

The early theoretical development of Konrad Lorenz

The motivating factors behind his instinct concept

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Abstract

The present study discusses the early theoretical development of Konrad Lorenz in the period from 1930 to 1937. In this period Lorenz developed his position on instinct in the first place, and thus his theoretical views were subject to change. Despite this change, the paper points to relatively stable features of Lorenz's approach, which emerged relatively soon in his scientific career and guided his theoretical development in this and beyond this early phase.

The focus is on the emergence of Lorenz's instinct concept—his main theoretical and conceptual innovation, which proved to be fundamental for the formation of ethology as a scientific discipline. 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; and flexible or intelligent behavior does not evolve from instinctive behavior. 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. Despite this critique Lorenz never abandoned his strong innate-learned dichotomy.

I view Lorenz's early theoretical development as being guided by four conceptual and methodological decisions as to how to study and explain behavior. These aspects, 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. These four general aspects of Lorenz's approach are: 1) the idea that the study of innateness has primacy over studying

learning, 2) the idea that we need a physiological rather than a psychological explanation of behavior; 3) the taxonomic and phylogenetic approach to behavior; 4) and the use of ideas from experimental embryology to think about the development of behavioral characters. The taxonomic-phylogenetic approach was particularly crucial in promoting Lorenz's idea that innate behavior patterns do not evolve into flexible behavior components. 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. Lorenz developed his early theory of instinct primarily on his own. Several of the intellectual influences on Lorenz are best viewed not as providing direct contributions to Lorenz's ideas but as supporting his general approach as embodied in the four aspects of his framework.

The origin of ethology as a scientific discipline was first and foremost due to the intellectual efforts of Konrad Lorenz and Niko Tinbergen. After the second world war it was largely Tinbergen rather than Lorenz who developed new theoretical ideas and who was concerned about the institutional and intellectual unity of ethology (Burkhardt forthcoming). But most of the very ideas and concepts of ethology were formulated by Lorenz in the 30s. My discussion focuses on this theoretical development of Lorenz from 1930 to 1937, which was so important for the formation of his own ideas as well as the origin of ethology. The goal of the present paper is to understand the early development of Lorenz's instinct concept by concentrating on some methodological and conceptual factors that were stable features of Lorenz's perspective despite the fact that his views changed—factors that drove Lorenz's intellectual development.

Crucial about Lorenz's theoretical ideas from early on is his distinction between innate and learned behavioral characters. Overall behavior sequences have to be analyzed into innate and learned components, and only the former qualify as instinct. The tradition in comparative psychology before Lorenz usually viewed instincts as innate rather than learned behavior

features, but Lorenz breaks with this tradition by endorsing a fundamental innate-learned dichotomy. For unlike everyone else before him he assumed that there are neither *ontogenetic* nor *phylogenetic* transitions between instinctive and insightful behavior. On Lorenz's account, instincts are inflexible and do not get modified by learning during ontogeny at all. Moreover, instincts do not evolve into more flexible or learning-based behavior components, that is, an instinct is never homologous to insightful behavior. When Lorenz was formulating his idea, the theory that instincts are phylogenetically derived from habits—as defended by Romanes—was often criticized because of its seeming Lamarckist views of inheritance. However, Lorenz's contemporaries generally assumed both that instincts get ontogenetically modified by experience and that insightful and flexible behavior evolved from instinctive and inflexible behavior. For this reason, Lorenz's instinct concept was a complete novelty.

After the second world war, Lorenz's strong innate-learned dichotomy was subject to vigorous criticism from animal psychologists, most prominently Lehrman (1953). Many ethologists abandoned the assumption that the difference between the innate and the learned is to be viewed as a dichotomy rather than a continuum. However, this is paper not about the scientific merits of Lorenz's or the innateness concept in general. Instead my discussion is purely historical in that I want to understand Lorenz's early theoretical development and his central theoretical views such as his instinct concept and his innate-learned distinction.

My goal is not to retell the often well-known details about Lorenz's theoretical development.¹ Rather, we can understand Lorenz's theoretical development by paying attention to some general and unchanging features of Lorenz's approach. I view Lorenz's theoretical development as being guided by four conceptual and methodological decisions as

¹ Burkhardt (forthcoming) gives a masterful discussion of the intellectual history of ethology and in particular of the contribution of Lorenz and Tinbergen. For a biography of Lorenz see Taschwer and Föger (2003).

to how to study and explain behavior. These aspects, 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. In a nutshell, the four factors motivating Lorenz's instinct concept are: 1) the idea that the study of innateness has primacy over studying learning, 2) the idea that we need a physiological rather than a psychological explanation of behavior; 3) the taxonomic and phylogenetic approach to behavior; 4) and the use of ideas from experimental embryology to think about the development of behavioral characters. The taxonomic-phylogenetic approach was particularly crucial in promoting Lorenz's idea that innate behavior patterns do not evolve into flexible behavior components. 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. Lorenz developed his theory of instinct until 1937 for the most part on his own. As I will explain later in more detail, several of the intellectual influences on Lorenz in this period of time are best viewed not as providing direct contributions to Lorenz's ideas but as supporting his general approach as embodied in the four factors of his framework.

