The Instinct Concept of the Early Konrad Lorenz

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Abstract. Peculiar to Konrad Lorenz's view of instinctive behavior is his strong innate-learned dichotomy. He claimed that there are neither ontogenetic nor phylogenetic transitions between instinctive and experience-based behavior components, thus contradicting all former accounts of instinct. The present study discusses how Lorenz came to hold this controversial position by examining the history of Lorenz's early theoretical development in the crucial period from 1931 to 1937, taking relevant influences into account. Lorenz's intellectual development is viewed as being guided by four theoretical and practical commitments as to how to study and explain behavior. These four factors, which were part of the general approach of Lorenz but not of other animal psychologists, were crucial in bringing about his specific position on instinctive behavior.

Keywords: Konrad Lorenz, ethology, instinct, innateness

Konrad Lorenz was undoubtedly one of the main founders of ethology as a biological discipline. In fact, the conceptual and theoretical framework of classical ethology was developed to a large extent by him. Crucial for Lorenz's view was that behavioral patterns have to be analyzed into sequences of innate and learned behavior components. Only the innate components qualify as instinctive behavior. Peculiar to Lorenz's position from early on is the strong dichotomy between the innate and the learned: there are neither *ontogenetic* nor *phylogenetic* transitions between innate and learned components of behavior. Instinctive behavior patterns are rigid and do not get modified or become more flexible due to experience in the course of ontogeny. In addition, flexible or intelligent behavior does not evolve from instinctive behavior—a tenet that might sound un-Darwinian and might be initially surprising given Lorenz's commitment to largely gradual evolution by natural selection. When formulating this position Lorenz contradicted virtually all former and contemporary assumptions about instinctive behavior. His innate-learned distinction became subject to vigorous criticism by psychologists in the 50s and 60s (most prominently Daniel Lehrman),[1] who argued that this approach was conceptually problematic and fruitless as a means to understanding behavior and its development. Despite this critique Lorenz never abandoned his strong innate-learned dichotomy.[2]

The aim of the present paper is to discuss how Lorenz came to hold this view of instinct. I view Lorenz's early theoretical development as being guided by four theoretical and practical commitments. These are views as to how to study and explain behavior that emerged very early on in Lorenz's career. Taken together, these four factors guided Lorenz's further development. The four commitments are 1) Lorenz's focus on innate, rather than learned, behavior, 2) the idea that behavior has to be explained by physiological rather than psychological means, 3) the comparative and taxonomic approach to behavior, and 4) the use of ideas from embryology to account for the development of instincts. These four aspects of Lorenz's general approach to

behavior emerged very early and were stable features of his perspective. The four commitments constrained and drove his intellectual development, and they make intelligible why he ended up with his strong tenet that instinct and experience are exclusive and that instinctive behavior does not evolve into more flexible behavior. Other approaches in animal psychology did not endorse these four components, and this difference in perspective explains why it came for instance to a clash between the Lorenzian ethologists and the Dutch purposivists tradition in animal psychology. Even though Lorenz developed his theory until 1935 on his own, I will suggest that there are important influences on Lorenz. As I will explain later in more detail, several of the intellectual influences on Lorenz are best viewed not as providing direct theoretical contributions to Lorenz's novel ideas but as supporting his general approach as embodied in the four aspects of his framework.

Lorenz's intellectual background and influences

Lorenz's own education was important in determining his early theoretical development. Konrad Lorenz (1903–1989) was the son of the internationally reputed orthopedic surgeon Adolf Lorenz. Konrad's elder brother Albert was a physician, as was Konrad's wife Margarethe. Adolf Lorenz was a dominant father figure, and even though Konrad would have preferred to study zoology, he compelled his son to go to medical school first. From 1923 onwards Konrad studied at the Second Anatomical Institute in Vienna and received his medical doctorate in 1928. Lorenz was a student of the comparative anatomist Ferdinand Hochstetter, and his work focused on the comparative anatomy of vertebrates. Once passing his doctorate in medicine, Lorenz enrolled at the Zoological Institute, where he received his Ph.D. in zoology in 1933. The director of Zoological Institute was Jan Versluys, a comparative anatomist as well. In fact, zoology at the University of Vienna was dominated by comparative morphologists and embryologists. While

Lorenz was working towards his Ph.D. in zoology, he still worked as Hochstetter's assistant at the anatomical institute and he was teaching as a demonstrator (laboratory instructor) in anatomy, which was his primary income apart from his wife's. For several years Lorenz could work in anatomy while at the same pursuing his main academic interest—the time-consuming study of bird behavior. While Lorenz was working on the 'Companion,' the monograph-long essay on animal behavior that secured him wide recognition among ornithologists,[3] he was still teaching anatomy. This situation, however, became problematic once Hochstetter retired in 1933. His successor was unsympathetic to Lorenz's work on animal behavior. In 1934 Lorenz made up his mind and left the field of anatomy, pursuing a career as an animal psychologists. The upshot of this brief overview of Lorenz's education is clear—Lorenz's intellectual background was medical and his primary competence was the field of comparative anatomy. The discussion below will reveal why this is so crucial for Lorenz's theoretical development.[4]

Despite the anatomical work with Hochstetter in Vienna, Lorenz's primary scientific mentor was the ornithologist Oskar Heinroth (1871–1945).[5] Heinroth was assistant director of the Berlin Zoo and dedicated his life—as did his first wife Magdalena—to the study of birds and especially their behavior. Out of years of observations grew detailed comparative studies of bird behavior, in particular a work on the birds of middle Europe encompassing four volumes.[6] In fact, Heinroth was one of the few before Lorenz who realized the taxonomic importance of behavioral patterns, i.e., the idea that behavior patterns are characteristic of taxonomic groups and can be used to classify organisms in the same manner as morphological characters are. From 1930 onwards Lorenz had an intense correspondence with Heinroth.[7] Despite detailed comparative studies of instinctive patterns, Heinroth's work was not of a theoretical nature. Indeed, Heinroth largely avoided scientific terminology and wrote in a style accessible even to lay readers. Explicit theoretical discussions of the nature of instinct or the literature on animal psychology were

absent from Heinroth's work. Instead, theoretical assumptions were only implicit in the perspective that Heinroth took. The Heinroth–Lorenz correspondence dealt primarily with reports about new animals obtained, their keeping, some observations on them, and the loss of animals. Discussion about instincts did not take place, and Heinroth seemingly had no explicit intellectual influence on Lorenz developing his new theoretical ideas on instinctive behavior (published from 1932 onwards). Due to Lorenz's ambition to found ethology as a distinct biological discipline, he was trying to develop a theory of instincts. It appears that Lorenz developed his novel theoretical ideas until 1935 primarily on his own. Lorenz sent his early theoretical manuscripts to the editor of the *Journal für Ornithologie*, Erwin Stresemann, and only later gave them to Heinroth, because he was afraid that Heinroth would view Lorenz's account as mere speculation.[8] Heinroth seemingly liked Lorenz's account,[9] but the point is that he did not directly suggest any of these ideas about the definition of instinct to Lorenz. Despite the fact that Heinroth had no specifically theoretical contribution to Lorenz's conceptual innovations, he nonetheless influenced and supported Lorenz as regards the general scientific perspective on and approach to instinctive behavior, as I will discuss in detail below.

Now I want to lay out the intellectual scene that the young Lorenz entered. It is beyond the scope of this paper to offer an overview of the different approaches to and theories of animal behavior that existed before the emergence of ethology. I will restrict my discussion to a few issues that help to understand how Lorenz's approach differed from most former traditions and why his views were novel. Focusing on those aspects of the tradition that Lorenz rejected makes sense for the purposes of understanding his theoretical development because Lorenz's early theory was based on his personal ideas and practical needs, rather than on a thorough consideration and reflection of former accounts on the nature of instinct. Lorenz developed his

own approach, ignoring a good deal of prior debates and insight, and selectively addressed and adopted a few theoretical considerations, which he deemed useful for his purposes at the time.

This holds to some extent for early ethology as a new discipline and research tradition in general. Even though traditional animal psychology did not exist as a discipline distinct from psychology or zoology, research in animal psychology was institutionally and theoretically well established. In particular in the United States, research in animal psychology was carried out in universities. Whereas animal psychologists often worked in laboratories, the early ethologists instead observed animals in relatively natural conditions—as field naturalists like Tinbergen, or as an animal keeper like Lorenz. There were surely 'forerunners' of this ethological practice, such as the British field naturalists, or American ornithologists such as C. O. Whitman and Wallace Craig. But as Richard Burkhardt has documented, it is far from obvious that something like ethology would have developed out of these small traditions in Great Britain or America.[10] The emergence of ethology was by no means an event to be expected; and the early ethologists largely created their own research tradition and theoretical approach.

Before the emergence of ethology there were a variety of theories on instinct and behavior. Different approaches disagreed on basic issues such as the relation between animate and inanimate nature, the relation between humans and animals, or the question as to whether and how evolutionary considerations have any bearing on the explanation of instinctive behavior. One theory of instincts that was quite popular among biologists and in particular physiologists in the first decades of the 20th century was the *chain reflex theory* of instinct. This theory viewed instincts as complex sequences of reflexes and was inspired by physiological studies of invertebrate behavior and reflexes in vertebrates (as conducted by Jacques Loeb, Charles Scott Sherrington, Ivan Pavlov, Vladimir Bechterev, and in Germany by Heinrich Ernst Ziegler). Many animal psychologists and proponents of more traditional theories rejected the chain reflex theory

because it could not account for the *spontaneity* of behavior. They argued that whereas a reflex goes off in the presence of a stimulus only, animals are active and behave spontaneously even without particular stimuli. Many of the approaches that rejected the reflex theory as inadequate coincided with approaches that Lorenz would later label '*purposivist.*' This name surely lumped together quite different approaches, but Lorenz was not particularly interested in the details that distinguished them. Instead Lorenz's own theory focused on a limited set of issues and his views on these matters clearly distinguished his approach from those of others—the purposivists thus became Lorenz's primary target. These were approaches that emphasized the purposiveness or goal-directedness of behavior. The idea is that behavior changes flexibly depending on the situation and that we can understand behavior only if we view it as directed towards a goal that persists despite variation in the behavior performed. Sometimes goal-directedness was taken as a mere descriptive category in that it was stressed that one has to individuate different types of behaviors according to the different goals that are pursued. Often teleology and goal-directedness were taken as explanatory categories. For instance, it was assumed that animals have a representation of the goal and act accordingly.[11] Many animal psychologists stressed consciousness, an animal psyche or mental states. Subjective states and experiences of the individual were invoked to account for the motivation, spontaneity, and goal-directedness of behavior. An influential case is the psychology of William McDougall. On his picture, instincts were viewed as psychological drives or dispositions that motivate behavior. McDougall offered a taxonomy of basic and subordinated instincts in accordance with the goals they pursue. Some researchers endorsed vitalism in that they claimed that instincts and the goal-directed-ness of behavior cannot be explained by physiological means only; instead specific and irreducible psychological factors need to be taken into account.

