertation thesis which reveals much more the trend away from reflexology and the questions put forward by traditional sensory physiologists, Kramer’s study seems to stay more within this frame.

However, below the surface there are also some indicators for the upcoming paradigm shift. For instance, G. Kramer, like E. v. Holst, tended to conceive the afferent leg of the nervous circuit not only by taking into account the modalities of peripheral sensation, the sensory capacities in a narrow sense, but also the process of reduction, abstraction and centralization in the upper regions of the circuit. We remember, ascribing priority to this set of enquiry and thus making it a constitutive part of a now heterogeneous scientific orientation was in fact one of the epistemic shifts that finally led to Classical Ethology. G. Kramer does not go so far in his dissertation thesis as to raise this type of inquiry upon a paradigmatic level but it is present in the particular segments of his argumentation. Moreover, the comparison with E. v. Holst’s simultaneously

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1292 For both parts see Kramer, “Untersuchungen über die Sinnesleistungen”, 630–634, 674–676.
1293 An analysis of other reductive sections such as the one being concerned with the restriction of the topic can substantiate this hypothesis.
1294 For E. v. Holst’s dissertation thesis which has been written more or less simultaneously with the same advisor see E. von Holst. “Untersuchungen über die Funktionen des Zentralnervensystems beim Regenwurm”. In: Zoologische Jahrbücher. Abteilung für Allgemeine Zoologie und Physiologie der Tiere 51.4 (1932), 547–588 and E. von Holst. “Weitere Versuche zum nervösen Mechanismus der Bewegung beim Regenwurm”. In: Zoologische Jahrbücher. Abteilung für Allgemeine Zoologie und Physiologie der Tiere 53.1 (1933), 67–100. The study has been published in two parts whereby the entire order of the project becomes evident only if both parts are taken together. Thus the later of the two publications appears to be more a sort of appendix which frames the more holistic tenor of the main study so that both parts as a whole could be linked with the tradition of Experimental Physiology.
written thesis shows that both scientists were representatives of different styles of (physiological) thinking. While E. v. Holst’s thesis was a manifestation of his holistic thinking which only could be disciplined by adding a second more classic part to the main study, Kramer’s procedure allowed reasoning in holistic terms only at the end of an otherwise strictly atomistic process of research. These observations are the first indicators that G. Kramer and E. v. Holst, though mutually respected colleagues and friends, should approach the upcoming synthetic movement in the biological disciplines of the mid-1930s from different starting points and with quite different outcomes.

Transition One. (R₁) This should become evident already in the next period of G. Kramer’s intellectual life-history. To identify the relatively short life span between early 1933 (date of PhD) and mid-1934 (move to Rovigno) as a separate period in G. Kramer’s life-history is justified for several reasons. At first, Kramer’s research took place within another environment. While his dissertation project was carried out under R. Hesse’s supervision, the papers Kramer published in the years 1934 and 1935 originated in the Institute for Pathology of the Kaiser-Wilhelm Institute for Medical Research. The KWII for Medical Research had been founded in Heidelberg in the year 1927 as a conglomerate of four departments, namely the institutes for Pathology, Physiology, Physics and Chemistry. The institute as a whole was led by L. v. Kreipl between 1929, the start-up date of the institute, and 1937. During the period G. Kramer was fellow at the KWII for Medical research, that is, between 1933 and 1934, Kreipl also functioned as the director of the Institute for Pathology with which Kramer was formally associated and this is most likely the primary reason why his support is acknowledged in Kramer’s papers of that time. Second,
together with G. Kramer’s institutional shift occurred a shift in his research topics. While his PhD thesis had examined the sensory capacities of the Clawed Frog with a special emphasis upon its orientation behaviour, Kramer now was mainly concerned with gas-exchange analyses in poikilothermic animals.\footnote{According to H. Kant, L. v. Krehl’s expertise was mainly in the areas of metabolism and thermoregulation of the human body. See Kant, “Integration und Segregation”, 176. Whether there was a crucial influence is something I cannot claim with definite certainty. G. Kramer mentions in the publications of that time that he was supported by a fellowship of the “Notgemeinschaft der Deutschen Wissenschaft” and in this context we might find the sources that answer this question. For the information that Kramer was supported by the Notgemeinschaft see Kramer, “Der Ruheumsatz von Eidechsen”, 616, Kramer, “Weitere Untersuchungen über die Umsatzgröße von Eidechsen”, 39, and Kramer et al., “Verbesserungen und Vereinfachungen in der Gaswechselmethodik”, 389.}

In concrete Kramer’s research consisted of placing Lizards – his main experimental animal – in closed or semi-closed respiratory systems while asking the question how much oxygen the animal consumed and how much carbon dioxide it produced under certain controlled circumstances. The parameters Kramer tested, for instance, included temperature, the animal’s state of activity, the animal species (i.e. different varieties of Lizards), its size (i.e. state of ontogenetic development) and the size of the body surface. Altogether the gas-exchange was treated as a measure of metabolic activity. I have already mentioned that with his move to Heidelberg the Lizard became his primary experimental animal. This is true but an insufficient information because his studies of that time reveal that he tested also amphibia (less prominent in the papers) and albino rats (i.e. a mammal animal) with the same method (the reasons will be explained later). Kramer published mainly three papers which mention explicitly the connection with Krehl’s institute two of which authored by G. Kramer only, while the last study of the series included the results of a joint endeavour with his colleague H. Wollschitt.\footnote{The improvement of the so-called “Tierkalorimeter” (animal calorimeter) was a joint undertaking of the Institutes for Pathology and Physics the latter of which was headed by W. Bothe since April the 1\textsuperscript{st} 1934. See Kant, “Integration und Segregation”, 186, 189–190. H. Wollschitt, formally affiliated with Krehl’s institute, apparently functioned as the mediator between the different departments not least because of his close cooperation with W. Bothe.}

The latter of the mentioned papers is also the one which is more or less unspecified as to the use of a particular experimental animal since it is primarily focused upon mechanical details but in one of the final sections the paper also describes results obtained with albino rats. In general, one may eventually say that the results of Kramer’s gas-exchange analyses raised questions concerning the figures they put forward. The cooperative study with H. Wollschitt was triggered by these uncertainties and finally was aimed at fixing the problem by naming several sources of measurement error related both to the apparatus used for the experiments and its application. As a provisional result, one may say that G. Kramer’s research during his Heidelberg period can be approached from two different angles. On the one hand, there were his own studies which ended with the irritation of his heuristic system that was therefore challenged to reorganize on a higher level. On the other hand, however, it was exactly the moment of this irritation which gave the impulse for a research cooperation whose outcome, in turn, was meant to stabilize his primary research. As a result, we may therefore presume that we have to do with two heuristic systems that were closely intertwined with each
other since they mutually supplemented one another. Kramer’s cooperative paper with H. Wollschitt reveals that solving the problem of measuring accuracy involved taking into account both the meticulous details of the experimental apparatus and the mathematical abstraction of the findings. On a historiographical level the history of Biology thus has to meet with technical history and both need to be resolved in a common framework providing means of descriptiveness in direction of both areas. The following paragraphs of my thesis thus can also be read as a test of my epistemological approach with a view of this kind of research question. Moreover, it has to answer the question whether Kramer’s cooperation cannot be read as an indicator for a deeper-lying epistemic transformation in his intellectual development that consisted of merging two qualitatively different heuristic programs together to one single “heterogeneous” scientific orientation – as was typically the case in the life histories of other ethologists who developed their own scientific identity simultaneously at the beginning of the 1930s. Finally, considering this possibility I shall have a closer look to the inner constitution of each heuristic realm as well since the changed composition of Kramer’s scientific orientation as a whole might have produced repercussions on each of its realms. In the following I will therefore examine how the studies G. Kramer published in the years 1934 and 1935 are structured to the inside and, beyond that, how they are related to each other.

The first of the three papers in question was submitted to the journal at the end of March in 1934. It is not a study which delivered entirely new and revolutionary results but, instead, was aimed at extending a basic hypothesis’ scope of applicability. Thus the argumentation of the paper proceeds in two steps. At first, it puts forward a core hypothesis. This hypothesis includes two propositions. The majority of authors, Kramer argues, agree that the gas-exchange rate not only in warm-blooded but also in cold-blooded animals increases slower than the weight of the animal and more or less proportional to the animal’s size of the surface of its body.1301 Kramer adopts this thesis and aims to prove its applicability to a wider range of objects. Thus he writes:

Bei alledem bleibt das Bedürfnis, sich von der Breite des Bereichs zu überzeugen, innerhalb dessen eine konstante Beziehung von Umsatzgröße zu einem Flächenmaß sich nachweisen läßt, und zwar bei möglichster Gleichmachung aller Bedingungen mit Ausnahme der zu untersuchenden. Vor allem bedarf es einer Zusammenstellung von Versuchstieren, die etwas Bindendes aussagen läßt über den Umsatz in Beziehung zu altersbedingtem Größenunterschied innerhalb der gleichen Art einerseits, zu artbedingtem Größenunterschied gleichaltriger Tiere andererseits.

[In all that, there remains the need to assure oneself of the width of the scope within which a constant proportion can be proofed between the amount of gas-exchange and the size of the body surface whereby all experimental conditions except the one to be examined are to be kept constant. In particular, there is a need for a sample of experimental animals which tell us something about the gas-exchange rate in relation to animals within the same species that vary in their size that is determined by their age, on the one hand, and in relation to animals of different species sharing the same age.][transl. CL]1302

1301 Kramer, “Der Ruheumsatz von Eidechsen”, 600.
1302 Ibid., 600–601. G. Kramer establishes here two types of comparison which anticipate his later allometry studies: Different age – same species and different species – same age! As to the latter type I need to add that G. Kramer was interested in “different species” that were closely related to each other. This information reflects back upon his reasoning on systematics in Bewegungsstudien an Vögeln (1930) and supports my thesis that he was interested in the
This overall gesture of extension, however, includes, so to speak as constituting part inside the scheme itself, a gesture of argumentative reduction: The extended scope of applicability can only be proved if a larger number of tests with objects of both different age and kind shows a constant (or at least regular) exchange rate. The latter step of argumentation is therefore reductive: Many cases are to be reduced statistically to one principle which is here a constant quantity of gas exchange. A binominal analysis of the paper’s organization can make visible both steps of argumentation (Fig. 2.20). While the former of the two argumentative steps is represented by the node in the tree below the title, the second step coincides with the node I have termed “Experiments”. My analysis of this latter step suggests that the data Kramer obtained in experiments with mainly six test groups and which he outlines in chapter three with the title “Besprechung der einzelnen Gruppen” (Review of the Single Test Groups) culminated in two further sections which can be read as the inferences that can be derived from this data. These two concluding sections bear the titles “Der respiratorische Quotient” (The Respiratory Quotient) and “Umsatz und Tiergröße” (Gas-Exchange Rate and Animal Size). It is not unimportant to mention that the latter section ends with some remarks concerning the proportion of energy a hibernating Lizard consumes relative to its lipid reserves and that it is exactly this wider view upon the biological meaning of Kramer’s findings that will become the topic of the penultimate section, “Die Bedeutung des Nachweises der Energie-Flächenbeziehung an Wechselwarmen” (The Meaning of the Proof of the Correlation between Energy Consumption and the Size of the Body Surface in Poikilothermal Animals), with which it therefore coincides thematically, at least partly.\[1303\] Next to the structural information derived from the performative forms of knowledge organization Kramer’s own outline substantiates my analysis. Most likely, with a view of the parts I have called “Experiments” he writes:

Bei der weiteren Darstellung gehe ich so vor, daß ich nach Beschreibung der Methode zuerst Nebenfragen behandle, die als Voraussetzung zur Kernfrage notwendig und auch für sich von Interesse sind.

[In the further course of my account I will proceed in such a way that, after having described the methodology, I will at first treat secondary auxiliary questions which [to raise and answer] are necessary for the central question but are also of interest in themselves.\[1304\]]

I identify the “Nebenfragen” (auxiliary questions) with chapter three and four, whereas the “Kernfrage” (central question) seems to coincide with chapter five.\[1305\] It is important to realize that Kramer speaks in both cases of “question” and in the latter of “core issue” or “central question”. As a result, we can say that the epistemic

\[1303\] See Kramer, “Der Ruheumsatz von Eidechsen”, 613.

\[1304\] Ibid., 601.

\[1305\] It would be theoretically also possible to group four and five together but this option is excluded by G. Kramer’s own statement. At the end of chapter four it reads: “Diese Erörterungen über den respiratorischen Quotienten bilde deswegen noch eine Vorbereitung auf unsere Hauptfrage, weil wir ja Energieraume vergleichen wollen” [This discourse upon the respiratory quotient is still a preliminary to our main question because it is the energy values we want to compare].\[transl. CL\]

See ibid., 610. The statement makes clear the hierarchies.
G. Kramer, *Der Ruheumsatz von Eidechsen und seine quantitative Beziehung zur Individualgröße*, Binominal Analysis
pattern of the publication mirrors its argumentative purposes. If my hypothesis was true each of the single parts of the paper must reveal its own characteristic order of propositions. In other words, the macro perspective provides a tentative hypothesis to be tested by entering the micro levels of the account. Without going into detail too much this, I think, can be confirmed. Thus G. Kramer shows in chapter three that in all six examined groups both the $O_2$ intake as well as the $CO_2$ exhaustion decrease slightly over the time period of the experiment. A first quantitative reductive gesture consisted therefore of finding a procedure to determine an average of both values for each sample group which could be used as basis for further comparisons and calculations.\footnote{The chapter with the title “The Respiratory Quotient” contains four major propositions.} At first, the reader is informed that the quotient is not a static entity but can change due to temperature increase or increased motility.\footnote{Second, we can read in-between the lines that the found $CO_2$ values were too low in order to be a direct indicator for the amount of oxidized substances. As a result, Kramer infers there might be other reasons for the observed retention of $CO_2$. Third, we are informed that the respiratory coefficient in different varieties of Lizards turned out to be constant. Finally, Kramer treats the question how the respiratory coefficient can be translated into a corresponding size for metabolic activity that can be a valuable variable for the amount of oxidized substances. On closer inspection all four propositions either reduce gradually (two and three) or extend one aspect with another (one and four) so that their overall composition seems to be more like the scheme in proposition one and four. The following section “Umsatz und Tiergröße” again makes an attempt to establish a correlation between the rate of gas-exchange, on the one hand, and morphological qualities such as weight or size of the surface. I see mainly four aspects treated. At first, we find a list of the six test groups each time comparing the amount of respiratory gases with the allegedly amount of produced heat (i.e. metabolic activity). This table is followed by a statement that comes to a conclusion:}

Also: Auf die Gewichteinheit gerechnet, ergibt sich ein regelmäßiger Anstieg der Stoffwechselgröße mit abnehmender Tiergröße.\footnote{As a result: Referred to the weight entity thus there is a regular increase of the metabolic value with decreasing size of the animal.} \[transl. CL\]

The second aspect correlates the gas exchange rates with the size of the body surface and claims there is a constant ratio.\footnote{In a third step the metabolic activity is compared with the size of the fat pads (and other organs) in each of the examined groups.}
subspecies.\textsuperscript{1315} His account seems to suggest the existence of a direct proportionality. Finally, we find some remarks about the biological relevance of the findings for the Lizard’s hibernation. The chapter as a whole thus makes the attempt to extend the perspective by reading biological significance into the obtained results. In doing so Kramer’s results raised questions: At first, the energy consumption he had calculated was much lower than the values of other authors.\textsuperscript{1316} Second, he struggled with the fact that his Lizards seemingly accumulated much more fat than needed during hibernation which raised the question how the calculation looked like with summer animals.\textsuperscript{1317} The last major section picks up the question of biological meaning, emphasizes the found constancy but exceeds the mere results by putting them into perspective with the findings obtained by other authors. In doing so, the paper ends with a feeling of uncertainty: The CO\textsubscript{2} values Kramer had obtained were too low in comparison to those found by others and Kramer’s first reaction apparently was to think about the relevance of the factors “season” and “temperature”.

I have argued that G. Kramer’s research on gas exchange and metabolism marked a paradigmatic shift in his scientific development because they indicate the point when his scientific interests merged into a heterogeneous formation. This can be proved by pointing out the heterogeneous realms themselves or by revealing possible repercussions to the inside. The latter aspect, in this case, becomes manifest as a loss of structural variety. That is to say, in contrast to Kramer’s dissertation thesis in which eventually the entire main part was not structurally identical with the epistemic pattern of the paper as a whole, the “Introductory Sections” in “Der Ruheumsatz von Eidechsen” fulfil this request. This can be proved easily by examining the order of the two chapters in which Kramer outlines his methodology. Thus in the chapter with the title “Technik” he gives us a meticulous account of the apparatus with which he measured the gas-exchange ratio.\textsuperscript{1318} In “Erzielung des Ruheumsatzes. Einfluß der CO\textsubscript{2} Konzentration” he discusses measures to calm down the experimental animal and comes to the conclusion that neither narcotization nor lesion is as adequate a means as the performing of the experiment by night when the animals enter into a condition of natural rest.\textsuperscript{1319} As a result reasoning on methodology in Kramer’s sense turns out as a dualism of both the conditions provided by the technical apparatus \textit{and} its adequate usage as a whole, that is, including the animal to be tested.

Lastly, with a view of possible succeeding transformation processes it seems wise to clarify how the interplay of reducing and extending epistemic schemata in Kramer’s study is correlated in terms of causation. My impression thereby is that the causal interventions we know from the biography of other ethologists have not yet taken place. Quantification is still experimental in a sense of testing under controlled conditions. Observation is still linked with the kind of holism Kramer’s early papers shared with O. Heinroth’s work. It is an interesting question whether it was

\textsuperscript{1315} Ibid., 612–613.
\textsuperscript{1316} Ibid., 613.
\textsuperscript{1317} Ibid.
\textsuperscript{1318} Ibid., 601–604.
\textsuperscript{1319} Ibid., 604–605.
not this more constructive holism which prevented Kramer from realizing earlier that his data was partly flawed because of measurement errors. If we have a closer look upon the sections in which he aims to explain the too low CO$_2$ values he had obtained we might see that he, in the first place, thought about additional CO$_2$ absorption by the skin, incomplete oxidization, or some kind of equilibrium between the different states determined by the Lizard’s biological rhythms.$^{1320}$ In any case, Kramer favoured natural explanations and less the failure of the experimental setting itself (viz. an ultimate over a proximate cause). In sum, I am therefore inclined to argue that the causal architecture of the upcoming neo-Darwinian scientific paradigm to which I count Ethology – so to speak – as an early conception of an Extended Synthesis was not yet established in Kramer’s writings of the year 1934. However, we must be aware that published sources represent developmental processes with a certain delay of time.

The second paper of the series is a follow-up study of the first. My interpretation is that Kramer’s results were too optimistic as to amount of gases exchanged by the Lizards during the test. Consequently, also the extent of metabolic activity seemed to be too optimal in comparison to some morphological peculiarities (such as the amount of stored fat). In other words, Kramer’s data did not match with the Lizard’s morphological constitution. And since, in the last consequence, systematic questions were at stake – which required that the animal’s morphological shape as a whole needed to be functional – Kramer’s interest shifted to non-hibernating Lizards. Maybe, he thought that the Lizard’s morphology would become more comprehensive if the values of hibernating and non-hibernating animals were taken together and considered as a whole. In other words, the paper Kramer published under the title “Weitere Untersuchungen über die Umsatzgröße von Eidechsen, insbesondere ihre Abhängigkeit von der Temperatur” (1935) may be read as the attempt to take into account all those factors related to the experimental animal which to correct was necessary in order to obtain a comprehensive picture. In concrete the paper begins with a definition of the so-called temperature coefficient, mentioned measurement examples of both Lizards and a toad only to conclude that the derived parameter has a species-specific character.$^{1321}$ According to Kramer, this result makes interspecific comparisons more difficult.$^{1322}$ Then Kramer adds the results of his experiments with summer animals.$^{1323}$ The average quotient of O$_2$ consumption and size of body surface reveals a relatively drastic increase. In addition, he thinks it possible that a certain amount of CO$_2$ might be absorbed by the skin of the animal. Beyond that, Kramer explained this lack of carbon dioxide with an erroneous disappearance (“fehlerhaftem Verschwinden”) and confirmed this hypothesis with a blank experiment.$^{1324}$ Due to the increased O$_2$ consumption, Kramer argues, the respiratory coefficient had to be conceived even lower than in the preceding study. The oxygen values (which had been the basis for his metabolic calculations) remain untouched by this result. Finally, G. Kramer felt compelled to

$^{1320}$ Kramer, “Der Ruheumsatz von Eidechsen”, 610, 613.
$^{1322}$ See ibid., 44–45.
$^{1323}$ See ibid., 45–46.
$^{1324}$ See ibid., 46–47.
add a correction of a general kind, too. If an animal breathes within a closed respiratory chamber, he argues, not only the respiratory quotient changes but also the absolute volume of enclosed gases. This increase of the absolute amount of enclosed gases must be taken into account when calculating the changed proportions at the end of the respiratory experiment. If this aspect is considered rightly the values for \( \text{O}_2 \) consumption still increase. The proportion of \( \text{O}_2 \) and \( \text{CO}_2 \) changes even more critically. In conclusion, Kramer’s follow-up study mentions four sources of potential error which might be able to explain the partly questionable results of his previous paper: The species-specific character of the temperature coefficient and thus the decreased applicability of interspecific comparisons, the increased \( \text{O}_2 \) consumption of non-hibernating animals, thus the lowered carbon dioxide proportion and therefore the possibility of erroneous disappearance of gases, the possibility of further absorption / retention by the animal and, finally, a general calculating error. On closer inspection at least three sources of error seem to have the same effect: They lower the absolute value of the respiratory coefficient by increasing the amount of oxygen, while the proportion of carbon dioxide apparently remained on its low level. In sum, the experiments with non-hibernating Lizards therefore did not exonerate the previous study but, quite the opposite, made the question of measurement errors even more pressing. To raise the question of knowledge organization seems a more difficult undertaking in this case. Two readings seem to be possible in principle. On the one hand, the paper can be taken as an independent study and thus can be read as an expression of G. Kramer’s self-critical understanding of research which, despite the pressing open questions, is capable to generate heuristic certainty on higher levels. On the other hand, however, it is possible to read the paper in connection with the first study of the series – as might be indicated by the title “Weitere Untersuchungen [...][1]. In this case also the epistemic scheme of the paper as a whole changes its character and indeed may turn out to be an accumulation of errors finally reaching a point of obvious certainty, namely the fact that measurement failures might be involved. I’d like to leave the question open at this point and think the answer lies in the order of the single parts of the study. Thus it might be argued that chapter one creates a mathematical size (the temperature coefficient) in order to obtain a phylogenetic principle. In chapter two and four the extension of the oxygen intake corresponds with a reduced carbon dioxide proportion. In chapter three the same effect is achieved by a preceding absorption of carbon dioxide by the animal.[2]

To deal with the problem of accuracy in measurement was the purpose of G. Kramer’s joint study with H. Wollschitt. I treat the study as representation of a separate realm of G. Kramer’s scientific orientation of the mid-1930s. I think, it is not commensurable with both preceding papers on gas exchange and metabolism. There are at least three arguments for this decision. At first, \( \text{Verbesserungen und} \)

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1325 See ibid., 47–48.
1326 In addition, I think it possible that \( \text{Weitere Untersuchungen} \) might be the first paper where we can observe indicators of Kramer’s upcoming shift to a neo-Darwinian framework. For instance, while the notion of carbon dioxide absorption still conveys the old causal architecture, the idea of oxygen \( \text{intake} \) might not. And what about the semantic connotation of the idea of emitting exhausted gases?
Intellectual Life-Histories

Vereinfachungen in der Gaswechselmethodik, as already mentioned, is a cooperative work and as such it is more difficult to determine G. Kramer’s part of the paper. Second, the study is mostly indifferent to the question of choosing an adequate experimental animal since it is mainly concerned with technical details of the apparatus. However, in a particular section nearing the end of the paper the authors add experiments with albino rats. As to the usage of characteristic experimental animals one may therefore say the study is either indefinite (since concerned with technical issues) or uses an untypical scientific object. Finally, and eventually most important, the epistemic character of the experimental apparatus which is treated in the current study has changed qualitatively. While Kramer’s previous gas-exchange analysis were carried out with a closed respiratory system, the new model turns out to be an open respiratory system. That is to say, whereas the former of the two models consisted of a closed chamber, the new experimental device allowed a constant perfusion with respiratory gases. In general, Verbesserungen und Vereinfachungen includes an introduction of the new device, the discussion of some aspects of its usage and, beyond that, the attempt to “calibrate” the apparatus by carrying out experiments with a scientific object used by other researchers for the sake of establishing comparability. Altogether the paper thus was aimed at establishing one common basis that guaranteed the mutual exchange of research results and their comparability beyond the own institute. The almost behaviourist inclination to find one principle or one technical norm and use one animal for all research is even mirrored in the title. It reads “Improvements and Simplifications” in this linear order and not the other way round. Moreover, both terms use the plural form which can be read as a sign for the quantitative nature of the paper. Finally, the term “Gaswechselmethodik” (“lit. Gas-Exchange-Methodology”) combines both a notion of permeability and the idea of reducing complexity which is usually part of any kind of methodological reasoning. Both scientific practices, improvement and simplification, therefore can be referred to one and the same subject, the methodology of gas-exchange analysis, but there is also a more specified reading: The improvement refers more to the gas-exchange analysis and its technical preconditions while the methodology is the domain where reduction of complexity primarily takes place. If I was to translate the branching root of the study into a binominal diagram it would look like the following (Fig. 2.21).

The basic idea of the graphic is that G. Kramer might have applied the ideas of “improvement” and “simplification” recursively on various levels and segments of his argumentation. For instance, it is usually the final concluding parts of a paper which provide some kind of simplification, while the main parts ought to include some sort of scientific progress. Most likely it is a speciality of Kramer’s and Wollschitt’s paper that this double-logic also applies to the main parts of the study. The very first sentence of the paper reads:

1327 For the information that previous experiments were performed with a closed respiratory chamber see Kramer, “Der Ruheumsatz von Eidechsen”, 601. For the description of the new model as “open respiratory system”, see Kramer et al., “Verbesserungen und Vereinfachungen in der Gaswechselmethodik”, 386, 389.

1328 Eventually to avoid the problematic of general volume increase discussed in the “Berichtigung” of the previous paper.
Fig. 2.21

G. Kramer, *Verbesserungen und Vereinfachungen der Gaswechselmethodik* (1935), Alleged Order
Nachdem durch Carpenter die Technik der biologischen Gasanalyse eine so hohe Steigerung der Feinheit und Zuverlässigkeit erfahren hat, daß sie bei weitem allen zur Zeit an sie gestellten Anforderungen entspricht, würden wir es für überflüssig halten, uns über diesen Gegenstand zu äußern, wenn wir nicht glaubten, für den von uns neuerdings benutzten Apparat den Vorzug größerer Einfachheit und Billigkeit beanspruchen zu können.

After the technique of biological gas analysis has experienced such an increase in precision and reliability through Carpenter that it is by far capable to meet all the requirements made on it at the time, we would consider it superfluous to comment upon this issue if we did not believe that we could not claim an advantage of simplicity and cheapness [also connoted: “appropriateness”][1] for the device recently used by us.]

We see how the introductory section expresses the dualism of improvement and simplification in itself or some parts within itself and, beyond that, applies it to the relation between itself and the sections which follow. For me it is quite interesting to see that Kramer’s and Wollschitt’s narration mentions an extrinsic impulse (Carpenter’s technique) as the trigger for the study and not the critical discussion of Kramer’s own problems in achieving accuracy in his measurements. This neglect or sidelong might be counted as a clear indicator that Kramer more or less deliberately interpreted epistemic schemes. In general, the paper does not make use of headings with exception of the sections called “Zur Ventilationsfrage” (On the Question of Ventilation) and “Zusammenfassung” (Summary) so that we have to rely on performatory information while reconstructing the organization. I see mainly four aspects of methodological readjustment. At first, Wollschitt and Kramer provide us with a description of the new device and how it has been developed. From the epistemological point of view, it is important to realize that the new device is not an entirely new invention rather than the product of the modification of an already existing apparatus or – even more precisely – the results of a process of decomposition and recomposition. In other words, Wollschitt and Kramer adopted the so-called Haldanian apparatus for gas-exchange analysis, dropped the parts from which they thought they were liable to produce measurement errors and replaced these parts (which were apparently responsible for the measurement of the gas volumes) with the so-called “Toeplersche Libelle” they had taken from the old device which as a whole turned out to deliver insufficiently accurate values. In general, the mechanism to measure the emission of $O_2$ and $CO_2$ consisted of using chemicals (potash lye and pyrogallic acid, respectively a combination of the both chemicals) that absorbed the respective gases and then measure the amount of absorption-products in each case. In addition, Kramer and Wollschitt discuss in their paper the potential source of measuring error when using the gas meter actively and not passively. That means the apparatus apparently included a so-called “Gaszühr” (gas meter) which was responsible for both the production of a constant perfusion of the emitted gases and, simultaneously, the measurement of their amount. Wollschitt and

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Gustav Kramer (1910–1959)

Kramer emphasize that if this gas-meter-pump is used actively, that is, as driving force or the perfusion, it is a principle source of error within the open respiratory system. In other words, Kramer and Wollschitt supplemented their description of their apparatus with explicit considerations of the potential source of error of one of its constituents and as a result, in order to avoid the mistake, modified the experimental setting once more: They inserted a throttled blower device after the gas meter, in other words, they separated the technical functions of measuring the stream of gas, on the one hand, and the instance which guaranteed a constant stream (not so much by blowing rather than drawing the air), on the other. Now that I have described the succession of practices that led to the new device I am able to put them in a nutshell. Two major processes can be observed. At first, Kramer and Wollschitt applied the practices of de- and recomposition which resulted in a modified and refined Haldanian apparatus. In a second step, they picked one principal source of error (the gas meter) which they aimed to eliminate by separating the measuring from the driving function. All further considerations are less concerned with the technical device itself rather than its application. Thus, Kramer and Wollschitt elaborate upon a special feature of open respiratory systems, namely the “Question of Ventilation” and their potential liability of error.\(^\text{1332}\) If I understand correctly this means that the apparatus is permanently perfused by a constant stream of gas mixture and the effect the animal produces is then measured as a deviation of this basic concentrations. This practice, however, seems to require a special skill of the experimenter, namely to be able to recognize the correct starting point of the experiment, that is, the right point of time when the output of gases has reached a new state of equilibrium after the experimental animal has been put into the chamber. The chapter with the title “Zur Ventilationsfrage” proceeds in two steps. At first, Kramer and Wollschitt make some general remarks concerning the parameters this calculation of the right starting point is dependent (size of the chamber, etc.) and then add a supplementary mathematical calculation of the correct time span. “Für Stoffwechselversuche”, Wollschitt and Kramer ask,

> will man aber erfahren, welche Mindestzeit vom Einsetzen des Tieres an verstreichen muß, ehe man mit der Gasanalyse des Abstromes beginnen kann.

[In case of experiments on metabolism, however, one would like to know which minimal span of time beginning with the placement of the animal must elapse before one can begin with the analysis of the gases in the output stream.](transl. CL)\(^\text{1333}\)

If I am not mistaken, Kramer’s and Wollschitts calculation operates with the idea that in an open respiratory chamber the concentration of \(CO_2\) cannot exceed above a certain value if the influx is adjusted correctly.\(^\text{1334}\) Therefore the \(CO_2\)-emission curve of a freshly inserted animal has a limes value in relation to which the proper starting point (here a concentration of carbon dioxide) can be defined relatively and arbitrarily (that is in the same manner for all the tested individuals).\(^\text{1335}\) The start-value of \(CO_2\) concentration then can be expressed as a value of time. From my epistemological standpoint it is important to keep in mind how the argumentation

\(^{1332}\) In the following *ibid.*, 384–389.


\(^{1334}\) This value seems to be a combination of the \(CO_2\) concentration of the influx and the exhaustion.

\(^{1335}\) *Ibid.*, 385, fig. 5.
itself behaves, namely that Kramer starts with an open question that refers to the right behaviour of the experimenter and his skills in the first place, which is answered with the help of a mathematical calculation in the second place. The paper finally ends with the description of model experiments that were carried out with albino rats. I have called these experiments “calibrating” because I think Wollschitt and Kramer chose quite deliberately an experimental animal, that is, the white rat, that was commonly used by experimental psychologists and physiologists. The experiments were therefore suitable to assess in how far the results obtained with the new apparatus matched with those published by other authors. The general epistemic thrust of the section with the paper’s final paragraphs is to level out possibly existing differences as a result of measurement errors or technical peculiarities of the new model. It is therefore not an accident that Wollschitt and Kramer emphasize the more or less complete agreement of their values with the ones of others. From the epistemological standpoint this gesture includes the translation of a moment of divergence into convergence. “Vergleichen wir unsere Kalorienwerte mit denen von Benedict c.s. gewonnenen”, they write,

If we are comparing our calorific values with the ones obtained by Benedict c.s. it turns out that there is complete agreement with the results conveyed in 1934 where 3 albino rats (2 male) of a slightly smaller size than ours after \(\frac{1}{2}\) to 1 days of starvation are said to have metabolized 607, 636 and 782 cal./m\(^2\)/24 h. By contrast, the values of the year 1929 are lying slightly higher. Also our RQ.–Values show complete agreement with the one of the American author if we ignore our last experiment.

To summarize my analysis of the final of Kramer’s papers being related to metabolism and gas exchange I would like to stress my impression that the paper was primarily meant to meet the uncertainties that originated in course of Kramer’s Lizard research. These dubiousness of the values he had obtained and published in his previous two publications in the series turned out to be partly due to technical reasons. To abandon these uncertainties was the impulse for Kramer’s cooperative endeavour with H. Wollschitt that was meant to develop an experimental device which was able to guarantee a certain level of intersubjective comparability. The overall overtone of the paper slightly contrary to its own statement therefore was more to obtain heuristic certainty and less simplicity. Like in other publications of Kramer’s, the general overtone of the study seems to determine the parts and its composition. What strikes me thereby is the impressive sensitivity with which G. Kramer used spatial and temporal relations, mechanical peculiarities (e.g. sucking vs. blowing pump, etc.) and his own epistemic practices (e.g. de- and recomposition, improvement and mathematical simplification) to order his ideas so that the entire composition could obtain paradigmatic meaning. Conversely, even the smallest details seem to be charged up with epistemic value so that reading Kramer’s accounts requires an extraordinary high degree of sophistication, similar to the one we need

to understand Darwin’s writings. Taken together all the information that I was able to collect while reading Kramer’s works written while being part of L. v. Krehl’s institute I think it is legitimate to conclude that Kramer between the years 1933 and 1935 developed a “heterogeneous” scientific orientation. This becomes evident both in the combination of more or less incommensurable though mutually related research projects and the loss of structural variability within the two realms being involved. On the one side, there were his own Lizard studies that intended to combine medical research with the question of biological meaning and thus raised a series of questions concerning the accuracy of the used experimental instruments. On the other side, however, we find the attempt to meet the raised uncertainties by means of scientific cooperation and the reflected development of an alternative apparatus for gas-exchange analysis that was based not only on other epistemic presuppositions (e.g. open vs. closed respiratory system) but also was meant to meet the need for one single technical norm. Despite the “heterogeneous” character of Kramer’s scientific orientation they still staid mostly within the non-Darwinian framework of causation since the typical linkages of gradual variability and ultimate causation, on the one hand, and holistic reasoning and proximate causation, on the other, was not yet established. In other words, simplification, in Kramer’s view around the year 1934, was still an issue of mathematical effort, while improvement of the experimental situation was primarily related to making technical progress.

**Migrating to Rovigno d’Istria (1934–1936)**

Transition Two. The following period in G. Kramer’s intellectual life-history was mostly characterized by an intervention on the level of causation similar to Ch. Darwin’s so-called “Malthusian turn”. In the following I will explain why. Already in early 1934 (summer 1934 at the latest) the German biologist M. Hartmann had recommended G. Kramer for a position as research assistant at the German-Italian Research Station for Marine Biology in Rovigno (Italy). The reasons for Kramer’s move are not fully clear to me yet. Maybe, the fact that L. v. Krehl’s vision of an interdisciplinary institute was about to fail, influenced Kramer’s decision: Since April 1934 the Institute was headed by R. Kuhn deputizing L. v. Krehl who, seriously ill, finally died in 1937. O. Meyerhof, head of the Institute for Physiology, had to emigrate in 1938 as a consequence of the “Nürnberger Rassengesetze”. His institute was formally dissolved but informally perpetuated as Institute for Biology. Both positions remained vacant and R. Kuhn, for the time being, functioned as executive director of both departments – in addition to the di-

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1338 See SBB, NL 150, file 37, letter G. Kramer to E. Stresemann (03/02/1934) and also Stresemann, “Gustav Kramer”, 258.

1339 The only available document of this period, a letter of Kramer’s to E. Stresemann, is painting an ambiguous picture. Kramer acknowledges to have profited yet also in a very general sense speaks of “very bitter” experience. See SBB, NL 150, file 37, letter G. Kramer to E. Stresemann (03/02/1934) and also Stresemann, “Gustav Kramer”, 258.

rectorship of the entire institute, a position he had covered since 1934 vicariously and since 1938 with the formal approval of the senate of the Kaiser-Wilhelm Society. As a result, it is probably not quite false to say that there existed a successive concentration of power and influence in R. Kuhn’s person – someone who was, or was about to become involved in the development of chemical weapons. And although Kramer certainly could not foresee future events he might have been able to read the signs and the general trend.\textsuperscript{1341} In addition to that, Kramer’s position at the KW\textsuperscript{I} for Medical Research seemed to be more the one of a Research Fellow, financed by the “Notgemeinschaft der Deutschen Wissenschaft”, so that being appointed Research Assistant simply was an improvement.\textsuperscript{1342} The new job opportunity could have been even more attractive for other reasons such as, for instance, the advanced technical equipment of the Institute for Marine Biology in Rovigno or the availability of fresh animals as scientific objects.\textsuperscript{1343} We do not know yet for

\textsuperscript{1341} G. Kramer’s political attitude cannot be deduced from his scientific publications and to answer the question requires to take into account other more biographical types of sources. In E. Stresemann’s obituary G. Kramer is described as someone with an “extraordinary fine sense for good and evil”. See fn. 1220, page 384. Another document providing some indirect evidence for Kramer’s political attitude might be the declaration in lieu of an oath Kramer made after 1945 in favour of F. v. Medem. There Kramer underlined Medem’s anti-Fascist statements and that the Zoological Research Station in Naples had been an “anti-Fascist enclave” during the Second World War. Since Kramer himself was a member of the staff of the Naples Research Station between 1936 and 1941 this also might reflect his own political attitude – at least the way he saw himself later. See MPG-Archives, III. HA, Rep. 77, file 1, Declaration in Lieu of an Oath in Favour of F. v. Medem (10/07/1947). See also ibid., file 1, Declaration in Lieu of an Oath in Favour of R. H. Fritsch (24/07/1947). In the latter document Kramer mentions that he wasn’t member of the NSDAP nor any of its subdivisions except the NSV (National Socialist People’s Welfare) (between 1937–1941 without official function). Furthermore, he emphasizes that he had been admitted by the military government of Heidelberg as university lecturer. See to this also UAH, PA 4639, “Meldebogen auf Grund des Gesetzes zur Befreiung von Nationalsozialismus und Militarismus vom 5. 3. 1946” (03/06/1947). In a letter of recommendation R. Dohrn confirms that G. Kramer disapproved the aggressive and intolerant National Socialist ideology as well as Hitler’s politics. Instead he is said to have been attracted by the international atmosphere of the Stazione Zoologica and that his personality was characterized by the appreciation and the understanding of otherness and foreign people. See UAH, B-6779/2, letter [?].\textsuperscript{3} Rupp to Provost of UH (19/07/1946), incl. R. Dohrn, letter of recommendation (01/07/1946). After the war, in the 1950s, the subject how to deal with researchers implicated with National Socialism became a matter of discussion between G. Kramer and E. Stresemann. While Stresemann seemed to have preferred a more rigid course, Kramer argued that a scientific community should not evaluate more sensitively a researcher’s political sins of the past than the rest of the public community. From this correspondence it can be eventually inferred that both Kramer and Stresemann had shared a latent but decidedly anti-National Socialist attitude. See MPG-Archives, III. HA, Rep. 77, file 5, letter G. Kramer to E. Stresemann (21/04/1951) and ibid., file 5, letter E. Stresemann to G. Kramer (25/04/1951).

\textsuperscript{1342} The German version of G. Kramer’s CV does not include any information concerning the formal title of his position at the KW\textsuperscript{I} for Medical Research. In the English version it reads: “1933 assistant at the ‘Kaiser-Wilhelm-Institut für medizinische Forschung (Institut für Pathologie)’. Work on metabolism in poikilotherms: relation of production of energy to size of the animal, temperature relationship of \textit{O}_2-consumption”. The position in Rovigno is also called “assistent” in the latter source. See MPG-Archives, II. HA, Rep. 29, Nr. 1, “Lebenslauf” and “Curriculum Vitae of Dr. Gustav Kramer” (ca. 1959).

\textsuperscript{1343} For some more details concerning the institute see J. Hämmerling. “Das Deutsch-Italienische Institut für Meeresbiologie zu Rovigno d’Istria”. In: Die Naturwissenschaften 29.32/33 (1941), 500–503 and D. Zavodnik et al. “The 110th Anniversary of the Marine Research Station at Rovinj (Adriatic Sea, Croatia). Reference Collections”. In: Natura Croatica 10.1 (2001),
certain Kramer’s motives to move to Rovigno. What we can keep in mind is that the change of research institutes once more seems to be correlated with a major epistemic shift in G. Kramer’s scientific development. It should be treated as an open question whether or not this is a more general principle.

When I, in the following, analyze the studies G. Kramer carried out while being associated with the German-Italian Institute for Marine Biology it is important to keep in mind that this publications represent Kramer’s scientific development with some delay in time. Thus we are informed in E. Stresemann’s obituary that Kramer spent ca. two years in Rovigno, between 1934 and 1936, before he moved to the Naples Zoological Research Station. However, if we have a closer look upon his bibliography we can see that all papers published in 1937 and 1938 (1936 and 1939 is unfortunately not represented) mention the affiliation with the institute in Rovigno. Depending on the point of time each paper has been actually written.

53–60. J. Hämmerling, the author of the former of the two accounts, was nominated director of the institute in 1940 and later became director of one of the five departments of the Max-Planck Institute for Marine Biology in Wilhelmshaven which was founded in 1947 / 1948. Hämmerling’s department in the newly founded institute at the North Sea coast was considered to be the legal successor of the German part of the Institute in Rovigno which had been founded in 1891 as “outpost” of the Berlin Zoological Garden and its aquarium, had been integrated into the Kaiser-Wilhelm Society in 1911 and had been passed into Italian ownership after the first World War before it was continued on basis of a German-Italian cooperative agreement as joint research institute since the year 1930. The heads of the other departments of the new institute in Wilhelmshaven next to J. Hämmerling were G. Kramer, E. v. Holst, H. Bauer and, finally, A. Bückmann. K. Lorenz’s department which was temporarily established on the estate of Baron v. Romberg in Buldern (Westphalia) was formally attached to the Wilhelmshaven institute later in July 1951 before the departments of E. v. Holst and K. Lorenz finally were hived off in form of the newly founded MPI for Behavioural Physiology in 1954 (date of the move to Seewiesen 1957). For the very long institutional tradition and its origins in Rovigno see Kazemi, “Eine Gründung in schwerer Zeit”, here especially 345–346 and E. Henning et al., eds. Chronik der Kaiser-Wilhelm- / Max–Planck–Gesellschaft zur Förderung der Wissenschaften 1911-2011. Daten und Quellen. (100 Jahre Kaiser-Wilhelm- / Max–Planck–Gesellschaft zur Förderung der Wissenschaften Teil I). Berlin: Duncker & Humbolt, 2011, 332, 350, 374, 385, 389, 390, 391, 416. For the old plan to establish an institute for Kramer, v. Holst and Lorenz see Archives of the Max-Planck-Society, Berlin [quoted as: MPG-Archives]. Erich von Holst Papers [quoted as: III. HA, Rep. 29], file 320, letter E. v. Holst to A. Kühn (13/11/1950) and ibid., file 320, letter E. v. Holst to A. Kühn (11/02/1952). For the integration of Lorenz into the MPI for Marine Biology see particularly ibid., file 182, letter E. v. Holst to O. Hahn (11/12/1950). For the separation of Lorenz’s and v. Holst’s department from their mother institute see ibid., file 183, letter E. v. Holst and K. Lorenz to O. Hahn (05/09/1953). For the founding of the MPI for Behavioural Physiology see ibid., file 3, ms. “Vorschlag zur Gründung eines Max-Planck-Instituts für Verhaltensphysiologie” (12/10/1952).


we might therefore have to date back the epistemic shifts these studies express. The publications of this period show a more heterogeneous range of research interests. At first, we find continued the former interest in metabolism but applied to another species, the sea anemone. Then there is more classical study on locomotion and colour change in *Tremoctopus violaceus Delle Chiaje* which is a particular species of octopus. In addition, the older passion with Lizards breaks through again, first in form of more classical studies of social behaviour, reproductive biology and ontogeny, but then more and more with a focus on Evolutionary Biology.\textsuperscript{1346} Thereby it is important to realize that Kramer’s interest in evolution was primarily one in systematics, (“allopatric”) speciation and its mechanisms such as geographical isolation. A first superficial glance at his evolutionary biological studies suggests that G. Kramer had a wider understanding of the Modern Synthesis beyond its core theorems, gradual heritable variability, natural selection, and increasingly complex phylogenetic development starting from one common origin.\textsuperscript{1347} It is also a peculiar, though quite interesting, coincidence that G. Kramer’s evolutionary biological studies of the respective period again were cooperative studies, carried out together with R. Mertens. To order these studies from a more epistemological point of view will be my concern in the following paragraphs. In doing that I will not, as usual, only reconstruct full epistemic tableaus but, with a more adjusted methodology, focus on the linkage between the levels of variability and causation. In order to achieve this objective I will give at first a brief description of each study and clarify its overall tenor, and then will try to assess in how far the neo-Darwinian causal architecture has been transformed into textual reality in each account.

\textsuperscript{1346} That Kramer drifted away somewhat from his former interest in metabolism can eventually be inferred from his hesitation to write an article for the journal “Fortschritte der Zoologie”. Although M. Hartmann formally asked, Kramer finally seems to have refused politely. See Archives of the Max-Planck-Society, Berlin [quoted as: MPG-Archives]. Max Hartmann Papers [quoted as: III. HA, Rep. 47], file 797, letter G. Kramer to M. Hartmann (06/12/1935) and ibid., file 797, letter M. Hartmann to G. Kramer (20/12/1935).

\textsuperscript{1347} How this hypothesis needs to be refined will become clear in the following parts of my thesis.


do with a piece of research of another more physiological kind. The experimental core of the study itself – next to the canonical parts “Material, Methodisches” and “Zusammenfassung” – consists of four sections two of which are related to gas-exchange analyses, while the remaining elaborate on aspects of metabolism and, as a result, coincide more with the paper’s overall theme (as named in the title). These four part-themes are (1) the sea anemone’s oxygen consumption (which allowed to determine the respiratory coefficient), (2) the question whether the respiratory activity can be increased through additives such as glucose, lactic acid, and pyruvic acid, (3) the question how much CO$_2$ is emitted with and without glucose additive and lastly (4) the identification of the anaerobically produced fission products. Each of these sections including the introductory part has not only its own characteristic inner composition but also a typical causal overtone, that is to say, whether the respective topic is treated in terms of proximate or, conversely, ultimate causation is not arbitrary. When I use the concepts of “proximate” and “ultimate” it is important to keep in mind that they are used as abstractions in biological narrations and as such encompass a wider range of sometimes even more metaphorical phenomena. For instance, which substance an organism consumes and which is “emitted” has a causal connotation just in the same way as whether a living organism adapts to its environment or, conversely, it is the environment that “inscribes” itself within the organic constitution of a living being, to put it metaphorically myself. It is not quite a simple undertaking to find a common denominator for these organism-environment relations and, even more difficult, to find a proper and comprehensive word for them. In any case, it must be kept in mind that organism-environment reference systems establish a dimension of behaviour which is independent from the level of variability (which becomes manifest, for instance, in nature-nurture issues) and the question of a behaviour’s complexity (which I used to call the anthropological dimension of behaviour). The reason for this claim for independence is simply a historical one, namely the fact that since Darwin at the latest the reference systems on each level of behaviour must be accounted for as freely combinable with each other theorem on any other level of a scientific paradigm. If we would like to find a geometric correlate or translation of this notion we may use the concept of space and, in doing so, claim that we can only speak of an independent “dimension” of space when each point in any chosen dimension (for the sake of clarity here also any “axis” in a system of coordinates) is freely combinable with any point in any other dimension. Asides the fact that the geometric code restricts our perceptibility to the notion of a three-dimensional space we can see very well that the idea of an increasing number of “dimensions” is closely linked with a notion of arbitrariness and relativism. G. Kramer’s studies, since his Rovigno period, reveal a transposition of epistemic reference systems on the level of causation which is not dissimilar to the one Darwin’s theorizing in his so-called notebook program underwent one time layer before. In Kramer’s sea anemone paper this begins already in the introduction with some remarks concerning the choice of the experimental animal. To put it provocatively: While Amphibia, Reptiles and Mammals function as a whole that is when the entire organism is kept intact, a see anemone can be cut to pieces and still live. Moreover, those body parts which seem to be suited best for a study of
metabolism can be picked and treated in an isolated way. Kramer apparently chose the tentacles because their thin-walled anatomy and thus the increased permeability of their membranes let them appear as highly promising object of metabolism research. “Dank der geringen Dicke ihrer Gewebeschichten”, Kramer underlines, eignen sich die handschußfingerartigen Tentakel von *Anemonia sulcata* sehr gut zu Stoffwechselversuchen, bei ihrer Kleinheit zudem besonders für die manometrische Methode, die hier ausschließlich Anwendung fand, soweit es sich um Gaswechselversuche handelt. Dazu kommt ihre Eigenschaft, im isolierten Zustand tagelang zu überleben, so daß einige Stunden nach dem Abschneiden die Intensität des Stoffwechsels nur in völlig zu vernachlässigendem Maße absinkt.

[Thanks to the small thickness of its tissue layers the glove-finger-like tentacles of *Anemonia sulcata* are suitable very well for experiments related to metabolism. To this is to be added their characteristic to survive in a state of isolation for days, so that some hours after cutting them off the intensity of the metabolism decreases only to a totally negligible extent.]\(^{(1350)}\)

Finally, Kramer’s scientific objects were available in masses, showed hardly any individual differences, and therefore could be examined in parallel experiments.\(^{(1351)}\) In other words, Kramer’s remarks concerning his choice of the sea anemone as experimental animal show that he combined an atomistic stance with the question of suitability (which is an ultimate question). And this linkage is a new quality which marks an epistemic shift in comparison to his previous works and turns out to be the first step of his metamorphosis to a neo-Darwinian thinker. The understanding of methodology must have changed simultaneously: Thus, in contrast to earlier respiratory experiments the tests with *Anemonia sulcata* took place in a liquid environment (viz. under water, in sea water). Beyond that, Kramer manipulated the natural oxygen concentration in the sea water by using what he called “Bombensauerstoff” that is pure aeriform \(O_2\).\(^{(1352)}\) Additional shaking guaranteed higher rates of oxygen supply. The test itself consisted of comparing the concentration of the respiratory gases in the water before and after the *Anemonia sulcata* (its tentacles respectively) was / were put into the container and kept breathing for a certain period of time. In sum, we may say that Kramer’s methodology in his sea anemone study appears to be more manipulative, in particular, as to the intake of \(O_2\). It certainly makes a difference (also from an epistemological standpoint) whether an animal is examined in a closed respiratory system (which in fact leads to a deprivation of oxygen), or in an open respiratory system (which is based on free absorption) or, finally, the experimenter uses a so-called “manometric” approach: That is the measurement of volume changes after having increased the pressure in a chamber and / or the concentration of one or the other gas. Measuring the oxygen consumption and calculating the respiratory quotient was the first analytical step.\(^{(1353)}\) From the epistemological standpoint it is important to realize that the \(O_2\) consumption refers to an absolute value, whereas the respiratory quotient is a relative physical size or variable. And here also I see a different quality of Kramer’s research with

\(^{(1350)}\) Kramer, “Untersuchungen über den Stoffwechsel der Seeanemone”, 163, also 174.

\(^{(1351)}\) Ibid., 166, 167. G. Kramer simply numbered the specimens such as “Anemone ‘I’”, “Anemone ‘II’” and so forth (Ibid., 167, 169).

\(^{(1352)}\) Ibid., 164–165.

\(^{(1353)}\) Ibid., 166–167.
Sea Anemone in comparison to the results of the earlier studies. While the Lizard’s metabolic activity (including respiration) had turned out to be dependent from natural factors such as seasonal rhythms and temperature, these factors now turned out to be more or less irrelevant. By contrast Kramer’s focus shifted to the organism’s nutritional condition and this, I believe, also implies a modified affiliation with causal terms. “Ich erwähne nur”, G. Kramer claims,

|くだ| eine Beziehung zwischen Größe des Sauerstoffverbrauchs und Jahreszeit oder Durchschnittstemperatur, bei der die Tiere gehalten wurden, nicht festgestellt werden konnte, verweise jedoch auf S. 167 unten ff., wo die Abhängigkeit vom Ernährungszustand behandelt wird. 

[I mention only that a correlation between the amount of oxygen consumption and the season or the average temperature with which the animals were kept could not be made evident. Yet I would like to refer to the bottom of page 167 and the following pages where the dependency from the nutritional condition is treated.]

My argument now is, that the “nutritional state” implies another, more proximate, form of causation, whereas causal parameters such as “season” and “temperature” refer not only to the activity of the organism as a whole but also more natural and therefore ultimate forms of causation. The causal “vector” either points from the outside to the inside (nutrition) or, conversely, from the animal into its environment (e.g. adjustment through biological rhythms). It is the measurement of the respiratory quotient (RQ) which allows to make use of the advantages of the experimental animal, that is, parallel measurements. “Für die Bestimmung des respiratorischen Quotienten kam die älteste, von Warburg angegebene Methode in Anwendung”, Kramer says and continues:

|V on 3 Gefäßen dient das eine zur Bestimmung des O₂-Verbrauchs, das 2. zur Bestimmung der zu Versuchsbeginn, das 3. der zu Versuchsende austreibbaren sowie der während des Versuchs frei auftretenden CO₂ [Menge ?]Cl. Voraussetzung ist die gute Vergleichbarkeit sowie die quantitative Bemessung des Materials; ersteres ist in zufriedenstellendem Maße der Fall, letzteres wird durch Wägen erzielt. 

[For determining the respiratory quotient the oldest method, i.e. the one provided by Warburg, has been applied: Of the three basins the first served to determine the O₂ consumption, the second to determine the [amount of] Cl CO₂ at the beginning of the experiment, and the third for the [amount of] Cl CO₂ at the end of the experiment and the CO₂ that appears freely during the test. A precondition for that is the good comparability and the quantitative measurability of the material. The former of the two is the case to a sufficient extent, the latter is achieved by weighing.]

In addition to that, I believe, determining the RQ in sea water included a more ecological component as well. While the medium air seems to be more uniform, the medium sea water seemed to be more specific as to the geographical location (e.g. because of changing pH-values) so that calculations needed to be adjusted. This would mean that the respiratory quotient for animals living in sea-water turns out to be an ecologically determined size, at least as to its calculation. My argument is, if the respiratory quotient is not only dependent on the physical conditions of an organism (nervous system, shape of organs etc.) but also from the environment (the sea water) then it obtains another connotation in terms of causation: It shifts

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\[1354\] Ibid., 166.
\[1355\] Ibid., 166–167.
from a proximate to an ultimate biological entity or size. Next to the calculation of the O₂-consumption G. Kramer asked whether the respiratory activity could be increased through additives. In doing so he tested three substances, glucose, lactic acid and pyruvic acid, two of which were acids, as the name tells, and one an organic compound. The two mentioned acids are also two decomposition products which originate during metabolism. Thus they are also bearing another epistemic connotation, in a sense of being dysfunctional or being a "waste product". The result was that adding glucose increases the respiratory activity but that the rate of increase is dependent in a non-trivial way from the time span the organism had starved before. Moreover, Kramer found out that lactic acid increases the respiratory activity definitely, whereas the tests with pyruvic acid led to indefinite and complex results: Initial acceleration was followed by stagnation and physically conditioned decrease. G. Kramer deduced this decrease from the harmfully stimulating effect of the added substance. In sum, like in other subsections the interplay between different epistemic patterns (including the establishment of paradox and tautological semantic relations) is paralleled also here on the level of causation so that the neo-Darwinian causal architecture is substantiated: Stagnation is harmful / dysfunctional, while variability turns out to be a result of the organism’s adjustment to its environment (proved by reactions to added substances). The final two sections of the experimental part of the study which are concerned with particular aspects of metabolism seem to support this result. According to G. Kramer’s account, the amount of measured CO₂ (without and with glucose additive) show that the Sea Anemone under anaerobe conditions metabolizes only a small fraction of the available amount of oxygen. “Eine Überschlagsrechung zeigt”, Kramer writes,

daß dementsprechend die anaerobe Energieproduktion auf wenige Prozent der aeroben gedrosselt ist. Anemone ist also obligatorischer Aerobiont.

[A short-cut calculation reveals that the anaerobic production of energy is throttled to a few percent of the aerobic one. Anemone thus is an obligatory aerobe.] (transl. CL)

The quotation shows that G. Kramer interpreted the respiratory habit of the Sea Anemone in terms of the animal’s biological fitness. Two modes of energy production (metabolism) are distinguished, that is, under aerobic (using O₂) and under anaerobic (not using O₂) conditions. Only one of them, the aerobic one, turns...

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1356 This question exactly refers to the ecological character of the respiratory activity. Do organisms adjust to their surrounding environment?
1358 That is, the potential to increase stagnates after several months of starving although usually the increase rate is dependent mostly on the basic value, that is, the increase is proportional to the extent of starvation. Kramer writes: “Es wiederholen sich also dieselben Verhältnisse wie bei ‘I’, auch der merkwürdige Umstand, daß beim sehr lang hungernden Tier die Steigerungswerte sich denen des kurz vorher gefütterten Tieres annähern” (Ibid., 169). Although Kramer does not draw a definite conclusion the result can be interpreted as such that the organism eventually adapts to the situation of starvation, eventually even in a malfunctional way. For instance, it is a well known phenomenon that starving organisms, after some time, begin to live from autologous reserves or even own tissue.
1360 Ibid., 171.
1361 Biologists distinguish between organisms which use oxygen for metabolism, the so-called...
out to be an efficient way in case of the Sea Anemone. The final section of the paper’s experimental part is concerned with the waste products of the Sea Anemone’s metabolism and their identification. This and the fact, that Kramer’s account focuses on anaerobic metabolism reveals the causal implications of the section. Kramer thus, in a first step, wants to clarify whether the $CO_2$-value measured at the end of each test is the product of the organism’s direct emission or, conversely, the indirect product of a secondary reaction in the sea water with what Kramer calls “eine fixe Säure”.\textsuperscript{1362} The concepts “direct” and “indirect” have causal implications ever since. Direct causation is proximate, indirect causation ultimate. Kramer favours the latter explanation and refuses the former possibility.\textsuperscript{1363} In a second step, he elaborates on further leading tests with tentacles of Anemonia (“Approach 1”, “Approach 2”, “Approach 3”) to identify the fission products. The tests showed that Sea Anemones make use of anaerobic respiration because lactate, the typical fission product, was built. The oxidation of this lactate however produced more $CO_2$ than would be expected if the lactate was the only existing waste product. As a result, Kramer argues, there must be another type of fission product which he has not identified yet. From the epistemological point of view, it is important to notice that the account remains open at this point. These final parts of the section on fission products are functional in as much as they confirm a hypothesis. But they take a paradox position within the entire frame because it is concerned with waste products. To sum up my analysis of G. Kramer’s Sea Anemone paper I’d like to emphasis that it is eventually the first paper in the entire series of published sources which reveals the neo-Darwinian causal architecture. This, I think, becomes evident in all the part-sections of the paper, that is, in the choice of the experimental animal, the re-conceptualization of the respiratory quotient as a more ecological quantity, the intention to prove the organisms adaptability / responsiveness to additional substances and, finally, the idea of applying an analytical procedure to dysfunctional phenomena (here the waste products of the metabolic reaction). In other words, the intervention on the level of causal reasoning Kramer’s work experienced since his move to Rovigno both asked for another scientific object and generated a model of causal analysis that fitted perfectly well to the analysis of metabolic reactions: The basic epistemic scheme underlying any chemical decomposition is that an ordered molecule structure disintegrates into different constituents while releasing energy and, in doing so, changes into another state of entropy. In a neo-Darwinian’s view this energy has functional value since it maintains the vital function of living cells within an organism.\textsuperscript{1364} His sea anemone study thus was most likely the first step of G. Kramer’s metamorphosis to a neo-Darwinian thinker. This result raises the question what gave the impulse for this shift. I cannot be sure but we know from other


\textsuperscript{1363} Kramer, “Untersuchungen über den Stoffwechsel der Seeanemone”, 171, also 170, fn. 1.

\textsuperscript{1364} Ibid., 172.

It is important to note that G. Kramer’s understanding of causal analysis, although it developed simultaneously, is not identical to the one applied by other classical ethologists when they translated disorder into order, for instance, in their deprivation or discriminatory experiments.
life histories (N. Tinbergen, E. v. Holst, J. Huxley) that the physically perceived experience of the failing of what was conceived naturally functioning before may have given an impulse. In E. v. Holst’s case, I think, his heart condition might have played a role. In N. Tinbergen’s, J. Huxley’s and also Ch. Darwin’s case we know that they experienced mental depressions. From these instances we may infer with some caution that we might have to do, at least partly, with an acquired disposition of physico-mental character. Whatever this factor x in G. Kramer’s life was is unknown. The need to revise his views in his studies on metabolism in Lizards (i.e. to have generated “false” or “erroneous” results) could have played a role as well as his immediate confrontation with the consequences of the National Socialist Dictatorship for the sciences. Another reason for Kramer’s move could certainly lie in the impacts his new research environment provided. This raises the question not so much for the scientific transfers that were allowed to happen in the German-Italian Institute for Marine Biology in Rovigno but more whether, why and how the contact with other scholars and researchers could have generated an epistemic shift of this kind. At this point it would be nice to have more archival sources capable to mediate between the mere scientific output of a researcher and the observable structural shifts becoming evident in these manifestations, on the one hand, and the causes of these shifts, on the other hand – even in case they have the character of induced or evoked causes.

The paper with the title “Einige Beobachtungen an Tremoctopus Violaceus Delle Chiaje” (1937) is a brief accumulation of observational data published in the Note dell’ Istituto Italo-Germanico di biologia marina di Rovigno d’Istria. The origin of the study was an accidental event. Fishermen, Kramer reports, brought living and dead *Tremoctopus violaceus* to the research station in July and August 1936. That is the scientific object of the study was neither chosen nor actively collected. Kramer’s observations finally led to some new insights, in particular, as to the loss of the so-called umbrella membrane. The paper includes mainly four bits of information: Thus in a first section G. Kramer takes into account the aspect of colour change and its behaviour in general. Then he elaborates upon shape and appearance of the so-called “umbrella membrane”. The following paragraphs treat ontogenetic aspects of the membrane, in particular the fact the adult animals
under certain circumstances slough off this part of their body. A final section elaborates upon the so-called spawn clump (“Laichtraube”) that has been detected in some of the caught animals. Two of these parts, one and two, are concerned with morphological and behavioural aspects, while the latter two refer to ontogeny and reproduction and therefore are more related to the idea of “development”. Do these parts contain any information concerning G. Kramer’s understanding of biological causation? Kramer’s account on the octopus’ behaviour and colouration suggests that the two aspects subsumed under this heading are connected with quite different attributes. *Tremoctopus violaceus*’s life style is described as “pelagic”, that is, it is living in the open sea. In addition, its behaviour seems to be static so that it can be caught easily on the surface of the water. If kept in a basin their orientation behaviour seems to be anything but adjusted. “In den großen Steinbecken unseres Instituts”, Kramer writes, war das Verhalten der lebenden Stücke ebenso typisch phelagisch: sie schwammen, ungereizt, mit ruhigen Trichterstößen langsam an der Oberfläche herum, allerdings nur so lange, bis sie an die Wand stießen. Dort schwammen sie dann buchstäblich unbegrenzt, “auf der Stelle”, offenbar ohne jedes Verständnis für ein mechanisches Hindernis, das in ihrem Lebensraum nicht vorgesehen ist. Das gleiche trat in der Vertikalen ein, wenn ein Tier nach unten schwimmen wollte und senkrecht auf den Boden aufstieß. Nur ganz selten, öfter z.B. in der engen Holzbütte der Überbringer, sah ich kurze Kriechgänge auf den mit langstieligen Saugnäpfen besetzten Tentakeln. [In the large stone basins of our institute the behaviour of the living specimens turned out to be equally pelagic: without being excited in any kind they were swimming at the surface while the infundibulum was performing regular repelling motions – however only as long as they hit one of the walls. There they were literally swimming unlimitedly at the very same spot, apparently without any understanding of the mechanical obstacle that is not part of their natural environment. The same happened in vertical movements, that is, when an animal tried to swim downwards and vertically hit the ground. Only very rarely, and more often in the wooden tub of the deliverers, I saw short crawling movements on their tentacles which are furnished with long-stemmed suckers.]

Although Kramer’s account is merely descriptive at this point it shows that he was liable to take into account dysfunctional and more or less static behaviours. This is an indicator for a modified understanding of causality. The same applies to his remarks on the animals’ habit to change the colour of its membranes. This behaviour is called “eindrucksvoll” (“impressive”), that is, it is attributed with an adjective that refers to the effect of something. Moreover, according to G. Kramer’s account, *Tremoctopus violaceus* makes use of its ability to change its colour when it is stimulated. In sum, we may therefore say that Kramer picked two types of behavioural appearances: “static”, “non-stimulated”, and “dysfunctional” behaviours, on the one hand, and “variable”, “stimulated”, and implicitly “functional” (since part of the protective repertoire) movements, on the other. The description of the umbrella-membrane, Kramer’s second thematic emphasis, and the functioning of this organ proceeds from the behaviour revealed in a situation of

1370 Ibid., 7–10.
1371 Ibid., 10.
1372 Ibid., 4.
1373 Ibid.
rest to states of ever more (artificial) excitation. The octopus apparently responds to the experimenter’s stimulation by stretching the tentacles and finally revealing a conspicuous morphological pattern. Attributes referring to the level of causation (non-excitation vs. excitation) are correlated with phenomenological concepts (behavioural and morphological appearances) so that proximate causation (here the artificial stimulation) is correlated with a holistic nuance (here eventually the entire spreading of the membrane including its characteristic colour pattern). The idea of conspicuousness and self-protection establishes a heuristic tension which I have described as “Darwin’s paradox” and in course of the second half of the 20th century should become one of the driving forces in ecological theorizing. I think the following section repeats this epistemic pattern. Kramer observed that adult specimens of Tremoctopus violaceus, when strongly stimulated, repel their umbrella membrane. In other words, Tremoctopus violaceus tears off at a predetermined breaking point. This loss of an essential body organ, however, seems to be compensated by the ability to grow again. The question is: Can the loss of the membrane – a per se disadvantageous event – claim functional value on a higher level of biological conceptualization? The general tenor of G. Kramer’s answer to this question is ambivalent: His explanation is not fully ultimate since it partly relies upon the physiology of ontogenetic growth. “Man wird so zur Vermutung geleitet”, he summarizes,

däß die Spannhaut und Dorsaltentakel von Tremoctopus dauernd weiter anwachsen und von Zeit zu Zeit eine rein autonome oder durch äußere Einflüsse unterstützte Verkürzung erfahren.

[One is thus directed to the conclusion that the elastic membrane and the dorsal tentacle of Tremoctopus grow permanently and from time to time experiences a reduction either autonomously or supported by outward influences.][transl. CL]

In other words, a modern ecologist would even go one step further and try to interpret the investment of building and rebuilding the tissue of the umbrella membrane within a handicap theoretical framework as a measure for the protective value of the overall behaviour and therefore also for the selective pressure the octopus is subject of. That G. Kramer somewhat sticks to the idea of ontogenetic growth mechanisms is a very strong indicator that he, around the year 1937, has adopted the neo-Darwinian causal architecture but not yet the typical epistemic re-evaluations. The description of the spawn clumps presupposes that the examined specimens were females only. According to Kramer’s account, the clumps of eggs are attached to the body of the female Tremoctopus in a fitting way. In sum, we may therefore conclude that G. Kramer’s observations of Tremoctopus Violaceus reveal the

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1375 Please see to this my account on N. Tinbergen’s ecological turn.
1376 Ibid., 7, 8. This phenomenon is called “autotomy”. Other species than Tremoctopus violaceus reveal this behaviour as well such as the Lizards. Is it pure chance that G. Kramer very often chose experimental animals that have this feature? Or is it another expression of a more homoeostatic epistemic scheme that translates abruptly dysfunction into function similar to the one underlying the idea of chemical decomposition? Be it as it may be, the act of separation in Kramer’s account seems to be resolved in a wider functional context.
1377 Ibid., 9.
1378 Ibid.
1379 Ibid., 10.
modified neo-Darwinian causal architecture which is expressed in four different thematic (semantic) contexts. However, my hypothetical comparison with modern Behaviour Ecology suggests that one crucial epistemic step on the way to the Modern Synthesis has not taken place: Kramer has not played Newton!

The year 1937 yielded another publication which fitted in this scheme. It was concerned with the biology of pairing and the social behaviours in Lizards and has been published under the German title “Beobachtungen über Paarungsbiologie und soziales Verhalten von Mauereidechsen”. The core of Beobachtungen über Paarungsbiologie und soziales Verhalten is built by the introductory sections and two further sections which are concerned with sexual and non-sexual (social) behaviours. The introduction does not, as usual, operate with a dichotomy of “material” and “methods” but distinguishes between “Animals and their Keeping”, on the one hand, and the “Studied Responses and their General Meaning”. The latter of the two sections, again, has the character of an inventory or “canon” of behaviours. Within this section again a bifurcation is noticeable. On the one side, Kramer names two very definite behaviours namely “Imposing” and “Treading”. On the other hand, he opens the account by elaborating on “Some other Movements”. Definite naming is thus supplemented by indefinite naming. To a certain degree this epistemic scheme is repeated by the sections which are related to the two main topics, sexual and social behaviour: While sexual behaviour, per definitionem is based on the idea of a definite dyad, the two sexes, social behaviour, on the contrary, is concerned with many individuals in a community and therefore with less definite entities. The chapter on sexual behaviours, again, apparently operates with a binominal order: On the one hand, there are two sections including descriptions of concrete sex-related behaviours. They are bearing the titles “The Behaviour of Conspecifics of the Same Sex” and “The Behaviour of the Sexes During and Outside the Mating Season”. On the other hand, however, Kramer added two sections which have a more typological character. Thus he elaborates on the “Differentiation of the Sexes” and finally concludes with a discussion of “Lorenz’s Types of Pair-Building”. The section on social behaviours consists of two parts, namely the personal recognition of conspecifics and what Kramer calls the “The Partial Restriction of the Responses Towards Conspecifics”. The former of the two seems to ask for the definite part in the Lizard communities since the idea of “personal recognition” is based on perceiving another specimen as identifiable and therefore definite individual, maybe in a sense of being able to isolate this individual by means of perception. From the epistemological standpoint, this section thus operates with a paradox: The definite within the indefinite. In all, the tableau of the entire outline thus can be legitimately represented in a tree-like shape. The overall character of the study turns out to be both descriptive and observational. Moreover, the arrangement seems to reveal its

For the complete reference see fn. 1345, page 427 of my thesis. The project generated another paper with supplementary information that, according to G. Kramer’s own words, has nothing to do with the original objective of the primary study but, nonetheless, deserves to be communicated. See Kramer, “Angaben über die Fortpflanzung und Entwicklung der Mauereidechsen”, here 66. On closer inspection, the supplementary paper turns out as a study of the life-cycle mostly of Lacerta sicula Rafinesque, so to speak, from the egg to the egg. Both papers together therefore eventually build an intertextual or conceptual unit whereby the latter of the two studies seems to take a more supplementary status.

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inner logic which originates in the way the parts are composed into one whole. I suggest the following figure to illustrate the overall scheme (Fig. 2.22). My question is now, whether the parts of the binominal scheme are also interpreted in causal terms. In other words, what is the causal architecture like in G. Kramer’s study on mating biology and social behaviours in Lizards? I would like to pick out some characteristic examples. I think it is in agreement with the overall organization of the study and its introductory part that we, within this introduction, find a discussion of the used scientific objects and their keeping. The objects, that is, the Lizards, are described with mainly two attributes. At first, the different species of Lizards Kramer used are said to be closely related with each other and, beyond that, reveal similar behavioural and morphological qualities.\textsuperscript{1381} We can therefore presume that Kramer’s study is a further development of his micro-systematic interest in behaviour. Second, these objects are correlated with the scientific method of observation and less with experimentation, although the latter is present in some sections of the study. By tradition, the method of observation – independent whether it is more connected with the practice of (quantitative) description or part of a holistic natural history – is linked with the idea of ultimate causation because the observer usually “goes into” the wild and/or adjusts his practices to the object’s behaviours more or less without manipulating the circumstances. The practice of keeping animals, by contrast, is closely linked with an idea of proximate causation in Kramer’s account not only because they are cultivated in a precisely defined environment (wooden boxes of 50 x 100 x 30 cm size) but also because we are informed that Kramer has made experiments on breeding these animals.\textsuperscript{1382} We may therefore conclude that Kramer’s description of his objects and the mode of keeping them implied a dualism of causal concepts. The way of linking terms of variability and causation is typically neo-Darwinian. Moreover, it is perhaps important to note that both practices are represented in a more descriptive and introductory mode as well as Kramer perceives object and keeping in connection with each other (i.e. syntactically through an “and”-connector in the headline). Second example. The introduction of the canon of the behaviours Kramer has examined for his study begins with the following quite significant sentence:

\begin{englishquote}
\end{englishquote}

\begin{germanquote}
To avoid the difficulty, that the description of the behaviours disturbs the systematic account of the interconnections I will deal first mostly with the description of the behaviour types and, in addition, with their meaning, whereby the latter will be treated only in as much as to ascribe the described matters their location for their later usage. The types of mating and the fighting I do not consider as a part of this. By contrast some in our context not so important responses
\end{germanquote}

\textsuperscript{1381} Kramer, “Beobachtungen über Paarungsbiologie und soziales Verhalten von Mauereidechsen”, 752–753.

\textsuperscript{1382} Ibid., 753.
Fig. 2.22

G. Kramer, *Beobachtungen über Paarungsbiologie und Soziales Verhalten von Mauereidechsen* (1937), Supposed Order
The quotation includes metalinguistic information about the paper’s organization. We are informed that the account of the examined behaviour types is separated out of the succeeding systematic main section because it might “disturb” (“stören”) it. Due to the disturbing potential of this part we may consider it dysfunctional in the main part but more adequate within the non-systematic introductory framework (I consider the secluded section a part of a wider introduction). Within this behaviour typology, there is a dualism between the types themselves and their meaning. The latter of which is an extension and related to a functional perspective (i.e. refers to the communicative meaning or has metalinguistic function) but is superimposed with a notion of restriction possibly both from the outside and the inside (only the allocation of a place for certain ideas is intended). Kramer’s account reduces at this point and marks a preference: The mating and the fighting are excluded, while seemingly unimportant gestures are included. The practices of exclusion and inclusion are bearing a connotation in terms of causation as well as the question of importance. The hint on the later usage of these seemingly unimportant behaviours includes a performative cross-reference to later sections or epistemic regions of the paper. To keep the question of causation on the upper levels of the argumentation one may say the mentioned typology of behaviours itself as well as the entire section is referred to in terms of dysfunction, while the aspect of meaning has an ultimate connotation because it says something about the biological meaning or otherwise has a metalinguistic function. In the typology itself the dualism is becoming manifest in the distinction between definite behaviours (imposing, treading) and what Kramer calls “Some other Movements”. The latter part deals with “waving” and “tail beating”. The former of the two is declared socially irrelevant, while the latter is described as a sign of general excitement and is also applied towards humans. Both behaviours seem to be peripheral to the question of sexual and social behaviour – either due to a lack of communicative significance or because they have a more interspecific character. Altogether I am inclined to read the section with the title “Studied Responses and their General Meaning” as a latent mirror image of the two main sections related to sexual and social behaviour whereby the section called “Some other Movements” would refer to the section on social behaviours, however, in a rather sophisticated way, or as Kramer himself says, only insofar as to allocate a space for these two peripheral sets of questions, that is, the question of the communicative relevance of the behaviour within the animal society and the question whether a behaviour is directed towards a conspecific or addressees beyond the boundaries of the own species. That G. Kramer claims a certain relevance of these seemingly irrelevant behaviours for what he calls “Differenzialdiagnostik des Wichtigen” can be read as another expression of

1384 Ibid., 755–756.
1385 For the way how these questions are addressed in the section on social behaviour please see ibid., 780–782. Due to the complexity of the cross-reference it is therefore not quite correct to speak of a “performative coincidence”. A better description would be “performative inversion”.

