

1

the study of animal behavior

JOHAN J. BOLHUIS AND LUC-ALAIN GIRALDEAU

INTRODUCTION

The scientific study of animal behavior is also called **ethology**, a term used first by the nineteenth-century French zoologist Isidore Geoffroy Saint Hilaire but then used with its modern meaning by the American zoologist Wheeler (1902). Ethology is derived from the Greek *ethos*, meaning “character.” There is some resemblance with the word “ethics,” which is derived from the same Greek word. This makes sense, seeing that ethics is basically about how humans ought to behave. Unfortunately the word “ethology” is often confused with the word “ethnology” (the study of human peoples), with which it has nothing in common. In fact the very word processor with which we are writing this chapter keeps prompting us to replace “ethology” by “ethnology”! For whatever reason, the word “ethology” is not used as much as it used to be, although there is still an active animal behavior journal bearing this name. Instead of “ethology,” nowadays many authors use the words “animal behavior” or “behavioral biology” when they refer to the scientific study of animal behavior.

A Brief History of Behavioral Biology

Early days

Scientists (and amateurs) studied animal behavior long before the word “ethology” was introduced. For instance, Aristotle had many interesting observations concerning animal behavior. The study of animal behavior was taken up more systematically mainly by German and British zoologists around the turn of the nineteenth century. The great British naturalist Charles Darwin (1809–82), pioneer of the theory of

evolution by **natural selection** (1859), devoted a whole chapter of his classic book to what he called “instinct.” As early as 1873, a British amateur investigator called Douglas Spalding recorded some very interesting observations on the behavior of young domestic chicks, a phenomenon that was later called **imprinting**, after the German *Prägung*, introduced by Konrad Lorenz (1935, 1937a,b; see Chapter 6). At the beginning of the twentieth century, the behavior of animals was also studied in the context of **learning** by the Russian physiologist Ivan P. Pavlov (1927) and the American psychologist Edward L. Thorndike (1911) (see Chapter 7).

Lorenz and Tinbergen

In the middle of the twentieth century, the study of animal behavior became an independent scientific discipline, called ethology, mainly through the efforts of two biologists, the Austrian Konrad Lorenz (1903–89) and the Dutchman Niko Tinbergen (1907–88). It can be said that Lorenz was the more philosophical, theoretical of the two, whereas Tinbergen was very much an experimentalist, who together with his students and collaborators conducted an extensive series of field and laboratory experiments on the behavior of animals of many different species. Lorenz put forward a number of theoretical models on different aspects of animal behavior such as evolution and **motivation**. He was also the more outspoken of the two men, and some of his publications met with considerable controversy. In 1973 Lorenz and Tinbergen were awarded the Nobel Prize for Physiology and Medicine. They shared their prize with Karl von Frisch (1886–1982), an Austrian comparative physiologist and ethologist who had pioneered research into the “dance language” of bees (see Chapter 10).

Ethology versus comparative psychology

During the early days of ethology there was a certain amount of scientific rivalry between mainly European ethologists and North American experimental psychologists, who also studied animal behavior in what was usually called **comparative psychology**. The European ethologists emphasized that animal behavior is a biological phenomenon, and as such a product of evolution. This is exemplified by the use of the word “instinct” (e.g., in the title of Tinbergen’s 1951 classic book *The Study of Instinct*), which referred to the “**innate**” components of behavior that are subject to natural selection. A prominent critique of this way of thinking came from the American psychologist Daniel Lehrman, in his 1953 paper “A critique of Konrad Lorenz’s theory of instinctive behavior.” In this paper he argued against Lorenz’s theory that behavior can be dissected into “innate” and “acquired” (or learned) components (see Chapter 6 for a more detailed discussion of these issues). In general, American psychologists emphasized the effects of learning on behavior. Pavlov had already demonstrated the importance of what we now call **Pavlovian** (or **classical**) **conditioning**. Later, Thorndike studied learning processes that are now known as **instrumental** or **operant conditioning** (see Chapter 7). Another difference between the ethologists and experimental psychologists was that the former

often observed animals (of many different species) in their natural environment, whereas the latter (despite the name comparative psychology) often concentrated on one species (such as the rat or the pigeon) that was studied exclusively in the laboratory.

