

From Ethology to Behavioral Biology[☆]

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Abstract

Understanding behavior has been a crucial aim for philosophers and scientists since Aristotle and, particularly, Charles Darwin. In the first half of the 20th century, a coherent scientific discipline – ethology – emerged as a field initially concerned especially with the causation of behavior at the proximate level. Early ethology had its origins in psychology and physiology and employed often a comparative approach; using behavior as a tool to analyse phylogenetic relationships was a prime target. With help of cybernetic models researchers like Konrad Lorenz and Niko Tinbergen aimed at understanding instinct and the origin and organization of drives. Ethologists were aware of the limitations of a purely mechanistic approach, though, and therefore strived to study behavior at the levels of ontogeny, immediate causation, function and evolution. With the emergence of behavioral ecology as a sub-discipline concerned solely with the function and adaptive value of behavior, ethology got a new impetus. Its power to develop hypotheses based on evolutionary theory and to test their specific predictions experimentally gained this research field great popularity, even at the expense of a narrow perspective. Eventually, after the turn of the millennium ethologists returned to a more balanced approach in the study of behavior, considering ontogeny, causation and evolution besides function. This has coincided with a new name for the discipline: behavioral biology.

Keywords

Adaptive value; Behavioral biology; Behavioral ecology; Ethology; Evolution; Function; Instinct; Konrad Lorenz; Niko Tinbergen; Ontogeny; Oskar Heinroth; Ultimate and proximate causation

The Very Beginning

Like for so much else in biology, Charles Darwin can be safely viewed as the great grandfather of ethology. In his endeavor to understand the continuity between biological traits across different taxa including humans, he realized that behavior was an important component of his evidence for biological evolution. He devoted a whole chapter of “On the Origin of Species” (Darwin, 1859) to the study of instinct, and in “The Expression of the Emotions in Man and Animals” (Darwin, 1872), he observed: “With mankind some expressions, such as bristling of the hair under the influence of extreme terror, or the uncovering of the teeth under that of furious rage, can hardly be understood, except on the belief that man once existed in a much lower and animal-like condition.” Despite such precursors, the systematic study of animal behavior began with the work of the eminent Chicago biologist Charles Otis Whitman and his student Wallace Craig, who gained significant insights in the behavior of animals by their systematic and comparative studies of pigeons. The term “ethology” was coined by American zoologist Wheeler (1902). In 1910, Oskar Heinroth, who later became the director of Berlin Zoo and Aquarium, published his “Beiträge zur Biologie: namentlich Ethologie und Psychologie der Anatiden” (Contributions to the biology, especially ethology and psychology of the anatids) a few years later (Heinroth, 1910), a paper that might be considered as a milestone in the infancy of ethology. Heinroth was particularly interested in the behavioral displays, social signals and rituals among conspecifics. In good Darwinian tradition and using ducks, swans and geese he argued that species-specific instinctive behavior could be used, like morphology, to determine the genetic affinities of different taxa, a view fully shared by C.O. Whitman in Chicago. Together with his wife Magdalena, Heinroth raised numerous young of a great variety of bird species in “Kaspar Hauser conditions”, i.e., in isolation from other birds, with the ambitious aim to systematically study the instinctive behavior of all the bird species of central Europe. This massive piece of work was published from 1924 to 1934 in the four-volume classic of “Die Vögel Mitteleuropas” (The Birds of Central Europe, Heinroth 1924-1934).

Development of Concepts

Heinroth's work was influential to a number of naturalists, mostly ornithologists, who readily accepted his view that behavior is a species-specific trait suited for comparative studies in order to reconstruct phylogeny. Most prominent among his disciples was to become the Austrian zoologist Konrad Lorenz, a zealous observer of behavior with an unrivalled intuitive knowledge of animals. Lorenz was strongly influenced by the idea that instinctive behavior patterns are innate and invariable, rendering them suitable to

[☆] *Change History:* August 2017. Michael Taborsky changed the title from “Ethology in Europe”, which focused on the emergence and development of this discipline in Europe. The new contribution takes a broader aspect and deals with the progression of approaches and foci in behavioral research over the last 120 years worldwide.

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reconstruct phylogenies just like any other bodily structure. In this view, instincts are equivalent to organs. Lorenz regarded the concept of instinctive behavior patterns not as a hypothesis to be tested, but as a fundamental assumption. Like his much admired mentor Heinroth, Lorenz used mainly birds as model systems, particularly because of the opportunity to raise them by hand and due to their similarity to humans with regard to sensory biology, conditions greatly facilitating systematic study. Lorenz' declared approach was to start with impartial observations devoid of any hypothesis. On the basis of these observations he developed ideas and concepts, above all the hypothesis of "innate releasing mechanisms". He also took up Heinroth's concept of imprinting (which the latter had never called by this term) and elaborated it, first in his seminal paper on "Der Kumpan in der Umwelt des Vogels" (The companion in the bird's world; Lorenz, 1935).