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thinking in terms of mathematical limes structures in which an account approaches successively and approximatively a previously projected thesis, here eventually the micro-systematics of Lizards. However, it must be admitted that Kramer in this study fills his “Differenzialdiagnostik” with communicative relevant observations. The secluded seemingly irrelevant action patterns then would be a hint on a later rapprochement of the same theme on another stage of knowledge and with an emphasis on non-functional behaviours – hence a sort of projection.\textsuperscript{1386} And the more I think about it, the more I come to the conclusion that it is eventually Kramer’s supplementary account Angaben über die Fortpflanzung und Entwicklung der Mauerelchsen which fills this gap or allocated location with content.\textsuperscript{1387} Third example. The behaviour of conspecifics of the same sex is described in a differentiated way as well. Kramer thus introduces three categories, the behaviour of male to male, female to female and, finally amongst young Lizards. Male Lizards are territorial animals and create their dominance by imposing behaviour which consists of chasing after another rival and biting it. Only one specimen rises to become the tyrant. Fleeing stimulates further the aggressiveness of the tyrant. Although the tyrant is described as the active part, the catching has proximate connotation because it consists not simply of driving the rival from the territory but includes biting. Further, Kramer’s account may have a quasi-experimental character at this point because the fact that the animals were kept and combined in cages influenced their mode of fighting. The circumstances of the observations thus were partly controlled and the outcome of the fights was potentially deadly.\textsuperscript{1388} “Man kann also”, Kramer writes, unabhängig von der primären Kampfveranlagung der Tiere und sogar gegen sie, ganz verschiedene Gruppierungen zwischen Siegern und Unterlegenen herstellen. Als beeinflussende Faktoren erweisen sich die Eingesessenheit im Territorium und der Ausgang vorausgegangener Kämpfe.\textsuperscript{1386} The term “differential diagnosis” originally comes from a medical context and here describes a technique to identify and determine the right diagnosis in demarcation of all other possible diagnoses within a field of closely related diseases. The basic idea standing behind thereby is that different diseases can possibly have very similar symptoms thus making different diagnoses possible amongst which a gradual reduction to the correct one has to take place. Kramer’s adoption of the term shows that he conceived his micro-systematic program similar to a physician’s strategy to determine the probability of a certain disease. In both cases the idea of a recursive binominal analyses may be in the background. Kramer’s paper then could be read as the attempt to determine the right type of behaviour for micro-systematic studies by extending the range of sexual behaviours by the social ones and within this latter field to filter out (i.e. reduce) the relevant type of behaviour. The main piece of evidence for this reading is a lecture manuscript which can be approximatively dated to the year 1946. In this handwritten source Kramer draws an explicit connection between the method applied by systemtists (i.e. his favoured method) and a more pre-scientific form of aetiological intuition (i.e. his method of diagnostics). See MPG-Archives, III. HA, Rep. 77, box 1, ms. “Vorlesung über Tierpsychologie” (ca. 1946), especially lecture VIII. For further information concerning the medical concept of “differential diagnosis” see M. Döpfner et al. “Differentialdiagnose”. In: H.-C. Steinhausen et al., eds. Handbuch ADHS. Grundlagen, Klinik, Therapie und Verlauf der Aufmerksamkeitsdefizit–Hyperaktivitätsstörung. Stuttgart et al.: Kohlhammer, 2009, 249–255 and J. P. Kassirer et al. “What Is a Differential Diagnosis?” In: Hospital Practice 25.8 (1990), especially 24, 27–28.\textsuperscript{1387} This would mean that Kramer’s projection applies both within his primary account and beyond its boundaries so that both mentioned studies need to be read as intertextual unity that, as a whole, reproduced the frame of the primary study.\textsuperscript{1388} For the deadly character see Kramer, “Beobachtungen über Paarungsbiologie und soziales Verhalten von Mauereidechsen”, 761.
[One can therefore compose quite different groups of winners and losers, independent of the primary inclination of the animals to fight and even against it. Influencing factors turn out to be the extent of autochthonousness in the territory and the outcome of previous results.] (transl. CL) 1389

The spatial logic of the imposing itself, the partly manipulative character of the experiments and the relevance of previous experience show that Kramer discusses male dominance and imposing in terms of proximate causation. According to Kramer’s account, in female groups tyrannies occur more rarely but newcomers are attacked. In general, mutual habituation leads to peaceful relationships. Kramer describes the behaviours of the youngsters as more arbitrary. Chasing occurs but more rarely. From my epistemological standpoint it is important to note that Kramer’s ontogenetic perspective leads to the result that fighting differentiates sex-specifically during the youth period. He writes:


[These observations of young animals supplement in a reasonable way the idea of the conditioned character of the fighting behaviour which could be made on basis of the results with adult males and females. Fighting is inborn in any Lizard, the sexual differentiation of this behaviour constituent shapes later on. The fact that also females fight and that the fighting of the males is dependent of the season is going to be made plausible from another perspective.] (transl. CL) 1390

The causal level of the behaviour of the females and the non-adult animals is not fully clear at this point although it is included in Kramer’s intention to provide supplementary information to make a basic thesis more comprehensible. In addition to that, we might interpret the ontogenetic process of sexual differentiation in respective behaviours as process of functional differentiation on basis of one common heritable disposition. 1391 Altogether the section on “On the Behaviour of Con specifics of the Same Sex” thus seems to substantiate the neo-Darwinian understanding of causation. Forth example. The behaviour of the sexes during and outside the mating season is described from three different angles each of which is revealing its own causal structure. Thus pairing and foreplay seems to share some similarity with the males’ fights insofar as they also display imposing to females. However, this gestures, according to Kramer’s account, occur on a much lower level of intensity and, in general, the entire action pattern seems to be conceived on different epistemic grounds. While the fights between males mostly consist of chasing, biting and even killing potential rivals, the pairing is described from the perspective of the females. Their general attitude towards the male is rejection which can be overcome only temporarily by the male when it is able to grasp its partner whereby the applied biting, according to Kramer, is of a quite different kind than in case of male-male

1390 Ibid., 764.
1391 In any case the entire narrative frame seems concerned with diffuse (i.e. dissociative), hierarchical behaviour, namely biting. The final state of the second sub-frame (i.e. sexual differentiation) is also the starting point of the chapter frame as a whole.
For my argumentation it is quite important to note that it is the female sex which is attributed with the quality of “rejection”, while the male is the one who tries to catch, keep and bite. Approach and withdrawal are correlated here with the sexes in an unusual way since in many traditional narrations it is the female which is described as the conceiving sex, while the male is figured out as the one who rejects rivals and, literally spoken, penetrates the female. In other words, in Kramer’s account, the female Lizard is representing the phallic sex. The partly inversion of the sex roles is a clear narrative indicator for a modified causal architecture. The interesting aspect in all this is that researchers need to find an adequate scientific object which matches the modified epistemic deep-structure. Let’s move on a little bit within the scheme. Kramer emphasizes that females outside the mating season are treated by the males as if they were males, that is, the males display imposing yet do not make an attempt to mate. However, he has observed that new females can be integrated by habituation and that females under certain circumstances can display male behaviours or action patterns stemming from a phase before the sexual differentiation of the drive to fight. The causal level of behaviour is not very obviously articulated at this point. However, we may realize that the behaviours displayed outside the mating season are approached from the perspective of the males and the whole issue is also discussed with castrated males. Castration is an experimental technique just like Kramer’s re-grouping experiments and these experiments are followed by observations which in turn lead to a final conclusion. Hence it can be argued that there exists an epistemic scheme consisting of the experimental manipulation of the males and the observation of their behaviour against the females. In a scheme like that both the technique of observation and the role of the female have a paradox position. “Mit Rücksicht auf dies letzte, das eigentlich schon die Bedeutung einer Paarungseinleitung ausschließt, bleibt folgende Auffassung”, Kramer concludes and continues:

Da das fremde Weibchen nicht nur Träger von Geschlechtsmerkmalen, sondern auch Träger der allgemeinen Merkmale eines Artgenossen ist, so ist das Männchen zweierlei Reizgruppen gegenübergestellt, und es reagiert auf beide. Die feindselige Komponente seiner Reaktion schwindet in dem Maße, wie Gewöhnung an das neue Tier stattfindet, genau so, wie das auch außerhalb der Paarungszeit der Fall ist, wo die erste Komponente, nämlich die Begattungsabsicht, von vornherein in Wegfall kommt. Wir kommen also zur Ansicht, daß den Männchen von *L. melisellensis* und von *L. sicula* eine eigentliche Paarungseinleitung fehlt.

[With a view of the last aspect, which alone suffices to exclude the relevance of the pairing introduction, the following standpoint remains: Since the foreign female is not only the carrier of the sex-specific qualities but also the carrier of the general characteristics of the conspecific, the male is confronted with two groups of stimulation and it responds to both of them. The hostile component of its response vanishes to that extent as the habituation to the newcomer takes place, just as it is the case outside the mating season where the first component, namely the intention to mate, comes to be dropped anyway. We therefore come to the conclusion that the males of *L. melisellensis* and *L. sicula* lack a genuine introduction to the pairing.]

In sum, we may say, that the whole habituation system at this point in Kramer’s account is thought from the perspective of the male and the aspect of “excitation”

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1392 For the pairing in general and the rejection of the females see *ibid.*, 765–768, here 766.
shows the proximate connotation. As to the females’ changing readiness to mate one can say the scheme once more changes. Kramer emphasizes the general reluctance of the females but, on basis of statistical data, marks exceptions within the behaviours of the females. Since this exceptional periods are correlated with their readiness to mate the causal connotation is clear. Fifth example. The section with the heading “Die Unterscheidung der Geschlechter” (“The Differentiation of the Sexes”) – if we leap over the introductory section of the chapter and concentrate on the remaining parts – is a typical example of G. Kramer’s understanding of causal analysis since it treats two discrete sets of qualities one of which is definite, namely the red belly, while the other set turns out to be indefinite in as much as it is a conglomerate of several different unspecific characteristics. Can anything be said about the mechanism with which these two sets of stimulation are being performed by Kramer’s scientific objects. Kramer used the experimental method to determine the relevance of the quality “red belly”, that is to say, he painted the animals with nail varnish and measured the responses. The result of these tests was that red colour partly functioned as releasive stimuli but Kramer also realized the high variability of this characteristic amongst the different geographic Lizard populations of Istria. But on basis of this result Kramer concluded that the quality in question is not enough fixed to function as a “key” of an innate releasing mechanism (IRM) in the Lorenzian sense – which, as a matter of fact, also questioned the taxonomic usefulness of behaviour characters. Kramer thus considered it possible that the responsiveness of some Lizards to “red belly” might be an individually acquired association. The idea of an “ontogenetically acquired association” also includes a proximate connotation which lies mainly in the acquired character.

This passage in Kramer’s study of the pairing biology and the social behaviours of Lizards most likely marks one of the beginnings of his interest in modern Evolutionary Biology because it raised the question how deviating morphological characteristics of the different geographic varieties of Lizards correspond with their behavioural traits. Kramer’s answer to the question of how Lizards recognize the other sex in 1937 still was that there are other primary characters which enable the recognition, while the character “red” was described as secondary and individually acquired. In addition to that, he presumed the relevance of some features other than “red belly” for the recognition of the sexes such as chemical indicators or other morphological characteristics such as size of the head, size of the torso, or skin patterns. In this context, Kramer also mentions the heuristic value of erroneous identifications in case of which the Lizard’s perceptual mechanisms respond inadequately. Kramer deduces from this observation the manifoldness of the perceptory

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Ibid., 772–778.

Ibid., 775–776.

See ibid., 776. In a later passage of the paper Kramer describes this process of acquisition more precisely (Ibid., 779). According to his view, there might exist preformed gaps for supplementary self-conditioning. This is an implicit reference to what K. Lorenz called instinct-conditioning intercalation – an idea the latter had adopted from O. Heinroth who had applied though not explicitly formulated this idea.

At this point we may see how his later interest in allometry gets into the act.
mechanisms. Although he does not mention it explicitly, we can infer that these “Other Features of Sex Differentiation” are *not* individually acquired. More likely they are the result of phylogenetic adaptation simply because they *are* anatomically fixed. As a result, the internal differentiation of the section on sex-differentiation operates not only with the dichotomies of definite vs. indefinite, morphological vs. non-morphological and visual vs. non-visual characters but also with attributes that refer to the causal level of behaviour such as “individually acquired” vs. “product of phylogenetic adaptation” (less explicit). The correlation of the dichotomies and their framing substantiates my hypothesis that Kramer’s paper operates with a modified causal architecture. Sixth example. G. Kramer’s discussion of K. Lorenz’s so-called types of pair formation shows that both researchers had quite different understandings of causal analysis. K. Lorenz had defined three types of pair formation according to the fixed rules of game that regulate the interaction of the sexes in each case. According to their purest occurrence he called this types Lizard-, Labyrinth fish-, and Chromid-type. This idea is based upon an end-tautological epistemic scheme because the reaction of one animal triggers the release of a corresponding action pattern in the potential partner which in turn disinhibits an action pattern in the first animal and so forth. The behaviour thus determines the mental state which is the result of integration and coordinating the behavioural information. The works of classical ethologists such as K. Lorenz and N. Tinbergen presupposes the existence of such fixed stimulus-response-correlations on different levels of central nervous integration. At least with a view of the behaviour of his Lizards G. Kramer questioned this hypothesis. According to his account, the recognition of the other sex has already been performed *before* the reaction of the potential partner can be perceived or takes place. In other words, the behaviour of the partner is not the decisive impulse for the recognition. The response of a male Lizard to a rival, once recognized, is always the same quite independent whether this rival flees, displays imposing or responds with indifference. In other words, in Kramer’s model the primary recognition of the sex determines the response and not, as in Lorenz’s model, the behaviour the recognition. Both models are based on different epistemic presumptions. While K. Lorenz, E. v. Holst and also N. Tinbergen developed – partly influenced by Gestalt theory – a reductive model of causal analysis or nervous causation in general, G. Kramer stays within O. Heinroth’s framework and developed it further into the framework of the Modern Synthesis of Evolution, that is, more precisely, into the more original part of the synthesis. Most interestingly, and in accordance with the chapter’s outline he does not see a principal contradiction between the two models and claims they might exist parallel to each other in Lizards. He substantiates his view by referring to the works of G. K. Noble and H. T. Bradley. Although he does not fully agree, his thesis is therefore supplemented by the results of “others”. This gesture of Kramer’s shows two things: At first, we find once more an expression of his practice to overcome antagonistic scientific positions by formulating a third position which consists of a qualitatively different “both-and”. This gesture is placed at a significant position within the overall scheme of his paper. Second, his *synthesis* is of interest from the epistemological

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1400 In the following see *ibid.*, 778–780.
standpoint because it seems to think into one unified model the aspects of both the primary and the secondary orientations of the Modern Synthesis of Evolution just like Darwin combined less and more problematic fields into the core of his *Origin of Species*. Therefore if we ask for the causal architecture of this specific section in his paper we need to take into account both how the twofold mechanism of primary sex recognition and succeeding action work together in the Lizard’s mechanism to recognize the other sex and the fact that Kramer might have been a very early advocate of an *Extended Evolutionary Synthesis* that encompassed both what I tend to call the “Modern Synthesis” and the “Ethological Synthesis”. And he may have rated this “Extended Synthesis” more useful just as the Lizard’s primary sex recognition mechanism appears to be rather inadapted (as to the response of the counterpart) although the mechanism in itself is differentiated and increasingly complex. Moreover, in some subspecies of Lizard this mechanism seems to have a learnt character.\footnote{1401}{See Kramer, “Beobachtungen über Paarungsbiologie und soziales Verhalten von Mauereidechsen”, 779.} In sum, we may say the section in question interprets a specific epistemic scheme in different contexts and we can infer from the way Kramer places the quality “acquired” that the new causal architecture remained intact. Seventh example. Kramer had observed that female newcomers are treated differently both by males (more sexual attention during the mating season and more liability to fight them outside the mating season) and in female communities. This observation suggested that Lizards can recognize each other individually.\footnote{1402}{For the following see ibid., 780–781.} Kramer argues here that the stability of a social community becomes evident only in cases when it is not extended to certain individuals, that is, the unusual stands out in the usual. The unusual state thereby is associated with a state of fight which, in Kramer’s view, is caused by an over excitation which blocks the differentiated treatment and the individual recognition. The stability of a Lizard community is thus described in terms of habituation and lower levels of excitation, while the fights superimpose this former state by a more of excitation. The practice to take the maladaptive exception in order to demonstrate the rule of normal functioning is another modified circumcision of what I have called “Darwin’s paradox”. Maybe, I go a little bit too far, but Kramer seems to have put forward the basic idea of the later handicap theoretical approaches. What makes appear Kramer’s approach to paradox functioning different from later functionally upgraded versions of the frame is the prevalence he ascribes to nervous over excitation which shakes the stability of the Lizard communities from beneath. In addition to that, it is worthwhile to mention that Kramer took into account both olfactory and optical signals. In general, the dualism of non-excitement and over-arousal marks the causal level of behaviour in this section. Final example. Kramer mentions that different communities of Lizards belonging to different subspecies can coexist next to each other without interfering.\footnote{1403}{Ibid., 781–782.} The epistemic scheme of the section with the title “The Partly Restriction of the Responses Towards Conspecifics”, however, becomes evident if we realize that this general rule of coexistence experiences exceptions. The picture Kramer draws from his cage-communities thus is the one of more or less separated communities. In or-
der to explain the inhibition mechanism that prevents the individuals of one variety from attacking the individuals of another Kramer puts forward the idea of olfactory recognition. “Bei anderen Käfiggemeinschaften waren die Beziehungen nicht so getrennt”, G. Kramer writes and proceeds,

besonders war ol $\sigma^1$ oft, wenn auch gleichsam gedämpft aggressiv gegenüber sicula-Männchen. Und zwar entstand der Eindruck, daß die “Dämpfung” im letzten Augenblick vor dem Zubeißen wirksam wurde, wodurch die Vermutung entsteht, daß die in diesem Augenblick einsetzende chemische Nahwahrnehmung nochmals hemmend wirkt.

[In other cage communities the relationships were not separated so strictly, especially the ol $\sigma^1$ was often aggressive towards sicula-males, though in a subdued way. In fact there emerged the impression that the “attenuation” becomes effective in the very last moment before the bite whereby the suspicion is raised that the chemical close-distance perception which is exerted in the last moment has once more a subduing effect.] (transl. CL)

The epistemic scheme of the section is obvious. Two states are differentiated, coexistence and exceptions to this state which are the result of contacts. These contacts, however, turn out to be damped due to an olfactory close-distance perception or recognition of the otherness of the other individual which leads to the inhibition of the aggressive action pattern. For my argumentation it is important to note that closeness is correlated with a loss of aggressive excitation because the olfactory inhibition becomes prevalent.

I’d like to sum up now my analysis of G. Kramer’s study Beobachtungen über Paarungsbiologie und soziales Verhalten von Mauereidechsen. I went more into detail than it was originally planned because I realized that the study in question might be a key text in G. Kramer’s transition. In the first place, I have reconstructed a rough outline of the paper’s binominal overall scheme. In a second step, I approached the microlevel of the argumentation with a twofold purpose. At first, I wanted to see whether the organization below chapter-level supported the idea I had of the entire outline. This, I think, can be confirmed. In a second step, I was particularly interested how the various different parts of Kramer’s “differential diagnosis” are correlated with expressions of causal reasoning. Again, I think, the result seems to suggest that the text fulfils the requirements of a neo-Darwinian account as to its causal architecture. In addition to that, I reckon the paper of high importance due to its transitional character: Particularly, while discussing the mechanisms of sex recognition, Kramer enters into the field of geographic distribution of various subspecies of Lizards, their different morphological outfit and the question of behavioural correlates. His later interest in Evolutionary Biology and especially in the study of allometric relations seems to have one possible origin in this paper. Moreover, in the discussion of the three types of pair formation put forward by K. Lorenz we can see a clear indicator that G. Kramer’s way to the Modern Synthesis did not coincide with the one of other ethologists such as K. Lorenz, E. v. Holst or N. Tinbergen. While the latter put forward a reductive form of causal analysis that found its expression in various kinds of circumscriptions such as the dualism of appetite and consummatory act or the hierarchical system of instincts, Kramer’s understanding of causal analysis more staid within O. Heinroth’s framework. In concrete, this
led towards a different understanding of the Lizards’ mechanism of sex recognition (primary recognition independent from behavioural stimuli displayed by the other individual) and eventually also to a more integrated perspective upon the upcoming Modern Synthesis in the sense of an “Extended Synthesis of Evolution”. Lastly, a brief comparison with the *Angaben über die Fortpflanzung und Entwicklung der Maureidechsen*, the paper Kramer published a year later in 1938 in order to communicate some supplementary information he had sidelined in the primary study, shows that *Beobachtungen über Paarungsbiologie und soziales Verhalten* was primarily interested in functional behaviours, that is, behaviours that have a communicative meaning either within the narrower context of pair-formation or, with a wider scope, for establishing and maintaining a social structure in the Lizard communities. In *Angaben über die Fortpflanzung und Entwicklung*, by contrast, we can find a more explicit discussion of so-called comfort movements, that is, behaviours that have primarily no communicative function but instead serve to maintain homoeostatic equilibria which is the case, for instance, in thermoregulation. Altogether, I am inclined to read Kramer’s encounters with the Lizard behaviours as the attempt to leave – on basis of repeated diagnostic procedures on various argumentative levels – successively behind the idea that behaviours can be an adequate object for micro-systematic study: Kramer neither accepted Lorenz’s typology of pair formation, nor did the extended social behaviours fully prove their taxonomic value, nor could the maintenance behaviours apparently fulfil this request. Kramer’s ensuing systematic micro-studies did primarily not rely upon behavioural characters.

**R**

G. Kramer’s stay at the German-Italian Research Station for Marine Biology generated mainly three types of research work. Next to the continuing interest in metabolism and his study of certain types of behaviours (mating and social behaviour) in Lizards which I have already discussed we find also represented an advanced dedication to zoogeography, that is, the study of the geographical distribution of animal populations and animal societies. This research was carried out, too, with Lizards so that we can deduce a connection or even an intertwining with Kramer’s behaviour studies and his zoogeographical accounts. Mainly two zoogeographical studies need to be taken into account, *Rassenbildung bei westistrianischen Inseleidechsen in Abhängigkeit von Isolierungsalter und Arealgröße* and *Zur Verbreitung und Systematik der festländischen Mauer-Eidechsen Istriens*. Both papers appeared in the year 1938 but the research work they are based upon can be dated back to the years 1935 and 1936. This fact in combination with the examined geographic region, that is, the mainland of Istria and several islands just off the Istrian coast, as well as the institutional reference at the beginning of each study reveal that these studies fall into Kramer’s Rovigno period.

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1405 Kramer had this extended view in so far as he was thinking both systems of recognition coexistent next to each other and correlated with particular experimental animals each.

1406 See Kramer, “*Angaben über die Fortpflanzung und Entwicklung der Maureidechsen*”, 68.

1407 For the time frame during which the field work was carried out see Kramer et al., “*Rassenbildung bei westistrianischen Inseleidechsen*”, 190.

1408 For the reference to the two research institutions both authors were affiliated with see Kramer et al., “*Zur Verbreitung und Systematik der festländischen Mauer-Eidechsen Istriens*”, 48 and Kramer et al., “*Rassenbildung bei westistrianischen Inseleidechsen*”, 189.
ographical isolation within this process. From this particular focus we can deduce that G. Kramer, since the end of the year 1935 at the latest, had begun to develop a profound interest in Evolutionary Biology, particularly of the Lizard species. We may therefore justly argue that he contributed to the Modern Synthesis. However, especially his zoogeographical papers show that he – at least in a very initial stage of his interest in Evolutionary Biology – entered this synthesis from a specific angle: While other architects such as, for instance, R. A. Fisher, put great emphasis upon the two core theorems “genetic mutability” and “selection”, Kramer, at first, seemed primarily interested in allopatric speciation and those mechanisms being involved in this process such as geographical isolation. As a provisional result, we may therefore say that the two zoogeographical papers which originated from research projects conducted during his stay in Rovigno represented those epistemic realms of the Modern Synthesis that architects used to describe as secondary just as Ch. Darwin had conceived the core of his vera causa argumentation as a combination of both his core ideas “gradual variability” and “natural selection”, on the one hand, and some additional partly Lamarckian theorems, on the other, such as “correlation of growth” or what he called the “direct action of the conditions of life”. This means that Kramer – at least at this stage of his scientific development – was an advocate of a wider understanding of the Modern Synthesis just as Th. Dobzhansky, E. Mayr or S. Wright, who were prepared to take into account evolutionary mechanisms other than and in addition to sympatric speciation. For the time being, this leaves untouched the idea that Kramer might have relocated epistemologically his theorizing on speciation in course of his further scientific development or (on the contrary ?) might even have had in mind the integration of still wider realms including Ethology. Quite independent whether one or the other hypothesis or even both hypotheses was / were true, we would expect that Kramer’s zoogeographic papers fulfil the requirements of their epistemic placement not only with a view of their content and the theses put forward but also their way of organizing knowledge. These hypotheses are to be tested in the following paragraphs.

At first sight, it stands out that both zoogeographical papers seem to build a unit. The following arguments support this interpretation. At first, they are both cooperative studies carried out and written together with R. Mertens who was affiliated with the “Natur-Museum Senckenberg” in Frankfurt a. Main at that time. In addition to that, the reader of the studies is informed that there existed a division of

1409 Darwin, The Origin of Species, 99–100. For the restricted validity of direct environmental causes see also, ibid., 67.

labour between both authors. While G. Kramer collected the animals in Istria, R. Mertens seemed to be the one who was responsible for their conservation and morphological evaluation. Moreover, both studies seem to be related to each other from a geographical point of view. While *Zur Verbreitung und Systematik* dealt with different species of Lizards on the mainland, *Rassenbildung bei weststrijianischen Inseleidechsen* was mainly concerned with both different species and subspecies on a number of small islands off the coast of Istria. The focus upon the geographic periphery thus corresponded with less definite species-boundaries and eventually an emphasis of closely related varieties within one and the same species. In sum, it is therefore eventually wise to treat both studies as a whole whereby the one which was published slightly later turns out to be an extension of the former into the periphery (both geographically and phylogenetically). On closer inspection, this division of labour between the two publications is reflected in each of them. Thus, I think, *Zur Verbreitung und Systematik*, taken as a whole, is the extension of a previously acquired research opinion. Not three different species of Lizards exist on the mainland of Istria but at least six or seven. G. Kramer and R. Mertens reach the amount of their species sample by adding new species to F. Werner’s list, by differentiating more detailed Werner’s classificatory entities but also by excluding those species which live on the Istrrian islands (*Lacerta sicula* Rafinesque) and two others (*Lacerta viridis viridis* Laurenti and *Algyriodes nigro-punctatus* Duméril & Bibron) living on the mainland so that, ultimately, five species remained to be examined. From the epistemological point of view, it is important to note that Kramer’s and Mertens’ sample emerges through a gesture of extension whereby from the number of added species some are subtracted. Altogether this operation keeps the character of a limitation since the insular varieties of *Lacerta sicula* is excluded per definitionem and does not appear substantially in this calculation at all: The examination of the insular forms of *Lacerta sicula* Rafinesque is reserved for the later paper. The empirical core of the study’s main part consists of describing the remaining five species by applying each five descriptive categories, namely the “material” or “amount”, the “size”, “squamosity and shielding”, “colouration and patterning” and, finally, “distribution”. These categories are applied repeatedly in a fixed order. The main part ends with a special treatment of the geographical distribution of two species and some remarks regarding their ecology. As a result Kramer and Mertens mention five aspects. At first, *Lacerta horváthi* turned out to be a new Lizard species for the mainland of Istria. Second, F. Werner’s *Lacerta muralis* appears in two different varieties in Istria, the “Nominat”- and the “maculiventris” race. The former of the two lives in the eastern and inner parts, while

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1411 See Kramer et al., “Rassenbildung bei weststrijianischen Inseleidechsen”, 190.
1412 *Zur Verbreitung und Systematik* was published in Senckenbergiana, Issue 1/2, that is, in March 1938, while *Rassenbildung bei weststrijianischen Inseleidechsen* appeared in Archiv für Naturschichte, Vol. 7, Issue 2, that is, in June 1938.
1413 See in the following mostly Kramer et al., “Zur Verbreitung und Systematik der festländischen Mauer–Eidechsen Istriens”, 49.
1415 See ibid., 65.
the latter dwells in the West of the Istrian peninsula. The boundary between the two geographical races hits through Triest. Third, *Lacerta muralis maculiventris* lives mainly close to human settlements, while the “Nominatform” also dwells far away from them. Fourth, there are transitional forms between both forms of *Lacerta muralis* and in captivity hybrids could be bred. Fifth, *Lacerta melisellensis fiumana* could be made evident in the western parts of Istria for the first time, *Lacerta sicula campestris* with certainty in the central and eastern parts. Lastly, near Rovigno, *melisellensis* and *sicula* reveal an additional peculiarity: While *sicula* dominates larger roads, *melisellensis* mostly occurs near footpaths, in the Macchia and in heathland. I need not go into detail. The order is clear. It consists of what Kramer in a former study described as “differential diagnosis”: An already existing sample is extended so that within this wider sample the most relevant parts (here two species) can be isolated. Why was the distribution of *Lacerta sicula campestris* and *Lacerta melisellensis fiumana* of special importance for Kramer’s and Mertens’ argumentation? My personal opinion in this matter is that both zoogeographical studies were meant to carve out primarily the phylogenetic relationships between the closely related varieties of the western Istrian islands. This eventually was the primary objective. However, this simply raised the question from which mainland species the different insula varieties might have originated through isolation in course of the islands’ separation from the mainland (see to this later). And without mentioning it explicitly, Kramer and Mertens may have thought that only those mainland species could be descendants of a common prototype which are living close to the western coast of the Istrian peninsula whose offshore islands they had focused upon. This would explain the special emphasis of the comparison between *Lacerta sicula campestris* and *Lacerta melisellensis fiumana* in the penultimate section of the paper.

This result makes appear *Zur Verbreitung und Systematik* more as a preparatory work of the later paper *Rassenbildung bei westistrianischen Inseleidechsen* and indeed the latter publication is more than twice as long as the former. Beyond that, it raises more explicitly questions that go beyond mere (geographical) systematization. I reckon it the main study and, maybe, it is also of some interest that *Rassenbildung bei westistrianischen Inseleidechsen* was dedicated to R. Hesse on the occasion of his seventieth birthday in January 1938. Since gestures of dedication or expressions of gratitude use to have the character of “giving something back” they connote an ultimate form of causation. Alike to the earlier published paper, *Rassenbildung bei westistrianischen Inseleidechsen* was a joint publication with R. Mertens but in contrast to the former study the reader is informed at the beginning of each section who the author was in each single part of the paper. This gives the entire paper a more atomistic character. Also the object of study has considerably changed its character. While *Zur Verbreitung und Systematik* picked one single coherent geographic area, the Istrian peninsula, and within this area as a whole examined different species of Lizards, *Rassenbildung bei westistrianischen Inseleidechsen* chooses altogether eighteen separate islands to reconstruct the phylogenetic relationships of several different geographic varieties that, according to Kramer and Mertens, mostly belong to one and the same species of Lizard. It reads:

In other words, the focus drifts from species to subspecies level and within this group both authors intended to carve out a rule, namely a constant correlation between the deviation of the respective Lizard population from the mainland type, on the one hand, and another combined parameter, which consisted of an arithmetic operation between a factor representing the size of the respective insula and a factor that represented the duration of the island’s isolation. “Aus später auseinanderzusetzenden Gründen”, Kramer and Mertens underline,

verzichten wir darauf, uns über Abhängigkeiten der Rassenbildung von Außenfaktoren zu äußern. Dagegen schien uns das vorliegende Tatsachenmaterial zum Versuch geeignet, auf etwa vorhandene Zusammenhänge zwischen dem Grad der Abgeändertheit einer Inselpopulation einerseits und Isolierungsdauer sowie Arealgröße andererseits zu achten.

This intention to deduce one single rule for all examined island populations reveals the heuristic thrust of the paper as a whole. How does this epistemic scheme reflect in the knowledge organization of the study? Or how is the argumentation like that it can lead to a reduction like that? For the sake of clarity I have added another binominal scheme of the paper’s order how I see it (Fig. 2.23). The illustration shows which parts of the paper are marked as written by G. Kramer (“G.K.”), which by R. Mertens (“R.M.”) and which has been written together (“G.K. / R.M.”).

Like in my other illustrations the terms and phrases in brackets are my own abstractions. They are based on both explicit and non-explicit, that is, performative, structural information. Asides the speciality that the paper is a cooperative study the arrangement of the knowledge it provides seems to be quite similar to the one G. Kramer had used in his previous empirical publications. As it appears, there is a larger section consisting of chapter two and three which includes prior information about the methodology and the scientific objects and thus has a more introductory character. These parts are written by G. Kramer himself and discuss the geological history of the islands’ isolation, their absolute age and their relative grade of separation, that is, their relative age. Further, Kramer informs the reader which islands are populated with Lizards at all and, if so, what kind of populations can be

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1417 Ibid., 190–191.
1418 “Introduction” and “Summary” are unmarked.
1419 For this twofold focus on “absolute” and “relative” age in chapter two “History of the Islands; Particularly their Age”, see ibid., 191. Within this bifurcation the binominal differentiation perpetuates onto lower levels. Thus, while discussing the absolute age of the islands, Kramer evolved two theories. Either the tectonic plate which Istria is a part of slants or bends westwards.
G. Kramer, Formation of Races in West-Istrian Island-Lizards As a Function of the Duration of the Islands' Isolation and their Area Size (1938), Alleged Organization
found. Some concluding remarks concerning the ecological conditions supplement Kramer’s first approach to his scientific object, that is, the Lizard populations of eighteen west-Istrian islands. At this point it is important to keep in mind that G. Kramer considers the amount of food and the size of an island as relevant factors that decide whether or not an island can be populated but he does not presume that ecological factors cause directly the shape of the inhabitants of a respective island.

“Es gibt wohl keinen Fall”, Kramer underlines,

in dem man mit genügender Begründung spezielle Eigenschaften von Inseln mit speziellen Eigenschaften der darauf lebenden Populationen in Verbindung bringen könnte (wohl dagegen kann man manche allgemeine Eigenschaften von Inseltieren als Anpassung an das allgemeine Inselmilieu ansehen, wie z.B. den Verlust des Flugvermögens).

[Eventually there is no case in which one, with sufficiently substantiated certainty, could connect specific characteristics of the inlands with particular qualities of the populations living upon them (however one can interpret general characteristics of the island animals as adaptations to the general milieu of the island).]

In other words, Kramer is inclined to refuse any kind of Lamarckian inheritance and favours instead the adaptionist perspective put forward by neo-Darwinians although this latter affiliation turns out to be still rather moderate. “Wir können nun gerade bei den von uns behandelten Inselpopulationen in sehr geringem Maße hoffen”, he continues,


[Especially in case of the island populations treated by us we can hope only in a very restricted manner to determine qualities specific for one insula as a cause of the specific qualities of the population dwelling upon it: Firstly, none of our Lizard races reveals a that far-reaching deviation from the mainland form or any other examined variety that it would legitimately entail such an inference; secondly, there are existing doubts, at least in some of the cases, whether the current milieu of the island is the original one or, more likely, one that has been changed artificially in recent times. Thus the number of Pinus halepensis on San Giovanni, Conversada, Asino and Bagnole can only be the result of [changes] in the recent past, while, by contrast,

so that the western islands lower and thus separate from the mainland or, on the other hand, there is the possibility of a general rise of the water level due to climatic shifts after the last ice age. In one case something drops, while in the other something rises. See Kramer et al., “Rassenbildung bei westistrianischen Inseleidechsen”, 192. According to Kramer’s account, both theories seem to generate the same result (another dissolving of antagonistic positions): The oldest island separated before 18.000 years, at the most, but more likely not earlier than 9.000 years before our time (Ibid., 193, 194). The relative age of the islands is simply more or less a function of their relative height above sea level (Ibid., 194).

See ibid., 194–197.

Ibid., 196.
Gustav Kramer (1910–1959)

It seems likely that the gras-islands Figarole, La Longa, Polari were populated with Macchia before the intervention by human hand. That those drastic changes of the flora influenced the earth’s soil and thus the population with prey animals is self-evident. However, this moderate attitude does not mean that the adaptive character of the modified qualities is to be neglected a priori.

In sum, one may say that Kramer’s account of the islands and their population fulfils the neo-Darwinian causal architecture. From the amount of relevant islands those are separated out which are not populated while in doing so the question for the causes is raised (lack of food, too a small size). The question of the island’s colonization is treated from an environmentalist perspective whereby the role of direct causation is discussed though widely rejected. Yet he does not neglect in general the adaptive quality of the deviated characteristics. And the interesting aspect of the quoted passage seems to be that Kramer apparently interpreted “Darwin’s paradox” in the current study as if he counted the drastic changes of the flora that were caused by humans in the last 9,000 years to the environmental factors in correlation to which living organisms needed to adapt. From the epistemological point of view, one can therefore argue that G. Kramer’s account argues within a functional framework but that the idea of adaptation is somewhat superimposed by the idea that lastly Man functions as a quite drastic causal factor. And with a view of my epistemological research question this would mean that G. Kramer adopted the neo-Darwinian causal architecture but did not apply the epistemic re-evaluations that should become characteristic for later accounts. Instead the entire adaptive framework – maybe as a result of taking into consideration R. Hesse’s position to whom the study was dedicated – kept a somewhat paradox overtone that still mirrored the affiliation with Hesse’s conception of animal geography. What follows is the core of the study. It consists of four main sections two of which seem to have a more systematic character, while the latter two seem to extend this perspective by bringing in the idea of actual phylogenetic transformation. The easiest way to describe the inner argumentative logic of these sections, I think, would be to apply once more G. Kramer’s concept of “differential diagnosis”. Pure systematics (including the geographical distribution of the species and their taxonomic relatedness) needs to be extended by a wider transformationist perspective so that within this wider area of phylogenetic variability one single principle of evolutionary change can be carved out. “Jede Arbeit von der Art der vorliegenden”, it reads in the introduction,

wird über das Deskriptive hinaus bestrebt sein, den Gesetzmäßigkeiten der Rassenbildung näherzukommen.

[Any research work of the kind of this present one will be aimed at exceeding the mere description and intend to approximate the rules of the formation of the races.]

This approximative reduction of the principles of race formation takes place mainly in the last of the four part-sections bearing the title “VII. The Insula Varieties in Relation to Area-Size and Duration of Isolation”. It can be read as an anticipated conclusion and thus turns out to be a provisional approximation of the paper’s final or concluding sections. In concrete, the four chapters (IV.–VII.) that together

\[1422\] Ibid., 196–197.
\[1423\] Ibid., 190.
build the core of the paper can be read not only as a pathway within a graphical scheme but also as discrete argumentative steps finally leading to an approximative conclusion. The first of these steps consists of an accurate description of the morphology of each island population.\textsuperscript{1424} I need not go into detail at this point since it suffices to mention the categories according to which the data is presented in each case. These categories are the “topography” of the islands, the “material”, that is, the amount of examined specimens, “general indicators”, the “size” of the animals, their “squamosity and shields” and, finally, their “colouration and patterning”. In so far one may say chapter four, “Description of the Island-Populations” is the one that coincides most with the procedure in the previous study which was concerned with mainland species of Lizards. Moreover, it is noteworthy that R. Mertens and G. Kramer distinguish between three different geographic regions, that is, islands “North of the Canal di Leme”, “South of the Canal di Leme” and the “Islands of the Brioni Group”. This differentiation shapes the outline of the chapter and beyond that conveys the bifurcation onto the lower levels of argumentation: Two of the regions are related to a geographical boundary, while the third group of islands is thought or defined independently of this boundary. This way of presenting knowledge is not arbitrary and fulfils the structural requirements at this particular location of the overall study. The second step in Kramer’s and Mertens’ argumentation is to translate the found geographic distribution into a taxonomic system.\textsuperscript{1425}

This part is exclusively R. Mertens’ contribution. Since all examined insular Lizard populations belong to one and the same species (\textit{Lacerta sicula Rafinesque}) the chapter has to deal with the problematic of micro-systematic classifiability. How many “pure races” need to be distinguished and where are the classificatory boundaries to be drawn? R. Mertens discusses two extreme solutions to the problem: Either there is only one variety (not likely) or each island population establishes its own independent race (more likely). However, Mertens finally refuses both of these extreme solutions and chooses a combined explanation.\textsuperscript{1426} In his view there are only two main geographic races, the \textit{Lacerta sicula campestris} of the mainland and the more short-tailed and darker \textit{L. sicula insularum}.\textsuperscript{1427} In addition to that, he presumes the existence of four further insular varieties which inhabit only one island each and whose characteristics match with neither of the before mentioned taxonomic entities. From an epistemological standpoint the chapter in question thus operates with a gradual reduction: The great amount of empirically raised data is to be translated into an artificial, though adequate, classificatory system. Mertens’ account reflects this procedure by presuming more possibilities to classify than he actually finally makes use of. The rest of the chapter discusses both the mainland (\textit{L. sicula campestris}) and the endemic varieties (\textit{L. sicula insularum} plus the four additional) populating the west-Istrian islands. Thereby it is important to note that

\textsuperscript{1424} See Kramer et al., “Rassenbildung bei westistrianischen Inseleidechsen”, 197–212.

\textsuperscript{1425} See to this chapter five, “The Island-Populations and their Taxonomic Relationships”, ibid., 212–217.

\textsuperscript{1426} See to this the last paragraph of the chapter’s introduction ibid., 213.

\textsuperscript{1427} This would mean that the species \textit{Lacerta sicula Rafinesque} appears in mainly two varieties or races, the \textit{Lacerta sicula campestris} which lives on both the mainland and on several islands, and a specific additional form, \textit{Lacerta sicula insularum}, which populates the islands only.
R. Mertens’ concept of geographic “variety” or “race” is a *plastic* one because not all insular populations being counted to one variety need to be fully identical.\(^{1428}\) The next step in G. Kramer’s and R. Mertens’ argumentation is to measure and quantify the extent of the deviation (“Differenzierungsgrad”) with which each of the insular populations differentiates from the mainland type and from the other island populations.\(^ {1429}\) This step again is based upon a quantitative reduction since the argumentation finally aims to carve out a developmental trend. The section is marked as written by R. Mertens. In the introductory paragraph of the chapter it reads:

Aus dem Vergleich der auffälligeren Variationen der Inselbewohnenden Eidechsen West-Istriens, soweit sie in der Größe, Körperform, Beschildung, Beschupfung, Färbung, Zeichnung und im Geschlechtsdimorphismus in Erscheinung treten, mit entsprechenden Variationen artgleicher Tiere vom istrianischen Festlande, wird sich ergeben, ob es Merkmale von Inselpopulationen gibt, die über die Variationsbreite auf dem Festlande hinausgehen oder nicht. Dabei wird sich zeigen, ob gewisse gemeinsame Richtungen der insularen Variabilität zu erkennen sind; auf Grund dieser Feststellungen wird später der verschiedene Differenzierungsgrad der einzelnen Inselpopulationen zu beurteilen sein.

[On basis of a comparison of the more conspicuous variations of the insular Lizards of West-Istria – as far as they become manifest in size, body shape, shielding, squamosity, colouration, patterning and sexual dimorphism – with corresponding variations of conspecific animals of the Istrian mainland it will be deducible whether or not there exist characteristics in insular populations which exceed the range of variation on the mainland. Thereby it will become evident whether there are recognizable common directions within the insular variability; on basis of these results it will be possible later to evaluate the different extents of deviation of each single insular population.][\(\text{transl. CL}\)]\(^ {1430}\)

In other words, R. Mertens’ applies a number of categories (size, shape, colouration, etc.) to determine the evolutionary trend and, in the last consequence, the grade of separation of each insular variety from the main type and from each other. While each of the parameters in question is treated in a separate subsection (A–E) of chapter six, the final reduction mainly concentrates on the subchapter with the title “The Range of Insular Variability and the Direction of Variability”.\(^ {1431}\) The main result of this section is that insular forms of *Lacerta sicula* in fact reveal a wider range of variability than the mainland varieties.\(^ {1432}\) This applies to most or all of the examined criteria. Many deviations are missing in the mainland form. However, despite the broad range of variability, R. Mertens is able to determine the developmental trend in some series of characters. “Trotz des bunten Variationsbildes, das die inselbewohnenden Rassen und Populationen in Istrien zeigen”, he argues,

\(^{1428}\) See *ibid.*, 213, 214.

\(^{1429}\) See to this chapter six, “The Varieties of Istrian Lacerta Sicula Rafinesque on the Islands and the Mainland”, *ibid.*, 217–228.

\(^{1430}\) *Ibid.*, 217.

\(^{1431}\) See *ibid.*, 226–228. It’s an interesting question whether the linear arrangement of subsection A to E can be resolved in a binominal order. Maybe, the categories “size” (A) and “body shape” (B) have another quality than “Shielding and Squamosity” (C) and “Colouration and Pattering” (D) since the former two refer to proportional entities, while the latter two seem to address more specific aspects of the animals’ outfit, particularly as to their surface. A–D eventually applies to all specimens in a group. The criterion “sexual dimorphism” (E) does not and partly involves ontogeny.

\(^{1432}\) See *ibid.*, 227.
It is remarkable that the reduction R. Mertens’ account displays does not only affect its argumentative logic (the reduction of variability to a trend) but also becomes partly manifest on a more concrete realm of the narration since many deviations are reductions such as the decrease of overall size, number of scales etc. Moreover, R. Mertens does not only name the developmental trends he also aims to determine how they might be interrelated. This partly holistic stance leads to a differentiation of two forms of relatedness. Either the observed mechanisms operate independently from each other or they are correlated. In the latter case we meet with an idea that already Darwin had circumscribed as correlation of growth. Altogether we may therefore state that the third step of Kramer’s and Mertens’ argument culminates into a threefold certainty: The insular forms show a more of variability, this variability can be abstracted to some developmental trends and, finally, these trends can be rated in terms of their correlation. Mertens concludes his argument by remarking that the extent of differential deviation between the single Lizard populations might be due to the different developmental velocities each series of characters may be subject of. The final stage in G. Kramer’s and R. Mertens’ “long argument” consists of translating qualitative taxonomic differences in quantitative sizes and, in doing so, fulfils the precondition to establish a measurable correlation between grades of phylogenetic deviation and the size of the islands and the duration of their isolation. This section of the study is marked as been written by both G. Kramer and R. Mertens. It is the point where the entire line of thought culminates into a principle. As such the section functions as a reduction in the overall argumentative scheme. In itself, however, chapter seven “The Insula Varieties in Relation to Area-Size and Duration of Isolation” puts forward a hypothesis in a first step which

1434 Ibid., 227–228.
1435 The latter aspect applies for instance to the overall reduction of body size which, in R. Mertens’ view, is correlated with the shortening of the tail (Ibid.). This eventually substantiates my hypothesis that there is an inner order in the subsections A–E. A and B refer to correlated characteristics, while C and D apparently do not – not being neglected that within this paragraphs Mertens also refers partly to correlated characters.
1436 Ibid., 228. This idea is of interest for G. Kramer’s later scientific development because it underlines the importance of allometric research while examining the role of geographic isolation.
The suggested procedure to prove both dependencies is quite elegant. As I have already suggested before, it seems to consist of two independent steps. At first, Kramer and Mertens translate qualitative differences in quantitative ones. This applies to all parameters which are of interest. Thus Kramer and Mertens grasp the duration of an island’s isolation in terms of its “Trenntiefe” (“depth of separation”) which seems to be an arbitrary number representing the utmost depth of the sea between the island and the mainland (other islands respectively). This figure is a measure for the relative age of an island. The area size of an island has been determined by cutting out the forms of the islands from a map. The physical weight of the paper cuttings may then be taken as an approximative arbitrary value for the size of an island. Finally, Kramer and Mertens needed to translate the qualitative phylogenetic differences into an arithmetic measure they termed “Differenzierungsgrad” (“grade of differentiation”, meaning the “extent of derivation”). Although the study is not quite clear at this point, I think, Kramer and Mertens re-interpreted the characteristics of one specific series (e.g. lighter vs. darker ground colour) in form of a graded scale to which they attributed arbitrary numbers. In a later critical remark it reads:

[...]

die Stufung der Populationen in Gruppen verschieden fortgeschrittener Variationen ist sehr willkürlich. Eine solche Wertung könnte nur dann gerecht sein, wenn Veränderungen nach gleicher Richtung, also gleicher Qualität, aber verschiedener Stärke zu beurteilen wären. Hier dagegen bleibt es bei einer Stufung nach Anzahl der Charaktere, in denen eine Population vom Festlandstyp abweicht; freilich tritt dann die Intensität der Abweichungen bei der Bewertung noch hinzu.

[the grading of the populations in groups of more or less advanced variations is quite arbitrary. Such a rating could only be justified if changes were to be evaluated that are pointing into the same direction, and hence are of the same quality but of a different intensity. Yet here, we stick with a rating based on the number of characters in which a population deviates from the mainland type; certainly the intensity of the derivation then is added as a criterion of the valuation.]

The second step of this “differential diagnosis” then consisted of establishing the

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1437 See ibid., 228–229. By the way: Kramer’s and Mertens’ way of testing a hypothesis is not exclusive that is negative. On the contrary it is more like testing a hypothesis’ applicability.

1438 Ibid., 231.
rule. “Wertet man nun die Trenntiefe positiv, die Flächenzahlen negativ”, Mertens and Kramer conclude,

so erhält man Summen, deren Größe dem Grade der Differenziertheit der Populationen im großen und ganzen parallel geht. Ordnet man dagegen einfach nach Inselgröße ohne Berücksichtigung der Trenntiefen, so ergibt sich eine Reihe, in welcher der Schwerpunkt des Differenzierungsgrades zwar bei den kleineren Flächen liegt; jedoch mit Unregelmäßigkeiten, deren teilweise Beseitigung durch das oben genannte Verfahren eben zeigt, daß sie durch das Inselalter bedingt sind.

[Now if one rates the depth of separation negatively and the figure for the area size positively one gets sums whose sizes are running more or less parallel to the extent of a population’s differentiation. By contrast, if one orders a series simply relative to the size of the area without considering the depth of separation one obtains a series in which the centre of the extent of the differentiation lies upon the smaller islands; however with irregularities whose elimination through the before mentioned procedure reveals that they are indeed caused by the age of the islands.]

In other words, Kramer and Mertens claim a direct proportionality between the extent of the differentiation of the populations, on the one hand, and the sum consisting of a negatively counted area size and a positively rated age of the island, on the other. If I was to translate this rule into mathematical formula it would like the following simple quotient:

\[
\frac{\text{Extent of Differentiation}}{\text{Depth of Separation} - \text{Area Size}} = \text{const}
\]

It is to be read: The quotient of the extent of differentiatedness, on the one hand, and the sum total of the size for the relative age of an island and its area, on the other hand, is constant for each examined case p. However, G. Kramer and R. Mertens also notified some exceptions to this rule. For instance, the population of the island Galiner revealed a smaller “Differenzierungsgrad” than was expected on basis of the presumed age and area size. The populations of the islands Rivera and Zumpin, on the contrary, showed more deviating populations than could be expected considering the relatively small “depth of separation” (i.e. relative age of the island). In sum, we may therefore conclude that G. Kramer’s and R. Mertens’ reduction of complexity finally ended with a gesture expressing uncertainty and caution. This impression is further confirmed by the fact that both authors explicitly elaborate on potential sources of errors at the end of the chapter. These potential sources of mistake are the arbitrary scaling of the populations, the fact that the “depth of separateness” might be an inaccurate measure for the relative age of an island and, finally, the possibility of animal migration between the insula and the mainland, as well as the changes of the vegetation caused by human hand. But after all, according to G. Kramer and R. Mertens, the fact that the obtained principle does not stand out more clearly does not belittle the overall result of the study. This result is that the smallness of an island accelerates the velocity of genetic development. “Wir können also mit der Feststellung schließen”, Mertens and Kramer conclude, daß Kleinheit des Areals den Veränderungsvorgang der Population beschleunigt. Im Hinblick auf die Frage nach der Wirkungsweise des Inselmilieus und auf das damit verquICKte Inzuchtproblem

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1440 See ibid., 230–233.
Gustav Kramer (1910–1959)


[Hence we can conclude with the statement that the smallness of the area speeds up the process of change within a population. This aspect is of interest with a view upon the question how the insular milieu exerts its influence and the problematic of inbreeding which is intertwined with it this aspect. Thus it can be presumed that the size of the area exerts an effect not or not only as such but also indirectly through the limitation of the number of inhabitants. However, further discussion in this direction should not be undertaken.][transl. CL]1441

Lastly, if an absolute age for the oldest island of ca. 9,000 years is taken for granted the evolution of the single island population must have taken place, relative to the island’s extent of separateness, within a few thousand years.1442 To sum up my reading of G. Kramer’s and R. Mertens’ paper Rassenbildung bei westtistrianischen Inseleidechsen in Abhängigkeit von Isolierungsalter und Arealgröße, one may say that it reveals the attempt to carve out a principle of evolutionary change applicable to isolated populations. As such its general heuristic overtone deviates both from Kramer’s and Mertens’ earlier study on mainland Lizards and the composition of the unity both studies build together: After all the constitution of the various different insular populations is explained as a derivation of the mainland type. As a whole Kramer’s and Mertens’ studies on Istrian Lizard population thus are “experiments” in the study of allopatric speciation. As the last quotation shows they apply population thinking in the background but, beyond that, put emphasis on additional mechanisms of evolution besides sympatric speciation. I think some words need to be dropped about the question in how far Kramer’s and Mertens’ model of speciation fitted into the socio-political context of the mid- and late 1930s. I do not consider the Modern Synthesis fully compatible with other simultaneously emerging and developing biologisms of human kind such as the one put forward by National Socialist racial ideology. One of the demarcation points lies within the Darwinian idea that all living creatures share more or less one common origin from which they descended through gradual variation (and additional forms of speciation). Kramer’s and Mertens’ model of speciation is of some interest in this context because it shows that biologists in the late 1930s were aware of the so-called “inbreeding”- or “selfing”-problematic, that is, the idea that limitation of population size or restriction of migration may have a negative effect upon the genetic constitution of a population due to the loss of genetic variability. This is a population genetic argument that speaks against and not for any kind of closed society from National Socialism to Sarrazin. In other words, eventually it was exactly the scientific accomplishments of some of the so-called architects which deprived National Socialist ideology from its quasi-scientific legitimation already in the late 1930s by undermining several core ideas of its vulgar biologism. Correspondingly to this, I think, it can be shown that many neo-Darwinians such as J. Huxley, J. Haldane, E. Mayr, E. Stresemann, and G. Kramer were latent or overt opponents of the National Socialist regime including the manner it instrumentalized the sciences. This thesis should be examined more thoroughly historically because K. Lorenz’s

1441 See ibid., 233.
1442 See ibid.
example shows that the epistemic interventions which had generated the Modern Synthesis obviously did not prevent him from putting forward his theory of “degeneration through domestication” within the epistemologically complementary realm although he was criticized for this by his colleagues. In general, Kramer’s and Mertens’ study on Istrián mainland and island populations of Lizards show that they were on the way to the Modern Synthesis but also that they approached this synthesis by putting into the foreground the more secondary aspects. This hypothesis is confirmed if we have a closer look on the causal architecture. Kramer’s and Mertens’ joint papers show the inverted way of causal reasoning that was typical for both neo-Darwinians and ethologists and can be traced in Kramer’s works since his move to Rovigno. However, I think, the epistemic outfit of the Modern Synthesis was not fully elaborated in Kramer’s research of the late 1930s because the typical re-evaluations are still missing which regroup the occurrence particularly of the paradox semantic relations within the epistemic schemes. One example for this might be that Kramer put forward a functional framework when discussing the relevance of the milieu but his account also suggests that he considered human interventions an essential part of the constitution of this milieu. Later neo-Darwinian theorists and most likely later behavioural ecologists would have argued in strictly handicap theoretical framework, that is, they would have used consequently quasi-malfunctional animal characteristics for their phylogenetic studies. This aspect is still underdeveloped in Kramer’s studies of the late 1930s. However, altogether it can be confirmed that the works of his Rovigno period took place in mainly two different realms. While the studies on metabolism and the general behaviour studies were carried out within an ultimate framework, the joint project with R. Mertens, as a whole, wasn’t. It focused on geographic isolation and the description of the developmental lines that seemed to be characteristic for island Lizards and very often implied regressive forms of evolution.

Moving to the Stazione Zoologica di Napoli (1936–1942)

Transition Three. In E. Stresemann’s obituary we are informed that G. Kramer changed once more his employer in 1936 when he moved from the German-Italian Research Station for Marine Biology in Rovigno to the Zoological Research Station in Naples.\textsuperscript{1443} According to J. Hämmerling’s judgement both institutions were breathing a different spirit: While the Rovigno institute was thought to be more like a Kaiser-Wilhelm Institute, that is, in the foremost it was to provide an excellent research environment for a restricted number of privileged scholars, the Zoological Research Station was considered the melting pot for zoological research in the era between the First and the Second World War.\textsuperscript{1444} The reasons why the Naples Station, at least in its early heyday, could advance to one of the first addresses for

\textsuperscript{1443} See Stresemann, “Gustav Kramer”, 258. Kramer mentions the possibility to move to Naples in a letter to M. Hartmann dated to Mai 1936. See MPG-Archives, III. HA, Rep. 47, file 797, letter G. Kramer to M. Hartmann (23/05/1936). In addition see ibid., file 797, letter M. Hartmann to G. Kramer (18/06/1936), in which the former evaluates the chance that the Station can employ a German assistant.

scientific exchange were lying both in the structure of the institution itself as well as in the personal characters of the directors of the institute. Thus it was mainly the fact that researchers from all over the globe – or their parental research institution respectively – could rent a table or a workplace that created the possibility to get in touch. In other words, the Naples Station had more the character of a private-enterprise research institute which was aimed at selling a product. In this context, we must understand also that the institute saw itself as a mediator between zoological research, on the one hand, and the popular scientific interest of the wider public community, on the other. Building up the great aquarium was the main step in this direction since it attracted a certain amount of interested visitors per year. Furthermore, the institute established business relations with renowned companies with mutual benefit. For example, the Carl Zeiss Factory (Jena) provided the latest optical instruments. In exchange Zeiss, by presenting their technology to an international community of potential clients, could hope to win new customers. Finally, the Naples Zoological Station met the growing need for preserved marine organisms in museums and research institutes by selling such collections to clients all over the world. In doing so the institute maintained an entire department for preservation and in 1877 an independent “Export Department” was established successfully. The Naples Station had been founded by A. Dohrn in 1872 to create a


1446 For the so-called “table-system”, see Groeben, “Catalysing Science”, 58, 59–60. Renting a table included free access to lab space, daily fresh experimental animals, access to the lasted technical instruments, assistance from well trained stuff, access to an excellent library and, last not least, the opportunity to publish quickly in one of the in-house publications such as the journal Mitteilungen aus der Zoologischen Station zu Neapel or the monograph series Fauna and Flora of the Gulf of Naples.

1447 Therefore it is not an accident that the Naples Zoological Station and its success was approached from an economic perspective. See M. T. Ghiselin et al. “A Bioeconomic Perspective on the Organization of the Naples Zoological Station”. In: M. T. Ghiselin et al., eds. Cultures and Institutions of National History. Essays in the History and Philosophy of Science. San Francisco: California Academy of Sciences, 2000, 273–285.

1448 Ibid., 277.

1449 See Groeben, “Catalysing Science”, 58. Other cooperative agreements existed with the Jung company (Heidelberg) for microtomes and Merck (Darmstadt) for dyes and other chemicals.

1450 See ibid., 60. The fundamental biological problems raised around 1900 such as the organizational plan of living systems, embryogenesis, general physiology, evolution and phylogeny, coincided with a boom of marine biological research. See B. Fantini. The History of the Stazione Zoologica Anton Dohrn. An Outline. Naples: Stazione Zoologica Anton Dohrn Napoli, 2002, 5–6. The advent of new branches of biological research in the first half of the 20th century, especially the modern sciences of hereditary, seemed to break this alliance and, amongst several other reasons, this matter of fact possibly endangered the economic basis of the Naples Zoological Station which, in turn, responded with structural reforms. See to this aspect Gemelli, “A Central Periphery”, 186, 188–192, especially 191. G. Kramer’s affiliation both fell into and mirrors this period of transition.
place where scholars found the prerequisites to answer the questions of “modern – i.e. post-Darwinian – biology”, as C. Groeben has put it.\(^\text{1451}\) Since then – and in spite of major changes in the institutional organization – the directorship passed on from father to son, first to Reinhard (director between 1909 and 1954) and later to Peter (director between 1954 and 1967), until 1967 when the Dohrn’s alliance with the station was ended.\(^\text{1452}\) It was part of this family tradition that the directors intended to provide a research environment without any doctrinaire restrictions.\(^\text{1453}\) Thus the directors saw themselves as catalysts for scientific innovation, that is, they aimed to assist and inspire when it was wished and, beyond that, fostered the establishment of social contact between the researchers. For instance, the prestigious institute building in the Royal Park right on the sea shore was designed by A. Dohrn so that it had a room in the first floor dedicated to music and leisure.\(^\text{1454}\) After the Second World War, G. Kramer writes in retrospect: “Die Station blieb übervölkisch und eine Freistatt der Humanität” (The station remained supranational and a sanctuary of humanity).\(^\text{1455}\) It would be an interesting further leading research question in how far the “constitution” and the particular intellectual climate of the Naples Zoological Research Station mirrored the Darwinian attitude of its founder (and the succeeding directors) and what is even more pressing: In how far did A. Dohrn’s understanding of “Darwinism” actually match with Darwin’s own epistemic orientation? “Dohrn [i.e. Anton Dohrn]\(^\text{c1}\), the scientist”, C. Groeben writes, should be defined, as Michael Ghiselin has shown, a “comparative anatomist with a functional outlook”. Dohrn applied the same “functional outlook” to the Zoological Station, shaping it as a co-adapted system of independent parts where labour was both divided and combined within the organization, optimising resources. This can well be seen in Dohrn’s assignment of tasks to his collaborators. Guest investigators had the highest priority at all times, their needs and wishes came first. But at the same time each of the assistants and some of the technical stuff also had several other tasks and commitments.\(^\text{1456}\)


\(^{1453}\) See Groeben, “Catalysing Science”, 56–57, 58. G. Kramer, later after the Second World War, asked in a memorandum for the reasons of the persistence of the Stazione Zoologica and came to the conclusion that R. Dohrn’s avoidance of influences not being excluded the possibility of being inspired by the muses was one of the reasons. See MPG-Archives, III. HA, Rep. 77, file 1, ms. “Die Zoologische Station Neapel lebt” (n. d.), page 1.


G. Kramer became Vice Director of the Research Station’s Department of Physiology in 1936 and I presuppose that the particular research environment fostered his metamorphosis to a neo-Darwinian thinker. In a letter to M. Hartmann, he writes:

Es geht mir gut hier, ich kann sagen, dass der Geist der Station schnell Besitz von mir ergriffen hat. Meine Rovigneser Schulung kommt mir natürlich sehr zugute.

[I am fine here. I can say, that the spirit of the Station has quickly taken possession of me. My training in Rovigno thereby proved to be of advantage.] (transl. CL)

The quotation suggests that the institutional environment Kramer had picked in the first place had a certain reverse impact upon his way of thinking and his personality as a whole. However, it would be incorrect, I think, to make his affiliation with the Naples Zoological Research Station the sole factor of his scientific development since G. Kramer like other ethologists and evolutionary biologists had begun already earlier to take the path in direction of the Modern Synthesis. This view is confirmed to a certain extent by the fact that Kramer himself saw a continuity between his education in Rovigno and his later employment. Rather the question must therefore be how the new milieu fostered the solidification of this transformation process. In the following paragraphs I would like to carve out how the formation of G. Kramer’s neo-Darwinian theorizing became manifest in the research works that originated in his Naples period. Maybe it is not to far-fetched, when I presume further that this epistemic solidification built the foundation for a longer period of research in which no further epistemic transformation processes occurred and which therefore was mainly characterized by interpreting and reinterpreting one and the same scientific paradigm. In a second step, thus, it is to be shown that Kramer’s neo-Darwinian convictions lasted well into the mid-1950s and therefore, so to speak, as a conservative moment of his research, ran across the drastic socio-political changes of the war and post-war period as well as they resisted Kramer’s moves to other institutional environments such as the Zoological Institute of the University of Heidelberg in 1946 or the MPI for Marine Biology in 1947 / 1948.

As it appears there are altogether four major publications which can be linked chronologically to the time Kramer spent in Naples and / or reveal even a connection in content to the local area. Three of them are reptile studies, while the fourth stands out of the series insomuch as it is an ornithological paper written for the “Festschrift” dedicated to O. Heinroth on the occasion of his seventieth birthday. I will elaborate on Kramer’s revived ornithological interest later and begin with his research in reptiles. Amongst the research papers concerned with Lizards there is the study of the so-called “con-colour”-trait (the lack of patterning) and its inheritance. The project began still in Rovigno in the year 1936 but was completed in Naples between 1937 and 1939.

Another project was dedicated to small populations of Lacerta sicula Rafinesque on the Sorrentinian peninsula and the island of Capri. This paper seems to continue and transfer G. Kramer’s interest in the

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1458 For the latter study see G. Kramer. “Beobachtungen über das Verhalten der Aaskrähe (Corvus corone) zu Freund und Feind”. In: Journal für Ornithologie 89. Ergänzungsband III (1941), 105–131.

mechanisms of speciation in the new regional environment.\textsuperscript{1460} The final paper of the series is a comparison between island and mainland Lizards with a view of the size of the newly hatched offspring, the annual amount of produced offspring and the age distribution of respective populations.\textsuperscript{1461} Next to these four main publications which appeared during or relatively shortly after G. Kramer’s stay in Naples there are two further papers which are also based on research projects carried out in the Naples period but were published at a point when the author was already in Wilhelmshaven. Due to this chronological delay I would like to keep these studies in the background of my analysis without neglecting them altogether.\textsuperscript{1462} Both of these studies are related to insular populations of Lizards or provide a comparison of island and mainland populations. Also I would like to draw my reader’s attention to the fact that the period between 1942 and 1945 is not represented in form of published sources since G. Kramer’s research activities were partly interrupted through military service and the captivity as a prisoner of war.\textsuperscript{1463} A loose comparison between G. Kramer’s research on Istrian mainland and island Lizards, on the one hand, and his comparative studies of populations dwelling on the Sorrentinian peninsula and the island of Capri, on the other, reveals several slight differences. At first, although both research endeavours were cooperative projects the style or mode of cooperation seems to have changed with Kramer’s move to Naples. While in the previous project it was G. Kramer himself who collected the animals and then sent them to Frankfurt where R. Mertens preserved and classified them, the cooperation with Count F. v. Medem turns out to have taken place on the spot and simultaneously by applying another form of division of labour.\textsuperscript{1464} In contrast to \textit{Rassenbildung bei westistrianischen Inseleidechsen} (1938)


\textsuperscript{1461} See G. Kramer. “Veränderungen von Nachkommenziffer und Nachkommengröße sowie Altersverteilung von Inseleidechsen”. In: \textit{Zeitschrift für Naturforschung} 1.11/12 (1946), 700–710.


\textsuperscript{1463} G. Kramer’s bacteriological research which was carried out during the Second World War apparently for medical purposes as well as his interest in blood serum which can eventually be dated back into this period could only be examined if I was able to get hold of additional and other types of sources. For Stresemann’s remark that Kramer was concerned with bacteriological research see Stresemann, “Gustav Kramer”, 258.

\textsuperscript{1464} Thus G. Kramer informs us that both authors measured the material in order to obtain more reliable results. For the double measurements see, for instance, Kramer et al., “Untersuchungen an Kleinpopulationen”, 101. For F. v. Medem’s biography see W. W. Lamar. “Federico Medem (29 August 1912 – 1 May 1984)”. In: \textit{Herpetologica} 40.4 (1984), 468–472. According to W. Lamar, v. Medem completed the research for his doctorate in Naples (1940–1942). He obtained his PhD from Humboldt University in 1942. The title of his thesis which had been advised by M. Hartmann was “Beiträge zur Frage der Befruchtungs-Stoffe bei Marinen Mollusken” (Ibid., 469). See to this M. Hartmann’s review MPG-Archives, III. HA, Rep. 47, file 965, ms. “Referat über die Dissertation von Friedrich Graf von Medem über die Befruchtungsstoffe der Mollusken” (23/04/1942), page 1–2 and ibid., file 964, ms. “Gutachten” (17/06/1941). Some letters exchanged between G. Kramer and M. Hartmann, Medem’s formal advisor, and also between F. v. Medem and M. Hartmann reveal that G. Kramer had a certain impact upon Medem’s succeeding project. See ibid., file 797, letter G. Kramer to M. Hartmann (20/11/1940),
Gustav Kramer (1910–1959)

in *Untersuchungen an Kleinpopulationen* (1940) there is no allocation of single chapters to one specific author. The author is named as indefinite “we”. Second, G. Kramer and R. Mertens did not offer a fully fledged genetic theory of speciation in their paper on Istrian Lizards nor did they drop many sentences on the actual mechanisms of inheritance underlying their idea of geographical isolation. However, what their study provided though was an epistemic frame within which the process of derivation could be thought. This frame implied the idea that the west-Istrian islands developed into relatively autonomous milieus accommodating relatively discrete populations of Lizards. It also included the notion that there was, though not exclusively, a general tendency to nanosomy in the insular populations and the fact that Kramer and Mertens raised the idea of “selfing” suggested that evolution in small isolated populations might possibly take a disadvantageous course, too. With Kramer’s move to Naples this framework seemed to become less certain. For instance, in *Untersuchungen an Kleinpopulationen* we read that in case of the examined Southern Italian Lizard populations body proportions turned out to be a non-distinctive feature. “Die einzelnen Populationen”, Medem and Kramer write,

This possibly raised the question which characteristics can function at all as distinctive qualities in a comparative study of different island and mainland Lizard populations. *Untersuchungen an Kleinpopulationen* therefore can be read as a preparatory study to answer this question and hence is placed in a more open epistemic framework. The structure of the last mentioned paper shows that it aims to obtain approximative certainty. In the paper’s core (yet less with a view of the paper as a whole) this is reached by a heuristic operation very similar to what Kramer in an earlier paper called “differential diagnosis”: The more distinctive morphological characteristics are supplemented by those which seem to be less discrete. Within the latter category, Kramer and Medem then aim to carve out those types of traits that might have a distinctive value nonetheless. In other words, the examination of the organization of the provided knowledge suggests that G. Kramer’s later cooperative study operated with a complementary heuristic scheme. In case this heuristic shift is to be interpreted as epistemological relocation of Kramer’s theorizing on

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1465 See fn. 1433, page 458 of my thesis.
1466 See fn. 1441, page 461 of this thesis.
1467 Kramer et al., “Untersuchungen an Kleinpopulationen”, 117.
1468 Kramer and Medem claim that their present study has a “prospective” character since it provides the foundations for further work on Lizard populations both within and beyond the Southern Italian area. See ibid., 86–87.
speciation we would also expect that Kramer henceforth took a more adaptionist standpoint – even in questions of *allopatric speciation*. My impression is that Kramer, in later stages of his theorizing on animal speciation, deviated slightly from other advocates of a wider understanding of the neo-Darwinian Synthesis such as, for instance, E. Mayr, insofar as he was not prepared to give up the idea that even in small isolated populations there might be selective pressures at work.\footnote{This characteristic adaptionist stance of Kramer’s Evolutionary Biology persisted eventually well into the mid-1950s and also went into his early studies on allometry. Therefore I would like to direct my readers’ attention already at this point of my account to the controversy Kramer had to fight out with M. Hartmann in the early 1950s in matters of racial formation in Italian Lizards. See to this MPG-Archives, III. HA, Rep. 77, file 11, letter G. Kramer to M. Hartmann (25/08/1953), Hartmann’s reply MPG-Archives, III. HA, Rep. 47, file 798, letter M. Hartmann to G. Kramer (17/09/1953), Kramer’s rejoinder ibid., file 798, letter G. Kramer to M. Hartmann (21/09/1953) and for Hartmann’s persisting view ibid., file 798, letter M. Hartmann to G. Kramer (28/09/1953). In this context, it is also important to take into consideration Kramer’s correspondence with M. Eisentraut who was employee of the *State Natural History Museum Stuttgart* (Staatliches Museum für Naturkunde, Stuttgart) and shared Kramer’s adaptionist standpoint but thought of other sorts of selective pressures than Kramer being at work in small insular Lizard populations. See MPG-Archives, III. HA, Rep. 77, file 8, letter M. Eisentraut to G. Kramer (15/09/1953), ibid., file 8, letter M. Eisentraut to G. Kramer (30/09/1953), incl. ms. “Der Inselmelanismus bei Eidechse und seine Entstehung im Streit der Meinungen” (ca. 1953), page 1–7 and ibid., file 8, letter G. Kramer to M. Eisentraut (13/10/1953).}

population thinking, Dobzhansky offered a purely population genetic mechanism to explain the possibly arbitrary development in small populations by introducing what he himself used to call “scattering of variability” and population geneticists nowadays describe as “drift”. From a mere epistemological point of view, this concept of inheritance mechanism in small populations reveals already the modified neo-Darwinian re-evaluations because it explains the more or less cataclysmic and arbitrary changes traceable in small populations with the statistic principle of chance. In addition to that, Dobzhansky’s drift-concept is not restricted to insular populations since it applies to any small self-enclosed genetic population, that is, also to isolated mainland populations. Both aspects suggest a slightly modified epistemic framework which G. Kramer seems to have adopted in 1940 at the latest.

In sum, we may therefore say that G. Kramer’s and F. v. Medem’s joint work has not only a preparatory and open character and thus applies an epistemic scheme complementary to the one used in the earlier study, it also reveals, so to speak, in its constituent parts the typical epistemic re-evaluations we can observe both in advanced neo-Darwinian theory and the consolidated scientific paradigm upon which Classical Ethology rested since ca. 1940 (in N. Tinbergen’s case slightly earlier). Epistemic re-evaluations, that is, shifts in underlying hierarchies, are difficult to make evident but I think it is possible if we have a closer and more careful look upon how particularly the paradox semantic relations change within the examined epistemic patterns. In the following I’d like try to give some examples. The first example I have chosen is Kramer’s and v. Medem’s treatment of methodology. From the paper’s introduction we can deduce that Kramer and Medem approached the issue of “methodology” from two different angles. One is mentioned in the introduction itself and therefore has a more universal character. The other idea of “methodology” is chapter-specific. That is to say, like R. Dawkins later claimed as editor of Animal Behaviour, Kramer and Medem suggest that the methodology should be discussed separately for each section of the paper and thus be individually adapted to the respective experiment or observations presented in the respective section. In doing so, the idea of “methodology” becomes ambiva-


\[\text{Clear indicators that G. Kramer had adopted population genetic models in general and the drift concept in particular can be found later in the lectures he delivered at the University of Heidelberg between 1946 and 1947. See MPG-Archives, III. HA, Rep. 77, box 1, ms. “Ökologische Genetik” (ca. 1946), II. Vorlesung, pages 4–7.}\]

\[\text{In other words, Kramer’s scientific development at this point makes both a progressive linear shift and “switches” the realms. This is difficult to explain.}\]

\[\text{Kramer et al., „Untersuchungen an Kleinpopulationen”, 87. This is why chapter three and chapter four both have a separate subsection at their beginning which is called “Methodologisches”}\]
lent not only because it appears in different parts of a scientific treatise but also because it is superimposed with the idea of multiplication and chapter-specific adjustment. This ambivalence shapes not only the methodological framework as a whole it equally applies to its universal part. Thus we are informed that G. Kramer in comparison to his earlier studies changed the scientific practices with which he used to preserve the caught specimens. While the Lizards so far were killed and preserved as a whole animal, Kramer now conserved only particular body parts, that is, mainly the skin. “Wir gehen bei der Darstellung so vor”, Kramer and Medem ascertain,


And later on it reads:

Wie schon erwähnt, wurden die Eidechsen mit wenigen Ausnahmen als Häute konserviert. So konnte ohne weiteres unterm Binokular gezählt werden.

The quotations show that Kramer’s and v. Medem’s practices of animal preservation shifted away from conserving the whole animal in liquid because they were looking for a method that was adjusted to their needs, mainly their interest in more particular anatomical details (i.e. the inner side of the skin), the space-economic storage and finally, the opportunity to count easily. In other words, the scientific objects partly loose their holistic shape. Instead they are reassessed as conglomer-
ate of valuable body parts – highly adjusted to the very specific research interest of Kramer and his coauthor. My argument now is that the modified preservation methods corresponded with a re-evaluated epistemic scheme that became manifest in these practices: Just like the idea of Drift reinterpreted the inheritance mechanisms in small populations in a statistic manner, Kramer’s and v. Medem’s revised method of animal preservation paved the way for a more of quantification and allowed for asking more particular research questions. In neo-Darwinian theorizing the idea of wholeness becomes less definite, certain and uniform. And analytical reductions needed to be substantiated by quantification.

Another example is Kramer’s and v. Medem’s assessment of the geographic regions in southern Italy where they chose the prototypical populations for their study. It has already become clear that Untersuchungen an Kleinpopulationen examines geographical varieties of one subspecies (Lacerta sicula Rafinesque) from a comparative perspective. Thus the study in question defined mainly five representative collecting areas two of which were located on the Sorrentinian peninsula, while the other three located on Capri Island. In each case one set of area was near the narrowest point of the watershed that divided mainland and insula, while the other collecting sites were more in the hinterland each (or better: more remote from the strait). If I read correctly it is also the sites in the hinterland which were located on higher plains so that the representative populations can be classified in the following scheme (Fig. 2.24).

The series (A, B, C.1, C.2, D) proceeds from East to West, that is, from the mainland into the direction of the island. The crucial question now is how the relation between the mainland and the island is conceived both with a view of geography and the Lizard population each area accommodates. My argument is, that in contrast to Kramer’s earlier cooperative study where the idea of isolation prevailed over the moment of continuity, in Untersuchungen an Kleinpopulationen we find a modified view in as much as the island is thought more as a separated continuation of the mainland. “Capri”, Kramer and Medem underline,

besides other possible reasons, this issue might be the reason why the cooperation with R. Mertens had not persisted. Maybe, a museum taxonomist, though interested in real geographic distribution, might have had and interest in the whole animals because a museum like the Senckenberg Natural History Museum collected and preserved with a view of a wider range of research interests. It would be of interest to include more archival sources at this point.