Behaviorism

The emphasis of the North American psychologists on learning was epitomized by the rise of **behaviorism** in the 1930s. Behaviorism was a very influential school of thought initiated by the American psychologist John B. Watson (1878–1958), with his book *Behaviorism* (1924). Essentially, Watson considered psychological phenomena to be physical activity rather than some kind of mental event. Watson proposed that we cannot make any scientific statements about what might be going on in our minds, and that introspection was unreliable. Rather, psychologists can only investigate the physical manifestations that we can observe in the form of behavior. For behaviorists, psychology is the study of behavior and of the external physical factors that influence it. They find that it is not possible to make scientific statements about mental processes. This may sound odd to us, but at the time behaviorism was extremely influential in science and beyond. Within North American psychology it was the dominant school of thought for several decades. Behaviorist theory also affected education practice, particularly with Watson's book *Psychological Care of Infant and Child* (1928). Watson once made the famous statement:

Give me a dozen healthy infants, well-formed, and my own specified world to bring them up in and I'll guarantee to take any one at random and train him to become any type of specialist I might select – doctor, lawyer, artist, merchant-chief, and, yes, even beggarman and thief, regardless of his talents, penchants, tendencies, abilities, vocations, and race of his ancestors.

This epitomizes behaviorist ideas about child rearing. Watson considered the upbringing of children to be an objective, almost scientific exercise, without the need for affection or sentimentality.

Watson's most famous student was Burrhus Frederic Skinner (1904–90), who applied behaviorist ideas to the study of learning. For Skinner and his behaviorist colleagues, learning had to do with changing relationships between visible entities, not with what might be going on inside the animal's head. In particular, behaviorist learning theorists suggest that learning involves the formation of associations between a stimulus and a response. Most of their experiments involve **instrumental conditioning** (see Chapter 7), where a certain response by the animal (e.g., pressing a lever) is rewarded (“**reinforced**”) with food.

Cognitive psychology

Within experimental psychology there came a reaction to behaviorism that took the form of what we now call **cognitive psychology**. In contrast to behaviorism, cognitive

psychologists start with the assumption that individuals (humans and other animals) have a mental life that can be investigated (see Chapter 8). For instance, Skinner (1957) maintained that language development in children was a learning process, where responses (i.e., uttering certain sounds) were reinforced. The great American linguist Noam Chomsky (1959) wrote a lengthy and highly critical review of Skinner's book on language development, in which he suggested that language acquisition is not a case of instrumental conditioning but the development of certain cognitive mechanisms, the so-called universal grammar (see Chapter 8). Another important publication that signaled the beginning of the cognitive revolution is the book by the British psychologist Donald Broadbent (1958) who, in contrast to Skinner, analyzed learning and memory in terms of cognitive mechanisms rather than stimulus–response relations. Hogan (1988) has noted that what cognitive psychologists call “cognitive structures” are in fact the same as the causal mechanisms that were proposed by ethologists such as Lorenz and Tinbergen (see Chapter 3).

Four Questions in the Study of Animal Behavior

Niko Tinbergen published a very important paper in 1963, in which he outlined the four major questions in the study of animal behavior, namely **causation**, **development**, **function** (Tinbergen called this **survival value**) and **evolution**. Tinbergen readily admitted that these questions were not very original, as three (causation, function, and evolution) had already been put forward by the British biologist Julian Huxley as the major questions in biology, and Tinbergen merely added a fourth, development. Tinbergen's four questions are sometimes collapsed into two categories: **proximate** and **ultimate** level questions, or “how” (causation and development) and “why” (function and evolution) questions respectively. No matter how these questions are broken up, it is crucially important that students of animal behavior be quite clear as to the type of question they are addressing when they study animal behavior. Tinbergen's analysis is so important that we would say that you cannot really understand animal behavior if you do not also understand the meaning of Tinbergen's four questions. Some of the more heated contemporary debates in the field of animal behavior can often be traced to misunderstandings about the meaning of the four questions (Hogan 1994; Bolhuis & Macphail 2001). It is essential, therefore, that any productive discussion about animal behavior involves participants capable of clearly stating which of the four questions they are addressing. This view of animal behavior has also served the organization of the present book, with Part I covering mostly causal and developmental topics and Part II dealing with functional and evolutionary questions.

