Animal BEHAVIOR

Fifth Edition

Mechanisms · Ecology · Evolution

Lee C. Drickamer
Northern Arizona University

Stephen H. Vessey
Bowling Green State University

Elizabeth M. Jakob
University of Massachusetts

Boston Burr Ridge, IL Dubuque, IA Madison, WI New York San Francisco St. Louis
Bangkok Bogotá Caracas Kuala Lumpur Lisbon London Madrid Mexico City
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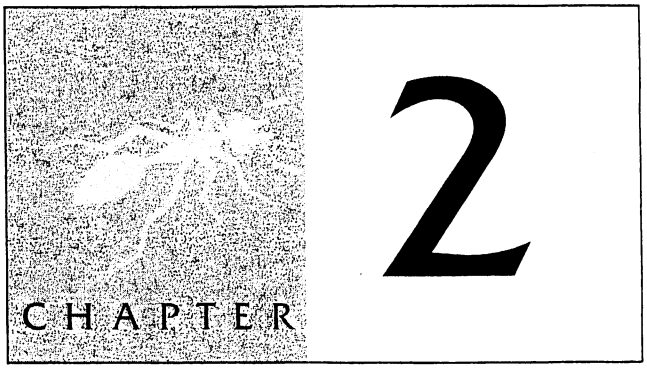

History of the Study of Animal Behavior

Humans and their prehuman ancestors have left evidence—both deduced by us from archaeological explorations and drawn, sculpted, and written by them—of their interest in the natural world. We know that some of this interest originated in need. Animals were a primary source of food, clothing, and materials for tools and shelter; thus, knowledge concerning their behavior was necessary for successful hunting. During the course of history, interest in animal behavior has also stemmed from human curiosity about the natural world. In this chapter, we examine how and why people have studied animal behavior—from the early days of human evolution, through the emergence of animal behavior as a scientific discipline in the nineteenth century, to the experimental and theoretical approaches of the present.

INTEREST IN ANIMAL BEHAVIOR

Early Humans

For many thousands of years, humans and their ancestors were hunters and meat-eaters. The early hominids and the first *Homo erectus* practiced a crude variety of hunting techniques. Peking man, a form of *Homo erectus* that lived approximately 400,000 years ago, was an accomplished hunter, used fire, and made tools from animal bones.

L. S. B. Leakey (1903–1972), an anthropologist known best for his discoveries of early hominid remains in Tanzania, proposed and tested a hunting strategy that was based on knowledge of animal behavior—a strategy that early hunters may have used to capture rabbits or other small prey. Leakey suggested that, upon sighting the prey at about fifteen meters distance, the hunter should sprint directly toward the animal (a small animal often initially freezes in such a situation).

Within two or three meters of the prey, the hunter should turn sharply either left or right, because the typical escape behavior of the prey is to make a sudden dash in one direction or the other. If both prey and hunter go to the left, the hunter is upon the animal and can grab it bare-handed (as Leakey demonstrated), or he might use a club or stone to strike it. If the hunter guesses incorrectly, he should stop, turn, and wait for the animal to stop. The process is then repeated and perhaps results in a successful capture.

Early *Homo sapiens* must have been keen observers of animal habits and characteristics. They needed to be familiar with the behavior of animals, not only to know where and how to hunt their prey, but also to protect themselves from potential predators. Hunters of the Upper Paleolithic (35,000 to 10,000 years ago) probably used fire to drive animals over cliffs or into cul-de-sacs or bogs where they could be slaughtered with rocks or clubs (figure 2.1). A ravine with at least 100 mammoth carcasses has been located in Czechoslovakia, and the remains of thousands of horses that were stampeded over a cliff have been discovered in France.

Prehistoric cave paintings in France and Spain reveal other aspects of humankind's relationship to animals. These paintings realistically depict many types of game animals in ways that suggest close observation of the animals at various times in their life cycles. In addition, some of the drawings are symbolic representations of actual hunting scenes. However, while early people were aware of the animals in their environment, their knowledge of animal behavior was probably limited to mostly practical concerns.