A geographical representation of this scheme can be found in Kramer’s and Medem’s text. See ibid., 88, fig. 1.
The phrase “abgetrennte Fortsetzung” (“separated continuation”) describes also the relationship between island and mainland in paradox terms and the fact that the entire geographic system obtains a stronger continuous nuance is a clear indicator that we have to do with a re-evaluated system in comparison to the former studies. It remains to ask whether and how later sections of the paper substantiate this view. A further example for a shifted paradox might be Kramer’s and Medem’s hypothesis that squamae and shields of the Lizards can serve as a distinctive feature. Thus both authors submitted the body surface of the Lizards to a quantitative analysis counting scales and shields along several previously defined and more or less species-specific parameters. The result of this quantitative analyses (which were carried out for male and female specimens separately) was that the obtained values for several parameters differed slightly from population to population and thus a graded stepping could be proposed which Kramer and Medem in their joint paper write as “Pta. Campanella > Pta. S. Elia > Mte. Tiberio > Mte. Solaro”. The series shows that it is not a simple “from-East-to-West” distribution and that each site may partly have its own regularities. However, the series also reveals the lower values for the insular populations. For my argumentative purpose it is important to keep in mind that this scale was obtained by more sophisticated quantitative analyses of morphological characters. Moreover, the mere counting was partly supplemented by additional calculations such as the multiplication of the “Querzahl” with the “Längszahl” to one (hypothetical) “Gesamt-Rückenzahl”. Finally, Kramer and Medem put emphasis on those data which contradicted the series. This was the case, for instance, with the “Längszahl” of the male Lizards collected at “Mte. Solaro” and “Mte. Tiberio”, on the one hand, and the amount of sub-digital lamellas in the population of the Landfaraglione.

In sum, we may therefore eventually say that Kramer in his later study applied a more statistic-oriented approach of assessing morphological qualities and, in contrast to the extreme mathematical reduction of his earlier cooperative study, turned out to be more open for possible exceptions. Heuristic certainty thus appears as a matter of statistical reduction and standard deviation rather than the mere outcome

1479 Kramer et al., “Untersuchungen an Kleinpopulationen”, 89.
1480 To the more fixed parameters belonged, for instance, the number of back scales in one specifically defined transverse row (“Querzahl”), the amount of transverse rows of belly shields, the number of transverse rows of back scales corresponding with ten belly segments (counted in a particular mode) that is the “Längszahl”, the amount of so-called femoral organs, and the number of sub-digital lamellas under the fourth tow of the hind leg. For these parameters and the conventions of counting see ibid., 90–92.
1481 For these results see ibid., 92–97.
1482 Maybe, it’s also important to realize that Kramer and Medem analyzed the surface of the body and not the skeleton. The emphasis was thus on peripheral morphological features.
1483 Ibid., 95–96.
1484 Ibid., 94–95, 97 and 115 for the population of the Landfaraglione.
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of aprioristic presumptions. And this seems to presuppose a more of potential uncertainty inside the system.

The modified paradox in G. Kramer’s and F. v. Medem’s treatment of the categories “Measures and Proportions” consists in the relative lowering of the distinctive value of the two parameters in comparison to the earlier study on west-Istrian Lizards. Mainly two longitudinal (length of the torso including the head, length of the tail) and one transversal size (the breadth of the stretched out hind limbs) were measured. The objects used for the results that Kramer and Medem present in the fourth section of their joint paper is described as “frisches Material” (“fresh material”).

The usage of preserved material apparently led to distorted measurements, while living animals, though narcotized, generate more adequate results. The account of “Measures and Proportions” thus reveals an upgrading of both the living animal and, simultaneously, the idea of scientific accuracy. What were the results like and what do they tell us about the modification of the underlying epistemic framework? Thus Kramer and Medem found out that there was no significant difference between the single populations as to the average size of head and torso nor the proportion of body and tail size. “Die Höchstmasse für Kopf-Rumpf sind in Tabelle 3 gegeben”, Kramer and Medem summarize and continue:

Wir sind auf Grund der vorliegenden Zahlen nicht befähigt, eine Verschiedenheit in der Körpergrösse der untersuchten Populationen festzustellen. Die genaue Beurteilung der Körperschwanzer Proportionen ist durch die Seltenheit unversehrter Schwänze erschwert. Lassen wir die 4 Werte vom Landfaraglione zunächst beiseite, so kann man immerhin sagen, dass Unterschiede zwischen unseren Populationen, sollten solche überhaupt bestehen, sehr gering sein müssten.

The absolute measures for the length of head and torso are shown in Table 3. On basis of the given figures we are not entitled to claim a difference in the body sized of the examined populations. The exact evaluation of the body-tail-proportion is more difficult due to the rarity of intact tails. If we leave unnoticed for a moment the 4 values of the Landfaraglione we can at least say that the differences between our populations, if they exist at all, must be extraordinary small.

In addition to these two results, the measurement of the transversal extent of the hind legs revealed that the relative “Quermass” that is the quotient of the transversal extent of the hind limbs, on the one hand, and the sum of head length plus torso length, on the other, decreases from a certain body size onwards. However, Kramer and Medem were able to demonstrate that this regularity applies to all the populations examined by them, so that what they called the “relatives Quermass” could not serve as distinctive quality either. As a result one may therefore say that in Untersuchungen an Kleinpopulationen there is a trend to more scientific accuracy while assessing body size and body proportions but that the values obtained in this way downgrade the relative significance of both morphological categories and their distinctive value. The interplay of both theorems thus might have changed in comparison to the earlier study since G. Kramer and R. Mertens had suggested in

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1485 Please take into consideration the turn of other ethologists to more cautious approaches of taxonomy which occurred simultaneously in other heuristic frameworks. A prototypical example for this move is K. Lorenz’s Anatinae paper of the year 1941.
1486 Ibid., 100.
1487 Ibid., 102.
1488 At least when it comes to compare Sorrentinian populations with those of the Capri Island.

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their comparison between Istrian mainland and island Lizards that the latter were deviating in their body size from the former. Also it is not clear whether R. Mertens had measured the body size of the Lizards while they were living.1489 This result can also be interpreted from a more methodological perspective. While the usage of less fresh material may lead to partly distorted results and these results may have a negative feedback effect upon both the method itself and the relationship between the methodology and the result, the usage of fresh material leads to more adequate results and the quantitative assessment as a whole becomes more productive. In addition to that, the practices of raising the “material” for the studies seem to rest on an altered disposition as well. It makes quite a difference whether living animals are transferred over a wider distance from Italy to Frankfurt where they are killed, subdued to a morphological analysis and then stored or, on the contrary, they are kept in situ, narcotized and measured as living creatures. In the former case “fixation” is absolute and renders the entire purpose of assessing living creatures somewhat paradox as a whole, while in the latter case the fixation is temporarily and dominated by the idea that the quantitative assessment of a living specimen generated more precise results. Only in the latter case we face the productive paradox epistemic constellation I have described as “Darwin’s paradox”. Most likely with discussing the distinctive value of the characters “Patterning and Colouration” Kramer’s and Medem’s account reaches a crucial point.1490 In this section of their paper they examine mainly four traits, namely the intensity of the patterning, the basic green pigmentation, the tendency to blue colouration and, finally, the darkening. The result of this comparative measurements revealed that some of these features are typical for a single population but in a highly location specific way. Thus Kramer and Medem showed – again in an examination of living animals – that Capri populations have less intensive skin patterns than mainland Lizards but that the Landfaragliione population is an exception to this rule since the patterns in this collection turned out to be more intensive.1491 Whether a Lizard is coloured green, non-green or somewhere in-between is depending on the season and, beyond that, is a quality that varies from individual to individual and its age.1492 It is therefore not a primarily population-specific quality. Moreover, according to Kramer and Medem a normal system of blue colouration can be distinguished from a coexisting additional system they called “Extrablau”.1493 The latter of the two reappears at typical locations of the body independent of the normal blue-system in one third of all examined animals, that is, quite independent of the collection site. “Wir haben gesehen”, Kramer and Medem therefore summarize, dass alle Populationen Individuen mit Extrablau liefern, und wir sind nicht in der Lage zu sagen, dass die eine oder andere eine stärkere oder häufigere Ausprägung dieser Eigenschaft aufweise. [We have seen, that all populations generate individuals with extra-blue and we are not ca-

1489 For sure is that G. Kramer had sent them to Frankfurt as living animals. See Kramer et al., “Rassenbildung bei westistrianischen Inseleidechsen”, 190.
1490 See to this, for instance, the high esteem Kramer and Medem hold for the aspect of the blue colour trait with a view of future systematic studies. See Kramer et al., “Untersuchungen an Kleinpopulationen”, 110.
1491 Ibid., 108, 117.
1492 Ibid., 108.
1493 Ibid., 111, 117.
pable of saying that one or another reveals a stronger or more frequent expression of this characteristic.

The appearances being connected with the extra-blue-system thus seem to be no characteristics which distinguish the examined populations – at least at first sight. As to the character “darkening” one may say that Kramer and Medem could answer the question in how far the feature is population specific only provisionally. This is most likely due to the fact that the anatomic mechanism underlying the lack of colouration was still waiting to be examined in detail. We are only informed that the trait shows an extremely high extent of variability both with respect of the inner and the outer side of the skins. What remains is a paradox, quasi-negative result. “Letztere Folgerung stellt natürlich den Wert eines Vergleichs des äusseren Aussehens in Frage, da es ja auf verschiedene Weise zustandekommen kann”, Kramer and Medem conclude and proceed:

Jedoch ist das Ergebnis ohnehin ein negatives: Soweit bei der herrschenden Variabilität innerhalb der einzelnen Populationen und bei der Schwierigkeit einer quantitativen Wertung etwas auszusagen ist, müssen wir gleiche Dunkelheit der Populationen feststellen. Diese Aussage ist für die Innenseite der Häute immerhin durch sorgfältige, aber subjektive Vergleiche der konservierten Häute begründet.

[The last inference certainly questions the value of a comparison of the outer appearance since it can originate in quite different ways. However, the result is a negative one anyway: In as much as the prevailing variability inside the single populations and the difficulty of obtaining a quantitative evaluation allows telling something definite we must state the existence of equal darkening in each population. This statement can legitimately be confirmed for the inner side of the skins at least through careful yet subjective comparisons of the conserved skins.]

To sum up, I need not tell that the four discussed aspects of patterning and colouration appear in a regular order so that the organization of the chapter can fulfil its function in the overall composition of the text as a whole: Only the intensity of the patterns has a distinctive value. All other aspects – the green colouration, the blue-systems and the darkening, cannot or at least not on a superficial level of taxonomic analysis claim to distinguish the populations of the different collection sites. The latter of the four aspects at least establishes a new model for comparative study by interpreting the dark skin colour (or the lack of colouration) as a combination of the colour of both the inner and the outer side of the skin. The chapter on colouration and patterning thus altogether leaves the impression that Kramer and Medem raised partly population specific yet mostly highly variable and partly individual morphological characters. With a view of the purpose of the overall “differential diagnosis” we can therefore ascertain that these, at first glance non-distinctive, characters can only claim to be of taxonomic value if they, in future studies, turn out to be pop-

1494 Ibid., 113.
1495 And nonetheless, Kramer and Medem underline that it is exactly this quality which is of an utmost importance for a future study which aims to derive the insular from the mainland populations. See ibid., 110, 111. The reason might be that such an extreme micro-systematic project requires the existence of a hereditary characteristic which all the individuals of a sample share but, within this sample, shows an extraordinary high grade of variability. “Extra-blue” seems to fulfil this request.
1496 Ibid., 114–115.
1497 Ibid.
population specific on still finer levels of micro-systematic examination. For the time being, they seem to bear a paradox character or, as Kramer and Medem put it, they might have a “prospective” potential. We have already seen in other contexts such as N. Tinbergen’s late turn to Ecology that “Darwin’s paradox” turned out to be an extraordinary innovative heuristic figure which generated many new research endeavours in the second half of the 20th century. G. Kramer’s “prospective” account is another example because it suggests that morphological characteristics that seemingly have no taxonomic value might obtain this value in later more sophisticated reassessments, so to speak, despite their momentary handicap. On the other hand, we see: There is no general developmental trend “from-the-mainland-to-the-insula” in the phenotypic appearances such as colouration, patterning, body size or body proportion. Kramer’s and Medem’s late study shows that each attribute needed to be assessed individually both with a view of its taxonomic value and its expression in each single population. In other words, what Kramer called “differential diagnosis” obtained a more atomistic stance and the re-evaluation of the underlying analytical epistemic scheme turns out to be a precondition of this modified and more cautious view. It remains to ask how does this result fit to the new chance model of geographical isolation that has been put forward by Th. Dobzhansky in his book *Genetics and the Origin of Species*? In general, one may say that Kramer’s more cautious mode of assessing the problematic of speciation, in the last consequence, led to a differentiation between those qualities which were subject of selective pressures and those that were distributed randomly as a consequence of genetic drift. As to the latter model of explanation one essential aspect most likely is that a drift model can explain the highly arbitrary and individual development Kramer and Medem had observed particularly in the population they found in the collecting area they called the “Landfaraglione”. With Dobzhansky’s book one may say that each micro-population, independent whether on the mainland or the island, can be subject to drift and take its own accidental course if the population is isolated by barriers. In this very particular developmental possibility the populations examined on the Capri Island do not seem to be very different from the mainland populations so that the new view upon isolation legitimates the description of Capri as “abgetrennte Fortsetzung” of the mainland. Concluding, I’d like to profile once more the epistemic transformation that took place with G. Kramer’s move to Naples by providing a condensed comparison between Kramer’s earlier and later cooperative research – that is to say, the comparable parts of each study. At first, both studies, that is, *Rassenbildung bei westi-strianischen Inseleidechsen* (carried out with R. Mertens) and *Untersuchungen an Kleinpopulationen* (carried out together with F. v. Medem) make use of more or less the same morphological categories with which R. Mertens had analyzed the west-Istrian Lizards morphologically (i.e. squamosity and shields, body size and proportions, patterning and colouration). However, in Kramer’s later work, though keeping these analytical categories, we can make evident a more sophisticated statistical usage of them. In general, the methodology is adjusted to the needs of each

1498 For Kramer’s and Medem’s interpretation of the found data in terms of Dobzhansky’s theory see Kramer et al., “Untersuchungen an Kleinpopulationen”, 115–116.
part of the study. In addition, Kramer more explicitly reflects upon the taxonomic value of each category in each sample population. Moreover, while in the former project phylogenetic development was primarily conceived as a *function of geological change*, this view turned out to be too simplistic: Although Kramer and Medem found qualities shared by the island populations that separated them from the mainland samples, there is *no complete uniformity* in phylogeny since the phylogenetic scale Kramer and Medem established between the collecting sites (with a view on some characters) did *not* coincide with a simple geographic distribution of the found features “from-east-to-west”. Some results even partly inverted the presupposed phylogenetic scale itself. The findings of some places (especially the Landfaraglione) broke up the series altogether. These findings required a more relativistic approach to the problematic of speciation which Kramer eventually found in Th. Dobzhansky’s drift model for small populations – if he felt it was applicable at all. Correspondingly, the mere *geo-*graphic representations of animal phylogeny changed into *graphic* expressions of statistical correlations.

In the following I’d like to show that all Lizard studies G. Kramer published during and shortly after his Naples period, as well as those that appeared with some further delay of time, perpetuated the preparatory character of *Untersuchungen an Kleinpopulationen* – partly even by picking up some particular aspects raised in this paper. Thus all these works seem to be centred around the question whether and how seemingly non-distinctive morphological characters could obtain taxonomic value in a still finer micro-systematic perspective. Furthermore, it must be clarified in how far Kramer’s more cautious approach to animal speciation coincided with a turn to the core theorems of the Modern Synthesis, namely gradual accumulation of heritable variability and natural selection. Both questions, in particular, apply to Kramer’s account of the so-called “concolor”-trait, that is, the absence of skin patterns. G. Kramer had already touched this issue in his chapter on “Patterning and Colouration” in *Untersuchungen an Kleinpopulationen*. There he had concluded that the examined sample populations differed in the intensity of the skin patterns but not in the factor that regulated the overall darkness of the skin. In *Über das “concolor”-Merkmal (Fehlen der Zeichnung) bei Eidechsen und seine Vererbung* he reassesses the question and aims to prove that the lack of skin patterns is regulated by one single recessive mendelizing hereditary factor which, though, is occurring in varying quantitative proportions with corresponding phenotypic effects. Kramer’s vision apparently was that the proportion of animals with and without skin patterns was specific in each population and that, therefore, a large scale comparison of the populations along this trait could clarify the taxonomic relationship between living Southern Italian populations of Lizards. “Gezeichnete und Concolor-Tiere”, Kramer argues,
kommen gewöhnlich in der gleichen Population nebeneinander vor, aber in unterschiedlichem Häufigkeitsverhältnis. Wir verfügen hierin erst über wenige exakte Daten, und es wird eine wichtige Aufgabe sein, die Häufigkeiten dieses Eigenschaftspaares in recht vielen und recht weit auseinanderliegenden Populationen festzustellen.

Patterned and concolor-animals usually coexist in the same population however in varying proportions. As to this question we have still only a limited amount of data and it will be an important job to assess the proportions of this pair of traits in quite many and rather distant populations.

Before this project could be tackled it needed to be clarified whether the concolor-trait had taxonomic value presupposed the systematic entities in question could be determined in accordance with the new biological, that is, genetic based, concept of species in particular and any other taxonomic unit in general. This, roughly spoken, seemed to be the purpose of G. Kramer’s account. In order to achieve this objective Kramer again applied an approximative narrative scheme: The first step of this argumentative scheme consisted, as I have mentioned already, in reducing phenomenological complexity to one explanatory principle – the thesis that one mendelizing factor (in combination with a virulent drift mechanism) might be sufficient to account for the geographic distribution of the concolor trait. In the second step of Kramer’s argumentative scheme this thesis is substantiated further by applying its basic ideas to ever wider scopes of applicability. This is why Kramer, in the core of the paper, supplements mere Morphology with Histology, why the complex of both areas of research is supplemented with a zoogeographic approach and, finally, why the entire complex, then, once more is tested by making use of additional breeding experiments. Having a closer look upon the paper’s organization, one may eventually say that this argumentative scheme, in its core, consists in extending the traditional zoogeographical set of inquiry with what might be called a “hybridization test”: Only if the artificially bred hybrids turned out to be viably (and revealed the expected phenotype) it was possible to claim that the traits in question (i.e. concolor and non-concolor) were homological (i.e. were shaped by Mendelian factors covering the homological loci of the chromosome pair in question) which, in turn, for Kramer was apparently a necessary precondition for the comparability of the trait itself.

In other words, each comparison requires a common third (terium datur) and Kramer wanted to make sure that he was actually comparing expressions of one and the same hereditary “factor” – in concrete the chromosomal sections that were correlated with this “factor”. Or still in other words, Kramer realized that he was not allowed to infer simply from the phenotype to genotype (which a mere superficial view upon the geographic distribution eventually might have entailed) since seemingly similar phenomena might have quite different genetic origins. This inference was only legitimate on basis of an argumentation and the current paper provides this argument approximatively. I think it is not necessary to go into further detail. It may suffice to point out some examples for the epistemic re-evaluations that Kramer had introduced in Untersuchungen an Klein-

1502 In all this surely Th. Dobzhansky’s genetic approach to the problem of geographical distribution is in the background. Thus Dobzhansky had interpreted the extent of the chromosomes’ deformations which naturally originate in hybrids as measure of the varieties’ genetic relatedness.
Gustav Kramer (1910–1959)

populationen and now became the basis for his consolidated neo-Darwinian way of thinking. A first example might be G. Kramer’s re-evaluation or reassessment of already existing taxonomic units or conventions. He had picked mainly two different Lizard species for his study (Lacerta melisellensis or L. fiumana and Lacerta serpa Rafinesque) yet his research report shows that biologists who were concerned with the concolor-trait tended to “invent” more classificatory entities than necessary by declaring those specimens which had no patterns a separate subspecies in every single species. Kramer’s approach to make evident the homological character of the quality across the species boundaries thus was meant to reduce the extent of taxonomic differentiation by applying a more plastic concept of species (or subspecies, respectively). “Das nomenklatorische Prinzip, parallele Varietäten bei verschiedenen Arten mit getrennten Namen zu belegen”, Kramer says,

führte zur Akzeptierung von imitans Werner für ungezeichnete Tiere der L. melisellensis fiumana. Diese nomenklatorische Regel, die Wettstein (Fußnote S. 274) im Hinblick auf die hier behandelte Eigenschaft erneut betont, wird gegenstandslos in dem Augenblick, wo Anlaß besteht, die vorher nur deskriptiv geordneten ähnlichen Eigenschaften für genetisch homolog zu halten. Dies ist hier der Fall.

[The nomenclatural principle to attribute parallel varieties in different species with separate names has led to the acceptance of imitans Werner for the unmarked specimens of L. melisellensis fiumana. This nomenclatural principle, which Wettstein (footnote p. 274) emphasized once more with a view upon the trait that shall be dealt with here, becomes obsolete in the moment we have reason to believe that the characters that had been classified before only descriptively turn out to be genetically homologous. This is the case here.]

As a result, we may say that Kramer’s attempt to evince the concolor-trait as genetically homologous cross-“specific” (specific on basis of the more complex taxonomic nomenclature) trait is not only a necessary prerequisite for further comparison but also had an effect on existing nomenclatural doctrines. My focus is epistemological and my impression here is that Kramer’s more plastic understanding of the systematic entities in question is another example that in neo-Darwinian theorizing those theorems which are expressing wholeness become more flexible, less absolute and, beyond that, want to be more adjusted to the actual needs of the taxonomist. Another example might be the methodological reassessment of the disciplinary boundaries that were separating Morphology from other neighbouring branches of zoological and anatomical research. We can infer indirectly from G. Kramer’s account that the more a systematist entered in ever finer realms of micro-classification and, in the last consequence, intended to establish correlations between phenotypic expressions and corresponding genes, the more urgently Classical Morphology was requested to open itself for other neighbouring disciplines. This is most likely the reason why we find in Über das “concolor”-Merkmal an entire chapter dedicated to “Morphology and Histology” (“Morphologisches und Histologisches”). 1504 Thereby it is important to realize that Kramer connected both research areas with an “and” in the heading of the respective section of his paper. In concrete the extension of Morphology with Histology meant that the appearance “lack of skin pattern” was not only assessed on basis of the traditional morpholog-

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1503 Ibid., 1–2.
1504 Ibid., 2–5.
ical classificatory categories (species, age, sex) but also with an even more microscopic view upon the Lizards’ skin, its tissue and the histological peculiarities of the scales that appeared either dark or unmarked. Thus Kramer was able to show that unmarked squamas consisted mainly of three different layers that is an outer epidermis with epithelial melanophores (A), an intermediate layer with connective tissue in which lipophores andallophores were woven together (B) and, finally, a deeper lying layer consisting of so-called iridocytes (C). In black (i.e. marked) scales, by contrast, layer B and C were absent, while layer A turned out to be equipped with more densely located melanophores. From the graphic with which the author aims to explain the effect of each layer upon the visibility of the marked color and the explanation of this illustration G. Kramer further provides we can easily infer that the absence of skin patterns is a paradox appearance since it rests upon the presence of two further layers of tissue in unmarked scales. In concrete Kramer claims that melanophores and iridocytes interact with each other in a complementary manner, or in the sense of a trade-off. The more of iridocytes in unpatterned scales automatically reduces the concentration of melanophores and thus leads to a balance of both concentrations which is perceived as lack of patterning. These additional tissues thus have the effect that the squama as a whole appears unmarked and indifferent as to its colouration. Needless to say that the type of paradox Kramer develops here at this point of his paper in an admittedly highly sophisticated manner coincides structurally with the other holistic paradox appearances I have examined so far: From a more concrete argumentative perspective, Kramer’s findings that it is the histological composition of the scales which determines the appearance of skin-patterning and not the skin itself – the colour of the inner side of the skins remained constant – substantiated his hypothesis that the observed phenomenological differences between the populations were not qualitative but due to quantitative proportional shifts of a particular hereditary factor. Another example is how Kramer conceives the relation between appearance and its occurrence, in other words, the geographical extension (here: distribution) of the phenomena in question. From Kramer’s account in his paper Über das “concolor”-Merkmal we can deduce again more indirectly that he considered it insufficient if systematists concentrated exclusively upon the geographic distribution of a predefined taxonomic entity (species, subspecies) in which they examined the occurrence of a taxonomic trait. By contrast, his approach implied a wider understanding of occurrence beyond the boundaries of each single taxonomic unit. As a result, we can therefore say that the more plastic notion of species mirrored in the corresponding conception of “geographical distribution”. Zoogeography thus was challenged with a need for large scale comparisons of gradually deviating hereditary qualities. If we consider the data Kramer provides both for non-Neapolitan and Neapolitan populations we get the impression that considering the geographical distribution of the varying proportions for unmarked and marked animals can make evident the population specific character of the trait. However, for my argumentative purpose it is essential to realize that

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1506 See ibid., 3–4.
1507 For this argument see mainly chapter “III. Vorkommen”, ibid., 5–7.
1508 See to this the paragraph I have quoted in fn. 1501, page 478 of my thesis.
Gustav Kramer (1910–1959)

Kramer somewhat downgraded the mere binary opposition “marked vs. unmarked” by presuming the dichotomy might be the extreme end of a graded scale. “Für die serpa-Populationen der Neapeler Gegend lassen sich die bestehenden Verhältnisse nicht so einfach im Sinne ‘gezeichnet oder ungezeichnet’ ausdrücken, da die Extreme Endglieder einer ununterbrochenen Variationsreihe sind”, Kramer underlines and proceeds,


[As to the populations in the Naples area the appearances cannot simply be described in terms of “patterned vs. non-patterned” since the extremes turn out as the final element in an uninterrupted series of variations. Kramer and v. Medem classified the Lizards of two populations of the Sorrentinian peninsula by applying the criterion of skin pattern intensity and found out that the proportion of the less intensively patterned to the more intensively patterned classes was 0.66:1 (Pta. Elia) and 0.61:1 (Pta. Campanella). On the island Capri, by contrast, the proportion shifted in favour of the lack of patterning. Two populations revealed the corresponding figures 1.18:1 (Mte. Tiberio) and 1:1 (Mte. Solaro). The Landfaraglione, a piece of rock which is still connected with Capri but whose population can be considered isolated and self-contained towards migration, accommodates only marked animals. – Mertens, already in 1916, had distinguished between more and less marked, respectively unmarked individuals in the population of Positano which is lying close to Pta. S. Elia. Of 300 individuals about the same proportion belonged to both groups. Considering the subjective methodology of Kramer and Medem as well as of Mertens the results certainly cannot be brought down to one common denominator.] (transl. CL)

The examined populations thus differed not only in the relative proportion of the concolor-trait (to the inside) but also, and more general, in the intensity of the expression of the contrast itself (from population to population). This implies that Kramer’s concolor-trait was the expression not only of one single allele but of many whereby the extreme contrast is to be understood as drastic proportional imbalance providing the reaction norm for the respective phenotype. The epistemic downgrading of the moment of discreteness as mere extreme end of a graded scale thus opens a window for the idea of the involvement of multiple alleles (of the same type) and thus of population genetics in general. However, this population thinking, as E. Mayr put it, also affects the way how to conceive the dualism between appearance and occurrence since, in the last consequence, the appearances are more conceived from their occurrence-side that is as mere populations of genes and their proportions. From the epistemological point of view, we can therefore say that the

1509 Ibid., 6.
upgrading of the population thinking affected both the way how to rate phenotypic alternations within a population and the relatedness of the populations as such: One population thus appeared as gene pool within a gene pool. This questioned the idea of qualitative discreteness and corroborated the notion that phenotypical differences can be resolved in proportional shifts of more or one hereditary factor. The final example I’d like to mention is related to Kramer’s breeding experiments. 1510 These, by the way, can only be carried out with living animals. Kramer’s breeding experiments proceeded in two steps. At first, he crossed concolor with non-concolor individuals of both examined species (L. serpa and fiuman) separately (intraspecific crossings). The tests consisted both of crossings with allegedly homozygous parent animals and of so-called back-crossings of heterozygous F₁ individuals. According to Mendel’s laws the F₂ generation then must reveal all phenotypes in a fixed proportion. Since Kramer claimed that the concolor-trait was based on a single, recessive factor this proportion was expected to be 3:1. 1511 The final result was that L. fiuman revealed a more alternating distribution, while the variability in the L. serpa sample was much more gradual or gliding. Kramer explained this matter of fact with an incomplete dominance and additional combining modifiers next to the main alleles. 1512 Hence the final results, once more, turned out to be more complex and the observation of a more graded scale of variability in Lacerta serpa raised the question for additional modifiers. Applying Mendel’s laws, although they seemed to hold in principle, required additional presumptions. However, there is one reason why Kramer’s experiments with intraspecific crosses was an essential step in his overall train of thought, too: Asides the dissonance in the extreme expressions of marked vs. unmarked the phenotypical expressions of the character was identical in both species which was a veritable indicator for the homology of the factor and an essential precondition for Kramer’s succeeding attempt to breed interspecific hybrids. “Dem phänotypischen Verhalten nach unterscheidet sich die Zeichnungslosigkeit von L. fiuman durch nichts von jener der L. serpa, es sei denn durch die oben besprochenen Unterschiede in der Variation und der Ausprägung”, Kramer writes and proceeds:

Diese Feststellung phänischer Gleichheit gilt auch für die histologischen Bilder. Da zudem die beiden Arten nächst verwandt sind, ist es von vornherein wahrscheinlich, daß es sich um parallele Mutanten handelt.

[In their phenotypic appearance of the lack of patterning in L. fiuman does not differ from the one in L. serpa, except in the above mentioned differences in their variation and their expression. This declaration of phenotypic equality also applies to the histological pictures. Since both species are closely related, too, it is very likely right from the start that we have to do with parallel mutations.]

1510 See to this the chapters “IV. Artgleiche Kreuzungen” and “V. Versuche zum Nachweis der Homologie”, Kramer, “Über das ‘concolor’-Merkmal”, 7–12, 12–15.

1511 See ibid., 7. Here it reads: “Die daraus sich ergebende Voraussage des Ergebnisses, daß das Fehlen der Zeichnung durch einen einfach mendelnden Faktor rezessiv übertragen wird, bestätigte sich in der Folge in den kontrollierten Versuchen” [The hypothesis which could be inferred from these results, namely that the lack of patterning is transferred through one simply mendelizing factor in a recessive way was confirmed in the following controlled experiments][transl. CL]. It is unclear in how far Kramer thought the concolor factor was sex-specific.

1512 See ibid., 12.

1513 See ibid. With a view upon the organization of the entire paper one may therefore say that the
I have already mentioned that I regard Kramer’s breeding of hybrids as precautionary measure to avoid the possibility of flawed comparisons. To guarantee comparability meant to proof that the observed phenotypical appearances could be traced back to one and the same genetic source (i.e. were the expressions of homological chromosomal sequences) in every sample population. Providing genetic proof for homology, in turn, could only be achieved approximatively by breeding interspecific hybrids and observe whether the hybrids were revealing the expected phenotypes and, beyond that, were viable at all. “Expected” here means in accordance with the Mendelian laws of heredity. “Kreuzt man in unserem Fall ein homozygotes Concolor-Tier der einen mit einem ebensolchen Tier der anderen Art, und die $F_1$-Bastarde fallen gezeichnet aus”, Kramer argues,

so ist dadurch nachgewiesen, daß diese Nachkommen in bezug auf das Vorhandensein oder Fehlen der Zeichnung in zwei verschiedenen Faktoren, deren jeder sich nur im Fall der Homozygotie manifestiert, heterozygot sind. Die genische Verschiedenheit der Concolor-Eigenschaft bei den Arten wäre damit nachgewiesen. Fallen dagegen in einem solchen Versuch die Nachkommen ungezeichnet aus, so steigt dieses Ergebnis die Wahrscheinlichkeit einer Homologie der betreffenden Allele bei den beiden Arten. Der Beweis der Homologie ist dadurch im strengen Sinn nicht erbracht, da es vorstellbar ist, daß auch zwei nicht allelomorphe Faktoren, von denen jeder für sich bei heterozygotem Vorhandensein wirkungslos bleibt, bei ihrem Zusammentreten sich derart ergänzen, daß ein Effekt zustande kommt, der dem der jeweils homologen Faktorenpaare gleich.

[If we cross, in our case, a homozygous animal of the one with an equally homozygous animal of the second species and the $F_1$-hybrids turn out to be marked then it is proved that these descendants, as to the presence or the absence of the patterning, are heterozygous in two different factors each of which becomes manifest [phenotypically] only in the homozygous case. The genetic dissimilarity of the concolor-trait in both species would evidently be proved. By contrast, if in such an experiment the descendants turn out to be unmarked, this result would increase the probability that the respective alleles are homological in both species. A proof of the homology is thereby not provided in a strict sense because it can be possibly imagined that also two non-allelomorph factors – each of which remains silent in the heterozygous state – complement each other in such a way when they are combined that the effect resembles the one which is produced by a homologous pairing of the alleles.]

Kramer simply applies Mendel’s first law to homozygous individuals of different though closely related species. Being granted that the concolor-trait is recessive it can be expected that the heterozygous individuals (meaning heterozygous in this specific factor) are unmarked if the trait is homological in both species and marked if non-homological. With a view of the epistemic scheme that governs this section one may say that Kramer puts forward a hypothetical alternative which, in a second step, was to be decided approximatively in favour of the second alternative. The paradox within this epistemic scheme originates simply through the fact that this second alternative was apt to corroborate the plastic (less absolute) species

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1514 See ibid. For those who would like to dig deeper into Mendel’s laws which here are the basis for the two hypothesis Kramer’s tests intended to discriminate, see G. Mendel, “Versuche über Pflanzenhybriden”. In: Verhandlungen des Naturforschenden Vereins zu Brünn 4 (1866), 3–47, and Plomin et al., Gene, Umwelt und Verhalten, 11–22.

1515 For Kramer’s final conclusion see Kramer, “Über das ‘concolor’-Merkmal”, 15.
concept put forward by neo-Darwinian geneticists. If the concolor-trait turns out to be homological in different species large scale comparisons are possible and, beyond that, the taxonomic over-differentiatedness could be boiled down by applying a more efficient since more plastic biological conception of the systematic entities in question.

A later study which was published shortly after the end of the war when G. Kramer already had moved from Naples to Heidelberg shows that both the number of offspring and the size of the young descendants can be used as a characteristic for comparing mainland with insular Lizards to evince that the principles of micro-evolution might be sufficient to explain the process of speciation even on small islands. The paper thus is mainly based on research carried out during Kramer’s stay in Naples and is therefore related to this period in his life. Especially by putting emphasis on the criterion of “body size” Kramer proved the taxonomic value of a characteristic that seemed to have less distinctive potential in one of his earlier studies. Moreover, in contrast to the population specific body size of the adult specimens the size of the young seemed to fit much more into a strictly adaptionist framework of evolutionary theorizing. To demonstrate the usefulness of the latter criterion thus was not only another essential preparatory step in direction of a comparative micro-systematic of Italian Lizard populations but also a veritable manifestation of Kramer’s particular selectionist approach to the problematic of speciation. The paper has the “limes structure” we’re already acquainted with, that is, the experimental results that are recapitulated in the core of the paper’s main part are reduced approximatively to one single causal explanation. In contrast to earlier studies, this explanation operates more explicitly with the idea of the organisms’ adaptiveness and thus involves the level of causation. In the abstract of the paper it reads:


[Newly hatched insular Lizards are relatively (and mostly also absolutely) bigger than the offspring of mainland populations. Instead the annual rate of produced offspring is much higher]

1516 See for this general thrust of the paper EGI Alex. Lib., D. Lack Papers, V. Work on clutch size, file 67, letter G. Kramer to D. Lack (24/07/1946) and ibid., V. Work on clutch size, file 67, letter E. Mayr to D. Lack (19/06/1946).

1517 The author makes explicit this aspect by naming the Zoological Research Station in Naples on the title page of his paper. See Kramer, “Veränderungen”, 700.

1518 See Kramer et al., “Untersuchungen an Kleinpopulationen”, 102.

in mainland than in island populations. On basis of the body size distribution and with the help of a combined method of age estimation in adult Lizards it will be shown that the age distribution in insular Lizard populations has shifted in favour of the older age groups. The common cause for all these differences made evident in this study will be explained by 1. the exclusion of the predators from the equation ruling the survival of the species in insular populations; 2. by the aggravation of the conditions of life in summer through which cannibalism is put into place as a particular selective pressure. The last mentioned group of factors favours the increase of the size of the young, while the former allows a progressive development in this direction which is only possible on the expenses of the actual rate of produced offspring. This is so because the rate of produced young has lost its value as selective pressure after the predator factor had become irrelevant.

G. Kramer’s ultimate explanation is highly sophisticated. It presumes that a given species of Lizard is capable of performing two types of reproductive strategies: Either the parents produce many small descendants or they produce fewer but bigger ones. Both strategies are thought to be complementary simply because the reproductive resources of an individual and thus of a population appear to be limited. Furthermore, Kramer presumes a kind of equilibrium or shifting balance between both strategies whereby in insular populations the balance has shifted in favour of the production of a reduced number of more viable offspring. The causes of this equilibrium shift are thought to lie in the particular environmental conditions provided by the insular milieu. Thus G. Kramer names two main reasons, namely the lack of predators (interspecific selective pressure), on the one hand, and the increase of cannibalism (intraspecific selective pressure), on the other. A more epistemological perspective reveals that both causes are connected with each other in a highly complex mode. On the one hand, it is the lack of predators which, according to Kramer’s account, allows at all that an insular Lizard population can switch to a reproductive strategy which favours fewer fitter young. This absence of an interspecific selective pressure is supplemented by a second active and positive force, namely the selective pressure which is exerted by the probability of intraspecific cannibalism: The bigger the young the greater the chance to survive the critical early stages of their lives which is why this reproductive strategy developed at all. The selective pressure exerted by the cannibalism thus is an ultimate cause for the tendency to produce fewer fitter offspring. On the other hand, however, it is this tendency which “checks” the success rate of the cannibalism. In other words, the relation between the tendency to produce fewer fitter young and its ultimate cause – at least from a conceptual perspective – rests upon a veritable paradox since the increased body size “checks” the selective pressure which “generates” it in the first place. I have added another graphic to my account which might illustrate the paradox which originates through the upgrading of the ultimate cause that is thought to be exerted by possible intraspecific cannibalism (Fig. 2.25). My illustration can be read as if the “the tendency to produce fewer fitter young” mediates between a proximate cause, the “absence of predators”, and an ultimate cause, the selective pressure exerted by the phenomenon of “intraspecific cannibalism” while in doing so the proximate cause “allows” the modified reproductive strategy to exist at all and the relationship between the ultimate cause and its phenomenological effect is ambivalent in

Ibid.
as much as the effect “checks” its ultimate cause (and thus, in turn, seems to be its proximate cause). I have somewhat extrapolated Kramer’s account to a certain extent because my graphic suggests a causal relationship between the “lack of predators” (“-Pr”), the amount of young individuals within a population (“+Off”) and the existence of the phenomenon of “cannibalism” (“+Can”). My argument now is that the paradox conceptual relation between the ultimate cause and the appearance it affects is typical neo-Darwinian since it is transferred into the overtone of this particular holistic epistemic frame which G. Kramer had applied to the special case of isolated populations. G. Kramer’s model is of interest not only because it anticipates later ecological studies by claiming the existence of competing reproductive studies but also by revealing the coexistence of antagonistic selective pressures within one and the same population under extreme conditions of life and, in doing so, provides a more integrated view that enabled him to formulate further leading hypothesis, for instance, as to the shifting velocity of phylogenetic development. I have anticipated G. Kramer’s all encompassing final explanation, revealed its paradox epistemic structure and thus demonstrated that the neo-Darwinian re-evaluations can be made evident also on the level of causation. Are there some more examples to substantiate my argument? The first example I aim to pick out is related to the phenomena Kramer calls the “relative constancy of the mainland

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1521 I think that it is this paradox conception which generates the notion that terminating the selective pressure may lead to a stagnation of the phylogenetic development in a population. The question of varying phylogenetic dynamics therefore is raised at this point!

1522 G. Kramer argues that both the extreme climatic conditions on the islands during the summer months and the higher population density may be a cause for the increase of intraspecific cannibalism. In addition, he considers it possible that the inhibition to feed from own kind is reduced when the potential prey object is young and small. See Kramer, “Veränderungen”, 705–706.
populations”.1523 This presumption is mentioned in the introductory section of the paper, that is, more precisely in the section on the applied methodology: Kramer, at first, had named three reasons why his scientific object is a suitable scientific object for a population genetic study.1524 Then he entered into his methodology by providing a rough account on what he calls “Phänoanalyse”, that is, the zoo-geographical comparative assessment of hereditary traits.1525 As a methodological presumption Kramer then names the mentioned constancy-thesis: According to his account, both the geological age of the geographic areas in question and the larger size of the populations on the mainland prevent these populations from accidental cataclysmic changes. In other words, in a population genetic framework the overall quantity prevails and thus restricts the possibility of accidental change. A second example expressing the complementary epistemic scheme is how G. Kramer conceives the correlation between the number and the size of the offspring. Thus, in a longer train of thought, he wants to demonstrate that both factors are complementary and, furthermore, that in small populations the reproductive strategy shifts from producing many small to fewer fitter offspring. In doing so, he demonstrates statistically that the clutch size in island populations is smaller and that the progeny is bigger. Furthermore, this basic double thesis is substantiated by crossing experiments proving that both egg number and egg size is determined by a hereditary factor that is transferred by female specimens only. Further argumentative steps consisted of evincing that egg size and egg number are correlated in principle by a trade-off relationship (the more eggs an organism produces the smaller they are) but that both parameters are determined by independent factors. Additional tests in which Kramer measured not the weight of the young but the length of their body (i.e. head plus torso) confirmed the basic presumption: Insular progeny is bigger. Kramer finally projected the number of produced offspring per year on basis of the annual number of egg dispositions, on the one hand, and the average clutch size, on the other only to evince that the found discrepancy between insular and mainland populations were not singular but mirrored in the annual average rates as well. The entire line of thought finally ends with naming the reasons why the reproductive strategy may have shifted: The bigger body size of the young may be of advantage in milieus where extreme climatic conditions increase the probability of intraspecific cannibalism. An additional lack of predators on the islands allows the population to adjust its reproductive strategy. To sum up Kramer’s line of argument we may therefore say that two basic hypotheses are named in the first place, in a succeeding step, are substantiated by a number of further arguments. These arguments not only confirm each basic thesis for its own but also their intertwining, that is, their character as independent though mutually connected parameters. This ambivalent character implies that both appearances must be accounted for as a

1523 See ibid., 700–701.
1524 See ibid., 700. These reasons are: The individual variability of the Lizards, their ubiquitous occurrence and the density of their populations, and the occurrence on small islands.
1525 Ibid., 700–701. Mainly two aspects are mentioned: If a character is shared by all insular populations Kramer presumes a common formative environmental factor. If, by contrast, a trait turns out to be population specific he presumes a milieu-independent course of differential development leading to this quality.
whole though independently as to their causation, too. This is why G. Kramer distin-
guishes between an active selective pressure and what he calls “Nachgiebigkeit
der Populationsstruktur” (“plasticity of the population structure”). In a concluding
remark it reads:

Im Vorausgegangenen wurden die Eigenheiten des Inselmilieus erörtert, von denen wir an-
nehmen, daß sie einen “Selektionsdruck” im Sinne einer Begünstigung der größeren frischge-
schlüpften Jungtiere ausüben. Ebenso wichtig wie dieser aktive Druck ist die Nachgiebigkeit der
Populationsstruktur in der vom Druck angestrebten Richtung, nämlich im Sinne einer Ernied-
rigung der Nachkommenziffer, ohne welche eine Erhöhung der Nachkommengröße offenbar
nicht zu erreichen ist. Diese Nachgiebigkeit ist offenbar in dem Augenblick gegeben, wo die
fressenden Feinde in der Bilanz der Arterhaltung gestrichen werden können. Es ist eine alte
Erkenntnis, daß eine wesentliche Eigenheit des Inseldaseins eben im Wegfallen der die Art
zehnenden Feinde ist. | Man kann überzeugt sein, daß prinzipiell die gleiche Konkurrenz beider
Tendenzen – nämlich einerseits recht große, andererseits recht zahlreiche Nachkommen zu
erzeugen – auch in der Festlandpopulation besteht. Nur ist ihr Kräfteverhältnis ein wesentlich
anderes, so daß die resultierende Gleichgewichtslage, der die Entwicklung zustrebt, anders zum
liegen kommt. Man kann das so ausdrücken, daß die optimale Anpassung ein Kompromißergeb-
nis darstellt, mittels dessen sich die Fortpflanzungsgemeinschaft aus einer “Selektionsklemme”
windet, die durch gegensinnig wirkende Selektionsdrucke zustandekommt. Dies gilt sicherlich
ganz allgemein, nicht nur für unsere Inseleidechsen. – Die optimale Anpassung wird übrigens
wohl niemals vollständig erreicht, da die Annäherung an diesen Zustand in späteren Phasen des
Anpassungsvorganges an diesen unmerklich langsam erfolgt und weil die Außenbedingungen
nicht unbegrenzt stabil bleiben.

The final example I’d like to mention is Kramer’s argumentation revealing and in-
terpreting the superannuation of the examined island populations. In general, this
train of thought consists of a reduction of the empirical data to a sort of conclu-
sion. The empirical section thereby consists in the attempt to translate categories
of size into an estimation of age (here the class of adult animals).\textsuperscript{1527} The reductive
part then consists of two further steps.\textsuperscript{1528} At first, Kramer names the reasons why

\textsuperscript{1526} Kramer, “Veränderungen”, 706.
\textsuperscript{1527} On the details see subsections “Einteilung in 3 Größenklassen” and “Altersschätzung innerhalb
\textsuperscript{1528} See to this part of the argumentation the two subsections with the titles “Die Gründe für die
the age distribution of insular Lizard populations has shifted in favour of a prevalence of older individuals. Kramer’s main argument at this point is that the lack of predators on islands not only leads to a reduction of the young but also allows the older individuals to exist. In a succeeding step this aspect is interpreted with a view of the population dynamics in general. Kramer’s calculations here show that the succession of the generations in island populations is twice as slow as the one of the mainland populations. This result, however, turns out to be paradox since it was the insular populations that usually deviated from the mainland populations in their more conspicuously changed appearances. Moreover, these changes must have taken place in the not too long period of 9,000 years. G. Kramer, however, was able to resolve this paradox by developing the idea that phylogenetic development may proceed with varying velocities. “Das Wegfallen der Feinde, das wir ja für die Ursache der Verlangsamung der Generationenfolge halten”, Kramer argues

Kramer’s reasoning on age distribution and population dynamics in insular Lizard populations thus turns out to be another example for the innovative potential of what I have called “Darwin’s paradox”. In the latter case it appears as growth-inhibiting factor that is resolved in a wider framework of changing population dynamics.

I have argued that G. Kramer’s self-characterization of his study Untersuchungen an Kleinpopulationen (1940) as “prospective” should be taken literally. This implies that the papers that were published in the following years can be read as if they picked up the categories Kramer had raised in Untersuchungen an Kleinpopulationen and tested them as to their usefulness for a large scale comparative study. It is of some interest that these characteristics usually did not refer to the behaviour of the Lizards but staid within the framework of morphology. Thus Veränderungen von Nachkommensziffer und Nachkommengröße (1946) had at least integrated the criterion of body size, while Über das “concolor”-Merkmal (1941) had proved the distinctive value of the intensity with which the skin patterns are expressed. All these follow-up studies shared a similar argumentative scheme and, beyond that, have in common that they clarified basic research questions. This preparatory char-

Überalterung der Inselpopulationen” and “Bedeutung der Altersverschiebung für die Wandlung des Populationsbildes”, ibid., 708–709, 709–710.
1529 Ibid., 710.
character seems to apply also to those studies that appeared with some delay in the years 1949 and 1951, that is, at a point when G. Kramer had his own department in the newly founded MPI for Marine Biology.\textsuperscript{1530} Thus Über Inselmelanismus bei Eidechsen (1949) is mostly dedicated to the criterion of “skin darkness” but also elaborates on the “blueness”. We can read this piece of research as the attempt to determine approximately the adaptive value (“Anpassungswert”) of two different though correlated morphological characters, that is, “skin darkness” and “blueness”. Kramer had observed that skin darkness in Lizards could be both due to the advanced age of an individual and a more general phylogenetic tendency.\textsuperscript{1531} His view was substantiated by the comparative data he had gathered during his stays in Istria and Naples. Thus he had found out that the skin of island Lizards throughout tended to be darker but in some cases (e.g. the Lizard’s juvenile stage) appeared slightly lightened up. The fact that in both cases the inner side of the skin turned out to be dark brought Kramer to the conclusion that in case of the lighter skins the commonly more advanced melanism was only masked by a secondary increase of the iridocytes concentration (\textit{viz.} the guanine in this tissue). On the other hand, the skins of mainland animals not only appeared optically lighter but their underside turned out to be bright, too. This seemed to apply even to those cases where the individuals appeared to be darker on superficial inspection. As a result, Kramer claimed there were existing two different variability systems interacting with each other while determining the animal’s appearance but apart from this division of labour needed to be considered independent. “Eine große Anzahl von Hauten wurde präpariert (Festland etwa 80, Gallo Maggiore 29, Castelluccio 34; Tonda 41) und besondere Aufmerksamkeit darauf verwendet, ob ein Zusammenhang zwischen äußerer und innerer Dunkelheit besteht”, Kramer writes and continues:

\begin{quote}
\end{quote}

\textsuperscript{1530} The founding date of the new institute was 1 August 1947. See MPG-Archives, III. HA, Rep. 77, file 10, ms. “Entwurf zu den Satzungen des Max Planck-Institutes für Meeresbiologie” (ca. 1947). Research began ca. one year later.

\textsuperscript{1531} Kramer, “Über Inselmelanismus bei Eidechsen”, 157.
Gustav Kramer (1910–1959)

versa. This corresponds with the equivalent earlier statement made by Kramer and Medem (1941) with a view of the mainland skins only. The lack of a strict correlation between actual density of pigmentation and the darkness of the outer appearance reveals that there are at least 2 systems involved in the melanism of Lizards, namely the one of the melanophores and the one of the secondary covering iridocytes. Both systems are varying independently from each other.

| The independence of the greater melanin concentration in the skins of island animals from their average age can be inferred not only from the (at least widely observable) independence of the inner pigmentation (in which we see the reliable measure of the actual pigmentation) from the outer appearance but also in that the ranges of variation, as drastic as they may be, do not transgress [eventually: blend into each other]. In addition, also the skins of adolescent island Lizards are darker than the ones of even-aged mainland animals. (Material: 7 mainland Lizards, 5 island Lizards. Three unbiased persons grouped these skins in independent evaluations in a sense of the greater brightness of the mainland animals).

Kramer’s paper Über Inselmelanismus bei Eidechsen is the attempt to assess the functioning of both variability systems independently but also to carve out the adaptive value of their combination. If we wanted to apply once more the idea of a “differential diagnosis” we might say Kramer extended the phylogenetic variability system with an ontogenetic one only to test in as much the individual development may anticipate or guide further phylogenetic development. The fact that ontogeny turned out to have a phylogenetic function then approximatively substantiated the overall claim of the adaptive value of both variability systems and their specific combination. I have added another figure to illustrate both variability systems (Fig. 2.26). Kramer has dedicated a single subsection to each system.

Fig. 2.26

G. Kramer, Island Melanism in Lizards (1949), Phylogenetic and Ontogenetic System of Variability

in each case mirrors the order of the respective system. As to the “Phylogenetic System” I’d like to point out two structural moments. At first, as it appears, within a frame that is characterized by a genuine tendency to darkness, which is marked by the darkness of the skin’s inside in all island animals, the state of relative brightness turns out to be a paradox situation. In Kramer’s account itself this aspect appears as description of breeding experiments intending to prove that even newly hatched

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1532 Ibid., 159.
1533 These subsections are “II. Melanismus bei istrianischen Inseleidechsen, auch bei frisch geschlüpften Jungtieren” and “III. Das Verbläsen der schwarzbahlen Faraglione-Eidechsen bei Haltung und Züchtung im veränderten Milieu”. See ibid., 160–161, and 161–163.
insular Lizards show the increased melanism quite independent of their age and the fact that they were born within an artificial environment. In other words, Kramer’s test was meant to show that nature overcomes nurture without necessarily dominating it. The second aspect I’d like to mention is that G. Kramer apparently conceives this paradox relation differently depending on whether he is speaking of Istrian Lizards or Southern Italian populations. In contrast to the former, the latter mentioned populations, he argues, reveal an additional tendency to blueness which is due to a difference of the guanine concentration or what he calls their “Feinstruktur” (“fine structure”). “Dieser verschiedene Guaninreichtum”, Kramer explains, oder die verschiedene Feinstruktur des Guanins der beiden Rassengruppen dürfte auch erklären, warum bei süditalienischen Inseleidechsen eine allgemeine Tendenz zur Blaufärbung besteht, im Norden dagegen nicht. [This enrichment of guanine or the deviating micro structure of the guanine in both groups of varieties may also explain why there is a general tendency to blueness in Southern Italian island Lizards, whereas it ain’t in the north.]

This can be interpreted as such that the specific constitution of the iridocytes in Lizards of the south has a feed-back effect upon the entire variability system. The theorem of brightness and the physical causes that can be thought in combination with that idea seem to be upgraded in their formative power upon the system as a whole. With a view of my epistemological research question this little detail would be of utmost interest because it would confirm my thesis that G. Kramer’s move to Naples coincided with essential epistemic re-evaluations of core theorems having structural and formative importance. Moreover, it would prove that Kramer himself after a period of some years interpreted his scientific development in the same way. His differentiation of Northern vs. Southern Italian Lizards, that is, the data obtained at an earlier stage of his career with the one he collected during his stay in Naples, then could be read as a late scientific self-reflection of his own course. With moving to the description of the “Ontogenetic System” Kramer’s account shifts from Istria to Naples where the mentioned breeding experiments had been carried out. According to Kramer, the Faraglione Lizards – after several weeks of captivity – began to change their morphological appearance in so far as they loose their shining habitus. In addition to that, the non-patterned areas of their bodies begin to lighten up. Kramer explains this transformation partly with a reduction of the melanin concentration in the epidermis. The development of the young seems to run logically across this tendency: Young Faraglione Lizards are born grey and develop their characteristic colouration until they reach their adolescence. However, according to G. Kramer’s account young Lizards born in captivity do not reach the extent of skin darkness and blueness. As a result, one may argue that Kramer used the counter-logical development of the young to demonstrate the nurture character of the transformation and, beyond that, to clarify the nature of

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1535 Ibid., 160.
1536 For the location of the experiments see ibid., 161.
1537 For the symptoms of captivity see ibid., 161–162.
1538 Ibid., 162, 163.
1539 Ibid., 162–163.
the mechanism of the variation. If the young in captivity never reach the extent of skin darkness of the wild ones, that is to say, if captivity increases the trait’s range of variation even beyond the natural range of variation, one may speculate that the lower extent of darkening might by due to some kind of acquired disposition: In further experiments Kramer wanted to substantiate both the “modifikatorische Natur der beobachteten Veränderungen” and that the changes were based on a mendelizing hereditary factor. The latter of the two theorems most likely is a logical precondition to include ontogeny in phylogenetic theorizing. Alike to my reading of the previous subchapter I am inclined to interpret the paradox which is produced by the account of juvenile development as flexible semantic relation which could be adjusted depending on whether G. Kramer was speaking about “captive” or “wild” young insular Lizards. The structural or epistemic correlate of this plasticity again seems to be the evaluation of the involved core theorems. While in natural island populations the tendency of the young to dark skin colour seems to have a restrictive impact upon the range of variation of the trait “fading darkness”, this theorem appears to be downgraded in a system of captive animals. The idea of a wider range of variation both overwhelms and controls the theorem of the “Darkening of the Young”. In the latter case the young can only be described in paradox terms as something which is dark without being it. It remains to discuss how G. Kramer places his account on the adaptive value of both systems and their intertwining. In chapter four of the paper, “Anpassungswert von Inselschwärzung und Inselbläuung” we can find in principal two argumentative trains of thought. At first, the adaptive value of the phylogenetic system is explained. A darker skin, Kramer argues, is of advantage in a milieu in which the Lizards are exposed to extreme lighting conditions because it both protects from harmful light rays and, through a higher rate of light absorption, helps to increase the temperature optimum of the poikilothermic animals. If I have understood correctly, the additional ontogenetic option to modify the skin colour in direction of blueness and blackness – which seems to be inverted under conditions of captivity – provides a transitional possibility to increase this effect. According to Kramer, in the following natural selection, however, works towards fading of guanine and condensation of melanin. From this perspective blueness appears as transitional phylogenetic stage in direction of more advanced darkening, or “total melanism” as Kramer puts it. An ontogenetic effect thus seems to have a guiding or directing influence upon phylogenetic development. I think it can be discussed whether Kramer had in mind a sort of Baldwin effect. What makes me hesitate to postulate this is that the secondary phylogenetic development in Kramer’s view does not work into the same direction as the ontogenetically modified phenotype but effects the neutralization of this feature. “Auf dem Weg zum totalen Melanismus”, Kramer concludes, stellt die Bläuung offenbar einen leicht gangbaren Weg der Neutralisierung reichlich vorhandenen Guanins dar.

[On the path to total melanism the blueness apparently turns out to be an easily feasible way to neutralize the guanine which is available in masses.][transl. CL]
From the epistemological point of view, Kramer’s construction in any case means that the ontogenetic system might be able to give a formative feedback impulse upon the entire system of variability systems. To put this very colloquially, the “Wilhelmshaven G. Kramer” thus perpetuated the Naples reading and not the Istria Reading of the system. That is to say, Kramer’s postwar writings perpetuated the re-evaluations he had introduced with his move to Naples.

With Body Proportions of Mainland and Island Lizards G. Kramer’s direct engagement with Italian Lizards ended although his interest in reptiles certainly persisted further. The paper was published in 1951 in Evolution, the journal of the Society for the Study of Evolution. Both the fact that Kramer published this study in English language and the journal in which the paper appeared indicated that his move to a neo-Darwinian thinker had reached a provisional peak: Kramer published in the journal of the scientific community which propagated the Modern Synthesis and the literature cited in the paper shows that he had begun to receive the works of B. Rensch, J. Huxley and other architects. We remember, Kramer had already raised the question whether body size and body proportions might be of taxonomic value in Untersuchungen an Kleinpopulationen (1940) but there still had to concede far-reaching indistinguishability in this set of morphological characters. This situation now seems to have changed. “The original scope of the measurements in this paper was to provide evidence regarding the following questions”, Kramer begins his paper and continues:

(1) Do island populations differ in their proportions from conspecific mainland populations? (2) If so, are these differences genetic or not? (3) Is the variation haphazard or are there parallel trends in island populations? (4) Are there any indications to suggest an adaptional value of

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1542 Thus, it can be inferred from G. Kramer’s papers that he, in the early 1950s, supervised a dissertation thesis being concerned with relative growth in Lizards. See to this the instructions he sent to H. Becker in 1952, MPG-Archives, III. HA, Rep. 77, file 6, letter G. Kramer to H. Becker (19/01/1952) and ibid., file 6, letter H. Becker to G. Kramer (15/01/1952). Moreover, Kramer seemed to breed further Lizards in Wilhelmshaven. See to this ibid., file 8, letter G. Kramer to M. Eisentraut (13/10/1953). Also Kramer’s correspondence with H. Maschlanka shows that she collected further data concerning relative growth in Italian Lizards. See, for instance, ibid., file 7, letter H. Maschlanka to G. Kramer (30/03/1953), ibid., file 7, letter G. Kramer to H. Maschlanka (17/03/1953), ibid., file 7, letter G. Kramer to H. Maschlanka (09/03/1953), ibid., file 7, letter H. Maschlanka to G. Kramer (03/03/1953), ibid., file 7, letter G. Kramer to H. Maschlanka (11/12/1952), ibid., file 7, letter G. Kramer to H. Maschlanka (01/12/1952), ibid., file 7, letter H. Maschlanka to G. Kramer (22/11/1952), ibid., file 7, letter H. Maschlanka to G. Kramer (n. d.). Related to this paper there exists a small correspondence in Kramer’s personal papers which confirms that E. Mayr who edited the journal before the editorship passed on to E. H. Colbert, also thought that Kramer’s paper would fit into Evolution. See ibid., file 2, letter G. Kramer to E. Mayr (25/02/1949), ibid., file 2, letter E. Mayr to G. Kramer (19/04/1949) and ibid., file 2, letter G. Kramer to E. Mayr (20/05/1949). Further letters show that the manuscript was submitted as early as 1949 and that it was printed only with a certain delay in time. See ibid., file 4, letter G. Kramer to E. Mayr (11/07/1950) and ibid., file 4, letter E. Mayr to G. Kramer (14/08/1950). For additional information concerning the editing and review process see the correspondence with E. H. Colbert, that is, especially ibid., file 5, letter E. H. Colbert to G. Kramer (15/02/1951), ibid., file 5, letter G. Kramer to E. H. Colbert (21/02/1951), and ibid., file 5, letter E. H. Colbert to G. Kramer (21/03/1951). Another source for additional information concerning this paper might eventually be Kramer’s correspondence with E. Stresemann. For Mayr’s vivid response see SBB, NL 150, file 37, letter G. Kramer to E. Stresemann (30/06/1947) and with some caution see eventually also ibid., file 37, letter G. Kramer to E. Stresemann (14/08/1947).
The quotation shows that the discovery of population specific differences in body proportions, however small they may be, was a late achievement of Kramer’s which allowed him to give another set of morphological characters the status of a promising research object in his zoogeography of Italian Lizards.\footnote{Kramer, “Body Proportions of Mainland and Island Lizards”, 193.} The narratological organization of Body Proportions of Mainland and Island Lizards does not differ in principle from the one Kramer had applied in his former Lizard studies but does display a more sophisticated mode of approximative coincidence or limes structure: Two morphological parameters are discussed separately from a comparative perspective in the core of the paper, namely the “relatives Quermaß” or “relative span” (RS) and the “relative tail length” (RT) whereby, in a supplementary step, the question is raised in how far both sizes can be correlated and a combined size can be developed. Particularly a comparison between inter- and intraspecific variations of the combined parameter thereby showed that the intraspecific variability could not be explained by accidental drift. Hence, another explanation was to be introduced in the discussion of the results which Kramer called “early allometric shifts”. In the following I try to reconstruct the entire train of thought in greater detail. Nonetheless, I think, it may suffice to clarify how each parameter is defined and what the findings are. Thus Kramer defines the relative span as a size being “established by expressing the actual span of the hind legs in per cent of the head-plus-trunk length (to be abbreviated subsequently as H + T)”.\footnote{Ibid., 194.} The “actual span” thereby is “measured under certain precautions [...]CL from tip of toe to tip of toe”.\footnote{Ibid., 193.} As objects for his measurements Kramer had chosen newly hatched Lizards because the relative span turned out to be subject of allometric change, that is, the length of newly hatched animals were found to be relatively longer than those of adults so that a common denominator needed to be found.\footnote{Ibid., 194–195.} Comparisons generated a number of graphs plotting the relative span (given in per cent of the body length) as a function of body size. The result of these comparative data assessments was that both the Istrian and the Southwestern Italian island populations – with some exceptions – had relatively shorter hind legs in comparison to their mainland equivalents.\footnote{Ibid., 205–206.} In adult animals the same feature appeared only if the Lizards were living on flat islands. In island milieus where longer legs are more adaptive the overall trend to adaptive regression appeared to be somewhat smoother (please note the end-paradox constellation of the epistemic frame).\footnote{See to Kramer’s favour of adaptiveness as explanation for the gradation of the relative spans within island populations, ibid., 198–199. In agreement with neo-Darwinian theorizing he had ruled out before the possibility of direct impacts exerted by different hatching temperatures. See ibid., 197 and with a view of the relative tail length ibid., 201.} “Quick snakes (Zamenis) which chase Lizards \textit{par force}”, Kramer argues,
represent a factor selecting for long-leggedness. [...] This factor is lacking on the islands, and our views as to “degenerative” evolution go to show that a feature brought about by special conditions tends to be regressive if such conditions break down. However, the regressive development, initiated by the absence of predators on the islets referred to, will be slackened in the particular cases where habitat conditions require special climbing agility.1551

What Kramer calls the “Relative Length of the Tail” in fact is a parameter consisting of the quotient of the tail length, on the one hand, and the sum total of the length of the head and the length of the torso, on the other. Kramer’s measurements here indicated that insular populations of Lizards – independent whether they are living on Northern or Southern Italian Islands – also have shorter tails.1552 Considering the micro-systematic purposes this overall harmony however would have been a poor result. Yet, on closer inspection Kramer was able to raise a more sophisticated parameter that was more apt to mark population specific differences. He had observed that in some Lizard populations the young were born with relatively longer tails than in others, a matter of fact that triggered the idea to compare the relative increment of the tail’s growth during the Lizards’ early adolescence. For how many per cent of its size at birth does a tail have to grow till it reaches the size of its adult stage? This proportion could be plotted against the overall body size and the ultimate result was a veritable correlation: “The bigger the hatching size of a population (H + T at hatching stage)”, Kramer concludes, “the less its RT at hatching stage will differ from its ultimate RT”.1553 In other words, the bigger the hatching size, the less the tails need to develop. The smaller the Lizards at birth, the higher the increment of tail growth.

If on the strength of the values for the young the variance between sexes is represented together with the variance for comparison of populations, high significance is obtained. As with the length of hind legs, the young Lizard is also differentiated as to sex with regard to the length of its tail.1554

And slightly later in the text it reads:

On the other hand, the relation between mainland and island values has undergone a change. While there is a definite though not certifiable suspicion that RT is increased with part of island young, as can be inferred from table 4, the corresponding values of adults show a marked decrease, which is statistically secured for all populations included in this table.1555

This passage can be read as if the relative tail length at birth in island populations was even higher than in mainland equivalents so that the increment rate represented a more “reductive program” of body growth.1556 As soon as Kramer had found this parameter he was interested in corroborating its distinctive value. Thus he correlated the relative tail length with the absolute size of the body and the number of tail vertebrae just to find out that the number of tail vertebrae in mainland populations is higher than in insular Lizards but that the tails of the island Lizards require less growth in post-embryonic stages. Kramer aims to substantiate this thesis by putting
forward the additional proposition that the tail length of newly hatched Lizards is
dependent only on the amount of yoke in the eggs and the eggs of island Lizards are
usually bigger. This ontogenetic speciality was apt to explain why the range of
relative tail growth in island Lizards could appear significantly higher. A further
move of Kramer’s to prove the distinctive value of the relative growth rate of Lizard
tails was to demonstrate the “Ecological Importance” of the tail length. In his
view long tails were as advantageous in matters of locomotion as the longer hind
legs quite regardless of the fact that autotomy is an effective method of protection
from predatory enemies.

To summarize the core account of Kramer’s paper, one may say, he both demon-
strated that an obviously discrete factor might be less discrete under certain cir-
cumstances as well as he proved that a seemingly non-distinct character on closer
inspection turned out to be of taxonomic value after all. Needless to say that this
deconstructive gesture generated paradox figures in the final regions of both epis-
temic frames. That there was a distinctive character that might serve for micro-
systematic purposes as well as there was a seemingly non-distinctive feature that
turned out to have taxonomic value raised the question whether both parameters
could not be thought together in one common combined factor or correlation with
more advanced taxonomic value. This question is discussed in the chapter with the
title “The Correlation between RT and RS”. The correlation Kramer now estab-
lished consists of the span of the hind legs (expressed in percent of the total length)
and the tail length (expressed in per cent of the total length). In the following it is
tested in three different contexts, the data available from his own studies of Italian
Lizards, the data provided by W. Hellmich in his study of Chilean Liolaemus and,
finally, a suitable sample of varieties within one and the same population Kramer
has drawn again from his own data collection. The result was apparently that a
proper correlation between the length of the tail and the length of the legs could
be established on the level of interspecific but not of intraspecific comparison. “Subsequently”, Kramer argues,

all suitable material (nine groups) was graphically examined for a correlated variability of length
of tail and span with individuals of the same population and belonging to a well defined age
group (the only choice in this respect being the hatching stage). The result was negative, which
seems to indicate that this relation, which was established in a comparison of various races and
species, constitutes a result of environmental selecting influences working in the same sense on two features that vary independently of each other.\textsuperscript{1563} This negative result is also the reason why the section entitled “Discussion” differentiates between “Island effects” and “Allometric shifts”. While the former of the two discusses the phenomena that could be explained with adaptive regression and, beyond that, with accidental drift, the latter subsection makes an attempt to explain the phenomena contradicting this account. “There is no indication”, G. Kramer writes in a concluding remark,

that the intrapopulation variability of the features examined is restricted by the effect of small population numbers. The relative growth of hind legs and tail makes possible a distinction between allometric changes in early and later ontogenetic stages. Presumably the latter only can be considered indicative in a sense of evolutionary allomorphism.\textsuperscript{1564}

I have argued that all of Kramer’s detail studies of Lizards finally were driven by the same objective namely to carve out those seemingly non-distinctive qualities which, on closer inspection, after all did prove to have a taxonomic value. With Niko Tinbergen’s words one may say that G. Kramer intended to bring order into chaos. This overall intention mirrored in the organization of the texts, that is, their approximative or limes structure. In \textit{Body Proportions of Mainland and Island Lizards} (1951), however, we find a slightly modified interpretation of this scheme. In contrast to Kramer’s earlier preparatory studies it is not the moment of discreteness, the \textit{tertium comparationis}, or the homological trait that is to be carved out approximatively. On the contrary, the intended argumentative reduction or proof ends with an ambivalent result. One side of this result thereby opens the field for a new type of inquiry namely the comparative assessment of “allometric changes in early and later ontogenetic stages”. Kramer’s move becomes clearer if we take into consideration once more J. Gayon’s classification of allometric research foci.\textsuperscript{1565} Gayon distinguished between four types of allometry, namely ontogenetic, phylogenetic, intraspecific and interspecific allometry. We historians would eventually call the former two “diachronous” because they operate with comparisons of different points within one and the same lineage, either of the individual or a wider taxonomic entity. The latter two are “synchronous” because they compare two different entities on one and the same stage of a time line. Kramer’s interest in allometry, that is, the comparative assessment of changing body proportions, so far may be connected more with the synchronous types of allometric inquiry simply because he was keeping the wider zoogeographic perspective at the back of his mind and thus was interested in morphological characters that proved to be of taxonomic value in a potential large scale micro-systematic study of Italian Lizards. “Of taxonomic value” in this context means that the qualities in question needed to be distinctive in small taxonomic units, they must be hereditary and possibly have adaptive value (except they turned out to be the result of accidental drift). In \textit{Body Proportions of Mainland and Island Lizards} this focus seems to have shifted partly. With focusing on newly born Lizards and asking for the relative increment of their tail length

\textsuperscript{1563} Kramer, “Body Proportions of Mainland and Island Lizards”, 204.
\textsuperscript{1564} Ibid., 206.
\textsuperscript{1565} See fn. 1231, page 390 of my thesis.
as a function of the overall body length Kramer raised an ontogenetic parameter which he intended to make productive for his systematic interests. The fact that the combined correlation between relative tail length and relative span (in each case to be thought relative to the overall body length) did not prove to be of systematic usefulness raised the opportunity to examine ontogenetic proportion shifts for their own sake and in a realm for their own. I interpret this slight modification as a signal that G. Kramer abandoned his plan of writing a comparative zoogeography of Italian Lizards on basis of all the preparatory detail studies in the aftermath of his joint project with R. Mertens. By contrast what appeared to be preparatory work so far and thus indicated the mutual intertwining of both of Kramer’s realms now becomes a thematically independent register of its own right – eventually with another model organism, the crocodiles. In addition to that, since his move to Heidelberg, G. Kramer had resuscitated his passion for Ornithology and most likely it is his newly revived interest in orientation and homing of birds which was meant to fill the complementary realm of his academic trajectory. The paper which I should discuss next, that is, G. Kramer’s contribution to the “Festschrift” which has been published on the occasion of O. Heinroth’s seventieth birthday in 1941 can be interpreted as an early harbinger of this change of course in Kramer’s intellectual life-history.

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Beobachtungen über das Verhalten der Aaskrähe (Corvus corone) zu Freund und Feind (1941) most likely was not only the first ornithological publication since 1932 it eventually was also the only pure causal analytical study during the period of time G. Kramer was affiliated with the Zoological Research Station in Naples. This suspicion, if it was true, would render this study a research endeavour complementary to the simultaneously carried out Lizard studies. Moreover, I think, we cannot understand the deeper sophistication of this paper if we do not read it in connection with the parallel development that had led to the founding of Classical Ethology. It was especially K. Lorenz who had reconfigured the epistemic frame provided by O. Heinroth’s and also J. v. Uexküll’s works into two different directions neither of which were actually structurally compatible with the original complex. On the one hand, Lorenz – under the influence of W. Craig’s concepts and also stimulated by Gestalt theory – created what he casually called “pure Leicology” that is a specific causal analytical framework that was particularly designed to explain instinctive action patterns as combination of a directing component and an final act of disinhibition but also appeared in other circumscriptions.\textsuperscript{1566} One of these interpretations was Lorenz’s model of behavioural taxonomy which he had shaped in his study of the social Corvidae (1931) and applied later, in a more refined form, in his famous Anatinae (1941) study that appeared right next to Kramer’s paper in the “Festschrift” for O. Heinroth. On the other hand, Lorenz, especially in his Companion study and later in his critical reassessment of some of I. Kant’s writings,\

had developed step by step a biotic environmentalism which was rooted in philosophical realism and as such had claimed a genuine correlation between “key” and “lock” – later more between the pithy species-specific “releasers” and their summarily working receptory correlates. I have already mentioned that G. Kramer obviously did not follow these epistemic moves that were leading to Classical Ethology in a narrow sense but, instead, perpetuated Heinroth’s legacy by reinterpreting it in several key concepts which shaped his own course to a neo-Darwinian thinker such as his (shifting) understanding of “zoogeography”, his vision of micro-systematic research or even his concept of “differential diagnosis” which turned out as an essential heuristic concept structuring his argumentations since his affiliation with the KWl for Medical Research. This discrepancy in the trajectories of researchers who, after all, were members of the same epistemic community and, beyond that, were even friends, raises the question how G. Kramer himself conceived the relation of the position taken by his research and the scientific paradigm that provided the frame for Classical Ethology. This question is of still greater interest because it touches the relationship between the Ethological Synthesis and its counterpart, the Modern Synthesis of Evolutionary Theory, which took shape both simultaneously and complementarily in the second half of the 1930s. In other words, Kramer’s relationship to his colleagues is of volatile nature because it touches the now widely discussed question whether or not even the wider understandings of the Modern Synthesis have left epistemic space for an “Extended Synthesis”. All this seems to be at stake when we read Kramer’s seemingly “innocent” observations of the Carrion Crow’s behaviour. While reading and analyzing Beobachtungen über das Verhalten der Aaskrähe we need to keep in mind a peculiarity: In retrospective view, it provides a more or less structured panorama of observations that go back to the early and mid-1930s – obviously mostly of the year 1932. This can be read as a narrative indicator: Many events are evolved from one common standpoint which lies in present time. The observations Kramer recollects in this paper apparently also originated in quite different geographic regions such as a park in Heidelberg, the “Damsbrücker Jagdrevier”, the Mark of Brandenburg, the Curonian Spit, and


1568 For some concrete indicators concerning the dating of the actual observations see Kramer, “Beobachtungen über das Verhalten der Aaskrähe”, 114.
Gustav Kramer (1910–1959)

the Isle of Cherso in the Adriatic Sea.\textsuperscript{1569} The date of the publication and also the dates of the quoted works, by contrast, indicate that Kramer’s account was written in 1940 or 1941, that is, shortly before it appeared in Heinroth’s “Festschrift”. All these information suggests that we might have to do with a later recollection and, at least as to the arrangement of the data, a reconstruction of earlier observations.\textsuperscript{1570} That Kramer’s account has more the character of a recollection includes a very subtle though latently existent hint upon the idea of causation in which the entire account is bathed. While this aspect points to later epistemic shifts in Kramer’s life course, the latent argumentative structure of the account is in accordance with Heinroth’s way of thinking. A central idea, namely that conspecifics establish an environment in J. v. Uexküll’s sense, is tested in several different contexts such as the formation of the pair (chapter 2), the defence of the territory (chapter 3), the behaviour towards different kinds of enemy (chapter 4), the endangerment of the offspring by humans (chapter 5), the hazard of the conspecific (chapter 6) and, finally, the harmed conspecific and the relation towards to members of other species (chapter 7). In all these part accounts Kramer seems to be interested in the mechanism that correlates stimulus and reception including the constitution of both sides of the communicative interaction in the Carrion Crow. These considerations finally lead to some further leading thoughts concerning the taxonomic relationship between Carrion Crow, Common Raven and Jackdaw (chapter 8). Maybe, it would be a good idea to begin with the end and compare Kramer’s behavioural systematics of the \textit{Corvidae} with the one proposed by K. Lorenz in his paper of the year 1931.\textsuperscript{1571} If my reading was correct, K. Lorenz had suggested a wider taxonomic gap between the Magpie, on the one side, and the Jackdaw and the Common Raven, on the other, while the relationship between the latter two was conceived in terms of minor differences. In doing so Lorenz was advocating a heuristic procedure he (later) used to call “Analyse in breiter Front”, that is, the conviction that taxonomic differences can be made evident from the periphery to the core, that is, from loser to narrower degrees of phylogenetic relatedness just as one may peal of the layers of an onion. Lorenz’s taxonomy – if read from left to right – therefore also implied a tendency to increasing abstraction which Kramer interpreted as increasing “intellectualization”:\textsuperscript{1572} Not only that inadequate objects (such as humans) stimulated defensive protection if they were personally known – no – even own conspecifics either fail to release the defensive reaction or actually trigger aggressive responses

\textsuperscript{1569} For the references to all this places see ibid., 109–113, 114 fn. 2, 121–122, 124, 126.