The development of Lorenz's early ideas

As Lorenz's early ideas on instinct are for the most part well-known, I do not intend to give a detailed overview of his theoretical development. Rather, I will briefly recall those aspects of his conceptual development that are relevant for the present paper. This includes in particular his intellectual influences. The focus will be on the development of his ideas on instinct and innateness, so that the next section can lay out and discuss the influence of the above mentioned four factors on his theoretical development. The function of this section is to provide a chronological framework for the following more thematic and conceptual discussion.

Lorenz's first important publication, appearing in 1931, gives a detailed overview of the observations that Lorenz conducted with his jackdaws (Lorenz 1931). It is non-theoretical insofar as it does not offer explicit reflections about the nature or definition of instinct. But the paper embodies a focus on certain behavioral phenomena and uses criteria of innateness. In fact, it is very much a paper like the ones Lorenz's scientific mentor Oskar Heinroth wrote. Rather than using the term 'instinct' (or 'Instinkt'), Lorenz adopts Heinroth's term 'Triebhandlung', which refers primarily to innate motor patterns, particular bodily movements that are part of the overall behavior of an individual. From early on, Lorenz focuses in his observations and discussion mainly on what later will be called fixed action patterns. Lorenz assumes two criteria of innateness: first, that a certain type of behavior is always performed in the same manner even though in certain situations a different behavior may be more adaptive (Lorenz says that these behavioral patterns are sometimes carried out reflex-like). The second criterion is that these 'Triebhandlungen' are elicited in a relatively specific situation (foreshadowing the later concept of an innate releasing mechanism).

In this very early period of Lorenz's intellectual development, his mentor Oskar Heinroth was of crucial importance. From 1930 onwards Lorenz had an intense correspondence with Heinroth.² But it is not the case that Heinroth proposed specific theoretical ideas about the nature of instincts to Lorenz. As it seems, Lorenz developed his later explicit theoretical ideas on his own. Still, even though Heinroth's work hardly offers any theoretical discussion about instincts (Heinroth and Heinroth 1924–1933), it still embodies a certain approach to and perspective on behavior. It is in this respect that Heinroth was a crucial influence on Lorenz. In the next section I will return to the way in which Heinroth influenced what I called Lorenz's four aspects.

² Posthumously published in Heinroth and Lorenz (1988).

While Lorenz (1931) is not theoretical in nature and does not go beyond Heinroth's views about instinctive behavior, Lorenz's next publication can be viewed as his first theoretical step. Lorenz (1932) discusses criteria of innateness in detail and in particular endorses a particular definition of instinctive behavior. Lorenz is apparently influenced by the chain reflex theory of instinct, even though Lorenz (1932) actually does not explicitly mention or even endorse this theory. The chain reflex theory views instinctive behavior as sequences of reflexes, and it was used by many biologists working in neurophysiology (especially the physiology of invertebrates). An aspect of this approach that Lorenz explicitly endorses is the instinct definition of Heinrich (1910), a physiologists working in the tradition of the chain reflex theory. Lorenz follows Ziegler in defining the difference between instinctive and insightful behavior as the difference between innate and acquired neural pathways. While many animal psychologists characterized instinctive behavior—in contrast to insightful behavior—by the absence of consciousness or subjective factors, Ziegler's definition permitted Lorenz to draw this distinction in purely physiological rather than psychological terms.

Apart from this instinct definition, Lorenz elaborates on some of his former ideas. At one point he talks about the releasing pattern (Auslöser) of an instinctive behavior pattern, in accordance with the idea of instincts as reflexes. A new important criterion of the innateness of a behavior pattern is the activity being carried out without their normal object or without any object. Lorenz calls them activities that are performed 'in vacuo' (auf Leerlauf)—a forerunner of the concept of vacuum activities. Lorenz now clearly expresses his conviction that instinct are rigid and inflexible rather than being modified by experience. A new argument is to compare them with organs. Just like morphological structures, which are inherited and can be used as taxonomic characters, instinctive behavior patterns exhibit developmental fixity, i.e., their development is insensitive to environmental inputs. Lorenz states that environmental and physiological disturbances result in the loss or complete

breakdown of instinctive behavior patterns, but not in their alterations or the performance of new behavior patterns. This idea will prove to be important for Lorenz's later ideas about the evolution of instinctive behavior. In order to reconcile his idea that instincts are rigid with the fact the overall behavior of an individual is modifiable and influenced by learning, Lorenz makes a fundamental theoretical move. He introduces the idea of *instinct-conditioning intercalation* (Erbtrieb-Dressur-Verschränkung). The overall behavior can be analyzed into a sequence of components. Some of them are innate and are instincts in Lorenz's sense, i.e., rigid behavior patterns. But components of the overall behavior sequence are variable as they involve prior learning, predominantly conditioning and in a few cases insightful behavior.