Tinbergen's four questions are sometimes also called the “four whys,” because they represent four ways of asking “Why does this animal behave in this way?” Let's consider a bird singing at dawn, say a male song sparrow (*Melospiza melodia*). The question is: why is this bird singing? This seems a perfectly straightforward question, but in fact it is not so easy, because it can take any of four different forms. These

different forms – you’ve guessed it – have to do with Tinbergen’s four whys. The first of the four questions concerns causation: what causes the bird to sing? Another way of asking this is: what are the mechanisms underlying the male’s singing behavior? These mechanisms involve the “machinery” that operates within the animal and which is responsible for the production of behavioral output. Topics include the stimuli or triggers of behavior whether they be internal or external, the way in which behavioral output is guided, factors that stop behavior, and the like. These are questions concerning the generation of behavior. Sometimes this is called motivation, a subject discussed at length in Chapter 3. The second question is about development: how did the singing behavior of the bird come about in the lifetime of an animal? It turns out that a male song sparrow does not sing immediately after it has hatched from the egg – quite some time elapses before it has developed a song, a process that involves learning. Such questions that concern development of behavior, sometimes also called **ontogeny**, are discussed explicitly in Chapter 6. The third question has to do with function: what is the function of the bird singing and what is it singing for? This question has to do with the consequences of singing for the singer’s **fitness**. Does singing help the bird keep intruding males away from his nest? Or does it simply serve to attract females? The topic of function, its methods of enquiry and main findings are discussed explicitly in Chapter 9 and provide the framework for all chapters in Part II. The fourth question concerns evolution: how did this behavior come about in the course of evolution? Behavior does not leave many fossils behind and so the study of its evolutionary history requires the development of special methods. These methods, based on taxonomy and comparisons among species, are discussed in detail in Chapter 13.

The previous paragraph illustrates that the question “Why does this bird sing?” is not very useful, as it can have four different meanings. It can be very confusing if a biologist studying birdsong does not make it clear which of the four “why” questions is being asked, and it could lead to futile arguments about whether the bird is singing to attract mates or because it learned its song. The same problem arises in all other areas of animal behavior and so it is very important to make it clear which of the four questions is to be addressed in any study. Of course, it is possible that a particular investigator wants to address more than one question at a time. This is perfectly legitimate, as long as it is made explicit which of the questions is addressed at what time. A famous example of this is an experimental paper by Tinbergen et al. (1962) on the behavior of black-headed gulls (*Larus ridibundus*). After the chicks have hatched, the adult birds remove the empty eggshells from the nest. Tinbergen et al. investigated both the causation and the function of this behavior using elegantly simple field experiments and reported results of both levels in the same paper. There is also considerable overlap between some of the four questions. For instance, the development of behavior is essentially a causal problem but may also involve functional aspects (see Chapter 6). The evolution of behavior often depends on mechanism. For instance, emergent properties of an animal’s sensory and perceptual capabilities (mechanisms) may create opportunities for **sexual selection** to evolve extravagant traits (see Chapter 13). Finally, questions in one domain (e.g., function) can provide clues for questions in another domain (e.g., causation). For instance, a number of bird species cache food, some for a few hours, others

for months (Vander Wall 1990). It is plausible that the ecological circumstances that have given rise to these different forms of food caching may have also influenced the animals' ability to memorize spatial locations. In fact, a large number of studies at a mechanistic level (e.g., learning, memory, cognition, **neuroethology**) are concerned with the spatial memory of food-caching versus nonfood-caching birds (see Chapters 5 & 8).

Trends in the Study of Animal Behavior

Behavioral ecology: from mechanism to function

Much of the early research and theorizing of early ethologists such as Lorenz and Tinbergen was concerned with the causation of behavior. When Tinbergen was invited to move from the Dutch University of Leiden to the University of Oxford, he established the Animal Behaviour Research Group while the famous ornithologist David Lack was taking over the newly founded Edward Grey Institute of Ornithology. The coincidence of having both these scientists and their followers in the same department in Oxford sowed the seeds of a discipline that was to blossom much later in the mid-1970s under the name of **behavioral ecology**.

