The Behavior of Animals

Mechanisms, Function, and Evolution

SECOND EDITION

Edited by
JOHAN J. BOLHUIS
LUC-ALAIN GIRALDEAU
JERRY A. HOGAN

WILEY Blackwell

THE BEHAVIOR OF ANIMALS

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Second Edition

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foreword

Robert A. Hinde

Writing a foreword for such a stimulating series of chapters, which represent the state of animal behavior studies at this time, is a considerable responsibility. Perhaps I can do best by looking not forward, as might seem appropriate, but backward, and thus attempt to provide a context for the chapters that follow. Of course it cannot be a fully objective backward view, because I am looking from where I am now, and what I see is biased by my own experience. It is bound also to involve simplification. But I hope that it will provide a useful perspective.

In the early decades of the twentieth century, most studies of animal behavior fell into two groups. In one were the naturalists, mostly amateurs, without scientific pretensions but with a long tradition stretching back beyond the nineteenth century. In the other were the psychologists, producing an increasing body of data and theory mostly concerned with learning processes. Of course this dichotomy is already unjust and simplistic. Darwin himself could be called a naturalist; and an originator of learning theory (J.B. Watson) started from naturalistic observation. However, the work of the learning theorists, impressive in its own right, was not to have much impact on the traditions that led to the chapters in this book until much later.

Those traditions can be said to stem from the emergence of ethology in the 1930s. This was due to Lorenz, an Austrian MD with a PhD in comparative anatomy, and Tinbergen, a Dutch zoologist who moved to England a few years after the end of World War 2. Both men had a passionate interest in animals, but this was expressed in very different ways. Lorenz kept a menagerie of diverse animals in his home, though also studying the local jackdaws and the semi-tame geese that he reared. Tinbergen, by contrast, was a dedicated field naturalist. Although he later worked with captive animals, it was always with problems that he had brought in from the field, and he liked best to be in the field himself. Tinbergen's first pupil, Baerends, suggested that the contrast lay in their attitudes to their subjects: Tinbergen saw himself as a nonparticipant hidden observer of animals, Lorenz as an adopted alien member and protector. Lorenz was a thinker who tried to relate or contrast his observations with current biological

and philosophical views, while Tinbergen was much more empirical, an experimenter as well as an observer.

But both rejected the vitalist view that the phenomena of "instinct" were unanalysable and the misuse of the Gestalt concept to imply that analysis is unnecessary because the whole is always more than the sum of its parts. They also rejected the focus of most learning theorists on the input/output relations of the whole organism, with neglect of the "physiological machinery," and the sterility of the artificial environments used to study animals in many psychological laboratories.

The term "ethology" has been applied primarily to the work of students who, though differing widely in the problems they tackled, the methods they used, the level of analysis at which they worked, and the theoretical interpretations (if any) that they adopted, shared certain orienting attitudes. They insisted that the proper description of behavior is a necessary preliminary to its analysis; and that the behavior of an animal must be studied in relation to the environment to which it has become adapted in evolution. In addition they held that full understanding of behavior required knowledge not only of its development and causation but also of its biological function and its evolution. The result was a vast amount of data on the behavior of animals and a certain amount of model-building to elucidate the mechanisms underlying behavior. In 1973 Lorenz and Tinbergen (together with von Frisch) were awarded the Nobel Prize in Physiology and Medicine.

Although ethology was primarily a European phenomenon in the early postwar years, two research workers in the USA were to have a considerable influence on its development, though in very different ways. Beach, a behavioral endocrinologist interested primarily in the hormonal control of sexual behavior, met Tinbergen in the USA and became a powerful supporter of ethology. Schneirla, a comparative psychologist working at the American Museum of Natural History, was intensely critical. One of his students, Lehrman, published a hard-hitting critique of ethology in 1953. There were three main issues. Lehrman and Schneirla took exception to Lorenz's distinction between "innate" and "acquired" behavior as neither empirically valid nor heuristically valuable. They objected to the energy model of motivation that Lorenz used, though this also came in for criticism from within ethology. And both were unhappy about the ethologists' tendency to apply concepts across a wide range of species differing in their levels of cognitive capacity. On their side, the ethologists felt that the adjective in "comparative psychology" was a sham, for contrasting distantly related species did not constitute comparison in a biological sense. They were also unhappy about the manner in which many comparative psychologists (though not so much those influenced by Schneirla) generalized on the basis of studies of a few mammalian species, predominantly the laboratory rat. For a while the differences between the two groups seemed irreconcilable. However, soon after his critique was published, Lehrman came to Europe and met a number of European ethologists. Tinbergen, Lorenz, and Lehrman were all bird watchers, with a passionate enthusiasm for natural history. Lehrman had an infectious geniality, and friendships were soon made. This brought about a rapprochement between ethology

and many of the members of Schneirla's group, a rapprochement that came not so much from academic discussion, but from the compatibility of personalities. On the issue of ontogeny, both sides changed their emphasis, the comparative psychologists withdrawing from their extreme emphasis on experience, and the differences in approach to the "comparative" issue were recognized.