Lorenz's next important paper is the famous 'Companion' (Lorenz 1935). As this and Lorenz's following theoretical papers are well-known, I will only mention a few aspects of them. The 'Companion' contains virtually all features of Lorenz's early theory of instinct. Lorenz restates his conviction that instincts do not get modified by experience and criticizes others as ignoring the possibility of instinct-conditioning intercalation. Due to experience or insight the very same and rigid behavior pattern might be used in new situations and for new purposes, but there "is some difference between *construction of a novel tool* through insight and conditioned use of an *inherited tool*".³ Lorenz pushes the instinct-organ analogy further by the notion of *maturation*. Even though the performance of some instinctive pattern might 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 just innate but needs to mature in the course of development—like organs, which are nothing but innate structures that need to develop during ontogeny until the adult performance is reached. In his theoretical discussions so far, Lorenz has stressed the fact that there are no ontogenetic transitions between instinctive and insightful behavior. The 'Companion' makes the novel claim that

³ Quoted from the translation Lorenz (1970), p. 110, my emphasis.

there are no *phylogenetic* transitions between instinctive and flexible behavior. Lorenz says that he does “*not* regard the instinctive behaviour patterns as *homologous* with all acquired or insight-based behaviour patterns”.⁴

An important conceptual innovation is the notion of imprinting. I will return in the next section to an aspect of Lorenz’s views of imprinting that is relevant for my discussion. In addition, Lorenz explicitly introduces the concept of an innate releasing mechanism. Lorenz specifically discusses releasers of social behavior and points out that there are innate releasing mechanisms as well as releasing mechanisms acquired by conditioning. Thus the releaser needs to be distinguished from the instinct it triggers—while the former may be acquired, the latter is always innate. Lorenz briefly specifies his relationship to Ziegler’s chain reflex theory of instinct. Lorenz apparently uses this theory as a way to think about instinctive behavior and states that instincts are reflex chains, but he is also aware of the fact that Ziegler’s theory as it stands is incomplete and cannot account for all aspects of instinctive behavior. Lorenz mentions the work of Wallace Craig (see in particular Craig 1918) and integrates Craig’s concept of appetite into his framework by pointing to threshold lowering and the search for a releasing stimulus. However, the discussion is very brief and at this stage the account does not give a systematic theory of how these ideas combine.

In May 1937 Lorenz’s famous (first) instincts paper appears (Lorenz 1937a). Compared to the ‘Companion’, this paper hardly introduces new concepts or novel theoretical insights. But this paper is so important because it does not deal much with observations, but is purely theoretical in nature. Lorenz gives a focused restatement of his theory of instinct, and in particular criticizes other approaches to instinctive behavior. Lorenz’s main target is Lloyd Morgan and McDougall. Now Lorenz integrates Craig’s ideas such as his notion of appetites

⁴ Quoted from the translation Lorenz (1970), pp. 116–117.

more fully than the ‘Companion’ did. This instinct paper is the first time that Lorenz discusses his relation to Ziegler and the chain reflex theory of instincts in detail. Lorenz states that phenomena such as appetitive behavior show that the reflex theory is incomplete. A crucial difference is that instinctive behavior goes together with subjective experience, an instinct is a reflex pattern whose elicitation is sought after. But so far Lorenz still broadly thinks along the lines of the reflex theory of instincts.

The second instinct paper (Lorenz 1937b), published a few months after the first instinct paper, restates Lorenz’s position. The fundamental theoretical innovation taking place in this paper is the shift from regarding instinctive behavior as elicited by external factors to a position that includes endogenous factors in the production of instinctive behavior. This is a crucial move away from the perspective of standard reflex theory. So far Lorenz had assumed that since the performance of an innate behavior pattern (the consummatory act) looks like a reflex, it is—like a reflex—fully caused by an external stimulus. Now Lorenz acknowledges that factors internal to the organisms play an important role in the production of instinctive behavior. It is well-known that this important theoretical shift and conceptual novelty was solely due to the influence of Erich von Holst.

Both Wallace Craig and Erich von Holst were important influences on Konrad Lorenz. And they were direct influences insofar as Lorenz explicitly took over some of their ideas on the nature of behavior. However, the following discussion will not mention these two influences. The reason is that I focus on features of Lorenz’s theoretical development that occurred largely before Lorenz interacted with Craig and von Holst or that are independent of their influence. This applies to the four factors of Lorenz’s perspective and his innate-dichotomy, to be discussed in the remainder of the paper. In particular Lorenz’s strong innate-learned dichotomy was already formed before the shift away from the reflex theory took place, and it was not affected by it. Even after the change in perspective, he viewed instincts

as ontogenetically inflexible and unchangeable by experience, and never homologous to conditioned or intelligent behavior. While von Holst's influence on Lorenz proved to be important for the establishment and success of ethology as a scientific discipline, in my view there is a sense in which this influence was less crucial for Lorenz.

The four factors guiding Lorenz's views on instinct

After this review of Lorenz's theoretical development and some of his influences, I turn to the more interesting and crucial part of my paper. I will lay out and discuss four factors of Lorenz's general perspective that guided Lorenz's theoretical development. These four factors can be viewed as key conceptual and methodological decisions on to how to study and explain behavior that Lorenz—unlike several other scientists—made. Most of these factors were present from very early on, and they remained constant features of Lorenz's post-war approach to behavior. Taken together, these factors constrained Lorenz's theoretical development, guiding it into a certain direction. The four aspects help to make intelligible why Lorenz ended up with his own instinct concept and his strong innate-learned dichotomy that distinguished him from other scientists. Because of the explanatory importance of these four factors, intellectual influences on Lorenz in this respect will be of particular interest for my discussion. In fact, my suggestion is that most of the early influences on Lorenz before 1937 did not offer explicit theoretical contributions to Lorenz's views on the nature or definition of instinct. Instead, they are best viewed as providing support on the four aspects of Lorenz's general perspective.