This selective exposition of the intellectual scene that Lorenz entered serves the purpose of explaining the novelty of his position and understanding his intellectual development. Lorenz (and later ethology to a large extent as well) broke with this broad purposivist tradition as follows. Lorenz urged the need to break down behavior into relatively small components, and an instinct is only a small part of an overall behavioral sequence. Lorenz viewed instincts as innate motor patterns or what ethologists later called fixed action patterns. An example is the movement of the neck and the beak a bird of a particular species makes when it catches an insect. Thus, instincts on this account are bodily movements that can be cinematographically recorded. They are not certain subjective states such as mental drives or desires that cannot be directly observed. The final purpose of a behavior sequence or the animal's awareness of this purpose is not the feature that explains behavior; in fact, Lorenz assumed that birds do not have any awareness of the purpose of their behavior (as we conceive it). On his account, the final goal such as the building of a bird nest is reached because it is the outcome of a sequence of individual behavioral components, where the performance of one leads to the next one. When a bird perceives nest-building material, it carries out the movement to grasp this object with its beak, and this in turn causes the next behavioral element that makes the bird to integrate the object into the nest. Once this action is completed, the bird is ready to react to further stimuli from building material. This is how the building of a nest is explained without assuming that the bird has a representation of the nest to come into being or an insight into the goal of its actions. Lorenz viewed the purposivists as constantly conflating *proximate* and *ultimate* causes (to use terms later introduced by Ernst Mayr). Lorenz acknowledged that we need to recognize the adaptedness and goal-directedness of behavior in that we give an evolutionary explanation of it. But these evolutionary causes of behavioral adaptations are not to be confused with proximate causes such as physiological and environmental triggers of behavior. The latter have nothing to do with the biological purpose of

behavior. An important argument for Lorenz's position was the existence of so-called *vacuum activities*. This refers to the situation when a behavior pattern is carried out while the normal releaser is absent. For instance, a bird may carry out the insect-catching movement (an instinct in Lorenz's sense) even though there is no insect present. Vacuum activities show that instinctive behavior may be performed even though it is not adaptive and does not meet its usual goal. In particular, the goal cannot explain instinctive behavior.

Lorenz developed his early views in a sequence of publications. His first important paper "Contributions to the study of the ethology of social Corvidae" (1931) reported detailed observations; in fact, it was very much a paper like the ones Lorenz's scientific mentor Oskar Heinroth wrote.[12] Despite the absence of theoretical discussions, the paper assumed that a certain type of behavior is instinctive if it is always performed in the same manner even though in certain situations a different behavior may be more adaptive. This foreshadowed Lorenz later explicit conviction that instincts are rigid and stereotypical behavior patterns that may occur independent of the purpose they serve. Lorenz's 1932 paper "A consideration of methods of identification of species-specific behavior patterns in birds" can be viewed as his first theoretical step. The notion of vacuum activities was introduced in this publication, thus explicitly separating instinctive behavior and insightful-purposive behavior. The famous essay "Companions as factors in the bird's environment: The conspecific as the eliciting factor for social behavior patterns," the so-called 'Companion' paper from 1935, brought about Lorenz's intellectual breakthrough in the ornithology community. This paper contained Lorenz's complete early theory of instinct, introducing notions such as the innate releasing mechanism. The well-known first instinct paper "The establishment of the instinct concept,"[13] published in May 1937, did not introduce new concepts or novel theoretical insights. But now Lorenz gave for the first time a detailed critique of former theoretical positions on instincts, clearly contrasting his theory with others. This paper

secured Lorenz wide recognition among biologists and animal psychologists beyond the ornithological community. The second instinct paper "On the concept of instinctive behavior,"[14] published a few months after the first instinct paper, restated Lorenz's position with modifications.

A main focus of my discussion is Lorenz's strong innate-learned dichotomy. Apart from neo-Lamarckists and behaviorists, most animal psychologists emphasized the clear difference between innate and learned behavior, and took instincts to be innate features. However, virtually everyone assumed that instincts could be modified, shaped and fine-tuned by the influence of learning and experience. (In 1935 Lorenz stated that the British zoologists Elliot Howard was the only one besides him who denied the influence of experience on instincts.)[15] Animal psychologists who viewed instincts as innate drives assumed that these innate factors motivate behavior and guide it in a certain direction, but that the actual performance of behavior, its repetition and the experiencing of a particular environment modify instinctive behavior. Even researchers such as Conwy Lloyd Morgan, who viewed instincts as being based on inherited rather than individually acquired neural features, assumed that they can be influenced by learning. Lorenz, however, maintained that instinctive behavior patterns are rigid and cannot be modified by experience—a conviction he clearly expressed in his publications from 1932 onwards. To reject arguments to the contrary, Lorenz introduced in his 1932 paper the notion of *instinct-conditioning intercalation*. The idea is that overall behavior can be analyzed into a sequence of components. Some of them are innate and are instincts in Lorenz's sense, i.e., fully inflexible behavior patterns. But other components of the overall behavior sequence are variable as they involve prior learning, predominantly conditioning and in a few cases insightful behavior. Thus the *overall* flexibility of behavior is compatible with Lorenz's tenet that instinctive behavior components are inflexible. Lorenz's 1935 'Companion' offered a further argument for his

position by viewing instincts in analogy to organs and stressing the idea of *maturation*. Even though the performance of some instinctive patterns may improve during ontogeny, this does not mean that this is due to the influence of *experience*. Instead, one has to consider the possibility that the behavior pattern is fully innate but needs to mature in the course of development—like organs, which are nothing but innate structures that have to develop during ontogeny until the adult performance is reached. A maturation process is not necessarily a learning process. On Lorenz's arguments, standard observations and arguments of animal psychologists regards the flexibility of behavior need not show that innate instincts are modified by learning.

Lorenz rejected not only the idea that there are ontogenetic transitions and influences between innate and learned behavior components, he also maintained that instincts do not gradually evolve into more flexible behavior. One traditional view about the evolution of instinct was the theory that instincts are lapsed intelligence. The idea is that instincts are derived from acquired habits. Due to the intelligence or the flexibility of animals, habits are formed that become part of the hereditary equipment of an animal and thus turn into inflexible instincts. This theory stemmed from the work of Charles Darwin and was endorsed prominently by George John Romanes and Herbert Spencer. As this view assumes Lamarckist mechanisms of inheritance such as use-inheritance, it was not very often endorsed by Lorenz's contemporaries. But instead everyone else assumed that flexible or insightful behavior is gradually derived from instincts. The evolution of higher animals and intelligent behavior was viewed as a process whereby primitive instincts become less and less rigid and instead the influence of ontogenetic adaptation and learning increases. In the 'Companion' from 1935, Lorenz claimed for the first time that there are no *phylogenetic* transitions between instinctive and flexible behavior. He emphasized that he did "*not* regard the instinctive behaviour patterns as *homologous* with all acquired or insight-based behaviour patterns."[16] On Lorenz's account, flexible behavior does not gradually evolve out of

instinctive behavior. Instead, instinctive behavior components are lost and later replaced by (non-homologous) insight-based behavior components. I shall explain Lorenz's evolutionary views in more detail below when we are trying to understand why he endorsed this rival view.

After the war Lorenz claimed that his early theoretical papers, such as his first important publication from 1931 or the 1932 theoretical discussion "was written without any knowledge of the theories held on the subject by purposivistic and behaviouristic psychologists".[17] This bold claim was not quite right. Some of Lorenz's later statements about his ignorance of other theoretical accounts are probably to be viewed as part of the rhetoric used to justify his new discipline.[18] For Lorenz, good empirical science and the development of theories had to start with extensive 'theory-free' observation, so that theoretical prejudices do not affect later interpretation.[19] Thus, Lorenz tried to represent his personal theoretical development in accordance with his own philosophy of science. In actuality, Lorenz's relatively theoretical paper from 1932 on the criteria of instinct was partially influenced by Heinrich Ernst Ziegler's book *The Instinct Concept in Past and Present Times*.[20] Ziegler's treatise gave a historical and systematic overview of different approaches and accounts of instincts before defending his own theory, including a discussion of purposivist, vitalist, and Lamarckist approaches. So when working on his first papers Lorenz knew about some of the possible methodological and theoretical possibilities for studying instinctive behavior. Even though Lorenz was not totally ignorant of some of the literature on animal psychology, he still was at best a very selective reader, in fact, he actually was a highly unsystematic reader. He read some of the main figures in animal psychology such Conwy Lloyd Morgan and William McDougall not very long before working on the famous 'Companion' paper, probably in 1933.[21] But at this time some of Lorenz's early theoretical views were already in place. This holds for his basic view of what instincts are and his tenet that innate instincts are not influenced by learning. Thus, when we shall later be

trying to understand Lorenz's strong innate-learned dichotomy and his position on the evolution if instincts, we have to keep in mind that these novel and controversial ideas were not at all based on a thorough reflection on the existing literature in animal psychology. Instead, Lorenz was unaware of large parts of the literature, he came up with his ideas primarily on his own and disagreed with other traditional accounts once he became aware of them.