It seems to happen not infrequently in the history of science that those regarded as originating a branch of science are subsequently seen to have been wrong in many of their generalizations. For instance, Freud (psychoanalysis) used a misleading model of motivation, Piaget (developmental psychology) based generalizations on a tiny sample of subjects, and Jeffreys (geophysics) refused to accept the evidence for continental drift. This was also the case with ethology. Many of the concepts that had been invaluable tools in the early days of ethology—the "innate releasing mechanism" and "fixed action pattern" for instance—were subsequently seen to involve oversimplification, and now seldom figure in the literature. But not surprisingly the change in outlook was not adopted simultaneously by all ethologists, and this led to some divisions within ethology. Lorenz, whose influence was particularly strong in Germany and the USA (through two research workers who had worked with him, Hess and Barlow), was slower to relinquish the innate/acquired dichotomy and energy model of motivation than Tinbergen and workers in the Netherlands and the UK.

An issue important for the nature/nurture debate became prominent in the 1960s. Both Tinbergen and Lorenz had long argued on the basis of empirical evidence that species were specially equipped for particular learning tasks that were biologically important for them. Thorpe's book on birdsong, published in 1961, showed that the chaffinch was predisposed to learn the species-characteristic song pattern. A few years later, Rozin, Garcia, and others demonstrated a predisposition to avoid toxins in mammals. Such findings were directly contrary to the orientation of the learning theorists, who were searching for laws of learning valid for all species and all situations. It thus became apparent that, in many cases, what was "innate" was a predisposition to learn some things in particular contexts. This was to be of special importance for the study of human behavior.

Lorenz, originally a comparative anatomist, had used species differences and similarities as a taxonomic tool, and Tinbergen had always had an interest in the function of behavior. But, of the four problems of causation, development, function, and evolution, the main (though by no means the only) emphasis in ethology had been on the first two. In the 1970s this changed with the publication of Wilson's *Sociobiology*. The orienting attitudes of ethology continued but the motivational models disappeared and many of the old concepts fell into disuse. Behavioral ecology came to the fore, and new theoretical approaches made possible the study of function in a quantitative fashion. Data on foraging behavior were compared with the behavior to be expected (on certain assumptions that were not always made fully explicit) from an organism foraging with maximal efficiency. Later, attention turned to such issues as sperm competition and the role of fluctuating asymmetry. Hamilton's work on kin selection, first published

in 1964 but neglected for much of the next decade, made possible a new approach to social behavior. Game theory was recruited, and mathematical modeling came to be a much used tool in studies of behavior.

At the same time, the influence of ethology started to penetrate into a number of other disciplines. Lehrman and Rosenblatt, as well as Beach and his many students, adopted the orienting attitudes of ethology in their work on behavioral endocrinology. Von Holst had already studied the elicitation of fixed action patterns by brain stimulation through implanted electrodes, and the importance of using unconfined animals where possible was recognized by neurophysiologists. Bowlby, a psychoanalyst concerned with the effects of maternal deprivation in children, realized that what had been called the "irrational fears of childhood" (fear of falling, being alone, etc.) would have been highly adaptive in the environments in which early hominids lived, and an ethological element was incorporated in the "attachment theory" which he elaborated, an approach that was to become central in studies of child development. The study of human nonverbal communication profited from the input of ethologists, such as Eibl Eibesfeldt. The techniques of the behavioral ecologists were applied in studies of preindustrial human groups. An ethological influence is to be seen in studies of human personal relationships, and even in studies of religion and morality. Thus, while ethology as a set of concepts or as a theory of animal behavior has been largely superseded, the influence of its orienting attitudes has increased and is potent in other disciplines.

While behavioral ecology took center stage in the study of animal behavior, many felt it to be impoverished by the neglect of problems of development and causation. This book will go a long way toward setting the balance straight. Each of the four problems is covered, and the chapters introduce the growing points in the study of animal behavior at the start of the twenty-first century.

Preface

The idea for this book arose out of a need that we (and many of our colleagues) felt for a comprehensive textbook on animal behavior. There is no shortage of animal behavior textbooks, so why did we want to produce a new one? First, animal behavior is a dynamic field of research, and we believe that a modern textbook should incorporate all the contemporary subdisciplines of behavioral biology, such as animal welfare, evolutionary psychology, animal cognition, and behavioral neuroscience. In some ways, the science of animal behavior has become a victim of its own success, as it covers a much wider field than it did initially. Gone are the days when one author could write a textbook both comprehensive and authoritative: Robert Hinde's classic *Animal Behaviour: A Synthesis of Ethology and Comparative Psychology* (1970) is an outstanding example of such a book, and it continues to inspire many of us. Given the breadth of contemporary animal behavior research, we felt that it was important to invite experts in the respective subdisciplines to write a chapter about their specialist topic.