Interestingly, Lorenz and the other early ethologists in Europe focused on questions that had been of interest mainly to psychologists, despite their highly divergent approach. The emphasis was on internal states and environmental influences, but the ethologists' concern extended beyond the question of immediate causation of behavior (Lorenz, 1950). Comparative Ethology was thus intended to be an alternative to B.F. Skinner's behaviorism, which prospered as an influential psychological discipline in North America, and the "reflexology" of Russian Ivan Pavlov. The European naturalists' aim was to teach psychologists the comparative and evolutionary approach, and the necessity to understand behavior of whole animals in their natural environment. The pre-eminent advocate of this approach was Niko Tinbergen, a Dutch naturalist who turned out to become, besides Lorenz, the second prime mover of ethology. Together they developed the concept of instinct based on a hierarchical organization of drives, assuming as key categories of behavioral causality action-specific energy and consummatory acts, together with innate releasing mechanisms (Tinbergen, 1951). These concepts were strongly shaped by an imagination of energy flow, but without assuming a material counterpart. The most conspicuous concepts of the day were Lorenz' psycho-hydraulic model and Tinbergen's hierarchical organization of drives.

The concepts of instinct developed first and foremost by Lorenz and Tinbergen were important sources of testable hypotheses enabling young researchers to scrutinize resulting predictions by experimental, physiological and cybernetic approaches. It is important, however, to consider these developments in historical context. In the end, the original concepts proved to be too simplistic and partly mistaken, and considered in retrospect they seem to have lead nowhere. If the concepts of the "classical" period of Ethology might be now viewed as scientific dead ends, at the time they were immensely important for the emergence and development of a behavioral science. Researchers like Gerard Baerends at Groningen, Robert Hinde at Oxford and the comparative psychologists Theodore Schneirla at New York and Daniel Lehrman at Rutgers University were sparked by early ethological theory and took it to its first acid test (Hinde, 1966; Bateson and Klopfer, 1973–1995). The intense discussion that ensued proved to be as important to the field as was the preceding development of the theory (Burkhardt, 2005).

Lorenz and Tinbergen

Despite their common interest and general agreement, the roles of that important, odd couple, Lorenz and Tinbergen, diverged greatly. Lorenz was mainly concerned with the causality of behavior as a result of the interaction of external stimuli and innate, preprogrammed action patterns. He was interested in imprinting as a mechanism causing long-lasting effects of early experience, and in the origin and function of ritualised social interactions. His major tool was the hand raising of birds, mainly ducks and geese, which enabled him to observe his study organisms at close hand and largely undisturbed. Lorenz was no keen systematic experimenter but had a rather philosophical interest in the mechanisms underlying behavior at any level. In contrast, Tinbergen loved the systematic experimental approach, which he preferably used under field conditions. He formalized the concept of instinct and strived for closer connections between the causal analysis of behavior and a physiological approach. Like Lorenz he was a keen naturalist and exceptionally gifted observer, but in addition he was also an excellent experimenter.

Over several decades, the rise and charisma of ethology was firmly in the hands of these two characters. Even if Karl von Frisch shared the 1973 Nobel prize of medicine and physiology with them for establishing ethology as a scientific discipline, von Frisch's role in this endeavor was negligible. He was an outstanding experimenter and his research on the dance language of bees is a masterpiece, but he was not actively involved in the conceptual and practical establishment of ethology. In contrast, Lorenz and Tinbergen, in their own ways, strived for constructing the foundations for a scientific study of behavior. While Lorenz was the hyperactive motor developing and disseminating concepts of behavioral regulation, outspoken, self-confident, sometimes dogmatic, but well connected among his colleagues, Tinbergen was more modest and careful in his attempt to gain attention for his ideas and for the sake of ethology, always integrative in his actions and arguments, but nevertheless pushing hard towards the establishment of ethology as a biological science on an equal footing with, say morphology or physiology. Tinbergen realized that confining ethology to the study of causation would be too narrow a discipline. He wanted survival value and evolution incorporated in a systematic study of behavior, just as ontogeny and causation – the four "Tinbergen questions" (Tinbergen, 1963) that today still serve as the undisputed guideline for the study of behavior (Bateson and Laland, 2013; Taborsky, 2014).

Eventually, ethology gained momentum and Lorenz and Tinbergen obtained prestigious positions with the Max-Planck Society and at the University of Oxford, respectively. Their continuous effort to establish this new discipline included the foundation of scientific journals, with "Ethology" being first in the field, co-founded by Lorenz under the name "Zeitschrift für Tierpsychologie" (Journal for Animal Psychology) in 1937. They organized international conferences that became increasingly popular, with the 1952 meeting at Lorenz' Max-Planck Institute in Buldern being the first of a series of "International Ethological Conferences" (IECs) that still continue today, with biannual intervals. These activities spawned numerous disciples, and ethology groups emerged at universities throughout the world. The most conspicuous centres of ethology were the Max-Planck-Institute for Behavioral

Physiology at Seewiesen, where Lorenz finally gained ground, and departments at the Universities of Oxford, Cambridge, Leiden and Groningen. For several decades, Germany, Great Britain and The Netherlands stood at the forefront of this new discipline. While the research directions pursued in German and British ethology diverged increasingly, ethology in the Netherlands kept its broad scope.