The four commitments guiding Lorenz's approach

As is well-known, Lorenz's papers on instinctive behavior from 1935 onwards had an enormous impact. Established scientists such as the American ornithologist Wallace Craig, who had done substantial work on animal behavior and influenced Lorenz himself, were impressed.[22] The early theoretical framework of classical ethology was largely created by Lorenz. Even his collaborator Niko Tinbergen, who played a crucial role in bringing ethology as an accepted discipline into existence, was clear about the fact that the first fundamental theoretical steps were due to Lorenz.[23] This section of my study will discuss what I perceive as the four key *conceptual and methodological commitments as to how to study and explain behavior* that Lorenz—unlike several other researchers—endorsed. Not all of these aspects of Lorenz's general approach were fully present from the beginning of his intellectual development. But they emerged relatively soon; and once they were fully formed and spelled out, they strongly guided Lorenz's further theoretical development and guided it into a certain direction. In the following section I will show how these four factors help us to understand why Lorenz ended up with the strong tenet that instinct and experience are exclusive and that instinctive behavior does not evolve into more flexible behavior. Because of the crucial importance of these four aspects, the biographical and intellectual influences that relate to this level of Lorenz's theoretical development are the most interesting ones and will be highlighted in the following discussion.

The primacy of the innate

As is well-known, Lorenz approached the study of behavior from a zoological rather than a psychological point of view. On his view, animal behavior was the model for human behavior. In fact, Lorenz assumed that we do not need a human psychology that works independently of zoology and animal psychology. But many animal psychologists did not necessarily disagree with this. What was more peculiar to Lorenz is his emphasis on innateness. While it was standard practice among animal psychologists to make the distinction between innate and learned behavior and to recognize the existence of instincts, most animal psychologists stressed the importance of learned and intelligent behavior.[24] Lorenz disagreed with many animal psychologists in that he claimed the innate rather then learned as the core of behavior. He argued that the focus in the study of animal behavior has to be on the instinctive instead of the insightful. Lorenz claimed that the study of intelligence makes sense insofar as the set of innate behavior patterns is known and previously understood. A consequence of this focus is that while Lorenz's early theory was good at analyzing innate behavior and what he termed instincts, it left him without a real framework for conceptualizing and explaining the various behavioral phenomena that involved learning. The Dutch animal psychologist Bierens de Haan—whose approach I will discuss in more detail later—complained about Lorenz's notion of appetitive behavior that it lumped together the many quite distinct behavioral processes in which organisms react flexibly to their environment, from orienting movements in amoebae to insightful behavior in primates.[25]

If we take a look at Lorenz's views of human behavior and morality, we can understand that his commitment to the primacy of the innate was not just a methodological preference but fundamental to his views about the nature of behavior. From 1939 onwards a new topic appeared in his publications. Lorenz started to discuss human behavior, in particular human moral behavior, from the point of view of instincts, and he famously—or notoriously—warned against

the genetic degradation of moral behavior. Lorenz crucial assumption was that important features of human behavior such as ethical and aesthetical values are based on instincts. He viewed the process of human civilization in analogy to the domestication of animals, and argued that in both types of processes the original functional instincts get lost, leading to a step-wise disruption of behavior and a degradation of social behavior in the case of humans. During the Nazi period, Lorenz used this account in order to receive popularity and further his career.[26] As Lorenz's theory stressed the dangers of the accumulation of morally and genetically inferior people within a society or ethnic group, his account diverged somewhat from Nazi racial theories, which focused on alleged differences between ethnic groups. But Lorenz still tried to appeal to eugenic thinking in Nazi Germany and Austria. Even after the war, Lorenz continued to warn against genetically based moral degradation (whereas nowadays even the assumptions about genetics and evolution underlying this view are taken to be fundamentally misguided).

The issue of the social consequences of domestication was addressed in the correspondence with Heinroth not before March 1938,[27] and stressed in Lorenz's publications and public talks only from 1938 onwards.[28] But one ingredient of this view was present in Lorenz's thinking at an earlier stage—namely the idea that human moral and aesthetic values are inherited features encoded in instincts. Already in a letter from 1933 Lorenz clearly expressed the conviction that an action counts as moral only if it is done instinctively, but not if it is based on reasoning. He points to Oskar Heinroth as another person who views morality as an instinct: "If something good and decent is *not* done for pleasure … and purely instinctively, then it immediately loses the characteristic of a 'moral' act, … That is, my social reaction of gratitude responds only if 'the other' behaved instinctively toward me ('on his own,' 'from the heart'). As soon as he considers or reflects about it, he will at best receive a letter of thanks, but no gratitude. … Unfortunately, Heinroth's doctrine of 'morality' as a real complex of instincts goes against the grain with so

many people; for them it appears to be cynical and to degrade the nature of morality."[29] Thus, Lorenz viewed instincts as the basis of human behavior, in particular human moral behavior. He was convinced that the innate is the core of behavior.

Heinroth was a crucial influence as far as this first factor of Lorenz's perspective is concerned. I already pointed out that Heinroth's work was not really of a theoretical nature, and that he—unlike Lorenz—did not attempt at offering his definition or theory of instinct. But Heinroth's work clearly exhibits a certain approach to the study animals and their behavior. Heinroth was a supporter of Lorenz in that his research focused on instincts and innate behavior rather than on learning. In fact, his hand-rearing of young birds often occurred in isolation from conspecifics, so that Heinroth systematically conducted deprivation experiments that help to discern innate features of bird behavior.[30] Apart from the focus on the innate and the instinctive, Heinroth was convinced—just like Lorenz—that humans have many more instincts than is usually acknowledged and that the study of human instincts is crucial for understanding human social behavior.[31] As the above quoted letter from Lorenz shows, Heinroth viewed morality as based on instincts.

The need for physiological explanations

The second factor guiding Lorenz's approach was the idea that a biological rather than psychological explanation of instinctive behavior was needed. According to Lorenz, the physiological, not the mental is the core of behavior. Behavior is to be explained by means of its underlying physiological causal basis, but not by means of invoking psychological drives and subjective motivations of behavior. Animal psychologists with a purposivist approach such as McDougall or Bierens de Haan emphasized the goal-directedness of behavior and made recourse to subjective experiences and desires that motivate behavior. Even a zoologist such as Julian

Huxley assumed that an understanding of animal minds is a crucial factor in behavior studies; for instance, he argued that we need to appeal to psychological factors to explain courtship behavior in birds. For Lorenz, however, the goal-directedness was not an explanation of behavior, it itself needs to be explained by causal factors.[32] It is the focus on causal-physiological explanation that Tinbergen appreciated so much about Lorenz's approach. Tinbergen termed this an 'objectivistic' in contrast to Bierens de Haan's 'subjectivistic' (mentalistic) approach to behavior.[33] Lorenz's and Tinbergen's emphasis on a causal-physiological study and explanation of behavior proved to be important for the success of ethology as a biological approach to behavior.

Until 1937 Lorenz had certain sympathies with the chain reflex theory of instinct, which viewed instincts as sequences of reflexes. One reason for this was Lorenz's physiological approach to the explanation of instinctive behavior. For a reflex is caused by an external stimulus based on clear-cut neurological pathways and physiological factors—mental states of the animal are not needed to explain reflexes. On Lorenz's physiological approach, physiological triggers are more of a model for explaining instinctive behavior than psychological factors. This is why Lorenz deemed the chain reflex theory as a potentially useful way to think about instinctive behavior. In the second instinct paper from 1937, Lorenz fully abandoned the chain reflex theory.[34] The change of view taking place in this paper was the shift from regarding instinctive behavior as elicited by external factors to a position that includes *endogenous* factors in the production of instinctive behavior. Lorenz's tenet that the performance of an innate behavior pattern is carried out in a stereotypic fashion and thus looks like a reflex fits with the chain reflex theory. But the reflex theory assumed that an instinct—like any reflex—is fully caused by an external stimulus. Now Lorenz for the first time argued that factors internal to the organisms play an important role in the production of instinctive behavior. The idea is that if an instinctive behavior pattern is not released for some while, then nervous energy can build up within the

organisms and lead to appetitive behavior (the animal actively searching for the releasing stimulus) and finally to vacuum activities. It is well-known that this important theoretical shift was solely due to the influence of the neurophysiologist Erich von Holst, a student of Albrecht Bethe.

Theodora Kalikow has discussed Lorenz's commitment to the chain reflex theory.[35] Her account that Lorenz endorsed the reflex theory, in particular Ziegler's version, is probably right. However, Kalikow does not have real evidence for her claims and instead relies too much on Lorenz's post-war account according to which he "was a firm adherent of classical Sherringtonian reflex theory."[36] In addition, Kalikow's brief discussion simply portrays Lorenz as endorsing the chain reflex theory until he abandoned it in 1937 under the influence of von Holst, ignoring any previous changes in Lorenz's stance towards the reflex theory. It is true that Lorenz himself acknowledged in 1942 that he "still adhered to the Ziegler theory of instinctive motor patterns in its customary form in 1937",[37] but my impression is that Lorenz's relation to the chain reflex theory was not always as clear and unambiguous as he later asserted. In any case, it is admittedly hard to settle this issue because in his early papers Lorenz's does not mention the chain reflex theory, and when he addresses it from 1935 onwards, he already acknowledges that it cannot account for all behavioral phenomena.