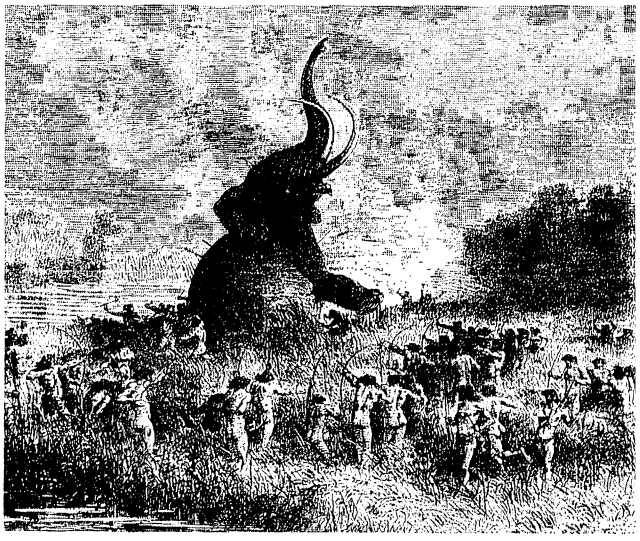

FIGURE 2.1 Early Hunters.
Early humans practiced various hunting techniques that were based, in part, on their knowledge of the behavior of the prey animals. In some instances, they successfully drove individuals or groups of animals, such as the wooly mammoths shown here, into swamps or bogs, where the animals became trapped and could be killed.

Classical World

Interest in animal behavior in the classical world stemmed from curiosity about natural phenomena and a desire to record and categorize observations. For example, Aristotle (384–322 B.C.) wrote ten volumes on the natural history of animals, in which we note the first extensive use of the observational method. The following brief excerpts, translated from the original Greek, give us a flavor of what Aristotle's observations were like (the first two passages are true, the last is false) (Ley 1968, 36–37):

> They say that the cuckoos in Hellice, when they are going to lay eggs, do not make a nest, but lay them in the nests of doves or pigeons, and do not sit, nor hatch, nor bring up their young; but when the young bird is born and has grown big, it casts out of the nest those with whom it has so far lived.
>
> In Egypt they say there are some sandpipers that fly into the mouths of crocodiles and peck their teeth, picking out the small pieces of flesh that adhere to their teeth; the crocodiles like this and do them no harm.
>
> The goats in Cephallaria apparently do not drink like other quadrupeds; but every other day turn their faces to the sea, open their mouths and inhale the air.

The Roman naturalist Pliny (A.D. 23–79) made extensive observations of the natural world. A quote from his *Natural History* provides some insight into the anthropomorphism (ascribing human characteristics or attributes to nonhumans) that characterized Roman perceptions of animal behavior (Nordenskiöld 1928, 55):

> Amongst land animals, the elephant is the largest and the one whose intelligence comes nearest that of man, for he understands the language of his country, obeys commands, has a memory for training, takes delight in love and honour, and also possesses a rare thing even amongst men—honesty, self-control and a sense of justice; he also worships stars and venerates the sun and the moon.

We can see from these brief passages that early scholars were attempting to record what they observed in the world around them. Their perceptions of behavior were often colored by the lack of full knowledge about what was taking place, or by biases based on religion or philosophy. However, for many centuries these early observations served as the basis for human understanding of the natural world.

FOUNDATIONS OF ANIMAL BEHAVIOR

The rigorous scientific study of animal behavior did not begin until the latter part of the nineteenth century. We turn now to three major developments that contributed significantly to the study of behavior as it developed prior to 1900: (1) publication of the theory of evolution by natural selection, (2) development of a systematic comparative method, and (3) studies in genetics and inheritance.