The *first factor* is Lorenz's focus on innate behavior. It does not need to be pointed out that Lorenz approached the study of behavior from a zoological rather than a psychological point of view. On his view, animal behavior is the model for human behavior, in fact, 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 is 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 (Morgan 1903; McDougall 1933; Bierens de Haan 1933). Lorenz disagreed with many animal psychologists in that he claimed the innate rather than learned is the core of behavior. 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.

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 1938 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 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. This topic was addressed in the correspondence with Heinroth not before 1938, and stressed in Lorenz's publications and public talks only from 1938 onwards (Lorenz 1940, 1943).⁵ But 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

⁵ For more on this issue see Kalikow (1976, 1983), Föger and Taschwer (2001), and Taschwer and Föger (2003).

points to Oskar Heinroth as another person who views morality as an instinct.⁶ Thus, Lorenz views instincts as the basis of human behavior, in particular human moral behavior. He is serious about his claim that the instinctive 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 helped to discern innate features of bird behavior (Heinroth and Heinroth 1924–1933).⁷ Apart from the focus on the innate and the instinctive, Heinroth was convinced—just like Lorenz—that human have much more instincts than is usually acknowledged and that the study of human instincts is crucial for understanding human social behavior (Heinroth 1911, p. 702). As the above quoted letter from Lorenz shows, Heinroth viewed morality as based on instincts.

⁶ “Wenn man nämlich etwas Gutes und Anständiges *nicht* aus Freude an der Sache ... und rein triebhaft tut, so verliert es sofort den Charakter der ‘moralischen’ Handlung, ... Das heißt, meine sociale Reaktion der Dankbarkeit spricht nur an, wenn ‘der Andere’ mir *instinktmässig* (‘aus sich heraus’, ‘von Herzen’) social entgegengekommen ist. Im Augenblick, wo er sich dabei was gedacht hat, was überlegt hat, kriegt er doch höchstens einen Dankesbrief, aber keine Dankbarkeit. ... Leider läuft so Vielen die Heinrothsche Lehre von ‘Moral’ als einem echten Instinktkomplex so furchtbar gegen den Strich und kommt ihnen cynisch und das Wesen der Moral herabsetzend vor.” (Lorenz, letter to Stresemann, March 5, 1933)

⁷ It is interesting to note that while for Lorenz the deprivation experiment was an important theoretical argument for the existence of innate instincts, it was hardly a part of his practical research and study of instinct.

The *second factor* guiding Lorenz's approach is the idea that we need a biological rather than a psychological explanation of instinctive behavior. The physiological, not the mental is the core of behavior. Behavior is to be explained by means of their 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 Lloyd Morgan, McDougall, or Bierens de Haan emphasize the goal-directedness of behavior and make recourse to psychological drives that guide behavior. Even a zoologist such as Julian Huxley assumed that an understanding of animal minds is a crucial factor in behavior studies. For Lorenz, however, the goal-directedness is definitely not an explanation of behavior, it itself needs to be explained by causal factors.⁸ It is the focus on causal-physiological explanation that Tinbergen appreciated so much about Lorenz's approach. (Tinbergen termed this an 'objectivistic' rather than subjectivistic-mentalist approach to behavior; see Tinbergen 1942.) 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.

In accordance with this physiological approach, physiological triggers are obviously more of a model for explaining instinctive behavior than psychological factors. This is the reason why the early Lorenz endorsed the chain reflex theory of instinct for some while (or at least used it for a general way to think about instinctive behavior). The reflex theory fitted Lorenz's observation that instinctive behavior patterns are carried out in a rigid and stereotypical way and it offered for an physiological explanation of how these behavior patterns are caused. But the commitment to physiological explanations remained even after Lorenz abandoned the view that instincts are reflexes. Lorenz's theoretical shift that was triggered by von Holst's

⁸ Russell (1934) states that it is unlikely that the migration of fish can be explained by a purely physiological theory (p. 42). In his copy of Russell (1934), Lorenz annotates this passage: "*why* in hell??"

influence replaced a focus on the neurophysiological reflex tradition of instinct with another neurophysiological approach to behavior. Now Lorenz assumes 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. The psychohydraulic model that was proposed in this period relies on a mechanical analogy (water and water pressure) to illustrate the causation of behavior. Thus, Lorenz's commitment to the second factor was unaffected by the shift towards von Holst's ideas. Indeed, the point of what I call the four factors of Lorenz's approach is precisely to lay out general conceptual and methodological aspects of Lorenz's general approach that remain unchanged and that guide Lorenz's theoretical development. These four factors are not about specific theoretical claims or definitions of instincts that Lorenz put forward.

As regards this second factor, 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, who wrote a whole book dealing explicitly with theories of instinctive behavior and defending a reflex approach of instincts (Ziegler 1910). But the aspect of Ziegler's influence that is of interest for me is not the fact that Lorenz (1932) took over Ziegler's definition of instinct, that 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 for 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.⁹

⁹ Lorenz says in 1931 about his draft of Lorenz (1932) that the paper 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,

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 reflexological tradition in this manner. The medical training helped Lorenz adopting a physiological approach to the causation of behavior.