\textsuperscript{1570} The mentioned observations are partly connected with a concrete date such as “13. IX”, “22. V. 7 h.” or “in May 1932”. See ibid., 126, 114–115, and passim. Mentioning exact dates and times suggest that Kramer’s account is based on written sources such as a notebook. The existence of such a notebook, though, is not mentioned in the publication. Yet Kramer mentions that he had noted observations. See ibid., 108. In letters Kramer exchanged with E. Stresemann we can finally find the explicit information that the paper in question was essentially drawn from earlier notes which Stresemann was asked to send to Naples. See SBB, NL 150, file 37, letter G. Kramer to E. Stresemann (28/09/1940), ibid., file 37, letter G. Kramer to E. Stresemann (05/11/1940) and ibid., file 37, letter G. Kramer to E. Stresemann (23/02/[1941]).\textsuperscript{52}


\textsuperscript{1572} Kramer, “Beobachtungen über das Verhalten der Aaskrähe”, 129.
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against themselves if they are not known in person. Kramer’s taxonomy differs from Lorenz’s at first sight in as much as he does not consider the Magpie next to Common Ravens and Jackdaws but the Carrion Crow. Also he does not share Lorenz’s urge to put forward a taxonomic order that proves an evolutionary trend to abstraction. “Nach Beobachtungen von Lorenz (1931)”, Kramer replies,

sohn Kollraben nur Freunde zu verteidigen, wobei die Artzugehörigkeit ohne Belang ist. Die Gefährdung des persönlich fernstehenden Artgenossen ruft eher Umbringenhelfen als Verteidigung hervor, umgekehrt wird der befreundete Mensch vor Angriff geschützt. Eine so weitgehende Intellektualisierung der Verteidigungsreaktion – gegenüber dem sehr rein reflektori-

schen Verhalten der Dohle – besteht bei der Aaskrähe zweifellos nicht. Unsere Versuche bauten sich ja fast durchweg auf das Ingangkommen der Reaktion durch persönlich fremde Artgenossen auf. Jedoch zeigt der besonders heftige Ausfall der Reaktion bei dem Krähennännchen, dessen totes Weibchen von mir getragen wurde, dass die persönliche Beziehung eine Rolle spielt.

[According to Lorenz’s observation (1931), Common Ravens seem to defend only friends whereby the membership to the species does not count. The endangerment of the personally distant conspecific elicits more assisting-in-killing instead of defending. Conversely, man being identified as friend is protected against attack. Such a far-reaching intellectualization of the defensive response – in comparison to the rather reflex-like behaviour of the Jackdaw – without doubt does not exist in the Carrion Crow. Our experiments indeed were mostly based upon the starting-up of the reaction through personally strange conspecifics. However, the extraordinary intensive expression of the response of the male crow whose dead female was being carried by me shows that the personal relationship plays a role.]

The quotation seems to show that Kramer replaced Lorenz’s comparison between Jackdaw and Common Raven which had served to prove the trend to “intellectualization”, as Kramer puts it, by a comparison between Jackdaw and Carrion Crow which does not show this trend. This also implies a greater similarity of both species which Kramer made evident in the releasing situation that triggers the defensive re-

action in both species. Kramer writes:

So gilt also die Fassung “Artgenosse in Gefahr” als die Verteidigungsreaktion auslösende Situation auch für die Dohle.

[Thus the conception “conspecific in danger” as the releasing situation for the defensive reaction also applies to the Jackdaw.]

We can therefore conclude that G. Kramer perceived finer systematic more in terms of graded slight differences. It is possible to approach Kramer’s argumentation once more if we change perspective and put K. Lorenz’s Companion-study into the back-

ground. To put it in more general semiotic terms Lorenz had claimed a complex correlation between stimulating situations and the receptory correlate in the mental apparatus of the organism in as much as the qualitative narrowing down of a recepto-

tory schema (in semiotic terms its “intension”) corresponds with the increase of the scope of its applicability (in semiotic terms is “extension”). In other words, if the recep-
tory schemata become less complex (poorer as to their amount of features) in a process of abstraction (“intellectualization” in Kramer’s words) they can respond to a wider range of releasing stimuli or stimulating situations. What I have described as process of “abstraction” in neutral terms is evaluated quite negatively in some

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1573 Kramer, “Beobachtungen über das Verhalten der Aaskrähe”, 129.
1574 Ibid., 129, also 130.
Gustav Kramer (1910–1959)

of Lorenz’s wartime publications as maladaptive and “degenerative” side-effect of domestication and / or modern civilization. Kramer, by contrast, does not follow this model and, most interestingly, translates Lorenz’s model of hypothetical realism (i.e. the adaptive correlation between mental apparatus and the environment it mirrors) back into Heinroth’s framework. What in Lorenz’s model appeared as “intellectualization” now, on the contrary, turns out as increased affection and enhanced readiness to display defensive behaviour which correspondingly goes hand in hand with a process of depersonalization of the releasing objects: Not only personal enemies match the defensive schemata but also quite impersonal sources of endangerment such as human beings. “Es liegen vorderhand keine Gründe dafür vor”, Kramer underlines,

\[\text{For the time being, there are no reasons to interpret the increased affection to fighting other than conditioned by the increase of endangerment that is connected with it. After new observations of Jackdaws have been contributed which to communicate I have been entitled by Lorenz and the similarities between Crows and Jackdaws appear to be stronger than previously realized this aspect at least is to be taken into consideration more carefully.}\]

(transl. CL)

If the trend to defensive empathy is made the criterion for a taxonomic classification and not the “intellectualization” we can understand why Kramer came to another systematic arrangement. Kramer’s model of defensive responses is partly what modern biologists nowadays might call a kin selection model, that is, the defensive schemata respond most decisively if endangerment affects members of the own kin or the offender is familiar. This basic model can be extended by the idea of increased affection which allows to respond to impersonal endangerment or if endangerment affects non-kin members. That is: The more unfamiliar the offender the more affection is necessary to release the protective defence reaction. In sum, we may say that Lorenz’s model is based on increased abstraction, while G. Kramer’s “Umweltlehre” is rooted in what – following roughly N. Luhmann’s early terminology and regardless of the deviating causal implications – might be called “Mittelschema” (means scheme). From this perspective we may now have a better access to the examples Kramer mentioned in the sections before the last. Maybe, it is possible to apply once more the concept of “differential diagnosis”. An introductory chapter with general marks concerning calls and behaviours of crows is supplemented with more extensive and more detailed aspects. Within this part the

1575 I have already mentioned that K. Lorenz eventually has not abandoned the deeper epistemic structure underlying his degeneration doctrine after the Second World War. More likely he has reinterpreted it as a theory of “dehumanization”. This is suggested, for instance, by the title of one of his later publications, “The Waning of the Human”. Lorenz’s later argument that humans are more prepared to kill members of their own kind if they can kill from remote distance through adequate weapons fits perfectly well with his abstraction scheme. P. Chavot seems to share my view in his thesis. See Chavot, “Histoire de l’ethologie”, 101–102.


1577 For N. Luhmann’s differentiation between “Zweckschema” (purpose scheme) and “Mittelschema” (means scheme) see Luhmann, Zweckbegriff und Systemrationalität, 43, 242–243.
empirical observations (chapter 2 to 7) are finally reduced to one principle which is the subject of chapter eight that interprets the findings in a model alternative to Lorenz’s taxonomy and his model of hypothetical realism. Considering this overall scheme I was wondering whether the internal organization of the empirical and observational sections is not proceeding from the familiar objects of stimulation to accounts of responses to foreign objects. What arguments does Kramer’s account provide which substantiate my hypothesis? First, I have argued that Kramer translated back Lorenz’s hypothetical realism in Heinroth’s and v. Uexküll’s frame because the latter suited more as a starting point for his own scientific development. This move implied also a greater scepticism towards Lorenz’s theses that signal movements and calls were strictly fixed hereditarily and, in addition, that there was a strict correlation between the phenomenological appearances and their causes – the basic presumption of his hypothetical realism. Kramer, by contrast, described the so-called “Spielrufe” of the Crows to demonstrate that single calls might not be fixed that statically and there existed a hereditary range of reaction within which the individual can vary pending of previously gathered experience. He also questioned the possibility to infer definitely from the appearances (the calls) to their meaning. “Unter der ungemein manigfaltigen Reihe von Lautäußerungen die man von Raben- und Nebelkrähe hören kann”, he writes,

We see, for Kramer the inference from utterance to meaning is not as straightforward as it is within the framework of Lorenz’s hypothetical realism. The accessibility of an utterance’s meaning is the exception rather than the rule. G. Kramer’s position remains more sceptical. The calls are usually accompanied with corresponding movements. But in Kramer’s view there are exceptions. The corresponding movements can be exhibited without the calls or, in case of great excitement, the wing-beat and the rhythm may be displayed without any sign of correlation. The latter aspect corroborates my interpretation of Kramer’s model. The more of excitement on the side of the mental apparatus entails a moment of disruption on the side of the appearances. Second, a structurally identical mechanism applies to the pairing ceremonies of the Carrion Crow: They greet objects they identify as conspecifics with calls demanding coition but drop these gestures as soon as the partner becomes more familiar. Again, emotional familiarization entails a reduction in the behaviour patterns. Also steady pairs reveal a stronger affiliation to a definite territory. Third, Kramer distinguishes more casual fights from severe attacks of

1579 Ibid.
1580 Ibid., 105–106.
1581 Ibid., 106.
a pair’s territory. Increase of threat strengthens the bonding of the pair so that the territory can usually be defended and is maintained over the entire year under certain circumstances. Fourth, G. Kramer also differentiates between defensive reactions against conspecifics, on the one hand, and severe predators, on the other. In the latter case the pair chases the intruder together and, beyond that, larger aggregations may form for defensive means. Increase of threat, for instance, by placing a young crow in close range of the predator increases the affective readiness to protect more aggressively. The shift to the rarer more hostile displays is accompanied by corresponding utterances each. Fifth, when adult crows defend their offspring they decrease their escape distance and approach even foreign intruders such as humans. Kramer says the radius of the circles with which they orbit around the offender becomes the smaller the stronger the excitement is. Correspondingly, the pair acts together. Also Kramer claims that other kinds of affects are touched while defending the young in comparison to the protection of other crows. That is, he claims the existence of multiple states of affection adjusted for occasions of lesser and greater threats. In a quite comprehensive passage it reads:

The quotation expresses quite well the two sides of Kramer’s model. Increased emotional excitement and huddling together goes hand in hand with a potential shift in the protective behaviours from less to more severe attacks. Sixth, Kramer’s experiments suggested that the trait which makes a Carrion Crow a worthwhile defensive object for another is “conspecific in danger”, that is, the fact of being related or a member of the same species and less – as K. Lorenz believed – the personal acquaintance. Basically, Kramer’s understanding of the Carrion Crow’s defensive response therefore rests upon what biologists nowadays would eventually call a “kin-selection” model. Correspondingly, he argues, the defensive affection is more or less statically attached with the source of the endangerment – in Kramer’s experiments he himself. Further tests revealed that less excited Crows do not simply respond to any inadequate, though prominent, releaser as Lorenz had demonstrated

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1583 Ibid., 111–113.
1584 Ibid., 113–116.
1585 Ibid., 115.
1586 Ibid., 117–118.
1587 Ibid.
1588 For the following ibid., 118–125, here 120.
1589 Ibid., 120.
with Jackdaws, but instead are capable of personal recognition.\textsuperscript{1590} As to the mental apparatus this requires a capacity to differentiate and memorize (which goes beyond a mere principle of heterogeneous summation). In addition to that, Kramer observed that crows can get used to a particular offender so that they concentrate their attacks exclusively upon him even in case this turns out to be dysfunctional because other sources of threats are likely to be neglected.\textsuperscript{1591} Once more the familiarization is correlated with a phenomenological reduction. A prototypical example for this reduction in Kramer’s account is the reduction of the flight distance in case of stronger excitement. In this latter case and in this case only, Kramer sees a corresponding summative mechanism at work in the mental apparatus of the animal. “Daraus geht hervor”, Kramer summarizes,

\begin{quote}
\noindent \textit{\textdaggerleft}This entails that in case of the previously mentioned observations we have to do with an additive effect which, so to speak, is determined by the algebraic summation of an anxious, distance-increasing and an aggressive, distance-reducing affective component. In the later stages of the longer lasting tests still another clearly recognizable effect of taming comes in,\textdaggerright\end{quote}

This quotation shows impressively how Kramer reinterprets the edifice of Lorenz’s hypothetical realism – in this case by repositioning the principle of stimuli summation. We can conclude indirectly: The memory based mode of personal recognition changes into a summative mode of reductive perception in course of greater affection. Seventh, and finally, Kramer aims to clarify whether and in how far the suggested model for defensive reactions applies to encounters between non-conspecifics.\textsuperscript{1593} Lorenz had claimed on basis of his model that raven birds are prepared to kill attacked members of another species – in the extreme case even members of their own species. According to G. Kramer, Lorenz had called this instance “Umbringenhelfen” (“assistance-in-killing”).\textsuperscript{1594} Kramer’s model seems to offer another vision: He had observed that sometimes defensive reactions are displayed even if no specific predator could be connected with the protective response.\textsuperscript{1595} Moreover, although in some cases Carrion Crows show hostile behaviours towards non-conspecifics in danger in other cases they don’t. He therefore refuses to subsume all these heterogeneous observations under Lorenz’s doctrine. Moreover, he apparently thinks it possible that the “subjective state of health” might be involved in releasing the protective reactions.\textsuperscript{1596} This could be read as the attempt to interpreted the increase of affection in connection with a tendency to empathy that, conversely, might have the effect that defensive responses are detached from the pri-

\begin{addendum}
\item Kramer, “Beobachtungen über das Verhalten der Aaskrähe”, 121.
\item Ibid., 122.
\item Ibid., 123, similarly 126.
\item For the following see ibid., 125–129.
\item Ibid., 127.
\item Ibid., 126.
\item Ibid., 128.
\end{addendum}
mary appearance of the conspecific and henceforth are applied to any kind of bird in danger. To put it provocatively, Lorenz’s “Umbringenhelfen” therefore stands against Kramer’s idea of solidarity – depersonalization against empathy. To sum up my reading of Beobachtungen über das Verhalten der Aaskrähe (Corvus corone) zu Freund und Feind (1941) one may say that all the different types of social encounters G. Kramer examines in his account substantiate a model of social interaction which marks an alternative to K. Lorenz’s hypothetical realism.

That Kramer reads back Lorenz’s model into the framework of Heinroth’s and v. Uexküll’s works that had partly served as a starting point of his own scientific development thereby coincides with the fact that Kramer’s recollections appeared in a “Festschrift” dedicated to O. Heinroth himself. It remains to ask whether we should dare have a glance behind the mirror and raise the question whether G. Kramer’s account could not be read as some kind of allegory or scientific fable. What can be said with certainty is that Lorenz’s model provided the epistemic grounds for putting forward his doctrine of “degeneration” which, as U. Deichmann and others have claimed, could be used as biological legitimation for killing humans. It is not an accident that Kramer underlined that the final stages of Lorenz’s abstraction model can lead to “Umbringenhelfen” – an accusation which certainly can be put forward against Lorenz’s accounts themselves if we take into consideration that it was the years before 1941 when most of Lorenz’s “domestication”-papers appeared. From this perspective it is only one step further to ask whether Kramer had not thought about concrete persons when he spoke of “Carrion Crows”, “Common Ravens” and “Jackdaws”. The idea of a joint research institute – E. v. Holst’s “desired Orplid” – most likely existed since the late 1930s.

Kramer picked up the theme of animal societies in a later more popular scientific paper of the year 1950. See G. Kramer. “Über individuell und anonym gebundene Gemeinschaften der Tiere und Menschen”. In: Studium Generale 3.10 (1950), 565–572. In this paper he distinguished between anonymous / open and closed forms of animal society only the latter of which were based on personal recognition. From this perspective Lorenz’s model appears to be based on de-individualization leading to neglect of the familiar conspecific, while Kramer’s model rests upon anonymization leading to solidarity with unfamiliar living beings (especially Ibid., 568–569).

Another study of the year 1951 seemed to attack Lorenz’s hypothetical realism by suggesting another model for the intertwining of releaser and releasing scheme. In bullfinches, Kramer argues, the inborn scheme of recognition allows responsiveness to a wide range of unspecific objects, whereas supplementary learning narrows down this range of responsiveness to a limited amount of isolated and closely related objects (which to recognize requires perceiving them as a whole). See G. Kramer et al. “Über angeborenes und erworbenes Feinderkennen beim Gimpel (Pyrrhula pyrrhula L.)”. In: Behaviour 3.4 (1951), 243–255. In this context, I’d like to mention U. v. St. Paul’s dissertation project and especially Kramer’s letter of evaluation. See MPG-Archives, III. HA, Rep. 77, file 11, letter G. Kramer to the Dean of the Science Faculty of the University of Münster (17/01/1950). I am not sure whether the results of Kramer’s pupil fulfilled the advisor’s intention. Also we know that U. v. St. Paul later switched to E. v. Holst’s department. Why? Her move is mentioned in letters to a colleague in Freiburg and to G. Kramer. See ibid., file 17, letter U. v. St. Paul to G. Birukow (13/09/1957) and ibid., file 17, letter U. v. St. Paul to G. Kramer (23/10/1957). And additional hint that Kramer was critical about Lorenz’s intercalation-theory eventually can be found in a letter to his mentor. See SBB, NL 150, file 37, letter G. Kramer to E. Stresemann (14/08/1947).

K. Lorenz’s implication with National Socialism has raised the interest of several historians. For more detailed references to their works see fn. 933, page 313 of my thesis.

For the circumscription of the planned institute as “Orplid” see Archives of the Max-Planck-Society, Berlin [quoted as: MPG-Archives]. General Administration, Institute Advisory Files.
Intellectual Life-Histories

have to interpret then the fact that Kramer altered Lorenz’s taxonomy in as much as he claimed a closer connection between “Jackdaws” and *Carrion Crows* and dropped the “Common Raven” altogether whereby the latter kind of bird, according to Lorenz’s own account, was the one amongst all other mentioned species which was capable most to kill one’s own kind if personal bondings forfeited. This allegoric reading of Kramer’s text is quite a far-fetched and speculative interpretation, of course. A matter of fact, however, is that the forms of cooperation which actually were established in the years after the Second World War were between G. Kramer and E. v. Holst (viz in Heidelberg and Wilhelmshaven) and less, as the later founding of the Seewiesen institute may suggest, between E. v. Holst and K. Lorenz. From this perspective Kramer’s seemingly innocent recollections may be even read as a highly subtle warning into the direction of the “Raven”. If Lorenz’s research was leading to “Umbringenhelfen” there would be no participation in a joint research institute. From a more structure historical point of view Kramer’s paper provides a translation of K. Lorenz’s hypothetical realism into the narrower core framework of the Modern Synthesis. In doing so he established a

MPI for Behavioural Physiology [quoted as: II. HA, Rep. 1A, IB-Files Behavioural Physiology], 3. Allgemein, I, letter E. v. Holst and K. Lorenz to O. Hahn (20/10/1952) incl. a proposal concerning the foundation of a Max-Planck Institute for Behavioural Physiology. E. v. Holst’s metaphor, the “desired ‘Orplid’” (“das ersehnte ‘Orplid’”), eventually is an allusion to one of E. Mörike’s poems. “Orplid” in E. Mörike’s work is the name for a desired fantasy land. Moreover, its invention is said to be the brain child of Mörike and his friend L. Bauer who together with W. Waiblinger constituted a band of three friends during Mörike’s period in Tübingen. This trio is also reputed full of personal tensions.

Most interestingly, we can infer from some letters exchanged many years later between N. Tinbergen and I. Eibl-Eibesfeldt that it was a characteristic of K. Lorenz’s to treat his close friends sometimes a bit raven-like. See to this Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3147, D 66, letter N. Tinbergen to I. Eibl-Eibesfeldt (25/10/1980) and ibid., Ms.Eng. c. 3147, D 66, letter I. Eibl-Eibesfeldt to N. Tinbergen (04/11/1980). See also E. v. Holst’s characterization MPG-Archives, III. HA, Rep. 29, file 292, letter E. v. Holst to O. Koehler (21/12/1949). From a letter written by G. Kramer to M. Hartmann in March 1937 we can infer that Lorenz met v. Holst in Berlin in early 1937 and, also that Kramer, tried to promote their cooperation. See MPG-Archives, III. HA, Rep. 47, file 797, letter G. Kramer to M. Hartmann (25/03/1937).

In this context, it might be also of interest that Kramer’s department, which finally was detached from the MPI for Marine Biology and incorporated into the newly founded MPI for Behavioural Physiology in 1959, originally was considered to become a department of the Radolfzell Bird Observatory which had become the formal legal successor of the former “Vogelwarte Rossitten”. See to this aspect Kramer’s correspondence with F. Frank in which these issues are discussed since around 1956, MPG-Archives, III. HA, Rep. 77, file 15, letter F. Frank to G. Kramer (10/02/1956). See also ibid., file 15, letter G. Kramer to O. Koehler (30/08/1956). And even after this plan had been discarded and Kramer’s institute (consisting of his and J. Aschoff’s department) was to be integrated into the MPI for Behavioural Physiology, Kramer apparently strictly refused any plan to unify both part-institutes spatially! For this information see ibid., file 17, letter K. Lorenz to G. Kramer (21/11/1957). The formal legitimation why G. Kramer’s department was not integrated into the Seewiesen institute was that he was bound in Wilhelmshaven by the special nature of his experiments with birds. See MPG-Archives, III. HA, Rep. 29, file 3, “Vorschlag zur Gründung eines Max-Planck-Instituts für Verhaltensphysiologie” (12/10/1952), here page 3 and ibid., file 183, letter G. Kramer to O. Hahn (20/04/1953).

Most interestingly, Kramer in a very early letter to his mentor E. Stresemann refers to K. Lorenz and the latter’s wife as the “Altenberger Kolkrabenpaar”. See SBB, NL 150, file 37, letter G. Kramer to E. Stresemann (03/02/1934).

However, from letters G. Kramer exchanged with J. Hämerling at the end of 1947 we can infer that Kramer, as soon as it was clear that Lorenz would return from captivity as a prisoner
connection between the neo-Darwinian and the Ethological Synthesis and, while doing so, the idea of an “Extended Synthesis”. What I have called “translation” thereby consists of both adopting a pre-existing and already elaborated epistemic framework and its reconfiguration. By filling with content this modified scheme then generates partly quite an antagonistic proposition so that we are confronted not only with an epistemic but also with a phenomenological tension. This tension, again, is somewhat alleviated in Kramer’s account by putting his focus upon another experimental animal, the Carrion Crow so that, finally, both frameworks may coexist. In some parts Beobachtungen über das Verhalten der Aaskrähe (Corvus corone) zu Freund und Feind even reads as if Kramer wanted to remind Lorenz of his roots and pull him on his side. In a letter written to E. Stresemann in 1943 Kramer, for instance, writes highly ambiguously:

 [...] Über Lorenz sind wir hier im Bilde. Ich glaube zwar, daß er auch aus der äußeren Experimentierbeschränkung eine Tugend zu machen weiß, wünsche ihm aber wie Sie, daß er bald und unter günstigen Verhältnissen wieder an seinen Wurzelort zurückkehren kann. Seine Arbeiten lesen wir hier an der Station mit großer Gier.

[As to Lorenz we are in the picture here. Though I believe that he knows, too, how to make a virtue of the restrictions imposed on the experimentation from outside, I wish him as you do, that he can soon return to his roots [literally: “root place”, “root location”] under favourable circumstances. Here at the Station we read his works with great greediness.]

The quotation eventually summarizes nicely G. Kramer’s standpoint regarding the derailment of his friend. Thus he seemed to explain his degeneration thesis as a gesture of opportunism – quite in agreement with and in terms of the narrative scheme provided by Lorenz’s own theorem: The more of outer restriction leads to a more of adjustment, that is, (a proximate) “less” is correlated with (an adaptive) “more”. And what is more: Both Kramer and Stresemann wanted Lorenz to return to the roots of his work which can be interpreted both very literally as “returning from war to research” or “from being soldier to being researcher”, but also as a “move back” to his scientific origins. Kramer’s attempt to intervene was well understood but, in the long run, did not have the desired effect since the MPI for Behavioural Physiology was later founded at first as double institute consisting of E. v. Holst’s and K. Lorenz’s department. There are several signs indicating that Kramer kept distance, both spatially and epistemologically, and this was the case even after his formal integration into the Seewiesen mother institute.

See ibid., file 37, letter G. Kramer to E. Stresemann (31.08.1943).
ii) The Return of the “Hopeful Monsters”?

In the previous paragraphs I have analyzed carefully the research works G. Kramer either published during the time he was affiliated with the Zoological Research Station in Naples or more or less shortly after this station in his career. My results show that the Naples period was characterized by the consolidation of the neo-Darwinian frame within which he had placed his research since his move to Rovigno at the latest. From an epistemological perspective this “consolidation” consisted of establishing the semantic re-evaluations that can also be made evident in the works of other ethologists. Although it is difficult to make evident these shifts of semantic hierarchies my special focus on paradoxa and their relocation within the epistemic patterns proved to be an effective tool. In Über Inselmelanismus bei Eidechsen, a later retrospective reflection of his research in Rovigno and Naples, I even found my hypothesis supported in G. Kramer’s own reasoning, that is, on a meta-level of scientific speech. It is also these later retrospective reappraising of data raised in Rovigno and Naples which make me believe that Kramer perpetuated his neo-Darwinian convictions after he moved to Heidelberg in 1946 and to Wilhelmshaven in 1948. A brief glance upon my statistical survey of G. Kramer’s research publications (Fig. 2.17) shows that the number of papers published between 1946 and summer 1948 is rather small. The lack of published sources becomes even worse if we take into consideration that Veränderungen von Nachkommenziffter und Nachkommengröße sowie Altersverteilung von Inseleidechsen (1946), one of the few published studies of those years, is actually a “reverberation” of research that has been carried out earlier in Italy. To a certain extent this proposition also applies to Wir Warmblüter (“We Warm-blooded Animals”) (1948), a comprehensive popular scientific account in which G. Kramer compared the metabolism of warm- and cold-blooded animals in different environments (i.e. in aerial environments and water) from an adaptionist’s perspective. He came to the conclusion that endotherm metabolism – despite the higher rates of energy consumption – finally turned out to be the more progressive option of evolutionary development. A historical account solely relying on published sources would let appear this period as silent as the time during which Kramer was prevented from research due to his military service (1942–1945). With a view of both periods of Kramer’s life-history, that is, the time between 1942 and 1945, on the one hand, and his early postwar research in Heidelberg it is therefore necessary to take into account more archive material. Although the amount of archival sources for this period is scarce, too, it gives us at least an impression of Kramer’s research activities. Thus Kramer’s personal paper’s hold a manuscript of an unpublished paper whose title can roughly translated as “Examinations Concerning the Denaturation of Blood-serum in Lizards”. The


paper mentions the author’s professional status when he carried out the study: “z. Zt. bei der Wehrmacht” (“Currently in the Armed Forces”). With this information the document can be dated between 1942 and 1945. The content of the paper is, simply speaking, concerned with the question how the blood serum of Lizards changes its consistence with increased temperatures. Kramer mainly compared the blood curves of his Lizards with the one he obtained with mammals (viz. Cows) but he also seemed to have tested the constitution of turtle blood. On basis of this information we might eventually approach G. Kramer’s serum study as the attempt to use the responsiveness of animal blood to heat as systematic characteristic. So far this study is the only scientific statement of Kramer’s between 1942 and 1945 I was able to trace. In E. Stresemann’s obituary we are informed that G. Kramer returned from captivity as a prisoner of war in 1945.\[1607\] He was not implicated with National Socialism and therefore not negatively affected by the laws of denazification.\[1608\] As a result he was re-employed since April 1946 and since then worked as assistant and adjunct professor at the Zoological Institute of the University of Heidelberg.\[1609\] The Zoological Institute was headed by E. v. Holst until both researchers decided to help establish together to the newly founded MPI for Marine Biology in Wilhelmshaven in summer of 1948.\[1610\] The cooperation between E. v. Holst and G. Kramer was both desired and had practical reasons.\[1611\] It was therefore not accidental. In fall 1946, Kramer obtained his habilitation (qualification by means of


\[1608\] See UAH, B-6779/2, letter Dean of UH Fac. Sc. Math. to Provost of UH (04/06/1946) and ibid., letter Leon P. Irvin (Military Government Office) to Provost of UH (06/06/1946).

\[1609\] UAH, PA 4639, “Meldebogen auf Grund des Gesetzes zur Befreiung von Nationalsozialismus und Militarismus vom 5. 3. 1946” (03/06/1947). For his employment as research assistant till 1\textsuperscript{st} April 1946 see UAH, B-6779/2, letter Minister for Education and Cultural Affairs of the Federal State Region of Baden to Provost of UH (23/07/1946). E. v. Holst thought that an ordinary post as research assistant for G. Kramer was inappropriate so that he intended to promote his colleague. See MPG-Archives, III. HA, Rep. 47, file 665, letter E. v. Holst to M. Hartmann (07/08/1946), asking for a letter of recommendation.

\[1610\] G. Kramer mentions his and v. Holst’s interest in becoming part of a newly founded institute in a letter to M. Hartmann dated to September 1947. See ibid., file 798, letter G. Kramer to M. Hartmann (29/09/1947). G. Kramer informed the dean of the “Naturwissenschaftlich-mathematischen Fakultät der Universität Heidelberg” (in the following: UH Fac. Sc. Math.) about his plans to move to Wilhelmshaven in a letter dated to December 1947. See MPG-Archives, III. HA, Rep. 77, file 1, letter G. Kramer to H. Schneiderhöhn [?]\[1611\] (10/12/1947) and also UAH, PA 4639, letter G. Kramer to Minister for Education and Cultural Affairs of the Federal State Region of Baden (03/03/1948). He resigned from his responsibilities as lecturer on January 31\textsuperscript{st} 1949 to build up the new research institute. See UAH, PA 10014, letter G. Kramer to Director of the Zoological Institute of UH (31/12/1947). Further letters show that Kramer was formally on leave till June 1949. See MPG-Archives, III. HA, Rep. 77, file 2, letter Dean of UH Fac. Sc. Math. ([A.\[1611\] Seybold) to G. Kramer (15/06/1949), ibid., file 2, letter G. Kramer to Dean of UH Fac. Sc. Math. ([A.\[1611\] Seybold) (20/06/1949), and also UAH, PA 4639, letter G. Kramer to Dean of UH Fac. Sc. Math. (01/06/1948), ibid., letter Dean of UH Fac. Sc. Math. ([A.\[1611\] Seybold) to Provost of UH (03/06/1948), ibid., letter Dean of UH Fac. Sc. Math. ([A.\[1611\] Seybold) to Provost of UH (17/12/1948), UAH, PA 10014, letter Provost UH to G. Kramer (18/12/1948) UAH, PA 4639, letter G. Kramer to Dean of UH Fac. Sc. Math. (20/06/1949), informing [A.\[1611\] Seybold that he does not want to transfer his “Habilitation” to another institution and UAH, PA 10014, letter Provost of UH to G. Kramer (02/07/1949), including a confirmation. A. Seybold was dean of the science faculty between 1 April 1948 and 31 August 1949. See D. Drüll-Zimmermann, ed. Heidelberger Gelehrtenlexikon 1933–1986. Berlin et al.: Springer, 2009, 585.

\[1611\] See MPG-Archives, III. HA, Rep. 47, file 798, letter G. Kramer to M. Hartmann (26/03/1946).
a postdoctoral thesis required to become professor at a German University) from the University of Heidelberg but later, when he finally moved to Wilhelmshaven, refused to transfer this qualification to another institution, which, in turn, complicated his nomination to “Professor” within the Max-Planck Society. In order to fulfil the requirements for his habilitation Kramer also had to deliver an inaugural lecture which took place on the 17th February 1947 and is of interest because of its more ethological title “Irrationale Motive in der menschlichen Einstellung zum Tier” (Irrational Motives in the Attitude of Humans to Animals). The rumours that G. Kramer never obtained a post-doctoral qualification (Habilitation) cannot be confirmed: G. Kramer’s postdoctoral thesis including several documents related to the process in course of which Kramer obtained this academic qualification are preserved in the personal files held by the Archives of the University of Heidelberg. However, up to now, I was not able to trace a larger published treatise bearing the same or a similar title as the original manuscript and the list of publications E. Stresemann added to his obituary does not include a treatise that is explicitly marked as “habilitation thesis”. This can mean that the treatise was not published as such at all, or that the results went in a number of smaller papers, or the thesis was


The title of Kramer’s inaugural lecture can be inferred from a letter he wrote to the Dean. See UAH, PA 10014, letter G. Kramer to Dean of UH Fac. Sc. Math. (L. Rüger) (13/01/1947). Two additional themes had been suggested by Kramer before, namely “Variabilität und Individualität” (Variability and Individuality) and “Zufall und Gesetz in der Entwicklung der Organismen” (Chance and Law in the Development of Organisms). See ibid., letter G. Kramer to Dean of UH Fac. Sc. Math. (03/09/1946). Another prerequisite was the so-called “Habilitations-Kolloquium” which took place on 21st of October 1946 in the Institute for Mineralogy and Petrography and was titled “Das persönliche Erkennen der Artgenossen” (The Personal Recognition of the Conspecific). See ibid., letter Dean of UH Fac. Sc. Math. to [?] v. Weizäcker (16/09/1946). Both chosen topics thus were more ethological, while the two more genetic themes were dropped.

Gustav Kramer (1910–1959)

published with another title. The latter option seems to be the case.1616 Although this sub-section of my thesis is mainly concerned with avian orientation and navigation I have to analyse at first Kramer’s evolutionary studies of the immediate postwar period because it is the epistemological vacuum they left which provided the space for a qualitatively different area of research such as orientation and navigation: Even stronger than the alleged published version, the typed manuscript of Kramer’s post-doctoral thesis seems to confirm my suspicion that the author during his stay in Italy had grown to a veritable, though somewhat atypical, advocate of the Modern Synthesis insofar as he, on the one hand, picked up the question of speciation in small isolated populations but, on the other hand, maintained the primary explanatory framework of neo-Darwinians to account for the phenomena of organic diversity: Heritable variability and selection. “Bei den ausgeklügelten Erscheinungen, die uns beim morphologischen, physiologischen und verhaltenskundlichen Studien der Organismen und ihrer Beziehungen untereinander stets von neuem entgegentreten”, Kramer writes,

The heuristic framework to which Kramer restricts his study on speciation by emphasizing the applicability of an orthodox selectionism also governs the composition of the text. Thus Kramer, after having narrowed down his theme in the introduction, enters into the empirical section of his thesis but within this part operates with an extension. Approximative reduction thus culminates in diagnostic

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1616 In a letter to M. Hartmann mentions a paper he intended to submit as habilitation thesis, the intention to publish it and to dedicate it to M. Hartmann. The title Kramer planned to give this paper is mentioned as “Wandlungen im Fortpflanzungsverhalten und in der Altersstatistik bei Inseleidechsen”. See MPG-Archives, III. HA, Rep. 47, file 798, letter G. Kramer to M. Hartmann (28/06/1946). This alternative title is bearing some resemblance with a study Kramer published in 1946 given the title “Veränderungen von Nachkommenziffer und Nachkommengröße sowie Altersverteilung von Inseleidechsen” so that I think it possible the results Kramer summarized in his post-doctoral qualification thesis went into this paper. For the complete reference see 1461, page 466 of my thesis. A more thorough comparison of the original ms. and the last mentioned publication seems confirm this hypothesis.

extension. This logic of extension is based on two steps. At first, Kramer mentions those forms of variability in Italian insular Lizards which can be explained by geographical isolation and chance (“B) Durch Isolation und Zufall zustandekommene Rassendifferenzierung von Inseleidechsen”). To this set of qualities he counts the red-colouration of the bellies, the concolor-feature and finally the body-size. In a second step, however, he goes beyond the explanatory framework that is based on direct and more cataclysmic impacts such as chance and isolation. In doing so, he discusses mainly two aspects of which Kramer thinks they might be connected in as much as they are both subdued to the particular selective pressures being exerted upon the individuals on small islands. One of these fields, which Kramer chose to demonstrate his view is the adjustment of the reproductive strategy of insular Lizards (“C) Eine Generelle Eigentümlichkeit von Inselpopulationen: Verringerung der Anzahl und Zunahme der Größe der Nachkommen”). In contrast to mainland animals, Kramer argues here, Lizards on small islands have viewer but bigger offspring. The second aspect which, in Kramer’s view, supports the applicability of an orthodox selectionism even in small populations is concerned with the modified age structure in small insular Lizard populations (“D) Die Verteilung der Altersklassen bei Insel und Festlandpopulationen”). Thus, Kramer shows that in island population the proportion of older and very old specimens is higher than in mainland populations. Both phenomena together, he summarizes, may be explained as the particular milieu-dependent solution of a conflict between two antagonistic selective pressures favouring one particular reproductive strategy each, namely either the production of many small or fewer bigger offspring. In his particular insular populations, he argues further, the equilibrium – or “trade-off” as ecologists nowadays might say – comes to an halt at a state which forces the production of bigger young, on the one hand, but, on the other hand, also allows, at least to a certain extent, the – per se maladaptive – decrease of the amount of offspring. The combination of selective pressures Kramer correlated with this particular state of equilibrium then consists of the non-existence of interspecific predators on geographically isolated islands (snakes etc.), on the one side, but also the negative effect of cannibalism, on the other hand, which is explained by more severe constraints with food supply particularly in hot summer months. While the proneness to intraspecific cannibalism enforces a reproductive strategy that favours the production of bigger, better protected and fitter young, the loss of predators allowed the decrease of the offspring numbers which Kramer made responsible for the relatively advanced ageing of the insular populations. In addition, Kramer interpreted his results with a view of the phylogenetic development by asking for the consequences of the modified reproductive strategy in insular milieus for both the age-structure of current a population (first step) and the linear succession of the generations (second step). The final stage of Kramer’s stepwise reduction then consisted in asking for the conclusion to be drawn from both previous steps for the problematic of phylogenetic development and the question of speciation. On the

one hand, Kramer here reasons, the longer duration of the generations in insular Lizards must have led towards a stagnation of the development since especially the factor of mutation (generation of variability) is bound to the process of reproduction. On the other hand, he guesses, too, that the drop out of the selective pressure exerted by predators in newly isolated islands in former times must have set free an enormous diversity of forms upon which natural selection could have acted upon at least in the immediate period after an island’s geological separation from the mainland. In sum, one may say that Kramer’s treatise operates with an orderly principle that is based on two steps: In a first step, he narrows down his theme to the peculiarities phylogenetic development reveals in exempt populations of low numbers. In a second step, however he exceeds the framework of canonical explanations which had been put forward by neo-Darwinian evolutional biologists so far (geographic isolation and suspension of the Hardy-Weinberg formula by applying the chance principle in small populations) by making plausible the applicability of the restricted explanatory framework (mutation and selection) even in small isolated populations. Altogether, Kramer’s habilitation thesis thus might be shaped by an epistemic reference system that rests upon the idea of gradualist reduction albeit in a somewhat unorthodox manifestation. This partly unconventional interpretation seems due to the fact that the problematic of speciation in small isolated populations is translated back into the orthodox frame which is guided by mutation and selection only. Kramer’s move had consequences for his life course, too. The above mentioned act of re-translation created a kind of a vacuum in the epistemic realm which neo-Darwinians used to fill with explanations for phylogenetic development based on discontinuous variability (e.g. allopatric speciation) and I believe Kramer filled this systemic position with an altogether different area of research: Animal behaviour and later research on avian orientation and navigation! In so far Kramer’s scientific development resembled Niko Tinbergen’s in as much as both researchers – soon after the Second World War – began to restrict particular scientific interests and practices to corresponding epistemic realms and thus created a free space that could be filled with other themes and practices, in Niko’s case, the founding of a research group.

Next to G. Kramer’s habilitation thesis, two further unpublished documents are available which might be able to cast some light upon the development Kramer’s research went through during the early post-war period. As adjunct professor he was supposed to give lectures two of which are passed onto us in form of handwritten manuscripts and which let us imagine already the future division of labour. Translated into English the titles read “Ecological Genetics” and “Lecture on Animal Psychology”.\[^{1621}\] “Ecological Genetics” operates with a logical bipartition. In the first part of the lecture Kramer intended to make his audience familiar with the latest achievements of neo-Darwinian population genetics. Thus he was mainly concerned with tracing the path leading from Mendel’s laws to the Hardy-Weinberg equilibrium. In the second part of the lecture, however, he seemed to be particularly eager to demonstrate those mechanisms of heritable variability which are at work

\[^{1621}\] See MPG-Archives, III. HA, Rep. 77, box 1, incomplete ms. “Ökologische Genetik” (ca. 1946), 48 pages and ibid., box 1, ms. “Vorlesung über Tierpsychologie” (ca. 1946), ca. 30 pages.
when the ideal case of unlimited large populations and lack of additional modifying factors (both presumption of the Hardy-Weinberg Principle) are not fulfilled. In doing so, Kramer wanted his students to appreciate the mechanism of genetic drift but also entered the question how to conceive the effect of mutation and selective pressures. Altogether, I regard Kramer’s lecture as an extraordinary important source which makes him appear not only as veritable exponent of the Modern Synthetic Theory of Evolution but also makes evident that he represented this synthesis in a wider sense, that is, as a combination of both population and ecological genetics whereby the mechanisms he mentioned in the latter case – Kramer’s emphasis – were closely related with the problematic of speciation (which Kramer interpreted partly orthodox in terms of mutation and selection). His “Lecture on Animal Psychology” is equally illuminating. The key to the text is eventually the information that Kramer distinguished in principle between two different types of holistic thinking which he called “Komplex- Qualität”, on the one hand, and “Gestalt” on the other.1622 Only the latter of the two is connected with the ideas of “transposability” and “positive diagnostic”, while the former of the two marks a form of holism lacking both features. Kramer’s concept of diagnostics which he had adopted from the medical sciences and translated into his systematic studies is less headed towards an exclusive reduction rather than the intuitive extension of one’s perspective into unknown territory. “Was übrig bleibt”, Kramer underlines in his lecture, “ist nicht eine Gestalt” which can be roughly translated with “What is left over is not a Gestalt”.1623 Kramer’s holism thus created a tension especially to Lorenz’s gestalt theory which becomes fully conspicuous, for instance, when he discusses the allegedly static character of the instinctive action patterns as it was put forward by K. Lorenz. “[...] die Instinkthandlung soll in ihrem finalen Ablauf unveränderlich sein (Lorenz)”. Kramer comments Lorenz’s theory and replies,

Wogegen zunächst + allerlei zu sagen ist! Früher wurde ja gerade [das] Gegenteil behauptet. [the instinctive action pattern is said to be static in its final stage (Lorenz). For the time being, a lot can be put forward against this view. In the old days it was quite the opposite that was claimed.][transl. CL]1624

My opinion is that Kramer’s alternative model of holism is also shaping the way he organized his lecture of 1946. Thus it doesn’t seem to be an accident that he begins with an outline of the historical origins of scientific Animal Psychology and after that proceeds with the more static behaviours, discusses learning only to finally end with the higher forms of problem solving and tool using. Both lectures thus most likely operate with different complementary and mutually intertwined epistemic patterns and therefore might cover well the two realms coexisting in Kramer’s life and research which can be roughly addressed in terms of “approximative reduction” vs. “diagnostic extension”. With a view upon the period after 1945 we may eventually say both realms were correlated relatively stably with one topic each. While Kramer’s interest in Evolutionary Biology culminated in a research

1622 See MPG-Archives, III. HA, Rep. 77, box 1, ms. “Vorlesung über Tierpsychologie” (ca. 1946), lecture VIII.
1623 See ibid., box 1, ms. “Vorlesung über Tierpsychologie” (ca. 1946), especially lecture VIII.
1624 Ibid., box 1, ms. “Vorlesung über Tierpsychologie” (ca. 1946), lecture III. For more background information see Köck, “Zur Geschichte des Instinktbegriffs”, especially 227–250.
program on relative growth, his ethological line of work was leading to the study of avian orientation and navigation. As I will show soon it was especially the latter topic which turned out to be a perfect interpretation of Kramer’s indefinite holism. For the time being, it may suffice to note that G. Kramer refurbished his passion for Ornithology in Heidelberg whereby he is said to have picked up even more consciously the thread of O. Heinroth’s research work which he had already acknowledged in his paper of the year 1941. In autumn of 1946, Stresemann and Kramer started to edit an ornithological journal with the title “Ornithologische Berichte” and which at the beginning mostly included reviews of research works that had been published outside Germany. In addition to that, American ornithologists – following the initiative of F. N. and F. Hammerstrom, M. M. Nice, and E. Mayr, had managed to establish a relief network for their German fellows soon after the end of the Second World War which consisted not only of sending care pack-

\[\text{Avian orientation and navigation is connected with Kramer’s former micro-systematic research insofar as the home finding capacity, in Kramer’s view, is quite a young phylogenetic appearance. See to this aspect the popular lecture with the following reference: MPG-Archives, III. HA, Rep. 77, box 1, ms. “Gr[1…] Vortrag” (>1950), here page 1–2. For Stresemann’s theory that Kramer returned to Ornithology in Heidelberg see Stresemann, “Gustav Kramer”, 259. See also MPG-Archives, III. HA, Rep. 77, file 7, “Lebenslauf” (n. d.). A fairly large bundle of letters preserved in E. Stresemann’s personal papers reveals the interaction between Stresemann and Kramer that was established by the founding of the review paper and the various themes that needed to be discussed. Concerning printing and distribution of the journal see for instance SBB, NL 150, file 37, letter G. Kramer to E. Stresemann (20/05/1947), ibid., file 37, letter G. Kramer to E. Stresemann (16/06/1947), ibid., file 37, letter G. Kramer to E. Stresemann (14/08/1947), ibid., file 37, letter G. Kramer to E. Stresemann (16/08/1948)[CL], ibid., file 37, letter G. Kramer to E. Stresemann (25/08/1948), and ibid., file 37, letter E. Stresemann to G. Kramer (20/01/1949). For editorial issues and, particularly, the organization of the contributions see, for instance, ibid., file 37, letter G. Kramer to E. Stresemann (11/07/1947), ibid., file 37, letter G. Kramer to E. Stresemann (22/07/1947), and ibid., file 37, letter E. Stresemann to G. Kramer (02/08/1947). For the lack of paper and, as a result, the attempt of the Military Government to shut down the journal, as well as the support of American ornithologists see, for instance, ibid., file 37, letter G. Kramer to E. Stresemann (21/10/1947), ibid., file 37, letter E. Stresemann to G. Kramer (24/10/1947), ibid., file 37, letter G. Kramer to E. Stresemann (27/10/1947), ibid., file 37, letter G. Kramer to E. Stresemann (15/11/1947), ibid., file 37, letter G. Kramer to E. Stresemann (01/12/1947), ibid., file 37, letter G. Kramer to E. Stresemann (08/12/1947), ibid., file 37, letter G. Kramer to E. Stresemann (09/01/1948), ibid., file 37, letter G. Kramer to E. Stresemann (22/01/1948), ibid., file 37, letter E. Stresemann to G. Kramer (10/02/1948), ibid., file 37, letter G. Kramer to E. Stresemann (03/03/1948), ibid., file 37, letter G. Kramer to E. Stresemann (26/10/1948), ibid., file 37, letter G. Kramer to F. Pitelka (01/11/1948), ibid., file 37, letter E. Stresemann to G. Kramer (08/11/1948), and ibid., file 37, letter G. Kramer to E. Stresemann (09/11/1948). For Kramer’s urge to establish a journal for pure science (“zweckfreie Wissenschaft”) see ibid., file 37, letter G. Kramer to E. Stresemann (07/01/1948), ibid., file 37, letter G. Kramer to E. Stresemann (13/03/1948). For more details concerning potential recipients see ibid., file 37, letter G. Kramer to E. Stresemann (09/03/1948) and ibid., file 37, letter G. Kramer to (?)[CL] Bader (Winter Publishing House) (26/08/1948). Kramer’s engagement with the Ornithologische Berichte might be also one of the reasons why there are some correspondences in his personal papers which are related to the exchange of reprints and papers. For instance, W. Craig sent Kramer his book The Song of the Wood Pewee (1943). See MPG-Archives, III. HA, Rep. 77, file 1, letter W. Craig to G. Kramer (04/08/1947). For Kramer’s scientific exchange with D. Lack see ibid., file 1, letter D. Lack to G. Kramer (31/10/1947). For more details concerning the founding and the intention behind the Ornithologische Berichte see ibid., file 3, letter M. M. Nice to G. Kramer (07/09/1948) and ibid., file 3, letter M. M. Nice to G. Kramer (19/10/1948).}
ages but also included the exchange of books and reprints.\footnote{1628} From the letters G. Kramer exchanged with friends and colleagues outside Germany we can infer that German scientists were desperately in need of those scientific publications which appeared during the war mainly in the English speaking parts of the world. This transatlantic scientific transfer of books and reprints finally resulted in establishing of so–called lending libraries inside Germany.\footnote{1629} That is, if I understood correctly, in each occupied zone there was at least one literature “depot” from which interested researchers could borrow the publications they wanted to read. G. Kramer most likely was one of these contact persons.\footnote{1630} Through this scientific transfer G. Kramer came into contact with H. L. Yeagley’s theory of orientation.\footnote{1631} Yeagley, an American physicist who was examining navigation of birds on behalf of the US military, had claimed that the orientation of pigeons could be explained by the bird’s capacity to calculate a position on basis of two physical systems, namely the magnetic field of the earth (that is the vertical intensity of this field), on the one hand, and the so–called Coriolis-field (that is the field of inertial forces being created by the rotation of the earth around its own axis), on the other.\footnote{1632}

\footnote{1628} The so-called “relief-Aktion” is documented in the letters E. Stresemann exchanged with G. Kramer. Several aspects are subject of discussion. For the delicate question of the profiteers see, for instance, SBB, NL 150, file 37, letter G. Kramer to E. Stresemann (20/05/1947), \textit{ibid.}, file 37, letter G. Kramer to E. Stresemann (16/06/1947), \textit{ibid.}, file 37, letter E. Stresemann to G. Kramer (30/06/1947), \textit{ibid.}, file 37, letter G. Kramer to E. Stresemann (22/07/1947), \textit{ibid.}, file 37, letter E. Stresemann to G. Kramer (02/08/1947), \textit{ibid.}, file 37, letter G. Kramer to E. Stresemann (15/09/1947), \textit{ibid.}, file 37, letter G. Kramer to E. Stresemann (21/10/1947), \textit{ibid.}, file 37, letter G. Kramer to E. Stresemann (10/12/1947). For the creation of this network of transatlantic exchange see also the documents in G. Kramer’s papers MPG-Archives, III. HA, Rep. 77, file 3, letter E. Mayr to G. Kramer (15/04/1947), \textit{ibid.}, file 3, letter E. Mayr to G. Kramer (02/06/1947), and \textit{ibid.}, file 3, letter E. Mayr to G. Kramer (05/12/1947). See also \textit{ibid.}, file 3, letter M. M. Nice to G. Kramer (11/09/1948).

\footnote{1629} The existence of such a library system is mentioned in SBB, NL 150, file 37, letter G. Kramer to E. Stresemann (10/02/1948).

\footnote{1630} The ornithological scientific community thus seemed to be standing out in comparison to other research branches through their highly advanced international scientific contacts soon after the Second World War. For instance, documents in G. Kramer’s papers which originated in context with the establishment of the new MPI for Marine Biology in Wilhelmshaven indicate that the marine biologists were not able to renew their contacts to Laboratories in Aberdeen and Lowestoft after the war. See MPG-Archives, III. HA, Rep. 77, file 10, ms. “Bericht über den Blount-Besuch” (ca. 07/1948), here page 1.

\footnote{1631} Kramer’s attention eventually has also been drawn to Yeagley’s work by a review in the German journal \textit{Natur und Technik}. See to this \textit{ibid.}, file 1, letter M. Sy to G. Kramer (23/11/1947). In a letter to E. Stresemann, Kramer reports that Yeagley has sent his orientation study and that he (Kramer) wants K. Heinroth to write a review. See SBB, NL 150, file 37, letter G. Kramer to E. Stresemann (03/03/1947).

once more reviving the scepticism of his student days, questioned this approach and henceforth began to carry out own experiments to explore the orientation mechanisms in birds.^{1633} “I have made the first attempts to join the study of homing”, Kramer writes in a letter to D. R. Griffin and continues: “I was induced to do that after having criticized Yeagley’s work. I think homing must be much more complicated than oriented migration is”.^{1634} The research in orientation and homing from then became one of the pillars, if not the prevailing theme, in G. Kramer’s research agenda until his tragic death in 1959.^{1635} In the following sections of my thesis I would like to reconstruct the transformation process that characterized G. Kramer’s research on orientation and homing in birds from 1946 to 1959. In doing so, I aim to answer the question in how far Kramer’s revived interest in Ornithology can be traced back to his mentor O. Heinroth. Furthermore, it must be clarified upon which epistemic grounds this research was carried out and, finally, how the increasingly sophisticated results interpreted and reinterpreted the underlying epistemic scheme over the years. In principle one may say, that G. Kramer’s intellectual life-history reveals a characteristic similar to the one of other ethologists namely that the epistemic development underlying their research had already reached a stage of consolidation at the beginning of the 1940s at the latest. Henceforth the trajectories of these researchers usually entered longer periods of epistemic continuity which in some cases once more took an unexpected turn in the late 1950s. Niko Tinbergen’s turn to Behavioural Ecology is one example of this type of life-history. I intend to show that G. Kramer’s life course is another, though of qualitatively different kind. Since Kramer’s research interests in the years after the Second World War were more or less strictly separated in two realms, that is, his passion for avian orientation and navigation, on the one hand, and his inclination to Evolutionary Biology (particularly the field of allometry), on the other, indicators for possible turning points in his life course need to be examined separately in each realm and with well adjusted methodological means in each case.^{1636}

\((R_1)\) I have argued that G. Kramer, in his very early ornithological accounts, has interpreted the epistemic scheme he had found a prevailing moment in his mentor’s works in two different antagonistic forms without abandoning the epistemic reference itself. These interpretations, in contrast to all later and deeper rooted epistemic interventions, were restricted to the mere phenomenological level of scientific speech. In this context, we were also confronted with two understandings of “orientation” each of which being connected with its own corresponding type of test.^{1637}

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1633 For Kramer’s criticism see G. Kramer. “Neue Beiträge zur Frage der Fernorientierung der Vögel”. In: *Ornithologische Berichte* 1 (1948), 228–238. In addition see also Kramer’s correspondence with H. L. Yeagley, MPG-Archives, III. HA, Rep. 77, file 1, letter H. L. Yeagley to G. Kramer (11/11/1947) and *ibid.*, file 1, letter G. Kramer to H. L. Yeagley (24/02/1948). Particularly for Kramer’s review paper see also SBB, NL 150, file 37, letter G. Kramer to E. Stresemann (07/01/1948[1949]).

1634 For the initial impulse Yeagley’s work had for Kramer’s own research see MPG-Archives, III. HA, Rep. 77, file 4, letter G. Kramer to D. R. Griffin (07/03/1950). See also *ibid.*, file 11, letter G. Kramer to K. Heinroth (27/10/1950).

1635 For Kramer’s shift of interests see once more fig. 2.17, page 388 of my thesis.

1636 For Kramer’s twofold interest in allometry and orientation in the period after World War II see also Lorenz, “Gustav Kramer”, 267, and also Thorpe, “Gustav Kramer”, 510.

1637 For another formulation of both understandings of “orientation”, see MPG-Archives, III. HA,
Either the natural state of the animal was conceived in terms of its closeness to the experimenter and the experiment consisted in the temporarily extension of the bird’s range of motility. In this case the theme of orientation appeared as the bird’s capacity to return to its keeper or a predefined location for the sake of feeding, sleeping or social contact. In the other case the natural state of the bird was constituted by its natural shyness towards humans and the experiment then consisted more in temporarily taming an otherwise wild creature. In other words, a natural distance was to be transferred into a, at least temporary, closeness for the sake of experimentation. The tragic paradox in the latter form of heuristic setting was founded in the overwhelming power of the bird’s natural instincts which often led to an ending of the acquaintance with its human companion because, for instance, its innate “Zugunruhe” finally gained the upper hand. In particular, the second interpretation was yielding accounts which ended with the loss of birds or even their withering – a narrative trait that can also be made evident in K. Lorenz’s early accounts which I tend to interpret as expressions of his juvenile scepticism. We can imagine that the epistemic interventions which basically reshaped Kramer’s scientific orientation between 1934 and 1940 also modified his understandings of “orientation”. In particular, what in former accounts had appeared as more or less futile attempt of taming wild creatures now turned out to be the modified basis for a new type of experiment, the so-called displacement experiment. Freighting the animal thereby created an initial distance between the experimenter and the animal in an artificial way and the animal was requested to transgress the obstacle that separated it from its host. Moreover, in contrast to the earlier “tragic” conception of orientation now the prevalence of the idea or the possibility of returning turned out to be a fairly constitutive moment of the new experimental setting and its presuppositions. As a provisional result, one may therefore say that orientation now was about to be conceived as the bird’s capacity to “sense” its home beyond pre-existing and artificially created distances. Considering the epistemic implications of G. Kramer’s orientation studies I think it quite amazing how his rejuvenated interest in Ornithology fitted into the secondary realm of the now consolidated neo-Darwinian orientation which, so far, was covered only if Kramer directly addressed the problematic of geographic isolation and speciation – that is to say in his more holistic ventures into Evolutionary Biology. Alike to N. Tinbergen’s trajectory where the practices of initial inauguration and supervising students ran like a thread through his entire career as an academic teacher, also in G. Kramer’s life course the epistemic logic underlying the theme of orientation established a strong moment of continuity that allowed epistemic modifications only below the surface even in case a thesis, treatise or scientific paper raised an alternative scheme onto paradigmatic level of sci-

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1638 For a prototypical example of this kind of narration see K. Lorenz. “Beobachtungen an Dohlen”. In: Journal für Ornithologie 75.4 (1927), 511–519.

1639 In other words, Kramer’s research on avian orientation and navigation shows a gesture similar to the one I have carved out in his systematic studies. The original framework he had adopted from Heinroth is multiplied on a mere phenomenological level of speech in the first place. In a second step, one of these interpretations is picked out and made the foundation for all further reasoning. The idea of micro-systematic and the displacement experiment thus are products of the same heuristic move.
entific speeches. My analyses have shown that G. Kramer reached out twice for more “General Analyses” (in H. Spencer’s sense) in his early career and in both cases the results turned out to be more fragile than relying on technical advances or the enticement of far-reaching mathematical reduction had suggested. And in both heuristic crises Kramer responded by changing his heuristic program in as much as he, from now on, switched to a more empirical mode of research and in doing so provided his extraordinary sensitivity a sphere of action within which it could flourish. I interpret both Kramer’s reflections upon the reliability and accuracy of the technical devices he had applied in his studies on metabolism and his micro-systematic detail studies as the result or the response of to previously experienced heuristic crises. Seen from this angle Kramer’s raised interest in orientation not only represented a return to Ornithology but also to a more risky way of research albeit under the slightly more moderate circumstances being provided by the fact that neo-Darwinian theorizing somewhat toned down the conciseness of those holistic theorems it put forward in some distinct areas of the new paradigm. 

To sum up my introductory remarks, I’d like to emphasize two aspects. At first, due to the fact that Kramer’s scientific orientation had already reached a state of fairly elaborate consolidation it is not necessary any more to reconstruct the epistemic scheme of every single paper in detail. Instead it may suffice to communicate the results of these analyses – which will be carried out nonetheless in the background – in a more casual manner. Second, this slight shift in my attention will allow me to focus more upon the finer phenomenological transformations which, in an additional step, then can be questioned for underlying so far unknown principles of heuristic variability. As a result, I’d like to suggest a two-step methodology for the following analysis of G. Kramer’s research of the decade after World War II. Thus, in a first step, I will try to provide a careful account of how Kramer’s understanding of avian orientation and navigation changed over the years. This account aims to be a phenomenological reconstruction of the finer steps of transformation which can be detected in Kramer’s reasoning upon the subject. In a second step, then I will make an attempt to carve out the more structure historical correlates of these shifts. A special emphasis thereby will be laid upon the turn Kramer’s ornithological research possibly experienced since around 1956. While it was primarily the conceptual paradoxes that served as an adequate tool to carve out the epistemic re-evaluations that had characterized Kramer’s consolidation to a neo-Darwinian biologist, it will be shown that it is the logical figure of tautology that turns out to be the appropriate tool to make evident the first indicators of the “turn” Kramer’s intellectual life-history experienced within the realm of his ornithological research. 

Step One: Phenomenological Overview. Altogether I see at least seven different phenomenological shifts in G. Kramer’s reasoning on avian orientation and naviga-

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1640 It was this pattern-inherent transformation process which was at stake when “Early Tinbergian Practice” changed into “Later Tinbergian Practice” and it is the micro-transformations of the orientation theme that might serve as an appropriate indicator for later shifts in G. Kramer’s life course running parallel to possible transformations in the realm he dedicated to his research on allometry.

1641 For Kramer’s sensitivity see Lorenz, “Gustav Kramer”, 266. Indicators for both of Kramer’s realms having different heuristic functions can be found in Thorpe, “Gustav Kramer”, 510.

1642 Please see to this aspect also E. Stresemann’s obituary, Stresemann, “Gustav Kramer”, 259–260.
The first of Kramer’s moves can be traced back to his Heidelberg period and consisted of extending already existing concepts of avian orientation and homing. I have already mentioned that the immediate impulse for G. Kramer’s revived research interest in ornithological issues eventually came from the outside of Germany. H. L. Yeagley, a physicist from Pennsylvania State University had carried out a project for the US Army Signal Corps during the Second World War in which he examined the geophysical basis of avian navigation. Both the US Army and the Navy had an interest in the physics of gravity and planetary motion since this knowledge was essential for the development for aircraft and missile guidance systems. Shortly after the war, in 1947 and 1951, Yeagley finally published the results of his studies in two separate papers the former of which raised Kramer’s attention. Kramer’s critical review was published in 1948 under the title “Neue Beiträge zur Frage der Fernorientierung der Vögel” in the *Ornithologische Berichte*, a journal he had founded in cooperation with E. Stresemann. His critical reflections of Yeagley’s theory marked the formal beginning of his research in avian orientation and navigation. H. L. Yeagley had put forward the spectacular hypothesis that homing pigeons, while flying, are able to sense the tiny increments either of the forces or of the secondary effects of the forces exerted by two different geophysical fields, namely the magnetic field of the earth (more precisely the vertical force within this field), on the one hand, and the field of inertial forces being created by the rotation of the earth, on the other (so-called Coriolis force). Both factors together built what Yeagley called a “navigational gridwork” or “grid system”, that is, a complex hypothetical pattern of field lines which provided the homing pigeon’s neurophysical orientation mechanism with the necessary raw data in order to process the two navigational coordinates, longitude and latitude, so to speak from the mode how both geophysical fields intersected with each other at each point of the bird’s flight. Although Yeagley did not neglect the possibility that homing pigeons use their previously acquired experience after entering the narrow radius of their home area, the model he put forward to explain that birds can find desired targets over huge distances and unfamiliar territories suggested a theory of true bicoordinated navigation. “It is well known”, Yeagley writes,

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For the data concerning H. L. Yeagley’s life and work see the references in fn. 1632, page 518 of my thesis.


For the complete reference of the paper see fn. 1633, page 519 of my thesis.

For the general thesis of the paper see Yeagley, “A Preliminary Study, Part I”, 1035. For a more elaborate formulation of the hypothesis see *ibid.*, 1039.

For the concepts “navigational gridwork” or “grid system” see *ibid.*, 1035, 1039 and passim. For Yeagley’s thesis that two or more overlapping navigational fields must be used as source of information while navigating see *ibid.*, 1036.
that many birds of the migratory species return to their breeding and nesting ground after being trapped and sent hundreds of miles into strange territory. Many such flights have been arranged so that the birds must orient themselves and fly hundreds of miles over water routes out of sight of land. One species, the Golden Plover, performs the remarkable feat of navigating 3000 miles from Alaska to the Hawaiian Islands with no landmarks over the broad expanses of the Pacific Ocean. Hundreds of individuals of the albatross family roam over thousands of square miles of the Southern Pacific area. Members of each species finally return to their own tiny island to breed and raise young. Hood Island of the Galapagos Archipelago group, is headquarters for one species of these birds. Since there are no “sign posts” of any kind over the ocean wastes, the flights must involve true navigation until the home island comes into view.

The idea of “true navigation”, however, required that the birds were not only furnished with the adequate sensory capacities but also with some kind of pre-existent memory or even “mental grid” that allowed the homing pigeon to store the information (i.e. the “navigational coordinates”) of the specific home locality in order to compare the spatial representation of this geographic place with the data sensed at any current point of its journey. Yeagley concludes “that the bird can recognize his home locality at the intersection of a characteristic line in the earth’s magnetic vertical field with a characteristic line of latitude”. He further claimed:

By this means, a bird, if flying in a location of magnetic vertical field intensity different from its home, can consciously fly in a direction which will bring its land-speed magnetic vertical-field effect back to that to which it is accustomed during its normal flight around home territory.

Kramer welcomed Yeagley’s theory of absolute orientation in as much as it exceeded the stagnant research on orientation and navigation in Germany at that point of time (i.e. ca. 1948). Ornithologists in Germany so far had mostly agreed with O. Heinroth’s scepticism that homing pigeons had no particular capacities of orientation. What homing birds in general were conceded to have was indeed a sort of innate instincts or acquired representations.

Kramer had already entered the question of “distance orientation” in his dissertation thesis on the Clawed Frog. There Kramer had argued that the proband animals were able to sense the location of a prey object and approach it by trial and error but the experimental situation now differed eventually in as much as the epicentre of the orientation process was not emanating impulses (shock waves, visual or olphactory cues) like a living prey object in the water. The location of the home loft seemed to be comparatively mute and under this circumstances Yeagley’s theory leads to the idea of some kind of representation of the target point, either in form of innate instincts or acquired representations.

When Yeagley speaks of a “characteristic line of latitude” he, in fact, has in mind two different possibilities. The latitude the bird processes can be a “magnetic latitude”. In this case the bird correlates its “Sensitivity” to the “effect of flying through a magnetic field” with its “Sensitivity to the forces produced by the earth’s rotation, acting on masses moving over its surface in a straight line” which, according to Yeagley, is “part of the well known Coriolis effect which is a function of latitude” (Ibid., 1037). In case the latitude the bird calculates is the “true latitude” the bird, according to Yeagley’s account, needs to correlate its sensitivity to the above mentioned Coriolis effect with a “Visual sensitivity to velocity over the earth’s surface (land speed)” (Ibid.).

Although Yeagley does not elaborate in detail upon the physical preconditions of this ability to “recognize” – we are only informed that the birds get “accustomed” with their home territory during explorative flights – the idea of any kind of memorized spatial representation seems to be a hidden presumption of his hypothesis even in case the bird approaches it target through trial and error.

For a research overview see Kramer, ”Neue Beiträge”, 228–229.
of apriori drive to fly which was meant to be refined by a supplementary capacity to read landmarks and thus to improve their homing performance by gathering experiences. In other words, Heinroth and others believed that homing performances to a large extent could be explained by a combination (or intercalation) of “Fluglust” and random search while circling in ever wider radii from the release place, that is, in the last consequence by trial and error. G. Kramer’s theoretical move in *Neue Beiträge zur Frage der Fernorientierung der Vögel* consisted in transcending the simple dualism of random seeking (O. Heinroth) and absolute orientation (H. L. Yeagley) by suggesting a third independent way which might be considered the starting point of experimental research on orientation in Germany. The order of the paper, however, shows that Kramer developed his view mainly by criticising only one of the antagonistic conceptions he aimed to leave behind, namely Yeagley’s. The latter had made use of mainly two different types of test to evince his hypothesis. On the one hand, he tried to manipulate the alleged orientation of the homing pigeons in the magnetic field by mounting small magnets on the underside of the pigeons’ wings between the first and the second joints. If the predicted deflections of the actual homing course indeed were observable this could be taken as an indicator for the effectiveness of the magnetic field. On the other hand, Yeagley had taken serious the negative homing results obtained by pigeon fanciers: In some geographic regions of North America homing pigeons seemed to be incapable at all to find their home loft, strayed or got lost altogether. Yeagley was inclined to explain this result as the product of ambiguities the intersection of the magnetic and the Coriolis field generated in some regions of the North American continent. That is to say, Yeagley claimed that in some locations the way both fields were intersecting with each other was more or less identical so that the pigeon’s calculating mechanism generated at least two different coordinates for the location of the home loft the navigating homing pigeons had taken aim at. This hypothesis predicted a non-random scattering of homing birds in these critical regions after the release. Yeagley performed quite a number of send up experiments and interpreted the actually obtained results in favour of his thesis: He also used to calculate a “total flight vector” which was meant to represent “the average result of all the recorded flights of that day” from a particular release site and claimed that several of these vectors either terminated close to one of the two predicted target points or even matched with them “with good precision”. Furthermore, Yeagley claimed that homing pigeons do not retrace the paths over which they have been transported to their release sites unless these latter locations “happen to be directly in the line from the home (or its conjugate point) to which they have been trained to pilot and to navigate”.

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1654 For an overview see Yeagley, “A Preliminary Study, Part I”, 1042.
1655 Ibid., 1042, for the entire test and the results, 1042–1044.
1656 For the failure of homing pigeons in some regions see ibid., 1039, with a view of possible test settings 1042.
1657 For these tests see Yeagley’s report of the experiments II-V, ibid., 1044–1051, 1051–1054, 1054–1056, 1056–1062.
1658 Ibid., 1046–1047. This total flight vector was calculated by building the sum total of all singular flights divided by the amount of all singular vectors. The usage of such a “total flight vector” was later criticized by Kramer from a methodological point of view.
1659 Ibid., 1053.
Thirdly, Yeagley’s graphical representation of the field lines of the magnetic and the Coriolis field in Northern America revealed that in some areas the respective lines approximate a condition of parallelism which, if the theory was correct, must lead to a lack of guidance and confusion in the birds. A number of release experiments were carried out along these “lines of tangency”, as Yeagley put it, and the obtained results seemed to corroborate Yeagley’s hypothesis although not in an entirely conclusive manner. Releases from places other than where the birds were trained entailed returns to the predicted conjugate points although the birds were released towards a compass direction other than it was the case during training.\textsuperscript{1660} Like several other ornithologists, G. Kramer questioned both Yeagley’s hypothesis and his proof by putting forward mainly two different counterarguments.\textsuperscript{1661} Besides some methodological objections Kramer thus questioned whether the homing pigeons had the physical capacities in form of adequate (i.e. adapted) sensory organs which enabled the birds to sense at all the extraordinary little gradients in both types of field whose readability – so to speak “on the fly” – was a necessary presumption of Yeagley’s theory of absolute orientation. On the other hand, Kramer compared the specific constitution of both fields of geophysical forces and their overlapping at critical conjugate points in North America with those existing in Europe. Since the latter allowed equally ambiguous homing results as in North America yet pigeon fanciers in Europe had not complained about some kind of blind spots as to their birds’ homing performances Kramer concluded that Yeagley’s experiments with geographical ambiguities might operate with wrong presumptions as well.\textsuperscript{1662} Kramer’s criticism ultimately culminated in two sets of conclusions. On the one hand, he discussed the birds’ general faculty to sense stimulation other than visual on basis of the organism’s physical conditions.\textsuperscript{1663} Kramer’s conclusion at this point perpetuated the view of his mentor insofar as he favoured orientation via visual over orientation via non-visual cues. And indeed the lack of sight, for instance in dense fog, seemed to lead to entirely random seeking in the homing birds – a result which supported Kramer’s thesis that processing of visual stimuli dominated in avian orientation and navigation and therefore, in his view, made any kind of geophysical navigational mechanism fairly unlikely.\textsuperscript{1664} On the other hand, however, Kramer distinguished strictly between homing, that is, true bicoordinated navigation: Thus, experiments with migratory birds had demonstrated that individuals being displaced geographically in course of their flight to their wintering areas (or to their breeding places in summer, respectively) maintain only the basic homing direction so that they missed their target locations in a predictable way.\textsuperscript{1665}

\textsuperscript{1660} Ibid., 1056, 1061–1062.
\textsuperscript{1661} See for both points of criticism, Kramer, “Neue Beiträge”, 230–231.
\textsuperscript{1662} For Kramer’s argumentation see also MPG-Archives, III. HA, Rep. 77, file 2, letter G. Kramer to F. Errulat (14/09/1951). Most interestingly, F. Errulat suggested to make experiments with different fields within the controlled environment of an observatory because he thought things were more complicate than it seemed at first sight. See ibid., file 2, letter F. Errulat to G. Kramer (05/04/1949).
\textsuperscript{1663} Ibid., “Neue Beiträge”, 236–237.
\textsuperscript{1664} Ibid., 237.
\textsuperscript{1665} Ibid.
\textsuperscript{1666} Ibid.
These results, however, contradicted the hypothesis that migratory birds have the more advanced ability of true bicoordinated navigation and hence required a conceptual distinction between true bicoordinated navigation (i.e. homing) and mere direction finding. Again, Kramer applied a principle of parsimony and focused on direction finding. As a result, one may say that G. Kramer’s initial conceptual extension allowed him to exceed the simple dualism between random and absolute orientation yet ultimately it also led towards a conceptual self-commitment. Thus, one the one side, it is surely legitimate to interpret Kramer’s focusing on visual means of orientation (in principal including the underlying physiological mechanisms) and his emphasis on direction finding as the two main conceptual pillars of his later discovery of the so-called sun-azimuth orientation. On the other hand, however, the implied restrictions turned out to be an impediment as soon as he felt ready to make a fresh start and enter the problematic of true navigation. W. H. Thorpe noted in context of another later scientific controversy that G. Kramer, in course of his orientation research, step by step re-integrated the aspects he had excluded from his horizon in the first place. To a certain extent, this proposition seems to hold even more with a view of G. Kramer’s initial criticism of H. L. Yeagley’s theory of geophysical navigation. However, although Kramer did not exclude the possibility of geophysical navigation completely from his agenda, he at least sidelined Yeagley’s idea till his death in 1959. On the other hand, as we will see, the idea of an absolute factor being effective in avian orientation soon re-appeared in his own theory of direction finding and slightly later (and even more pronounced) in his attempt to solve the riddle of true navigation. Although Yeagley’s theory was mostly rejected by his contemporaries, at least the idea of pigeons using the geomagnetic field of the earth for direction finding turned out to be valid later on and from this perspective Kramer’s early conceptual commitments eventually turn out to be a proper heuristic handicap. Finally, as I will show in the next paragraph,

1668 Although the idea that birds have the senses to navigate in the magnetic field was widely rejected in the 1960s, since the early 1970s more and more evidence indicated that both insects and birds might be able to exploit the input signals provided by the geomagnetic field. Nowadays magnetic field orientation has been confirmed in some birds, several other animal species and, at least to a certain extent, also in homing pigeons. See T. Ludlow, *Bird Navigation*. URL: http://www.modelresearch.com/science/lectures/navigate.pdf (accessed on Dec. 9, 2012), 5, Able, “Orientation and Navigation”, 595–596 and K. Schmidt-Koenig. “Zur Geschichte der Orientierungsforschung”. In: *Journal für Ornithologie* 142.Sonderheft 1 (2001), 114, 116. According to H. G. Wallraff, the sun and the magnetic field “are apparently not used by birds to determine their current position with respect to home, but are nevertheless substantial components of the homing process as a whole”. See H. G. Wallraff. *Avian Navigation: Pigeon Homing as a Paradigm*. Berlin et al.: Springer, 2005, Preface, 69–85, here vi. A possible effect exerted by the Coriolis force seems to have vanished from the ornithological research agenda (Ibid., 57, 183–184). In so far Kramer’s scepticism was legitimate.
1669 For the fact that Pigeons use the magnetic field for determining their preferred compass direction, for example, see ibid., 184, 185. Historically speaking, not all pigeon fanciers and professional researchers were convinced by Kramer’s criticism of Yeagley’s thesis. A. Bethe, for instance, informed Kramer that he was intrigued yet not convinced by Kramer’s review of Yeagley’s paper. See MPG-Archives, III. HA, Rep. 77, file 2, letter A. Bethe to G. Kramer (20/03/1949). See also Kramer’s correspondence with F. Wiese, a pigeon fancier who believed in the pigeon’s ability to sense the magnetic field of the earth, ibid., file 7, letter F. Wiese to G. Kramer (12/03/1953), ibid., file 7, letter G. Kramer to F. Wiese (07/11/1952), ibid., file 7, letter F. Wiese to [R.]}
Kramer sidelined not only non-visual forms of orientation and true bicoordinated navigation, his first attempts to clarify the principles of direction finding were made with experimental animals other than domesticated pigeons. The homing pigeons, however, soon re-entered his research agenda simply because of their aptitude as experimental animal. Altogether it may be not entirely incorrect to understand G. Kramer’s research on orientation and navigation in homing birds through the lens of the tension that was emerging by excluding something possibly true or valuable. (2) The second phenomenological shift in Kramer’s research on orientation was based upon the extension of the original scope of experimental animals. G. Kramer’s critical review of H. L. Yeagley’s theory of navigation reveals that his first assessment of the orientation theme after 1945 was related to the experimental animal “homing pigeon”. Soon after, however, he exceeded this narrow scope by taking into account non-domestic songbirds and made the choice of the right animal subject of another differential diagnosis finally leading to the Starling – the species of Bird that turned out suitable most for Kramer’s purposes. How is that? Already in Heidelberg Kramer found out that migratory songbirds such as shrikes and blackcaps, when put into round cages, reveal directed migratory behaviours during those phases of the day these birds usually set forth on their journey.1670 The pity, however, was that the revealed compass point did not coincide with the actual migratory direction so that Kramer inferred there must be involved other disturbing factors that caused this deflection. Further tests then showed that the deflections were due to species-specific differences or caused by distracting light sources such as the nightly silhouette of a lighted city in case the experiment was performed out in the open.1671 Particularly in order to neutralize the latter source of disturbance Kramer switched to a species of migratory bird whose individuals both reliably indicated the migratory tendency through actual flight movements or corresponding sublimates (i.e. behaviours Kramer called “Schwirren”) and which migrates during day light and not by night. The ideal proband animal that fulfilled both prerequisites was the Starling with which all further experiments were carried out until finally the focus was widened once more (see below). Additional technical facilities were meant to exclude the possibility of magnetic orientation.1672 This was not all: If I have understood correctly G. Kramer also made the technical device with which he recorded the migratory tendency of the bird, that is, the round

Drost (14/10/1952), and ibid., file 9, letter F. Wiese to G. Kramer (31/05/1954). Others like E. Stresemann and E. Mayr supported Kramer’s critical perspective, mainly for methodological reasons. See ibid., file 3, letter E. Mayr to G. Kramer (26/04/1948) and SBB, NL 150, file 37, letter E. Stresemann to G. Kramer (25/08/1948). See in addition also Schmidt-Koenig, “Zur Geschichte der Orientierungsforschung”, 116.