Theory of Evolution by Natural Selection

For several centuries, European ships made voyages of exploration and discovery to all parts of the globe. Often scientists were officially attached to the voyages, as Charles Darwin (1809–1882) himself was. These scientists and other crew members made observations of exotic fauna and flora and brought live and preserved specimens to zoos and laboratories in Europe, where scholars could observe, record, and speculate about the anatomy, behavior, and interrelationships of these newly discovered species. The following passage from Darwin's account (figure 2.2) of the marine iguana of the Galápagos Islands illustrates the kind of observations he made on animals in their natural setting (Darwin 1845, 336):

> They inhabit burrows, which they sometimes make between fragments of lava, but more generally on level patches of the soft sandstone-like tuff. The holes do not appear to be very deep, and they enter the ground at a small angle; so that when walking over these lizard warrens, the soil is constantly giving way, much to the annoyance of the tired walker. This animal, when making its burrows, works alternatively the opposite sides of its body. One front leg for a short time scratches up the soil, and throws it towards the hind foot, which is well placed so as to heave it beyond the mouth of the hole. That side of the body being tired, the other side takes up the task, and so on alternatively.

Like all major scientific paradigms, the theory of evolution drew upon contributions by and suggestions from the work of other scientists. In 1798, Thomas Malthus (1766–1834), in his *Essay on the Principle of Population,* hypothesized that humans have the reproductive potential to rapidly overpopulate the world and outstrip the available food supply. The inevitable result is disease, famine, and war. Malthus's theory was an important influence on Darwin's thinking about the competition for survival among members of a species. A contemporary and friend of Darwin's, geologist Sir Charles Lyell (1797–1875) was among those who made observations of rock strata and successions of fossils that gave evidence of a process of continuous change in living material through time, an idea that was at odds with the biblical suggestion of the simultaneous creation of all living things. This evidence of geological change led others to the idea that species themselves were not fixed entities. The artificial selective breeding of domesticated stocks by English farmers provided additional support for the thinking of both Darwin and A. R. Wallace (1823–1913).

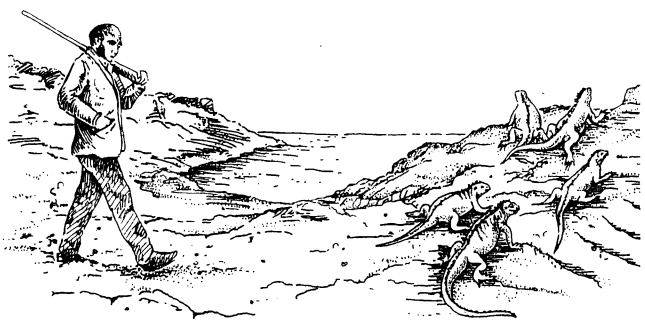

FIGURE 2.2 Charles Darwin investigating the unique marine iguanas of the Galápagos Islands.

Wallace's voyage to the Malay archipelago, Darwin's travels on the *Beagle* to South America and the South Pacific, and their other studies and the intellectual influences of the time, led each man independently to formulate the theory of evolution by natural selection. The original theory states that although each animal species has a high capacity for reproduction, the population size remains relatively constant over time. Thus, not all animals produce the maximum number of offspring. Heritable variation in traits exists within animals of one species. Because some traits are more advantageous than others, not all organisms produce an equal number of surviving offspring, and the operational process of natural selection occurs. Only those members of the species that are able to survive to produce more offspring contribute their characteristics to subsequent generations through their young.

Behavior, morphology, and physiology were all thought to be subject to the effects of natural selection. The following passage from *The Origin of Species* illustrates that Darwin clearly recognized the central role of animal behavior in determining the outcome of competition between animals (Darwin 1859, 94):

> Amongst birds, the contest is often of a more peaceful character. All those who have attended to the subject, believe that there is the severest rivalry between the males of many species to attract, by singing, the females. The rock-thrush of Guiana, Birds of Paradise, and some others, congregate; and successive males display with the most elaborate care, and show off in the best manner, their gorgeous plumage [figure 2.3]; they likewise perform strange antics before the females, which, standing as spectators at last choose the most attractive partner.

FIGURE 2.3 Male bower bird in display.
As in the passage quoted from Darwin, male birds of a variety of species display to attract females. The male bower bird builds a bower and adorns it with brightly colored objects.