The *third factor* is in my view the most important aspect of Lorenz's approach. It is the main factor driving Lorenz's theoretical development. This is Lorenz's taxonomic or phylogenetic approach to behavior. As it is well known, Lorenz homologized behavior characters and used them to classify taxonomic groups. Behavioral homology is a type of homology stemming from classical ethology. Many other psychologists used a comparative approach to behavior in that they studied organisms from different groups and compared their behavior. But Lorenz's approach meant much more than dealing with different groups of organisms. This is the reason why I prefer the label taxonomic or phylogenetic approach rather than comparative approach, because the latter does not point to the difference between Lorenz's approach and traditional comparative animal psychology. The taxonomic approach is the reason why Lorenz views instincts in analogy to morphological structures. Lorenz emphasizes 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 (Lorenz 1931). In fact, Lorenz claims that instincts are sometimes more conservative than morphological features (1932, 1935, 1937a). Tinbergen learned about this taxonomic approach to behavior from Lorenz (Röell 2000).

Erscheinungen, die meist nur von der psychologischen Seite betrachtet wurden, einmal möglichst physiologisch zu fassen." (Lorenz, letter to Stresemann, July 30, 1931)

One reason why the taxonomic-phylogenetic approach is such a crucial feature of Lorenz's approach is that it was strongly embedded in his research practice. 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 close proximity to his home so that he could observe them (Whitman 1919). 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 distinguishes instincts from intelligent behavior in terms of innate vs. acquired neural pathways. However, while Lorenz endorsed this neurobiological definition for some while, 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 their natural environment rather than investigating their neurophysiology. 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. 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 comparative anatomy classes when writing on the 'Companion'.¹⁰ 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 (Heinroth 1911; Heinroth and

¹⁰ In 1934 Lorenz decided to leave comparative anatomy and pursue a career in animal psychology.

Heinroth 1924–1933). Lorenz acknowledged this support by Heinroth, in particular his comparative-taxonomic approach, on many occasions.

The *fourth factor* concerns the way Lorenz's approaches the development of behavior. Lorenz uses ideas from embryology and the developmental biology of morphological structures to think about the ontogeny of behavioral features. However, this factor is not as influential as the other factors in driving Lorenz's perspective, and it is not always clearly and consistently present in Lorenz's account. 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.¹¹ But Lorenz pushed the analogy further by using the idea of maturation to support the claim that instincts do not get modified in ontogeny under the influence of experience. On his account, even though the performance of instincts may change during early ontogeny, this just reflects the fact that instincts as well as their underlying morphological and physiological basis has to mature, i.e., to develop in the first place. Sometimes Lorenz used more specific embryological ideas, such as theoretical concepts from developmental mechanics. Lorenz's account of imprinting shows this. Imprinting is an ontogenetic acquisition process. A bird has to be imprinted to its parents, for instance, 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 (1935) assumes that imprinting is like the process of embryological induction or determination. 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.

¹¹ Alverdes (1925), for instance, said that instincts are given to the organism the same way organs are.

The following remark by Lorenz nicely illustrates how he used the framework of developmental mechanics to think about the development of behavior. Koehler (1933) is an article dealing with the idea of wholeness in biology. 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 of Koehler (1933) “Prägung!” (Imprinting!). It is intriguing that this margin 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 on instinct and innateness

The four factors of Lorenz’s perspective are 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.¹² The taxonomic-phylogenetic approach is particularly important for Lorenz’s

¹² My account can only show why Lorenz was *more likely* to have his peculiar views on instinct and innateness than another theory. In contrast, Kalikow (1975) 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” (p. 334). McDougall (1933), for instance, talks 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” (pp. 98–99). So McDougall’s work contains an idea that has some of the main features of the innate releasing mechanism

theoretical development. Due to this theoretical commitment, which was strongly embedded in his research practice, in his study of instincts Lorenz does not focus on the overall behavior of an organisms or on long behavior sequences, that may be viewed as pursuing a goal. On the contrary, as it is well-known Lorenz restricts his instinct concept to specific behavior sequences, particular motor patters that are part of the overall behavioral repertoire of an animal. For these motor patterns can be clearly observed, homologized with the behavior pattern of closely related species, and found to be characteristic of a taxon.¹³ Heinroth dealt before Lorenz with behavior based on a phylogenetic framework. Just like Lorenz he focused on characteristic movements of certain parts of the body (Heinroth 1918, 1930). Lorenz's views that instincts are innate motor patterns fits perfectly with his focus on innate behavior and his phylogenetic-taxonomic perspective. It also promises the possibility of a physiological explanation of instincts. The definition of instincts as innate motor patterns is in strong contrast to the account of other animal psychologists, who often viewed instincts as innate drives that motivate behavior and account for its goal-directedness.

My claim is that other animal psychologists had an instinct concept that was very different from Lorenz's because they did not subscribe to all four aspects of Lorenz's perspective. 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

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 observation and the four aspects of his theoretical perspective.