Let us take a closer look at this matter. Lorenz's first theoretical paper from 1932 was clearly influenced by the work of Heinrich Ernst Ziegler (1858–1925), a German physiologist endorsing the view that instincts are sequences of reflexes. Lorenz explicitly stated that he uses Ziegler's basic definition of instincts: "I have defined the difference between instinctive and intelligent activities in the following way: the former are based upon *inherited* pathways and the latter on *individually-acquired* pathways. The psychological definition is thus replaced by a *histological* definition."[38] Whereas some animal psychologists characterized instincts by the absence of

insight or other subjective factors, using Ziegler's physiological definition of instincts Lorenz could define instinctive as well as intelligent behavior without any reference to mental factors. However, apart from this definition of instincts, Lorenz did not endorse the chain reflex theory of instincts. In fact, in the 1932 paper he did not even mention this theory or other aspects of Ziegler's work.[39] Despite Ziegler's partial influence on Lorenz, the latter did definitely not endorse Ziegler's whole theory. For instance, Ziegler assumed the existence of incomplete instincts, which need some practice or even experience. Incomplete instincts are a kind of drive or innate disposition for a type of behavior rather than a rigid reflex that is performed in the same manner from the very beginning.[40] This was surely incompatible with Lorenz strong innate-learned dichotomy, and already in his 1932 paper Lorenz heavily emphasized the inflexibility and rigidity of instincts and states at a few places that an innate behavior pattern is performed in a complete manner on its first performance.[41]

Lorenz's 1932 paper actually did not mention the chain reflex theory of instincts, but it was addressed in subsequent publications. However, while the 'Companion' stated that instincts are chain reflexes, it also mentioned limitations of Ziegler's definition of instinct.[42] In his first instinct paper Lorenz said that even though he presents himself "with some reservation" as a supporter of the reflex theory, "this does not mean that [he] regard[s] this as a particularly promising working hypothesis".[43] The reasons for this is that a reflex approach cannot account for certain phenomena. Vacuum activities were very important for Lorenz because they show that the same stereotypical behavior pattern is executed independent of its purpose. But as a vacuum activity occurs without the usual releasing stimulus, it is not a like a reflex. Craig's notion of appetites, that Lorenz acknowledged, refers to behavior without a clear-cut external stimulus as well. To be sure, the fact that Lorenz never explicitly endorsed the reflex theory does not mean

that he did not take it seriously. Lorenz probably viewed it as the best available starting point, despite many unsolved issues.

Kalikow views Lorenz commitment to the chain reflex theory stemming from his mechanistic, anti-vitalist view of nature.[44] 'Mechanism,' however, is a problematic label for Lorenz's point of view. In the early 30s, Lorenz might have been a mechanist in the sense that he was reluctant to accept the relevance of subjective experience for the explanation of behavior.[45] But later he seemed to accept the relevance of emotions and subjective states in animals, thus agreeing more with his mentor Heinroth. Heinroth countered the claim from his lay readers that he was viewing animals as mere reflex machines by stating that in fact he likened animals to human persons that are extremely emotional and of low intelligence. Independent of what Lorenz thought about emotions in animals, he was definitely not a mechanist as some proponents of the chain reflex theory were. The latter did neurophysiological work in laboratories and assumed that reflexes and instincts are performed by certain organs only. Lorenz, as an observer of animals in a relatively natural environment, was aware of the fact that instinctive behavior involves the whole organism. Lorenz emphasized that we have to break down and analyze phenomena, but unlike mechanists he still had the whole organism and its environment in view.[46] Moreover, proponents of the chain reflex theory were usually not interested in the purposiveness and adaptedness of behavior, which they associated with vitalist schemes of explaining behavior by reference to unanalyzable forces that make animals develop and behave goal-directed. Lorenz, however, was an evolutionary thinker and explicitly viewed the adaptedness as something that has to be studied and explained, albeit by evolutionary principles such as natural selection. This difference from strong mechanistic positions was due to Lorenz's research practice as a whole organism biologist, and because of this research practice and different perspective the orthodox chain reflex theory could not have been fully congenial to Lorenz.[47]

I offered some challenges to the standard assumption that Lorenz was a firm and unambiguous adherent of the chain-reflex theory of instinct until 1937. What I want to emphasize, however, is that the real point of my discussion of Lorenz's commitment to the reflex theory is actually to shift the historiographic focus away from the reflex theory issue. Based on the work of von Holst, Lorenz ultimately abandoned the reflex theory as a whole. But my discussion is about stable and thus more telling features of Lorenz's perspective. An example of this is his strong innate-learned dichotomy. Even though von Holst's work brought about a change in Lorenz's overall theory, Lorenz's views about innateness and the inflexibility of instincts were unaffected by this. Lorenz never wavered regards the innate-learned dichotomy or abandoned this tenet; this is the reason why I view it as a much more important and influential feature of Lorenz's thought. This also applies to my four factors as they are stable features guiding Lorenz's theoretical development. Relevant for this context is Lorenz's second commitment, i.e., the idea that we need a neurobiological or physiological explanation of behavior rather than a psychological explanation based on subjective factors. Lorenz's preference for the reflex theory was obviously driven by this commitment, but the later endorsement of von Holst's theory was as well. Now Lorenz assumed that endogenous factors play an important role in the production of behavior. But Lorenz is clear about the fact that these internal factors are not psychological drives but neurobiological stimuli—von Holst's work was purely neurophysiological. The psychohydraulic model that was proposed in this period relies on a mechanical analogy (gas, water and pressure) to illustrate the causation of behavior. Lorenz's commitment to the second factor—the physiological approach—was unaffected by the shift towards von Holst's ideas.

There is a received account as to how Erich von Holst convinced Lorenz that the reflex theory has to be fully abandoned. Lorenz met von Holst the first time in February 1936, when he gave a

talk about an early version of the first instinct paper. After the war, Lorenz stated that von Holst convinced him immediately at this meeting that the reflex theory was wrong.[48] Even though the history is often recounted in this manner,[49] Lorenz remembered incorrectly. Actually, it took Lorenz more than a year to fully appreciate von Holst's ideas and figure out how to modify his instinct theory so as to neatly integrate von Holst's insights. Even though Lorenz and von Holst did meet in February 1936, the first instinct paper did not mention von Holst's ideas, while the final version of this paper went to the publisher in September 1936.[50] As late as April 1937 von Holst criticizes Lorenz's draft of the *second* instinct paper, because it still uses ideas and terminology of the reflex theory, such as Lorenz's formulation that an instinct is an intended reflex. Von Holst points out that vacuum activities are much better explained by the endogenous production of behavior rather than Lorenz's idea that they are reflexes that can be caused by an unspecific external stimulus.[51] Based on von Holst's critique, Lorenz is revising his draft of the second instinct paper for several weeks. Indeed, the editor of *Folia Biotheoretica*, van der Klaauw, complains about Lorenz constantly reworking the manuscript rather than sending him the latest version, because the journal issue has to be printed.[52] But after receiving the final version at the end of May 1937, van der Klaauw states that he is glad that Lorenz was able to include his new perspective based on von Holst's results.[53] Already while reworking his manuscript, Lorenz tells the ornithologist Erwin Stresemann about the profound changes in his views that von Holst's ideas made necessary.[54] Given the fact that Lorenz met von Holst in early 1936, one may wonder whether von Holst attempted to convince Lorenz of the falsehood of the reflex approach to instincts at this meeting already. If yes (but this is unclear),[55] then it is not easy to answer why it took Lorenz more than one year to appreciate von Holst's points.[56]

Let us return to the main topic of this section—the need for physiological explanations of behavior as the second factor of Lorenz's perspective. An obvious influence on the early Lorenz

was the neurophysiological tradition stemming from the work of Sherrington that viewed instincts as reflex chains. The representative of this tradition with the largest influence on Lorenz was the already mentioned Heinrich Ziegler, by virtue of his 1910 book which deals explicitly with theories of instinctive behavior and defending a reflex approach of instincts. But the aspect of Ziegler's influence that is of interest for me is not the fact that Lorenz's 1932 paper took over Ziegler's definition of instinct (which characterizes instincts as based on innate rather than acquired neural pathways). The for my purposes crucial influence attaches to the second aspect of Lorenz's perspective. What Ziegler's work showed to Lorenz was that it is possible to have a potentially fruitful research approach to instinctive behavior that is based solely on neurophysiological factors and does not make recourse to psychological explanations.[57] Another likely intellectual influence was Lorenz's university education. Lorenz started out studying medicine and he passed his first doctoral degree in medicine before studying zoology. Due to his medical training Lorenz learned about physiology and probably got acquainted with the reflex physiology tradition in this manner. The medical training helped Lorenz adopt a physiological approach to the causation of behavior.

The taxonomic and phylogenetic approach to behavior

The third and most important feature of Lorenz's approach was his deep commitment to a comparative, taxonomic or phylogenetic approach to behavior that drove both his research practice and his theoretical development. Sometimes classical ethology is characterized as the comparative study of behavior. But the label 'comparative' can fail to express what was peculiar to Lorenz's approach. Traditional comparative psychology was comparative in that animal psychologists studied the behavior of different species from a variety of taxonomic groups. But Lorenz's approach meant much more than dealing with different groups of organisms. Lorenz

viewed instinctive behavioral patterns like morphological characters that can be identified in different species. In other words, Lorenz homologized behavioral features; in fact, the notion of behavioral homology is a type of homology stemming from classical ethology. Instincts as taxonomic characters can be used to classify taxonomic groups and study their phylogeny and evolution. This is the reason that I prefer the label taxonomic or phylogenetic approach rather than comparative approach. Lorenz made the same point in a post-war paper. In the section that has the telling title "Comparative anatomy of behavior," Lorenz states that he does not need to explain to biologists what the concepts of 'comparative' anatomy and physiology refer to, while psychologists use the term 'comparative' in a "very loose sense to all behavior studies concerned with different forms of life". Lorenz resents "when an American journal masquerades under the title of 'comparative' psychology, although … no really comparative paper has ever been published in it."[58]

The taxonomic-phylogenetic perspective was a crucial part of Lorenz's approach from the very beginning. His publications clearly show that Lorenz followed this research method. His first larger publication from 1931 contained detailed observational studies of different species from one taxonomic family of birds. Later publications offered an explicit theoretical account of the nature and importance of this method. The second instinct paper, for instance, started out with the taxonomic relevance of instincts, before discussing their development and physiology.[59] The taxonomic approach is the reason why Lorenz viewed instincts in analogy to morphological structures. Lorenz emphasized that both are inherited and often have a long phylogenetic history. They can be evolutionarily conservative, so that they serve as taxonomic characters that allow to characterize and classify biological taxa.[60] In fact, Lorenz claimed that instincts are sometimes more conservative than morphological features.[61] Tinbergen learned about this taxonomic (rather than just comparative) approach to behavior from Lorenz.[62]

The reason why the taxonomic-phylogenetic approach was such a crucial feature of Lorenz's approach is that it was strongly embedded in his research practice. The research practice of Lorenz and other behavioral researchers has been discussed in detail by Richard Burkhardt.[63] Lorenz's practice resembled that of Charles Otis Whitman. Neither Whitman nor Lorenz were field naturalists. Like Lorenz, Whitman kept many birds—primarily pigeons in the case of Whitman—in close proximity to his home so that he could observe them.[64] Both made comparative observations on closely related species that allowed them to gain insights into the phylogeny and evolution of behavior. Compare the taxonomic *practice* of Lorenz with some of his *theoretical* claims such as the definition of instinct taken over from Ziegler. Ziegler's definition is based on the difference between innate and acquired neural pathways. However, while Lorenz endorsed this neurobiological definition for some time, it never had an impact on his research practice. Ziegler and other neurophysiologists made neurobiological experiments and observations. Lorenz, on the other hand, stuck to observing living animals in a relatively natural environment rather than investigating their neurophysiology in the laboratory. The taxonomic-phylogenetic approach, in contrast, was part and parcel of Lorenz's research practice. What Lorenz did in his ethological research every day was to observe animal behavior from a comparative, taxonomic, and phylogenetic point of view.