Darwin concluded that species were not fixed entities. The theory of evolution by natural selection accounted for changes within a species through time and also for the gradual appearance of new species. Recent developments in other biological fields—genetics in particular—have modified the theory of evolution by natural selection proposed by Darwin and Wallace. Today, some evolutionary biologists believe that evidence from the fossil record and genetic mechanisms support the claim that rates of evolution vary through time (Stanley 1981). Change through evolution, in particular the appearance of new species, may occur more rapidly during some time periods than at other times. We will explore the theory of evolution and its consequences for animal behavior in chapters 4 and 5.

Comparative Method

George John Romanes (1848–1894) is generally credited with formalizing the use of the **comparative method** in studying animal behavior. For Romanes, the comparative method involved studying animals to gain insights into the behavior of humans. Romanes sought to support Darwin's theory with his proposal that mental processes evolve from lower to higher forms and that there is a continuity of mental processes from one species to another. He argued that although people could really know only their own thoughts, they could infer the mental processes of animals, including other humans, from knowledge of their own. For Romanes, the similarities between the behavior of humans and that of other animals implied similar mental states and reasoning processes in humans and in nonhuman species. He suggested that a sequence could be constructed for the evolution of various emotional states in animals. Worms, which exhibit only surprise and fear, were placed lowest on this scale; insects were said to be capable of various social feelings and curiosity; fish showed play, jealousy, and anger; reptiles displayed affection; birds exhibited pride and terror; and finally, various mammals were credited with hate, cruelty, and shame.

Romanes's theory relied largely on inferences rather than on recorded facts or direct observations of behavior; he made substantial use of anecdotes. A movement led by another Englishman, C. Lloyd Morgan (1852–1936), sought to counteract these faults by using the **observational method.** Morgan's basic tenet was that only data gathered by direct experiment and observation could be used to make generalizations and develop theories. Morgan is probably best known for his "law of parsimony," which is now axiomatic in animal behavior studies. "In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale" (Morgan 1896, 53). This statement has been interpreted to mean that in the analysis of behavior, we must seek out the simplest explanations for observed facts. Where possible, we should reduce complex hypotheses to their simplest terms to facilitate the clearest understanding of the mechanisms that control behavior.

Theories of Genetics and Inheritance

The third development that greatly influenced research in animal behavior was the birth of the science of genetics and the development of modern theories of inheritance. In the 1860s, Gregor Mendel (1822–1884) reported his findings from breeding experiments using garden peas. These studies established key principles of the laws of inheritance of biological characteristics. Present-day behavioral biology is based on the combination of evolutionary theory, which explains how traits can change through time, and genetics, which explains how traits are passed from one generation to another.

We now know that, like morphological and physiological traits, an animal's behavior has a genetic component. Thus, behavior may change as a species evolves. This means that, as scientists, we can explore the genetic variation underlying various behavior patterns, just as others have investigated the effect of genetic inheritance on morphology and physiology. Behavior-genetic analysis had its beginnings in these early studies of inheritance and was then greatly expanded in the 1930s by the work of R. A. Fisher (1890–1962) and others. Behavior-genetic analysis (e.g., Boake, 1994) is a powerful tool used by many animal behaviorists; we will learn more about this in chapter 5.

EXPERIMENTAL APPROACHES

The ideas, methods, and theories established during the latter half of the nineteenth century form the foundation of today's experimental approaches to the study of animal behavior. (1) Comparative psychologists and physiologists have sought to determine the underlying causes of behavior—the control mechanisms. (2) Classical ethologists have been concerned primarily with the functional significance and evolution of behavior patterns but have also developed explanations for behavior mechanisms, including drives, innate releasing mechanisms, and similar concepts. (3) Behavioral ecologists and sociobiologists have explored the ways in which animals interact with their living and nonliving environments and have applied the principles of evolutionary biology to the study of social behavior and organization in animals. We should now briefly examine the historical development of each approach. From these varied approaches to the study of behavior has come the modern synthetic view of animals living and behaving in their natural environment. Though we examine these approaches here as separate entities, bear in mind that they did not develop entirely independently of one another, and that in recent decades, they have become melded into a single discipline. The modern approach to the study of animal behavior contains elements of all three approaches. As we can see by looking at the animal behavior courses offered at various colleges and universities and the titles of the textbooks used to teach such courses, those who work and teach in this area may call themselves ethologists, animal behaviorists, or comparative psychologists. However, they are all really pursuing similar goals

using common theoretical frameworks, and practicing their craft using similar experimental techniques and methods.