1671 See G. Kramer, “Orientierte Zugaktivität gekäfigter Singvögel”. In: Die Naturwissenschaften 37.8 (1950), 188.

1672 See to this aspect the report Kramer gave in one of his popular lectures MPG-Archives, III. HA, Rep. 77, box 1, ms. “Gr[...] Vortrag” (>1950), page 7–8. That Kramer not only made experiments with caged birds within a magnetic field but also planned to attach small magnetic plates to the wings of the pigeons like H. L. Yeagley did before can be inferred
In other words, Kramer’s “Rundpavillon” (round pavilion) was installed out in the open so that the proband birds, pending on how the experimenter restricted the sight of the bird, could see the open sky. This reconfiguration of the experimental device not only exceeded the range of possible measurements in comparison to its predecessor it also helped to reduce further the number of possible sources of disturbance that were necessarily involved with the indoor setting (e.g. distracting light sources, marks on walls, etc.). More advanced experiments with the round pavilion finally involved the manipulation of the direction from which the light source came from and thus allowed a more thorough examination of the question to which visual stimuli the starling actually responded.

Recordings were made in form of handwritten notes (by using a specific short-cut system) and by applying the method of filming. As a provisional result, one may therefore say that not only the process in course of which the “right” experimental animal was to be found but also the developmental history of the technical device used for the experiments was following the epistemic pattern underlying Kramer’s understanding of “differential diagnosis”: In a first step, the view is widened upon a wider range of possibilities. In a second step, this wider range of options is made subject to a process of gradual experimental reduction, whereby the final result or ultimate state of knowledge then can be re-fed into the system – as a new hypothesis to be tested. This establishes a process in course of which one and the same scheme is recursively applied to changing and transforming scientific quests – a process which itself mirrors the scheme. In the former of the two examples mentioned this heuristic machinery was applied to the scope of adequate experimental animals, in the latter case it shaped the technical improvement of the experimental setting from the correspondence Kramer maintained with the company which was meant to produce the small magnetic strips. See MPG-Archives, III. HA, Rep. 77, file 2, letter G. Kramer to Magnetstahlwerk Aplerbeck (12/07/1949) and ibid., file 2, letter G. Kramer to Magnetstahlwerk Aplerbeck (20/07/1949).

A detailed description of the octagonal pavilion is passed onto us in Kramer’s personal papers. See ibid., box 1, ms. “Beschreibung” (n. d.). After the Second World War the research station in Rovigno became Yugoslavian, a second station for Marine Biology which was located on the Helgoland Island was bombed so that there existed a need for a new institute on German territory. This new institute was built in Wilhelmshaven by the Max-Planck Society. According to a memorandum which has been written most likely by J. Hämmerling, the new institute was meant to be established upon a broader scientific basis and, beyond that, should be adjusted to the needs of the researchers who would be appointed as heads of the single departments in the future. See to this ibid., file 10, ms. “Denkschrift über die Errichtung eines Kaiser Wilhelm Institutes für Meeresbiologie” (n.d), page 1–2. This broad scientific and person-oriented research focus is most likely the reason why Kramer’s ornithological research could be integrated into an institute for “Marine Biology”.


itself. Some of my readers might call my analysis “subtle”, far-fetched or even blame me for constructing this order. Maybe. However, this point of critique leaves unanswered why this construction is possible at all and, beyond that, neglects the possibility that it is the researchers themselves who construct their research environment in accordance to characteristic epistemic practices allowing them to place their scientific positions adequately within the epistemic space of their scientific community. Furthermore, although I think that behaviour researchers were highly sensitive in matters of knowledge reproduction it is not even necessary to claim that these dynamics need to be subject of conscious reflection in any case. Some events may remain in the realm of unspoken epistemic practices. Others may be raised to consciousness by later reviews or historical accounts in general. In any case, the humanities need to face the fact that the principles of cultural reproduction might pre-exist quite independent whether or not they are made subject to any kind of narration. In other words, the apple falls from the tree even in case Newton has not told us the story in this way.

To return to Kramer’s orientation studies it remains to ask which effect both the choice of the adequate experimental animal and the reconfiguration of the experimental setting finally yielded in the field of the scientific ideas itself. Kramer’s criticism of H. L. Yeagley’s paper had ended indirectly with the conclusion that the faculties of birds to find a particular location within the three dimensional space of their natural environment was restricted to mere direction finding on basis of visual cues only. This view needed to be refined partly as soon as it became clear that the migratory behaviours of birds reveal a common goal-directedness quite independent whether visual landmark cues were available or not. In a succeeding step G. Kramer and his associates were able to identify the sun as the primary source of stimulation. The results of these experiments suggested that it was the cues provided by the sun and less the landmarks which guide the birds on their oriented flights:

1676 The direction of the starlings directed movements in the cage turned out to be manipulable and predictable. Experimental deflections of the light source entailed the predicted deviations of the directed movements. The brighter central parts of the light source were preferred over the peripheral areas. It remained doubtful whether starlings use cues from the parts of the sky opposite to the side of the sun or the polarized light like Honeybees.

1677 More of cloudiness corresponded with more random and strayed movements in the round pavilion. Covering the windows with greaseproof paper simulating fog impaired the orientedness yet did not terminate it. Finally, the direction

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\[\text{\ldots} \]' Vortrag” (>1950), here page 13–14. See also ibid., box 1, ms. “Vortrag Münster” (n. d.), page 3 and a letter to E. Stresemann in which G. Kramer summarizes all the attempts he made in vain to evoke the relevance of polarized light, ibid., file 5, letter G. Kramer to E. Stresemann (16/02/1951). Kramer’s personal papers show that he, in questions related to the effectiveness of polarized light, conferred with H. Kaiser, a physicist working for the State Office for Material Testing (Staatliches Materialprüfungsamt) in North Rhine-Westphalia. See ibid., file 4, letter H. Kaiser to G. Kramer (01/06/1950). The correspondence might be of interest because Kaiser warned Kramer that the usage of mirrors could change linear polarized to elliptically polarized light so that the light rays being finally sensed by the proband bird within the cage might have another quality than natural light. In addition to that, see also Kramer’s correspondence with M. Kerz who, in contrast to Kramer’s results with birds, was able to evince that Crayfish is capable to sense polarized light, ibid., file.
tendencies remained constant all over the day independent of the sun’s movement. G. Kramer and his workmates thus concluded there must exist a neural mechanism which can compute the correct compass direction by using the data provided both by the sun and an internal clock. Kramer’s discovery therefore entered the field of biological rhythms and what is nowadays called “Chronobiology”. In sum, the discovery of the so-called compass direction went clearly beyond the Heinroths’ thesis according to which the homecoming-ability of birds was enabled by a mere intercalation of a primary “Fluglust” and a secondary experience factor (either in form of an already acquired familiarity with landmarks or random seeking). The dualism of “Fluglust” and “experience”, in a first step, was replaced by the dualism of “Fluglust” and “direction finding” without overthrowing Heinroth’s epistemic framework completely. The act of direction finding then consisted of a complex process that involved both the variable stimuli emanated by the sun and the impulses provided by an inner clock.

(3) To verify the hypothesis that starlings can calculate the migratory direction on basis of two parameters, that is, the course of the sun, on the one hand, and the time of the day, on the other, the methodology applied so far needed to be refined.

An aspect which cannot be read in Kramer’s publications is that he took into consideration M. Takata’s hypothesis according to which solar activity might have an impact upon the blood composition. Kramer thought it possible that the so-called blood flocculation could be used by the birds to “measure” the time of the day. This hypothesis which stood in the tradition of Kramer’s unpublished serum paper which he had written most likely between 1942 and 1945 finally could not be confirmed. The entire issue, however, demonstrates that Kramer was prepared to test any hypothesis no matter how far-fetched it appeared. See also ibid., file 11, letter G. Kramer to M. Takata (ca. 1952). For a summary of Takata’s results see K.-O. Kiepenheuer. “Zur Beeinflussung des menschlichen Blutserums durch die Sonne”. In: Die Naturwissenschaften 37.10 (1950), 234–235. For the doubts that Takata’s theories raised see MPG-Archives, III. HA, Rep. 77, file 10, letter H. J. Sarre to G. Kramer (02/05/1952) and H. Sarre. “Solare Einflüsse auf die Takata-Reaktion”. In: Medicin–meterologische Hefte 5 (1951), 25–28.

For a retrospective and more popular scientific account of this first revision see MPG-Archives, III. HA, Rep. 77, file 14, ms. “Vögel fliegen ohne Kompaß” (ca. 1955), here page 1–2. That Kramer was aware to have left behind his mentor’s position on a phenomenological level of explanation becomes manifest in a letter to Heinroth’s widow. See ibid., file 11, letter G. Kramer to K. Heinroth (27/10/1950). See also ibid., file 13, letter G. Kramer to A. Meyer (18/04/1949) and ibid., file 13, letter G. Kramer to “Verband zur Förderung der Reisetaubenzucht e.V.” (24/09/1952). Pigeon fanciers declined Heinroth’s thesis from the very beginning. See, for instance, ibid., file 13, letter [K.] Uhlenbrock to G. Kramer (19/01/1949) and ibid., file 13, letter A. Jacobsen to “Verband zur Förderung der Reisetaubenzucht e.V.” (06/09/1952).
once more. The mere recording of otherwise natural, directed migratory behaviours within the round pavilion now was exceeded by so-called conditioning experiments in which the proband bird did not indicate the compass direction of its migratory tendency through directed flight behaviours or corresponding sublimates but instead by choosing the correct feeding location amongst a number of food dispensers that had been installed in the round cage in accordance with the compass points.\textsuperscript{1680}

If I have understood correctly the conditioning of the bird, in concrete, consisted of rewarding the proband bird if it had redirected its migratory tendency towards a food dispenser which represented the right compass direction.\textsuperscript{1681} Whether the birds in question learnt to substitute their more or less completely exhibited flight intention movements with feeding behaviours is something I cannot tell with certainty. However, G. Kramer ascertained that conditioning experiments can be carried out independent from the migratory period.\textsuperscript{1682} In any case, Kramer’s starling learnt to indicate the compass direction of his momentary migratory tendency by picking food from a dispenser that represented the respective compass point. Kramer underlines that the conditioning method is more suited to examine the way how the starling calculates the migratory direction on basis of the movement of the sun.\textsuperscript{1683} Hence, one may say the result of the previous tests have been made subject of a new more advanced diagnosis whereby the new thesis required a further methodological refinement in order to obtain more elaborate results. The inner logic of the diagnosis thus seems to have shaped the scientific procedure. I think, the very first objective of these tests with starlings that had been trained in that way was to confirm the

\textsuperscript{1680} See to this G. Kramer et al. “Stare (Sturnus vulgaris L.) lassen sich auf Himmelsrichtungen dressieren”. In: \textit{Die Naturwissenschaften} 37.22 (1950), 526. In a later article reviewing his own research, Kramer himself marks the dualism between or shift from non-conditioning and conditioning experiments. See to this the order of “Part I. Direction Finding in the Starling”, G. Kramer. “Experiments on Bird Orientation”. In: \textit{Ibis} 94.2 (1952), 265–278. See also MPG-Archives, III. HA, Rep. 77, file 11, letter G. Kramer to A. Bethe (25/07/50).

\textsuperscript{1681} G. Kramer and his associates thereby used a particular feeding behaviour typical for Starlings which in German language is termed “Zirkeln” (lit. “circling”). The Starling when seeking food thrusts its bill into gaps of wooden branches and widens these openings with his bill in order to reach otherwise inaccessible prey object. This widening is called “Zirkeln”. See Kramer et al., “Stare (Sturnus vulgaris L.) lassen sich auf Himmelsrichtungen dressieren”, 526. Thus the bird cannot see what is included inside the food dispenser. See to this aspect also MPG-Archives, III. HA, Rep. 77, box 1, ms. “Gr[... ] Vortrag” (>1950), here page 15–16. For an additional description of the conditioning method see \textit{ibid.}, file 5, letter G. Kramer to M. Bizony (27/04/1951). In the year 1950, G. Kramer published a couple of research papers which have nothing to do with orientation and homing at first sight. Instead they are related to the predatory behaviour of Shrikes as well as nest building and moult in Red-backed Shrikes. I think it possible that Kramer with this supplementary research intended to obtain a better and wider understanding of the Starling’s feeding behaviour and the usage of the bill. The paper about the moult of the Red-backed Shrike is related to the reproductive cycle. At least two of these papers then could be indirectly related to the conditioning of Starlings. See G. Kramer. “Beobachtungen über Erwerb und Behandlung von Beute beim Rotrückenwürger (Lanius c. collurio L.).” In: \textit{Ornithologische Berichte} 2 (1950), 109–117, G. Kramer. “Der Nestbau beim Neuntöter (Lanius c. collurio L.).” In: \textit{Ornithologische Berichte} 3 (1950), 1–14, and G. Kramer. “Über die Mauser, insbesondere die sommerliche Kleingefiedermäuser, beim Neuntöter (Lanius c. collurio L.).” In: \textit{Ornithologische Berichte} 3 (1950), 15–23.

\textsuperscript{1682} MPG-Archives, III. HA, Rep. 77, file 5, letter G. Kramer to M. Bizony (27/03/1951).

\textsuperscript{1683} See Kramer et al., “Stare (Sturnus vulgaris L.) lassen sich auf Himmelsrichtungen dressieren”, 527.
results which had been already obtained by previous experiments. Deflections of the light source with mirrors entailed the expected deviations of the chosen directions. Again, the regions of the sky with stronger light sources were preferred over regions with less bright sources of light. Information of those areas of the sky that were located opposite of the sun was not used at all. Cloudiness obstructed but did not terminate the orientation, while complete deprivation from sun light was leading to random or at least scattered choices of direction. More advanced conditioning tests finally manipulated the course of the sun by presenting an artificial light source that was identified as natural sun by the proband birds. Both the conditioning under natural sun and succeeding tests with an artificial light source and the reverse test, that is, training under an artificial light source and subsequent testing under natural conditions, pointed into the same direction. Starlings only use the so-called azimuth angle and not the height of the sun as signal while calculating the migratory direction. Further experiments carried out by K. Hoffmann, a pupil of G. Kramer’s, were aimed at manipulating the internal clock through conditioning. The migratory directions clock-shifted Starlings used to choose showed the expected deflections so that the experiments in question confirmed the overall hypothesis that now more and more began to take form: Birds can perform oriented flights on basis of an internal mechanism that is able to calculate the adequate direction from two parameters namely the point of time (provided by an internal clock) and the so-called sun-azimuth angle. Kramer called this orientation mechanism "sun-azimuth orientation" and its discovery made him world-famous. Simultaneously to the experiments which were meant to confirm the effectiveness of visual factors G. Kramer and his associates ruled out the possibility that migrating birds orient themselves through perception of ultra short waves. Other hypotheses that Kramer and his co-workers disproved were related to the orienting function of

1684 For the results see Kramer et al., “Stare (Sturnus vulgaris L.) lassen sich auf Himmelsrichtungen dressieren”, 527.
1685 A letter to the Cambridge zoologist W. H. Thorpe shows that Kramer and his associates were about to carry out these tests at the end of the year 1950. See MPG-Archives, III. HA, Rep. 77, file 4, letter G. Kramer to W. H. Thorpe (16/11/1950). See also Kramer’s brief report ibid., file 5, ms. “Die Orientierung des Stars nach der künstlichen Sonne” (n. d.) and a later letter to Luuk Tinbergen which includes some more details concerning the experiment ibid., file 11, letter G. Kramer to L. Tinbergen (16/05/1951): For reasons of scientific objectivity Kramer suggested joint tests with Luuk in which each party tested the starlings that had been trained by the other researcher.
1687 For the high esteem of Kramer’s discovery see, for instance, Schmidt-Koenig, “Zur Geschichte der Orientierungsforschung”, 113–114.
1688 For Kramer’s disproof of the effectiveness of ultra short waves see G. Kramer. “Versuche zur Wahrnehmung von Ultrakurzwellen durch Vögel”. In: Die Vogelwarte 16.2 (1951), 55–59. That these experiments yielded a negative result can be also inferred from letters Kramer exchanged with the MPI Ionospheric Research which apparently provided the technical device Kramer had used for the tests. See MPG-Archives, III. HA, Rep. 77, file 4, letter G. Kramer to W. Dieminger (14/11/1950), ibid., file 4, letter W. Dieminger to G. Kramer (16/12/1950),
the moon or the question whether sun orientation might not be the basis for orientation during night as well. As soon as the hypothesis had passed through his diagnostic procedure and turned out to be firm enough Kramer felt ready to make the results accessible to a wider audience and make them subject of expert discussion. Kramer introduced the results he and his co-workers had obtained so far for the first time in a more coherent and elaborate form in a presentation he delivered during the International Ornithological Congress held in Uppsala in June 1950. His findings have been confirmed many times since then. They are still valid and quoted today. In sum, one may say that the refined methodology that finally led towards this discovery was based upon the model of the differential diagnosis as well: The experimental setting provided by the original form of the round pavilion and its usage was extended by the method of conditioning which allowed carrying out more adequate tests. The more of opportunity, in turn, was a precondition for determining the stimuli to which the proband animals responded. More advanced tests still narrowed down the number of qualities possibly serving as stimuli. In course of this reduction the sun-azimuth angle turned out to be the adequate stimuli which, in combination of the bird’s internal clock, provided the data with which the neural mechanism of the bird was able to calculate the migratory direction. Kramer presented his theory to a wider audience only after his theory had reached a certain reliability so that presenting would lead to further confirmation.

(4) Besides extending the range of applied methods G. Kramer and his associates intended to exceed the scope of applicability of their orientation theory by verifying it in various species of Bird other than the Starling. In this context, U. v. Saint Paul’s research must be mentioned. In various supplementary experiments she was able to make evident that besides Starlings also the Barred Warbler, the Red-backed Shrike and the Western Meadow Lark can utilize sun-azimuth orientation so that Kramer was able to conclude the orientation mechanism might be spread widely animal class of birds. This repeated widening of G. Kramer’s focus upon
a much broader range of potential experimental animals finally once more led towards a heuristic reduction in as much as the classical proband animal of orientation research, the homing pigeon, re-entered Kramer’s research agenda and from ca. 1952 onwards became the central scientific object of his research on avian orientation and navigation. Studies being concerned with homing pigeons were carried out since 1950. However, in the initial stage of this research on pigeon homing had a more preparatory character in as much as it was primarily concerned with evaluating critically the reports published by Italian and German pigeon fanciers.\textsuperscript{1694} The discovered differences in homing performance and speed raised the question whether not the more moderate climatic conditions in Italy might have a significant impact upon the homing speed and success. In particular, the effect exerted by winds in lower strata turned out to be vital reason for increased scattering north of the Alps and hence became subject of more thorough examination.\textsuperscript{1695} The evidence speaking for the possibility of more scattered results due to winds at this point still contradicted the idea of true navigation because if the homing pigeons were capable of bicoordinated navigation they would be able to compensate the negative effects of wind drift. Moreover, in a series of experiments G. Kramer and

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  \item See G. Kramer et al. “Heimkehrleistungen italienischer und deutscher Reisetauben”. In: \textit{Die Vogelwarte} 15.4 (1950), 237–242. Many letters in G. Kramer’s personal papers show that he corresponded with several pigeon fanciers in various issues such as the purchasing of pigeons, return of lost pigeons and assistance with releases. Amongst these letters we find also several ones in which Kramer requested so-called “Preislisten” (ranking lists) in order to examine them from a scientific point of view. See, for instance, MPG-Archives, III. HA, Rep. 77, file 13, letter G. Kramer to A. Kemmann (17/11/1950), \textit{ibid.}, file 13, letter G. Kramer to H. Hartwig (13/04/1951) and \textit{ibid.}, file 13, letter G. Kramer to G. Hochmuth (13/04/1951).
  \item G. Kramer et al. “Heimkehrleistungen von Reisetauben in Abhängigkeit vom Wetter, insbesondere vom Wind”. In: \textit{Die Vogelwarte} 15.4 (1950), 242–247. In this context, I’d like to direct my reader’s attention to the extensive correspondence G. Kramer maintained with H. Seilkopf who worked for the Meteorological Office for North-West Germany and whose task was to reconstruct the weather conditions during several historical and contemporary pigeon races. See, for instance, MPG-Archives, III. HA, Rep. 77, file 4, letter G. Kramer to H. Seilkopf (13/07/1950), \textit{ibid.}, file 4, letter H. Seilkopf to G. Kramer (26/08/1950), \textit{ibid.}, file 4, letter H. Seilkopf to G. Kramer (01/09/1950), \textit{ibid.}, file 4, letter G. Kramer to H. Seilkopf (04/09/1950), \textit{ibid.}, file 4, letter H. Seilkopf to G. Kramer (08/09/1950), \textit{ibid.}, file 4, letter G. Kramer to H. Seilkopf (09/09/1950), \textit{ibid.}, file 4, letter G. Kramer to H. Seilkopf (23/10/1950), \textit{ibid.}, file 4, letter G. Kramer to H. Seilkopf (31/10/1950) with more detailed information concerning the two papers of the series, \textit{ibid.}, file 4, letter H. Seilkopf to G. Kramer (03/11/1950), \textit{ibid.}, file 4, letter H. Seilkopf to G. Kramer (18/11/1950), \textit{ibid.}, file 4, letter G. Kramer to H. Seilkopf (20/11/1950), \textit{ibid.}, file 4, letter H. Seilkopf to G. Kramer (08/12/1950), \textit{ibid.}, file 4, letter H. Seilkopf to G. Kramer (19/12/1950), \textit{ibid.}, file 5, letter H. Seilkopf to G. Kramer (16/01/1951), \textit{ibid.}, file 5, letter G. Kramer to H. Seilkopf (17/01/1951), \textit{ibid.}, file 5, letter G. Kramer to H. Seilkopf (07/02/1951), \textit{ibid.}, file 5, letter H. Seilkopf to G. Kramer (09/02/1951), \textit{ibid.}, file 5, letter G. Kramer to H. Seilkopf (16/03/1951), \textit{ibid.}, file 5, letter G. Kramer to H. Seilkopf (23/03/1951), \textit{ibid.}, file 5, letter H. Seilkopf to G. Kramer (03/04/1951), \textit{ibid.}, file 5, letter G. Kramer to H. Seilkopf (12/04/1951), \textit{ibid.}, file 5, letter H. Seilkopf to G. Kramer (30/04/1951), \textit{ibid.}, file 5, letter H. Seilkopf to G. Kramer (02/05/1951), \textit{ibid.}, file 5, letter G. Kramer to H. Seilkopf (02/05/1951), \textit{ibid.}, file 5, letter H. Seilkopf to G. Kramer (25/06/1952), \textit{ibid.}, file 6, letter G. Kramer to H. Seilkopf (24/07/1952) and \textit{ibid.}, file 8, letter G. Kramer to H. Seilkopf (21/05/1953).
\end{enumerate}
his associates aimed to clarify whether the results of the test he had carried out with Starlings could be repeated with the homing pigeon. Despite the fact that the pigeons behaved differently and the methodology therefore needed to be adjusted it could be proved that also carrier pigeons could be conditioned to compass directions. Experiments with conditioned pigeons could take different forms. One of these test settings consisted of experiments that were performed in the open by releasing trained birds from distant places. Pigeon fanciers had managed to improve the homing performances of their birds by training, that is, they released the birds many times from or into the same direction but steadily increased the distance from the target point which is the home location. Kramer adopted the method of conditioning the animals to a certain direction but varied the experiment by releasing the pigeons from compass directions other than the one the pigeons were accustomed to.\(^{1696}\) The results of these tests, which were, in the final consequence, based on irritation of an acquired / learnt disposition, showed that previous conditioning turned out to be a handicap during release tests from unfamiliar grounds. Pigeons headed off into the learnt bearings and well trained birds needed more time to return from unknown places.\(^{1697}\) Kramer interpreted these results at first by claiming a possible coexistence of different orientation mechanisms (random seeking, usage of landmark cues, and on basis of direction training) and tended to explain the extraordinary homing performances in terms of conditioning effects.\(^{1698}\) Yet in the early 1950s he still avoided to refer to any kind or absolute navigation. “Kurz und gut”, Kramer concludes and continues:

> wir getrauen uns noch nicht, den hinreichenden Erklärungswert der drei Heimfindemethoden, die man bisher aufstellen kann, zu proklamieren: 1. Fliegen auf gut Glück – sei es in vielfach gekrümmter Flugbahn oder im Geradeausflug; 2. Fliegen nach bekannten Landschaftsbildern (hierzu gehört auch das Orientierrsein in der nächsten Schlagumgebung); 3. Fliegen in eingeübter Richtung. | Wohl aber getrauen wir uns, zu behaupten, daß das schnelle Durchfliegen unbekannter Gebiete auf annähernd kürzestem Heimkehrwege durch die Richtungsdressur zustandekommt. Dies steht im Einklang mit der Wettkampfpraxis der Brieftaubenzüchter der ganzen Welt, die ihre Tauben von Auflussungspunkten zunehmender Entfernung aus der gleichen Himmelsrichtung fliegen lassen. [In short: We do not dare yet to proclaim the sufficient explanatory value of either of the three methods of homing which so far can be put forward: 1. Random flying – be it in a manifoldly bent flight path or in straight forward manner; 2. Flying on basis of known landmark cues (to this kind is to be counted also the orientedness in close proximity of the loft); 3. Flying in conditioned directions. | Yet we do venture to postulate that the fast flying through unknown territory on more or less the shortest trajectory to the home location is a result of the direction training. This agrees with the racing practice of the pigeon breeders of all over the world who release their pigeons from increasingly wider distances albeit one and the same compass direction.](transl. CL)\(^{1699}\)

The extension of distance which can be obtained by training supported Kramer’s theory of direction finding via clues provided by the sun because it suggested, too,

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\(^{1696}\) For this type of tests see primarily the following paper, G. Kramer et al. “Ein wesentlicher Bestandteil der Orientierung der Reisetaube: die Richtungsdressur”. In: Zeitschrift für Tierpsychologie 7.4 (1950), 620–631.

\(^{1697}\) See ibid., 624–627, 627–629, 631.

\(^{1698}\) See ibid., 629–630.

\(^{1699}\) Ibid., 630.
that the crucial parameter would be the direction. Further release attempts in which birds either missed their target point or were flying too far into the otherwise correctly calculated direction but after some time partly managed to return properly seemed to question the idea of mere direction finding because the pigeons showed that they can readjust their course and therefore correct previous deflections. Other conditioning experiments with homing pigeons were performed in the round cage where the birds, as it had been common practice with Starlings, were meant to indicate compass directions by choosing a food source. In this case the experiments with light sources deflected by mirrors confirmed the results obtained with Starlings. “Damiß daß die Richtungsdressur auf der Grundlage der Sonnenorientierung im Versuchskäfig nachgewiesen wurde”, Kramer summarizes,

ist nahezu sicher anzunehmen, daß die Richtungsdressur heimfliegender Brieftauben der gleiche Orientierungsmechanismus zugrundeliegt, um so mehr als die Bewölbung die Straffheit des Abfluges sowie den Heimkehrerfolg ebenso beeinträchtigt wie die Wahlpräzision im Versuchskäfig. Ferner lehren diese Versuche, daß eine Richtungsdressur heimfliegender Tauben, auch zum Beispiel im Falle der üblichen Wettkämpfe, von der Tageszeit der Auffassungen unabhängig ist. [In evincing that direction conditioning on basis of sun orientation in the experimental cage, it can be presumed almost absolutely that direction training of homing pigeons is based upon the same mechanism of orientation. This holds even more as cloudiness impairs the straightforwardness of the departure and the homing success just in the same way as the precision of choice within the experimental cage. | Furthermore, these tests teach us that direction conditioning of homing pigeons, that is, for example, during flying competitions, is independent from the time of the day at which the release occurs.] [transl. CL]

All this data either had a more supplementary nature or was suitable to transfer already known results to a domestic species of Bird. Yet in 1952, after having proved the sun-azimuth orientation in Starlings, the homing pigeons raised Kramer’s attention also as an adequate experimental animal for his new research interests beyond mere orientation. In two pilot release experiments being carried out in the summer of 1951 from the Castle of Gleiberg near Gießen and from the Fehmarn Island with now entirely untrained homing pigeons G. Kramer was able to demonstrate that the birds were able to find their home over long distances without having any flight experiences at all. On the contrary, homing from lower distances which was considered fairly feasible by seeking, however, failed. Realizing this, at first sight, astonishing result, G. Kramer now was forced to take into consideration a direct-

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1702 Ibid., 249.
ing factor that was thought to become the more effective the greater the distance was.\textsuperscript{1704} If the results were interpreted positively, they suggested that the extraordinary homing performances of carrier pigeons could not be explained by a mere combination of direction finding and random seeking both of which could be improved by training. It suggested the existence of true navigation and this positive result opened the field for another more challenging research endeavour. Reducing the factors “experience” and “conditioning” therefore led towards the idea that next to sun-azimuth orientation another strictly separate and absolute mechanism of orientation must be effective in pigeons. In 1952 Kramer finally remarks:

\begin{quote}
\end{quote}

\textsuperscript{(transl. CL)}\textsuperscript{1705}

The quotation shows that G. Kramer’s attempt to transfer his theory of sun-azimuth orientation to another domesticated species of Bird, namely the homing pigeons, led him to an unexpected result insofar as also pigeons limited in experience achieved homing performances over great distances (less though over short distances) which could neither be explained by mere random seeking nor by a combination of direction finding and random seeking because both the departure and the homing itself were too directed over longer distances, while homing from immediate proximity failed.\textsuperscript{1706} Hence at least the possibility emerged that homing pigeons might possess a more precise sensation of the target location (i.e. an “Ortssinn”) than previously assumed. As a result, Kramer, during the annual conference of the German Zoological Society in 1952, claimed to reassess the navigation problematic but still believed that it was the sun with which birds determine the coordinates of their position.\textsuperscript{1707}

(5) Thus around the year 1952 G. Kramer began to reach out for solving the previously sidelined problematic of true bicoordinated navigation.\textsuperscript{1708} The choice of this “new” theme coincided both with a renewed focus on homing pigeons as experimental animals and a turn to a still more advanced experimental methodology.

\textsuperscript{1704} See Kramer et al., “Heimkehrleistungen von Brieftauben ohne Richtungsdressur”, 176.
\textsuperscript{1705} See to this the results of the tests with inexperienced bird and their discussion, Kramer et al., “Heimkehrleistungen von Brieftauben ohne Richtungsdressur”, 174–176 and 176–177 respectively and also Kramer, “Experiments on Bird Orientation”, 281–282.
\textsuperscript{1706} See Kramer et al., “Die Dressur von Brieftauben auf Kompaßrichtung im Wahlkäfig”, 251.
\textsuperscript{1707} Kramer, “Die Sonnenorientierung der Vögel [1952]”, 83.
\textsuperscript{1708} For the mere chronology of the events see also the brief research report G. Kramer sent to K. Dorn, an Eastern German veterinary physician, MPG-Archives, III. HA, Rep. 77, file 7, letter G.
which combined conditioning with so-called displacement tests, that is, the release of the pigeons from a distant place whereby the experimental situation, that is, the problem to be solved, consisted in returning to the home loft. However, in as much as the previously applied experiments also involved problem solving we may eventually say that the logic of exceeding the boundary which is established by the presentation of a problem (revealing a migratory tendency, finding the right food dispenser, etc.) and its solution also marks a moment of epistemological continuity. Moreover, Kramer’s attempt to solve the riddle of avian navigation surely was meant to translate and therefore to exceed the results of his previous research into so far unknown territory. If migratory birds can perform oriented flights by processing the data provided by both the azimuth circle of the sun and an internal clock why should true navigation not be explainable by the movement of the sun (in combination with the internal clock), too? The hypothesis Kramer henceforth intended to verify therefore was that avian homing might be based on some kind of bicoordinated sun navigation. This, however, implied that homing pigeons must be able to determine the coordinates of both the starting and the end point of their journey through the information that is provided by the movement of the sun. And this, in turn, is only possible if the pigeons not only can make use of the azimuth angle but also the height of the sun relative to the time of the day and, even more difficult, of the year. The experimental setting Kramer and his associates invented to test this hypothesis was highly sophisticated and time consuming. The experiments were carried out in three successive years between 1952 and 1954. The results appeared in two main articles being published in 1953 and 1955. The arrangement of the experiment was modified slightly from year to year both as to the preparation of the pigeons and the practice of releasing them. The core idea of Kramer’s so-called “Warteversuch”, however, remained the same and can be described as follows: A sample of homing pigeons was kept in Wilhelmshaven within an aviary where birds could study the daily movement of the sun. At a certain point of the year, Kramer deprived the pigeons of the possibility to see the sun. After a certain
time had elapsed – Kramer called this period “Wartezeit” – he shipped the animals to a well defined location further south in order to release them. This point was Gleiberg near Gießen. Both the geographical location and the point of time (the autumn equinox) were chosen deliberately so that – at least in one specific interpretation of the experiment – the sun curve the pigeons could see at the day of their release (subsequently referred to as the “Gleiberg curve”) – although the position was further south and hence the position of the sun at noon was in principle higher than it was the case simultaneously in Wilhelmshaven – still was lower than the last curve the pigeons were able to see in their home loft in Wilhelmshaven before their “Wartezeit” (subsequently referred to as the “Wilhelmshaven curve”). The birds were released at significant times of the day which were determined by the way how the Gleiberg and the Wilhelmshaven curve (in later experiments the hypothetical and the actual Gleiberg curve) were related to each other at significant points. For instance, at noon, that is, at the point of the day when the position of the sun was highest, the gradient of both sun curves is zero so that only the height and not the gradients of the sun could be used as information by the pigeons. As a result, the releases at noon tested only the factor “sun height”. Releases shortly before and after noon intended to test the effectiveness of the factor “gradient” (or the shape of the curve in general) in the pigeons’ processing of the right homing direction. Closely connected with this aspect is another: The point of the year could be chosen so that the Gleiberg and the Wilhelmshaven curve intersected in a particular way which allowed Kramer to chose release times in course of the day before, during and after the points of intersection in order to see whether the ambiguity caused by the hypothetical coincidence had a confusing effect or not. In sum, the entire arrangement of the test created a situation which was apt to deceive the proband birds in as much as they – as a result of the time span they had been deprived from seeing the daily course of the sun – could interpret the conditions at their release point, when they first saw the sky again, as a point further north, not further south of Wilhelmshaven. As a result of this possible deception the pigeons had the choice: Either they bought the deception, misinterpreted the release point, which was actually further south, as point further north and therefore headed off into southern direction or they interpreted the geographical location of the release point correctly and headed north. The results of the experiments Kramer carried out together with his associates over several years between 1952 and 1954 were all more or less the same: The homing pigeons could not be deceived once

1713 In later variations of the test, in fact the situation is even more complex since the release date was chosen as such that the actual Gleiberg curve was more or less identical with a hypothetical curve the birds would have been able to see if they had spent the last day before their “Warteperiode” in Gleiberg and not in Wilhelmshaven. At least this hypothetical Gleiberg curve coincided with the actual one of the release day in the highest point, that is, at noon. These precautions created deliberately the possibility for the pigeons to make significant errors but restricted the amount of suitable days in the year to only a few so that the tests needed to be repeated over several years! This test setting particularly refers to the report of the year 1953.

1714 This aspect, of course, does not apply to the points of time in the day where both sun curves intersect with each other and might alter for the time spans before and after the intersections. For the results of the tests of the year 1952 see Kramer, “Wird die Sonnenhöhe bei der Heimminderorientierung verwertet?” 213, 215–218. For the results of 1954 see Kramer, “Ein weiterer Versuch”, 174–176.
and continuously headed off correctly into northern direction. The information the pigeons could draw from the shape of the sun curve itself when they were released slightly before or after the critical points had no effect upon their homing behaviour either. In a letter to Niko’s younger brother, Luuk Tinbergen, G. Kramer writes in July 1952:

Mit der Heimkehrorientierung sitze ich fest. Die Sonnen-Navigation, welche die Hypothese war, konnte in einem kritischen Test nicht bestätigt, eigentlich nahezu widerlegt werden. Tauben fliegen auch dann gerichtet ab, wenn die Sonnenhöhe am Auflaßort genau gleich der des Heimatortes ist. (Das passiert bei N-S-Versetzung 2 mal am Tag).

[1 got stuck with the homing-coming orientation. Sun navigation, which had been the hypothesis, could not be verified in a critical experiment. In fact it could almost be declined. Homing pigeons set off in directed manner even when the height of the sun at the release location is exactly the same as it is at the home loft. (If the pigeons are displaced from North to South this happens twice a day).]

As a result and in contrast to G. V. T. Matthews, a colleague from the University of Cambridge (UK) who had postulated a slightly different version of sun navigation hypothesis and whose test results had substantiated the thesis, Kramer concluded that the height of the sun most likely was not a relevant parameter in avian navigation. However, if the height of the sun was not essential the whole hypothesis of sun navigation was doubtful either. After several years, G. Kramer ended the experiments testing the alleged sun navigation hypothesis and henceforth more and more turned into a critic of G. V. T. Matthews’ theory which therefore became also more and more the subject of a veritable scientific dispute between different sci-

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1717 MPG-Archives, III. HA, Rep. 77, file 6, letter G. Kramer to L. Tinbergen (22/07/1952). A similar statement can be found in a letter to J. Verwey who believed that Kramer’s pigeons were not able to study the sun long enough. ibid., file 7, letter G. Kramer to J. Verwey (13/11/1952). For the entire correspondence see ibid., file 7, letter J. Verwey to G. Kramer (11/11/1952), ibid., file 7, letter G. Kramer to J. Verwey (16/11/1952) and ibid., file 7, letter G. Kramer to J. Verwey (18/11/1952). See also Kramer’s later letter in which he confirms his disapproval of the sun navigation hypothesis, ibid., file 8, letter G. Kramer to J. Verwey (28/05/1953).


Thereby we can observe different stages or grades of Kramer’s criticism: Whereas Kramer, during the first stage of his own experiments – as they are communicated in his paper of 1953, – speaks in general of a “weakening” of the hypothesis, still believed in the possibility of sun navigation, and partly modified Matthews’ theory so that he was able to “rescue” the idea, on the later stage of his own experimentation – as it is represented in the article of 1955 – he required a reconsideration of G. V. T. Matthews’ results on basis of his more precise and more sophisticated methodological comments. Moreover, he suggested a completely different way how pigeons might read a sun curve. In some of his later accounts – after K. Hoffmann had repeated Matthews’ experiments in Cambridge by comparing Matthews’ with German pigeons – Kramer even vehemently disputed and therefore also refuted Matthews’ thesis so that his later reception therefore was clearly negative. Kramer’s transient reinterpretation of Matthews’ theory is of interest because it might indicate the direction his scientific development would have taken if he had lived longer: Whereas Matthews had suggested that the homing pigeon can identify the relevant sun curve by reading the tiny gradients while the sun is on the move and, so to speak, compares homologous sections of the curves being visible at both the release and the home location, Kramer, for a moment, considered it possible that the birds might only use the height and the azimuth of the sun as relevant information. Since each sun path can be described as a mathematical function he thought it possible that the birds extrapolated the rest of a curve on basis of these two bits of information. This however required that the pigeons were furnished with some kind of pre-established templates on basis of which an entire curve can be reconstructed even if only a tiny piece of it is readable. “Tatsächlich”, Kramer explains,

ist jede Sonnenbahn die klare geometrische Verwirklichung einer mathematischen Formel, so

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For both concepts see Kramer, “Ein weiterer Versuch”, 181–183.
daß ohne Rückgriff auf ein (erinnertes oder durch Extrapolation konstruiertes) Vergleichsstück und ohne irgend eine der Voraussetzungen, welche dem menschlichen Navigator bei Kenntnis des Datums in Tabellen verfügbar sind, die grundsätzliche Möglichkeit besteht aus einem Stückchen den Rest der Kurve und damit auch den Scheitelpunkt zu ergänzen.

[In fact, each path of the sun is the clear geometrical realization of a mathematical formula so that, without referring to any homologous bit (either remembered or construed through extrapolation) and without any of the presumptions the human navigator has at his disposal by knowing the dates recorded in tables, there is the principal possibility to complement the rest of the curve and hence also its summit on basis of this tiny piece.] (transl. CL)\textsuperscript{1724}

However, Kramer’s idea seemed to presuppose that the birds possess this “formula” or any equivalent representation of it in the first place, that is, some kind of almanac for sun curves. Hence he described both modes of orientation as “empirico-astronomic” (G. V. T. Matthews’) and “purely mathematical” (his) method\textsuperscript{1725} Yet after all, the experiments ended clearly with a negative result. And this negative outcome had eventually an enormous impact on how Kramer carried out research after 1955. In other words, the fact that Kramer and his associates were not able to evince sun navigation eventually marked a turning point in his further life course in as much as it was related to research in orientation and navigation.

Transition Four. (6) Abandoning the idea of true sun navigation, however, did not shake G. Kramer’s believe in the existence of some kind of bicoordinated orientation. The positive homing performances of totally inexperienced birds from great distance which Kramer had first observed in summer and autumn of 1951 could be repeated in further tests and therefore pointed clearly into this direction.\textsuperscript{1726} Thereby a new methodology was to be applied: The birds were raised in closed aviaries and thus were not able to become familiar with their environment on explorative flights. In other words, Kramer and his associates had begun to work with birds being deprived from experience. And nonetheless, despite this deprivation from experience, some of them found their way from great distance – a matter of fact that suggested the existence of some unknown bicoordinated orientation mechanism, just like pigeon fanciers had used to claim it.\textsuperscript{1727} The period after the failed Gleiberg experiments is characterized by the search of this unknown mechanism. Thereby it is essential to understand that Kramer, for the time being, did not put forward another alternative overall hypothesis he ventured out to examine in a second step. The starting point of his scrutinies changed in so far as Kramer more concentrated on isolated parameters which, in case their relevance was confirmed, were apt to narrow down the range of possible explanations. This is why the papers G. Kramer published in cooperation with others or alone in the years after 1955 concentrate on a number of seemingly isolated themes such as the effect of weather and season, the effect the direction and place of release exerts upon the

\textsuperscript{1724} Kramer, “Ein weiterer Versuch”, 181.

\textsuperscript{1725} It might be that Matthews interpreted Kramer’s proposal as if pigeons possessed a sort of “nautical almanac”. He considered the idea more reasonable if the stored information was not related to the sun azimuth but to the sun arc. See MPG-Archives, III. HA, Rep. 77, file 14, letter G. V. T. Matthews to G. Kramer (19/10/1954).

\textsuperscript{1726} See G. Kramer et al. “Das Heimkehrvermögen gekäfigter Brieftauben”. In: Ornithologische Beobachter 51.1/2 (1954), 4–12.

\textsuperscript{1727} For Kramer’s evaluation of the results see ibid., 11.
homing performance, or the distinction between long-distance and short-distance flights. The common denominator of these studies may be that Kramer, while seeking for relevant parameters to be tested, on the one hand widened his perspective on a wider variety of aspects that hadn’t been thought of so far, yet, on the other hand, maintained a strategy of thoroughly scrutinizing single isolated parameters. The diagnoses Kramer performed after it had turned out to be impossible to prove true sun navigation thus commenced from another starting point: A more extensive widening went hand in hand with a more explicit self-limitation as to what was to become the object of an empirical test in the second place.\footnote{There are some indicators that this “move” also led towards a scattering of G. Kramer’s work group in as much as single more or less isolated projects coexisted next to each other.} Examples which I have drawn from Kramer’s scientific publications may suffice to demonstrate the modified style of Kramer’s diagnoses which became characteristic for his studies after Gleiberg.\footnote{Kramer’s personal papers show that these published examples are only the tip of the iceberg of Kramer’s inventiveness. Next to M. Takata’s theory of blood flocculation he also took into consideration the possibility that the vibration of the ground could be dependent of the respective geographic position and therefore might be a clue with which the birds can calculate the relative position of their release point. See to this spectacular idea of Kramer’s correspondence with I. Kohler who worked at the Institute for Experimental Psychology at the University of Innsbruck in Austria, MPG-Archives, III. HA, Rep. 77, file 7, letter G. Kramer to I. Kohler (09/10/1952) and \textit{ibid.}, file 7, letter I. Kohler to G. Kramer (14/10/1952). From a science historian’s perspective Kohler’s reply is exciting, to say the least, because he mentions so-called disorientation experiments with blind and seeing human beings showing that blind people – without loosing their orientation – are capable to process more irritating movements such as spinning around their own vertical axis than proband persons with normal visual capacities. This observation points into the direction of an orientation mechanism which is based on a kind of proprioceptive memory including the possibility that an organism can reconstruct a cognitive map on basis of its own movements within the three-dimensional space.} (a) A number of tests is related to what Kramer called “the direction effect”.\footnote{For this thematic emphasis see G. Kramer et al. “Directional Differences in Pigeon Homing”. In: \textit{Science} 123.3191 (1956), 329–330, G. Kramer et al. “Two-direction Experiments with Homing Pigeons and Their Bearing on the Problem of Goal Orientation”. In: \textit{American Naturalist} 91.856 (1957), 37–48 and, finally, Kramer et al., “Neue Untersuchungen über den ‘Richtungseffekt’”. See also the paragraphs providing an overview of the topic in the following papers Kramer, “Experiments on Bird Orientation and Their Interpretation”, 203–208, G. Kramer. “Recent Experiments on Bird Orientation”. In: \textit{Ibis} 101.3/4 (1959), 405–409, and Kramer, “Long-distance Orientation”, 354–355. For a broader view upon the release site specific biases which puts Kramer’s early studies into perspective see Wallraff, \textit{Avian Navigation}, 18–22.} G. Kramer and his associates had recognized that the homing success of a sample group of proband birds differed depending on the direction the pigeons needed to fly in order to reach their home loft.\footnote{For Kramer’s explanation why the term “direction effect” should be preferred over the term “direction tendency” see MPG-Archives, III. HA, Rep. 77, file 14, letter G. Kramer to L. C. Graue (05/09/1955) and also \textit{ibid.}, file 14, letter G. Kramer to L. C. Graue (22/07/1955). From Kramer’s account we can infer that the modified concept allowed a more of arbitrariness especially as to the short-distance releases where directional preferences deviated.} Releases from geographical locations southerly of Wilhelmshaven (northerly flight direction) yielded significantly better homing performances than in those groups that were released from places easterly of Wilhelmshaven (fight direction to the west).\footnote{See Kramer et al., “Directional Differences in Pigeon Homing”, 329. The “direction effect” could also be made evident with pigeons from a second loft Kramer had established in Freiburg.} This insight sparked off quite an extensive research endeavour in the following years which was
carried out not only in Germany but also in the United States. In the years after 1952 G. Kramer had established a close cooperation with J. G. Pratt, a parapsychologist from Duke University. The contact between J. G. Pratt and G. Kramer was apparently prepared by a correspondence Kramer had begun with J. B. Rhine, the head of the Parapsychology Laboratory, in January 1951 at the latest. Due to time constraints Rhine seemed to have passed the issue to Pratt, his associate. Pratt, like H. L. Yeagley before him, had begun, or was about, to examine the mechanisms of avian navigation for the US military. Besides the promising financial opportunities research in avian orientation and navigation provided in the United States, the parapsychologists of Duke University also had a more intrinsic interest in the theme since as long as the actual physical orientation mechanisms were not found the issue “avian navigation” was apt to maintain the hypothesis that some kind of extrasensory perception (ESP) might be involved. Failure of physical explanations of the type Kramer had in mind thus in the last consequence supported the form of non-causal (i.e. non-proximate) explanation the parapsychologists intended to prove. “We do not hold to the rather traditional belief”, J. B. Rhine, for instance, writes in a letter,

that all animal orientation has to be explained in terms of sensory factors or perception, but, on the other hand, if extrasensory perception plays a part the fact could only be determined after exhaustive efforts to find the explanation in terms of more familiar processes had repeatedly failed.

G. Kramer certainly did not believe in any kind of extrasensory explanation of avian navigation but instead was interested in physical causes. Despite this clash of approaches, which I tend to interpret as deep-rooted epistemological deviations, Kramer rated highly Pratt’s and Rhine’s unprejudiced manner to treat the issue of avian navigation. He also valued Pratt’s methodological and practical skills. This can be concluded from Kramer’s letters to friends, colleagues and superiors. See to this MPG-Archives, III. HA, Rep. 77, file 14, ms. “Zweiter Rundbericht über Freiburger Auffassungen” (ca. 06/1955), pages 1–3 and ibid., file 15, ms. “Kurze Beschreibung der beiden Kreuz-Auffassungen mit Freiburger Tauben am 24. und 26. Mai 1955” (ca. 05/1955), pages 1–2.

See to this ibid., file 5, letter J. B. Rhine to G. Kramer (04/01/1951), ibid., file 5, letter J. B. Rhine to G. Kramer (26/04/1951), ibid., file 5, letter G. Kramer to J. B. Rhine (04/05/1951), ibid., file 5, letter J. B. Rhine to G. Kramer (09/05/1951), ibid., file 5, letter G. Kramer to J. B. Rhine (20/06/1951), ibid., file 5, letter J. B. Rhine to G. Kramer (26/06/1951), ibid., file 5, letter G. Kramer to J. B. Rhine (03/07/1951), ibid., file 5, letter J. B. Rhine to G. Kramer (07/07/1951), ibid., file 5, letter J. B. Rhine to G. Kramer (25/08/1951), ibid., file 5, letter G. Kramer to J. B. Rhine (17/09/1951), ibid., file 6, letter J. B. Rhine to G. Kramer (13/09/1951) and ibid., file 6, letter J. B. Rhine to G. Kramer (03/07/1952).

For the financing of Pratt’s research by the US Navy see, for instance, Kramer et al., “Directional Differences in Pigeon Homing”, 330, fn. 1. Here it reads: “These experiments were conducted under contract NR 160–244 between the Office of Naval Research, Department of the Navy, Washington, and Duke University”. See also MPG-Archives, III. HA, Rep. 77, file 12, letter G. Sprugel (ONR) to J. G. Pratt (04/06/1953).

Ibid., file 5, letter J. B. Rhine to G. Kramer (09/05/1951). See also ibid., file 12, letter J. G. Pratt to G. Kramer (25/08/1953).

How Kramer himself saw his cooperation with the parapsychologists can be inferred from a ms. for a radio broadcast. See ibid., file 14, ms. “Vögel fliegen ohne Kompaß” (ca. 1955), here pages 7–8.

See, for instance, ibid., file 8, letter G. Kramer to O. Hahn (30/01/1954) or ibid., file 11, letter
Gustav Kramer (1910–1959)

G. Kramer to O. Koehler (28/02/1953).


Several of the research proposals with which J. G. Pratt applied for funding are passed onto us in Kramer’s papers. See ibid., file 12, ms. J. G. Pratt [?] [Cl], [Homing Phenomena in Animals] [Cl] (ca. 1953), pages 1–14, ibid., file 12, letter J. G. Pratt to G. Kramer (20/03/1953), ibid., file 12, letter G. Kramer to J. G. Pratt (26/03/1953), incl. ms. “Comments to the Application” (n. d.), ibid., file 12, letter J. G. Pratt to G. Kramer (16/04/1953), ibid., file 12, letter J. G. Pratt to G. Kramer (18/09/1953) and ibid., file 12, letter J. G. Pratt to G. Kramer (23/11/1953). Pratt’s proposal is of interest for my argumentation because it shows that Pratt intended to carry out the experiments “along a broad general front”. And I think it was exactly this unprejudiced approach which unified Kramer’s and Pratt’s research groups. In the accompanying correspondence we are also informed that Kramer preferred not to be involved directly in an application for funds from the US Navy. His salary for the time he planned to stay in the States therefore was planned to be paid (partly) by Duke University. Pratt’s contract with the US Navy was renewed over several years till 1959, as far as I can see. This is suggested by the following source documents: Ibid., file 12, ms. J. G. Pratt [?] [Cl], “Renewal of ONR contract Nonr–1181(03), NR 160244” (16/04/1954), pages 1–11, ibid., file 12, letter J. G. Pratt to U. v. St. Paul (06/06/1955), ibid., file 12, ms. J. G. Pratt [?] [Cl], [Investigations of Orientation in Animals] [Cl] (19/02/1957), ibid., file 12, letter J. G. Pratt to G. Kramer (23/08/1958) and ibid., file 12, letter G. Kramer to L. C. Graue (06/10/1958). Additional funding was provided by the National Science Foundation (NSF). See to this ibid., file 12, letter J. T. Wilson to J. G. Pratt (22/06/1954), ibid., file 12, letter J. G. Pratt to J. T. Wilson (26/06/1954), ibid., file 12, letter J. G. Pratt to G. Kramer and U. v. St. Paul (26/06/1954), ibid., file 12, letter J. G. Pratt to G. Kramer (05/08/1954), ibid., file 12, ms. J. G. Pratt [?] [Cl], “Research Proposal and request for NSF grant” (08/1954), pages 1–9. For instance, see ibid., file 12, letter J. G. Pratt to G. Kramer (05/08/1953), ibid., file 12, letter J. G. Pratt to G. Kramer (25/08/1953), ibid., file 12, letter J. G. Pratt to G. Kramer (23/11/1953), ibid., file 12, letter J. G. Pratt to G. Kramer (17/12/1953), ibid., file 12, letter J. G. Pratt to G. Kramer (19/02/1954), ibid., file 12, letter J. G. Pratt to G. Kramer (03/04/1954), ibid., file 12, letter J. G. Pratt to G. Kramer (12/07/1955), ibid., file 12, letter J. G. Pratt to G. Kramer (21/07/1956), ibid., file 12, letter J. G. Pratt to G. Kramer (07/01/1958). See Kramer, “Experiments on Bird Orientation and Their Interpretation”, 204 and Kramer et al.,
compass directions under same circumstances, the landscape in the two Carolinas also seemed to be more homogeneous. Kramer and his coauthors write at the beginning of a joint paper published in 1957: “We were able to make a more thorough study of directional effects in the Durham, North Carolina, area than was possible in Wilhelmshaven because the topographical conditions are more homogeneous there (Kramer, Pratt, and St. Paul, 1956).” A more homogeneous landscape in principle ruled out the disturbing factor of orientation or distraction through landmarks or cities. This extensive research program finally culminated in more reliable and valuable results simply because they included a comparative perspective. Thus Kramer and Pratt had found out that for some unknown reasons the homing performances in Europe were in general better than in the two Carolinas. Moreover, the seasonal fluctuations of homing performances observable in Germany could not be confirmed for the release locations in the States. Beyond that, it could be shown that direction effects existed in both countries but that they were not identical. While in Northern Germany sent up attempts from the south yielded better performances than from the east, in the two Carolinas there existed a statistically significant south-over-north superiority. This irregularity even applied to releases from short distances which contradicted sheer landmark orientation. Cloudiness somewhat lowers the advantage provided by the direction effects without terminating them. Moreover, besides the direction a number of even more arbitrary factors turned out to be relevant such as the performance variation from day-to-day and possibly also the genetic stock of the proband pigeons. (b) A second parameter Kramer’s research on avian navigation was concerned with after 1955 was the distance which separated the release place from the target location. As long as no definite navigational mechanism was discovered any research on homing was confronted with the more parsimony theory that homing was only due to a

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1743 “Neue Untersuchungen über den ‘Richtungseffekt’”, 178. See also MPG-Archives, III. HA, Rep. 77, file 7, letter G. Kramer to L. Tinbergen (09/03/1953).
1746 For the fact that regional differences can be observed in both states see Kramer, “Long-distance Orientation”, 354.
1750 For the day-to-day variability see Kramer et al., “Two-direction Experiments”, 38 and ibid., 47.
1751 For Kramer’s interest in the factor “distance” see G. Kramer et al. “Über das Heimfinden von Käfigtauben über Kurzstrecken”. In: Journal für Ornithologie 97.4 (1956), 371–376 and also Kramer, “Long-distance Orientation”. 

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combination of mere direction finding and arbitrary seeking either randomly or on basis of previously acquired knowledge about environmental cues. This idea had produced a principal differentiation between long- and short-distance orientation whereby it was quite clear that direction finding from great distances could neither be random nor guided by experience. The critical aspect consisted more in the short-distance flights since it couldn’t be ruled out entirely that homing pigeons applied some kind of division of labour in so far as they bridged the wider distances via direction finding, while the final recognition of the home loft was performed on basis of previously acquired knowledge of any kind. A theory of true navigation which intended to go beyond the simple dualism of direction finding and arbitrary seeking therefore paradoxically needed to reduce one’s view, concentrate on short-distance flights and ultimately evince that the mechanisms of navigation were also effective during homing from short and ultra-short distances not being excluded that orientation via visual clues might be intact simultaneously as well, at least partly.

A considerable amount of Kramer’s argumentative investment was meant to clarify this question which also means that after Gleiberg the focus of the tests partly shifted from long- to short-distance flights. In a study Kramer published under the title “Über das Heimfinden von Käfigtauben über Kurzstrecken” he argued that inexperienced pigeons released from short distances in summer still performed better than experienced ones released in winter. The comparison of winter and summer results thus led to a re-evaluation of performances obtained over short distances of which ornithologists including G. Kramer used to think that they were mastered by random or experienced seeking. In a second test Kramer sent up untrained and trained pigeons from ultra short distances (viz. 2.8 km) and thus demonstrated that untrained birds headed off less directly yet managed to reach their home location equally fast. Kramer therefore concluded, even on short and ultra-short distances homing pigeons operate with an absolute unknown navigational mechanism and less via landmark clues.

(c) A third particulate aspect which is standing out in Kramer’s post-Gleiberg publications is the impact of varying climatic conditions upon the homing success of carrier pigeons. G. Kramer and his workmates had realized that the homing performances of carrier pigeons during the summer...
months were significantly better than in the winter months. The reasons for this observed matter of fact were unknown and required to take into account a wide range of possible effects and, subsequently, their discrimination.\textsuperscript{1756} Thus Kramer at first considered the option that in winter the “Fluglust” (internal motivation to fly) was somewhat diminished but comparative data contradicted, or at least, questioned this notion.\textsuperscript{1757} “Winter pigeons”, though less successful in homing, nonetheless turned out to be equally eager flyers. Also Kramer thought about some kind of physiological mechanism that was a direct effect of low temperatures, indirectly correlated with temperature changes or even with annual biological rhythms such as the breeding cycle.\textsuperscript{1758} Yet the impairment or disturbance of any kind of sensory mechanism could not be approved by experiments. Also the idea of a correlation with any kind of biological rhythm, either the reproductive cycle or the migratory activity, turned out to be unrealistic due to individual and day-to-day variations as well as the fact that the performance differences seemed to be connected with the climatic not the astronomical winter.\textsuperscript{1759} In addition, Kramer was confronted with G. V. T. Matthews’ suggestion that in winter the landscape might be covered with ice and snow and hence might provide less discrete cues.\textsuperscript{1760} But the so-called winter effect equally applied both to experienced birds and first timers besides the fact, that the winters in Northern Germany, in Kramer’s view, did not produce that homogeneous landscapes. One of Kramer’s workmates, H. G. Wallraff, even managed to correlate interdiurnal barometric variation with actually observed homing performances.\textsuperscript{1761} In sum, one may eventually say that the examination of the impact of climatic conditions was eventually the area of Kramer’s research in which he most consequently opened his horizon on so far discounted aspects but which also reveals the highest degree of scattering. The bottom line of this research finally was that neither the lack of motivational intensity, nor the lack of definite landmarks in winter, nor the low temperatures themselves acting upon the sensory mechanisms, nor the reproductive and migratory cycles of the pigeons turned out to be \textit{the} crucial factor.\textsuperscript{1762} Instead, as outlined in later accounts of the problematic, the correlation between homing performance and low temperatures \textit{itself} apparently was underlying annual fluctuations. “The phenomenon of a drastically lowered homing performance in

\textsuperscript{1756} For the general result that lower temperatures impair homing performances see Kramer, “Einfluß von Temperatur und Erfahrung”, 347 and their confirmation Kramer et al., “Weitere Erfahrungen”, 370. See also Kramer et al., “Über das Heimfinden von Käfigtauben über Kurzstrecken”, 372–374. For more background information concerning the annual periodicity see Wallraff, Avian Navigation, 38–41.


\textsuperscript{1758} Kramer, “Einfluß von Temperatur und Erfahrung”, 347.

\textsuperscript{1759} See Kramer et al., “Weitere Erfahrungen”, 369, 370. That is periods of high reproductive or migratory activity were correlated with bad homing performances and vice versa.


\textsuperscript{1762} For the list of non-relevant parameters see Kramer, “Recent Experiments on Bird Orientation”, 412 and Kramer, “Long-distance Orientation”, 356.
winter time has been given a considerable analytical development by Wallraff (1959 a, b)", Kramer summarizes and continues,

He has shown that the general effect consist of a cyclic fluctuation roughly paralleling the annual temperature curve (Fig. 10). During part of the year, September to March, an actual correlation exists between single performances and temperatures at the given occasions. Such a correlation does not appear in the rest of the year.\textsuperscript{1763}

On basis of this more advanced state of knowledge Kramer questioned whether the seasonal fluctuation with partial correlation to temperature changes really applied to the homing problematic at all but still answered the question in the affirmative and concluded: “All this tends to indicate that the variation of homing success in the course of the year is caused by variations in physical factors that serve as elements in the system of orientation clues, or (more likely) of factors related to such elements”.\textsuperscript{1764} Yet, despite the fact that Kramer was prepared to take into account the “physical” nature of the effect he did not go so far as to reconsider the effects exerted by the magnetic field.\textsuperscript{1765} This was status quo till Kramer’s death in 1959.

(7) The final aspect of my phenomenological survey I’d like to mention in order to sketch the development of G. Kramer’s research on orientation and homing between 1946 and his tragic death in 1959 consists of some conceptual changes which seemed to prepare a more integrated view upon the navigation problematic. Kramer had already in 1952 suggested to explain the mechanism underlying true navigation by distinguishing two fundamentally different steps. He hypothetically argued that homing birds, just like navigating human beings, in a first step use some kind of mental map upon which they can locate both the starting and the target point of their journey and from which they can draw the direction to which they need to fly in order to reach their target destination. In a second step, Kramer claimed, the navigating birds make use of their compass orientation. Both steps were thought to be discrete processes in one and the same neural mechanism he later called “map-and-compass orientation”.\textsuperscript{1766} This idea implied that only the former of the two steps was based on some kind of unknown absolute mechanism of position finding,

\textsuperscript{1763} Kramer, "Recent Experiments on Bird Orientation", 411.
\textsuperscript{1764} Ibid., 412.
\textsuperscript{1765} Yet other sources show that G. Kramer did not exclude the possibility that orientation in the magnetic field still could be made evident some day. See Kramer’s contribution for a radio broadcasting company, MPG-Archives, III. HA, Rep. 77, file 14, ms. “Vögel fliegen ohne Kompaß” (ca. 1955), here page 1.
\textsuperscript{1766} G. Kramer’s map-and-compass model turned out to be a valuable epistemological basis for further experiments. This can be inferred from Wallraff, Avian Navigation, 59–68, especially 64–66 where the author explains how the map and the sun compass component interact with each other. In short: According to H. G. Wallraff, pigeons must have some sort of rudimentary representation of olfactory (or other) gradients which they can correlate with the compass directions they can calculate from the daily shifts of the sun azimuth. When displaced, the pigeons apparently can recognize scalar decreases or increases of the gradients in question and – eventually while also processing the position of the sun and the time of the day – seem to be able to calculate the homeward direction. Most interestingly, Wallraff also believes that pigeons can correct their course on the fly due to updated incoming signals (Ibid., 144) but finally questions that Pigeons have a more elaborate “navigational map”, that is a (physiological) representation of spatial conditions far away from the birds’ home or of unknown territory (Ibid., 145). However, in Wallraff’s methodological distinction between a “positional” and a “directional” component Kramer’s map-and-compass model seems to live on, at least to a certain extent (Ibid., 145–146).
while the latter might operate with the well proved sun-azimuth orientation. For instance, Kramer’s map-and-compass model predicted that under overcast sky the mechanism of position finding which, in Kramer’s view, was independent of the astronomical data provided by the sun remained still intact, while only the latter step should be negatively affected. And indeed some of Kramer’s later results favoured his model. Experiments assessing regional or directional effects had revealed that overcast sky levels down the outstanding performances of those sample groups profiting from regional effects but did not affect the weaker performances of the control groups. Kramer interpreted these results in terms of his two-component model and claimed that cloudiness only affected the compass and not the map function. In a later statement he underlines for instance:

Three statements can be derived from these data: | (1) The directional differences do not disappear with overcast. | (2) Overcast has no or little effect upon homing flights of the slow class. | (3) Overcast diminishes noticeably the number of flights which would otherwise qualify in the top class. The deficit in the top class is covered by the middle class. | This result supports the map-and-compass concept. At the beginning of the foregoing chapter it was concluded that variations correlated to space and time must be attributed to shortcomings of the “map” component, while cloudiness is known to affect the compass component. Now clearly those birds have a chance to make full use of the compass who were successful in determining their proper position in relation to home. If deprived of the compass, their good “map” performance is wasted; they are reduced to searching for their direction by repeated position finding. Thus the proportion of top-class performers shrinks. On the other hand, poor position-finders can draw little advantage from a compass; therefore the slower groups are not noticeably affected.

Kramer’s map-and-compass model was first formulated in a rudimentary form in 1952 and was elaborated more detailed in 1953. Yet, after that, the idea was somewhat pushed into the background. After failing to prove true sun navigation the model regained more and more importance until it reached a paradigmatic status from ca. 1957 onwards. How was that possible. In addition to that, I would like to know whether the concept itself was subject of transformation over time. In order to answer these questions I should like to quote literally some passages in which Kramer elaborates on his map-and-compass model. In his statement of the year 1952 it reads:

Es sei daran erinnert, daß die bei uns Menschen angewandte Methode der astronomischen Navigation die gleiche Abhängigkeit der Präzision aufweist, sofern man nämlich die Bestimmung der geographischen Position als Grundlage zu einer Richtungsangabe benutzt.

[It should be kept in mind, that the method of astronomical navigation applied by us humans reveals the same dependency upon precision in so far as one utilizes the determination of the geographical position as a basis for the calculation of a direction.]

In 1953 Kramer explains:

Es leuchtet auf den ersten Blick ein, daß die Zielorientierung (im Gegensatz zur Richtungsnavigation) in zwei Teilprozesse zerlegt werden kann: 1. Die Schätzung des neuen geographischen Orts, 2. die auf dieser Grundlage mögliche Richtungsbestimmung. Daß die Taube instan-

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1768 Ibid.
1769 See also MPG-Archives, III. HA, Rep. 77, file 12, letter G. Kramer to J. G. Pratt (ca. 07/1952).
de ist, Himmelsrichtungen auf Grund des Sonnenazimuts zu bestimmen, ist nachgewiesen. So ist der Schluß scheinbar berechtigt: Die Schätzung des geographischen Orts wird ohne Sonne vollzogen; die anschließende Bestimmung der Flugrichtung dagegen ist einfach eine Sonnenazimut-Orientierung, daher ohne Sonne nicht darzustellen. Dagegen gibt es aber den Einwand, daß die Schätzung des geographischen Orts allein schon zur Bestimmung der Heimflugrichtung hinreichen müßte. Wenn die Taube in der Lage ist, gewissermaßen bei jedem Flügelschlag die Ortsbestimmung zu erneuern, so muß sie auch nach einigem Tasten die zum Erfolg führende Richtung ermitteln können. Wozu braucht sie dann die Sonne überhaupt noch? Diese letzte Frage sei gleich dahin beantwortet, daß im biologischen Geschehen die Bereitstellung verschiedener Methoden üblich ist. Es mag also sehr wohl sein, daß tatsächlich die Sonne nicht unbedingt nötig ist, sondern daß sie nur eine abgekürzte und sehr präzise, aber nur beschränkt anwendbare Orientierung ermöglicht. Wenn Orientiertheit der ohne Sonnensicht abfliegenden Tauben nicht feststellbar ist, so mag das nur bedeuten, daß ein weniger präzise arbeitender Mechanismus der Richtungsbestimmung in Kraft ist. – Wir selber (Kramer und v. St. Paul) haben früher die prompte Richtungnahme bei Turmabflügen als Indizium gegen das Bestehen von Orientierungsmethoden nach Art des Abtastens eines Gefälles gewertet, sind aber unter dem Eindruck der hier geschilderten Tatsachen vorsichtiger geworden.

It makes sense immediately that the goal orientation (in contrast to the direction orientation) can be divided in two part processes: 1. The Estimation of the geographical location, 2. the estimation of the direction which is possible on this basis. That the pigeon is capable to determine compass directions on basis of the azimuth of the sun is evident. As a result the conclusion seems justified: The estimation of the geographical location is performed without the sun; the subsequent determination of the flight direction, on the contrary, is simply a sun-azimuth orientation and therefore not performable without the sun. Against this view, however, there is the objection, that the estimation of the geographical location alone may be sufficient for the identification of the homing direction. If the pigeon is capable to renew the estimation of the geographical place – so to speak with every wing beat –, it must also be able after some groping to determine the direction which leads to success. If so, for what does it [the pigeon] need the sun? This last question is to be answered right away by pointing out that in biological processes a supply with different methods is common. Hence it might well be that indeed the sun is not necessary and instead allows only a curtailed and very precise orientedness which, though, is applicable only in a limited manner. If no orientation can be made evident with pigeons being sent up without having any view on the sun, this may only mean that a less precisely working mechanism of determining the direction has become effective. – We ourselves (Kramer and v. St. Paul) used to interpret the prompt taking up of a direction when pigeons were released from towers as an indicator against the existence of an orientation mechanism that is operating on basis of scanning gradients but have become more cautious under the impression of the data that have been reported here.  

In 1957 Kramer underlines:

I made one attempt (Kramer 1953) to formulate a hypothetical concept allowing for the effect of the visibility of the sun, which has been established for various distances, including very short ones where astronomical navigation is excluded anyway. I then argued that the goal-orientation process might be composed of two fundamentally different steps, one establishing the position of the release place, the other determining the direction of the flight. Both steps find their parallel in Human orientation, the first being represented by the procedure of studying the map, the latter by consulting the compass. It is clear that the compass is useful only after the position of the new place has been established on the map. It is also clear that initial orientation is impaired of the compass is missing. My suggestion was that the sun’s function was only that

of the compass, while the determination of the position was an unknown procedure without relation to the sun.\footnote{1772}

In a study of the year 1958 Kramer writes:


[On other occasions (Kramer 1953, 1957) it has been argued that we have reasons to believe that the process of goal orientation can be separated in two independent steps: 1. the determination of the geographical place relative to the home location, besides the homing direction which can be inferred from that. This step is unexplored. 2. the step of finding in the field the direction which has been derived before; this is done with the help of the sun. Since in human navigation the former of the two steps is performed by means of using a map and the second by using a compass the term “map-and-compass concept” has been introduced. The results obtained under overcast sky fit to this conception. Since the determination of the direction by sun cannot provide any difficulty during bright weather, the reason of the direction effect must be connected with the estimation of the location of which it is presumed that it is performed independent from the sun. The results obtained during cloudiness, indeed, are as it is expected if only the estimation of the compass direction is affected. From the lack of the sun compass primarily those flights are suffering which, as a consequence of the correct determination of the location, would have had a fair chance under bright weather condition to reach the target quickly. In case of incorrect estimation of the position, by contrast, the sun compass is not helpful at all. An additional impairment / delay due to cloudiness is not to be expected because repeated position finding, even while the sun is absent, may deliver the direction in the field anyway.\footnote{1773}] (transl. CL)

And in 1959 he claims:

If our “map-and-compass” concept holds good, any attempt to analyse homing orientation

\footnote{1772} Kramer, “Experiments on Bird Orientation and Their Interpretation”, 224. For Kramer’s defence of his two-step model against Matthews’ objections see ibid., 224–225. Thus Kramer replied to Matthews critique that the model would fail in cases of great longitudinal shifts that a bird could make adjustments after its position has been determined once. Matthews also seems to have claimed that under overcast conditions releases on training lines give better initial orientation than off the lines suggesting that the approximate sun position detectable even in overcast sky might be useful for azimuth determination. Kramer replied that training was useful regardless of the availability of the sun. Matthews’ third objection was that if the sun provided only the azimuth its absence would only impair not upset orientation but extremely poor results under overcast sky suggested the latter. Kramer answered that nobody knows how complete disorientation looks like.

\footnote{1773} Kramer et al., “Neue Untersuchungen über den ‘Richtungseffekt’”, 191.
Gustav Kramer (1910–1959)

will automatically centre upon the position-finding portion of the whole process. The source of all variations and “effects” encountered in homing must be sought in the position-finding element, not in the direction-finding. If we find regular fluctuations in successful homing, for example, in relation to season, the conclusion must be that in one part of the year physical data available for position-finding are more feeble than in another. Similarly, in any particular spot where scattering in the departure direction is wide, position-finding must be based on weak or conflicting data. It would be unreasonable to assume that sun-compass orientation should be more difficult in a particular season, or in a particular position, than in any other.\footnote{1774}

Finally, in 1961 Kramer summarizes:

The map-and-compass concept cannot properly be called a hypothesis for the same reason that nobody would care to call the old belief in a “sense of site” or “sense of position” a hypothesis. Nevertheless an organization of the problem is attained with the help of the two-step formulation. For instance, it may be concluded that in a number of “effects” described above – such as direction effect, winter effect, and day-to-day variations – it must be the map constituent that is affected. The two-step concept suggested also an experimental approach which starts from our knowledge that shifting the physiological rhythm (in other words, resetting the internal clock) produces predictable alterations of direction finding. If in goal orientation the sun gives only bearings, a shifted clock should produce the same alterations as in direction finding: clock shifted forward, counter clockwise; backward: clockwise. The expectation was already tentatively confirmed in one of a small number of long-distance releases made by K. and A. Rawson (1953, unpublished).\footnote{1775}

The synopsis of passages related to Kramer’s “map-and-compass concept” which is more or less complete reveals several aspects worthwhile to keep in mind. At first, the series of quotes shows a gap for the years 1954–1956 during which Kramer, as far as I can see, has not used his two-step concept explicitly or at least pushed into the background. After that, the concept re-enters Kramer’s writings whereby the idea now is connected with a comprehensive catchphrase. The reasons for this transitional silencing can be found in the quotations themselves. Kramer had reserved the former of the two steps, that is, position finding, from the very beginning for those mechanisms that did not utilize the sun as source of information. With his shift of interest to sun navigation, that is, position finding by utilizing the sun, the concept was pushed into background and not readjusted which would have been possible, too. After sun navigation turned out to be not the mechanism which is capable to explain the mapping part of the model, the concept seemed to become appropriate again. Hence I am inclined to argue that the usage and not so much the concept itself altered over the years. The revitalization of the concept had probably the function to provide a coherent conceptual frame within which the unsolved question of true bicoordinated orientation could be addressed adequately although it still remained unsolved. Second, the combination of position and direction finding, from the very beginning, has been discussed of one possible method of orientation amongst several others. One of these alternatives, as already Kramer’s account of the year 1953 shows, was a mechanism of direction finding on basis of repeated determination of the positions on the fly, that is, by assessing the gradients within a field. Thirdly, in later accounts Kramer’s focus shifted to the map component of the model and, in doing so, he began to address those parameters which

\footnote{1774}{Kramer, “Recent Experiments on Bird Orientation”, 405.} \footnote{1775}{Kramer, “Long-distance Orientation”, 357.}
allegedly affected the map and not the compass constituent (i.e. the direction effect, the day-to-day and the geophysical effects). I have already explained that Kramer’s emphasis on particulate aspects was based on an alternative model of analysis and my impression is that the epistemic deep structure of this model did not fully coincide with the logic that was underlying the map-and-compass concept as a whole. This created a sort of epistemic tension which, by the way, partly affected also the concept as a whole, namely always when the dualism of both mechanisms needed to be addressed on a heuristic level: The map-constituent was unknown and hence remained uncertain, while the compass orientation had been confirmed many times. In addition to that, I think, it can be discussed whether the alternative, that is, direction finding by repeated position finding under overcast skys, had not a similar epistemic effect. Maybe, it was this tension which contributed to the fact that Kramer connected the idea of a dualism in the process of goal orientation with a comprehensive catchphrase – a move whose sense was primarily lying in that it created order. Finally, it is quite astounding that Kramer developed the concept by drawing a connection between human and animal orientation. If I was to put it provocatively I’d say the map-and-compass concept owed its existence to an anthropomorphizing heuristic gesture of G. Kramer’s. In sum, I think it should be examined more precisely whether G. Kramer’s map-and-compass concept established not a scientific paradigm which – despite of all its superficial constancy – nonetheless was subject of a more representative transformation process taking place in the years between 1952 and 1959. For instance, it is possible to argue that in earlier quotations the linear understanding of the dualism (1. map, 2. compass) prevailed, while in later accounts the map-component more appeared as the logical inference of a number of varying parameters that were not affected by the sun. In the former of the two cases the dualism was more like a “Komplex-Qualität” in the latter like a “Gestalt”. If this reading was possible, it would support my thesis that the starting point (here the conceptual starting point) of Kramer’s diagnoses significantly altered after Gleiberg.