¹³ In fact, Lorenz does not talk about instincts because this term is too vague. Instead, he uses only the term instinctive behavior pattern.

psychologists working with the more traditional purposivist perspective criticized each other vehemently. Röell (2000) gives a detailed discussion of the Dutch tradition in animal psychology and ethology and addresses the interesting question of why the Lorenzian ethologists and the representatives of the traditional animal psychological approach did not want to collaborate or at least to coexist.¹⁴ In my view, one important factor was institutional. Lorenz and Tinbergen attempted at creating 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 a difference in perspective as well.

I focus on a brief comparison between Lorenz and J. A. Bierens de Haan, the most influential animal psychologists of the Dutch purposivists tradition. Bierens de Haan stresses the way in which instincts get modified in ontogeny under the influence of experience. Bierens de Haan (1940) is the statement of his mature theory. It is interesting to note that Bierens de Haan very well agrees 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 offer very different interpretations because the point of agreements are embedded in very different theoretical perspectives. Bierens de Haan accepts the idea that there is a morphological as well as physiological aspect of behavior. However, he states that we can focus on the psychological study of behavior alone, whereas for Lorenz psychological aspects such as subjective feelings make only sense as part of a biological approach to behavior. Bierens de Haan acknowledges the existence of reflexes and reflex-like behavior. But his focus is on intelligence, learning, and the goal-directedness of behavior (Bierens de Haan 1933, 1935). In

¹⁴ Among other things, Röell points out that National Socialism and anti-German sentiments played a role for the attitude of several Dutch animal towards ethologists such as Konrad Lorenz and Otto Koehler.

fact, he claims that the reflex is about causation, while the instincts is about teleology (the goal-directedness), so that instincts and reflexes cannot possibly be identified. Directly criticizing Lorenz, Bierens de Haan argues 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 factors motivating behavior. Objective (biological) issues such as behavior activities needs to be distinguished from subjective (psychological) issues such as instincts. Overall, Bierens de Haan disagrees with each of the four aspects of Lorenz perspective. He acknowledges the existence and importance of instincts and innate behavioral characters, but his theoretical focus is on learning, intelligence, and the goal-directedness of behavior. While Lorenz prefers physiological explanations of behavior, Bierens de Haan stresses the importance of psychological explanations and the existence of innate drives motivating behavior. The latter also does not make use of a taxonomic-phylogenetic approach to behavior, and he does not use embryological models to explain the development of behavior. Due to the fundamental difference of perspective the debate between Lorenz and Bierens de Haan leads to a clash. Bierens de Haan (1942) restates the critique of Lorenz and makes some polemical remarks. Lorenz (1942) strikes back, vigorously attacking Bierens de Haan's general purposivist and vitalist approach rather than addressing the interesting and critical points that Bierens de Haan (1942) raised.

The four aspects of Lorenz's perspective make intelligible why he came to view instincts as motor patterns rather than psychological drives motivating behavior. The four factors also shed light on his innate-learned dichotomy. As already pointed out, Lorenz claims that there are neither ontogenetic nor phylogenetic transitions between innate and learned behavior. Unlike virtually any one else, Lorenz assumes that instincts do not get modified by experience

at all.¹⁵ Driven by his taxonomic approach, Lorenz focuses on instincts as innate motor patterns. This suggests the idea that instincts are inflexible, and the analogy between instincts and morphological structures supports the idea of rigidity and—based on the notion of maturation—the independence of environmental influences. Using the notion of instinct-conditioning intercalation, Lorenz can account for the overall flexibility of behavior without abandoning the idea that instincts are rigid. This yields Lorenz's basic views about how behavior is composed into innate and learned components, and how it develops.

Moreover, 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. This position contradicted all former and contemporary accounts, and it might initially strike one as surprising given Lorenz's commitment to a Darwinian framework, as Darwin stressed the continuity between animal and human cognitive capacities. An interesting proponent of the more traditional view was the zoologist Charles Otis Whitman.¹⁶ In his influential lecture, Whitman (1899) discussed animal behavior and its evolution based on detailed observations. He argued in particular against the view that instincts are derived from acquired habits, a position on animal behavior quite popular at that time and sometimes based on Lamarckist assumptions. But even though Whitman had—like Lorenz—an explicitly biological and comparative approach to behavior, he assumed that instincts can evolve into more flexible behavior, agreeing with Spencer and Lloyd Morgan in this respect.

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,

¹⁵ In 1935 Lorenz stated that the British zoologists Elliot Howard is the only one besides him who denies the influence of experience on instincts (Lorenz, letter to Stresemann, August 3, 1935).

¹⁶ See Burkhardt (1988, forthcoming) on Whitman.

the importance of intelligence can only increase when instinctive behavior patterns get 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. Instead of evolving into more flexible components, instincts atrophy and get lost (Lorenz 1935, 1937a, 1992). 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. This shows how important his early focus on particular observations is for his later evolutionary account. Whitman (1899), in contrast, uses 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 plastic, behavioral sequences involving instinctive components get broken up and appetitive and condition-based components may be added (Lorenz 1937a).¹⁷

Apart from the fact that Lorenz has a different preferred hypothesis, why does he think that the alternative 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 (Lorenz 1935). The

¹⁷ When Whitman states that "intelligence would have a tendency to break up and render plastic a previously stereotyped instinct" (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! unless Plasticity=Breaking up". Lorenz finds Whitman's observation very useful, but thinks that they are erroneously interpreted. At the end of Whitman (1899) Lorenz annotates: "If Prof. Whitman wasnt influenced by Spencer and Lloyd Morgan he'd be much nearer the truth".