Studies of Mechanisms

Comparative psychology is the study of different animals' behavior patterns in order to determine the general principles that explain their actions. Comparative psychology can best be understood by looking at the variety of approaches to behavior studies taken over the past century, which eventually led to comparative psychology's development. In today's world, comparative psychology has melded into the larger discipline that we call animal behavior or ethology.

Perceptual Psychology

Several distinct approaches to discovering the mechanisms underlying behavior emerged during the mid-nineteenth century. Researchers who were concerned with the mind/body dichotomy studied the relationships between physical and mental processes. Investigators were interested in separating the processes of sensation (body) and perception (mind). This usually involved the objective measurement of sensation (the reception of stimuli through the senses, such as sight and hearing) and the comparison of this direct measurement to objective interpretation (perception) of the sensations. Today's subdiscipline of psychophysics is an outgrowth of these early studies. These types of studies still impact our understanding of animal behavior in terms of what an animal makes of its world, both with regard to sensory systems and with respect to the animal's interpretations of its sensations.

Physiological Psychology

Modern physiological psychology developed from early attempts to relate behavior with the internal physiological properties and events of the organism. For example, Marie-Jean-Pierre Flourens (1794–1867) surgically removed portions of the brains of pigeons and recorded the resulting changes in the birds' behavior. Hermann von Helmholtz (1821–1894) studied the conduction speed of nerve impulses, and later, the physiology of vision. He ingeniously measured the speed of nerve conduction by experimenting on the frog motor neuron that triggers muscle contractions. First he stimulated the nerve at one point near the muscle, and then at a second point farther away from the muscle. The difference in amount of time elapsed between stimulus and muscular contraction in the two measurements is the conduction time for the distance between the two stimulus points. From this information, he calculated the speed of conduction.

Physiological psychology remains an important subdiscipline today, and work in this realm and in animal behavior are interconnected. Another classic study is Sperry et al. (1956), in which he surgically manipulated the position of the eyes in newts (*Notophtalmus viridescens*). Sperry removed the eyes and then replaced them so that they were upside down! Newts treated in this way behaved as if they saw the world upside down; they moved their eyes upward in response to the movement of an object downward in their visual field. This effect persisted even after several years. We learn from Sperry's work that in the visual system of the newt, the neurons in the optic nerve traveling from the retina to the brain are labeled for spatial orientation. Thus, even though the eye has been rotated, the message sent to the brain along the nerve remains the same as if the eye were in the correct, normal orientation. For his work on the nervous system, Sperry shared the Nobel Prize in 1981.

Functionalism

By the late 1800s and early 1900s, Europe was no longer the exclusive center of behavioral studies, and individuals were conducting research investigations in comparative psychology at a number of laboratories in the United States. Two major new theoretical and experimental points of view arose during this period: functionalism and behaviorism. The **functionalists,** among them, John Dewey (1859–1952), studied the functions of the mind and how the mind operates, in contrast to studying how the mind is structured. Functionalists attempted to answer three major questions: (1) How does mental activity occur? (2) What does mental activity accomplish? and (3) Why does mental activity take place? Functionalism employed objective observation rather than introspection as its primary method.

The functionalist approach was the introduction into psychology of **adaptive behavior,** a notion prevalent in biology that behavior functions in the animal's survival in its natural habitat. To these early psychologists, the concept of adaptive behavior implied that the response to a stimulus changes the sensory situation in such a way that the original conditions that produced the response are altered. For example, pain disappears when a sharp splinter is removed from the hand, and the original condition—the existence of a splinter—is also altered.