Regional Divergence

The policy of the German Max-Planck Society was to merge ethology with physiology, which defined the research activities at the Max-Planck-Institute for Behavioral Physiology at Seewiesen from the start (1958) right to its end (1999). This was an obvious combination, not only because in essence behavioral causation is a physiological problem, but also because of the strong position of physiology in biological science in Germany; its keen focus on sensory and neural physiology prepared the ground for the study of behavioral mechanisms at the level of organisms, organs and cells. In Great Britain, on the other hand, where the tradition was strong in ecology and evolutionary thinking, the interest in the adaptive value of behavior gained momentum. While Tinbergen at Oxford strived to keep behavioral research in balance between the ultimate and proximate levels of explanation, his successors abandoned three of the four legs of ethology and capitalized entirely on the adaptive value of behavior – giving birth to the most conspicuous subdiscipline of ethology, behavioral ecology.

Behavioral Ecology and Beyond

The onset and expansion of behavioral ecology may be seen as the second success story of ethology, after its hype in post-war Europe that followed the birth of the discipline. It is also worth noting that behavioral ecology brought about the unification of behavioral research in Europe and America, despite the divergent history of this science on these two continents. The consequent application of evolutionary theory to the study of behavior revolutionized not only ethology, but the whole of organismic and integrative biology. William D. Hamilton of University College, London, achieved a breakthrough with his theoretical model of “The genetical evolution of social behavior” (Hamilton, 1964), where he concluded that “Species following the model should tend to evolve behavior such that each organism appears to be attempting to maximize its inclusive fitness”. This caused a paradigm shift from the focus on the maximization of individual fitness to the inclusion of effects on kin, which helped to understand the evolution of altruistic behavior such as known from eusocial insects – a dodgy puzzle to Charles Darwin. At Harvard, evolutionary biologists Robert Trivers and E. O. Wilson sparked behavioral science with their systematic application of evolutionary theory to the study of sociality (Wilson, 1975; Trivers, 1985).

The other significant conceptual progress in the early days of behavioral ecology was its focus on fitness effects of biological traits, which paved the way to the cost-and-benefit analysis of behavior. Richard Dawkins at Oxford has been perhaps the most radical proponent of a shift from the focus on the individual to a gene centered view of behavioral evolution (Dawkins, 1976). Further role models of this development include John Krebs and Nicolas Davies, also from Oxford University, who developed elegant experimental tests of qualitative and quantitative predictions of foraging, aggressive and reproductive behaviors. They spread the ideas and concepts of this new approach to the study of animal behavior by editing an influential series of books (Krebs and Davies, 1978–1997). John Maynard Smith from Sussex and Geoffrey Parker from Liverpool proposed a game theoretical approach to the study of behavioral decisions (Parker, 1974; Maynard Smith, 1982), which had been used already long before in economy and military strategy. At the Max-Planck Institute in Seewiesen, Lorenz' successor, Wolfgang Wickler, pursued a strict functional approach to behavior (Wickler and Seibt, 1977) that had lasting effects on the development of ethology in Europe by the dispersion of his disciples. In the Netherlands, behavioral research centres at the Universities of Groningen, Leiden and Utrecht thrived with a balanced approach to behavior that, remarkably, was not as narrowly confined to the study of its adaptive value as was the custom at many other centres of ethology worldwide. Australia, Canada, and several countries in Scandinavia and Southern Europe developed their own strong research programs in behavioral ecology, which has contributed substantially to the progress in theoretical and empirical behavioral research. More recently, behavioral research has gathered momentum also in South America and Asia, particularly in Japan, India and China.

Despite these positive developments, the unfavorably narrow focus of behavioral ecology on the adaptive value of behavior proved to obstruct a comprehensive understanding. The study of the causation of behavior was largely left in the hands of specialists from other disciplines, such as neurophysiology, endocrinology, developmental biology and experimental psychology. Despite the scientific progress in these fields, a synthetic view of the origin, causation, function and evolution of behavior has been largely missing. Only after the turn of the millennium, ethology has started to regain its balance (Kappeler, 2010; Rubenstein and Alcock, 2018). Due to the connotations of the word “ethology”, which is often equaled with the early history of this discipline, the regained breadth of research on animal behavior is as of late called “behavioral biology”, a term actually proposed already by Tinbergen (1963) (cf. Taborsky, 2014). We can now satisfactorily state that behavioral development, causal mechanisms, adaptive value and evolutionary patterns all have their firm place in behavioral research and university curricula at literally hundreds of institutions distributed all over the world. National and supranational behavioral societies thrive, small and large meetings on all aspects of behavioral research are popular and the job market for young researchers in behavior shows promise for a bright future of this discipline. Under its new brand name behavioral biology, ethology has come of age.

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