Second, a large proportion of extant textbooks are single-author volumes that approach animal behavior from a particular perspective, for example from an evolutionary point of view or with the emphasis on mechanisms. We believe that a modern science of animal behavior should encompass both functional and causal approaches. For such a comprehensive approach, we found the classic formulation of the aims and methods of ethology (the study of animal behavior) by Niko Tinbergen, one of its founding fathers, most useful. Tinbergen suggested that there are four basic questions in animal behavior, namely about causation, development, survival value (function), and evolution. We agree with Tinbergen that all these four questions are equally important. Hence all of them are represented in this book. Like Tinbergen, we also find it important to distinguish among the four questions. In particular, it is important to realize which of the four questions is addressed, and to use a research approach appropriate for that question. Most chapters in the book focus on one of the four questions, with cause and development being the main subjects of the first ten chapters, and survival value (function) and evolution being the main subjects of the last seven chapters.

But most chapters are also concerned with more than one question, noted separately of course, supporting Tinbergen's claim that all questions should be answered.

We are very pleased with the enthusiastic response we received from the authors invited to contribute to this book. They are all leaders in their respective fields, and we feel privileged that they participated in this project. Robert Hinde has passed away since his foreword was written, but his words are just as relevant to the second edition of this book as they were to the first. His influence remains.

1 the study of animal behavior

Johan J. Bolhuis, Luc-Alain Giraldeau, and Jerry A. Hogan

Introduction

The scientific study of animal behavior is often 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." The word "ethics" is also derived from the same Greek word, which makes sense, because ethics is basically about how humans ought to behave. Unfortunately, the word "ethology" is also 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 the 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," many authors now 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) have 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

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systematically, however, mainly by German and British zoologists around the turn of the nineteenth century. The great British naturalist Charles Darwin (1809–1882), in his classic book on the theory of evolution by natural selection (1859), devoted a whole chapter to what he called "instinct." As early as 1873, a British amateur investigator, Douglas Spalding, recorded some very interesting observations on the instinctive behavior of young domestic chicks, including a phenomenon that was later called "imprinting" (Chapter 7). 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; Chapter 8).

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 (1903–1989) and the Dutchman Niko Tinbergen (1907–1988). It can be said that Lorenz was the more philosophical and theoretical of the two. He 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. 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. 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 (Chapter 14).

Ethology and 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' theory of instinctive behavior." In this paper he argued against Lorenz' theory in which behavior can be dissected into "innate" and "acquired" (learned) components (see Chapter 7 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, and Thorndike studied learning processes that are now known as instrumental condition-

ing (Chapter 8). Another difference between the ethologists and experimental psychologists was that the former often observed animals of many different species in their natural environment, while 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. He proposed that we cannot make any scientific statements about what might be going on in our minds, and that introspection was unreliable. Rather, for behaviorists, psychology is the study of observable behavior and of the external physical factors that influence it. 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 (1904–1990), who applied behaviorist ideas to the study of learning. For Skinner (1938) 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 refers to changes in the frequency of responding due to its consequences. Most of their experiments involve operant conditioning (see Chapter 8), in which 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 in 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 (Chapter 9). For instance, Skinner (1957) maintained that language development in children was a learning process, in which responses (i.e., uttering certain sounds) were reinforced. The American linguist Noam Chomsky (1959) wrote a highly critical review of Skinner's book on language development, suggesting that language acquisition is not a case of instrumental conditioning, but a much more complex interaction between experience and internal cognitive mechanisms (Chapter 7). At birth the child is already endowed with essential knowledge of language, the theory of which is known as Universal Grammar. Clearly, learning is involved in the development of language, but it is not the only factor. Chomsky and colleagues have recently described the growth of language in the child as "the interplay of three factors: domain-specific principles of language (Universal Grammar), external experience, and properties of non-linguistic domains of cognition including general learning mechanisms and principles of efficient computation" (Yang et al. 2017). Another important publication that signaled the beginning of the cognitive revolution is a 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, 2017) 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 (Chapters 3 and 9).

Four Questions in the Study of Animal Behavior

Niko Tinbergen published a very important paper in 1963, in which he outlined four major questions in the study of animal behavior, namely **causation**, **development**, **survival value**, and **evolution**. As he readily admitted, Tinbergen wasn't original, because three of these questions (causation, survival value, and evolution) had already been put forward by the British biologist Julian Huxley (1887–1975) as the major questions in biology, but Tinbergen added a fourth question, development. Many authors, including ourselves, use the word **function** as a substitute word for survival value, but the term function is used in many different ways in biology (Wouters 2003), and care is necessary when using it. It should also be mentioned that the evolutionary biologist Ernst Mayr (1904–2005) in 1961 popularized a different categorization of problems in biology: proximate and ultimate causation. Proximate causation is similar to Tinbergen's causal question, but ultimate causation is a controversial term that deals with evolutionary issues somewhat differently from Tinbergen's questions of survival value and evolution. However, no matter how these questions are broken up, it is crucially important that students of animal behavior be quite clear about the type of question they are addressing when they study or speak of animal behavior.