A crucial influence on Lorenz in this respect was his university education. As already mentioned, Lorenz studied medicine, focusing on comparative anatomy, and his first doctoral degree was in comparative anatomy. Apart from anatomy at the medical school, zoology at the University of Vienna was dominated by comparative morphologists and embryologists. Lorenz was still teaching anatomy classes when writing on the 'Companion'. Lorenz's primary competence was in comparative anatomy above all other traditional zoological fields. Another influence or support came from Oskar Heinroth. Even before Lorenz, Heinroth homologized

behavioral patterns and used them as taxonomic characters.[65] Lorenz probably developed his research practice on his own, but he soon realized that Heinroth's research had made use of a similar practice. Heinroth's published work and the correspondence with him encouraged Lorenz in pursuing the taxonomic perspective on behavior. Lorenz acknowledged this support by Heinroth, in particular his comparative-taxonomic approach, on many occasions. In a paper after the war, for instance, Lorenz cites Heinroth and Whitman as forerunners of the taxonomic approach, and of ethology in the first place. Expressing in fact his own point of view, Lorenz states that given Whitman's and Heinroth's perspective (which differed from the approach of their contemporaries), it was actually no surprise that they avoided the pitfalls of former approaches and developed some early insights of ethology. He continues: "No very great tribute either is due to them for applying the phyletic method to the study of innate behaviour. *Being comparative morphologists, it was only natural for them to do so.* But by doing it, they discovered a fact which could not be discovered from any but the phyletic point of view; …"[66] Thus, my suggestion is that we have to view Lorenz primarily as a comparative anatomist and the taxonomic approach as the main factor guiding his theoretical development.

The embryological approach to behavior

The last factor concerns the way in which Lorenz approached the development of behavior. Lorenz used ideas from embryology and the developmental biology of morphological structures to think about the ontogeny of behavioral features. However, this feature was not as influential as the other theoretical and practical commitments driving Lorenz's perspective, and it was not always clearly and consistently present in Lorenz's account. This is due to the fact that Lorenz focused on the phylogeny and the evolutionary adaptation of behavioral characters, but was never really interested in studying and explaining the development of behavior—unlike behavioral

biologists such as Daniel Lehrman. But when Lorenz had to address the development of behavior, he used ideas from experimental morphology.

The embryological approach fits with Lorenz's general idea that instincts are like morphological structures and that instincts are to be studied from a causal-physiological point of view. Lorenz was not the first to use the analogy of instincts and organs.[67] But he pushed the analogy further by using the idea of *maturation* to support the claim that instincts are not modified in ontogeny under the influence of experience. On his account, even though there are cases where the performance of instincts changes during early ontogeny, this just reflects the fact that instincts as well as their underlying morphological and physiological basis have to mature, i.e., instincts have to fully develop in the first place—just like organs. This line of thought permitted Lorenz to maintain that change in instinctive behavior during ontogeny need not be due to the influence of learning or experience; a change in a behavioral character is compatible with it being completely innate. Lorenz stressed this point to rebut alleged evidence that was invoked to show that innate instincts can be modified by learning.[68]

Sometimes Lorenz used more specific embryological ideas, such as theoretical concepts from developmental mechanics. Lorenz's account of imprinting shows this. The notion of imprinting was introduced in the 1935 'Companion' paper. A bird 'recognizes' its parents as follows. When a young bird hatches from its egg it will be imprinted to the animals it encounters immediately after hatching (normally its parents), i.e., it will subsequently show any behavior that is normally directed at its parents towards the animal to which it was imprinted. If for example Lorenz was the first living being that the hatched bird encountered, then the bird would behave towards Lorenz as if he was one of its parents. A bird has to be imprinted to its parents and thus needs to acquire the external information (to 'learn') what its parents are. Lorenz, however, denies that imprinting is actually a learning process. He points out that imprinting can be carried out only in

a very short period of development and that it is irreversible—unlike standard learning processes. In fact, Lorenz assumes that imprinting is like the process of embryological induction or determination.[69] This is a well-known concept from the German tradition of developmental mechanics (the Spemann school) used to account for the development of specific morphological structures by means of stimuli from adjacent tissues. As a nice illustration of how Lorenz used the framework of experimental embryology to think about the development of behavior, consider a marginal note that Lorenz made in his copy of an article by Otto Koehler (Koehler, 1933). Koehler's essay deals with the idea of wholeness in biology; and at one point Koehler describes an instance of embryological induction by means of a dead organizer, i.e., non-living matter derived from animal tissue (p. 182). Lorenz annotates on the margin of his reprint "Prägung!" (Imprinting!). It is intriguing that this marginal note is about a dead organizer, because a bird can be imprinted not just to other animals, but to inanimate objects as well.

In sum, even though Lorenz was not primarily interested in the development of behavior and did not have a coherent theory of the ontogeny of behavioral features, in order to defend his views of instincts Lorenz thought along the lines of a kind of behavioral embryogenesis, using ideas from developmental mechanics.

Lorenz's early views on instinct and innateness

The four aspects of Lorenz's perspective are quite constant features of his approach. Taken together, these factors guided and constrained his early theoretical development. This holds in particular for the formation of Lorenz's instinct concept and his innate-learned dichotomy, so that these features that were so characteristic about Lorenz's theoretical position and that distinguished him from other animal psychologists can be understood based on the four factors.[70]

Before discussing in detail how Lorenz's perspective furthered his innate-learned dichotomy, I want to illustrate the explanatory relevance of the four factors by comparing Lorenz with a quite different tradition—the Dutch purposivists. From the late 30s onwards, the proponents of the ethological approach (Lorenz, Tinbergen, and their supporters) and the Dutch animal psychologists working with the more traditional purposivist perspective criticized each other vehemently. In my view, one important factor for this development was institutional. Lorenz and Tinbergen attempted to create a new biological discipline, which required emphasizing the difference between their discipline and other 'non-biological' approaches to animal behavior. But the fundamental disagreement was based on differences in perspective as well.

I want to focus on a brief comparison between Lorenz and Johannes Abraham Bierens de Haan (1883–1958), the most influential animal psychologists of the Dutch purposivists tradition at the time. When Lorenz's first publications appeared, Bierens de Haan was already a well established researcher and theorist. Bierens de Haan—a student of F.J.J. Buytendijk—was fundamentally influenced by William McDougall's psychology, adopting and developing his idea of instincts as innate drives motivating behavior.[71] Bierens de Haan viewed an instinct as the drive or striving to behave in a certain manner given certain subjective perceptions.[72] This was in direct contrast to Lorenz, who defined instincts as particular motor patterns, i.e., bodily movements that can be filmed, rather than subjective features of the psyche such as mental propensities. This disagreement as to how to use the term 'instincts' was not simply a terminological matter. It was a difference in view as to what is important about animal behavior, what is the nature of behavior, and how to explain it.

Bierens de Haan stressed the way in which instincts are modified in ontogeny under the influence of experience. In fact, one of his books, which states his mature theory, is entitled *Animal Instincts and their Rebuilding by Experience*.[73] On his account, the inflexibility that the

performance of some instincts exhibits is not due to the innateness of instincts—as Lorenz would have it. Quite on the contrary, habit and the repeated use of certain behavior patterns brings about stereotypic and potentially unadaptive behavior patterns. It is interesting to note that Bierens de Haan very well agreed with some of the important observations and arguments of Lorenz, such as Lorenz's point that we need to distinguish change of behavioral performance due to maturation and the influence of learning. But Lorenz and Bierens de Haan still offered very different interpretations because the point of agreements are embedded in very different theoretical perspectives. Bierens de Haan accepted the idea that there is a morphological as well as physiological aspect of behavior. However, he stated that he focuses on the psychological study of behavior only, whereas for Lorenz psychological aspects such as subjective feelings only make sense as part of a biological approach to behavior. Bierens de Haan acknowledged the existence of reflexes and reflex-like behavior. But his focus was on intelligence, learning, and the goal-directedness of behavior. In fact, he claimed that the reflex is about causation, while the instinct is about teleology (the goal-directedness), so that instincts and reflexes cannot possibly be identified. Directly criticizing Lorenz, Bierens de Haan argued that we cannot just equate instincts and instinctive behavior patterns. In his view, motor patterns are only the expression of instincts, while instinct is an explanatory and psychological concept referring to subjective factors motivating behavior. The intention of the individual is the fundamental feature of instinct. Bierens de Haan stressed the continuity between the human and animal psyche. The mental is a feature that emerged with the origin of animals. Instincts were viewed as a specifically psychological properties of an individual, which were contrasted with biological properties. A fundamental tenet of Bierens de Haan was that objective (biological) issues such as behavior patterns have to be distinguished from subjective (psychological) issues such as instincts.[74]

Overall, Bierens de Haan disagreed with each of the four aspects of Lorenz perspective. He acknowledged the existence and importance of instincts and innate behavioral characters, but his theoretical focus was on learning, intelligence, and the way in which innate features are embedded in and modified by subjective experience. And he did not view innate instincts as something that is to be explained by evolution and natural selection. Bierens de Haan vehemently rejected Lorenz's preference for causal-physiological explanations of behavior by stressing the necessity of psychological explanations and the existence of innate drives and subjective desires motivating behavior. I emphasized that I view the taxonomic-phylogenetic approach to behavior as the main factor driving Lorenz's theoretical development. Bierens de Haan, however, did not think much of Lorenz's taxonomic approach to behavior.[75] He also did not use models from embryology or experimental morphology to explain the development of behavior. Due to the fundamental difference of perspective the debate between Lorenz and Bierens de Haan led to a clash. In 1942, Bierens de Haan restates the critique of Lorenz and makes some polemical remarks. Lorenz strikes back, vigorously attacking Bierens de Haan's general purposivist and vitalist approach rather than addressing the interesting and critical points that the latter raised.[76]

Now that I have illustrated the difference between the perspective of Lorenz and more traditional approaches in animal psychology, I finally turn to the development of Lorenz's instinct concept. The four aspects of Lorenz's perspective make intelligible why he came to hold this particular instinct concept and the strong innate-learned dichotomy. Lorenz's views on these matters emerged very soon in Lorenz's intellectual development, and remained non-negotiable claims. Lorenz never wavered on his tenet that innate instincts and learned behavior components are different in nature and are clearly separate. In my view, the main reason for this is that Lorenz's taxonomic approach is the main factor guiding Lorenz's views on instincts, and the taxonomic approach is part of Lorenz's research practice from the very beginning.