presence of an instinctive component inhibits the development of intelligent components with the same function (Lorenz 1937a). 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 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 (Lorenz 1937a). An annotation by Lorenz puts this idea more strongly than we know from his 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, ..." (Whitman 1899, p.337). 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 might be due to the fact Lorenz was not really an evolutionary theorists. He was an evolutionary thinker in that he defended ethology as a biological, phylogenetic, and evolutionary approach to behavior (and proposed

his evolutionary epistemology), but he was not much engaged in discussion about the mechanisms of evolutionary change—despite the fact that during his biological career important evolutionary movements such as the Modern Synthesis and later on sociobiology emerged. In this respect he was very much unlike Whitman, who was at end of the 19th century at the forefront of discussions about Darwinism and evolutionary theory.¹⁸

The four factors of Lorenz's approach help to understand how Lorenz came to held his specific position on the evolution of instincts. First, they promote Lorenz's views on how behavior is composed and how it develops, which indirectly suggest his evolutionary position. Behavior is composed out of 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. Second, in particular Lorenz's taxonomic-phylogenetic approach has a more direct bearing on his evolutionary views. Lorenz states that the fact that instincts can be used for comparative purposes shows that they cannot undergo variation due to experience.¹⁹ The evolutionary

¹⁸ The absence of substantial discussions about the mechanisms of evolutionary change in the early theoretical work of Lorenz is quite striking. This is on the one hand simply 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 just not evolutionary biology. It is for instance not clear whether he ever read Darwin's book on emotions. Burkhardt (forthcoming) points out that the preface that Lorenz wrote for the Chicago edition (Darwin 1965) does not demonstrate any knowledge of Darwin's book. Lorenz's emphasis on ethology as the biological, in fact, evolutionary science of behavior is to some extent part of his rhetoric to create a new biological field (Burkhardt 1981, 1983).

¹⁹ "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

conservativeness of instincts and the analogy to morphological structures are—in his view—incompatible with the idea that instincts are influenced by experience and exhibit large evolutionary changes.²⁰ The use of instinct as taxonomic characters is the driving force for Lorenz's focus on motor patterns as what instincts actually are and the assumption that they are inflexible. This is the reason why I regard his taxonomic-phylogenetic approach as the most important aspect of his perspective. If we want to understand why Lorenz assumed that his research program might break down if he abandoned the view that there are neither ontogenetic nor phylogenetic transition 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 primary academic training. Independent of whether we can get really clear about Lorenz's motivations and arguments for his position on the evolution of instincts, the four factors guiding his theoretical perspective help us understand the development of his instinct concept, which distinguished him from other animal psychologists.

behavior patterns cannot undergo substantial modification through individual experience, as has been assumed by Spencer, Lloyd Morgan, and others.” (Lorenz 1992; quoted from the translation Lorenz 1996, p. 239)

²⁰ “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, ...” (Lorenz 1935; quoted from the translation Lorenz 1970, p. 249)

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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'. 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).

References

Alverdes, F. (1925). *Tiersoziologie*. Leipzig: C. L. Hirschfeld.

Bierens de Haan, J. A. (1933). Der Stieglitz als Schöpfer. *Journal für Ornithologie* 81, 1–22.

- Bierens de Haan, J. A. (1935). Probleme des tierischen Instinktes. *Die Naturwissenschaften* 23, 711–717, 733–737.
- Bierens de Haan, J. A. (1940). *Die tierischen Instinkte und ihr Umbau durch Erfahrung*. Leiden: E. J. Brill.
- Bierens de Haan, J. A. (1942). Der Kampf um den Begriff des tierischen Instinktes. *Die Naturwissenschaften* 30, 98–104.
- Burkhardt, Jr, R. W. (1981). On the emergence of ethology as a scientific discipline. *Conspectus of History* 1, 62–81.
- Burkhardt, Jr, R. W. (1983). The development of an evolutionary ethology. In D. S. Bendall (Ed.), *Evolution: From Molecules to Men*, pp. 430–444. Cambridge: Cambridge University Press.
- Burkhardt, Jr, R. W. (1988). Charles Otis Whitman, Wallace Craig, and the biological study of animal behavior in the United States, 1898–1925. In R. Rainger, K. R. Benson, and J. Maienschein (Eds.), *The American Development of Biology*, pp. 185–218. Philadelphia: University of Pennsylvania Press.
- Burkhardt, Jr, R. W. (forthcoming). *Patterns of Behavior: Konrad Lorenz, Niko Tinbergen, and the Founding of Ethology*. Chicago: Chicago University Press.
- Craig, W. (1918). Appetites and aversions as constituents of instincts. *The Biological Bulletin* 34, 91–107.
- Darwin, C. (1965). *The Expression of Emotions in Man and Animals*. Chicago: Chicago University Press.
- Föger, B. and K. Taschwer (2001). *Die andere Seite des Spiegels: Konrad Lorenz und der Nationalsozialismus*. Wien: Czernin.
- Heinroth, O. (1911). Beiträge zur Ethologie, namentlich der Ethologie und Psychologie der Anatiden. In H. Schalow (Ed.), *Verhandlungen des V. Internationalen Ornithologen-Kongresses in Berlin, 30. Mai bis 4. Juni 1910*, pp. 589–702. Berlin: Deutsche Ornithologische Gesellschaft.
- Heinroth, O. (1918). [Über reflektorische Bewegungsweisen im Lichte der Stammesverwandschaft]. *Journal für Ornithologie* 66, 111–114, 241.