We find Tinbergen's analysis so important that we would say you cannot really understand animal behavior if you do not also understand the meaning of his 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 these questions (e.g., Hogan 1994, 2017; Bolhuis & Macphail 2002). It is essential, therefore, that any productive discussion about animal behavior involves participants that are capable of clearly stating which of the four questions they are addressing. This view of animal behavior has also served as the framework for the organization of the present book, with the first half covering mostly causal and developmental topics while the second half deals with questions of survival value (or function) and evolution.

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, because answers can take any of four different forms. These different forms—you've guessed it—have to do with Tinbergen's four questions. The first question concerns causation: what causes the bird to sing? The answers 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 *causation* of behavior. Sometimes this is called motivation, a topic discussed at length in Chapter 3. Tinbergen's question of causation also concerns the mechanisms or structure of behavior. These mechanisms involve the "machinery" that operates within the animal and which are responsible for the production of behavioral output (Chapters 5 and 9).

The second question is about development: How did the singing behavior of the bird come about in the lifetime of an animal? A male song sparrow does not sing immediately after it has hatched from the egg, and it takes quite some time before it has developed a song, a process that involves learning. Such questions that concern *development* of behavior, sometimes also called **ontogeny**, will be discussed explicitly in Chapter 7. The third question has to do with the consequences of singing for the singer's **fitness**: What is the function of the bird singing; what is it singing for? Does singing help the bird keep intruding males away from his nest? Or does it serve to attract females? Or does it do both? The topic of function (survival value), its methods of enquiry, and main findings will be discussed explicitly in Chapter 11. The fourth question concerns evolution: how did this behavior come about in the course of evolution? Behavior does not leave 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, will be discussed in detail in Chapter 15.

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" he/she is asking, and it could lead to futile arguments concerning 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, so it is very important to make clear which question

is being 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 are addressed at what time. A famous example of this is an experimental paper by Tinbergen and his associates (Tinbergen et al. 1962) on the behavior of blackheaded gulls (*Larus ridibundus*). After the chicks have hatched, the adult birds remove the empty eggshells from the nest. Tinbergen and his students investigated both the causation and the function (survival value) of this behavior using elegantly designed simple field experiments. They discovered the stimulus characteristics of items removed from the nest and, in the same paper, also reported results relevant to nest predation.

There is also considerable overlap among the four questions. For instance, the development of behavior is essentially a causal problem but may also involve functional aspects (Chapter 7). 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 operate in the evolution of extravagant traits (Chapters 12 and 14). 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 birds' ability to memorize spatial locations. In fact, a large number of studies are concerned with investigating the spatial memory of food caching versus nonfood-caching birds (Chapter 8).

Trends in the Study of Animal Behavior

Behavioral ecology: from mechanism to function

Much of the 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 at the same time the ecological 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-seventies for such an event. In 1975 the Harvard entomologist Edward O. Wilson published *Sociobiology, The New Synthesis* (1975). Wilson's book was firmly grounded in population genetics and evolutionary biology. Its clear presentation of William D. Hamilton's concepts

of inclusive fitness, kin selection, the evolution of 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 at Oxford University and Nicholas B. Davies at Cambridge co-edited a book they called *Behavioural Ecology: An Evolutionary Approach*, which applies a similar evolutionary approach but this time to all, not just social, behavior. The publication of that book marks the official birth of behavioral ecology, which now includes sociobiology (see Chapter 17).

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 trade-offs between their evolutionary benefits and costs (Chapter 11). 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 (Chapter 11). When applied to communication it raised an important number of questions concerning the design of signals and their functions (Chapter 14). While 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 (Chapter 12) as well as conflicts of interests between mates (Chapter 14) have become exciting and rapidly developing areas of the discipline. Darwin himself pictured behavior as a character that was modified over generations by selection. Behavior, hence, has a history that can be and is studied with contemporary organisms (Chapters 15 and 16).

Neuroethology and cognitive neuroscience

The mechanisms underlying behavior are also represented in the workings of the central nervous system. In fact, Tinbergen often used neural analogies and metaphors in his models of behavior. We shall see in Chapters 2 and 5 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 its neurons are connected, led to increased interface between brain and behavior a new subdiscipline arose that is called neuroethology (Ewert 1980; Chapter 2). 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 simple 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. 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 (Chapters 5 and 9).