Behavioral ecology arose out of the fusion of evolutionary ecology, population ecology, and ethology. A number of conditions were ripe in the mid-1970s for such an event. In 1975 the Harvard entomologist Edward O. Wilson published *Sociobiology: The New Synthesis*, the birth of what is known today as **sociobiology**. Wilson's book was firmly grounded in population genetics and evolutionary biology. Its clear presentation of William D. Hamilton's concept of **inclusive fitness**, **kin selection**, the evolution of both **altruism** and social groups among others provided the essential foundations for a successful evolutionary approach to social behavior. Not long after that, in 1978, John R. Krebs of Oxford University and Nicholas B. Davies at Cambridge coedited a book they called *Behavioural Ecology: An Evolutionary Approach*, which was to apply a similar evolutionary approach but this time to all, not just social, behavior. The publication of this book marks the official birth of behavioral ecology, which now includes sociobiology.

Behavioral ecology today is more of an approach than a body of accumulated fact. Its initial success grew out of a combination of **optimality theory** and evolutionary thinking that pictures the expression of behavioral traits as constrained tradeoffs between their evolutionary benefits and costs (see Chapter 9). The development of the concept of the **evolutionarily stable strategy** (ESS) by the British evolutionary biologist John Maynard Smith (1982) allowed this cost-benefit approach to be applied to a wide range of behavioral interactions. Evolutionary thinking and the cost-benefit approach cast a new light on behavioral systems such as foraging, fighting, and **habitat selection** (see Chapter 9). When applied to communication it raised an important number of questions concerning the design of **signals** and their functions (see Chapter 10). Whereas early ethologists tended to picture sexual reproduction as a cooperative venture

between males and females, the evolutionary approach has somewhat subverted this idyllic view. **Mating systems** and mate choice (see Chapter 11) as well as conflicts of interests between mates (see Chapter 12) have become exciting and rapidly developing areas of the discipline. Darwin himself pictured behavior as a character that was modified over generations by selection. Hence behavior has a history that can be studied with contemporary organisms (see Chapter 13). When the evolutionary approach is applied to social groupings a number of interesting questions arise, especially in relation to apparently altruistic and **cooperative behaviors** that are often reported within groups (see Chapter 14).

Neuroethology and cognitive neuroscience

The mechanisms underlying behavior are also somehow represented in the workings of the central nervous system, in particular the brain. In fact, Tinbergen often used neural analogies and metaphors in his models of behavior. We shall see in Chapter 2 how the central nervous system obtains and processes **information** about its external world. As knowledge about the brain, both its gross and fine-level morphology as well as the way **neurons** are connected, led to increased interface between brain and behavior, a new subdiscipline arose that became known as neuroethology (Ewert 1980; see Chapters 2 & 5). In the early days of this new discipline, researchers concentrated on the study of the neural mechanisms of perception and movement, often in insects or lower vertebrates. More recently the study of the brain mechanisms of behavior is also directed at higher cognitive processes such as learning and memory or spatial orientation. Often, the terms “**behavioral neuroscience**” or “**cognitive neuroscience**” are used to describe these disciplines (see Chapter 5). Now the combination of an extraordinary array of powerful techniques, from electrophysiological recording to molecular analyses of RNA sequences, allows researchers to delve deeper into the connection between behavior and its neural substrate.

Cognitive ecology

Perhaps as a result of the success of behavioral ecology, the relationship between the brain and behavior has also been studied more recently from an evolutionary perspective. An animal's ability to collect and process information should be heavily influenced by its ecology. For instance, sexual selection operating within oscine birds has led to the development of diverse and complex songs that females are able to evaluate with great ability. How do the evolutionary pressures for complex birdsong affect the evolution of the underlying neural substrate? How does having a large **home range** affect the ability to navigate? Does having to store food place selective pressure on spatial memory? These questions, as well as those that explore the mental lives of animals and the way information is processed by brains, are treated extensively in Chapter 8.