Behaviorism

John B. Watson (1878–1958) was the principal founder of a new approach to the study of behavior, **behaviorism.** The basic tenet of behaviorists is that animal behavior consists of an animal's responses, reactions, or adjustments to stimuli or complexes of stimuli. Thus, most activities of an organism are products of its past experiences. Behavior, rather than the mind, became the primary focus for study. To what degree can we predict and control behavior based on a knowledge of an animal's previous experiences? The methods utilized by Watson and his followers, for example, B. F. Skinner (1904–1990), were strictly objective. Reports of subjective feelings or emotions were, by definition, not acceptable as scientific data. This restriction forced the behaviorists to study human behavior in much the same way they studied the behavior of any other animal, without benefiting from their subjects' verbal judgments or reports of feelings and perceptions. (It is noteworthy that Skinner's *earliest* papers dealt with innate aspects of behavior; studying the history of our discipline provides many insights and surprises!)

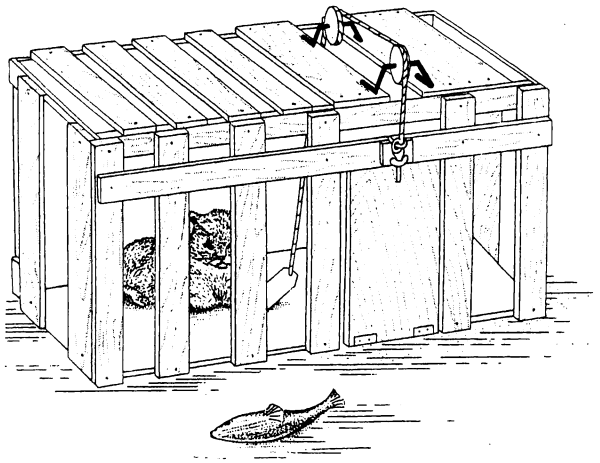

FIGURE 2.4 Thorndike puzzle box.
A cat inside the cage can clearly see the reward, in this case a fish, placed outside. In order to obtain the reward, the cat must learn to manipulate a shuttle-lever system that raises the door of the cage.

Animal Psychology

Concurrent with the development of these viewpoints was the emphasis by Edward L. Thorndike (1874–1949) on the need for systematic, replicable experiments in comparative animal psychology. Thorndike used the puzzle box (figure 2.4) to perform a series of task-learning experiments, using cats as test subjects. A cat was placed in the box, which was fastened shut; by manipulating a shuttle-lever, the cat could open the door and obtain a reward placed outside the box. From these experiments, Thorndike concluded that much of animal learning takes place by trial and error and that rewards are a critical component of learning processes.

In 1950, Frank Beach stressed that the discipline of comparative psychology was devoting too much attention to the white rat as a test subject, while ignoring many other types of available vertebrate organisms. Others, notably Lockard (1971) and Hodos and Campbell (1969), called our attention to the lack of an evolutionary perspective in comparative psychology and to the incorrect use of the rat as a model for other organisms, especially humans. These critiques stimulated more truly comparative investigations, for example, the work of Dewsbury (1972, 1975) on reproductive behavior in rodents. More attention has also been given to the natural context and actual field investigation of animals (Lockard 1971; Barash 1973a,b, 1974a,b).

Animal psychology today is a diverse mixture of subdisciplines, both new and old. The study of comparative learning and learning theory is still quite important, as the works of Bitterman (1975), Seligman (1970), and Roitblat and Meyer (1995) exemplify. Ecological aspects of learning in a variety of animal species have been examined by investigators like Kamil and Sargent (1981), Davey (1989), Balda et al. (1998) and Dukas (1999). The development of behavior is also a subject of continued investigation by researchers like Oppenheim and colleagues (Oppenheim 1982; Oppenheim et al. 1992; Caldero et al. 1998), who examines aspects of neural development; by Burghardt and colleagues, who are studying the development of feeding behavior in reptiles such as garter snakes (*Thamnophis sirtalis*) (Burghardt and Krause 1999); and by groups like the one developed at the Wisconsin Regional Primate Laboratory by Harlow and colleagues (Suomi and Harlow 1977) that explored primate behavior development. The study of the physiological processes underlying behavior has also diverged into several pathways: the relationship of hormones and behavior (Lehrman 1965; Crews 1980; Goy et al. 1988; Knapp et al. 1999; Strier et al. 1999); neural correlates of behavior (Hubel and Wiesel 1965; Brown et al. 1988; Glendinning et al. 1999) and brain chemistry; and psychopharmacology and behavior (Kelly et al. 1979; Ferris et al. 1999). The cross-fertilization between genetics and behavior also produced a new subdiscipline called behavior genetics, which is concerned with the hereditary bases of behavior and how the interactions of genetics and environment affect behavior (Hirsch 1967; Oliverio 1983; Miklosi et al. 1997; Kim and Ehrman 1998).