As second example of conceptual reconfiguration was sparked off by the fact that Kramer’s concept of “direction effect” became obsolete.1776 The idea of a positive correlation between the homing success and the compass direction into which the pigeons needed to fly in order to be able to reach their home appears somewhat attached to the idea of sun navigation. However, the discovery that direction effects were varying not only in Germany and the United States but, beyond that, seemed to alter highly arbitrarily from release site to release site – and there also relative to the release distance – proved that it is actually not the “direction” which is the distinctive factor but some kind of parameter which is connected with the geographical location of the release site itself.1777 Kramer’s concept of “direction effects varying...
effect” needed to be changed into “regional effect”. What this “regional effect” might be remained an open question at first or, more precisely, Kramer and Pratt answered this question negatively: The effect could not be explained solely with orientation through landmark clues. This might appear as tiny detail but on closer inspection it paved the way to reconsider forms of absolute orientation on basis of other data than provided by the sun. And although Kramer rejected H. L. Yeagley’s theory till his death in 1959, the question persisted whether it could not be the magnetic field which provided an explanatory model for definite orientation independent from the sun and, beyond that, could explain the arbitrary regional and eventually also the seasonal variations. What I would like to emphasis at this point is, that Kramer’s re-conceptualization of “direction” to “regional effects” implies an analytical gesture, a gesture of heuristic detachment of a key concept from an earlier explanatory framework (viz. sun-navigation).

**Step Two: Where is deep structure relevant?** My analysis of the epistemic schemes governing G. Kramer’s research works on orientation between 1946 and 1959 reveals that most of them followed the pattern of what might be called in his own words “Differentialdiagnose des Wichtigen”. From this sample must be excluded those papers which seem to have the character of a preliminary or supplementary study either within an intertextual context or in form of an autonomous paper. What Kramer once called “differential diagnosis” turned out to be an extraordinary important macro- and meso-structural principle of knowledge organization in his accounts and as such consists of two major procedures. That is in a first step an already confirmed proposition is extended by a wider range of potential causal factors, is applied to a wider scope of applicability or simply is read into unknown territory. The second step concentrates upon this wider field in as much as the wider range

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1778 Kramer did not fully drop the old term but de facto had to let it go. For the parallel usage of both concepts see Kramer et al., “Two-direction Experiments”, 47.


1780 In a paper published in 1957 Kramer at least re-approached Yeagley’s position in so far as he confirmed the starting point of the latter’s account: The regional differences H. L. Yeagley had interpreted as blind spots where avian navigation must fail due to the particularities of the magnetic field being virulent at these locations. See to this Kramer et al., “Two-direction Experiments”, 47. However, see also Kramer’s late rejection in Kramer, “Long-distance Orientation”, 360.
of data is made the object of a gradual reductive heuristic program which is finally aimed at carving out a more advanced answer to a problem that latter of which, in turn, can be fed or re-fed into the system as new and more advanced starting point. To put it in a nutshell one may say that the result Kramer’s studies generated between 1946 and 1954 / 1955 were the product of applying recursively this scheme of diagnosis – or “Prüfen”, as Kramer used to put it – without changing the heuristic program itself. The fact that G. Kramer and his associates had to note that true sun navigation could not be made evident in homing pigeons seemed to have a substantial effect upon the mechanism of this scheme in general and its “input-side” in particular. What formerly was meant to extend positively a proposition’s scope of applicability now turned out to be an extension that was meant to narrow down the range of possible explanations for the riddle of avian navigation. In one of his accounts G. Kramer used the significant expression of “coming closer the riddle” which can be read both in a sense of “coming closer the solution of the riddle” and “coming closer the riddle itself” while leaving it unsolved. While the optimism lying within the former of the two readings particularly applies to Kramer’s early postwar research on avian orientation, the more pessimistic reading may characterize his later research on true navigation. In other words, the heuristic program underlying the concept of “differential diagnosis” needed to be placed on new footings in as much as the “input-side” side of the model faced both a widening of perspective and a more rigid focussing upon single isolated parameters. On the phenomenological surface this move allowed G. Kramer to take into account a wider range of possible parameters governing the mechanisms of avian navigation and a more focused mode of testing these factors such as region, weather and distance. From G. Kramer’s own later accounts it can be inferred that the scattering of themes went hand in hand with an increasing independence of his co-workers and their projects. “Our experimental efforts”, Kramer writes in Recent Experiments on Bird Orientation (1959), “are proceeding along several adequate lines. Within a measurable time, it is hoped cross relations will be established between these different ways of approach. So far this has not been the case”. From the epistemological point of view, one may say that this shift mostly affected the tautological relations within the epistemic reference system just like the modes of knowledge organization the later Tinbergians applied in their PhD studies did not fully coincide with Niko’s understanding of an empirical ethological study. In case of G. Kramer’s intellectual life-history, particularly in the period after the Second World War, modifying tautologies in reference systems mostly affected the initial introductory sections of the research papers, that is, their method, the experimental setting, the research overviews or the choice of experimental animals and less the descriptions of the experiment themselves or the final conclusions. Just like the dualism implied in Kramer’s map-and-compass concept needed to be modified in as much as the map-constituent, that is, the act of position finding, needed to be put on alternative footings, the starting points of his diagnoses, too, required a funda-
mental re-conception. At least at this point the phenomenological transformation was coincident with epistemic variation. In the following I will first try to trace the beginnings of the epistemological shift that in my opinion shaped Kramer’s turn around 1956 and then provide some additional examples to demonstrate how the reconfiguration of initial tautologies may have led to another starting point of the research endeavour as a whole.

(1) From my phenomenological overview it can be inferred that the innovation achieved by G. Kramer and his workmates between 1946 and 1954 / 1955 was mostly due to a recursive application of one and the same heuristic scheme without altering the scheme itself. This can be called “phenomenological variability”. However, on closer inspection even then when the underlying reference systems remain unaltered the transformation of scientific concepts does not seem to be entirely random. The extension of key concepts, the extension of the range of used experimental animals, the refinement of the technical devices, the extension of the sun-azimuth orientation theory’s scope of applicability to other species of Bird and, finally, also the attempt to shift from sun orientation to sun navigation all have in common that they aim to exceed an already existing state of knowledge in order to find a more advanced solution of a problem within this unknown territory. In sum, we have therefore to do with a controlled modus of increasing positive knowledge. In contrast to the later years the input-side of this heuristic program consisted of whole positive hypotheses and less as isolated theorems.

(2) While examining the very early accounts of G. Kramer’s student years it became evident that his partly critical attitude expressed itself primarily in gestures of exclusion which were mainly placed at the beginning of his accounts. These aprioristic thematic exclusions seemed to disappear in favour of the before mentioned reference system as soon as he moved to the KWI for Medical Research. I presume it was there at the latest where G. Kramer adopted the medical concept of “differential diagnosis”. Yet my impression is, that in 1953 the old type of aprioristic exclusive opening gesture reappeared once again. After having proved sun-azimuth orientation he claimed that the theory was already confirmed sufficiently. Further arguments in favour of the idea need not be collected:

In dieser Besprechung wird nicht mehr diskutiert, ob Brieftauben (und Vögel überhaupt) über die Fähigkeit verfügen, primär, d.h. ohne Landschaftserfahrung, gerichtet heimzufliegen. Diese Fähigkeit wird als erwiesen vorausgesetzt. Besprochen wird vielmehr das Widerspruchsvolle, das in den folgenden Feststellungen enthalten ist.

[In this account it won’t be discussed any more, whether carrier pigeons (and Birds in general) have the ability, primarily, that is, without having collected landscape experiences, to fly home directly. This ability is presupposed as one that has been evinced. Rather the contradictory aspects shall be discussed which are included in the following statements.][transl. CL]

This gesture of ruling out something so decidedly reminds us of Kramer’s early accounts yet it remains positive in a sense that the entity which is ruled out refers to a positive achievement. Maybe, also Kramer’s attempt to rule out ultra short waves as potential physical clue alternative to sun orientation points already into the same direction due to the negative result of the study. However, in contrast to the aprior-

istic exclusions applied in the papers of the second half of the 1950s Kramer’s final
disprove of the effectiveness of radar waves is truly empirical and apart from this
fact had apparently no structural consequences.
(3) After the attempt to prove sun navigation turned out to be a dead end with a
clearly negative result the old scheme of recursively extending a scope of a theo-
rem’s applicability could not be maintained any more. A negative result, if it was
not to be ignored altogether, needed to be fed into the system. And my hypothesis
is that this happened not only (or even less) upon the level of phenomenological ex-
pressions but also and with more far-reaching consequences on the deep structure
level of scientific transformation. Furthermore, I think, the way that happened con-
sisted in a reacquisition of the criticism Kramer had applied in his student papers
albeit in a modified form – especially as to the causal architecture of the applied
epistemic frames and the occurrence of structural paradox. As I have already men-
tioned above this affected mostly the input-side of his diagnoses, that is, the starting
position and the initial decision “what is to be tested at all”. Kramer’s habit to widen
– one is inclined to say “radically” – his horizon on aspects not taken into account
so far while simultaneously focusing on single parameters of avian navigation most
likely is the most comprehensive expression of this “new” aprioristic criticism. To
put it in K. Lorenz’s words, since ca. 1956 Kramer placed a type of analytical ges-
ture at the beginning of his diagnoses Lorenz himself had used to call “Analyse in
breiter Front” and which did not fully coincide with the overall scheme of Kramer’s
diagnoses but, instead seemed to match J. B. Rhine’s postulate that a research ques-
tion can only be decided after exhaustive testing. However, the diagnosis as such
was certainly maintained as overall heuristic scheme. I will demonstrate a little fur-
ther down in my thesis how this modified model of diagnosis became manifest in
concrete expressions. For the time being, I am interested in the way how this tran-
sition from the old to the new model of diagnosis actually took place. The relevant
period of transition thereby seems to be the year 1956 and the publications that
appeared within this rather brief time span. Although I am not completely certain
yet, I’d like to mention the two forms of transition I see so far: (a) At first, I think,
Kramer operated skilfully with conceptual ambiguities. This becomes evident, for
example, in a paper that was published in 1956 under the title “Über Flüge von
Brieftauben über See” (“On Flights of Homing Pigeons over Open Sea”).\textsuperscript{1785} Since
D. R. Griffin’s paradigmatic accounts on pigeon homing the problem the birds had
to solve was to return from an artificially created distance to the home loft and this
transition from a state of far to low or no-distance used to coincide with another
unspoken convention: The birds returned \textit{from marked territory} – in case of both
D. R. Griffin’s and G. Kramer’s send up tests that means: \textit{From the mainland to
the coast}. In case of Griffin’s experiments this aspect can be explained very well
by his partial interest in the impact of landmark cues during homing. As to Kramer,
this aspect remains more mysterious since it was he who had wanted to rule out this
line of explanation from the very beginning of his involvement with orientation and

\textsuperscript{1785} See G. Kramer. “Über Flüge von Brieftauben über See”. In: F. Steininger, ed. \textit{Natur und Jagd in
Niedersachsen. Festschrift zum 70. Geburtstage von Herrn Museumsdirektor i.R. Dr. phil. Hugo
Weigold am 27. Mai 1956}. Hannover: Arbeitsgemeinschaft f. zoologische Heimatforschung in
Niedersachsen, 1956, 113–118.
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navigation. As a result one may speculate that – besides other practical aspects – it was also the epistemological implications of the experiments that commenced from homogeneous territory that prevented him to make this move earlier. In 1956, however, he did it, that is to say, as soon as the epistemic transformations allowing this move were on the way. At the very beginning of the paper Kramer writes:

Das Arbeiten mit Brieftauben auf hoher See ist das Ideal des Orientierungsforschers, weil er keine andere Umgebung findet, die physisch gleich neutral ist. Andererseits treten technische Schwierigkeiten auf, die zu überwinden erst dann geraten erscheint, wenn es sich zeigt, daß es anders gar nicht geht. Nach dem heutigen Stand der Dinge ist das zwar nicht der Fall; trotzdem habe ich einige sich bietende Gelegenheiten ausgenutzt, um aus eigener Anschauung zu einem Urteil über das Verhalten von Tauben über See zu gelangen. 

[The work with carrier pigeons on open seas is the ideal of the researcher who is concerned with the orientation problem because he does not find any other environment which is equally neutral. On the other hand, there are occurring technical difficulties which to solve is required only at a point when there is obviously no other alternative. According to our current state of knowledge this is not the case; Yet, nonetheless I have used some occasions that have come up in order to come to a conclusion concerning the behaviour of pigeons over open sea on basis of my own observations.] (transl. CL)

That Kramer describes release experiments on open seas as “ideal” can be read as an allusion to a more idealistic tradition of theorizing which is also implied in the notion of “Gestalt”. Both contexts have in common that they imply a reduction towards the essential, non-material and non-arbitrary. The exclusive model or reduction however does not fully coincide with Kramer’s model of diagnosis. In conclusion, one may say that as soon as the pigeons were released from homogeneous territory the inner epistemic logic of the entire homing experiment faced some kind of conceptual tension – a tension very similar to the one that lies within Kramer’s expression “dem Rätsel näherkommen” and eventually also the reconfigurations underlying his map-and-compass concept. As I will show below, it is Kramer’s move to transfer his homing experiments partly to the United States where the pigeon’s “homing” or “returning” *per definitionem* meant returning to a foreign place – at least from G. Kramer’s Wilhelmshaven perspective – which fulfils even more the scheme of a modified diagnosis. I add that one of the main motives to cooperated with J. G. Pratt was that in North and South Carolina the pigeons could be released from unmarked and homogeneous territory. My personal opinion is that G. Kramer was fully aware of these subtle epistemological implications. To sum up, one may say, that through the releases from homogeneous areas (over the North Sea or in North and South Carolina) the entire scientific paradigm of avian orientation attained an ambiguous nuance in so far as the basic problem (transition from far to no-distance) could lead to two different types of test namely release attempts from both marked and unmarked territory. This re-conception redefines the starting position of the diagnosis and not so much the realization of the experiment. (b) The second form of transition from the earlier to the later model of diagnosis is much more structural and refers to the question of knowledge organization. My analyses

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1786 Ibid., 113.
1787 For the fact that the send up attempts in the USA had the advantage that releases could be performed from homogeneous territory and this was possible from all four compass directions see fn. 1743, page 546 of my thesis.
of many if not all of Kramer’s scientific accounts revealed that he, as E. Stresemann emphasized, used to write up and present his results in a highly condensed and reflected way. This implied that each account was evolved systematically in a process of recursively applied differentiation over several levels – so to speak – from the root (i.e. the title, theme or core idea) to the periphery without neglecting the linear character of every written or spoken account. The idea of repeated bifurcation on various levels allows to determine precisely where, in which context and when epistemic interventions occur. Like it was the case with the Tinberians’ turn to Ecology it seems that turns of this kind commence with tiny modifications (eventually of the type I mentioned in 2) on lower levels before they break through to the roots and reach paradigmatic or semi-paradigmatic status. There is at least one text of G. Kramer’s which may be read as an expression of a transitional state in this structural process. *Weitere Erfahrungen über den “Wintereffekt” beim Heimfindevermögen der Brieftauben* was published in the year 1956 like the previously mentioned study. The relevant introductory section has no headline and is not numbered. It reads:


As we can see, the section as a whole consists of two paragraphs: Whereas the former of the two provides a review, the second gives as an outlook. The direction of the view (i.e. backward vs. forward) identifies the epistemic frame of each section by its causal level. To abbreviate my argumentation I suggest the following illustration which translates the propositions of each paragraph into a binominal scheme (Fig. 2.27). The comparison of the various different levels shows that on sentence and proposition level the scheme of the new model of diagnosis is applied already, while on paragraph level the old scheme is still intact just like as it is the case with the overall order. For instance, in the section I have named “Differences to early tests” the reference systems underlying the propositions are clearly end-

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1788 Kramer et al., *Weitere Erfahrungen*, 353.
Fig. 2.27

G. Kramer, *Weitere Erfahrungen über den "Wintereffekt" beim Heimfindevermögen der Brieftauben* (1957), Introductory Sections
tautological! This does not apply to the root level. I have interpreted this structural ambiguity as indicator for epistemic transition. (4) The next stage of epistemic transition then is marked exactly by the point when the new model of diagnosis frames not only subaltern sections of an account but, as it is the case with Kramer’s papers published after 1956, affect particularly those areas of the “Lineatur” which to alter would imply an intervention of paradigmatic meaning or importance. In order to demonstrate the formative effect of this intervention I’d like to mention some examples where I see possible correlations. As I have mentioned above the modifications mostly refer to the starting point of the release experiments.

(a) Next to Kramer’s release experiments from the North Sea which allowed to test the pigeons’ homing ability from entirely homogeneous and unmarked territory, I think, his cooperation with J. G. Pratt and the fact that further sent up tests were carried out in the United States can be also interpreted as an indicator that the epistemic foundations of the release experiments had changed. The basic structure of the experiments still remained the same: The pigeons were to solve a problem by translating artificially created distance into nearness to the loft. However, the preconditions of this type of experiment had altered after the Gleiberg experiments. While in former release experiments the pigeons were sent up from marked territory, G. Kramer and his collaborators now aimed to rule out the potential impact of landmark cues from the very onset. The releases in North and South Carolina alike to the sent up tests over the North Sea or from the Helgoland Island provided this opportunity but they were far less complicate to arrange and involved less negative side effects (e.g. like the disturbances that were caused by a rocking ship). In addition to that, if we have a look at the experimental setting from Kramer’s Wilhelmshaven perspective the idea of “homing” obtained necessarily another character since the birds’ home was not Wilhelmshaven but the lofts of Duke University. In other words, the target point of the pigeons’ journey was a well defined geographic location discrete from Wilhelmshaven. In sum, by transferring the release tests partly from Germany to the States the starting point of Kramer’s tests or diagnoses altered its deep structure. Or, if we would like to turn around the argument: The epistemic modification of the diagnosis model allowed another set of epistemic practices to become reality in the first place. I am inclined to favour the latter of the two perspectives.

(b) I have already demonstrated that the starting point of Kramer’s diagnoses altered in as much as he both widened the perspective for possible so far unknown parameters of orientation but, on the other hand, limited his actual analysis to isolated aspects. In this context, I have discussed G. Kramer’s studies of weather impacts, on direction or regional effect and his interest in short distances. It remains to add that in comparison to the former experiments which were aimed at testing the sun navigation hypothesis in later stages of the transformation we can find a multiplication of release places in general. That is to say, while the send up experiments related to the movement of the sun were highly fixed in time and space insofar as they were to be carried out only from one geographic location (Gleiberg near Gießen) and, even more significant, at a very restricted number of suitable days in the year, the later tests reveal a higher degree of variability in the chosen release sites.
This more of plasticity certainly must be understood in connection with Kramer’s interest in regional effects and his efforts to prove them by comparative release experiments from all compass directions and varying distances. Altogether, as to the release places, one may therefore eventually speak of a dualism between a common multiplication, on the one hand, and a deliberately comparative final experimental setting, on the other. A special variety of this new interpretation of release experiment was the so-called “two direction experiment” in which mixed samples from different lofts or different genetic stock were released simultaneously from one (or two) release sites so that they could choose either one or the other home loft. Again, I tend to argue that the epistemic shift provided the frame within which this new type of comparative experimental practice could be thought at all. The establishment of a new second loft in Freiburg in the fall of 1952 must be interpreted in this context since it provided the necessary preconditions to carry out two-direction experiments in Germany at all.1789

(c) Another aspect I’d like to mention next to the multiplication of places, times and samples in combination with a more comparative assessment of the homing results is a change in the way how the experimental animals were prepared for the tests. While in earlier experiments Kramer mostly used conditioned or trained animals, the release experiments of the late 1950s were performed with pigeons that were prepared by deprivation. In some remarks concerning the direction of future research on direction effects Kramer recommended:

Moreover the evidence indicates that further analysis should try to answer the following questions: – (a) What is the share of the release site? (b) What is the share of the loft site? (c) Are there differences in orientation facility depending on the direction of displacement, but independent of local effects as presumed under (a) and (b)? It will also be important to collect more evidence of variations as produced by large scale regional differences.1790

At least one of the raised questions, that is, (a) could only be answered by controlled deprivation experiments using closed aviaries. The second question seemed to demand more repeated releases under varying circumstances and successive exclusion of irrelevant parameters. Hence it suggested another type of deprivation test yet nonetheless a procedure of discrimination. And so does question three since Kramer asked for factors “independent” from the peculiarities of the specific locality. The usage of closed aviaries played a special role in Kramer’s understanding of controlled deprivation experiments since they allowed to control the visual field of the proband birds kept within the aviaries before they were released.1791 The later comparative assessment of the homing results delivered by samples that were treated differently in that way then allowed to determine those factors provided by the home that actually permitted the coming of the birds. It turned out that

1789 For the foundation of this loft see Kramer et al., “Two-direction Experiments”, 38. See also MPG-Archives, III. HA, Rep. 77, file 7, letter G. Kramer to O. Steidinger (14/08/1952) and ibid., file 14, letter G. Kramer to O. Benecke (29/11/1954).
pigeons that have been raised in aviaries below ground levels so that they could not see the horizon were not able to return successfully.\footnote{See MPG-Archives, III. HA, Rep. 77, file 15, letter G. Kramer to K. v. Frisch (07/11/1955).}

\footnote{See Kramer, “Experiments on Bird Orientation and Their Interpretation”, 196.}

\footnote{For Kramer’s claim to reassess the problematic of true sun navigation see Kramer, “Die Sonnenorientierung der Vögel [1952]”, 83. In this context, I’d like to direct my reader’s attention to a dispute Kramer sparked off with his colleague F. Sauer about the question who can claim originality over the discovery of sun-compass orientation. For me this dispute is not so much of interest because of Kramer’s claim for originality – in his view Sauer had described sun-azimuth orientation as congenial finding of both Kramer and Matthews – but the way he discusses retrospectively his own engagement with the problematic of true sun navigation. According to his account he was negative-critical from the very beginning. See MPG-Archives, III. HA, Rep. 77, file 19, letter G. Kramer to F. Sauer (02/09/1958), \textit{ibid.}, file 19, letter F. Sauer to G. Kramer (04/09/1958), \textit{ibid.}, file 19, letter F. Sauer to G. Kramer (16/09/1958), \textit{ibid.}, file 19, letter G. Kramer to F. Sauer (26/09/1958), \textit{ibid.}, file 19, letter F. Sauer to G. Kramer (06/11/1958), \textit{ibid.}, file 19, letter F. Sauer to G. Kramer (03/12/1958).}

(d) Next to the shifts that affected the form of the experimental setting there can be made evident some changes in those scientific practices that were related to the scientific discourse within the community of ornithologists. I think it is quite a significant information that G. Kramer communicated his rejection of true sun navigation in form of a scientific controversy with G. V. T. Matthews, his colleague from Cambridge University who had shared both the common interest and the basic methodological outline. Since it was Kramer himself who had tested sun navigation over several years it would have been also possible to convey his abandonment in more self-critical manners. This, however, would have established a stronger \textit{continuity} between his earlier and later research on navigation. Yet, my impression is that this is not how Kramer communicated his later doubts. Particularly in the introductory section of his paper \textit{Experiments on Bird Orientation and Their Interpretation} which was published in the British journal \textit{Ibis} in 1957 we can find a very pronounced criticism of Matthews’ theses. At the beginning of the paper it reads:

\begin{quote}
It was at this stage [the point when Kramer aimed to infer from sun orientation to sun navigation]\footnote{See MPG-Archives, III. HA, Rep. 77, file 15, letter G. Kramer to K. v. Frisch (07/11/1955).} that the present writer became acquainted with G. V. T. Matthews’ work on the subject of homing orientation. Since that time, work on pigeon orientation has been initiated in at least three other places besides Cambridge and Wilhelmshaven. Divergent views were formulated by Matthews, who conceived a special type of sun-navigation hypothesis, and other authors. It was only for a short time that sun navigation was retained as a likely possibility by the Wilhelmshaven team. Matthews’ special sun-arc hypothesis, in particular, is subject to criticism. It will be a primary purpose of this paper to explain the reasons, both factual and theoretical, for this critical attitude.\footnote{See Kramer, “Experiments on Bird Orientation and Their Interpretation”, 196.}
\end{quote}

Knowing the prehistory of Kramer’s criticism one may ask why he chose this and not that way of criticism. And this question is even more legitimate if we take into consideration that G. Kramer claimed to reassess the problematic in June 1952 at the latest and, beyond that, performed release experiments over at least three consecutive years together with several of his associates (1952–1954) – if we include K. Hoffmann’s experiments in Cambridge the time frame is even longer.\footnote{For Kramer’s claim to reassess the problematic of true sun navigation see Kramer, “Die Sonnenorientierung der Vögel [1952]”, 83. In this context, I’d like to direct my reader’s attention to a dispute Kramer sparked off with his colleague F. Sauer about the question who can claim originality over the discovery of sun-compass orientation. For me this dispute is not so much of interest because of Kramer’s claim for originality – in his view Sauer had described sun-azimuth orientation as congenial finding of both Kramer and Matthews – but the way he discusses retrospectively his own engagement with the problematic of true sun navigation. According to his account he was negative-critical from the very beginning. See MPG-Archives, III. HA, Rep. 77, file 19, letter G. Kramer to F. Sauer (02/09/1958), \textit{ibid.}, file 19, letter F. Sauer to G. Kramer (04/09/1958), \textit{ibid.}, file 19, letter F. Sauer to G. Kramer (16/09/1958), \textit{ibid.}, file 19, letter G. Kramer to F. Sauer (26/09/1958), \textit{ibid.}, file 19, letter F. Sauer to G. Kramer (06/11/1958), \textit{ibid.}, file 19, letter F. Sauer to G. Kramer (03/12/1958).}
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lier and his later research on avian navigation. Yet there is, I think another, more
deeper-lying argument. Redirecting the criticism was more compatible with the ex-
clusive analytical scheme which had begun to shape particularly the various aspects
communicated in the introductory sections of his papers since ca. 1956. And again
one may legitimately ask what was first, the hen or the egg. I cannot give a definite
answer to this question yet my impression is that Kramer’s criticism of Matthews’
theory is only one possible of several other forms how one particular paradigmatic
shift became manifest in concrete expressions. If we wanted to take the reverse
perspective, I think, it would be more fruitful to go back a few years and ask for
the psychological effect the experience of being unable to prove sun navigation
actually had on Kramer. I think it can be inferred from my analysis of Niko Tinber-
gen’s life course that one if not the crucial factor of his later turn to Behavioural
Ecology was the pressure that was exerted by the criticism younger generations
of ethologists including Niko’s own pupils directed against the holistic theorems of
the classical period. From this perspective, it cannot be excluded that obtaining neg-
ative results over several years might have had a similar impact upon a person that
was known for his hypersensitivity. A historiographical hypothesis like that would
lead to an approach which goes beyond mere epistemological phenomenology, for
instance, by bringing in a medical historical stance. Moreover, this approach would
require the existence of a considerable amount of archive sources and as long as
I do not see these holdings I need to leave open the question. What can be said
with certainty is that there occurred a paradigmatic shift in Kramer’s intellectual
life-history which coincided chronologically more or less obviously with the failed
Gleiberg experiments. Moreover, in some of the letters Kramer exchanged with
friends and colleagues we are informed that one or the other result was “difficult to
digest”.

e) A last aspect of Kramer’s late research on avian navigation which can be cor-
related with the structural transitions of the mid-1950s may be interpreted as a
reaction towards the steady increase of ornithological knowledge related to the
orientation problematic since the end of the 1940s. In a revealing passage in the
introductory sections of a later paper with the title “Recent Experiments on Bird
Orientation” (1959) it reads in the paper’s introduction:

A few years ago it was possible to give a critical review of recent work on bird orientation within
the limits of a lecture. Today this is impossible. I therefore shall not try to give a complete
picture of our present knowledge in this field. I shall rather concentrate upon what has recently
been achieved in the analysis of pigeon homing in Wilhelmshaven. In a final chapter I will try to
assign these studies their proper place in the framework of orientation research as a whole.1795

The quotation is more or less an explicit confirmation of the twofold shift the pre-
conditions of Kramer’s experimenting were subject of after 1956. The widening
of the perspective, in the quotation the extension of ornithological knowledge, re-
quired a more of exclusive reduction, in the quotation the restriction to the results
obtained by the Wilhelmshaven team. This double mechanism must be interpreted
as aprioristic setting before the tests could begin. Kramer’s modified understanding
of his diagnostic method thus can also be interpreted as his personal response to an

1795 Kramer, “Recent Experiments on Bird Orientation”, 399.
ever increasing scientific community and the huge amount of data it produced as a consequence.

To sum up my analysis of G. Kramer’s research on orientation and navigation, I would like to emphasize several aspects. At first, I thought it needed to be taken seriously that Kramer’s revived interest in ornithology began at a point in the transformation process of his scientific development when his neo-Darwinian convictions had already reached a state of consolidation and, as a consequence, the major epistemic shifts were already an issue of the past. It was therefore necessary to make a step back and begin with a more phenomenological survey of the transformations that can be observed on the surface of concrete expressions and their variation. In doing so, I was able to distinguish seven different developmental stages, namely: (1) the conceptual revitalization of the ornithological research on orientation and navigation in Germany, (2) G. Kramer’s seeking of the right experimental object and the discovery of migratory tendencies, (3) the methodological refinement and the application of conditioning which lead to the discovery of the so-called sun azimuth orientation, (4) the transfer of both methods and results to a “new” scientific object, the homing pigeon, (5) the failed attempt to exceed the theory of sun orientation by proving true biocoordinated sun navigation, (6) a succeeding double strategy of widening the perspective on so far discounted parameters and simultaneously testing isolated factors and, finally, (7) the conceptual reconfigurations preparing a solution to the problematic. In a second step, I have directed my attention towards the means of how these phenomenological shifts could be interpreted from a more abstract perspective. I doing so, I was able to evince a substantial dualism between an earlier and a later diagnostic scheme. Whereas the studies published between 1946 and 1955 consisted of exceeding an already confirmed state of knowledge in one or the other way, with the year of 1956 mainly the starting point of G. Kramer’s tests changed substantially: The setting of the “what” at the onset of the diagnoses was not, as it was the case in the years before, coincident with an overall hypothesis to be tested, verified or extended, but made subject of an initial reductive analysis in course of which a wider range of testable parameters was narrowed down to a few particulate ones. This encroachment of exclusive analytical gestures at the onset of Kramer’s studies apparently did not occur fully cataclysmically. Apriori exclusions can be made evident as early as 1954. The year 1956 marks a period of transition until finally, since ca. 1957, the new diagnostic model pervaded into quite a variety of concrete expressions ranging from the redefinition of the experimental setting to the modes of scientific discourse and Kramer’s own reflections concerning the development of his scientific discipline. If the phenomenological shifts are compared with the transformations I was able to evince on deep structure level we can see immediately that there exists no one-to-one correlation. There are phases in which one and the same reference systems find themselves expressed in manifold phenomenological variations. This applies to the period before and after the turn. Conversely, the years 1955 and 1956 seem to mark a period of epistemological transition in G. Kramer’s intellectual life-history during which central themes faced substantial reconfigurations and a more of punctuated epistemic variability. Before and after
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this period of transition the epistemic foundations of Kramer’s reasoning on avian orientation and navigation seemed to remain fairly stable.


E. Stresemann underlined in his obituary that G. Kramer’s research was strictly divided in two separate areas. With a view upon the decade after the war Stresemann’s observation applies very well. As we have already seen, there was certainly a rather strong interest in the mechanisms of avian orientation and, since 1952, in more advanced faculties of navigation, too. This line of research had its own dynamics – both on the phenomenological surface and the more conservative strata of scientific change. In particular, the years after the failure of the Gleiberg experiments led to a modified model of diagnosis which differed from previous conceptions insofar as its onset turned out to be both wider and more focused.

On the other hand, however, G. Kramer dedicated a considerable amount of his engagement to the study of allometry, that is, the examination of changing body proportions in onto- and phylogeny of living organisms. Kramer’s interest in “allometry” had had its origin in his comparative systematics of various Italian Lizard populations, in other words, in studies he had carried out during his stays in Rovigno and Naples. We remember, after the characters typically used in classical taxonomic studies turned out to be not enough distinctive to be used in micro-systematic studies, G. Kramer had opened his mind and for the following series of particulate research papers switched into another epistemic mode: Most of these studies had a preliminary investigative character since their main purpose was to raise and evaluate those morphological criteria which seemed to be appropriate for Kramer’s micro-systematic research program. The comparative study of body proportions was an essential constituent in Kramer’s repertoire but it was only one of several other analytical criteria guiding both the assessment of the data and Kramer’s written argumentation. The ambivalent outcome of these preparatory studies as to the taxonomic usefulness of relative growth is most likely the reason why Kramer pushed his micro-systematic approach to relative growth somewhat into the background in the immediate post-par period. Around 1951 we can observe a move in Kramer’s study of allometries: For the first time he not only compared different species but also various different ontogenetic stages of one and the same species. The ontogenetic study of body proportions from now on turned out to be a major characteristic of all further allometric research. Where inter-specific comparisons occurred in his papers, Kramer mostly used allometric series of ontogenetic growth as objects of comparisons and therefore combined intra- with interspecific research of allometries. As to the chronology of the events one may say that Kramer’s interest in allometry turned into a more or less independent research program since ca. 1951 (1954 at the latest). From this perspective it is legitimate to speak of a “heuristic reduction” in course of which one particular criterion of evolutionary study turned out to be a primary focus. On the other hand, however, Kramer – eventually also for pragmatic reasons – gave up partly his specific commitment to the Lizards, the species of animal which had served as the primary scientific object in most of his micro-systematic studies so far. Contrary to the fixation to one single animal species, Kramer’s postwar research on allometric growth was based
on various different species belonging to various classes such as Birds (Gulls), Fish (Dogfish, Cod), reptiles (Crocodiles and Caimans), and even mammals (Whalebone Whales). The twofold “logic” of both reducing the topic and widening the scope of adequate objects might be read as a first indicator that Kramer’s research of allometric growth operated with a heuristic program complementary to the diagnostic scheme he used to apply in his studies on orientation and navigation. All these preliminary observations lead to the question whether and, if so, in how far the realm of Kramer’s allometry research was also subject to transformation and, beyond that, whether this transformation can be correlated in any way to the dynamics I was able to make evident in the complementary realm (i.e. the study of orientation and navigation). Having a first glance at Kramer’s papers on allometric growth it stands out that since around 1958 there is no particular emphasis on one particular scientific object. Statements from now on were placed on a more abstract level, formulated in more general terms and references to data were treated in a more comparative fashion. Whether Kramer’s second realm was facing a “turn” simultaneous to the one I have made evident in his research on avian navigation and, if so, how it became manifest, must be examined with utmost caution. I therefore suggest once more to begin with a more phenomenology oriented survey of the transformation process that characterized Kramer’s allometry studies and ask in a second step for possible epistemological correlates of these shifts. Altogether I see at least six different stages in G. Kramer’s research on changing body proportion.

**Step One: Phenomenology**

1. The first of these stages I have already mentioned. It is marked by the date 1951, that is, the point of time Kramer for the first time realized the relevance of individual growth rates and thus introduced a new perspective which integrated both ontogenetic and phylogenetic development.

2. The second step might be called the formal beginning of Kramer’s engagement with allometry. It dates to the years 1954 / 1953 when he published two studies bearing the titles “Über Wachstum und Entwicklung der Vögel” (“On Growth and Development in Birds”) and “Über relatives Wachstum bei Bartenwalen” (“On relative Growth in Whalebone Whales”).

   The former of the two papers is a shortened version of a presentation Kramer had delivered on the 66th annual conference of the German Ornithological Society in Freiburg. It is divided in two parts one of which provided a general literature-based introduction, while the second section entered into the details of relative growth in bird skeletons. This part is based on Kramer’s own measurements. Kramer in principle distinguished the animal class of Birds in nest escaper (i.e. nidifugous birds) and nest cower (i.e. nidicolous birds). Both forms of development – Kramer argued the former of the two was the more original form of development shared by Reptiles – can be correlated with different growth processes: While proportional analyses of nest escaper revealed more or less linear development, that is, the body proportions remain more or less unaltered, ontogenetic growth in nidicolous birds turned out to be more asymmetric.
and partly hypertrophic. Particularly the examination of the extremities in nest cowers showed the advanced growth of the legs in earlier stages of development, whereas the forelimbs began to growth above average only later. Kramer interpreted the peculiarities of growth in nidicolous birds as functional ontogenetic adjustment to specific developmental needs. For instance, the growth curve of the domestic pigeon’s skeleton relative to the overall weight revealed a pit shortly before the hatching date which Kramer explained with the limitation of space within the egg. The cuckoo’s hind limbs show accelerated growth in early ontogeny and Kramer thought this could be explained by the bird’s habit to kick the host bird’s offspring out of the nest. In sum, one may say that Kramer, on this early stage of his reasoning on relative growth, interpreted ontogenetic allometries as species-specific adaptations to selective pressures. Ontogenetic allometries thus could be used as taxonomic characteristic. Conversely, relative growth turned out to be a field where phylogenetic development on basis of heritable mutability and selective pressures affected the development of the individual organism. “Über relatives Wachstum bei Bartenwalen” is not based on own empirical measurements but reinterprets the data drawn from research that was carried out before by J. F. G. Wheeler and N. A. Mackintosh. Both scholars had made the Whalebone Whales subject of an allometric study: They measured the size of the head over several growth phases, related the data to the growth of the overall body size and came to the conclusion that the head of Whalebone Whales in contrast to other vertebrates becomes relatively bigger, whereas the tail proportionally shortens. The neo-Darwinian J. S. Huxley picked up the thread and brought “the same figures into another shape”, as Kramer put it. Huxley’s result was that the growth coefficient of the head of animals sized between 17–26m was at least 1.55, while the growth rate during the embryonic stage was nearly isometric, that is, the growth coefficient (\(\alpha\) in Huxley’s formula) was approximately 1.0. G. Kramer adopted both Huxley’s habit to differentiate more carefully different ontogenetic stages and the practice to reinterpret already existing data from another theoretical angle. In doing so he considered it more appropriate to correlate the relative sizes of the whales’ heads not with the

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1799 See ibid., 194, 195.
1800 See ibid., 196–198.
1801 See ibid., 198.
1802 See ibid., 198–199.
1803 Kramer’s reception of N. A. Mackintosh’s work was accompanied by a correspondence including some additional information concerning relative growth in whales. Especially the later letters in the correspondence show that Kramer was particularly interested in the data drawn from foetuses and young whales. See MPG-Archives, III. HA, Rep. 77, file 6, letter G. Kramer to N. A. Mackintosh (19/03/1952), ibid., file 6, letter N. A. Mackintosh to G. Kramer (26/03/1952), ibid., file 6, letter G. Kramer to N. A. Mackintosh (08/04/1952), ibid., file 6, letter G. Kramer to N. A. Mackintosh (21/04/1952), ibid., file 6, letter N. A. Mackintosh to G. Kramer (21/05/1952), ibid., file 6, letter G. Kramer to N. A. Mackintosh (24/05/1952), ibid., file 7, letter G. Kramer to N. A. Mackintosh (11/08/1952), ibid., file 7, letter N. A. Mackintosh to G. Kramer (26/09/1952), ibid., file 7, letter N. A. Mackintosh to G. Kramer (09/10/1952), ibid., file 7, letter N. A. Mackintosh to G. Kramer (28/10/1952), ibid., file 7, letter G. Kramer to N. A. Mackintosh (07/11/1952), ibid., file 7, letter G. Kramer to N. A. Mackintosh (15/04/1953) and ibid., file 7, letter N. A. Mackintosh to G. Kramer (23/04/1953).
overall size of the animals but the length of the torso alone, that is, the overall length minus the length of the head. “Die Verarbeitung der Daten”, Kramer underlines, unterscheidet sich von den früheren Darstellungen hauptsächlich dadurch, daß das Kopfmaß nicht auf die Gesamtlänge, sondern auf die Körperlänge ohne Kopf bezogen wurde.

[The processing of the data differs from previous accounts mainly in that the measure of the head has not been related to the overall size but instead to the length of the body without the head.] (transl. CL) 1805

In addition to that, Kramer’s way of presenting his results graphically seemed to deviate partly from the practices applied by other authors in so far as he both filled gaps through “freie Interpolation” (“free interpolation”) and approximated the singular values to a more or less hypothetical non-disruptive but smoothly curved graph. “In den Strang der Einzelwerte des Kopfwachstums (Abb. 1)”, Kramer writes in a concluding methodological remark,

wurde eine geschwungene Kurve, nicht eine “gebrochene Grade” eingepaßt. Es gibt kaum einen Fall, in welchem die Orte, an welche man Bruchstellen von Geraden verlegt, nicht der Willkür unterworfen wären. Zudem ist in der Zerlegung der Kurve in gerade Teilstücke das Postulat enthalten, daß in jedem Teilabschnitt das Wachstum nach Art eines selbstmultiplikativen Prozesses verläuft. Reeve und Huxley haben aber gezeigt, daß dieses Postulat gar nicht erhoben werden kann. Es besteht keine Schwierigkeit für die Annahme, daß die relative Wachstumsgeschwindigkeit eines Organs in ebenso gerundeter Weise ab- und zunimmt, wie die Zeichenfeder dem Pfad der Einzelwerte folgt.

[Into the linear sample of the singular values it has been fit in a curved graph and not a “fractured curve”. There is hardly any case in which the locations at which the gaps of a curve are placed are not subject to arbitrariness. Furthermore, disassembling the curve in straight linear sections contains the postulate that in every part the growth proceeds alike to a self-multiplicative development. Yet Reeve and Huxley have shown that this claim cannot be maintained. There is no difficulty in presuming that the relative speed of an organ’s growth decreases and increases in the same rounded manner the drawing pen follows the path of the singular values.] (transl. CL) 1806

This quotation suggests that Kramer’s way of presenting his results graphically implied a process of approximation and rounding, that is, in the last consequence of reducing complexity and, beyond that, it seems to indicate Kramer’s believe that growth processes actually occurred that way. In other words, the graphical ways with which he represented his results indicate that he interpreted his findings as real abstractions just like any other natural law and less as “mathematical model” or anything like that. The results were threefold: At first, Kramer’s replacement of the reference quantity showed that the growth rate of the Whalebone Whale’s head during embryology was not only isometric as Huxley had claimed it turned out to be even negative allometric, that is to say, the head grows slower than the rest of the body. Nearing the end and after the embryonic phase the growth coefficient increases and approaches isometric growth. Second, according to Kramer’s account, the forelimbs grow stronger than the rest of the body. Huxley, by contrast had suggested isometric growth. Finally, as to the hind limbs, Kramer confirmed Huxley’s results suggesting positive allometric growth. Altogether, one may say, Kramer’s reassessment of J. F. G. Wheeler’s and N. A. Mackintosh’s data contrary

1806 Ibid., 64.}
to Huxley’s calculations showed a less than isometric growth of the head during embryology, whereas the forelimbs turned out to grow faster than Huxley had claimed before. Kramer’s calculations thus, at least to a certain extent, challenged Huxley’s formula of allometric growth because they showed that the growth rates of single organs were less uniform than Huxley’s general abstraction might have suggested or was able to represent. However, it is important to keep in mind that G. Kramer – at this point of his reasoning on allometric growth – did not question J. Huxley’s formula. Instead he defended Huxley’s abstraction by claiming that it provided valuable approximation over longer periods and, beyond that, a solid quantitative basis in those cases where the relative speed of growth oscillates a lot. “Es kann gefragt werden”, Kramer asks,


[It can be asked what sense does it make to maintain Huxley’s allometry formula and the corresponding method of double logarithmically plotting the data. Concerning this matter it can be said at first that the formula delivers valuable approximations in many cases of relative growth processing over longer time spans. Second, even in those cases where the relative speed of growth goes up and down permanently such as the head of the whale or the extremities of the bird (Kramer 1953), the method of representing the data that has been applied so far provides a solid methodological basis to be able to formulate quantitatively and compare at all. If numbers for $\alpha$ are to be obtained tangents can be plotted. This is inaccurate but still more precise than fitting in straight lines which will always generate an annihilation of differences in curves such as the one in Fig. 1. – The success of Huxley’s method is based upon the fact that its practical value holds independently from any growth theoretical meaning.] (transl. CL)

In sum, one may eventually say that Kramer’s engagement with relative growth from the very beginning involved a certain potential of criticism that could possibly be directed against neo-Darwinian theorizing, in this case J. Huxley’s attempt to reduce quantitatively the complexity of relative growth. Kramer’s results showed the limits of Huxley’s abstraction by proving that the relative speed of organic growth, if the periods of ontogenetic growth were distinguished more carefully, fluctuated more than Huxley’s method allowed to represent adequately particularly when the relative growth coefficient, $\alpha$ in Huxley’s formula or the increment of the growth curves correspondingly, was kept constant at all costs, for instance by filling gaps with straight lines. Consequently Kramer did not rate highly the overall bearing of a growth curve which he, instead, interpreted as the product of several antagonistic particulate forces. See to this MPG-Archives, III. HA, Rep. 77, file 6, letter G. Kramer to L. M. Klauber (27/12/1951).
ing and presenting the data. The usage of approximative quantitative methods such as rounding or plotting tangents etc. can be interpreted as means to maintain the quantitative framework beyond obvious limitations. Altogether one may therefore say that Kramer’s reassessment of relative growth in Whalebone Whales led towards a potential theoretical criticism of Huxley’s abstraction which to defend, in the last consequence and to a certain extent paradoxically, implied its strengthening. This strengthening was achieved by a reinterpretation of the quantitative-reductive framework by adjusting it concretely to the modified needs, that is, the representation of more complex and varying data. Altogether one may therefore say that Kramer was mainly interested in deviating data yet simultaneously was capable to frame or re-frame it in the neo-Darwinian reference system applied to phenomena of relative growth.

(3) The following period or phase of G. Kramer’s engagement with relative growth seems to continue the general tenor of the previous stage: G. Kramer directed his focus even more than before upon details which seemingly challenged J. Huxley’s theoretical foundations of the quantitative study of relative growth. In this context, I’d like to mention two studies of Kramer’s in which he restricted his attention on one single particular scientific object each yet, in doing so, intended to obtain a more or less complete or extended picture of as many different series of allometric growth as possible.\(^{1809}\) This particular focus necessarily raised the question of the relationship between the parts and the whole in matters of allometric growth. That is to say, Kramer’s attempt to reconstruct the growth processes of many part organs in one and the same species of organism provided the bases for comparing growth and transformation processes of these parts (inter se) and between the parts and the entire organism. The scientific objects Kramer had chosen for this research endeavour were the Dog Fish and the Cod both of which were belonging to the animal class of Fish so that they could be expected to be available in the North Sea around Wilhelmshaven.\(^{1810}\) Especially the paper on Dog Fish which G. Kramer published together with L. Dinnendahl in the *Pubblicazioni della Stazione Zoologica di Napoli* reveals a differentiation between the parts and the whole: Its main theme is the mechanisms of visual accommodation in the Dog Fish’s eye and the effect of allometric growth upon this mechanism.\(^{1811}\) In contrast to mammals whose visual accommodation is mainly an effect of the eye’s lens and its relative thickness, a Dog Fish eye’s focusing is determined by the size of the bulb in combination with the lens which is a comparatively more static organ.\(^{1812}\) Kramer was interested in those organic constituents which are involved in the mechanism of visual accommodation. In doing so, he at first examined those tendencies of allometric growth

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\(^{1809}\) For a parallel of this practice in neo-Darwinian systematics see also Stresemann, *Die Entwicklung der Ornithologie*, 282.


\(^{1811}\) For the interest in structural changes during ontogenetic growth see ibid., 28.

\(^{1812}\) Ibid., 32.
that affected the eye as whole. For instance, he found out that the lens of the Dog Fish’s eye grows relatively slower during ontogeny than the overall volume of the eye. \footnote{See ibid., 28.} In addition to that, Dinnendahl and Kramer made evident a second general tendency of growth: The shape of the eyelen more and more approached the form of a perfectly round ball whereby the bulb, too, turned out to grow slower than the fish as a whole. \footnote{Ibid. For the negative allometric growth of the bulb see ibid., 28–29.} Both tendencies together, that is, the negative allometric growth of the lens and the negative allometric growth of the eyeball, Kramer argues, are working into the same direction in as much as they increase the eye’s refraction. “Beide Tendenzen – die des schwachen disproportionalen Zurückbleibens des Linsenvolumens und deren zunehmende Annäherung an die Kugelform – mögen zusammenhängen”, Kramer summarizes and continues:

> Sie bewirken dioptrisch dasselbe, nämlich die Zunahme der relativen Refraktion. Unter relativer Fraktion verstehen wir die maximale Brechkraft des Auges bezogen auf die absolute Grösse des Bulbus, ganz unabhängig davon, ob das Auge sich dabei in Akkomodationsruhe oder in maximaler Akkomodation befindet. 

[Both tendencies – the one of the slightly disproportional lagging behind of the lens volume and its increasingly approximation of the shape of a ball – may be connected with each other. Dioptrically they have the same effect namely an increase of the relative refraction. By relative refraction we understand the maximal refractive power of an eye correlated with the absolute size of the bulb, quite independent from whether the eye’s accommodation is at rest or at its maximum.][transl. CL] \footnote{Ibid., 28.}

If both organ constituents grew more or less isometrically (or in accordance with a strictly geometric growth rate), Kramer continued, this would have the effect that the depth of the Dog Fish’s visual field became larger than favourable. \footnote{Ibid.} The negative allometric growth of lens and bulb by contrast increases the refractive power of the Dog Fish’s eye so that the negative effect that is to be expected in case symmetric growth processes can be somewhat diminished. In sum, the Dog Fish’s visual apparatus as a whole therefore turned out to be subject to mostly negative allometric growth tendencies and this seemed to have a favourable effect. In a second step, Kramer and his co-worker, L. Dinnendahl, went into details. They picked out one single part of the visual apparatus, namely the eye’s retina, which they made the object of a thorough histological analysis. \footnote{Ibid.} That means they differentiated six tissue layers of the retina and asked for each of them separately how the constitution of this layer changed during ontogenetic growth. \footnote{For the following see ibid., 29–32.} The overall result of this examination was that the retina became thinner up to a certain age but also that this process affects each layer in quite a different manner. Thus Dinnendahl and Kramer found out that the relative size of those parts lying outside of the so-called Membrana limitans externa (“Aussenglieder und Ellipsoide”) increased and that

\footnote{These layers were the outer constituents of the layer of rods (“Stäbchen-Aussenglieder”), the inner constituents (“Innenglieder”), the outer granular layer (“äussere Körnerschicht”), the outer reticular layer and the Henle fibre layer (“äussere reticoläre und Henle’sche Faserschicht”), the inner granular layer (“innere Körnerschicht”) and, finally, the inner reticular layer including the ganglion cells (“innere retikuläre Schicht und Ganglienzellen”).}
new rod cells are built but that no new granular cells were built on the outer granular layer. The thickness of the outer granular layer remains more or less constant but the outer reticular layer and the Henle fibre layer becomes relatively thicker. The inner granular layer turned out to become thinner during ontogenetic growth and the relative amount of ganglion cells seemingly decreases, too. In sum, Dinnendahl and Kramer concluded that it was not legitimate to deduce the masses of the constituents of the retina from its overall size but that the ontogenetic growth processes of the retina corresponded more or less with the transitions that can be observed if small species are compared with big ones. Once more the growth processes turned out to be more complicate if single constituents of an organ were taken into account separately. Even negative allometric growth turned out to be a common option of organic growth. “Maschlanka hat schon darauf aufmerksam gemacht”, Dinnendahl and Kramer finally conclude in their paper,

dass auch in der übrigen Entwicklung der Proportionen, besonders derer des Gehirns, manches passiert, was nicht einfach als Weiterwachsen angesprochen werden kann.

[Maschlanka has already drawn our attention to the fact that also in the remaining development of the proportions, especially the one of the brain, there are many aspects that cannot be simply addressed as accrescence [literally: “further growing”]]\textsuperscript{1819} (transl. CL)\textsuperscript{1820}

All that seemed to restrict the scope of applicability of Huxley’s formula to the parts and constituents of an organ whereby its validity remained intact quite independent from the direction of the respective growth process. The heuristic procedure which G. Kramer and his coauthor, G. Huhn, applied in their joint paper on body proportions in Codfish resembles very much the program applied in the previously discussed account. Alike to the study of the Dog Fish’s eye the authors focused on one single animal species in their paper but in doing so intended to obtain a complete picture that included series of growth of as many organs and organ systems as possible. Selective reduction to one scientific object thus was combined with extensive widening as to the methodological approach in one heuristic reference system. In the paper’s introduction it reads:

Der Zweck der hier vorgelegten Messungen war, einen Überblick über das differenzielle Wachstum von möglichst vielseitig gewählten Organen und Organsystemen einer Fischart zu ermöglichen.

[The purpose of the measurements presented here was to make possible an overview of the differential growth in organs and organ systems which belong to one single species but have been chosen as variously as possible.]\textsuperscript{[transl. CL]}\textsuperscript{1821}

The introductory sections of the paper also inform the reader about the reasons why Kramer and Huhn have chosen a species of fish as scientific object:\textsuperscript{1822} Fish in general and the Codfish in particular reach advanced stages of growth already at a very early stage of ontogenetic development. Moreover, Kramer and Huhn argue that the equilibrium which is established between the body’s weight and the weight of the fluid medium “water” is both the simpler and the more original form of life.

\textsuperscript{1819} Kramer et al., “Über Änderungen im Aufbau der Augen”, 33.
\textsuperscript{1820} Ibid.
\textsuperscript{1821} Kramer et al., “Über Proportionsänderungen”, 1.
\textsuperscript{1822} Ibid.
As to the applied method one may say that Kramer and Huhn preferred to plot the results of their measurements in a graphical manner just like in all previous and all later papers being concerned with matters of relative growth. In the section of the paper which is dedicated to methodology both authors write:

Die Huxleysche Allometrieformel \( y = b \cdot x^\alpha \) approximiert in den meisten Fällen das gegenseitige Verhältnis zweier zu vergleichender Wachstumsgeschwindigkeiten gut. Dabei soll nur Gebrauch gemacht werden von der hinreichenden rein formalen Koinzidenz der mathematischen Darstellung und der natürlichen Verhältnisse. Mit Rücksicht auf die Verwendung des Exponenten \( \alpha \) als bündigen Ausdrucks der relativen Wachstumsgeschwindigkeit eines Körperteils werden auch die graphischen Darstellungen in doppelt logarithmischer Form gegeben, auch dann, wenn die lineare Darstellungsweise eine annähernd geradlinige Progression ergäbe. Im doppelt logarithmischen Diagramm ergibt der Tangens des Anstiegswinkels der Ausgleichgeraden ohne weiteres \( \alpha \).

(Huxley’s allometry formula \( y = b \cdot x^\alpha \) approximates well the mutual relationship of two growth rates which are to be compared. Thereby I should like to make use only of the sufficiently pure coincidence of the mathematical representation and the natural circumstances. As to the use of the exponent \( \alpha \) as an adequate expression of the relative speed of growth of a body part also the graphical representations will be given in double logarithmic form, even when the linear way of plotting would lead to an approximatively linear progression. In the double logarithmic diagram the tangent of the angle of gradient of the balanced straight line provides \( \alpha \) easily.) -- (transl. CL)

Kramer’s method of presenting his results remains widely unaltered in most of his allometric studies. It is graphical in the first place and consists of plotting the measured values of relative growth in a two-dimensional system of coordinates whereby the basic entity of both the x- and the y-axis is following a non-linear but logarithmic progression. This is most likely meant when Kramer speaks of “double logarithmic” plotting.\(^{1824}\) The gradient of the (straight) line which is fitted in approximatively in-between the singular values thereby represents the speed of the growth process. If the angle of gradient is exactly 45° the growth rate is “isometric” that is both organs or body parts grow equally fast during ontogeny. If the angle is steeper growth is “positive allometric”, if lower it’s “negative allometric”. From my epistemological investigative perspective it is important to note that Kramer’s way of plotting his results was aimed at reducing complexity via quantification – the many is reduced to the one (the relative growth coefficient). The double-logarithmic plotting thus allowed to maintain this overtone in seemingly deviating and even more complex cases (at least if the organ systems were treated in a particulate manner). In one of the passages I have quoted above Kramer and Huhn describe the range of body parts they have made the object of their measurements in terms of

\(^{1823}\) Ibid., 2. For Kramer’s method see also Kramer, “Über Wachstum und Entwicklung der Vögel”, 196–197 and Kramer, “Über relatives Wachstum bei Bartwalen”, 58, fn. 2. In the latter paper we find the logarithmic expression of Huxley’s formula: \( \log y = \log b + \alpha \cdot \log x \). The growth coefficient appears as \( \alpha \) in this formula. “\( b \)” stands for the initial growth (“Anfangsgröße”) of an organ. See also the terminological convention suggested by J. S. Huxley’s and G. Teissier’s in their joint paper J. S. Huxley et al. “Terminology of Relative Growth”. In: Nature 137.3471 (1936), 780–781.

\(^{1824}\) In a later letter Kramer himself explains the advantages (independence of absolute values) of his method. See MPG-Archives, III. HA, Rep. 77, file 18, letter G. Kramer to H. Wermuth (05/02/1958).
“möglichst vielseitig gewählten Organen und Organsystemen”. On closer inspection this phrase can be taken quite literally. Thus the paper includes the results of measurements of altogether five areas of the Codfish body, namely the size and the form of the head, the brains, the eyes, the inner organs and, finally the fins.\textsuperscript{1825} It can be easily seen that Kramer and his coauthor while presenting their results proceed from the centre (the head and its inner organs) to the periphery (the fins) of the Cod’s body. As I will discuss below this way of knowledge organization is a significant indicator for the epistemic patterns in the background. For the time being, I’d like to mention briefly the results of Kramer’s and Huhn’s measurements and ask what conclusions both authors have drawn from their results. Thus Kramer and Huhn found out that the overall body form of the mature Cod remains more or less constant. This means if the overall length (i.e. the cube of it) was plotted against the overall weight the obtained curves showed isometric growth.\textsuperscript{1826} As to the size and the shape of the head the measurements of Huhn and Kramer suggest that the head after all grows isometrically but that the mouth develops negative allometrically, while simultaneously the development of the back parts of the head shows a positive growth rate.\textsuperscript{1827} The weight of the Cod’s brain as a whole which Kramer and Huhn had assessed by applying a uniform method of conservation and measurement showed a slightly negative growth rate ($\alpha = 0.44$) after it had been plotted against the overall size of the body.\textsuperscript{1828} With a view upon single parts of the brain the picture was less uniform. While the so-called Tectum opticum and eventually also the Cerebellum grows negative allometrically, the Lobi inferiories revealed a constant growth rate.\textsuperscript{1829} Kramer and Huhn concluded that the more central parts of the brain grow relatively slower than the lower parts. The lower parts apparently grow faster but still slower than the overall body. The values for the weight of the eye scattered heavily and their graphical representation was leading to a curve with a much higher gradient than the one of the overall brain size (growth rate = 0.72).\textsuperscript{1830} However, as soon as Kramer and Huhn focused upon the retina alone the obtained values once more revealed another picture since a Cod’s retina grows as fast as the size of the brain (which revealed a lower growth rate). The examination of the inner organs yielded equally differentiated results.\textsuperscript{1831} The proportion of the weight of guts (sexual organs excluded) and the overall length of the body turned out to be constant quite independent of the Codfish’s age just as A. Bückmann, one of G. Kramer’s colleagues at the Max-Planck Institute for Marine Biology had already claimed before.\textsuperscript{1832} However, some of the inner organs seemed to grow faster, while others developed with lower growth rates than the average. The growth curve of other organs like the heart coincided 1:1 with the curve of the overall body weight. At this point Kramer and his coauthor confirmed

\textsuperscript{1825} Each body part is treated in one separate chapter. See to this Kramer et al., “Über Proportionsänderungen”, 3–4, 4–6, 6, 6–8 and 8 respectively.
\textsuperscript{1826} Ibid., 2–3.
\textsuperscript{1827} Ibid., 3–4.
\textsuperscript{1828} Ibid., 4–5.
\textsuperscript{1829} Ibid., 5–6.
\textsuperscript{1830} Ibid., 6.
\textsuperscript{1831} Ibid., 7–8.
\textsuperscript{1832} Ibid., 7.
Gustav Kramer (1910–1959)

a thesis which had been put forward by R. Hesse, Kramer’s teacher and advisor of his dissertation thesis. The area of the fins has been plotted against the square of the overall body length: The result was that both the pectoral and the caudal fin grow isometrically. In sum, one may say that G. Kramer’s and G. Huhn’s study on body proportions in Codfish confirmed the overall tenor of the previously discussed dogfish paper: The series of allometric growth that can be made evident in whole organs or organ system need not be identical or coincide with the ones of the constituents. Parts and whole can be subject to qualitatively different partly divergent ontogenetic development. And although G. Kramer does not draw explicitly theoretical conclusions in Über Proportionsänderungen im Laufe des Wachstums nach Eintritt der Geschlechtsreife beim Dorsch we can get the impression that his approach implied a more of differentiation. This more of qualitative differentiation, in turn, can eventually be read as a partly critical gesture against the neo-Darwinian attempt to reduce the complexities of organic growth by mere quantification. The validity of Huxley’s abstraction is implicitly limited to parts and part constituents. Conversely the question could be raised how the intertwining of each single growth process could be grasped – the entire system of organic growth. (4) The following stage of G. Kramer’s reasoning on relative growth is characterized by the fact that he treated the phenomena of allometry not only in terms of mere “variability”. Especially in the papers published in 1955 and later we can find also a more explicit reflection of the question of causation. Thereby we eventually have to distinguish more carefully. My impression is that in and around the year 1955, that is to say, in contrast to later phases, G. Kramer’s view upon allometric growth was more like the one of a pure adaptionist in so far as he both used to underline the functional character of the phenomena in question and tended to put emphasis upon the aspect of convergent evolution. The negative growth of the Whalebone Whale’s head during embryology and early youth was adaptive because it supported the sucking behaviour of the young. The isometric or even positive allometric growth of the Cod’s head which seemed to break the general principle that the growth rate of the head size in vertebrates is negative, in Kramer’s view turned out to be adaptive because within the medium “water” the rules of gravity do not hold as they do with creatures living under areal conditions. The increase of refractive power in dogfish during ontogeny has been discussed in functional terms because reducing the depth of the visual field seemed to be of ad-

1833 Ibid., 8.
1834 Ibid.
1835 In a report covering the research work done between 1 April 1952 and 31 March 1953 Kramer writes: “Die Studien über relatives Wachstum sind noch im deskriptiv-vergleichenden Stadium” (The studies on relative growth are still on a mere descriptive-comparative stage). See MPG-Archives, III. HA, Rep. 77, file 7, ms. “Jahresbericht über die Arbeit der Abteilung Kramer” (ca. 03/1953), page 1.
1836 See to this a letter to M. Hartmann ibid., file 14, letter G. Kramer to M. Hartmann (29/01/1955) and ibid., file 14, letter M. Hartmann to G. Kramer (08/02/1955).
1838 See to this Kramer’s comment to a presentation delivered by B. Rensch most likely during the annual meeting of the German Zoological Society in 1952, MPG-Archives, III. HA, Rep. 77, file 7, letter G. Kramer to W. Herre (09/07/1952), incl. ms. “Diskussionsbemerkungen Kramer” (ca. 1952), here page 1–2.
vantage for the organism. Kramer’s loyalty to the theoretical framework provided by neo-Darwinian Evolutionary Biology thus became not only manifest in his defence of J. Huxley’s formula but also in claiming the adaptiveness of the growth processes and their effect upon the organisms’ mode of life. In a number of papers published in and around the year 1955 this particular emphasis on adaptiveness became manifest more explicitly in Kramer’s attempt to link the phenomena of allometric growth with the idea of *convergent evolution*. In the previously discussed paper on relative growth in Codfish we are informed that nidicolous Birds are not a good scientific object for interspecific comparisons of allometric growth series especially when it comes to compare the relative growth of the brains because of their delayed development of body structure. Reptiles are said to be appropriate, while Fish and Amphibia are even described as optimal objects. Against this backdrop we need to understand eventually also that Kramer’s interest in convergences coincided with a move to another experimental animal, namely the crocodiles. "Krokodile gehören zu denjenigen Wirbeltieren", it reads at the beginning of one of Kramer’s crocodile studies,

> Crocodiles belong to those vertebrates whose body size covers a huge range of growth from hatching to their definitive size. Thereby a real deep-rooted change of their Gestalt or their mode of life does not occur. [transl. CL]

Crocodiles thus appeared to be the ideal object for interspecific comparisons of ontogenetic processes of relative growth: Crocodiles reveal extensive growth during ontogeny yet no drastic changes in their behaviours or Gestalt. The choice of the scientific object thus seems to indicate that Kramer, in addition to his thorough studies of individual species, developed a stronger interest in interspecific comparison of relative growth processes since 1955, so to speak as a necessary prerequisite to study convergences. Moreover, both the Cods and the Crocodiles – with a view of their body form – seem to reach the state of adulthood very early in their life, a matter of fact which let appear their growth as a more gradual and unilineal process.

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1839 Kramer et al., “Über Proportionsänderungen”, 5–6. Kramer’s methodological comment at this point was meant to clarify the conditions under which interspecific comparisons of one single factor, here the brains, could be carried out best. The answer was that the growth of all other body parts should be constant and this request is fulfilled best in those animals which reach full morphological maturity of their body structures at a very early stage in their development.

1840 In this context, two studies need to be discussed one of which is based on measurements which had been carried out by F. v. Medem in Colombia, while the other paper discusses phenomena of relative growth in a non-recent species (i.e. *Mystriosaurus bollensis*). For the complete references of both studies see G. Kramer et al. “Über wachstumsbedingte Proportionsänderungen bei Krokodilen”. In: *Zoologische Jahrbücher. Abteilung für Allgemeine Zoologie und Physiologie der Tiere* 66 (1955), 62–74 and G. Kramer, “Über wachstumsbedingte Veränderungen der Körperproportionen bei Mystriosaurus bollensis”. In: *Zoologische Jahrbücher. Abteilung für Allgemeine Zoologie und Physiologie der Tiere* 66 (1955), 75–78. Both research papers were published in one and the same volume of *Zoologische Jahrbücher*, refer to each other explicitly and therefore can be treated as an intertextual epistemic unit.


1842 And from Kramer’s statement it can be inferred that this principle applies to many or all species of crocodiles.
As I will show later this does not apply to Birds. As a provisional result, one may therefore argue that the choice of the experimental animal supported the maintenance of the gradualist epistemic framework. Maybe, it should also be mentioned that Kramer primarily did not use museum collections for his allometry studies of Crocodylia but relied on data obtained from freshly killed beasts. This both allowed more precise measurements and provided the opportunity to take into consideration those parts of the bodies which did not belong to the skeleton and would have been difficult to preserve and/or transport. On the other hand, this scientific practice of on-site assessment of scientific data required a person being apt at doing this line of work. Kramer found the ideal man for this project in his friend Count F. v. Medem who was responsible for collecting the material for Kramer’s reptile studies over several years, first on a more freelance basis, later as Kramer’s temporary assistant. A fairly large amount of letters which have been exchanged between both zoologists in the 1950s are preserved in Kramer’s personal papers. They reveal the division of labour that existed between Kramer and his co-worker. Thus there is a number of letters including the instructions Kramer gave and which were meant to be observed by Medem while he was collecting the material in the forests of Columbia. Medem’s expedition reports, in turn, allow some inferences as to the manner of hunting the specimens and the practices with which he assessed the data. Other parts of the correspondence are more related to Kramer’s and Medem’s joint publication of the year 1955. These letters, on the one hand, refer to editorial details and the data basis used for the study. On the other hand, there is a detailed comment of Medem which also seems to encompass Kramer’s supplementary more paleontological account. As exciting particularly Medem’s...
expedition accounts may be from a biographical point of view, it is not always that simple to make these letters fruitful from a science historian’s perspective. My impression is that the instruction Kramer gave in the forefield of the joint publication reveal clearly that he had extended his perspective from intra- to interspecific comparisons. The guidelines since 1956 show that Kramer wanted Medem to measure particularly the bones of the limbs, the skulls, the hip and shoulder girdles as well as the specimens as a whole. In addition to that, these instructions indicate that Kramer was also interested in the soft parts of the bodies, that is, especially the weights of the muscles but not so much the weight of the brains. As to the assessment of the data related to the muscles, we can observe a tiny though eventually significant shift in the practices around 1956: While so far the weighing of the animals’ muscles took place on site, Medem now was instructed to preserve the tissue and send it to Wilhelmshaven. In general, Kramer’s cooperation with Medem, in my opinion, is significant from an epistemological perspective because of the roles both zoologists played within this unit: While Medem was the one to deliver the data, it was more Kramer’s part to order and digest it from a comparative and theoretical standpoint. This division of labour or, more precisely, the epistemological scheme that was underling the cooperative endeavour as a whole gives us eventually also the clue how to read the intertextual unit of the two research papers of Kramer’s being explicitly concerned with relative growth in crocodiles: While his (later) paper on *Mystriosaurus bollensis* seems to bring in the comparative perspective, the main study of the unit seems to operate on well-tried grounds. Its heuristic procedure is more or less identical to the previously discussed studies. Kramer and his coauthor, F. v. Medem, chose only one species of crocodile, the Colombian Caiman, or at least a restricted number of comparative objects but in doing so went meticulously into details in as much as they treated various different organs and organ systems of this primary species. In concrete G. Kramer and F. v. Medem examined the relative size of the head, the form of the head, the limbs and the tail. Alike to the accounts I have discussed above the narrative order while presenting the results of the measurements proceeds from the centre (the head) to the periphery (the limbs and the tail). Thus Kramer and Medem found out that the head in principle grows slower than the torso in postembryonic stages of growth. However, having a closer look at single parts or (visceral) part organs of the head things turned out to be more sophisticated and required a more of differentiation: For instance, the snout of Caimans grows much faster than the back or cerebral

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1848 See to this particularly *ibid.*, file 15, letter G. Kramer to F. v. Medem (21/09/1956) and Medem’s earlier complementary letter *ibid.*, file 15, letter F. v. Medem to G. Kramer (15/09/1956).


1850 From this perspective it might be of interest, too, that Medem was temporarily institutionalized in Kramer’s department. These tiny issues eventually anticipate future developments.

1851 For the primary focus on different collections of Colombian Caimans see Kramer et al., “Über wachstumsbedingte Proportionsänderungen bei Krokodilen”, 62–63.

1852 *Ibid.*, 63. The growth coefficient for both of the examined species turned out to be approximately one: For *Caiman fuscus* $\alpha = 0.95$, for *sclerops* $\alpha = 0.94$. 

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parts of the head. In fact the mouth is the organ with the most extensive growth rate at all even in comparison with the growth rate of the torso. Thereby Kramer and Medem were able to trace a peculiarity of the Caimans, their primary scientific object. In most other species of crocodiles the snout after hatching is relatively shorter and broader. In young animals and early adult age this proportion changes radically as much as the length of the snout increases drastically, whereas its width decreases. In very old animals the proportion usually changes once more since the mouth’s length shows a negative allometric growth rate, while its relative width increases again. In other words, older specimens of crocodile usually show a tendency to develop broad powerful mouths. Yet G. Kramer and F. Medem found out that in Caimans this third phase of development which is characterized by negative allometric growth of the snout length and its simultaneous widening does not take place in the same way. “Bei Caimanen”, they conclude,

\[ \text{In Caimans the snout becomes thinner in accordance with its lengthening / stretching without – as it is the case in particular with Crocodylus – entering a final stage of secondary widening.} \] (transl. CL)

In addition to that, it could be shown that transformation process of the Crocodile’s skull usually responds to the requirement of being able not only to bite powerfully but also to open and keep open the mouth: To match this requirement crocodiles develop more advanced muscle insertion points for those groups of muscles that are responsible for the movement of the lower char and especially the lifting of the heavy head. Furthermore, the tail of young Caimans is as long as the sum total of the size of the head plus the size of the torso. Yet, with advancing years the relative tail length decreases. The same trend to relative shortening can also be made evident in the relative length of the extremities – a result which was agreeing with the findings Kramer had made in his studies of various different species of Italian Lizards in the late 1930s and early 1940s.

Kramer’s decision to dedicate an allometric study to the Colombian Caimans must eventually be interpreted in connection with the peculiarities of this animal’s ontogeny, that is, the fact that the relative shortening of the snout is not correlated with a simultaneous widening of the mouth in advanced stages of ontogenetic development as it is the case with most Crocodylus species. This interpretation is suggested the more by the supplementary

\[ \text{1853} \quad \text{Ibid., 65–66.} \]
\[ \text{1854} \quad \text{In the following see ibid., 66–68.} \]
\[ \text{1855} \quad \text{Ibid., 73.} \]
\[ \text{1856} \quad \text{For the following and the positive allometric growth of the so-called processus articularis see ibid., 69–70.} \]
\[ \text{1857} \quad \text{For putting special emphasis upon the lifting of the head, a peculiarity he thought to have discovered until he read Herodot’s comments on crocodiles. For this little anecdote see Kramer, “Das Bewußtsein des historischen Hintergrundes in der Naturforschung”, 60.} \]
\[ \text{1858} \quad \text{For the relative growth of the tail and the extremities see Kramer et al., “Über wachstumsbedingte Proportionsänderungen bei Krokodilen”, 71–73.} \]
\[ \text{1859} \quad \text{For a Caiman of 1m length the relative length of the tail decreases to 85% in Caiman scleropus and 90% in fuscus.} \]
\[ \text{1860} \quad \text{For this cross-reference to Kramer’s earlier Lizard papers see ibid., 72–73.} \]
study Kramer published simultaneously about *Mystriosaurus bollensis*. This extinct species of saurian resembles recent angustirostral species of crocodile in having thinner snouts but in contrast to them *Mystriosaurus bollensis* was a more aquatic animal.\textsuperscript{1861} A thorough examination of the saurian’s body proportions caused a surprise. *Mystriosaurus bollensis* resembles many recent species of crocodile which cannot be addressed as direct relatives (*Gavialis*, *Tomistoma*) not only in single isolated absolute body proportions – it also reveals a parallel in the proportional shifts characterizing the typical growth process of a crocodile’s mouth, that is, the succession of relative shortness, increased relative length and relative shortening in advanced adulthood.\textsuperscript{1862} In Kramer’s graphical representations the negative allometric growth of the snout length in later stages of ontogenetic development becomes manifest in growth curves which are slightly bent down in their upper regions.\textsuperscript{1863}

As to the relative length of the forelimbs and hind limbs of *Mystriosaurus bollensis* Kramer found a drastic deviation in comparison to recent terrestrial species of crocodile.\textsuperscript{1864} Since an aquatic animal does not have to compensate the forces exerted by gravity the limbs do not have to be shortened in order to gain more static stability. Moreover, the relative length of the tail turned out to be constant in all periods of ontogenetic growth and, beyond that, the tail was eventually much longer than in any other recent species.\textsuperscript{1865} Both texts together and the comparison between recent species of Colombian Caimans and the fossil *Mystriosaurus bollensis* seem to mark Kramer’s position at this point of his scientific development: Allometries can reveal phylogenetic convergences by proving parallel developmental series of growth in non-related species. These ontogenetic proportional shifts can be interpreted as approximation in direction of an optimum. This optimum, in turn, is ecological that means it is determined by the environment the respective animal lives within. “Die Interpretation lautet”, Kramer summarizes the parallel findings in *Mystriosaurus bollensis* and recent species of crocodiles

Es muß sich um Konvergenz handeln, da nicht davon die Rede sein kann, daß sich die rezenten schlanksnäuzigen Arten direkt von den Teleosauriern herleiten. Die Ansicht, daß die festgestellten Proportionsverschiebungen den Verschiebungen des funktionellen Optimums entsprechen, wird durch das parallele Verhalten zweier (möglicherweise gar dreier) phylogenetischer Zweige mit gleichen konstruktiven Voraussetzungen erheblich gestützt.

The interpretation is as follows: It must be a matter of convergence since it cannot be claimed that the recent angustirostral species directly descended from the teleosaurians. This view, that the detected proportional shifts correspond with the shifts of the functional optimum, is supported by the parallel behaviour of two (possibly three) different phylogenetic branches having the same constructive preconditions.\textsuperscript{1866}
Kramer’s argumentation is sophisticated: If under recent and related species of Reptilia deviating growth processes are possible (e.g. the lack of negative growth in the Caiman’s snout in advanced age eventually due to particular feeding habits) and, beyond that, phylogenetically non-related species of animals reveal similar proportional shifts in their series of growth, the tendency of the growth process must be headed towards an optimum which is determined by the respective ecological circumstances (e.g. land living vs. water living animal). Changing the habitat thus means a shift in this optimum and therefore another course of organic development. From this perspective the ontogenetic growth processes in organisms appear to have a systemic character (i.e. partly contrary selective forces interact with each other) but the growth systems as a whole seem to be adapted to particular ecological niches. From the epistemological point of view, this implies the maintenance of the adaptionist framework which, so to speak, suffuses the phenomena of ontogenetic growth. This raises a question: If these parallel developments turn out to be dysfunctional does this information not question the entire theoretical framework of a pure adaptionist in as much as the observed parallels are more likely to be proper homologies?