Animal welfare, conservation biology, and evolutionary psychology

Many people are interested in animal behavior out of mere curiosity, the need to know more about something. This is all very fine but there always comes a time where someone will ask “What is the purpose of studying animal behavior?” This question, whether from a research colleague, a friend, or a granting agency, requires an answer expressed in terms of benefits to society. We see three areas in which applications of animal behavior research can contribute to human society, **animal welfare**, conservation, and understanding human nature. These types of questions are addressed in the third and last section of the book.

Animals are important contributors to wealth and quality of life. They provide us with nourishment, the means to find cures and treatments for our illnesses, as well as invaluable companionship. Almost all the information contained in this book relies on experiments and research conducted with animals. However, there is a growing concern that animals used for human benefit be exposed to as little unpleasantness as necessary. Are housing cages too small, or densities of individuals too high? Is the knowledge acquired from experiments sufficiently important to authorize animal experimentation? The answer to such, often difficult, questions depends in many ways on knowing something about an animal’s behavior (see Chapter 15).

Population growth and economic development have led to the increasing precariousness of a good number of species and as a result the intensity of research on conservation problems has increased exponentially in recent years. The way an animal responds to anthropogenic changes in its environment and its ability to cope with such modifications are likely dependent on its behavior, social organization, mating system, and ability to innovate. In that context we ask whether animal behavior can provide important, perhaps crucial, information on the conservation of the earth’s biodiversity (see Chapter 16).

People are endlessly curious about people and the sheer number of disciplines devoted uniquely to the study of human beings is eloquent testimony to this fact (e.g., medicine, anthropology, psychology, sociology, criminology). Animal behavior can provide insight into human behavior in two ways. More conventionally, phenomena observed in animals can be generalized, although often in some modified way, to humans. For example, just as a new antibiotic drug that cures an infection in some nonhuman primate can also be used, perhaps in a slightly modified way, to cure infections in humans, so can knowledge about how an animal learns be extended and applied to human learning. The second way, however, involves generalizing an approach rather than a result. For instance, can we learn anything new about human behavior by applying an evolutionary cost–benefit analysis to the things we do? This is what a discipline known as **evolutionary psychology** does (see Chapter 17).

SUMMARY AND CONCLUSIONS

Animal behavior has grown into a highly diverse set of approaches and disciplines. Its subject area ranges from molecules and neurons to individuals and populations. One of Tinbergen's major contributions to the study of animal behavior has been to make its goals explicit and clarify the four types of questions that can be asked of behavior: causation, development, function, and evolution. In this book we strongly advocate Tinbergen's position that behavior can only be understood through research on all four questions. In addition, we suggest that it is made clear which of Tinbergen's questions is addressed when a behavioral problem is investigated: a problem in one domain should not be investigated with concepts from another. That is why the chapters in the current book are organized explicitly into sections. The first is devoted to mechanisms and covers both cause and development. The next section is on function and covers both survival value and evolution. We end the book with a section on animal behavior and human society, dealing with animal welfare, conservation and human behavior in the hope of illustrating that answers to important questions will require addressing all four levels of questioning advocated by Tinbergen.

FURTHER READING

Tinbergen's (1963) paper on the four whys is essential reading for any serious student of animal behavior. It was reprinted in Houck and Drickamer (1996), which is a collection of classic papers on all aspects of animal behavior. Tinbergen's (1951) classic book is still very much worthwhile. It was reprinted in 1992 and is still available. The great British ethologist William Thorpe (1979) has written a brief history of ethology, viewed from the inside, whereas Dewsbury (1989) provides a more recent account from the North American perspective. Boakes (1984) is an excellent review of the history of the study of animal behavior by psychologists, whereas Laland and Brown (2002) provide a very clear account of the different ways in which the behavior of animals (including humans) can be studied from an evolutionary perspective. Functional and evolutionary aspects of behavior are also discussed in the edited volume by Krebs and Davies (1978), of which there is already a fourth edition (Krebs & Davies 1997), with every edition containing new information.

ACKNOWLEDGMENTS

We are grateful to Jerry Hogan and Euan Macphail for their comments on the manuscript.