First, there was Lorenz's view that the concept of 'instinct' ought to refer to motor patterns—observable bodily movements rather than drives or disposition to behavior or even certain subjective states as many other researchers assumed.[77] Lorenz's taxonomic approach precisely suggested his account or definition of instinct. Once one views instincts as taxonomic characters or homologues, instincts have to be features that we can identify when observing the behavior of an organism. In addition, they have to be features that we can find in different species; thus they have to be relative small units of the overall behavior of an individual. As in the case of morphological structures, we have to break down an organism into smaller modules or homologues that we can compare with corresponding features in other species. In his daily observations of birds from closely related species, Lorenz could observe and study instincts in his sense of motor or behavior patterns. Even though Lorenz originally developed this taxonomic research practice on his own, before him Lorenz's scientific mentor Oskar Heinroth had dealt with behavior based on a taxonomic-phylogenetic framework. In fact, just like Lorenz he focused on characteristic movements of certain parts of the body.[78] Lorenz obtained crucial support from Heinroth in pursuing this approach to the study of instinctive behavior. Apart from the taxonomic-phylogenetic aspect of Lorenz's perspective, his view that instincts are in fact motor patterns fits perfectly with his focus on innate (as opposed to learned) behavior. Motor patterns are also amenable to experimental study and within the scope of physiological theories, so that instincts in Lorenz's sense are likely candidates for successful physiological explanation, in accordance with his views as to how behavior has to be explained.

Second, apart from Lorenz's definition of instincts, there was his peculiar and controversial claim that there are no ontogenetic transitions between innate and learned behavior components. Unlike virtually anyone else, Lorenz assumed that instincts are not modified by experience at all. Lorenz's view of instincts as motor patterns—driven by his four commitments and in particular

the taxonomic approach—actually supported the idea that innate instincts are stereotypic and inflexible. The behavior patterns that are characteristic of a species are quite rigid and do not appear to be much influenced by learning. The instinct-organ analogy and embryological ideas permitted Lorenz to put forward his notion of maturation. Pointing out that maturation processes are not to be confused with real learning processes, Lorenz could argue that instincts in his sense show full performance once they are developed and maturated, and are not modified by later learning. Using the notion of instinct-conditioning intercalation, he could account for the overall flexibility of behavior without abandoning the idea that the particulate components he calls instincts are rigid.

Lorenz's taxonomic-phylogenetic approach was the main force driving his notion of instinct, and thus an indirect cause of the idea that instincts are independent of experience. But there is a more direct bearing of the taxonomic point of view on Lorenz's strong innate-learned dichotomy. Lorenz assumed that the fact that instincts can serve as taxonomic characters and are often evolutionarily conservative is incompatible with them being modifiable. Linguists who currently use methods similar to the ones from taxonomy and molecular phylogeny to reconstruct the relationship and evolution of different human languages may be surprised about the claim that anything that is inherited over many generations and can serve as a taxonomic character cannot be learned. But Lorenz clearly made this assumption, and it was an important idea driving his innate-learned dichotomy. He made this point in several publications. It appeared for the first time in the 'Companion': "Nobody can deny that the phylogenetic mutability of an innate behaviour pattern possesses exactly the same characteristics as an organ and does not resemble that of a learning function. Its mutability is so similar to that of a particularly 'conservative' organ that the *instinctive behaviour pattern* actually carries greater weight as a *taxonomic* feature, …"[79] Both the first and the second instinct paper repeated this argument in a more explicit

form.[80] The clearest expression of this idea can be found in a book manuscript that Lorenz wrote during the war: "If highly complicated behavior patterns are reliable, phylogenetically interpretable characters of species, genera, and orders, like any morphological characters, then this fact alone is enough to demonstrate that these behavior patterns cannot undergo substantial modification through individual experience, as has been assumed by Spencer, Lloyd Morgan, and others."[81]

Finally, Lorenz had a bold view about how instinctive behavior changes in the course of evolution. He maintained that it is impossible for an instinct to evolve gradually into experience-based and intelligent behavior. More precisely, an instinct is never homologous to a flexible behavior component. This position contradicted all former and contemporary accounts. An interesting proponent of the more traditional view was the zoologist Charles Otis Whitman.[82] In his influential 1898 lecture, Whitman discussed animal behavior and its evolution based on detailed observations.[83] He argued in particular against the view that instincts are lapsed intelligence or derived from acquired habits, a position on animal behavior quite popular at that time and sometimes based on Lamarckist assumptions. He rejected the idea that instincts are relatively recent features, which originated much later than morphological structures. Rather than becoming later integrated into the given morphology and hereditary make-up of organisms, instincts evolved form the very beginning together with their underlying anatomical structures. But even though Whitman—like Lorenz—had an explicitly biological and comparative-phylogenetic approach to behavior, he assumed that instincts can evolve into more flexible behavior, agreeing with Herbert Spencer and Conwy Lloyd Morgan in this respect.[84] In fact, Whitman's lecture starts with a quote from Darwin's *Origin*, emphasizing the continuity between animal and human cognitive features: "*Natura non facit saltum*, is applicable to instincts as well as to corporeal structure."[85]

How did Lorenz come to hold his peculiar view about the evolution of instincts? He offers a different scenario on the evolution of behavior than other zoologists. On Lorenz's account, the importance of intelligence can increase only when the role of instinctive behavior diminishes. This may happen if in an overall behavior sequence, consisting of several components, new components that are based on learning are inserted. Thus instinctive behavior is broken up by newly introduced flexible behavior components, reducing the amount of rigid instincts that are part of the overall behavior. Alternatively, innate behavior pattern may be completely lost and experience-based components fill the corresponding functional positions. The overall behavioral sequence involving different components is modified, by the addition or deletion of specific instinctive or experience-based components. Lorenz's general picture is that instead of evolving into more flexible components, instincts atrophy, are lost, and replaced by new and distinct experience-based behavior components.[86] This is the reason why Lorenz can claim that instincts are not homologous to novel components that are based on learning. Lorenz described as early as 1931 the loss of instinctive patterns.[87] This shows how important his early focus on particular observations is for his later evolutionary account. Whitman, in contrast, used comparative studies of wild, semi-domesticated, and domesticated pigeon species to support his view that instincts become more plastic in the course of evolution. Lorenz does not really challenge Whitman's basic observations, but he offers a different interpretation of his results. Rather than becoming more flexible, behavioral sequences involving instinctive components are broken up and appetitive and condition-based components may be added.[88] When Whitman states that "instinctive action is *gradually* superseded by intelligent action",[89] Lorenz objects by annotating his copy of Whitman 1899: "no! step by step."

Apart from the fact that Lorenz has a different preferred hypothesis, why does he think that the received scenario about the evolution of instincts is impossible? One consideration he offers

in support of his view is that instincts and insight-based behavior components appear to be mutually exclusive, so that only one can fill the same functional role. The presence of an instinctive component inhibits the development of intelligent components with the same function.[90] This idea is rather about the development of instincts, and it alone cannot establish Lorenz's evolutionary position. For this argument does show that an inflexible component cannot correspond in the next generation to a less inflexible homologous pattern, which need not presuppose that an instinct gets more flexible during ontogeny. More interesting is Lorenz's idea that instincts do not get replaced by more flexible components because they do the adaptive job better than the intelligence of the corresponding animal permits.[91] An annotation puts this idea more strongly than we know from Lorenz's publications. Whitman quotes a passage from Lloyd Morgan expressing the idea that instinct evolve into more flexible patterns: "And this, if continued, would tend to convert what had been a stereotyped instinct into innate capacity; that is, a general tendency to certain activities (mental or bodily), the exact form and direction of which are not fixed, …"[92] Lorenz counters on the margin: "This would convert instinct into nonsensical action." So Lorenz seems to be convinced that instinctive behavior patterns are so adaptive that softening them up would make them less adaptive. This claim can actually support the idea that it is very unlikely that a flexible behavior pattern replacing a rigid instincts would be maintained by natural selection. Nevertheless, the idea that rigid instincts hardly ever evolve into more variable behavior components does not entail that such a thing never occurs, i.e., that an instinct is never homologous to a flexible behavior component in the descendant.

Overall, Lorenz does not give a conclusive argument for his rejection of the idea that non-instinctive behavior could be homologous to instinctive behavior patterns. As far as his own rival evolutionary scenario is concerned, Lorenz does not offer a theory of the evolution of instincts that is spelled out in detail and defended. This is probably due to the fact Lorenz was not really

an evolutionary theorist. He was an evolutionary thinker in that he defended ethology as the biological, phylogenetic, and evolutionary approach to behavior (and proposed his evolutionary epistemology), but he was not much engaged in discussions about the mechanisms of evolutionary change. Lorenz surely addressed instinctive behavior from the point of view of phylogeny and adaptation, but still the absence of substantial discussions about evolutionary mechanisms in the early work of Lorenz is quite striking. This is on the one hand due to the fact that Lorenz contrasted his theoretical ideas with other approaches in animal psychology, but did not relate them much to contemporary debates about evolution. On the other hand, Lorenz primary specialty was comparative anatomy, not evolutionary theory.[93] Lorenz's emphasis on ethology as the biological, in fact, evolutionary science of behavior was to some extent part of his rhetoric to create a new biological field.[94] In this respect Lorenz was very much unlike Whitman, who at end of the nineteenth century was at the forefront of discussions about Darwinism and evolutionary theory. While Whitman was fundamentally concerned with the relationship of evolution, development and heredity, Lorenz hardly ever acknowledged the fact that characters (including morphological structures) show variation within a species; at any rate, he definitely does not view the possibility of intra-specific variation as theoretically significant. Instead, he stressed the idea that an innate character is either present or that it is completely lost. This might strike the contemporary reader as an instance of what Ernst Mayr calls a 'typological' approach to species. Lorenz's taxonomic approach was the main reason why he emphasized that instincts are rigid and species-specific.