Studies of Function and Evolution

Ethology

The systematic study of the function and evolution of behavior, called **ethology,** is now a little over a century old. One of its most important principles is that behavioral traits, like anatomical and physiological traits, can be studied from the evolutionary viewpoint. For example, C. O. Whitman (1842–1910) made extensive observations of display patterns, which he termed instincts, in various species of pigeons. Whitman found that he could use displays (patterns of behavior exhibited by animals that function as communications signals) to classify animals according to similarities and differences in behavior. From its early beginnings, ethology developed into a separate science, with its own concepts and terminology, much as comparative psychology did. Today, as we noted previously, those working as ethologists are conducting the same sorts of studies as all others who study animal behavior.

The **ethogram,** an inventory of the behavior of a species, has been a starting point for many ethological studies. After making observations of an organism's behavior, ethologists then formulate specific questions about the adaptiveness and function of particular behavioral patterns. A student of Whitman's, Wallace Craig (1876–1954), defined two key categories of behavior patterns from his work with doves and pigeons. The first category includes the variable actions of an animal, such as its searching behavior to find food, a nest site, or a mate; these are called **appetitive behavior.** The second category includes stereotypical actions that are repeated without variation, such as the act of mating or the killing of prey; these are called **consummatory behavior.**

The ethological approach is used in another major area of inquiry: the determination of how key stimuli trigger specific behavior patterns. J. von Uexküll (1864–1944) demonstrated that animals perceive only limited portions of the

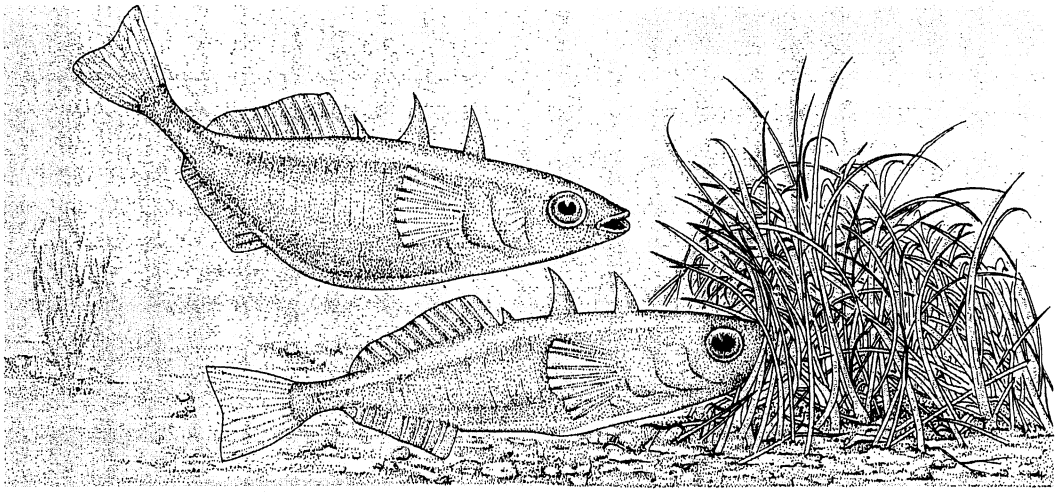

FIGURE 2.5 Courtship of male and female three-spined stickleback.
The enlarged belly of the female three-spined stickleback fish (top) is a sign stimulus for the male of the species (bottom) to court and to entice the female to enter the nest he has built.

total environment with their sense organs and central nervous systems. This sensory-perceptual world was termed the **Umwelt** by von Uexküll. Among the stimuli recorded by the sense organs, certain specific cues that ethologists call **sign stimuli** trigger particular stereotyped responses called **fixed action patterns (FAPs).** For example, the female three-spined stickleback fish's enlarged belly triggers courtship behavior in male sticklebacks (figure 2.5).