Transition Four. (5) Kramer’s more differentiated approach to the phenomena of relative growth had revealed that the growth process of the parts need not coincide with the one of the whole organ or organ system. If the biologist wants to make an attempt to reintegrate these deviating lines of data once more into one uniform explanatory system, two different interpretations are possible when it comes to explain the intertwining the various different growth processes. Either the biologist argues that each transformation process is subduced to the power of natural selection by itself (which also makes the entire guiding system adaptive) or, on the contrary, all series of organic growth are embedded in one single system of growth which can become subject of natural selection only as a whole and, beyond that, allows the existence of non-adaptive or insufficiently adaptive growth within the system.

In the former of the two cases the systemic nature of the organism’s genome remains uncertain while in the latter case the idea of genetically controlled ontogenetic growth processes gains more evidence. My impression is that G. Kramer, in his crocodile studies, was inclined to take the pure adaptionist stance, whereas the year 1956 marked a turn to the latter point of view. Maybe, it is not an accident that this move once more coincided with a change to another experimental animal, the Gull, that is, a species of Sea Bird. The study which must be discussed in this context is a paper that G. Kramer published together with L. Dinnendahl in the German Journal for Ornithology in 1956.¹⁸⁶⁷ In later papers being concerned with the

¹⁸⁶⁷ G. Kramer et al. “Über größenabhängige Änderungen der Körperproportionen bei Möwen”. In: Journal für Ornithologie 98.3 (1957), 282–312. The following background information is also of interest: Already in 1951, G. Kramer has supported an application of H. Maschlanka for a grant of the German Research Council. Kramer was in contact with Maschlanka, an American zoologist, since his own student years in Königsberg. Her project was meant to examine the changes of body proportions in Silvery Gulls relative to individual (i.e. non-age-dependent) growth differences. See MPG-Archives, III. HA, Rep. 77, file 5, letter G. Kramer to German Research Council (28/03/1951), incl. Maschlanka’s proposal (27/03/1951), page 1–2, ibid., file 11, letter G. Kramer to O. Koehler (07/02/1951) and ibid., file 11, letter G. Kramer to O. Koehler (08/11/1951). Kramer obviously wasn’t pleased with Maschlanka’s results and
problematic of relative growth we do not find any more a bonding to one specific animal species. Instead these papers have more the character of general abstractions on basis of interspecific comparisons. 

I will elaborate more thoroughly on Kramer’s and Dinnendahl’s paper of the year 1956 and then ask in how far the later abstractions eventually mark another stage of intellectual development. Maybe, it is useful to begin with the end and explain the punch line of Kramer’s engagement with Gulls in the first place. In his later works on allometry G. Kramer once more reassessed the theoretical framework within which classical neo-Darwinian biologists such as J. Huxley and B. Rensch had placed the concept of allometry. In doing so, Kramer found out that both authors used the concept for describing seemingly non-adaptive (at least non-lineal) growth processes without abandoning altogether the idea of adaptiveness. In other words, the potentially dysfunctional phenomena of relative growth appeared within neo-Darwinian theorizing in a paradox position and since it was traditionally the aspect of sexual selection which, in the view of many modern evolutionary biologists, partly suspended the effectiveness of natural selection within the overall network of adaptive forces it takes no wonder that especially Huxley had treated potentially dysfunctional phenomena of allometric growth in connection with the repercussions of the forces exerted by the mechanisms of sexual selection. It is one of the significant peculiarities in G. Kramer’s later theorizing on relative growth that he rejected this connection and, instead, concentrated on aspects of insufficiently adaptive or even dysfunctional phenomena of allometric growth quite independent from the aspect of sexual selection. The theme he had chosen in order to mark this shift was the static analysis of the bird’s skeleton relative to the stages of ontogenetic growth and in connection with, or comparison of the physical requirements resulting from various different movements (e.g. gliding, flapping flight, landing, etc.). “Die Aufmerksamkeit eis...
Gustav Kramer (1910–1959)

war vornehmlich auf die mathematische Erfaßbarkeit der Allometrien und auf den zugrun-เดopoιώνηδενγεγιαντντοστοχαστηκακια,στοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχασตικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχαστικακιακααλετευσηστοχα

[The attention of a group of English authors being superheaded by Huxley was primarily directed towards the mathematical comprehensibility of the allometries and their underlying mechanism. In this current examination was concerned with the evolution which breeds proportions in accordance with the overall size of the bodies. The two complexes of queries namely the one of the mechanisms and the one of the species-preserving fitness of the changes in the proportions can be treated separately in principle. Yet in J. S. Huxley’s work (1932) it can be made evident that he, due to their forced character, ascribes a role to allometries which is vastly independent from the functional; basically he considers them to be appearances without adaptive value (l. c. p. 214, 219). Huxley’s view is based primarily upon experiences with those organs whose involvement with physics is not as immediate as it is the case with the weight-bearing extremities. On the contrary, particularly Huxley’s basic scientific object, the chela of Uca, is without any doubt subject of severest intraspecific selection, just like probably the antlers of a deer and the mandibles of the beetles. The result will be a compromise between the concessions to intraspecific selection, the static capacity to bear weight and, in case of the crab’s chela, the even more original and more widely spread function to grasp. By contrast, as to the extremities of the Gull it can be said in that, most likely, the function of locomotory movement dominates so vastly that concessions to other selective impacts may be widely irrelevant.]

In contrast to Huxley, G. Kramer seemed to be interested in forms of organic growth independent from the forces exerted by intraspecific selection. Instead he concentrated on those environmental strains that are the result of purely physical forces

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For Kramer’s even more challenging scientific position see Kramer, “Funktionsgerechte Al-
– here the mere force of gravity. As a result, the choice of the topic suggests a strong transdisciplinary intertwining with aerodynamics, statics and comparative anatomy.\textsuperscript{1875} Kramer’s interest therefore ran counter to a tendency widely spread amongst other ethologists such as K. Lorenz and E. v. Holst to ban physics from the science of Ethology. Kramer’s and Dinnendahl’s method was simply to assess the load-bearing capacity of the various bones of both the forelimbs and the hind limbs and ask how this capacity changes in a phylogenetic series ranging from lower to larger species of Gull. The comparison with the actual physical forces exerted upon the respective body part during various types of flights allowed Dinnendahl and Kramer to draw conclusions as to whether the architecture and the material constitution of the extremities can cope with the requirements. The result of this measurements and calculations showed that the bones of the hind limbs if taken together grow more or less isometrically with the overall size (yet the proximal bones are slightly longer in bigger forms).\textsuperscript{1876} Moreover, measurements of bone structure and architecture in smaller and bigger forms showed that both the \textit{Femur} and the thinner but longer \textit{Tibiotarsus} were more or less able to meet the static requirements of higher body weights.\textsuperscript{1877} However, especially \textit{Tibiotarsus} seemed to fulfil the stability requirements only if it was exposed to a specific type of load, namely bending (“Knicken”). If this part of the hind limbs was exposed to other types of forces such as the ones caused by inflection (“Biegen”), Kramer and Dinnendahl argue hypothetically, the bone structure would eventually not match the minimum stability requirements.\textsuperscript{1878} The static examination of the wing skeleton yielded more negative results. The overall length of the wing skeleton grows more or less isometrically and the proportion of the relative length of the parts of the wing turned to be constant (in contrast to the hind limbs).\textsuperscript{1879} Furthermore, cross-section analyses of both the \textit{Humerus} and the \textit{Ulna}, the main constituents of the wing skeleton, revealed a higher investment in a more of bone material in larger species of Gull.\textsuperscript{1880} However, comparisons with the actual physical forces exerted upon the wings when the body size increases showed that both growth processes are not able to cope with the physical loads (which are exerted mainly in form of bending forces) – neither during the static gliding flight nor when the birds make use of wing-beat movements or need to slow down abruptly.\textsuperscript{1881} Summarizing their analysis of the wing skeleton Kramer and Dinnendahl write:

Abschließend läßt sich über die Untersuchung des Flügelskeletts sagen, daß die Phylogenese – wenigstens im speziellen Fall der Möwenreihe – darauf verzichtet hat, beim Bau größerer

\textsuperscript{1875} See for instance Kramer’s letter to the orthopaedist F. Pauwels, MPG-Archives, III. HA, Rep. 77, file 15, letter G. Kramer to F. Pauwels (25/01/1956).
\textsuperscript{1876} Kramer et al., “Über größenanhängige Änderungen der Körperproportionen bei Möwen”, 284.
\textsuperscript{1877} Ibid., 287–288 and for a summary 290.
\textsuperscript{1878} Ibid., 290.
\textsuperscript{1879} Ibid., 290–291.
\textsuperscript{1880} Ibid., 291.
\textsuperscript{1881} For calculations of the loads during gliding and the shortcoming of the actual growth see ibid., 292. For the forms of steered flight see ibid., 293.
Concluding one may say about the examination of the wing skeleton that the phylogenetic development – at least in case of the specific lineage of the Gulls – refrained from taking up the evolutionary arms race with the rapid increase of the inflectional forces resulting from the modified architecture in larger forms.\textsuperscript{1882}

On the other hand, Kramer and Dinnendahl were able to show that this lagging behind the actual physical needs was partly compensated by supplementary phenomena of allometric growth such as the reduction of the area of the wing surface and the shortening of the wing feathers while keeping unaltered the skeleton of the forelimbs.\textsuperscript{1883} The lowering of the wing-beat rate and the increase of the feathers’ stiffness – both possible growth tendencies in bigger Gull species – pointed into the same direction. In addition to that, Kramer and Dinnendahl claimed that the inadequacy of the skeleton goes hand in hand with a readjustment of the flight behaviours of the Gulls.\textsuperscript{1884} Kramer and Dinnendahl therefore came to the conclusion that the growth of several isolated bone structures did not match the needs which originated by the fact that the birds live in a certain areal environment but that these deficits are partly compensated by supplementary mechanisms of allometric growth and behavioural adjustment. “Dieser Urteilspruch über die mit ansteigender Größe schwindenden athletischen Fähigkeiten soll nicht den Eindruck erwecken”, Kramer and Dinnendahl argue,

doß hiermit die Lebenseignung der größeren Species geschmälert sei. Selbstverständlich stellt jede Größenstufe eine optimale Kompromißlösung eigener Art dar, wobei die Freiheit in der Kompensation der Teileigenschaften eine universale ist. So mag angenommen werden, daß die Mantelmöwe das, was ihr an Beschleunigungsfähigkeit abgeht, durch gesteigerte Kampfkraft ausgleicht – was ein willkürliches Herauspicken eines als sich kompensierend aufgefaßten Eignungspaars bedeutet. Man kann auch in umgekehrter Richtung vorgehen und sagen: Was die kleineren Arten an Flinkheit gewonnen haben, geht ihnen an Kampfkraft verloren. Dadurch möge ausgedrückt werden, daß der Weg der Größenänderung, der tatsächlich in der Mehrzahl der Fälle von Klein nach Groß führt, genauso gut in umgekehrter Richtung fortschreiten kann, wenn nur ein evolutiver Anreiz dazu besteht, d.h. wenn sich Nischen (im ökologischen Sinn) bieten.

\textsuperscript{1882} Ibid., 296.
\textsuperscript{1883} For the negative allometry of the wing surface see ibid., 296–302. In evincing that the negative allometry of the wing area is not a matter of modifications of the wing skeleton but solely a result of the shortened feathers they contradicted K. Meunier’s opinion who had explained the negative allometry with modifications in the bone structure. For Meunier’s point of view see K. Meunier, “Korrelation und Umkonstruktion in den Größenbeziehungen zwischen Vogelflügel und Vogelkörper”. In: \textit{Biologica Generalis} 19.3 (1951), 403–443. For the rejection of K. Meunier’s stand point see Kramer et al., “Über größenabhängige Änderungen der Körperproportionen bei Möwen”, 282–283, 297, 299, 306 and also Kramer, “Funktionsgerechte Allometrien”, 430–431. See also MPG-Archives, III. HA, Rep. 77, file 6, letter K. Meunier to G. Kramer (06/02/1952), ibid., file 6, letter G. Kramer to K. Meunier (08/02/1952) and ibid., file 7, letter K. Meunier to G. Kramer (17/02/1952). For a brief account of Meunier’s life see G. Heidemann, “Dr. Karl Meunier verstorben”. In: \textit{Zeitschrift für Jagdwissenschaft} 33.1 (1987), 66.

\textsuperscript{1884} Big Gulls cannot slow down as abruptly as smaller species. See Kramer et al., “Über größenabhängige Änderungen der Körperproportionen bei Möwen”, 295 and also Kramer’s later account Kramer, “Funktionsgerechte Allometrien”, 428.
every stage of size creates an optimal compromise solution of its own kind whereby the freedom of compensation being possible between all part aptitudes is universal. Thus it may be presumed that the Great Black-Backed Gull compensates by increased fighting strength what it lacks in terms of acceleration. This, of course, is an arbitrary picking out of a dichotomy of aptitudes which can be conceived as compensatory. One can also argue the other way round and say: What the smaller species have won in terms of nimbleness they loose in fighting strength. By this I should like to emphasis that the course of size-related changes which actually proceeds in most of the cases from small to big, can proceed in the opposite direction as well, if this is evolutionary tempting, that is, if adequate niches (in the ecological sense) come up.

To put it provocatively, what we read in this paragraph of G. Kramer’s and L. Dinnendahl’s account is no less than a modified theory of “hopeful monsters”: Processes of relative growth, even if the final result in particulate organs is lagging behind the physical needs of the respective habitat may nonetheless lead to an “organic composition” which as a whole can be adaptive in a certain ecological niche.

I see at least three different though connected aspects. At first, G. Kramer in cooperation with his associate, L. Dinnendahl, began to understand the intertwining of the partly divergent growth processes from a systemic standpoint. “Hier wird deutlich”, Kramer and Dinnendahl underline, daß der Abstimmung der Wachstumsgeschwindigkeiten keine selbständige Rolle beim Zustandekommen der Proportionen zukommt, sondern daß im Genom ein Proportionsplan besteht, dem die Allometrien untertan sind. Dies wird dadurch bestätigt, daß bei Transplantationen eines Organs von älteren auf jüngere Stadien das Organwachstum so gezügelt wird, daß sehr bald die dem Wirtsstadium angemessene Proportion hergestellt ist (Twitty, zitiert nach Huxley 1932, p. 51–52). | Aber auch im evolutionistischen Sinn hat die Form das Primat vor der Wachstumsgeschwindigkeit. Nicht relative Wachstumsgeschwindigkeiten als solche sind den evolutiven Kräften der Außenwelt ausgesetzt, sondern die Körperform, so wie sie in jedem Augenblick ist. Es ist also richtiger zu sagen: Die Natur züchtet Proportionen nach Maßgabe der Gesamtgröße als: Sie züchtet relative Wachstumsgeschwindigkeiten, deren Ergebnis die Proportionen sind.
the allometries are subjugated to. This is confirmed by the fact that in transplantation of organs from a more advanced to a younger stage of development the organic growth is reined so that very soon the proportion is established which is adjusted to the developmental stage of the host organ. (Twitty, quoted after Huxley 1932, p. 51–52). | But also in the evolutionary sense the form has the primacy over the speeds of growth. Not the relative speeds of growth as such are subject to the evolutionary forces of the outside world but the form of the body like it appears in every single moment. Hence it is more correct to say: The nature breeds proportions in accordance with the overall size rather than: It breeds relative growth rates whose result is the proportions. [transl. CL

In this quotation we are informed how Kramer and Dinnendahl conceived the physiological basis of the growth system. According to the authors there is a “Proportionsplan” which is pre-determined in the genome and provides an integrated system of all relative growth processes.\(^\text{1888}\) As a result, it is not each single constituent which is subject of natural selection but only the form as a whole.\(^\text{1889}\) Second, the distinction between functional and potentially dysfunctional growth allowed thinking qualitatively different processes of growth. While Kramer seemed to have in mind a linear process of organic growth when he spoke of “unmittelbar funktionsgerechtem Wachstum”, he suggested to explain the more rapid forms of development as forms of preparatory or anticipatory growth. “Im Falle der ‘geradlinigen’ Entwicklungen, also etwa bei einem Krokodil oder einem ametabolien Arthropod, liegen die Verhältnisse deswegen einfacher, weil der Proportionswandel als unmittelbar funktionsgerecht erkennbar ist”. Kramer and Dinnendahl write and proceed:


\[\text{In case of the linear development, for instance in crocodiles or an ametabolic arthropod things are less complicate because the proportional changes can be immediately realized as functional. Where rapid changes of the form occur, there are, by contrast, accumulations of material which are not meant to be of immediate use but prepare functions for later stages of growth. Examples}\]


For the heritable basis of the growth regulators see also Kramer, “Funktionsgerechte Allometrien”, 434.

In Kramer’s personal papers there are indicators as early as 1952 showing that he at least planned to manipulate the growth of rats and birds in different ontogenetic phases by applying hormone treatment. These experiments could be of interest in this context because they might reveal in how far the artificially increased growth of an organism is following a construction plan, too. See MPG-Archives, III. HA, Rep. 77, file 6, letter E. E. Hays to G. Kramer (19/06/1952) and ibid., file 6, letter G. Kramer to E. E. Hays (ca. 06/1952). See also Kramer’s correspondence with F. A. Beach who assisted in purchasing the apt substances, ibid., file 6, letter G. Kramer to F. A. Beach (08/04/1952), ibid., file 6, letter G. Kramer to F. A. Beach (23/04/1952), ibid., file 6, letter F. A. Beach to G. Kramer (16/04/1952), ibid., file 6, letter F. A. Beach to G. Kramer (26/05/1952) and ibid., file 6, letter F. A. Beach to G. Kramer (04/06/1952). See also ibid., file 8, letter W. Donaldson to G. Kramer (09/10/1952) and ibid., file 7, letter Parke, Davis & Company to G. Kramer (21/10/1952), incl. invoice. In a later letter to M. Hartmann, however, we are informed that the experimental increase of vertebrate animals failed. See ibid., file 14, letter G. Kramer to M. Hartmann (29/01/1955).
for this sort of “preparatory growth” are the prenatal growth of the brain in Amniota and the growth of the wings in nidicolous birds. With the help of the concepts of functional and preparatory growth all processes of growth, at least those in later development, can be understood as functional and therefore also as products of natural breeding.)

This quotation shows that Kramer’s systemic understanding of relative growth not only implied the idea of compensatory growth processes but also the possibility of a more chronological asymmetry. From the epistemological standpoint this latter idea is quite interesting because it operates with an epistemic scheme which is similar to the one underlying the models of instinctive action patterns put forward by early ethologists such as K. Lorenz: In both concepts we find the anticipatory accumulation of some kind of potential (either nervous energy or ontogenetic variability) which in a final step is released or becomes available to be built in. In other words, Kramer’s concept of “Vorbereitungswachstum” implies the idea of some kind of functional foreshadowing – an initial moment of guidance in the overall plan or “subplan”. Finally, the shift to dysfunctional or insufficiently adaptive body structures went hand in hand with a stronger emphasis of the potentially homological character of the allometries. In other words, evincing the partly inapt nature of allometric growth prevented Kramer from putting forward still the pure adaptationist stance that had been the tenor of earlier accounts but, on the other hand, opened another far-reaching theoretical option: Potentially dysfunctional morphological characteristics are unlikely to be the product of convergent evolution like the streamlined form of the body that originated independently in different non-related and remote species such as Fish and Whales. By contrast, they indicate true homologies and therefore provide the option to use the study of individual, intra- and interspecific allometric growth processes as valuable criterion for classificatory purposes and systematic research. At this point one is eventually capable to understand that Kramer’s advanced engagement with relative growth has not lost its original systematic impetus. Quite the opposite! However, the emphasis on dysfunctional and insufficiently adaptive growth does not mean that Kramer and Dinnendahl altogether abandoned the idea of ultimate causation. Kramer and his coauthor just thought that only the organism as a whole could be subject of natural selection plus that trend to adaptiveness in some cases might not cope with the requirements at all. In sum, one may therefore say that G. Kramer’s late reflections on relative growth were characterized by a truly systemic and holistic stance.


For the homological characters see Kramer, “Funktionsgerechte Allometrien”, 435. In this context, I’d like to mention also a correspondence between the German zoologist A. Remane and G. Kramer which can be dated to early 1958. Remane claimed that divergent developmental velocities could be the result not only of functional adjustment but also due to what he called the “historical side”, that is, intrinsic conditions of the phylogenetic growth system. See MPG-Archives, III. HA, Rep. 77, file 19, letter G. Kramer to A. Remane (20/12/1958), incl. ms. “Zum Vortrag Kramer!” (n. d.), and ms. “Kramers Antwort an Remane” (20/01/1959).

Quite the opposite, Kramer and Dinnendahl, for instance, insist that the allometric growth of the Gull’s extremities, in contrast to Meunier’s view, is only seemingly an example for non-adaptive allometric tendencies. See Kramer, “Funktionsgerechte Allometrien”, 431.
which ascribes a restricted, formative and guiding but overwhelming role to natural selection yet with no immediate impact upon the isolated or particulate growth processes as such. The idea of adaptiveness is therefore stretched to the utmost extreme, that is, into regions of biological growth which, at first sight, seem to be non-adaptive. As a result, Kramer was able to conclude that all allometries might be the outcome of selection. I will discuss the epistemological implications of this revised holism below.

(6) It remains to ask whether or not G. Kramer’s late, more theoretical and comparative accounts, which were concerned with the problematic of relative growth, establish another stage in his scientific development just like his studies of avian navigation entered another qualitatively different stage after the failed Gleiberg experiments. I am inclined to answer this question in the affirmative for several different reasons. At first, I consider it a significant gesture that Kramer since 1958 avoided to elaborate his view upon the problematic of allometry by choosing one single species of animal or a restricted amount of objects of comparison. His accounts therefore have the character of general abstractions on comparative grounds. Corresponding to this move we can find a stronger emphasis upon intra- and interspecific comparisons. Second, I see another way in how the paradox constellation of adaptive dysfunctional phenomena is becoming manifest. While the earlier account on Gulls put great emphasis on compensatory phenomena of allometric growth and readjusted behaviours, the later accounts seemed to put forward another form of argument by comparing hypothetically the actual growth rates with the ones to be expected with fully and non-adapted control organisms: The growth rate of seemingly dysfunctional or insufficiently adaptive morphological characteristics is lower than they would be if they were adapted – in Kramer’s words if they showed a “mechanical” growth rate. Yet, on the other hand, they turned out to be still higher than it would be expected if the force of natural selection had no effect at all – in Kramer’s words if the curve showed a mere “geometric” growth rate. This intermediate position of the actually found curves of relative growth showed that the forces of natural selection and with them the effect of ecological adaptation were active yet in many organ systems are simply lagging behind the actual physical needs. I see a difference in the statements that nature reveals adaptive deficits and compensates them, or, that it takes up the arms race but does not reach a sufficiently high speed of organic growth, or, finally, that nature does not pick the arms race of evolution at all. Compared with this range of different possible utterances, my impression is that Kramer’s distinction between “immediately functional” growth and those processes which included “preparatory growth” somewhat smoothed the problematic of potentially inadequate growth since the lag-

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1895 For Kramer’s translation of both the optimal and the suboptimal growth rates into mechanical terms, see Kramer, “Funktionsgerechte Allometrien”, 426.
1896 And this aspect could apparently be proved not only in series of Birds but also of Medem’s Caimans. See MPG-Archives, III. HA, Rep. 77, file 19, letter G. Kramer to F. v. Medem (11/09/1958).
1897 For the compromises in nature between geometric and mechanical growth see Kramer, “Funktionsgerechte Allometrien”, 429.
To sum up my analyses of the phenomenological shifts in G. Kramer’s reasoning on relative growth and the problematic of allometry I would like to mention several aspects: At first, Kramer’s engagement with allometries from the very beginning had a potentially critical stance which could be directed against the classical neo-Darwinian framework in so far as his studies on relative growth were not interested in the whole organ or system of organs but also in the histological details. This more of differentiation eventually went against the intention to reduce complexity by mere quantification. The result of Kramer’s histological studies of relative growth (e.g. in Dog Fish and Cod) was, that the growth processes of the parts need not coincide with the one of the whole. Furthermore, Kramer tended to restrict the applicability of Huxley’s abstraction to single subprocesses of relative growth but simultaneously revealed the validity of the formula independent from the direction of the growth process. Secondly, this process of heuristic decomposition raised the question whether and in how far the singular growth processes could be reintegrated in one model of organic growth: Two extreme solutions, the adaptionist’s and the systemic model, are discussed in different stages of Kramer’s reasoning on allometries: While his studies on recent and fossil Reptilia stressed the idea of convergent evolution, the static analysis of the Gull’s extremities marked a turning point since henceforth the systemic character of the growth processes became the primary focus of Kramer’s attention without neglecting the possibility of “directly functional” forms of organic growth. Which model of organic growth was to be applied more and more became a matter of aprioristic decision which was closely connected with the question what scientific object was currently under examination. Kramer’s systemic view anticipated two lines of biological research reaching out even in our present time. First, the idea that individual development is regulated by some sort of fixed ground plan raises the question for the genetic basis of this plan. These genes actually do exist and are called “homeotic” genes of which so-called “hox-genes” build a highly topical subset of genetic enquiry. Second, potentially occurring developmental macro-mutations raise the question whether or not evolution involves saltationism. Both sets of questions have been put forward already by R. Goldschmidt and further developed within another epistemological frame by G. Kramer and later by S. J. Gould in his theory of punctuated equilibria.

1899 Although M. R. Dietrich does not seem to be familiar with G. Kramer’s research we can infer from his account that R. Goldschmidt played a pioneering role in several hotspots of biological inquiry which G. Kramer picked up such as the systemic view upon the hereditary system, the possibility of non-linear growth and, most importantly, the integration of development and intellectual histories.
**Step Two: Epistemology**

The key question to me is whether these phenomenological shifts can be correlated with corresponding epistemic transformation processes on the more conservative levels of scientific change. From this particular perspective one may eventually say that Kramer’s accounts on relative growth until the year 1956 reveal one common quality. They tend to begin with a primary reduction, mostly to one single species of animal, but within this reduced focus pursued a meticulous examination into the finest, even histological details. This epistemic scheme was as compatible with the epistemic framework provided by classical neo-Darwinian theorizing as all empirical preparatory studies of Kramer’s before his engagement with allometry and, beyond that, established a conceptual alternative to the model of differential diagnoses. There might exist both science historians and biologist who are liable to interpret Kramer’s late research on allometry within this framework as well. My opinion, however, is that Kramer’s emphasis of potentially dysfunctional, insufficiently adaptive and asymmetric growth processes was not fully compatible any more with the framework provided by the neo-Darwinian synthesis (in a narrower sense) within which his studies were placed before. Several arguments seem to substantiate my view. At first, with choosing forms of allometric growth which could be conceived independently from the aspect of sexual selection such as the static analysis of the Gull skeleton Kramer detached his study of relative growth from the framework within which neo-Darwinians such as J. S. Huxley and B. Rensch had located the allometries so-far. Second, in putting forward the idea of a pre-existent “Proportionsplan” Kramer suggested a systemic model of allometric growth which allowed him to integrate potentially dysfunctional, insufficiently adaptive and asymmetric forms of relative growth and, beyond that, ascribed only a restricted, guiding but overwhelming function to the forces of natural selection. On closer inspection Kramer’s systemic understanding therefore rooted in a paradox heuristic constellation which to solve, in my opinion, generated prototypical concepts such as the idea of “anticipatory growth”, the intermediate compromises between mechanic and geometric growth or the notion that antagonistic growth processes might be able to compensate the deficits of each other, not to mention the compensatory function of readjusted behaviour patterns. All these theorems are bearing paradox overtones in a sense of being somewhat open closed systems. As a result, I am therefore inclined to argue that Kramer’s late study on allometries took place within a more holistic framework that was similar to the mechanomorph frame within which many abstractions of classical ethologists had originated. For instance, I think it is not an accident that N. Tinbergen, while defending the classical holism against the growing tendency towards more ecological approaches
within his work group, explicitly argued in favour of Kramer’s holistic model of organic growth. 1902 Thirdly, another indicator that G. Kramer eventually more and more drifted away from the unilineal, gradualist and adaptive framework of his earlier studies on Lizards and allometry, might be the fact that he used to understand growth processes independent from their direction, for instance, independent from whether or not allometric growth rates turned out to be positive or independent from whether phylogenetic series proceeded from small to big or vice versa. This emphasis of bidirectionality is a clear indicator for a more systemic understanding of evolution, in general, and relative growth, in particular. Fourthly, despite the fact that Kramer puts a great deal of verbal emphasis upon function and adaptiveness he does neither solve nor exclude the problem that the speed of organic growth in some cases might never reach fully adaptive “mechanical” growth rates. Kramer says:


[As long as the particular qualities of the used materials cannot be improved – and nothing points into this direction –, the strict obedience of the mechanical similarity is probably not possible at all. However, between the ways of geometric and mechanic similarity there are compromises, and it is these compromises which are usually made use of by evolution.]

Finally, although I have not included in my account detailed analyses of forms and structures with which Kramer organized and presented his knowledge in his publications concerned with relative growth, nonetheless, I’d like to point out a striking detail. I have argued that Kramer’s early accounts of allometric growth combined a gesture of initial restriction with a secondary exemplification and elaboration in details. It is obvious that Kramer’s accounts on allometry before 1957 proceeded in these exemplifications from the centre to the periphery of the animal body. That is to say, Kramer used to treat the size and the form of the animal’s head in the first place and only after that provided the measurements of the forelimbs, the hind limbs and the tail. This canonical narrative order changed in Kramer’s Gull paper of the year 1957. Here, and as far as I can see, in all further accounts measurements – in accordance with their respective location in the overall scheme of the paper as a whole – were organized from the periphery to the centre, that is, from the extremities to the head or from the hind limbs to the forelimbs. This aspect is a clear indicator that the empirical parts of the texts altered their narrative order and therefore also that the epistemic schemes organizing the texts as a whole were apparently replaced around the year 1957. My previous analyses have revealed that the implicit and explicit modes of knowledge organization are one of the most reliable indicators for the moves taking place in the intellectual life-history of a researcher. In sum, I

1902 The highly exciting aspect in this cross-referencing is its chronology: Kramer turned to his evolutionary holism just in the moment when Tinbergen was about to abandon it, so that Tinbergen’s cross-reference made sense just at a very singular chronological moment – the moment of or around the turn itself.

therefore claim that G. Kramer’s reasoning on allometric growth drifted away from the neo-Darwinian Synthesis and entered those areas within the epistemic space of his scientific community which Ch. Darwin in his *Origin of Species* had marked, for instance, with his chapter on embryology.

It is time to sum up my account of the development G. Kramer’s intellectual life-history has taken in the decade after the Second World War. In principle I have distinguished between two separate epistemic realms and, in doing so, I have asked in how far both spheres are correlated with particular thematic fields of research. The answer to this question is that Kramer’s two main research foci of the late 1940s and the 1950s, that is, research on avian orientation and navigation, on the one hand, and his interest in relative growth, on the other hand, are loosely correlated with one heuristic machinery each. While in the field of avian orientation and navigation the diagnostic program seems to prevail (though not strictly), things appear to be less obvious in the realm of allometric research: With a particular view upon the empirical main parts of the papers in question, here we have to do with a combination of reduction and exemplification in the years up to 1957, whereas the later publications – in these empirical parts – seem to rely stronger on apriori thematic limitations in the first place. In a second step, this limited thesis is supposed to be substantiated with the help of a wide range of empirical data drawn from observations of several different species of animal. Moreover, I have asked for both realms of Kramer’s research separately whether his scientific development might not reveal a turn similar to the one I have made evident in N. Tinbergen’s life course. This question too, I think, can be answered in the affirmative for both realms: While in the field of avian orientation and navigation the failed attempt to prove proper sun navigation marked a turning point to another modified model of diagnosis, Kramer’s studies of relative growth apparently headed towards a more systemic and holistic epistemic framework which was more likely to be identified with the form of exclusive holism ethologists put forward in their mechanomorph period. Both moves together are a clear indicator that G. Kramer, on later stages of his life course, drifted away from the classical neo-Darwinian framework which had shaped his research between ca. 1938 and 1956. If this thesis was true, Kramer was about to reinterpret older neo-vitalistic epistemic frameworks within the modern neo-Darwinian epistemic community just as Niko Tinbergen had reinterpreted the older neo-Lamarckian position as Behavioural Ecology of animal and man. From a science historian’s point of view G. Kramer’s intellectual life-history is the more exciting as he unified in his person eventually both a late tendency to Cognitive Ethology (as indicated by his map-and-compass model of avian orientation) and a line of Evolutionary Biology that should become popular later in the works of, for instance, S. J. Gould. Kramer’s allusion to the idea of “hopeful monster” may be only one tiny but rather palpable parallel. In sum, one may therefore say that both N. Tinbergen’s and G. Kramer’s life histories in their later stages drifted away from the extended synthesis that was consisting of both the neo-Darwinian and the etho-

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[1904] Most interestingly, Kramer’s turn implied also a high esteem of classical humanist education and the ability of the historical perspective to put one’s position into perspective. For Kramer’s anti-materialist stance see Kramer, “Das Bewußtsein des historischen Hintergrundes in der Naturforschung”, 60–61.
logical amalgams. In doing so, they made the neo-Darwinian epistemic community a fully self-reproductive field of biological research. However, beyond the obvious parallel that both Tinbergen’s and Kramer’s research drifted away from their classical convictions and the equally obvious structural incompatibility of the scientific orientations both researchers were headed at, there are also some peculiarities in both life histories which are worthwhile to be mentioned. For instance, G. Kramer, in contrast to N. Tinbergen, has not outsourced one of the realms of his scientific orientation to his pupils. G. Kramer certainly cooperated with members of younger generations of biologists such as U. v. Saint Paul, G. Wallraff, K. Hoffmann, K. Schmidt-Koenig, L. Dinnendahl, or G. Huhn but the works of these youngsters covered more or less independent niches within Kramer’s research program and not, as it was the case with Niko’s pupils, a realm complementary to his own more theoretical reviews that were meant to maintain and form the ethological discipline in accordance to the vision Niko had of Ethology in the different stages of his life. Maybe, it is therefore not entirely false to say that Kramer’s idea of academic socialization was more organic, while Niko’s model rested upon a division of labour and mutual exchange. It is not an accident that Niko’s strategy of outsourcing generated one of the most famous research groups ever, the ABRG. However, on closer inspection, it was also Kramer’s reinterpretation of the problematic of animal speciation in the orthodox selectionist framework which created the epistemic space for an entirely different theme: Avian orientation and navigation. The comparison of G. Kramer’s and N. Tinbergen’s life courses leads also to the question in how far and, if so, how the two constitutive realms which can be made evident in both trajectories were intertwined in both cases. I think, the question can only be answered in a diachronic way that is relative to the time factor. Niko’s strategy to install a more or less clear cut division of labour gave his pupils a great deal of independence but on closer inspection Niko’s system also implied mutual stimulation. Ethological theory or at least the results obtained in previous studies were often the starting point of his pupils’ further leading works, but on the other hand, it was exactly the empirical data delivered by his pupils which went in his own theoretical and disciplinary formative comments. From time to time these theoretical accounts were written in cooperation with one or more of his pupils so that we can also speak of personal exchange in a very literal sense. In later stages Tinbergen seemed to have applied his practices of academic socialization to pupils below PhD level so that the PhD students, whose work space was separated from Niko’s also spatially till the new institute was built, were even more allowed to establish their own system of mutual tutoring. In Kramer’s case the relationship between both realms was much more determined by the needs of his own research. His abstractions, though embedded in sophisticated models of diagnoses, were partly liable to produce errors, especially in the earlier stages of his life course. In those cases, when a particular theme turned out to be supplementary or when the particular occasion required a modified mode of presentation, Kramer switched into a more empirical heuristic machinery complementary to the diagnostic model. In many of Kramer’s research publications, however, we can find a rather stable correlation between theme and scheme so that mutual exchange turns out to be a mere matter of “complementariness”, that is,
an epistemic relation between different complementary heuristic machineries. For instance, the application of the diagnostic scheme in his ornithological works of the early 1950s shows clearly that it worked very well as an autonomous heuristic machinery without systematic intertwining between the different realms: A thesis could be extended only to come to a more refined conclusion which, in turn, could be declared the starting point of a subsequent diagnosis. Complementarily, the reduction to one organ or one species in his allometric studies which was usually supplemented by an elaboration of ever finer details led to an accumulation of data which could be extended even more if further wider ranges of related scientific objects were chosen for additional studies. Both part systems of G. Kramer’s research therefore could be considered separately (E. Stresemann) also because they worked independently and stimulated themselves autonomously. Yet, in addition to that, there might be a kind of convergence of both realms as to the scientific objects used in later stages of Kramer’s life-history since both the realm dedicated to orientation and navigation and the late studies of allometries was related to the animal class of Birds. Due to Kramer’s early tragic death it is difficult to provide any reliable information of how his scientific development would have continued if he had lived longer, but it is not quite unlikely that the homogeneous emphasis of ornithological themes which coincided both with Kramer’s nomination as director of the Ornithological Research Station Radolfzell and his appointment as head of a department of the MPI for Behavioural Physiology would have led in the long run to a stronger amalgamation of his otherwise rather divergent research interests.1905

Growing Raven – Speculations beyond the Tragic Death

G . Kramer’s early tragic death was experienced as severe loss by his colleagues and friends.1906 Moreover, it provokes speculation how his life and research would have proceeded. Kramer died in a period of epistemic transition but in contrast to N. Tinbergen had proceeded farther when he died in 1959. What might have come must be discussed separately for each of the spheres within which his life and research took place. At the end I’d like to provide a perspective how these fields would have or could have merged together in a homogeneous scientific orientation.

Despite the fact that it is not possible to say which concrete forms Kramer’s future research on avian orientation and navigation would have taken if he had lived longer, we can find, nonetheless, some indicators in his late work which might show us into which direction his lines of thoughts would have gone. In addition to that, Kramer raised in a rudimentary form questions which later, after his death, developed into paradigmatic themes of ornithological research, not least, through the works of his own pupils. According to T. Ludlow, mainly four theories exist amongst ornithologists nowadays as to the question which clues pigeons and other


birds utilize during navigation. One theory presumes that the bird stores “every twist and turn” of its journey and as a result is able to compute any new location on the fly on basis of a mental map or representation of all its moves. In case this mechanism is simply based on adding up singular vectors no definite orientation marks (e.g. provided by astronomical data) are necessary. (2) The birds use celestial cues to calculate their current position within some sort of reference system (position finding) and/or can compute their homing direction on basis of celestial signals (direction finding). This theory, at least in its radical formulation (i.e. position and direction finding is based on celestial clues), mostly coincides with the sun navigation hypothesis which has been disputed by G. Kramer for his homing pigeons. Yet other ornithologists, for instance, F. Sauer seem to have proved that various species of Birds migrating by night can use star constellations as orientation cues. Further experiments revealed also that several species of Bird use polarized light – a hypothesis Kramer had excluded, on basis of his tests with the Starling. (3) A third theory presumes that birds navigate in the magnetic field of the earth and therefore partly coincides with H. L. Yeagley early thesis. Finally, a fourth theory which was postulated by H. G. Wallraff, one of G. Kramer’s pupils, claims that homing birds can learn to associate a particular odour with a particular direction of the wind which is characteristic at their home location.


See to this, for instance, what K. Schmidt-Koenig calls “Wegumkehr” and which is actually a navigation mechanism using inertial forces, see Schmidt-Koenig, “Zur Geschichte der Orien

G. Kramer mentioned and discussed F. and E. Sauer’s impressive results critically in several of his paper’s but they created a latent tension to his own results because they raised the question why birds apply bicoordinated orientation by celestial cues during night and not during day light. Can birds see the stars during day? And why do they use the stars and not the sun for true navigation. For Kramer’s discussions see Kramer, “Experiments on Bird Orientation and Their Interpretation”, 201–202. Kramer, “Die Sonnenorientierung der Vögel [1958]”. 55. Kramer, “Long-distance Orientation”, 362–365. Further archive material also shows that Kramer and his associates performed orientation experiments with pigeons testing their ability to return during the night. This required new techniques such as the usage of radar or radio engineering. For this merely technical aspect see MPG-Archives, III. HA, Rep. 77, file 16, letter G. Kramer to General a. D. [W.] Martini (30/01/1957), ibid., file 16, letter H. Ballreich to Oberpostdirektion Bremen (26/03/1957) and MPG-Archives, III. HA, Rep. 29, file 196, letter G. Kramer to W. Jechorek (21/01/1958). For the tests at night see, for instance, MPG-Archives, III. HA, Rep. 77, file 18, letter U. v. St. Paul to G. Kramer (20/08/1958) and ibid., file 18, letter U. v. St. Paul to G. Kramer (ca. 1958). The results seemed to suggest the existence of another orientation mechanism independent from the sun-compass, at least homing seemed to be non-random at night. In this context, see also H. O. Wagner’s further leading conclusions ibid., file 16, letter H. O. Wagner to G. Kramer (29/10/1956), ibid., file 16, letter H. O. Wagner to G. Kramer (16/11/1956) and ibid., file 16, letter H. O. Wagner to G. Kramer (04/12/1956). On the other hand, K. Schmidt-Koenig proved that shifting the pigeon’s internal clock had an effect upon the direction of their departure, that is, direction not position finding. See ibid., file 17, letter G. Kramer to A. D. Hasler (15/10/1957), ibid., file 17, letter G. Kramer to E. Mayr (28/10/1957) and ibid., file 18, ms. “Tätigkeitsbericht Abt. Kramer 1957/58” (ca. 1958). According to Schmidt-Koenigs later retrospective account, Sauer had discovered a form of star-compass orientation not “navigation” although he himself insisted to have discovered a form of true navigation.


For the gradual acceptance of magnetic orientation see also ibid., 595–596.

See for a discussion ibid., 598–599. H. G. Wallraff dedicated his career to solve the riddle of
When they sense this odour at the release site, which requires the distribution of these senses by winds, they choose the opposite direction. Theory (2)–(4) can differ relative to the extent with which a bird is capable to compute the overall homing direction from the very beginning of his release and therefore can return directly. The alternative would be that birds permanently readjust their current position by repeated position finding. In any case, at least the existence of a stored spatial representation of the home location in the bird is required which can be related to the current location of the release site. The more directed the flights and the less trial and error is meant to be involved in this process the more must ornithologists be prepared to concede the existence of more advanced spatial representations (including representations of the release site and, maybe, the homing direction itself). Theory four requires to a certain extent that the scents of the home location are distributed by winds in a regular or linear way so that birds can compute a sort of map of gradients on basis of relative scent concentrations in the air.\footnote{1913} From the epistemological point of view, this theory of orientation thus may re-approach the concept of orientation Kramer had put forward in his study of the Clawed Frog and eventually also implies another causal architecture since the release site is supposed to send out directly olfactory stimuli. Which of the theory has been prepared by Kramer’s re-conceptualizations – or did he have in mind a completely different alternative?\footnote{1914} For the time being, one may say that G. Kramer’s map-and-compass concept implies that he was prepared to concede his scientific objects highly advanced spatial representations: According to his view, the act of position finding includes not only determining the relative geographical position of the release site but also the development of a concept of the homing direction which then, in course of the second step, needs to be translated into concrete action in the field. His idea of pure mathematical extrapolation of the sun’s movement with which he, in a transitional stage of theorizing, intended to “rescue” G. V. T. Matthews’ (and his own) theory of sun navigation points into the same direction. This aspect raises the question whether G. Kramer’s theorizing on avian orientation and navigation might have approached theory one. What speaks against this option is that a theory of path integration would have sidelined previous achievements such as Kramer’s discovery of the sun-compass. What speaks for this hypothesis is that G. Kramer, in addition to his latent belief in highly advanced spatial representations, also considered it likely that pigeons can find their home by repeated position finding, for instance, when their sun compass is terminated by overcast sky. In a letter Kramer has written to L. Tinbergen at the end of the year 1952, for instance, we can find the hypothetical statement:

Ich frage mich im Zusammenhang mit Deinem “gedrehten Zug”, ob man überhaupt von einer “Normalrichtung” in anderem als einem rein statistischen Sinne sprechen darf. Vielleicht ist

\footnote{1913}{olfactory orientation. See Wallraff, \textit{Avian Navigation}, chapter 7, 87–147.} \footnote{1914}{In addition to Ludlow’s account see for the controversy on olfactory orientation Schmidt-Koenig, “Zur Geschichte der Orientierungsfororschung”, 118–120.}
Another indicator which points into this direction is that Kramer apparently was not prepared to reconsider navigation in the magnetic field.\cite{1916} It is eventually possible to clarify this exciting research question by taking into account more archive sources. One of the aspects that might become of importance in this context is the latent heuristic tension which was lying in Kramer’s cooperation with J. G. Pratt. Kramer the sensory physiologist had definitely another research interest in avian navigation than Pratt, the parapsychologist. From this interaction we can infer that Kramer was primarily interest in the broad variety of physical cues and the mechanisms of their sensory perception. I think it possible that another line of possible research that might have developed if he hadn’t died that early would have been related to the question how all these different factors work together in the Bird’s orientation system as a whole.\cite{1917} This is even more likely because Kramer’s Seewiesen colleagues shared this interest in questions of coordination. Also I think it can be inferred from archive material that Kramer was sceptical towards the idea that olfactory factors might be able to guide the pigeons when trying to find their home.\cite{1918} As a result, one may eventually say that this tension of not having proved true sun navigation while simultaneously excluding navigation by magnetic or olfactory clues eventually provided the “breeding ground” for a theory of spatial representations and / or a more systemic integrative position based on his research emphasis on Bio-climatology. And both the idea of overall mapping and the question how Birds process the wide range of possible geophysical parameters might have brought his research into the direction of Cognitive Ethology. That Kramer spoke of a “map” component in avian navigation seems to substantiate this hypothesis at least to a certain extent because calculating the position of the release site
relative to the home loft (i.e. via bicoordinated navigation), in the last consequence, requires some sort of spatial representation of the home location whose qualities are physically not present at the release site. I repeat, the very, very interesting aspect in G. Kramer’s intellectual life-history is that he unified in one person the interests we otherwise might find, for instance, in D. R. Griffin and S. J. Gould separately. 

Kramer’s studies on relative growth show a trend away from examining completely functional allometries (as a result of convergences) towards an interest in insufficiently adaptive though adjusted allometries as part of a whole growth system. This was only possible in another epistemic framework, one, which was similar though not identical with the model of causal analysis K. Lorenz and other classical ethologists had made a constitutive component of their scientific orientation. If we recollect that Kramer in his paper of the year 1941 latently attacked Lorenz’s “raven system” for interpreting the reductive gesture within this framework in terms of “degeneration” we may say that Kramer, with his department becoming a part of the MPI for Behavioural Physiology, partly adopted the paradigmatic outline of the Seewiesen mother institute. The crucial question, however, is how the adopted epistemic reference system would have been fleshed out in Kramer’s future research and within the particular setting of Kramer’s late scientific orientation. My opinion is, he might have used seemingly dysfunctional or insufficiently adaptive allometries as a homological characteristic for systematics and thus would have paralleled S. J. Gould’s theory of punctuated equilibrium whose inherent logic of discontinuous non-lineal development Kramer had already anticipated in his Gull study, however, in the field of ontogenetic not phylogenetic development and eventually also by applying a slightly different idea of holism. In other words, I believe, that S. J. Gould’s later theory of punctuated equilibria and G. Kramer’s concept of “Vorbereitungswachstum” (preparatory growth) share a common idea, namely the possibility of asymmetric or discontinuous development. What is unclear, however, which experimental animal Kramer would have chosen if he had continued his research on relative growth. Kramer had built up several lofts in Wilhelmshaven and Freiburg which provided him with animals for his release tests. In addition to that, we know from archive sources and U. v. St. Paul’s publications that Kramer planned to re-approach the question of night-orientation. This particular question could have stood in connection with his interest in non-domesticated forms of pigeons of which could be presumed that they were eventually furnished with this original sense more than the artificially breed carrier pigeons. The most original form of pigeon was the rock pigeon and it was the nest of one of them Kramer intended to approach when he fell down a rock wall in Italy and so died a tragic death. As a result, we may say with some certainty that Kramer’s interest in avian navigation would have been connected further to the pigeon as primary experimental animal. But what about his allometry studies? Kramer’s interest in relative growth developed from his studies of Italian Lizards but he had not systematically reassessed this species himself after having left Naples although we are informed that he was breeding Lizards in Wilhelmshaven and also that H. Maschlanka collected and measured Lizards in Italy.

1919 See to this also MPG-Archives, II. HA, Rep. 1A, IB-Files Behavioural Physiology, file “Walddorf”, ms. G. Kramer, “Plan eines Max Planck-Instituts für Ornithologie und Verhaltensphysiologie bei Tübingen” (29/05/1957), here page 1.
in the mid-1950s. Further material came from Medem’s Columbian Crocodiles and from Gulls which in North Sea region occurred in masses. Maybe, the latter two sources, too, were about to dry up. With Kramer’s move to Tübingen where his new institute was built the Gulls needed to be dropped and it is not quite clear whether Kramer’s teamwork with Medem persisted any longer. One of the reasons speaking against this hypothesis is that Kramer’s new program somewhat left behind Medem’s strictly functional orientation – the latter kept being the hunter and not the farmer so that Kramer’s attempt to domesticate his friend stagnated in a state of wishful thinking. Besides, Medem also signalled non-understanding towards Kramer’s new idea about allometry, while the former explanatory model to interpret the phenomena of relative growth as the outcome of convergent evolution was totally comprehensive for him. Also Medem took his own path in Columbia as honorary professor, later writing his own books on crocodiles. So Medem eventually was eventually not the one to play the role of the supplier in a teamwork constellation with Kramer as the head of the system for all days. As a result, one may say, that G. Kramer – if he had planned to continue his research on allometries at all – might have been seeking for a new experimental species. We know that he kept a wolf about which he also planned to publish a paper. According to the editors of the German Zeitschrift für Tierpsychologie (ZfT) where the paper appeared in 1961 posthumously, Kramer had partly edited this text before his tragic death.

It was completed by his wife using his notes. It is difficult to say whether and how Kramer had intended to spark off a new research endeavour related to wolves. In the paper we can find indicators that he planned to raise an entire series of specimens. Furthermore, we can only speculate about the direction into which this research would have gone. In contrast to most of the scientific objects Kramer had examined before, wolves are mammals living in groups with complex social organization. One the one hand, the paper includes some information concerning the relative growth of the wolf’s organs. On the other hand, however, we find also passages related to the animal’s sensory capacities and its ability to locate prey objects. Other sections are more explicitly concerned with the behaviour repertoire of the wolf and its transformation during ontogeny. Finally, there are some

1921 Ibid. This plan, however, turned out to be difficult to realize, not least, because Kramer’s wolf misbehaved and needed to be killed. I think it possible that Kramer’s motivation to raise and examine a wolf was a mixture consisting of his criticism of K. Lorenz’s erroneous instrumentalization of the wolf’s biting inhibition (thus continuing the list of fields on which Kramer used to attack latently the convictions of his friend such as the latter’s conception of instinct, his notion of “instinct-dressage” intercalation, his classification of animal societies by mating-system especially the “lizard-type”, his conception of personal recognition in animal societies, his definition of the (IRM) not to mention Kramer’s epistemological criticism of Lorenz’s questionable theory of “degeneration through domestication”) and a return to his own past that is namely his early engagement with the “Clever Dog from Weimar” which eventually had been inspired by O. Pfungst’s studies. Most interestingly, in O. Heinroth’s memorial speech for Pfungst we can find the information that Pfungst had raised a wolf, too. See Heinroth, “Pfungst’s Beziehungen zum Tiere”, 26.
1923 Ibid., 98–99.
1924 Ibid., 99–104.
indicators that Kramer was interested in the wolf’s cognitive development as a part of its maturation. Altogether, I consider it possible yet doubtful that G. Kramer, corresponding with his appointment as director of the MPI for Behavioural Physiology and his move from Wilhelmshaven to Walddorf near Tübingen where his institute was about to be built, thought about raising a new field of research related to wolves. In any case, this would have marked a caesura and this is one of the reasons why I have not integrated this study in my graphic (i.e. Fig. 2.17). Also Kramer, just around the time when it had become clear that his institute would be part of the MPI for Behavioural Physiology seemed to have begun to breed ravens. This can be inferred from letters to F. Frank and has symbolic meaning because of his attempt to discipline Lorenz’s political derailment during National Socialism. Whether there was any plan to establish a research program on, say, behavioural allometries or biological rhythms in ravens is partly an open question and hence speculation. That Kramer started breeding ravens, however, can be confirmed and also that he planned to keep ravens together with Shrikes and Robins in his new institute. In addition to that, it can be confirmed too, that Kramer planned to translate his study of relative clutch-size, a topic he had raised with Lizards in his habilitation thesis, into an ornithological area of research. “Da ich aber eine Anzahl tüchtiger Mitarbeiter habe”, Kramer writes to H. Seeliger, 

Kramer’s interest in how far genetic determinants might regulate the clutch size in response to population size belongs into the chapter of “competing reproductive strategies” and the question in how far the equilibrium states built by these trade-offs can be adaptive might suggest that Kramer eventually planned to translate the classical neo-Darwinian studies of quasi-dysfunctional reproductive constraints into his new framework which allowed to think adaptiveness only in a very restricted sense. However, from Kramer’s brief remark, it cannot be inferred whether his approach to adaptiveness has changed in comparison to his former accounts on clutch-size. We can only infer from Kramer’s letters that he considered the raven an endangered species and planned to re-establish a wild population. This can eventually be read as an indicator because one is tempted to ask for the population genetic

1925 Ibid., 104–109.
reasons that made the ravens a species threatened by extinction. A further research interest Kramer connected with the Raven as scientific object was social and reproductive behaviour.\textsuperscript{1928} To find out how G. Kramer intended to combine population genetics with behaviour study would be of great interest.

A very important question, I think, is whether Kramer’s two souls would have merged closer together in his later research. I think this question can be answered in the affirmative if we take into account non-published sources related to the building of his new institute: Both Kramer’s allometry studies and his navigation research reveal, at least to a certain extent, the same trend. His allometry papers started to take into account statics, a strictly physical and environmental cause of phylogenetic change and not related to sexual selection. In his orientation studies, too, the failure to prove true sun navigation had led towards more particulate studies which tested the effectiveness of single climatic and geophysical factors. This trend to take into account proximate environmental causes merged together in a concept of “Bio-climatology” which was planned to become one of the pillars or research foci of the new institute. Archive sources providing more detailed information concerning the outline of his and J. Aschoff’s department in the new institute which already was about to be built in 1959 when Kramer died show several aspects: At first, Kramer saw his institute – despite the fact that it shared the name “Behaviour Physiology” with the Seewiesen Institute – straightened out along different lines.\textsuperscript{1929} Second, Kramer mentions three major research foci which should be unified in the Walddorf Institute namely research on orientation with a special emphasis upon geophysical impact factors, research on biological rhythms and, finally, what he called “Bioklimatologie” (Bio-climatology).\textsuperscript{1930} All three areas of research, he argued, have in common that they stress the physical environment – a tendency I was able to carve out already in his later allometry studies, too.\textsuperscript{1931}

As a result, one may eventually say that heterogeneous research interests finally...
were about to be bound together in a homogeneous scientific orientation which became manifest in a veritable interest in forms of proximate causation provided by the physical environment such as geophysical factors in case of avian navigation and, in the last consequence, the forces of gravitation in his static analysis of the various kinds of extremities in Gulls. It would be an interesting further leading research question whether and how Kramer hoped for synergetic effects between both realms.
Forms of Epistemic Variability

a) Discussing “Epistemic Landscapes”

My dissertation thesis suffers from a “presentation problem”. The reason for this problem lies within my methodology which is aimed at making evident that a researcher’s textual and eventually also trans-textual expressions reveal his scientific orientation because they observe particular rules of differentiation. To make evident this commitment to certain principles of composition, however, requires evolving the entire tree of ideas structuring a scientific publication. These forms of knowledge organization certainly can be analyzed as such and the analysis, in turn, can be translated in a written text. However, the difficulties begin when these readings need to be re-translated into a comprehensive visual imagination in the reader. To find efficient and even more effective forms of presenting my results belonged, at least to a certain extent, to the scope of my own research questions. If the process of re-translating text into imagination is not comprehensible per se and readers, in the last consequence, need to repeat reading eventually both the primary and the secondary texts the question is raised why not present the mere results in the first place. The model for this type of presenting research results then would be the natural sciences. Like it is likely to be the case in a physicist’s or a biologist’s paper, readers are informed about the experimental setting, the final results and their value. However, the recipient of such a piece of research is usually not capable to re-enact each single step of the processes underlying a complex scientific experiment. For instance, if we are informed that G. Kramer released so and so many pigeons from the tower of the castle of Gleiberg we know at the end of the account how many pigeons returned, what the weather was like or how directed the departure of the birds actually was. But we cannot re-enact in our mind the actual flight of each single bird. Not even G. Kramer himself had this opportunity since his visual capacities (despite the use of binoculars) were not apt to observe the entire trajectory from the release site to the home loft in case of each single bird. In other words, there might be involved some kind of blind spot, a sort of black box, and the question is whether the accounts of us science historians do not have to accept this matter of fact. In the following I will therefore present the results of my reading experiments in two different forms one of which is qualitative, while the other makes an attempt to assess a life course from a more quantitative perspective. The former
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of the two strategies is going to be applied to N. Tinbergen’s life-history, while the latter aims to illustrate G. Kramer’s life course.

i) **N. Tinbergen**

The trajectory of N. Tinbergen’s intellectual life-history can be illustrated in the following graphic (Fig. 3.1). It shows the four major transitions in his science

![Graphic showing the transitions in N. Tinbergen's intellectual life-history](image)

**Dislike of Statistical Reduction**  
**Affection for Team Sports & Social Interaction**  
**Dislike of Museum- and Zoo-Zoology**  
**Affection for Hunting / Photography**

### I. Merging Divergent Interests

- \( T_{m1} - m_{1} \)
- \( m_{2} - T_{m2} \)
- \( c_{2} - fct_{1} \)
- \( desc_{2} - asc_{1} \)

“Über die Orientierung des Bienenwolfs”, I (1932)

“Über die Orientierung des Bienenwolfs”, II–IV (1935–1938)

### II. Causal Interventions

- \( T_{m1} - T_{m2} \)
- \( m_{2} - m_{2} \)
- \( fct_{1} - c_{2} \)
- \( asc_{1} - desc_{2} \)

“An Objectivistic Study of Behaviour” (1942)

“Physiologische Instinktforschung” (1948)

“The Study of Instinct” (1949)

**Tinbergen Theorizing** (1949–1959)

### III. Re-Evaluation of Theorems

- \( T_{m1} - m_{2} \)
- \( c_{1} - fct_{2} \)
- \( desc_{2} - asc_{1} \)

“Über die auslösenden und die richtunggebenden Reizsituationen” (1940)

“Die Ethologie als Hilfswissenschaft der Ökologie” (1940)

“Die Balz des Samtfalters” (1942)

“On the Stimulus Situation Releasing the Begging Response” (1930)

**Tinbergen Practice** (1949–1959)

### IV. Drift to Functional Ethology

- \( T_{m1} - m_{1} \)
- \( c_{1} - fct_{2} \)
- \( desc_{2} - asc_{1} \)

“Early Childhood Autism” (1972)

“Zur Paarungsbiologie der Flussseeschwalbe” (1931)

“Field Observations of East Greenland Birds”, I–II (1935–1939)

“Eine reizbiologische Analyse” (1937)

“Über die auslösenden und die richtunggebenden Reizsituationen” (1939)

“Die Ethologie als Hilfswissenschaft der Ökologie” (1940)

“Die Balz des Samtfalters” (1942)

“On the Stimulus Situation Releasing the Begging Response” (1930)

**Tinbergen Practice** (1959–1974)

“Early Childhood Autism” (1972)

“Über die auslösenden und die richtunggebenden Reizsituationen” (1940)

“Die Ethologie als Hilfswissenschaft der Ökologie” (1940)

“Die Balz des Samtfalters” (1942)

“On the Stimulus Situation Releasing the Begging Response” (1930)

**Tinbergen Practice** (1959–1974)

“Early Childhood Autism” (1972)

N. Tinbergen’s Intellectual Life-History (1930–1983)

and life (merging of divergent interests, intervention on the level of causation, relocating paradoxa within the epistemic reference systems and, finally, drifting to a homogeneous scientific orientation). I have not reconstructed Niko’s very early life-history on basis of scientific publications but, instead, have drawn relevant information from biographical and autobiographical data. Thus it seems that Tinbergen’s...
dislike of statistical reductions (his brother Jan’s domain), his affection for playful forms of social interaction, as well as his repudiation of keeping animals (dead or alive) and his passion for foraging in the wild and photographing might be early forms of scientific practices, based on dispositions, some of which shaped his further development. The interesting question at this point is whether we are prepared to see a connection between his early papers on social and reproductive behaviour and his affection for team sports or between his passion for symbolic hunting and the Digger Wasp’s predatory behaviour. In any case, Niko’s very early scientific works show that he merged exactly those reference systems which G. Kramer rejected. All further stages of Niko’s life course take place in two different realms whereby I have plotted in each case the inner constitution of the reference systems shaping both the textual and – as it seems – also the non-textual scientific expressions. The short-cuts I’ve used (m, Tm, Fct, Asc, etc.) follow the conventions I have outlined in the introduction of my thesis. In concrete, the biased dichotomies in each case represent the “root-areas” of the textual representations, a combination of connected texts or a system of practices. Thus Niko’s first study about the Digger Wasp’s hunting behaviour operates with a methodological distinction between close-distance and long-distance orientation. The study of the tern’s reproductive cycle describes the transition between social and sexual life. The two papers being concerned with the behaviour of East Greenland birds build a unit in as much as they both treat atypical reproductive systems. However, they differ from each other insofar as one paper deals with the behavioural effects of reverse sexual dimorphism, while the other examines the relation between morphology and behaviour in a species without sexual dimorphism at all. The follow-up studies on orientation in Digger Wasps pick up the primary distinction between close and remote orientation on basis of an altered causal architecture and evolve both themes in separate studies: While the study published in the year 1935 combines the question of close-range orientation with the actual act of hunting and killing (II.), the two subsequently published studies elaborate upon the mechanisms allowing the recognition of the nest, both with a view of homing from known (III.) and remote unknown territory (IV.). Niko’s handbook *The Study of Instinct* and all other more theoretical papers of that period are clear expressions of the causal analytical framework that shaped advanced ethological theorizing. At the foremost, this epistemic reference system generated studies which were concerned with the questions of organization and centralization of the nervous system but also led towards a new model of behavioural systematics which was based on a broad basis of comparative data and “soft” reduction. Most of the empirical studies Niko published between 1938 and 1949 were related to cooperative research projects he had conducted with pupils. Moreover, all these studies were related to K. Lorenz’s special phylogeny of releaser, which Tinbergen had acquired in a first step but after that developed further without modifying the basic framework (as for instance G. Kramer and some of Niko’s pupils did). In developing further J. v. Uexküll’s environmental theory and by re-reading some of I. Kant’s works, Lorenz had postulated a direct adaptive correlation between an organism’s receptor schemata, on the one hand, and the bundle of stimulating qualities being apt to release a particular response, on the other. Moreover, Lo-
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Renz’s model of adaptive correlation included two mutually intertwined processes. The decrease of a schema’s inherent complexity (in linguistic terms its intension) was thought to be correlated with an increase of the number of releasive situations (the extension of a concept, respectively). Tinbergen adopted this dual and mutually intertwined logic but concentrated on non-plastic correlations of “key” and “lock”, namely the correlation of so-called innate releasing mechanisms (IRM) with corresponding species-specific signal movements (releaser in a narrow sense).¹ Niko’s cooperate projects carried out between 1938 and 1949, in the last consequence, were aimed at finding further sub- and sub-sub-differentiation of both mentioned categories so that Lorenz’s idea of mutual correlation could be not even maintained but also substantiated on further subaltern levels of the model. Since his move to Oxford in 1949, and despite the fact that on the deep-structure level of his scientific development epistemic continuity persisted further, Tinbergen introduced a fundamental division of labour with far-reaching consequences. While henceforth theorizing was his part, the more empirical side of the Classical Ethological Synthesis was left to his PhD students. The latter of the two realms of Niko’s life and research reactivated the technique with which he initiated cooperate research projects already before by applying a dual gesture: The PhD projects of Tinbergen’s students usually began with an initial impulse provided by himself, very often in combination with a gesture of critical reception. Yet, after this initial act of inauguration, Niko’s pupils usually profited from a high degree of academic freedom. This pattern of reception had already guided Niko’s own acquisition of Lorenz’s environmental theory but henceforth was developed further into a highly sophisticated system of academic socialization which finally resulted in a rather advanced, and some might even say self-enclosed, peer-to-peer tutoring system. This system – G. Beale described it as “Tinbergian Practice” – most likely was kept intact until Niko’s retirement in 1974 no matter whether his later students reinterpreted this system, for instance, in writing theses that represented those epistemic realms Niko had side-lined between 1949 and 1959 but finally adopted in his turn to Functional Ethology in a slightly modified version in 1962, as I believe. As long as Niko defended the classical ethological outline of his still young scientific discipline, his theorizing maintained the causal analytical reference system, not only in that it incorporated the idea of adaptive radiation (which Niko in a gesture of partial misreading identified as neo-Darwinian) into his overall concept of Gull systematics but also by discipling his “renegade” pupils by means of a highly sophisticated boundarying and re-boundarying procedure which finally generated the idea that only the organic system as whole can be made subject of natural selection.²

¹ In a later more popular manuscript for a radio broadcast N. Tinbergen puts great emphasis upon the adaptiveness of the releaser to a signal function but also stresses their handicap potential. See Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3143, C 235, ms. “The Courtship of Animals” (n. d.). See in addition the follow-up talks ibid., Ms.Eng. c. 3143, C 235, ms. “Fighting and Threat as Means of Spacing-Out” (n. d.) and ibid., Ms.Eng. c. 3143, C 235, ms. “An Explanatory Theory of Courtship” (n. d.).

² For the more recent reassessment of the idea that “organisms themselves represent the determinants of selectable variation and innovation” – a theorem shared by G. Kramer – see Pigliucci et al., “Elements of an Extended Evolutionary Synthesis”, 13–14.

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c theorizing altered once more in as much as he adopted a reference system which I have circumscribed as “Darwin’s paradox” and which was reinterpreted in Niko’s works after 1962 in the form of a handicap theoretical approach (in a wider sense) to animal and human behaviour.3 Thus, Tinbergen tried to answer the question why parent gulls carry away egg-shells from their nest just in the moment when the young ones are in need of their protection most. He tackled the question how visual discrimination can be both functional and non-deliberate and, finally, he entered the question why organisms sometimes prefer to live in more or less drastic isolation although social aggregations are thought to provide a more of comfort and protection. All these themes which Niko partly raised in his pioneering ecological studies and which later partly developed in extensive areas of research in Behavioural Ecology can be interpreted as the output of a heuristically highly productive end-paradox epistemic framework. Finally, even Niko’s late engagement with childhood autism can be interpreted on basis of the two epistemic realms which guided both Tinbergen’s own ecological studies and his later pupils’ research. This perspective reveals that Elisabeth and Niko Tinbergen’s engagement with a behavioural malfunction in humans was subject of a historical transformation process. Thus it seems that the autism project began as any other Tinbergenian project before, namely in a gesture of critical reception whereby the act of criticizing the works and positions of others finally was leading to an own, more theoretical, contribution. According Elisabeth and Niko Tinbergen, the autistic disorder could be explained as motivation conflict which, in their view, was common in normal children but in “autistic” ones remains unsolved. Like in Niko’s ecological studies Early Childhood Autism thus seems to operate with a dualism between normal and non-normal by simultaneously applying the question how the non-normal can be normal (and, from the standpoint of the autistic child, even functional) as well. The Tinbergen’s later encounters with “autistic” children seems to be shaped by this dualistic framework as a whole. Niko’s nomination for the Nobel Prize in 1973 and his so-called “Nobel Lecture” marked a turning point. On basis of the wider human ecological perspective N. Tinbergen had outlined in his acceptance speech the focus had shifted from aetiology to the question of cure. The measures the Tinbergen’s suggested were, in the last consequence, based upon a specific homoeostatic understanding of an organism’s life functions, its psyche but also its relation to its wider biotic (i.e. social) and abiotic (i.e. inanimate) environment. From the Tinbergen’s later accounts we can infer that their model of homoeostatic equilibrium system defined the intervention caused by an impulse from the outside as productive and advantageous in as much as emotionally stagnated bondings were forced to experience the opposite impulse, so to speak, as suffusion backwards and from beneath. I think, the method of holding, the Tinbergen’s adopted from M. Welch and henceforth propagated against all kinds of resistance, might be a clinical practice that fulfills this disposition and this could be one of the reasons why it turned out to be so attractive for the Tinbergen’s. Lastly, their intervention into the clinical field can be interpreted according to this homoeostatic model of social interaction and its underlying epistemological dispo-

3 For Niko’s widening of perspective beyond mere studying of homologies see Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3156, E 2, letter N. Tinbergen to R. Burkhardt (19/06/1982).
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sition as well since the Tinbergen’s intended to gain acceptance for a more balanced perspective on both the aetiology and the problematic of curing autistic children. The qualitative analysis I have suggested to reconstruct N. Tinbergen’s life course is a compromise inasmuch as it deduces significant shifts from an incomplete, albeit representative, sample of events and accounts. It has to face the problematic that not all stations in a researcher’s life become necessarily manifest in written documents. In other words, textualization (semiosis in general) can be a gradually increasing phenomenon. The main advantage of a qualitative, graphical representation of an intellectual life-history is that it lets participate the reader in the heuristic process which had led to this reduction in the first place. Moreover, it is capable to make visible when single textual representations establish larger (intertextual) units. And, finally, evolving epistemic reference systems leads a historical reconstruction reliably and precisely to the relevant breaking points of the transformation process a researcher’s life is subjected. In all life courses I have examined so far the reproductive dynamics which is keeping alive an epistemic community is caused by the productive altering of the reference systems establishing a respective scientific orientation – either in form of their replacement but also by shifting the overtone, inverting the inherent directionality or, in some cases, even both. A qualitative analysis of these reference systems including their transformation over time therefore can make evident the forms of epistemic variability the process of knowledge production and reproduction can take.

ii) G. Kramer

In course of my study I became aware that both implicit and explicit forms of knowledge organization might eventually be one of the most significant indicators for the epistemic shifts structuring the scientific development of individual researchers, which, in turn, might be considered representative expressions of the reproductive dynamics of a scientific community as a whole. I have therefore analyzed carefully most of the studies G. Kramer has published in course of his academic career. My primary intention thereby was to carve out the guiding epistemic patterns and classify Kramer’s publications by using these schemes as criterion. If translated into graphical form the result turns out as an impressive visual illustration of Kramer’s scientific development between ca. 1930 and 1959 (Fig. 3.2). I would like to use this graphic and the explanation of its details to summarize the course of G. Kramer’s intellectual life-history. At first, I’d like to direct my reader’s attention to the fact that Fig. 3.2 is a three-dimensional graphic plotting Kramer’s publications – each study is represented by one cube – by using three different independent criteria, namely the type of epistemic scheme regulating the order of the study, the year of its publication and the amount of publications per year. As far as I can see the list of scientific publications I have worked through is almost complete with the exception of two studies: So far, I was not able to get hold of Kramer’s contribution to an Italian dictionary with the title “L’orientamento”.

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G. Kramer’s Intellectual Life-History (1930–1959 / 1961), Overview

Fig. 3.2
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addition to that, I have excluded a posthumously published account of observations Kramer had made with a wolf which he had raised. As to the date of a publication, it is important to keep in mind that each study appears with some delay of time so that the scientific shifts these studies potentially represent need to be slightly dated back. I have differentiated altogether eight different epistemic schemes in one scientific community and treated further derivatives as transitional forms. The number eight is a result of the fact that I have actually worked with four qualitatively different schemes but these patterns change slightly their shape depending on their epistemological environment, that is to say, pending on with which other scheme they are combined and whether they appear in a homogeneous or a heterogeneous environment. These nuances are difficult to assess on a phenomenological level. Like N. Tinbergen, G. Kramer’s very early research interests seemed to be both divided and distributed over antagonistic scientific orientations. And like Tinbergen’s life course, Kramer’s trajectory seems to have merged these two realms finally together, thus putting his life and research upon a track that finally made him a veritable representative of the Modern Synthesis of Evolution. It is one of the most impressive results of my thesis, that Kramer’s intellectual life history does not at all cover those epistemic schemes which establish the synthesis of Classical Ethology and which are represented in the works of N. Tinbergen, E. v. Holst and K. Lorenz (with exception of his late homogeneous orientation where he adopted the causal analytical framework which was typical for Classical Ethology, albeit in a slightly modified form). Altogether, the graphic shows that Kramer’s life-history went through three major stages, namely an initial period during which his interests were divided between two extreme positions, a subsequent phase of synthesizing and, finally, a last phase in course of which his scientific development drifted to one of the homogeneous scientific orientations. On closer inspection of the figure, especially the synthetic parts of his scientific development, show exactly the three major epistemic shifts (expressed with different intensities of red and green colours in the graphic) Kramer’s development shares with all other neo-Darwinian and ethological trajectories I have examined. These shifts are: A trend to establish a heterogeneous scientific orientation, in other words, to build an epistemic synthesis, the transposition of epistemic patterns on the level of causation and, finally, the epistemic re-evaluations within the epistemic frames primarily leading to a re-location of the paradoxa within these frameworks.

In G. Kramer’s intellectual life history, like it was the case with other neo-Darwinians and ethologists these major shifts occurred in the first half of the 20th century, thus establishing a longer period of epistemic continuity beyond the political caesuras provided by the Second World War and related historical events. Only the mid-1950s, again, appear to be another historical period of increased epistemic dynamics. A second point I’d like to discuss besides the three dimensional way of plotting Kramer’s textual expressions is the question how to treat larger epistemic units consisting

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5 Kramer, “Beobachtungen an einem von uns aufgezogenen Wolf”.
6 I have illustrated the intervention on the level of causation also with gradient colouration so that all shifts can be expressed on one and the same plane. If the very nature of this transition was interpreted as the signal for a switch into another epistemic community I would have to place all further “cubes” on another parallel plane in my graphic.
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of two or more textual representations. My approach to correlate scientific manifestations with epistemic schemata presupposes that the complexity outlined in these accounts can be reduced. In most accounts this procedure seems to be possible simply because behavioural scientists gave their narrations a form, structure or organization. In many, if not all, the publications written by E. v. Holst, N. Tinbergen, K. Lorenz and G. Kramer there is a tendency to present the results of their studies in a highly sophisticated and differentiated way which was apt to mark positions and moves within the epistemic space of their scientific community. In other words, the function of the scientific manifestations I have examined is not only to present results but also to keep alive the self-reproductive dynamics of an epistemic community. When we intend to correlate scientific manifestations of all kinds with epistemic reference systems and present the results quantitatively we must be aware of a phenomenon literature scientists use to describe in terms of “intertextuality”.\(^7\) This is to say, that in some cases not one single account but two or more accounts together establish one epistemic unit whereby this entity as a whole usually builds the epistemic scheme, that is, a complex of semantic relations including direction, tautology, paradox, overtone and hierarchies. In some cases the intertextual unit might even coincide with the entire scientific orientation. For instance, W. James’ *Principles of Psychology* can be assessed correctly from an epistemological standpoint eventually only if we understand the dyad which is established by the fact that this work is divided in two separate though connected parts. E. v. Holst’s dissertation thesis obtains its adequate position within the epistemic space of his scientific community only as a combination of the two publications in which the results appeared. In case of G. Kramer’s works I have declared a publication an “intertextuality phenomenon” only on very rare occasions, that is, when two texts referred to each other not only by the usual system of academic cross-referencing but, beyond that, reveal a stable logic relationship. For instance, Kramer’s cooperation with R. Mertens resulted in two publications one of which was treating Istrian *mainland lizards*, while the other was concerned with *insula forms*. In this case the dichotomy of mainland vs. insular established the logic or semantic relation between the two accounts. Moreover, usually one of the two combined studies turns out to have a more supplementary character or is “framed” as I’d like to put it. In my graphic the publications linked together in one intertextual unit appear as separate cubes but the dependent or subaltern studies are marked as “framed”.\(^8\) A final aspect I’d like to pick out and discus is the question how arbitrary the correlation between epistemic reference systems and concrete phenomenological expressions actually is. As I have already explained, in G. Kramer’s intellectual life-history, the two main epistemic schemes in which most of his scientific accounts are “bathed”, appear as two different “heuristic machineries” but also as different realms of his en-

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7 If I remember correctly, the concept of “intertextuality” has first been introduced by J. Kristeva in the late 1960s in order to describe the network of mutual cross-references particularly in literary texts. My adoption of this concept is lose and adjusted to my own needs.

8 In concrete this means that these studies appear as cubes with red line and green fill colours or, vice versa, green lines and red fill colour. The frame determines the rubric under which I have classified the text epistemologically. These texts are read as “x is supplementary part of a larger unit together with and possibly ruled by y”.