The four aspects of Lorenz's approach help us somewhat to understand how Lorenz came to hold his specific position on the evolution of instincts. For they promoted Lorenz's views on how behavior is composed and how it develops, which indirectly suggest his evolutionary position. On Lorenz's account, behavior is composed out of distinct units, some of which are instinctive

behavior patterns, others are conditioned reflexes, taxes, or appetites. Each component is either innate or it involves experience. Given this framework, it is theoretically hard to see how an instinctive behavior pattern could gradually evolve into a more flexible component. Innate motor patterns obviously are not homologous to conditioned reflexes in the next generation. Thus Lorenz's overall conceptual framework suggests that instincts to not evolve into flexible behavior.

Ultimately, it is quite unclear what actually motivated Lorenz's views on the evolution of instincts—whether it were certain arguments that Lorenz used to defend his position or whether it were deeper factors such as his taxonomic approach. Lorenz does not have an elaborated theory of the evolution of instinctive behavior and it was not important for his research practice to have elaborated ideas about the mechanisms of evolutionary change; which makes it hard to assess the roots of his position on the evolution of instincts. But independent of whether we can really understand his claim that there are no phylogenetic transitions between instinct and learning, we saw that what I called Lorenz's four theoretical and practical commitments explain some crucial aspects of his early theoretical development. The four factors make intelligible why Lorenz chose to view instincts as nothing but innate motor patterns, and why he maintained that instincts are inflexible and not influenced by learning. As I tried to show, the main driving force behind this position was Lorenz's use of instinct as taxonomic characters. If we want to understand why Lorenz assumed that his research program might break down if he abandoned the view that there are no transitions between instinctive and learned behavior, then we have to look at his taxonomic-phylogenetic approach that was so deeply embedded in his research practice. The early Konrad Lorenz has to be viewed as a comparative anatomist much more than as an evolutionary theorist, which fits with his academic training. These features explain Lorenz's strong innate-learned dichotomy.

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Note on archival sources

The correspondence between Konrad Lorenz and Erwin Stresemann is stored at the Staatsbibliothek zu Berlin, Preußischer Kulturbesitz (Germany) as 'Nachlaß 150 (E. Stresemann), Kasten 40.' Any letter from Lorenz that is part of this source is referred to in the paper as 'Lorenz, letter to Stresemann.' Some of Lorenz's correspondence is in the possession of his daughter Agnes von Cranach and is referred to in the notes as the 'Konrad Lorenz Family Papers.' Annotations by Lorenz referred to in the paper are from the books in Lorenz's library, which is preserved in the library of the Konrad Lorenz Institute for Evolution and Cognition Research, Altenberg (Austria).

Notes

[1] Lehrman, 1953.

[2] Lorenz, 1981, p. 261.

[3] Lorenz, 1935.

[4] For more details about Lorenz's life see Taschwer and Föger, 2003; Burkhardt, 2005.

[5] For a biography see Heinroth, 1971.

[6] Heinroth and Heinroth, 1924–1933; see also Heinroth, 1911.

[7] Heinroth and Lorenz, 1988 provides a posthumous publication of the correspondence from 1930 until 1940.

[8] This holds for Lorenz's first theoretical paper from 1932 (Heinroth and Lorenz, 1988, p. 71; Lorenz, letter to Stresemann, July 30, 1931) as well as the 'Companion' from 1935 (Lorenz, letters to Stresemann, November 21, 1934 and August 3, 1935).

[9] Heinroth's response to Lorenz's 1932 paper is lost, but a reply from Lorenz suggests that Heinroth approved of Lorenz's account (Heinroth and Lorenz, 1988, p. 77).

[10] Burkhardt, 2005.

[11] E. S. Russell is a zoologist who emphasizes the goal-directedness as a purely descriptive category, but sometimes slides into a view that seems to invoke these goal as an explanation of the behavior (Russell, 1934).

[12] Virtually all of Lorenz's relevant publications in the period discussed are translated and reprinted in the collection Lorenz, 1970.

[13] Lorenz, 1937a.

[14] Lorenz, 1937b.

[15] Lorenz, letter to Stresemann, August 3, 1935.

[16] Quoted from the translation Lorenz, 1970, pp. 116–117.

[17] Lorenz, 1970, p. xviii.

[18] Burkhardt, 1981.

[19] Lorenz, 1996; Brigandt, 2003.

[20] Ziegler, 1910.

[21] On Lorenz's account (which is credible), the Vienna psychologist Karl Bühler, with whom Lorenz worked for some while when he decided to leave anatomy and pursue a career in animal psychology, made him read this literature (Lorenz, 1970, p. xviii).

[22] Lorenz's 'Companion' made use of Craig's notion of 'appetite' (Craig, 1918). Craig wrote to Lorenz about his 'Companion' and first instinct paper: "Your paper, 'Der Kumpan in der Umwelt des Vogels' is by far the greatest paper on instinctive behavior of birds I ever read in my life." (Craig, letter to Lorenz, April 27, 1937, Konrad Lorenz Family Papers). "You have solved so many problems while other observers (including myself) have merely hacked at them." (August 16, 1937). "To a great extent, your papers have persuaded me that your views are correct and that my former views were wrong." (September 19, 1937). So not only did Craig's work on appetites have an impact on Lorenz, but conversely Craig adopted some of Lorenz's ideas. However, based on empirical examples Craig did not accept Lorenz's absolute distinction of appetitive and instinctive behavior (as he says in the letter from September 19, 1937).

[23] A note on the first page of Lorenz and Tinbergen, 1938 specifies that it is based on Lorenz's instinct concept and that the theoretical part of the paper is mainly due to Lorenz. Tinbergen himself suggested to Lorenz to add this note (Tinbergen, letter to Lorenz, October 12, 1937, Konrad Lorenz Family Papers).

[24] Morgan, 1896; McDougall, 1933; Bierens de Haan, 1933.

[25] Bierens de Haan, 1942, p. 100.

[26] Kalikow, 1976; Föger and Taschwer, 2001; Taschwer and Föger, 2003.

[27] Heinroth and Lorenz, 1988, p. 244.

[28] Lorenz, 1939a, 1940, 1943.

[29] Lorenz, letter to Stresemann, March 5, 1933; my translation.

[30] Heinroth and Heinroth, 1924–1933.

[31] Heinroth, 1911, p. 702.

[32] E. S. Russell stated that it is unlikely that the migration of fish can be explained by a purely physiological theory (Russell, 1934, p. 42). In his copy of this monograph, Lorenz annotated this passage: "*why* in hell??"

[33] Tinbergen, 1942.

[34] Lorenz, 1937b.

[35] Kalikow, 1975.

[36] Lorenz, 1970, p. xvii.

[37] Lorenz, 1942; quoted from the translation Lorenz, 1970, p. 362.

[38] Lorenz 1932, quoted from the translation Lorenz, 1970, p. 57. Compare Ziegler, 1910, p. 46.

[39] Kalikow gives a list of five criteria of innateness "which Lorenz first justified, in 1932, by means of the chain reflex theory" (1975, p. 334). It is true that these criteria are consistent with a chain reflex approach and that Lorenz might have had the chain reflex theory in mind when formulating these criteria. But it is not the case that Lorenz justified them by means of the chain reflex theory in his paper—he did not even explicitly mention this theory.

[40] Ziegler, 1910, p. 45.

[41] Lorenz [1932] 1970, p. 90. Ziegler's work was actually influenced by Herbert Spencer and Conwy Lloyd Morgan. Ziegler stated explicitly that he follows Spencer in taking instincts as complex reflexes (1910, p. 44) and that the instinct concept he uses agrees with the one employed by Morgan in *Habit and Instinct* (p. 47). Spencer and Morgan, however, became one of the main targets of Lorenz's later critique (in particular Lorenz, 1937a).

It also is interesting to note that Ziegler mentioned C. O. Whitman and gave a full-paragraph quote from his seminal 1898 lecture on animal behavior (Ziegler, 1910, p. 49; compare Whitman, 1899, p. 328). Lorenz seemingly overlooked this passage, because he effectively learned about Whitman's work only from his student Wallace Craig and read Whitman's lecture not before 1934. This is peculiar because the passage that Ziegler quotes starts with "Instinct and structures are to be studied from the common standpoint of phyletic descent", the famous statement that Lorenz will later on quote several times in support of his approach (Lorenz, 1937b, p. 21; 1939b, p. 71; 1996, p. 238). Even though using instincts as taxonomic characters was one of the earliest theoretical ideas of Lorenz and a very important one, he apparently did not pay attention to this quote given by Ziegler.

[42] Lorenz [1935] 1970, pp. 116, 121, 249, 250.

[43] Lorenz 1937a; quoted from the translation Lorenz, 1970, p. 305.

[44] Kalikow, 1975, pp. 331f.

[45] In a letter to Heinroth from October 1931, Lorenz complained about a paper that Heinroth sent him. (It is very likely that Lorenz referred to Loeser, 1930, who had argued against the instinct concept, claiming that it is non-explanatory. To put Loeser's account very roughly, apart from real reflexes that involve only a part of an organism, animal behavior has to be explained by principles of gaining pleasure and avoiding discomfort.) Lorenz mentioned that he and Heinroth had talked several times about pleasure accompanying instinctive behavior. Lorenz, it seems, was more skeptical than Heinroth about this issue, stating that he rather agrees with Ziegler that pleasure and discomfort exist only where corresponding

associations can be formed, i.e., where they have a biological meaning. Lorenz seemed to admit subjective experience, but not in every case and not as an explanatory principle (Heinroth and Lorenz, 1988, p. 79).