- Heinroth, O. (1930). Ueber bestimmte Bewegungsweisen der Wirbeltiere. *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin*, 333–342.
- Heinroth, O. and M. Heinroth (1924–1933). *Die Vögel Mitteleuropas, in allen Lebens- und Entwicklungsstufen photographisch aufgenommen und in ihrem Seelenleben bei der Aufzucht vom Ei ab beobachtet*. 4 volumes. Berlin: Hugo Bermühler.
- Heinroth, O. and K. Lorenz (1988). *Wozu aber hat das Vieh diesen Schnabel? Briefe aus der frühen Verhaltensforschung 1930–1940*. Edited by Otto Koenig. München: Piper.
- Kalikow, T. J. (1975). History of Konrad Lorenz's ethological theory, 1927–1939. *Studies in the History of Philosophy of Science* 6, 331–341.
- Kalikow, T. J. (1976). Konrad Lorenz's ethological theory, 1939–1943: 'Explanations' of human thinking, feeling and behaviour. *Philosophy of the Social Sciences* 6, 15–34.
- Kalikow, T. J. (1983). Konrad Lorenz's Ethological Theory: Explanation and Ideology, 1938–1943. *Journal for the History of Biology* 16, 39–73.
- Koehler, O. (1933). Das Ganzheitsproblem in der Biologie. *Schriften der Königsberger Gelehrten Gesellschaft* 9, 139–204.
- Lehrman, D. S. (1953). Critique of Konrad Lorenz's theory of instinctive behavior. *Quarterly Review of Biology* 28, 337–363.
- Lorenz, K. (1931). Beiträge zur Ethologie sozialer Corviden. *Journal für Ornithologie* 79, 67–120.
- Lorenz, K. (1932). Betrachtungen über das Erkennen der arteigenen Triebhandlungen der Vögel. *Journal für Ornithologie* 80, 50–98.
- Lorenz, K. (1935). Der Kumpan in der Umwelt des Vogels. Der Artgenosse als auslösendes Moment sozialer Verhaltensweisen. *Journal für Ornithologie* 83, 137–215, 289–413.
- Lorenz, K. (1937a). Über die Bildung des Instinktbegriffes. *Die Naturwissenschaften* 25, 289–300, 307–308, 324–331.
- Lorenz, K. (1937b). Über den Begriff der Instinkthandlung. *Folia Biotheoretica* 2, 17–50.
- Lorenz, K. (1940). Durch Domestikation verursachte Störungen arteigenen Verhaltens. *Zeitschrift für angewandte Psychologie und Charakterkunde* 59, 2–81.
- Lorenz, K. (1942). Induktive und teleologische Psychologie. *Die Naturwissenschaften* 30, 133–143.

- Lorenz, K. (1943). Die angeborenen Formen möglicher Erfahrung. *Zeitschrift für Tierpsychologie* 5, 235–409.
- Lorenz, K. (1970). *Studies in Animal and Human Behaviour*. Volume I. Cambridge, MA: Harvard University Press.
- Lorenz, K. (1992). *Die Naturwissenschaft vom Menschen: Eine Einführung in die vergleichende Verhaltensforschung*. Das “russische Manuskript” (1944–1948). Edited from the author’s posthumous works by Agnes von Cranach. München: Piper.
- Lorenz, K. (1996). *The Natural Science of The Human Species: An Introduction to Comparative Research*. The “Russian Manuscript” (1944–1948). Edited from the author’s posthumous works by Agnes von Cranach. Cambridge, MA: MIT Press.
- McDougall, W. (1933). *An Outline of Psychology*. London: Methuen.
- Morgan, C. L. (1903). *Instinkt und Gewohnheit*. Leipzig: B. G. Teubner.
- Röell, D. R. (2000). *The World of Instinct: Niko Tinbergen and the Rise of Ethology in the Netherlands (1920–1950)*. Assen: Van Gorcum.
- Russell, E. S. (1934). *The Behaviour of Animals*. London: E. Arnold.
- Taschwer, K. and B. Föger (2003). *Konrad Lorenz: Biographie*. Wien: Zsolnay.
- Tinbergen, N. (1942). An objectivistic study of the innate behaviour of animals. *Bibliotheca Biotheoretica* 1, 39–98.
- Whitman, C. O. (1899). *Animal Behavior*. Reprinted from the *Biological Lectures of The Marine Biological Laboratory, Woods Hole, 1898*. Boston: Ginn.
- Whitman, C. O. (1919). *The Posthumous Works of Charles Otis Whitman*. Volume III: *The Behavior of Pigeons*. Edited by Harvey A. Carr. Washington: The Carnegie Institution of Washington.
- Ziegler, H. E. (1910). *Der Begriff des Instinktes einst und jetzt. Eine Studie über die Geschichte und die Grundlagen der Tierpsychologie*. Jena: Gustav Fischer.