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tire personality or as two different types of researcher. Thus Kramer differentiated in *Das Bewußtsein des historischen Hintergrundes in der Naturforschung* (“The Consciousness of the Historical Background in the Natural Sciences”) (1955) between the aesthete or inventor who does research for its own sake and feels inner satisfaction when he is able to build abstractions and share them with others, on the one hand, and the pugnacious goal-oriented professional, on the other. As E. Stresemann has remarked correctly in his obituary, G. Kramer was simultaneously both – and, what is even more exciting, he seemed to have switched deliberately between the two realms of his personality. That is to say, if we compare his research interests and the topics his works covered over the years with the heuristic programs he applied to deal with his current theme we will be able to find only a rather loose correlation before, and a more stable correlation after, his move to the MPI for Marine Biology in Wilhelmshaven. That means Kramer’s studies on animal metabolism appear in both realms and so do his micro-systematic works of Italian lizards. After his move to Wilhelmshaven there is a stronger correlation between his interest in avian orientation and navigation and the diagnostic scheme, on the one hand, and between his research on allometries and a more histological approach, on the other. However, there are also exceptions to this rule. For instance, the presentation Kramer delivered before the German Zoological Society in 1958 and which was later published under the title “Über die Heimfindeleistung von unter Sichtbegrenzung aufgewachsenen Brieftauben” (1959) seems to reveal a non-holistic scheme most likely because of the scientific practices governing the speeches of the society, that is, namely the fact, that the presentations were usually supplemented by a discussion involving the auditorium. Other ornithological accounts have clearly a preparatory character or treat peripheral aspects of the main theme so that it apparently seemed to be more appropriate if the respective aspect was singled out in a first step but amplified in a second. My impression is also that Kramer switched to the mode of the preparatory account when his abstractions turned out to be problematic or insufficient. According to G. Kramer’s own statement which is also quoted in E. Stresemann’s obituary this occurred at least three times in the former’s career. “Ich hatte ursprünglich nur vor”, Kramer comments on his early research on avian orientation,

in noch drastischerer Weise als Heinroth die visuelle Seite und Erfahrungsgrundlage des Brieftauben Such- und Heimfindevermögens aufzuzeigen. Aber sie benehmen sich ganz anders. Es ist, glaube ich, das 3. Mal in meiner wissenschaftl. Tätigkeit, daß ich meine Ausgangshypothese widerlege. (Ich gestehe mir das Durchdringensein von einer vorgefaßten Meinung stets offen ein und versuche sie nicht zu vermeiden. Das ist besser, als wenn man sie weguheucheln versucht; wenigstens liegt es mir mehr.) – Dies ist natürlich noch im Stadium der privaten Mitteilung. [Originally I only had planned to evince, in an even more drastic way than O. Heinroth did, the visual side and the experiential basis of the searching and home-finding-ability of carrier pigeons. Yet, they behave quite differently. It is, I believe, the third time in my research that I disprove my initial hypothesis. (I always admit frankly that I am pervaded by a presupposed opinion and do not try to avoid it. This is better than if one attempts to deny it hypocritically; at least this applies more to me.) – This, certainly, is still in a state of private notification.]\(^9\)

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Kramer’s account does not mention what these three occasions precisely were when he had to revise his presupposed opinions except the latest one. However, I think that – besides the heuristic crisis which occurred during his studies on metabolism – his early geological theory of geographic isolation established a very strong, even mathematical, abstraction of the process of speciation which was eventually not suitable to represent the arbitrariness involved in the development of insular populations. This morphological arbitrariness eventually could be grasped better with a concept of drift or, very simply, by the persistence of selective pressures which Kramer was not prepared to sacrifice even in small populations. The years after Kramer’s cooperation with R. Mertens are characterized by a more cautious approach to the micro-systematic problematic. This means that Kramer began to raise empirically and step by step those characters which turned out to be valuable for his research endeavour. His style in these studies was more questioning, reductions were established gradually on basis of arguments and had a more provisional character. Heuristic uncertainty and openness of the accounts went hand in hand. I presume that Kramer, at first, eventually planned to tie once more the knot in a larger micro-systematic study on Italian Lizards. And it is not entirely unlikely that this study was meant to be his habilitation thesis. However, as it turned out, his reasoning on speciation in Lizards stayed within the frame that was guided by genic variation and natural selection. His actual habilitation thesis proves this impressively and herewith also documents his neglect to accept the canonical division of labour in neo-Darwinian theorizing between the idea of sympatric speciation in larger populations and allopartic speciation in small ones. In sum, I think that the choice which scheme Kramer was prone to apply was dependent on the heuristic function each program promised to have and less the scientific object (i.e. the experimental animal) or the environment (e.g. lab vs. field) within which the current research project was carried out. My results substantiate therefore my view that it is problematic when science historians aim to abstract scientific transformation processes on mere phenomenological level, for instance, by claiming the existence of representative model organism or the formative impact of the respective environment of research since these reductions are endangered to presuppose a one-to-one correlation between the phenomenological expressions and the desired abstractions. Although I certainly admit that any kind of phenomenological terminology is necessary to tell a history and the mentioned approaches do have a legitimate scope of applicability, my analysis of G. Kramer’s (and others’) life-histories clearly reveals that there is no fixed one-to-one correlation between epistemic deep structure and phenomenological expression. I consider it therefore necessary to differentiate between the more and the less conservative strata of scientific variability which presupposes also that one scheme can precipitate in several different manifestations and, vice versa, one manifestation can be the expression of different quite antagonistic schemes. The prototypical example for the latter type of correlation is K. Lorenz’s reinterpretation of his early instinct concept (put forward by O. Heinroth or H. E. Ziegler) finally leading to a more gestalt theoretical account that was compatible with W. Craig’s dualism of appetence and consummatory act. In other words, Lorenz kept the word but changed the underlying concept or structure. Kra-
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mer’s subtle criticism of Lorenz’s hypothetical realism also belongs to this type of variability. Examples for finding manifold expressions for one and the same epistemic scheme are many. I just like to mention the various contexts within which G. Kramer applied the model of diagnostic analysis (which was different from the reductive causal analysis classical ethologists put forward). The latter form of epistemic variability particularly applies to the phases of a life course during which the epistemic foundations remain constant over a longer period of time. This was the case in all the life-histories I’ve examined between 1938 and ca. 1956, in case of the classical ethologists even longer. Yet, in contrast to classical ethologists, and alike to N. Tinbergen’s life course, G. Kramer’s trajectory reveals a final drift to a homogeneous scientific orientation which, however, established an antagonistic pole to Tinbergen’s position. While Tinbergen turned to Functional Ethology, Kramer’s development was pointing towards a more holistic position. His concept of “bio-climatology” and the emphasis of static physical causes (weather, gravitation, geophysical parameters, etc.) substantiate this view.

A quantitative representation of a life-course has the advantage that it can make evident the high degree of orderliness with which a researcher’s life-history may have developed. In G. Kramer’s case we find represented only those lines which finally were leading to the Modern Synthesis and not one single representation (except after his turn) which used to be a constituent of the Ethological Synthesis. Moreover, a quantitative representation can show the preferences for one or the other epistemic reference system at a given point in time. For instance, in G. Kramer’s very early research we can find a preponderance of the sceptical narrative scheme he applied in his ornithological accounts or the evaluation of a “clever” dog. His dissertation thesis, by contrast, is the only strictly purely physiological work of this period. From this perspective we may ask whether such preponderances indicate the direction of a later turn. The form of representing results thus leads to another hypothesis that can be tested in further comparative studies. Another advantage may be the gradual character of the representation. Especially in periods of long epistemological continuity quantitative shifts might indicate or anticipate future developments. The gradualist perspective might also lead to another interpretation of the forms of epistemic variability underlying each transition. Who says that what I have called “re-evaluations” and the mechanism underlying G. Kramer’s and N. Tinbergen’s final turns are not actually the same or, at least, similar so that the later of the two shifts appears only as an extreme expression of the former? Finally, it should be discussed whether it is allowed to extrapolate from the orderly structure Kramer’s life course reveals to the existence of what I have called “epistemic cycles”. What the graphic does show is that researchers build synthetic constellations and eventually follow a trend or relent a pressure when they drift to another orientation in their later lives. Especially my examinations of the works written by the two cohorts of N. Tinbergen’s pupils shows that students either maintain and complete the orientation of their teacher or they form their own orientation by synthesizing divergent interests just like the generation of their teachers did before them. A large scale quantitative assessment of these response patterns in various different chronological cross-sections could eventually solve this question. N. Tinbergen’s
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and G. Kramer’s life histories both seem to respond to these subversive moves of their pupil generation each in their own way with a third discrete period in their academic trajectories. This and the way how the interplay between academic socialization and break through of one’s disposition (the latter potentially giving a further impulse in the lives of the socializers) is distributed in my trajectory model, at least in my opinion, seems to prove some kind of “force” underlying the dynamics of the cycles in question upon which the systems of scientific ideas act somewhat inert. If we could accept that inertia is a common quality of cultural representation it would be possible, so to say as a reverse conclusion, to deduce some kind of underlying driving force which is permanently undermining these representations but is becoming overt particularly in epochal times of upheaval. Next to the advantages, a quantitative representation of a life course also has some disadvantages. One of them surely is that the entire process of complexity reduction which was leading to a particular placement of a scientific manifestation cannot be traced back or be re-enacted. In the last consequence, the reading experiments must be repeated so that another form of intersubjective quality control possibly emerges in the humanities.

b) Approximating Modes of Scientific Change

i) Within the Epistemic Community

One reference system – Different paths. At the beginning of my dissertation thesis I put forward the hypothesis that cyclic transformation processes might have a formative impact on a person’s life course. This especially seems to be the case if the scientific paradigm within which a researcher receives her or his academic education and the orientation of a person’s disposition do not coincide with each other. In this special case a person’s disposition is supposed to break through in a process during which a researcher’s scientific orientation as a whole is built of two divergent constituents which had been parted before as a result of the researcher’s previous academic socialization. I’d like to call this principle the “‘Two’-to-‘One’-Rule”. It applies independently whether an academic socialization takes place in heterogeneous orientations and the breakthrough points into the direction of a homogeneous scientific paradigm or, vice versa. The life-histories of all ethologists I have examined so far, including the ones I have put into the centre of my dissertation thesis, seem to confirm this rule. N. Tinbergen and G. Kramer were socialized in a time of cultural polarization early in the period between the two World Wars and built their orientation as combination of constituents which they adopted from the former antagonists, in the “no-man’s-land” between vitalism and mechanism, as K. Lorenz once put it with a view of the position of the niche Ethology had occupied within the field of the behaviour sciences. However, if both life courses are

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10 In several respects similarly to how I use the concept of “orientation” R. Jaeggi recently defined “forms of life” as “normatively structured inert bundles of social practices”. If I understood correctly, Jaeggi derives the inertia of social practices from the resistances their usage is subject to or their change has to face (especially as a consequence of materialization per se or non-transparent expression). See R. Jaeggi. “Towards an Immanent Critique of Forms of Life”. In: Raisons politiques 57.1 (2015), 18 and 15 for the quotation. If the crisis is the reason to reflect and possibly alter practices this raises the question what the origin of this crises actually is.

11 For the corresponding references see fn. 758, page 266 of my thesis.
translated into the reference system I have suggested in the introduction of my thesis – this system here functions as the tertium comparationis – it becomes evident that Kramer’s and Tinbergen’s courses were not identical rather than complementary.\textsuperscript{12} The one fused the constituents the other declined. As a result, Kramer turned out as a representative of the Modern Synthesis, while N. Tinbergen became a typical, if not the most typical, advocate of the Classical Ethological Synthesis. Both researchers have in common that their life course reveals an additional transition beyond and after their synthetic period. Yet, the direction of the turns the trajectories of both researchers exhibited since 1956 (Kramer) and 1959 (N. Tinbergen) was different – both life courses headed towards antagonistic poles. Thus N. Tinbergen developed into pioneer of Functional Ethology which could take concrete forms in Behavioural Ecology, new forms of Functional Anatomy and Physiology and well as in early interpretations of Human Ecology. G. Kramer, by contrast, eventually approached a position upon which S. J. Gould once laid his finger while speaking of the “Return of the Hopeful Monsters” in alluding to R. Goldschmidt who had coined the catchphrase. G. Kramer himself did not speak of “hopeful monsters” in his late studies of relative growth but, instead, preferred the phrase “not hopeless” monsters which signals a slightly deviating nuance. My hypothesis, a hypothesis which is to be tested still though, is that Kramer’s late scientific orientation (and eventually also S. J. Gould’s) differed from R. Goldschmidt’s position, to which they alluded, in the modified causal architecture which reasoning on evolution in neo-Darwinian and post-synthetic terms necessarily implied. In conclusion, one may say that the trajectories of both researchers proceeded complementary without overlapping at any point in time. However, it must be kept in mind that Niko’s turn to Ecology implied the adoption of a neo-Darwinian theorem, while Kramer’s turn to Bio-climatology included a form of reductive causal analysis which was similar to the one classical ethologists such as K. Lorenz, E. v. Holst and also N. Tinbergen in their mechanomorph period between 1938 and 1959 had put forward as one essential pillar of their still young scientific discipline. In other words, G. Kramer eventually adopted a stance he, in his allegory of the year 1941, eventually associated with the position of the Raven. It is one of the really nice coincidences that G. Kramer in the second half of the 1950s began to breed ravens so that just in the right moment, that is, when it became clear that his new institute would be part of the MPI for Behavioural Physiology, this “raven issue” appeared repeatedly in letters he exchanged with friends and colleagues.

Different paths – Analogous forms of transition. I have tried to present the life courses of both G. Kramer and N. Tinbergen in a both structured and more or less synchronized way. In doing so, I have placed “markers” in my account of both paths which I called “Transition One”, “Transition Two” and so forth and whose function is to compare the forms of epistemic variability which were accompanying each transition in both life courses. The result is quite astounding: Although the trajectories of both researchers covered complementary scientific orientations within the epistemic space of their scientific community, they definitely share sim-

\textsuperscript{12} My qualitative analysis of N. Tinbergen’s life course provides the necessary argument, my quantitative assessment of Kramer’s publications provides both the necessary and the sufficient argument for this proposition so that it can be postulated with some certainty.
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ilar or even the same types of epistemic transition their life-histories went through and, what is even more astonishing, these transitions share the same chronological order. The fact that too many individuals change similarly and simultaneously in different environments and even different time layers is a clear indicator that theories of “pure” transmission are insufficient to explain human culture.\textsuperscript{13} In case of my study this is substantiated by the fact that both life courses, at first, united heterogeneous constituents (Transition One) and that both life courses experienced causal interventions around and after 1933 (Transition Two). Furthermore, the epistemic schemes, which can be placed in the two realms both protagonists covered each in their own way, experienced a substantial re-evaluation of theorems around the year 1938 (Transition Three). For instance, G. Kramer’s understanding of diagnosis became more cautious and relied on intersubjective confirmation (which included independent testing by co-workers and pupils) just in the same way as classical ethological reductions turned out to be less rigid in as much as they were performed on a much wider basis of empirical data. In other words, in this period instinct began to be spelt with a small “i”. Finally, both protagonists drifted to new epistemic regions since around 1956 (Kramer) and 1959 (Tinbergen) (Transition Four). And although both researchers were headed in opposite directions the mechanism of each “turn” appears to be similar. Thus G. Kramer replaced the purely adaptive framework which had guided his studies on relative growth till 1956 with an alternative system that allowed to take into account the “functional character” of insufficiently adaptive or even seemingly maladaptive phenomena of relative growth. Niko Tinbergen, on the other hand, replaced the causal analytical framework he had still defended in his theoretical accounts and reviews in the 1950s against the challenges put forward by his pupils by, in the widest sense, more handicap theoretical paradigm (“Darwin’s paradox”) he adopted from the neo-Darwinians. Both shifts seem to be based primarily, though not exclusively, on a change of the overtone in the respective epistemic frame. And moreover, from a phenomenological point of view both shifts within the “R\textsubscript{2}-realms” in the animated Fig. 1.1, page 43, of my thesis turn out to be inverse-complementary: Kramer adopted the mode of holistic thinking right in the moment the latter refuted it and Tinbergen adopted the mode of adaptionist thinking right in the moment Kramer refuted it. The realms of Kramer’s and Tinbergen’s scientific orientation which seemed to remain constant at first sight, that is the “R\textsubscript{1}-realms” in Fig. 1.1 of my thesis, eventually experienced structural changes which are at least worthwhile to be compared with each other, too. Thus, Kramer’s technique of diagnosis which he mostly applied in his studies on avian orientation and navigation slightly changed its character in so far as the starting point of this diagnoses turned out to be both wider and more exclusive. N. Tinbergen’s strategy of academic socializing altered also in as much as the works of his PhD students did not fulfil any more the overall tenor or ideal Niko had from em-

\textsuperscript{13} To explain the dissemination of theorems within societies, theories of “pure” transmission sometimes bring in an almost epidemic nuance, operate with media theory, or refer to technical innovation in means of communication. From a point of view, which is simultaneously interested in historical structures, this theories fail to explain phenomena such as congenial innovation, epistemic reconfiguration without structural prototypes or, as mentioned above, spatio-temporal coincidences in deviating environments.
Approximating Modes of Scientific Change

pirical ethological research: While the theses of the early Tinbergians began with a critical reception and then intended to exceed the results of the works they had received, later Tinbergians found ways to reduce complexity in their projects. Prototypical examples for this shift may be seen in M. Bastock’s and E. Cullen’s theses revealing the almost behaviourist stance to reduce many behavioural appearances to one gene mutation (Bastock) or one peculiarity of the natural habitat, namely cliff-nesting (Cullen). As a provisional result, I am therefore inclined to argue that even in these seemingly unaltered epistemic reference systems the tautological relations obtained another modified quality as soon as they were placed within a homogeneous scientific orientation! In sum, I’d like to emphasize therefore that the forms of epistemic variability which are guiding the linear order in both examined life courses share a high degree of structural similarity. The reasons for these astonishing parallels are unknown so that I suggest to begin with more careful and sophisticated phenomenological comparisons. What can be said so far is, that the fact that both life courses do not interfere with each other might exclude the possibility that the forms of epistemic variability underlying the four transitions in each life course can be interpreted as expressions of the non-shared epistemic schemes like other appearances such as the reconfiguration of a scientific concept (e.g. “instinct”) or the manifold expressions of one scheme such as the interpretation of the causal analytical frame in terms of central nervous organization or the comparative systematics of the Gull species. The linear order seems to be a supra-individual phenomenon or the consequence of shared epistemic schemes which I have not taken into account. Next to the more structural coincidence of both life courses there are also a number of partly more arbitrary similarities: Thus, K. Kramer and N. Tinbergen, each in his way, shared common believes and experiences: Both researchers were internationalists in different ways. N. Tinbergen intended to make popular the science of Ethology in the Anglo-American World and founded a new international journal for behaviour studies. G. Kramer moved to an international zoological research station and maintained scientific correspondences with many researchers after the war such as Luuk Tinbergen, G. V. T. Matthews and J. G. Pratt. Both trajectories show a silent period between 1942 and 1944 / 1945, due to imprisonment in a hostage camp (Tinbergen) or war service and imprisonment as prisoner of war (G. Kramer). Both life courses show a long period of epistemic continuity between 1938 and 1956 / 1959 but also relatively drastic phenomenological changes after 1945: While G. Kramer attached his two souls with two fixed research interests, avian orientation and navigation, on the one hand, and the study of relative growth, on the other, N. Tinbergen sourced out the realm of empirical research and thus created one of the most famous research groups in the world. Same forms of transition – Qualitatively different forms of researcher-environment interaction. Being granted that the epistemological shifts in different life courses can be similar in each case and, moreover, even seem to occur in a chronologically synchronized manner, it is legitimate to ask for the “causes” that might have given a (reverse) impulse for each shift. In doing so, I presuppose that the question of causation – that is to say, for both environmental modifiers and more community-inherent forms of dynamics – must be discussed separately for each form of transition. (1)
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The first transition (merging divergent constituents) is based on a process of approach and withdrawal: Some constituents are adopted, while others are refused. In Niko’s life course statistics and museum- / zoo-Zoology are refused, while the interest underlying team sports and the photographing (surrogate of hunting) are adopted and – somehow – become represented in his early scientific accounts. As the hunting of the Digger Wasp, on the one hand, and the interest in social and reproductive behaviour in various species of birds, on the other. Eventually the interest in species with no clear-cut or reversed sexual dimorphism is something which is paralleled in the role play that exists in team games such as hockey – the passion of Niko’s youth – because in play certain rules of social interaction are suspended. This is the very definition of “play”. Kramer exactly liked what Niko despised: Museum and zoo-Zoology, on the one hand, and experimental physiology, statistics and mathematical reductions, on the other. The latter of the two interests became more than obvious in his geological theory of speciation in Istrian Island Lizards. While alternative and / or additional explanations drawn from trauma- or biological optimality-theory can be possibly applied, too, for the time being, I don’t think that this primary transition requires much external formative impact upon underlying dispositions. By contrast, I think it is an indirect consequence of both the cyclic dynamics which seems to govern social systems and the result that cognitive life course features seem to be plastic in youth and stable in more advanced periods of life. Comparisons with other structurally different epistemic communities could reveal parallels in this point (e.g. in the mid-17th and mid-19th century I can confirm this for communities related to behaviour studies). (2) The second transition, the intervention on the causal level of behaviour, by contrast, seems to be a form of epistemic variability of a different kind. In both life courses we find this shift correlated with a drastic change of environmental conditions. In Niko’s case, as Hans Kruuk put forward, it might be his trip to Greenland where Tinbergen became a real hunter in the real world. In Kramer’s case things are less obvious but I think the reasons for leaving Germany in the year 1934 were primarily scientific and professional. In addition they might have had to do with the impact of National Socialism upon the KW1 for Medical Research and the realignment of the institute which was a consequence of this impact. In a first draft of my thesis I presumed stronger than I do now the possibility that this shift might have something to do with how humans experience physical handicaps. E. v. Holst suffered from an acquired heart condition which finally led to his too early death. Niko Tinbergen struggled

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14 In this context please re-read once more Niko’s letter to R. W. Burkhart describing his course of becoming an advocate of “Darwinian” functionalism, Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3156, E 2, letter N. Tinbergen to R. Burkhart (05/05/1979).

15 Without meaning to over-interpret, I tend to read Kramer’s octopus-paper a little bit as allegory for both his and O. Meyerhof’s (apparently one of Kramer’s mentors) leaving the KW1 for Medical Research: The Octopus – and, by the way also the Lizard – can strip off a now dysfunctional part of his body in order to live when being attacked by the predator.

16 For some more detailed information concerning E. v. Holst’s health problems see Heidelberg University, University Archives [quoted as: UAH]. Zoological Institute and Museum, General Issues [quoted as: B-6778/2], letter E. v. Holst to Provost of UH (06/12/1946), Heidelberg University, University Archives [quoted as: UAH]. Personal File E. v. Holst I [quoted as: PA 10036], letter E. v. Holst to Minister for Education and Cultural Affairs of the Federal State Region of Baden (21/11/1947), informing the addressee about the resignation from his
most likely with endogenous depressions. Similar phenomena can be made evident in J. Huxley’s biography and K. Lorenz eventually suffered from stomach ulcer. All these conditions could have led to a more acquired mental condition which says: What is supposed to function naturally has turned out to be dysfunctional, while the functional has become object of varying circumstances. In case of G. Kramer this disposition is not evident per se. We know from E. Stresemann’s obituary that he was a highly sensitive person but, as far as I know, had no drastic physical handicaps. On the contrary, Kramer is described as a sporty (also sportive) and athletic person by E. Stresemann. The experience of National Socialism which declared naturally talented researchers such as Kramer’s colleague O. Meyerhof in Heidelberg a second rate human being just because he was Jewish, however, could have been an event that was experienced similarly. However this is speculation. What can be confirmed is that G. Kramer experienced the National Socialist Berlin of the 1930s as “socially cold” environment. And this information, I think, must be read against the background of Kramer’s criticism he had put forward against K. Lorenz’s theory of “urban degeneration” and the fact that Kramer till his death in 1959 claimed institutional independence from the Seewiesen mother-institute. (3) Similarly related to environmental conditions is the third transition (re-evaluations of theorems inside reference systems). The move to Naples – the private economically and Darwinism-oriented international research station in Italy – possibly could have given Kramer a push similar to the one Niko experienced through his acquaintance with E. Mayr and his work. We know that the period around and after 1938, in N. Tinbergen’s life, was connected with travels abroad and the personal contact with his companion, K. Lorenz. Niko realized at that time that his research was of value and that he won confidence not least because of the academic position he had obtained at the University of Leiden. Similarly G. Kramer: He was nominated deputy director of the physiological department of the Stazione Zoologica. This suggests that transition three might be correlated with a changed attitude of a person towards responsibilities as professor and director of the Zoological Institute and Heidelberg University, University Archives [quoted as: UAH]. Personal File E. v. Holst II [quoted as: PA 4284], letter E. v. Holst to Provost of UH (02/12/1947), incl. a medical certificate (01/12/1947). See also MPG-Archives, III. HA, Rep. 47, file 665, letter E. v. Holst to M. Hartmann (04/12/1950).

For J. S. Huxley’s depression see, for instance, Huxley, *Ein Leben für die Zukunft*, 244–245. T. Munz has interpreted the various figurations Lorenz had provided of his goose “Martina” as expressions of both his changing scientific persona and his discipline. The fact that K. Lorenz, advanced in years, readdressed his goose as “an exemplar of the abnormal and a veritable catalogue of stress-induced dysfunction” (T. Munz) in combination with the quasi-autobiographic character of his late account on his geese suggests that Lorenz eventually suffered from stress-induced dysfunctions himself. For T. Munz’s argumentation see Munz, *My Goose Child Martina*, 4–5, 29–35.

However, in a letter to E. Stresemann, written soon after the war, we are informed that Kramer, at that time, suffered from (frontal) sinusitis (Stirnhöhlenerkrankung) and hay fever. See SBB, NL 150, file 37, letter G. Kramer to E. Stresemann (20/05/1947). Moreover, a military doctor certified that Kramer could not work as interpreter in Africa or tropical regions in general. See *ibid.*, file 37, letter G. Kramer to E. Stresemann (23/02/1941)\(^\text{19}\)).

This can be inferred from a letter G. Kramer wrote to O. Koehler in 1941 discussing the possibility to become O. Heinroth’s successor as director of the zoological garden. See MPG-Archives, III. HA, Rep. 77, file 11, letter G. Kramer to O. Koehler (01/04/1941). Please remember also Kramer’s attempt to discipline his friend Lorenz.
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oneself and the position she or he takes within a social environment (here the scientific community). This however, does not explain the synchronized nature of this and the previous transition nor does it explain why the linear successions of these shifts paralleled the trajectory of Ch. Darwin’s intellectual development a century before. (4) Experiencing shifting social hierarchies seems to be part of this process, though. (4) The final and fourth transition seems to be an effect of the social pressure exerted by an epistemic community and / or the pressure that is exerted by the scientific results when they have to resist critical screening in a social community. In N. Tinbergen’s case the driving moment appears to be his own work group in combination with the criticism that was put forward against Classical Ethology after the so-called Lehrman controversy. The sensed causes of this transition therefore seem to be similar social / environmental as in the previous two forms of transition but the effect, the drifting movement, is significantly different. The overtones in the epistemic reference systems change, the relative hierarchy of the constituents stay the same. In transition three the hierarchies change, the overtones remain unaltered – at least this is how I see it. After all, I am inclined to conclude that a simple dualism of academic socialization and breakthrough of dispositions does not seem to hold, at first sight, since transition two, three and four imply the influence of additional environmental modifiers with different structural effects in each case. In other words, I think it possible that a general trend towards a more of agency might be superimposed by additional environment-induced modes of personal variability to which particularly sensitive individuals respond more overtly than others. This result may support R. W. Burkhardt’s postulate to understand the history of Ethology by taking into account the changing environmental settings within which the protagonists combined science and life ("Ethology’s Ecologies"). However, I believe, “Ecology” might be a concept being too coarse when it comes to explain the complex forms of expressions in human cultural evolution as long as we mean to imply the effect of simple selective pressures when we refer to “ecological” conditions of life. Thus, behaviour geneticists distinguish more carefully between passive (cataclysmic environmental events), evoked (induced influences) and active (constructed) forms of organism-environment interaction. (21) And I think the idea standing in the background of this terminological differentiation, namely that cultural and social environments may have a constructed character, might particularly apply to the history of the sciences. (22) In other words, I believe, that a research environment such as a particular work group, a peer-reviewed journal

20 From V. B. Smocovitis account of the Modern Synthesis we can infer that main protagonists such as E. Mayr were not deliberately pursuing the unification of biological sub-branches. Asides the fact that this semi-conscious nature of the synthesis might be an expression of one of the Modern Synthesis’ primary epistemic schemes and therefore some kind of posthumous narrative strategy I also think it possible that the so-called architects did not gain full insight into the full tableau of knowledge reproduction. See Smocovitis, Unifying Biology [1996], 202–203.
21 Plomin et al., Gene, Umwelt und Verhalten, 222–224. For a plea to replace models of unidirectional with bidirectional or mutual influence between organism and environment in social theory see also Alwin et al., “Generations, Cohorts, and Social Change”, 44.
22 In the social sciences, in general, and life course theory, in particular, this aspect is discussed in terms of “agency”. See Elder et al., “The Emergence and Development of Life Course Theory”, 11–12, 15.
or an institute cannot have the same causal implications as, say, the cataclysmic event of an earthquake. In concrete, if this more thorough terminological differentiation is applied to the transitions that shaped G. Kramer’s and N. Tinbergen’s life-histories, we may eventually say that the observed causal interventions correspond with an *evoked* form of researcher-environment interaction. With his choice to live amongst Inuit N. Tinbergen chose more or less actively the conditions of life in the first place of which H. Kruuk later claimed they might have had considerable formative impact upon Niko’s further live course. The same applies to G. Kramer and his choice to move to Rovigno. His teamwork with R. Mertens which fell into this period here is of particular interest because Mertens was the expert in lizard taxonomy at that time with a dissertation and a habilitation thesis in the field and two decades experience as museum taxonomist. Kramer played the role of the junior partner in this teamwork and we can suppose that he chose Mertens because he was attracted by his works and expertise. The differences of knowledge and expertise which makes one researcher attractive for another might be experienced subjectively as different developmental velocities yet, in fact, they might be the simple outcome of another researcher’s deviating scientific orientation which the junior partner chooses in the first place to experience induced influences in the second. G. Kramer’s cooperation with R. Mertens, could possibly be an example of such an evoked researcher-environment interaction. Most interestingly, also in Niko’s encounter with the Inuit culture we find someone who played the role of the “instructor” – the shaman Karale. The third transition appears to be a mixture of both evoked and – in later stages – *actively constructed* forms of interaction. They have not only a geographic component (Greenland and Rovigno as places chosen to carry out research) but also an essential social nuance. The cooperate projects N. Tinbergen carried out with pupils (D. J. Kuenen, A. C. Perdeck, J. van Iersel, J. J. ter Pelkwick) indicate that these cooperations established actively constructed social and professional environments, and so does Niko’s early cooperate research with K. Lorenz or his contact to E. Mayr. This tendency became even stronger as soon as Tinbergen moved to Oxford and outsourced the realm of empirical ethological research in the first place which was meant to stimulate his theorizing in the second place. Again the same applies to G. Kramer who, as soon as he had moved

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23 R. E. Kohler, by contrast, writes with a view of the disrupted careers of many “new naturalists” who had tried to combine lab with field methods: “But when so many individual career choices show a similar tendency, personal factors begin to seem an inadequate explanation, and one suspects underlying social structures that can shape the careers of entire generations”. See Kohler, *Landscapes and Labscapes*, chapter 6, “Troubled Lives”, 175–211, here 179.

24 In Niko’s recollections of his legendary research with Lorenz in Altenberg he emphasizes the playful and childish atmosphere in which this research took place. See Niko’s contribution to the Festschrift published on the occasion of K. Lorenz’s 85th birthday, Bod. Lib., *N. Tinbergen Papers*, Ms.Eng. c. 3156, E 16A, ms. “Für K. Lorenz’s ‘Festschrift’” (ca. 1988).

25 Moving to Oxford, of course, was the result of free choice and at least Niko’s life as a researcher provided the opportunity to shape his environment. In a radio broadcast titled “On Turning Native”, Tinbergen explained to have gone through different stages after his emigration, namely a phase of euphoria, a period in which bliss turned into criticism and finally a more biased third phase whereby he described his present state (i.e. 1961) as “qualified happiness”, that is, as somewhat fallen between the stools. Moreover, Niko’s account shows that he thinks it possible that immigrants have an impact upon the new country (they introduce new ideas) but he also ascertains to have experienced drastic reverse effects such as loosing the bonding to his native
to Naples, began another teamwork with F. v. Medem whereby now Medem played the part of the junior researcher. And all later cooperations with Medem, who was collecting beasts in Columbia for Kramer’s allometry studies in the 1950s, repeated this constellation: F. v. Medem collected the material, whereas Kramer was the one to reflect it theoretically. That Kramer became head of a department in the MPI for Marine Biology and later in the MPI for Behavioural Physiology supports my thesis that Kramer actively shaped the environment in the first place which then influenced his course in the second. In other words, the so-called “Harnack Principle” according to which the Max-Planck institutes used to be established supported the active construction of a social and institutional environment. The “turns” (transition four), however, seemed to be of a different kind. Here Burkhardt’s ecology concept at first sight seems to apply particularly well because both Kramer’s approach of Bio-climatology and Tinbergen’s turn to Functional Ethology seemed to be influenced by deviating views and / or non-expected results. This pushed both researchers into a more passive position whereby the pressure was exerted either more directly through deviating results (Kramer) or more indirectly and mediated by the factor “fellow human being”, that is, by critical pupils and their results or by critics outside the epistemic community (Tinbergen). On the other hand, however, it can be asked whether Kramer’s and Tinbergen’s turns were not also an act of choice since, for instance, the example of K. Lorenz shows that deviating research results do not necessarily lead to the abandonment of a scientific orientation. In sum, I am therefore inclined to argue that the intervention on the level of causation, the re-evaluations and the final drift to a homogeneous scientific orientation involved forms of epistemic variability which were also correlated with different forms of researcher-environment interaction. These forms of interaction became manifest in different modes in each life course. And finally: How do I have to interpret that the form of researcher-environment interaction is correlated at all with shifts displayed in the epistemic outline of a scientific orientation?

Different environmental modifiers – common patterns? In the following paragraph I’d like to think through the consequences of this view. The critical discussion of my results so far led to the following inferences: Firstly, I think, the mere dualism of academic socialization and breakthrough of pre-existent dispositions does not hold – at least at first sight. In case of transition two, three and four secondary environmental impacts either overlap or supplement the formation of a researcher’s scientific orientation. Moreover, the mere postulate to examine “Ethology’s ecolo-

country including the command of his mother tongue. See Bod. Lib., N. Tinbergen Papers, Ms.Eng. c. 3143, C 236, ms. “On Turning Native” (ca. 02/1961).

26 One of the aspects expressing this change in roles might be that Kramer tried to promote v. Medem in as much as he tried to obtain financial assistance for their joint research. See MPG-Archives, III. HA, Rep. 47, file 797, letter G. Kramer to M. Hartmann (01/07/1938) and, for Hartmann’s support, ibid., file 797, letter M. Hartmann to G. Kramer (09/07/1938).


28 For this process of disintegration see also Bolduc, “Behavioural Ecology’s Ethological Roots”, 677.
gies” is not sufficient as long as alluding to the biological concept of “ecology” implies the mere emphasis of effective selective pressures. Behaviour scientists distinguish between passive, evoked and actively constructed organism-environment interaction. From this perspective transition two and three turn out to correspond with choices of induced and/or constructed environments, while transition four shows Kramer and Tinbergen partly in a more passive role (results deviated, pupils contradicted). This result, if it could be further substantiated, so to speak as a reverse conclusion, has far-reaching implications for my understanding of scientific change and its underlying mechanisms because it shows that the disposition to which researchers break through might eventually be complex so that this process of breaking through requires further epistemic investment (more transitions) which in each case seem to be accompanied or assisted by choosing either induced or actively constructed researcher-environment constellations. One of the preconditions of this line of thought might be, that in one and the same person there are existing different variants of scientific orientation all of which can become manifest in adequate researcher-environment constellations. The idea that human beings can develop multiple personalities within a predetermined range of options also seems to be implied in C. H. Waddington’s concept of “epigenetic landscape” which I adopted in a very loose form by coining the analogue “epistemic landscape” and by which I mean the orderly sequence of the scientific orientations a researcher covers in course of her or his life in interaction with corresponding environmental settings. Another argument for my thesis that constructed environments are more likely to yield an impact is the observation that both examined life courses display long periods of epistemic constancy between 1938 and 1956/1959 whereby the environmental causes that originated from the events of the war, that is, for instance, imprisonment and estrangement between former colleagues, apparently had no effect upon the more conservative epistemic level of the scientific development in each case, while the mid-1950s, on the contrary, provided adequate impulses for a further move.29 An indicator which points into the direction of an answer to this question is provided in Niko’s life history: He did not alter his formal attitude towards his German colleagues after the war because the ethological scheme (here of causal analysis) was able to interpret this relationship in a sense that the initial sympathy changed into distance but still provided a somewhat overwhelming sympathetic affection which was apt to keep the ties together. This shows that it is not the impact

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itself which makes a researcher switch her or his scientific orientation but, more likely, how she or he perceives these impulses on basis of the underlying schemes.30 It almost appears as if a shift in scientific orientation occurred whenever the silent contract between a person and the environmental setting she or he selected, evoked or even actively constructed breaks because the expected self-confirming feedback fails to arrive or stays out. Feedback models of this kind are not a new idea: They can be found, for instance, in C. Bazerman’s Vygotsky-Fleck model or, more recently, in R. Jaeggi’s understanding of forms of life as tools for problem solving. The crucial question to me is how to explain the discrepancy between experienced reality and anticipated feedback, which seems to be a driving moment for epistemological re-configuration, when we take constructivism seriously and accept that individuals make their reality, to a very large extent, in accordance with their forms. This inconsistency, which I consider as one of the results accomplished by studies of so-called epistemic cultures, and the particular spatio-temporal distribution of epistemic patterns suggest that discrepancies between anticipation and subjective experience originate eventually more form intrinsic organismic plasticity than previously expected.

At this point eventually the bigger picture begins to appear. The driving impulse for the modes of scientific change I have examined in a particular epistemic community seems to be a process of representation of pre-existent orientations not being represented so far in the community concerned with behaviour study. The researchers I examined managed to find results that could be interpreted in their reference systems and built a match with actual observations so that the schemes they wanted to express could be verified intersubjectively. The dispositions can be less or more complex whereby the investment it takes to hypostasize them is dependent from the epistemic outfit of the paradigms within which the initial socialization took place. In case of my epistemic community ethologists were required to translate their observations from the older Cartesian system into a Darwinian. This was only possible by applying the transitions my thesis was able to carve out. Later generations of ethologists eventually did not / do not have to repeat these steps because they found an already fully reproductive epistemic community which could absorb their ideas and represent their life courses. The transitions were assisted by corresponding researcher-environment interactions which are of great interest because the ethnologists’ choice of adequate reference persons and institutions in the given period of time (ca. 1930–1975) eventually reveals the complete range of scientific orientations within the epistemic community I have examined. This provides a unique opportunity of scientific / historical examination. Altogether the importance of the dualism between socialization and breakthrough is somewhat upgraded by this results.31

However, it should be discussed whether the turns in N. Tinbergen’s and G. Kramer’s lives exceed this dualism. What might be the reasons? Eventually it can be

30 The crucial role of subjective experiencing is strongly emphasized in recent studies concerned with modifications of the human genome due to impacts of social conditions on cell specific gene expression patterns. See Slavich et al., “The Emerging Field of Human Social Genomics”, 331, 333, 336, 337 and 341.
31 For the complementarity of interpretations based on cohort replacement effects, on the one hand,
demonstrated that the two turns I was able to track might be a consequence of shortened epistemic cycles since a researcher after having reached his predisposed destination could have been confronted with deviating pupils who had to repeat his own history. In the long 19th century we are confronted with a long cycle from 1830/50 to 1930/50. In the 20th century we find a short cycle lasting from the mid-1930s to the mid-1975s. While the long cycle embraced the time span of three or more generations, the short cycle encompasses eventually only the life-time of one generation. That means, that in a 20th century life-history a researcher, after having reached his/ her zenith, might have been confronted with a new generation of pupils which like he himself was challenged to perform a paradigmatic change and form her/his own scientific orientation. The generation of the teachers then is forced to make a decision: The teacher can either stay and defend his convictions or he can join the move of his pupils. The life-histories of those who met the challenges reveal another fourth transition towards one of the orientations their pupil generation was headed at. In conclusion, this means that the shortening of the epistemic cycles in the 20th century, at least in some case histories, extends the life-histories by a fourth transition and makes them more complex. If we interpret this fourth transition as an act of choice as well, we have to be consequent and ask whether it cannot be also part of a human’s condition to choose a form of interaction between self and other which allows a reverse construction. The fact that both G. Kramer and N. Tinbergen were highly sensitive persons points into this direction.

**ii) Across Communities**

Predictable Points of Friction. As soon as the epistemic community of neo-Darwinians and ethologists became not only a draft of orientations in one of Darwin’s books but a real social entity, the new community came into contact with other communities which were and still are underlying the same (?) cyclic dynamics as the community I have examined. These contacts were partly loaded with conflicts and my model of epistemic community (Fig. 1.1) predicts exactly the spots at which these disputes sparked off, certainly without knowing the exact concrete forms these conflicts took in each case. I pick out two examples of conflicts both of which can be explained as a result of the interaction between different varieties of an epistemic community (here in a wider sense of the word). These examples are the controversy between N. Tinbergen and professional psychiatrists about aetiology and cure of autistic children, on the one hand, and G. Kramer’s contest with J. G. Pratt for the right understanding of the pigeons’ homing ability, on the other.32

—and period effects, on the other, see Alwin et al., “Generations, Cohorts, and Social Change”, 41. For the connection between increased heritability and “the increasing capacity of the person to select and mold his or her context, which in turn strengthens the active correlation”, see also Shanahan et al., “Biological Models of Behavior and the Life Course”, 610. Other points of conflict could be added such as N. Tinbergen’s engagement in East Africa or G. Kramer’s controversy with K. Meunier in matters of relative growth. Particularly the latter would be worthwhile to be examined in more detail since Meunier was implicated with National Socialism and this raises the question how zoologists related themselves to their history after the war. My impression is that G. Kramer used to translate his protest into scientific controversy. Yet, how did this practice change over time in comparison to Kramer’s encounter with K. Lorenz?
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N. Tinbergen’s dispute with clinical psychiatrists in matters of childhood autism is a good example for the mode two competing scientific orientations, the older Experimental Psychology, and the newly emerging Functional Ethology, came into conflict. If taken into consideration the two major transitions which were leading to the Ethological Synthesis (the intervention on the level of causation and the re-evaluations) and, moreover, we presume that the new functional paradigm inherited these two epistemological modifications from Classical Ethology we may be able to correlate the observed points of friction with deeper-lying deviations in the epistemic architecture of the competing scientific orientations: At first, the dispute between N. Tinbergen and clinical psychiatrists was about whether or not the symptoms of the autism disorder syndrome can be located on a gradual scale ranging from “normal” to “autistic” behaviour. While psychiatrists such as M. Rutter and L. Wing insisted that autistic behaviour need to be treated as a qualitatively discrete behavioural phenomenon which was due to inherited dispositions, it is one of the primary characteristics of N. Tinbergen’s encounter with “autistic children” to postulate a continuous relation between “normal” and “non-normal” behaviour. In his view, normal children reveal symptoms covered by the list of abnormal behaviours Tinbergen had adopted from psychiatrists in a modified form, while, on the other hand, the so-called “autistic” children, in his view, suffered from a temporary disorder – a “derailment” in his words – and therefore could be cured. In taking a decidedly gradualist perspective in matters of childhood autism Tinbergen thus anticipated at a very early stage of the debate what nowadays is self-evident and becomes manifest when professionals speak of “autism spectrum disorders”. There are at least two more indicators for Niko’s more continuous perspective. In contrast to psychiatrists, he was prepared to take into account a wider range of aetiologies. First of all, this move had a strategic function since he was able to demonstrate that childhood autism might be a much more widely spread phenomenon than previously supposed – a result which seemed to support his opinion that autism might have an epidemic character. In addition to that, Tinbergen, by widening the scope of case histories, intended to make evident statistically cases of autistic children that had been cured but who, in his view, did not appear in any statistic so far because their symptoms seemingly did not match the clinical definition of autism. In doing so, he sought to prove the curability of the autistic behavioural disorder. Another aspect, which is closely connected with the previously mentioned one, is Tinbergen’s integration of a wider public into his argumentation – both with a view upon his wide definition of the phenomenon and the question of an adequate cure. In Niko’s view, autism, in the last consequence, was a disease caused by the maldevelopment modern western civilizations were experiencing since they left behind Niko’s archaic ideal of living in kin groups to which, he thought, the genetic outfit of us humans was particularly well adapted, especially with a view of our social behaviours. According to his homoeostatic understanding of the social economy in us humans, Tinbergen therefore thought the best therapy for autistic children would be a return to intact social relationships of which he thought they were still existent in some recent families. What he at least implicitly postulated was a process of

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self-healing by applying a set of behavioural practices which he regarded to be co-
incident with the innate paternal instincts, especially maternal instincts, that is, in
the last consequence, the genetically stored behavioural heritage of us humans. The
key to Niko’s argument is that he – eventually due to his own distrust of clinical psy-
chiatry – thought, this form of therapy would be possible only outside the clinical
profession. The fact that he dedicated his book “Autistic” Children to the so-called
“Do-It-Yourself” (DIY) mothers is only one of the more obvious expressions of
his attitude to widen his perspective on non-professionals and lay culture in order
to find and popularize an adequate cure. The second point of conflict between N.
Tinbergen’s approach to autism and his clinical opponents was related to the ques-
tion of causation. Many or most of the psychiatrists writing about autism in the
1960s and 1970s – contrary to L. Kanner’s early environmentalist theory of autism
– claimed that the actual causes for autistic symptoms were proximate. That is the
results of the 1960s and 1970s more and more suggested that the behavioural dis-
orders covered by the concept of “autism” had mostly genetic reasons. Tinbergen
did not neglect the effectiveness of genetic dispositions – in this context he spoke
of genetic or inherited “vulnerability” – but he insisted upon the existence of the
virulence of ultimate causes which he called “psychogenic” or “functional”. “Func-
tional” causes, according to Tinbergen’s view, referred to secondary environment-
induced parameters that changed, at least to a certain extent, the physical condition
of an autistic child but “nothing more”, as Niko put it in one of his letters to J.
Prekop. This “nothing more” thereby means that “psychogenic” causes in Niko’s
view, were not due to inherited factors. I have argued that N. Tinbergen, although he
grossly underestimated the heritability of the autism spectrum disorders, nonethe-
less threw a pioneering idea into the debate in as much as his “functional” causes, at
least from a structural or epistemological point of view, anticipated what nowadays
is conceived in terms secondary “epigenetic” modifications of the genome. How-
ever, although he spoke of “psychogenic” causes, Tinbergen, simply missed to real-
ize the possibility that his “functional” factors might affect the human genome. In
sum, N. Tinbergen’s dispute with clinical psychiatrists in the 1970s over the causes
of autism and the question of curability not only shows that the clash of opinions
was the result of competing epistemic regimes but also how these epistemic ref-
ence systems work, that is, the range of propositions they generate, where they
produced errors and where they turn out to have finally yielded pioneering ideas
nonetheless.

The second example I’d like to discuss is G. Kramer’s cooperation with J. G. Pratt
in matters of homing in pigeons. If my hypothesis was true and G. Kramer’s path
through life finally entered the “reign of the hopeful monsters” it seems to be a
promising undertaking to ask if and, if so, in how far Kramer came into contact with
representatives of the more neo-vitalistic orientation Kramer himself was blamed
to foster by some contemporaries. The “parapsychological laboratory” J. G. Pratt

In a letter written by G. v. Wahlert there is a hint that some of Kramer’s colleagues had blamed
his late studies of relative growth to have some kind of “vitalistische Tönung” (a vitalistic
overtone, nuance or shading). This suggests that Kramer’s contemporaries understood perfectly
well his move and the implied consequences. See MPG-Archives, III. HA, Rep. 77, file 19,
letter G. v. Wahlert to G. Kramer (10/02/1959).
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was employed at had been founded by J. B. Rhine, his boss, in cooperation with W. McDougall:35 In 1927 McDougall moved to the newly founded Duke University where he became the head of the recently founded psychology department.36 This is where McDougall’s cooperation with J. B. Rhine and his wife Louisa started and which finally “led to the foundation of the first autonomous research institute for parapsychology at an American university, marking the discipline as we know it today”.37 The reason why J. G. Pratt and G. Kramer finally found each other in a joint research program that lasted more than half a decade most likely need to be sought in the different heuristic motives both researchers connected with their scientific object but also in the latent rivalry which may have existed between the two different explanatory frameworks advocated by both researchers. While J. B. Rhine and J. G. Pratt thought avian navigation could be one of the fields to profile their hypothesis that extrasensory forces or capacities were actually existing, G. Kramer, by contrast, was primarily interested in the physical conditions allowing the carrier pigeons to display their extraordinary home finding performances. In other words, while the parapsychologists, in the last consequence, were claiming the existence of some kind of mystical or unknown ultimate cause, Kramer’s bio-climatological approach, on the contrary, was interested in proximate causes. In a letter to O. Hahn, the president of the Max-Planck Society at that time, Kramer writes in order to explain his overseas engagement:


[Especially the head of the laboratory, Dr. J. E. [J. B.] Rhine, hopes that the power of orientation in many species of birds (and other animals) has an “extrasensory” basis, analogous to clairvoyance in humans. I myself and my people do not believe that and Rhine and Pratt know that we do not believe that. The common basis upon both parties can operate is the one of common experimenting. The ability to do that cannot be questioned neither in Rhine nor in Pratt; From the latter who is also the head of the experimental site I know that because of a 1 1/2 year lasting partly written and partly personal contact. Thus the cooperation can only be fruitful for the clarification of the actual problematic. I let you know these things because you wanted to be informed about the foreign contacts.][38]

The quotation shows that both parties, the parapsychologists and the zoologists, favoured deviating explanatory models but also that they had some kind of gentleman agreement: They agreed in carrying out experiments in order to find out

36 Ibid., 139–140.
37 Ibid., 140.
the actual grounds of the homecoming ability quite independent whose explanation the results would favour. Despite the epistemological rivalry, Kramer’s cooperation with J. G. Pratt, in contrast to N. Tinbergen’s dispute over autism, had a more harmonious character but was based also on mutual benefit. Kramer in his letter to O. Hahn even speaks of “Filialenbetrieb” in the States.\textsuperscript{39} Next to the question of causality it seems worthwhile to discuss the heuristic pros and cons both parties connected with the experimental test area USA. As I have already mentioned further above, G. Kramer favoured the release sites in the United States because of their climatic advantages. In a letter to L. Tinbergen he writes:


[My pigeon policy becomes more and more adventurous. The parapsychologists who had adopted my tradition of treating the pigeons and designing the tests had invited me to come to America. I think that Pratt (Duke University Durham, North Carolina), favoured by geographic and climatic conditions will soon reach a top position amongst the experimentalists. We have performed a winter release with young pigeons which shows that everything necessary is available: Especially an eager and intelligent man (Pratt himself) and useful pigeons.][trans. CL]\textsuperscript{40}

According to Kramer, releases in the United States were also possible during winter and therefore at a higher rate, and this more of testing, Kramer argues, will win J. G. Pratt a superior position amongst the experimenters. Pratt and Rhine, by contrast, seemed to be more interested in incorporating Kramer’s expertise and also to convince him of their theoretical point of view. They were the ones who applied formally for the funding and therefore functioned as the “manager” of the project. Besides the mere scientific side of the conflicts across the competing epistemic communities points of friction can also be made evident in what I’ve called “transtextual representations” of reference systems, that is, in the behaviours of the protagonists themselves. In my methodological comments in the introductory part of my dissertation thesis I have put forward the hypothesis that epistemic reference systems can not only become manifest in form of textual expressions but also in other forms of non-textual epistemic practices. I’d like to pick up this question in a very limited extent by asking in how far G. Kramer’s and N. Tinbergen’s contacts with corresponding representatives of coexisting epistemic communities were translated into action. In order to examine transtextual epistemic practices it seems useful to find alternative circumscriptions of the three methodological levels I have ascribed to behaviour. Especially the question of causation thus seems to be translatable into the question how researchers use scientific resources (both material and immaterial) and whether they conceive themselves more as the “giver” or the “taker”. G. Kramer’s encounter with J. B. Rhine and J. G. Pratt is pervaded latently by this context. This begins with the simple fact that the correspondence between both parties

\textsuperscript{39} See \textit{ibid.}, file 8, letter G. Kramer to O. Hahn (30/01/1954).
\textsuperscript{40} \textit{Ibid.}, file 7, letter G. Kramer to L. Tinbergen (09/03/1953).
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appears to be one-sided. Although we cannot presume that in Kramer’s personal papers all his outgoing letters are preserved in form of copies, there seems to be an imbalance nonetheless. The amount of letters G. Kramer has written is fairly limited in comparison to the number complementary letters. This ascribes the role of the recipient to Kramer, while especially J. G. Pratt seems to have delivered a huge amount of data, test results and shared thoughts. Reading Kramer’s correspondence with J. B. Rhine turns out to be highly exciting if it is seen from this angle: Rhine seemed to have suffered from the conflict that he wanted to win Kramer’s expertise but this act simultaneously pushed him into the role of the “receiver”, a matter of fact which contradicted his scientific orientation (since any form of neo-Vitalism or Utilitarism usually involves the idea of ultimate causation). The solution to the problem was – and this is the latent tenor of his letters – that he adapted to Kramer’s role as the “receiver” by acting as a profiteer, too. Moreover, the parapsychologists provided the funding. Their application with the Office of Naval Research (ONR) in 1953 was successful and was renewed several times until it ended in 1958/1959. In addition to that, there was some extra funding provided by the National Science Foundation. G. Kramer had helped to obtain these funds by sharing his expertise but he also profited in return both in a more direct (compensation of expenses) and in a more indirect way (shared results, funding of associates). If we look at the entire system from the parapsychologists’ side we may interpret the entire constellation as a “giver-system” with G. Kramer as a major recipient but also with the parapsychologists taking advantage of the cooperation. This benefits apparently were more of financial kind and maybe less theoretical. After all I doubt whether the final results supported their hope to prove extrasensory perception in homing pigeons. From G. Kramer’s perspective we might interpret the cooperation as a “taker-system”, a “Filialenbetrieb” abroad, which was built up with a certain and considerable amount of investment (mainly Kramer’s theoretical and U. v. St. Paul’s practical) expertise but also with an ulterior motive, namely to profit from the results obtained in a more favourable geographical and climatic region. From a purely formal and organizational perspective the parapsychologists surely dominated the cooperation, not to say, J. G. Pratt revealed himself as a master organizer. From a more scientific point of view, however, the entire system shows very much G. Kramer’s handwriting. The practices related to the keeping of the animals, the technique of releasing them, the experimental setting and, most important, the research questions and the direction of the entire undertaking were mostly his. Summarizing G. Kramer’s and J. G.

41 This directiveness in vitalist orientations often appears as expressions of “teleological” thinking which is actually a linkage between a directional and a deterministic denotation. It is one of the main characteristics of Darwinian theorizing that this linkage broke apart.

42 In this context it is of interest to mention that the cooperation with J. G. Pratt was not the only teamwork G. Kramer maintained. Besides Pratt there were also H. Seilkopf (meteorologist), F. v. Medem (expedition zoologist, collecting reptiles), and H. Maschlanka (zoologist, collecting and measuring lizards and gulls), who supplied Kramer with material, data and preparatory research results. Similar forms of cooperation could be made evident in E. v. Holst’s and, in a different form, in K. Lorenz’s life-histories.

43 For instance, the experiments J. G. Pratt conducted with G. Kramer in cooperation were not apt to test extrasensory perception. This is why Pratt partly carried out own tests with mobile lofts which, however, led to negative results.
Pratt’s transtextual epistemic practices, one may say that it was more Kramer who was the “taker” and Pratt who was the “supplier” albeit in a more complex form than this simple dichotomy might suggest.

The epistemic practices N. Tinbergen applied during the period he was engaged with childhood autism and particularly the one which supported his fight with the psychiatrists actually need to be differentiated more carefully relative to the time period of his encounter. As to the question of the usage of scientific resources, I see four major complexes which can also be distinguished by the media the Tinbergen's used to popularize their view. The first stage consisted of picking up the theme in a gesture of critical reception and commenting the statements of others. The correspondence that has been preserved in N. Tinbergen’s personal papers shows that this early critical phase was accompanied by the exchange of ideas, opinions and opposing views between the Tinbergen’s and a number of experts in the field. The second stage was sparked off by the rejection of an article the Tinbergen's had planned to publish in the *Science* magazine and as a response and a means to convey their opinion into the wider public they wrote *Early Childhood Autism* (published in 1972). The fame Niko reached by being awarded the Nobel Prize in 1973 again marked a turning mark and we can presume that Tinbergen henceforth used his fame to propagate his view into a even wider public community. His so-called “Noble Lecture” is only one example for this strategy. Other means to popularize his view were the television and radio interviews. Whether Niko approached childhood autism in another documentary film like he did before with the behaviour of Gulls must be clarified still. The final stage is characterized by a partial withdrawal from the wider public stage. However his correspondence with J. Prekop, M. Zappella, M. Welch, Ph. Elmhirst and other therapists shows that Tinbergen still propagated his views on aetiology and curability of childhood autism, albeit within a narrower community of therapists, interested researchers and concerned parents. Niko’s scientific practices here were more to function in the background as broker of scientific contacts, organizer of personal meetings and, last but not least, to propagate M. Welch’s holding therapy. It would be of great interest to correlate N. Tinbergen’s transtextual scientific practices with corresponding argumentative strategies applied by the psychiatrists from whose standpoints Tinbergen differed. So much can be said so far: The initial informal exchange of opposite scientific standpoints changed into a scientific controversy that was carried on in scientific journals beyond Niko’s awarding with the Nobel Prize and eventually also with changing intensity. Finally, from Niko’s letters to friends and colleagues we can infer that he latently maintained ambitions to function as therapist by himself. These ambitions were refused not only by his professional opponents but also by therapists who at least partly shared Niko’s perspective.
My dissertation thesis put forward the hypothesis that scientific transformation is based on reproductive processes which are embedded in wider cultural systems with their own inherent cyclical dynamics. My particular research question thereby was how cyclic fluctuations in epistemic systems affect the life courses of researchers in the behaviour sciences of the 20th century. Focusing on behaviour was leading to a promising thematic emphasis since behaviour researchers not only made behaviour an object of their scientific reflections. Beyond that, their implicit and explicit utterances include additional information how they place themselves or move within the epistemic space of their scientific community – in other words – they fulfil an additional communicative function over and above the mere scientization of the observed phenomena. In order to raise this extra communicative function of scientific manifestations, I made an attempt to develop an adequate methodology that allows to treat a researcher’s scientific expressions relative to the stage of her / his scientific development. This method consists of both building a reference system and a reading tool which allows to locate scientific manifestations within this reference system. The former of the two puts the epistemic community in the centre of my methodological approach but within this wider reference system defines further and finer investigative sub- and sub-sub-units (scientific orientation, dimensions, realms and epistemic frames). The second component of my methodology is called “binominal analysis”. In the last consequence it is a tool to reduce the complexity of scientific manifestations by carving out the rules of differentiation pervading their textual and non-textual representations in both explicit and performative ways. This methodology was able to solve several problems with which my project was confronted at the beginning. At first, there was the question of finding an adequate periodization. This problem could be solved by the observation that the cyclic dynamics in epistemic communities reveals itself as interplay between periods of synthesesization and subsequent polarization. Connecting this at the foremost mere topographical peculiarity with R. Koselleck’s late concept of “Zeitschichten” it was possible to define precisely the short epistemic cycle between ca. 1930 and 1975 as my primary chronological period of examination. Second, at the beginning of my project it turned out to be doubtful whether the caesura of the year 1945 which is actually motivated by the political history of the 20th century can be defended in
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a project which is concerned with processes of knowledge transformation in epistemic communities. This question now can be answered in a differentiated way on basis of empirical results: Although the two intellectual life-histories I have put in the centre of my study, reveal long periods of epistemic continuity and duration between 1938 and 1956 / 1959 there are also significant indicators on a more or less phenomenological level of scientific transformation revealing that the immediate post-war period brought significant changes for both researchers. G. Kramer connected the two epistemic machineries which had shaped his research so far with more or less fixed themes, that is avian orientation and navigation, on the one hand, and the study of relative growth (allometry), on the other. N. Tinbergen “outsourced” the realm of empirical ethological research by leaving it mostly to his PhD students. In doing so, he not only created one of the most famous research groups but also a system of two mutually stimulating realms of ethological research (“Tinbergen Theorizing” and “Tinbergian Practice”). Finally, my initial focus upon scientific transfers excluded researchers which did not match the criterion insofar as their innovative ideas were not primarily the product of scientific exchange between different persons rather than the result of intensive interaction between scientific object and researcher. The solution to this problem, which I suggest, consists of putting the human being and not the material scientific object into the centre of our attention. Moreover, I suggest to understand the fact whether or not scientific transfers occur, whether or not researchers cultivate scientific contacts with others, or whether or not they participate in international ethological or ornithological conferences, as epistemic practices that might be ruled by underlying personal dispositions just like any other textual or transtextual representation. With this “practice-oriented” and even more relativistic re-interpretation of the transfers it is possible to obtain a more differentiated picture of the parameters that shaped the process of knowledge transformation not only relative to an individual person’s life-course but also – and what is even more exiting – relative to each single period a person went through in course of his (possibly also: her) intellectual life-history. In the main part of my thesis I ventured out to reconstruct the life courses of two protagonists of the 20th century behaviour sciences, N. Tinbergen and G. Kramer, both of whom chose different life paths. N. Tinbergen advanced to one of the architects of the Classical Ethological Synthesis and then drifted to Functional Ethology – a scientific orientation which was shaping not only his pioneering work in Behavioural Ecology but also his late engagement with early childhood autism which I interpreted as a pioneering encounter with Human Ecology. G. Kramer, by contrast, became a, in several respects atypical, advocate of the Modern Synthesis of Evolution but at a later stage of his life seemed to have drifted away from this paradigmatic framework and, in doing so, was about to create a new research program he described with the term “Bio-climatology”. Putting together G. Kramer’s and N. Tinbergen’s life courses in one reference system which here serves as the tertium comparationis provides a unique constellation for a more reflected historical comparison and this for several different reasons. At first, as it turned out, G. Kramer’s and N. Tinbergen’s life courses seemed to be complementary in a sense that one researcher covered the epistemic realms the other refused. This hypothe-
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sis could be confirmed by the results of my thesis. With the exception of the later stages of both life-histories both researchers therefore did not affiliate their research in epistemic schemes covered ever by the other. Eventually observed similarities in both trajectories therefore are more likely to have a superindividual character and therefore are less likely to be readable as expressions of those individual epistemic frameworks I have taken into consideration in distinguishing three dimensions of behaviour. Second, the life courses of both researchers reveal a fourth transition (the “turns”) of which I think they eventually do not add up in a simplified double logic of primary academic socialization and subsequent breakthrough of individual dispositions which, in some cases, shapes the formation of the researchers’ scientific orientation. The fact that we have to do with more complex life courses with more than three transitions provided the unique opportunity to integrate the effects of tertiary processes of reverse socialization or personality construction which I am inclined to interpreted as a necessary consequence of the fact that the epistemic cycle between 1930 and 1975 is an extraordinary short cycle in comparison to the long cycle between 1830/1850 and 1930: The shortening of the cycles thus seems to lead to an increased probability for the occurrence of generation conflicts within one life time. Finally, the group of behaviour scientists which shaped their epistemic community between 1930 and 1970 is a unique object of historical inquiry in as much as they translated their research from the old and further co-existing Cartesian into a new Darwinian epistemic system which they, in doing so, filled with life. This required a more-of epistemic investment, a matter of fact which articulates itself in that both the researchers who established the Classical Ethological Synthesis (with N. Tinbergen as representative) and the so-called architects of the Modern Synthetic Theory of Evolution (to which I count G. Kramer) had to go through several qualitatively different epistemic transitions in course of their life-histories. This constellation, in this particular form, existed eventually neither before (with the exception of Ch. Darwin’s life-course which ethologists and neo-Darwinians repeated obviously in a structurally analogous way) nor after, since the generation of biologists coming after Kramer and Tinbergen found an already fully fledged neo-Darwinian epistemic community which was apt to absorb their ideas and styles of research in an adequate way. The fact that N. Tinbergen and G. Kramer’s life-histories reveal a more complex structure eventually provides further insight into the inner constitution of an epistemic community because each transition turned out to be connected with particular forms of (subjectively sensed) researcher-environment interaction. Moreover, the fact that there exists at all a correlation between epistemological societal phenomena may help in future studies to assess more precisely the organismic basis of each transition. So far it can be claimed that the transitions I have observed in both life courses are of a supra-individual, often globally modifying and environment-related kind.

In the third section of my thesis I made the attempt to discuss the results I had obtained in my case studies in a still more reflected manner by applying a series of systematic comparisons. Thus, in a first step, I summarized my findings by presenting them in two different forms of graphical illustration. In doing so, I also intended to make the pros and cons of both ways of representing life courses subject of a crit-
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ical discussion so that the subsequent reflections could proceed in a more fruitful way. Placing G. Kramer’s and N. Tinbergen’s life-histories in a common reference system reveals, besides the differences (i.e. the complementary courses), also similarities: N. Tinbergen and G. Kramer, each in his own way, merged divergent theorems, modified the causal architecture of their scientific orientations, performed re-evaluations within the epistemic reference systems and, finally, drifted “back” to a “homogeneous” scientific orientation. All four transitions including the forms of epistemic variability which are correlated with these transitions occurred more or less simultaneously in both trajectories (and not only there) so that I presume they may be of a superindividual nature. Despite their similar structural nature each transition is connected with different historical events and their subjective sensation in Kramer’s and Tinbergen’s life history. Thus Tinbergen’s modification of his idea of causation seems to be linked with his stay in Greenland (1932 / 1933), whereas in Kramer’s life course it is connected with his migration from the KWI for Medical Research to the German-Italian Zoological Research Station in Rovigno. Hierarchical shifts of theorems in N. Tinbergen’s life-history are connected with obtaining a more advanced academic position at the University of Leiden and international recognition of his works, while in case of G. Kramer’s scientific development his move to the Stazione Zoologica di Napoli and the new institute’s international, economic and Darwinian spirit might have given a vital reverse impulse. As to the “turns”, there might be a significant difference, too. While Niko’s drift to Functional Ethology appears to be more a response to his pupils’ criticism and therefore a product of social interaction, Kramer’s reconception of both the framework within which he carried out his orientation research and the one which shaped his studies of relative growth seems to be more the effect of having perceived scientific results that could not be integrated in the extant framework. In another more advanced step of comparison I, then, made the attempt to find the parallels in these seemingly so arbitrary historical events. In doing so, I started with R. Burkhardt’s postulate for a study of “Ethology’s Ecologies” but suggested to differentiate more carefully between different forms of researcher-environment interaction. From this slightly modified methodological perspective it is especially the changes of the geographical environments which suggest that the causal interventions might be induced and correlated with evoked forms of researcher-environment interaction. The re-evaluations seem to be correlated with constructed forms of academic milieu since both in Kramer’s and Tinbergen’s life-history the periods between 1938 and 1949 / 1959 provided the opportunity to build a research institute (G. Kramer’s contribution to the establishment of the MPI for Marine Biology), to shape the profile of a chair (Tinbergen in Leiden after the war), to coin the spirit of research group (N. Tinbergen’s ABRG) or to establish various forms of research cooperation (e.g. Kramer’s teamwork with F. v. Medem). The “turns” which are traceable in both life courses, by contrast, show both researchers in a more passive role and it can be discussed whether N. Tinbergen and G. Kramer chose actively a form of interaction with social and inanimate environments that allowed some kind of reverse socialization or construction of their orientation. Yet, it can be ascertained that both researchers shared a common disposition to sensitivity of even hyper-sensitivity.
Conclusion

Besides the forms of epistemic variability within the community, my methodology also allows to take into account the forms of interaction that took place in-between different co-existent epistemic communities. As an example to demonstrate the insights that can be reached by this approach I have picked N. Tinbergen’s dispute with professional psychiatrists over questions of aetiology and cure of autistic children and G. Kramer’s cooperation with the parapsychologist J. G. Pratt. The particular structural deviations of overlapping analogous scientific orientations (which is a necessary consequence of a self-multiplying epistemic community, here in a wider sense of the word) thus allows to predict precisely the locations where disputes might occur without being able to anticipate their concrete form in each case.

I made an attempt to compare both Kramer’s and Tinbergen’s final stage of their scientific development with analogous constellations both as to the mere textual representations of the respective epistemic reference system and their transtextual and behavioural expressions. Tinbergen’s approach to childhood autism thus differed from the psychiatrists’ in as much as he postulated earlier and more consequently that autistic symptoms can be described as a spectrum of disorders. In addition to that, he – in accordance with his functional ethological understanding of causation – concentrated on “psychogenic” non-inherited causes. Both components can be made evident in his scientific practices. Thus N. Tinbergen operated with a more widely conceived concept of expert culture when he intended to verify his aetiology of autism and substantiate his suggestions for a possible cure. Moreover, his engagement with childhood autism was exhaustive and was driven by the aim to convey his views into a wider public of interested and concerned people. Tinbergen’s engagement with autism thus had the character of a grass-roots missionary movement. G. Kramer’s encounter with the parapsychologist J. G. Pratt, despite the harmonious form of interaction, reveals clearly the deviating motives both research parties connected with their cooperation. While J. G. Pratt and J. B. Rhine intended to make evident extrasensory perception in avian navigation, that is a mysterious vitalist force, Kramer, the zoologist, was interested in proximate (i.e. physical causes). Both epistemic regimes also seemed to shape the behaviours of the researches and the mutual relationships these behaviours generated. Thus it appears that the parapsychologists were the formal organizers of the joint research endeavour. They took care for funding of which Kramer and his associates profited.

But it was also primarily Kramer who helped obtaining the funding by sharing his advanced practical skills and his theoretical expertise. Kramer, in turn, conceived the joint research endeavour which took mainly place in the United States as “Filia- lenbetrieb” of his own research in Germany under more advantageous geographical and climatic conditions whereby his investment promised to pay back. In both G. Kramer’s and N. Tinbergen’s life course textual and non-textual representations of epistemic reference systems thus provide a coherent picture. This means, that textual practices of knowledge organization and forms of shaping human relationships by behaviours eventually might be expressions of one and the same underlying epistemic reference systems and / or organismic basis. However, it is too early to decide this question definitely.
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Appendix A
N. Tinbergen’s Pupils 1949–1975

First Generation 1949–1959
Niko Tinbergen’s research group included his own PhD students but also pupils who were writing their thesis with other professors (e.g. R. A. Hinde) or finally received their degree under another advisor (e.g. L. de Ruiter). The group was not restricted to PhD students only. There were also pupils who had already received a doctorate degree before and came to Oxford as post-docs in order to join up with N. Tinbergen. To this group belonged U. Weidmann and E. Sager (later E. Cullen). Altogether, Niko’s pupils can be differentiated in two cohorts. The members of the older generation was born between the mid-1920s and the mid-1930s. I have listed them in the following table (Table A.1). The list does not include the pupils who had received their PhD under N. Tinbergen’s supervision while he was still professor in Leiden such as G. P. Baerends and J. van Iersel, nor does it include undergraduate and graduate student projects below PhD level.

Second Generation 1960–1975
Niko’s second generation of pupils consists of a younger cohort of zoologists who were born between the mid-1930s and mid-1940s. I have listed them in table A.2. The information I have compiled in this table is partly drawn from G. Beale’s and H. Kruuk’s works but is also based on my own investigations. The table includes only Niko’s PhD students and not the post-docs who were carrying out projects in Oxford in the 1960s such as D. Franck and M. Impekoven. The sample includes only PhD projects so that in most cases a relatively close relationship between advisor and student can be presumed. Moreover, the PhD students Mike Cullen supervised and who can be also counted to the ABRG are not listed either.

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### Table A.1  List of N. Tinbergen’s Pupils, 1949 – ca. 1959

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<td>A Comparative Behaviour Study of the <em>Paridae</em></td>
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<td>M. Bastock</td>
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<td>An Analysis of Mating Behaviour in <em>Drosophila</em>, With Special Reference to Isolating Mechanisms</td>
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<td>U. Weidmann</td>
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<td>A. D. Blest</td>
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<td>The Relation Between Birds and Insects With False Warning Colouration</td>
<td>Eyed Hawkmoth</td>
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<td>J. Delius</td>
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<td>Skylarks</td>
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<td>St. A. Crossley (née Pearce)</td>
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<td>R. N. Liley</td>
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<td>misc. rel. art. in <em>Science, The Canadian Entomologist</em>, etc.</td>
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<td>Captive Chicks / Birds</td>
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*End of Table*
List of Editorial Symbols and Abbreviations

Editorial Symbols

<...> Source author’s deletion
«...» Source author’s insertion into his own writing
*italics* Highlighted by primary author (underlined, in italics or otherwise)
**bold type** Source author’s later annotation
[... ] or (…) Primary author’s complements or comments
e Wholly or partly excised page
‘[…]' Text or section illegible
· inserted space
| New paragraph
|| New page
[... ]Ed. Editor’s complements to source
[... ]CL. My complements to source (Claus Ludl)
(...)CL. My omissive correction of source (Claus Ludl)
[... ](trans. CL.) My translation (Claus Ludl)
[... ](appr. trans.) Third-party translation approved by the author, or published otherwise
fn./Fn. Footnote
ms./mss. Manuscript / manuscripts
NB Notebook
rel. art. Related article
unpubl. unpublished
incl. including / included
N. N. Nomen nescio; Unknown name
n. d. No date

Abbreviations

ABRG Animal Behaviour Research Group, Oxford University
AMNH American Museum of Natural History
ARM Acquired Releasing Mechanism
ASAB Association for the Study of Animal Behaviour
### List of Editorial Symbols and Abbreviations

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<th>Abbreviation</th>
<th>Definition</th>
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<td>ASD</td>
<td>Autism Spectrum Disorder</td>
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<tr>
<td>ATP</td>
<td>Adenosine Triphosphate</td>
</tr>
<tr>
<td>BAP</td>
<td>Bureau of Animal Populations, Oxford</td>
</tr>
<tr>
<td>BSC</td>
<td>Biological Species Concept</td>
</tr>
<tr>
<td>CBF</td>
<td>According to D. Morris, a Behavioural Unit Consisting of: Collecting, Boring, Fanning</td>
</tr>
<tr>
<td>CCICED</td>
<td>China Council for International Cooperation on Environment and Development</td>
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<tr>
<td>CNS</td>
<td>Central Nervous System</td>
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<tr>
<td>CNTNAP2</td>
<td>Contactin-associated Protein-like 2</td>
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<td>CNV</td>
<td>Copy Number Variation</td>
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<tr>
<td>DIY</td>
<td>Do-It-Yourself Mothers</td>
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<tr>
<td>DNA</td>
<td>Deoxyribonucleic Acid</td>
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<td>EES</td>
<td>Extended Evolutionary Synthesis</td>
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<td>EGI</td>
<td>Edward Grey Institute of Field Ornithology, Oxford</td>
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<td>ESP</td>
<td>Extrasensory Perception</td>
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<td>EU</td>
<td>European Union</td>
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<tr>
<td>GABA</td>
<td>$\gamma$-aminobutyric acid</td>
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<tr>
<td>HPA</td>
<td>Hypothalamic-Pituitary-Andrenocortical (Axis)</td>
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<tr>
<td>IRM</td>
<td>Innate Releasing Mechanism</td>
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<tr>
<td>IRME</td>
<td>Innate Releasing Mechanism Modified by Experience</td>
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<tr>
<td>ISAB</td>
<td>Institute for the Study of Animal Behaviour</td>
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<td>KLI</td>
<td>Konrad Lorenz Institute for Evolution and Cognition Research in Altenberg (Austria)</td>
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<tr>
<td>KWI</td>
<td>Kaiser-Wilhelm Institute</td>
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<tr>
<td>MPG</td>
<td>Max-Planck Gesellschaft, General Administration</td>
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<tr>
<td>MS</td>
<td>Modern Synthesis of Evolution</td>
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<tr>
<td>NJN</td>
<td>Nederlandse Jeugdbond voor Natuurstudie</td>
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<td>NSF</td>
<td>National Science Foundation</td>
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<td>NSV</td>
<td>National Socialist People’s Welfare</td>
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<tr>
<td>ONR</td>
<td>Office for Naval Research</td>
</tr>
<tr>
<td>OU</td>
<td>Oxford University</td>
</tr>
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<td>PKU</td>
<td>Peking University</td>
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<td>RM</td>
<td>Releasing Mechanism</td>
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<td>RPA</td>
<td>Repetitive / Recursive Partitioning Analysis</td>
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<tr>
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<td>Respiratory Quotient</td>
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<td>RS</td>
<td>Relative Span</td>
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<td>Relative Tail Length</td>
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<td>RTT</td>
<td>Rett Syndrome</td>
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<tr>
<td>SEB</td>
<td>Society for Experimental Biology</td>
</tr>
<tr>
<td>SRI</td>
<td>Serengeti Research Institute</td>
</tr>
<tr>
<td>TPr</td>
<td>“Tinbergian Practice”</td>
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### List of Editorial Symbols and Abbreviations

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<th>Symbol</th>
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<td>TTh</td>
<td>“Tinbergian Theory”</td>
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<tr>
<td>UH</td>
<td>University of Heidelberg</td>
</tr>
<tr>
<td>UH Fac. Sc.</td>
<td>Faculty for Sciences and Mathematics of the University of Heidelberg (Naturwissenschaftlich–Mathematische Fakultät der Universität Heidelberg)</td>
</tr>
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<td>Univ.</td>
<td>University</td>
</tr>
<tr>
<td>USA</td>
<td>United States of America</td>
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<td>WSSE</td>
<td>Whitney South Sea Expedition</td>
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<tr>
<td>WWF</td>
<td>World Wide Fund for Nature</td>
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<td>ZfT</td>
<td>Zeitschrift für Tierpsychologie</td>
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### List of Illustrations

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<td>Nervous Circuit of the “Erkkoordination” (epistemologically reinterpreted version)</td>
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