[46] In a letter from 1936 Lorenz complained that so many physiological chemists are incapable of viewing animals as an organic wholes: "Ich kenne aber so viele Physiologische Chemiker, die alle ganz unfähig sind, im Tier eine organische Ganzheit zu sehen." (Lorenz, letter to Stresemann, October 4, 1936)

[47] One of Lorenz's marginalia on McDougall shows additionally that Lorenz did not view himself as a mechanist. In a passge where McDougall points out that animals have the capacity to learn (McDougall, 1933, p. 94), Lorenz annotated on the margin: "Who denies this. McD is always argumenting as if the assumption of an unintelligent instinct, not to be influenced by experience implies that the man who makes it is a mechanist."

[48] Lorenz, 1985.

[49] Wuketits, 1990.

[50] F. Süffert, letter to Lorenz, September 5, 1936, Konrad Lorenz Family Papers.

[51] "… so finde ich ihre Schlussdefinition: 'angestrebter Reflexablauf' nicht völlig ideal … 'Angestrebt' ist natürlich ausgezeichnet, aber gegen 'Reflex' (Reflexkette) werden sich alle wenden, die in den letzten Jahren, besonders an den Insekten, gerade die Undulationstätigkeit hervorgehoben haben. … Ihre Leerlaufreaktion hat Sie ja selbst dazu geführt zum mindesten Reflexe mit u. U. *unendlich* niedriger Reizschwelle anzunehmen und damit das wesentliche (für die Reflexlehre wesentliche) des Reflexes, dass er Hineinströmendes herausspiegelt, aufzuheben. Wenn Sie annehmen, dass jeder Instinkthandlung ein an sich schon aktives Ganglienmaterial zugrundeliegt … dann erübrigt sich natürlich auch die Suche nach der speziellen Ursache der *Leerlaufreaktion* vollkommen." (von Holst, letter to Lorenz, April 1, 1937, Konrad Lorenz Family Papers)

[52] Van der Klaauw, letter to Lorenz, Mai 16, 1937, Konrad Lorenz Family Papers.

[53] "Nicht gerne hätte ich die Arbeit ohne diese Neuorientierung auf Grund der Ergebnisse von Holst in Druck gegeben." (van der Klaauw, letter to Lorenz, Mai 25, 1937, Konrad Lorenz Family Papers)

[54] "Sachlich ist zunächst festzustellen, dass die Dinge von Holst eine ganz unglaubliche Förderung meines eigenen Verständnisses der von Lorenz beschriebenen Erscheinungen zu Folge haben. Vieles wird falsch, z. B. die Definition des 'angestrebten Kettenreflexes'. Es spricht eine überwiegende und überzeugende Zahl von Tatsachen, Schwellenerniedrigung, Leerlaufreaktion, Intensitätsabnahme nach ein oder mehrmaligem Ablauf, unabhängig von Zielerreichung usw. usw. dafür, dass wirklich alle eigentlichen Instinkthandlungen Holstsche automatisch-rhythmische Prozesse sind. Wirklich unbedingte Reflexe sind die angeborenen Auslösemechanismen. Damit kommt die Notwendigkeit, analytisch viel schärfer zwischen dem Ablauf der Instinkthandlung und ihrer Auslösung zu unterscheiden usw. usw. usw. Dass die Reflexlehre einfach falsch ist, ist nicht meine Schuld, sondern die der Physiologen und eine unglaubliche Zahl von aus der Reflextheorie heraus unverständlicher Dinge werden auf einnmal *einer* überzeugend einfachen Erklärung zugänglich." (Lorenz, letter to Stresemann, April 16, 1937)

[55] In January 1937, long after Lorenz met von Holst, Otto Koehler commented on Lorenz's first instinct paper (that was to appear in a few months) and recommended him to read some articles of von Holst on the neural coordination of rhythmic movements, because these experimentally founded ideas fitted with Lorenz's gas-pressure model of the causation of instinctive behavior: "Lesen Sie ferner v.Holsts 4 Arbeiten im Pflüger 1935/6 über die Koordination der Rhytmen der Flossenschläge, so finden Sie dort Vorstellungen über deren Zustandekommen, die Ihrem Gasdruckkessel weitgehend parallellaufen und zudem physiologisch experimentell gut begründet sind." (Otto Koehler, letter to Lorenz, January 9, 1937, Konrad Lorenz Family Papers)

[56] Klaus Taschwer and Benedikt Föger have already pointed to the fact that von Holst did not convince Lorenz before April 1937, but they did not lay out the chronology and evidence in detail (Taschwer and Föger, 2003).

[57] Lorenz says in 1931 about the draft of 1932 paper that it is the attempt to deal in a physiological manner with features that are usually approached from a psychological point of view: "Es ist nur ein Versuch, Erscheinungen, die meist nur von der psychologischen Seite betrachtet wurden, einmal möglichst physiologisch zu fassen." (Lorenz, letter to Stresemann, July 30, 1931)

[58] Lorenz, 1950, pp. 240, 241.

[59] Lorenz, 1937b.

[60] Lorenz, [1931] 1970, p. 21.

[61] Lorenz [1932] 1970, p. 95; [1935] 1970, p. 249; [1937a] 1970, p. 282.

[62] Röell, 2000.

[63] Burkhardt 1999, 2003, 2005.

[64] Whitman, 1919**.**

[65] Heinroth, 1911; Heinroth and Heinroth, 1924–1933.

[66] Lorenz, 1950, p. 222, my emphasis. From the perspective of Burkhardt it becomes clear that the frequent citation of Heinroth and Whitman had the function of justifying the existence of an emerging discipline (Burkhardt, 1981).

[67] The German biologists Friedrich Alverdes and Friedrich Hempelmann used an instinct-organ analogy before Lorenz, saying that instincts are given to the organism the same way organs are, or inherited like morphological structures (Alverdes, 1925; Hempelmann, 1926).

[68] Lorenz [1935] 1970, pp. 117, 250; [1937a] 1970, pp. 262, 314; 1937b, p. 23.

[69] Lorenz, 1935.

[70] My account can only show why Lorenz was *more likely* to have the unusual phylogenetic position than another one. In contrast, Kalikow is too bold when she claims that the concept of innate releasing mechanism "could not have been invented without an over-all optic such as that provided by the chain-

reflex theory" (Kalikow, 1975, p. 334). McDougall, for instance, talked about organisms being "endowed by nature with a lock", to be unlocked by "a key", i.e., "a specific object that evokes an instinctive response" (McDougall, 1933, pp. 98f). So McDougall's work contained an idea that has some of the main features of the innate releasing mechanism concept. The difference is not that Lorenz had some ideas with which other authors could not have come up. Other authors might have had similar ideas, albeit embedded in a completely different theory. The difference is that Lorenz was more likely to take certain steps given his observations and theoretical assumptions. (Lorenz actually read this passage of McDougall's, probably when working on the 'Companion.' His annotations show that he was very sympathetic to McDougall's key-lock metaphor.)

[71] His research practice was also similar to that of American animal psychologists.

[72] Bierens de Haan 1935, 1937. He actually took a vitalist stance by assuming that instincts are brute facts that we cannot explain. Instincts and the goal-directedness of behavior are fundamental explanatory principles that cannot even be explained by the fact of evolution (1935, 1940).

[73] Bierens de Haan, 1940.

[74] For the points made in this paragraph see Bierens de Haan, 1933; 1935, p. 735; 1937, p. 9; 1940, pp. X, 24, 35; 1942.

[75] Bierens de Haan, 1942, p. 100.

[76] Bierens de Haan, 1942; Lorenz, 1942.

[77] In fact, Lorenz did not talk about instincts because this term is too vague. Instead, he preferred the term 'instinctive behavior pattern' (*Instinkthandlung*).

[78] Heinroth 1918, 1930.

[79] Lorenz, 1935; quoted from the translation Lorenz, 1970, p. 249

[80] Lorenz [1937a] 1970, p. 314; 1937b, p. 23.

[81] Lorenz, 1996, p. 239.

[82] On Whitman see Burkhardt 1988, 2005.

[83] Whitman, 1899.

[84] Whitman, 1899, pp. 331ff, 338.

[85] Whitman, 1899, p. 285

[86] Lorenz [1935] 1970, p. 120; [1937a] 1970, p. 291; 1996, pp. 245f.

[87] In 1931, Lorenz described the absence or loss of a specific innate behavioral pattern and its sudden reappearance, depending on the physical condition or the social developmental environment of an organism. He remarked that intelligence cannot compensate for the loss of these patterns (Lorenz [1931] 1970, pp. 55f). One year later, he observed that environmental and physiological disturbances can result in the loss of instinctive behavior patterns, claiming that "these disturbances always result in the absence of components of such patterns and never in the performance of novel ones; there is always breakdown rather than an alteration." (Lorenz [1932] 1970, p. 85)

[88] When Whitman states that "intelligence would have a tendency to break up and render plastic a previously stereotyped instinct" (1899, p. 337), Lorenz annotates on the margin: "break up and render plastic are two very different things!!!" Whitman emphasizes the continuity of instinct and intelligence: "Plasticity of instinct is not intelligence, but it is the open door through which the great educator, experience, comes in and works every wonder of intelligence" (p. 338), while Lorenz disagrees by annotating: "Error! unles Plasticity=Breaking up." Lorenz finds Whitman's observation very useful, but thinks that they are erroneously interpreted. At the end of his copy of Whitman 1899, Lorenz writes: "If Prof. Whitman wasnt influenced by Spencer and Lloyd Morgan he'd be much nearer the truth."

[89] Whitman, 1899, p. 329.

[90] Lorenz [1935] 1970, p. 120; Lorenz [1937a] 1970, p. 290.

[91] Lorenz [1937a] 1970, p. 290.

[92] Whitman, 1899, p. 337.

[93] It is for instance not clear whether he ever read Darwin's book on emotions. Burkhardt points out that the preface that Lorenz wrote for the Chicago edition (Darwin, 1965) does not demonstrate any knowledge of Darwin's account (Burkhardt, 2005).

[94] See Burkhardt 1983, 2005.

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