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Ethology and the Study of Behavioral Evolution

While many individuals have contributed to the development of ethology, the Austrian Konrad Lorenz (1903-1989) and the Dutchman Niko Tinbergen (1907-1988) are regarded as its central figures, whose efforts established ethology as a recognized subdiscipline of evolutionary biology. Lorenz and Tinbergen first met in 1936 when Lorenz traveled to Leiden and they became friends and collaborators. Lorenz was known for his great passion for watching animals and his visionary breadth, while Tinbergen brought a more analytical and experimental approach to the study of animal behavior.

As well as being practitioners of ethology, both Lorenz and Tinbergen wrote about its methodology. Tinbergen identified four questions that ethologists should attempt to answer about any specific behavior: How does it develop? What are its immediate causes? What is its function? How did it evolve? Lorenz stressed the importance of spending hours watching animals behaving spontaneously before formulating any hypotheses, and he professed himself shocked by the deep ignorance of animals that he thought he detected in behavioristic psychologists such as J.B. Watson (1878-1958). The development of an ethogram for a species -- a list of observed behaviors -- is the starting point for ethological research.

In 1973, Lorenz and Tinbergen shared the Nobel prize for medicine with the German zoologist Karl von Frisch (1886-1982). They were cited "for their discoveries concerning organization and elicitation of individual and social behavior patterns". Von Frisch is best known for his discovery of the dance language of honey bees. Von Frisch's student Martin Lindauer conducted a comparative study of the dances of several closely related bee species to reconstruct their phylogeny. The idea that behavior could be as reliable as morphology in reconstructing the relationships among species was significant for the acceptance of ethology as an important part of evolutionary biology.

Early ethologists were very interested in the concept of instinct (indeed, Lorenz and Tinbergen met at a workshop on this very topic). Lorenz is associated with the idea of a fixed action pattern -- a complex behavior that can be reliably and repeatedly elicited by a specific "sign stimulus". Tinbergen showed that a particular pecking behavior of herring gull chicks could be elicited by relatively simple models of the adult beak with a prominent red spot. While the general concept of a fixed action pattern applies across numerous species, particular sign stimuli and fixed action patterns are highly species-specific and can only be understood in the context of the particular developmental, adaptive, and evolutionary contexts faced by members of the species. Many years of fruitless nature versus nurture debates and wars about definitions have made current ethologists leery of the concept of instinct. Nevertheless, the study of inherited behavioral adaptations is still an important part of ethology. Areas of particular interest and activity include predator-prey interactions and the various systems of anti-predatory alarm calls found in a wide range of species, the social dominance structures that also vary widely across different species, comparative studies of social play, the memory demands of food caching and retrieval, tool manufacture and use, and the existence of culturally transmitted traits.

Ethology can also be understood by contrast to alternative approaches to the study of behavioral evolution in biology and psychology. Within biology, behavioral ecology applies population-level models of evolution to the understanding of animal behavior. Behavioral ecologists freely borrow models from economics and game theory which represent individual organisms as rational optimizers and allow analysis of interactions between environment and behavior on reproductive fitness and the distribution of behavioral traits. Unlike traditional ethology, behavioral ecology has been less concerned with immediate causes of the behavior of individual animals, or its development, and mechanisms responsible for generating optimal behavior are often simply assumed and not explained. Nevertheless, there has been significant crossover between the two subdisciplines.

Comparative psychology also takes an explicitly evolutionary approach to animal behavior. However, unlike biologists who tend to be very interested in differences among individuals and among species, psychologists are trained to look for general patterns of behavior and principles of learning (sometimes

referred to as "laws" of learning). Where comparative psychologists do see differences between species, they often regard these as revealing steps on an evolutionary ladder to full blown cognition, and they are often drawn to investigating tasks which mark thresholds of cognitive sophistication. Thus, for example, there has been much interest among comparative psychologists in finding out which species can recognize themselves in mirrors, can pass a "false belief" attribution task, or can learn a human language. Many ethologists prefer to observe animals in natural or naturalistic habitats. Some scientists, to be found on both sides of this divide, are pluralists who believe that the integrative study of animal behavior requires both field and laboratory investigation; others are less ecumenical.

Ethology has had several important offshoots. Both Lorenz and Tinbergen extended their approaches to the study of human behavior: Lorenz in his study of aggression, and Tinbergen (with his wife Elisabeth) in studying autistic children. The willingness of ethologists to treat humans as scientific objects of study like any other animal also importantly foreshadowed E.O. Wilson's extension of evolutionary models of the social behavior of insects to explain human sociality, thus giving rise to the field of sociobiology -- a field that also is tightly connected to behavioral ecology.

Another important offshoot of ethology is the comparative study of neural function known as neuroethology. Specific adaptations of neural systems to particular behavioral tasks have been described in a variety of species, such as the startle response of fish, the coordinated vocalizations of frogs, the directional hearing of owls, or the unusual sensory mechanisms of star-nosed moles.

Lastly, cognitive ethology is the label coined by Donald Griffin (1915-2003) to describe the reintroduction of issues of cognition and consciousness to the evolutionary study of animal behavior. Griffin made his early reputation conducting careful physical analyses of the echolocation capabilities of bats, before turning his attention to questions of animal mind and awareness. Many disagree with his approach which they find excessively anecdotal and anthropomorphic. Nevertheless, the cognitive revolution that took place in human psychology was slow in coming to the ethology, and Griffin was instrumental in getting other scientists to take seriously the idea that questions about the evolution of mind could be addressed by studying topics ranging from cognitive maps in honey bees to intentional communication in primates.

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