Credit for the synthesis of these early findings and for the further development of modern ethology belongs largely to two men, Konrad Lorenz (1903–1989) and Niko Tinbergen (1907–1988). Lorenz pioneered studies of genetically programmed behavior and investigated the importance of specific types of stimulation for young animals during critical periods of early development. Modern ethology's concern with four areas of inquiry—causation, development, evolution, and function of behavior—developed from a scheme proposed by Tinbergen (1963). (As psychologist Thomas McGill has noted, the first six letters of the alphabet can be used to remember these questions: Animal Behavior: Causation, Development, Evolution, Function.) Recognition for animal behavior as an independent discipline came in the fall of 1973, when the Nobel Prize for Physiology or Medicine was awarded to three ethologists: Konrad Lorenz, Niko Tinbergen, and Karl von Frisch (1886–1982). Von Frisch had conducted research on animal sensory processes and made important contributions to the study of bee behavior and communication.

Modern ethology is characterized by varied types of investigations ranging from more traditional observational studies in natural environments (Geist 1971; Joerman et al. 1988; Millesi et al. 1998) to experiments on the physiological bases of behavior (Bentley and Hoy 1974). The latter study is indistinguishable from those conducted by many physiological psychologists. Some ethologists work primarily with behavior genetics and the evolution of behavior (Manning 1971; Gerhardt 1979; Ukegbu and Huntingford 1988) or explore the relationships between hormones and behavior (Hinde 1965; Truman, Fallon, and Wyatt 1976) or the nervous system and behavior (Nottebohm 1981; Rose et al. 1988; Oliveira and Almada 1998). Others work on research problems in the field or in a laboratory setting that resembles the natural habitat. By employing experimental manipulation to test specific hypotheses, Kummer (1971) investigated the effects that transplantation of individuals from troop to troop had on the social behavior of baboons, Wickler (1972) studied the significance of color patterns in fish, Gowaty and Wagner (1988) tested the aggressive behavior of eastern bluebirds, and Panhuis and Wilkinson (1999) investigated the effect of male eye span on contest outcome in stalk-eyed flies.

Since the mid-1950s, the distinctions between ethology and comparative psychology have been slowly disappearing. Several events have opened communication between scientists of the two approaches. These events include the biennial meetings of the International Ethological Conference, many cross-visitations between researchers in Europe and America, and the publication of a number of international animal behavior journals. A common approach, which started with the notion of species-typical behavior, has emerged from this exchange of information. **Species-typical behavior** involves actions and displays that are broadly characteristic of a species and that are performed in a similar manner by all its members. The autobiographical sketches of many leaders in animal behavior (Dewsbury 1985) include a variety of perspectives, and provide excellent insight into the way the various approaches have developed independently, and how they have recently coalesced into a unified and integrated approach to the study of behavior.

At least one major long-standing controversy in animal behavior has been largely resolved during recent years. Early

ethologists believed that much of an animal's behavior was instinctive or preprogrammed and was not affected to any great extent by experience. Many psychologists claimed that learning and experience were the major determinants of behavior. Today, most animal behaviorists believe that neither of these viewpoints is entirely correct. Instead, as we shall see in chapter 10, the current focus is on the interaction of genotype, physiology, and experience as the determinants of behavior, and on how the relative contributions of genetic and environment effects differ among animal species.

Comparisons

Discerning whether a particular study has been conducted by an ethologist or a comparative psychologist may be difficult at first. If we understand the historical differences between these two approaches, we can better appreciate the synthetic approach that characterizes the behavior studies of the past several decades.

Ethology was developed, largely in Europe, by researchers trained in biology. Ethologists traditionally observed a wide variety of animals in nature and conducted experiments under conditions that mirrored the natural setting as closely as possible. They concentrated their efforts on exploring questions of ultimate causation—the "why" questions of the evolution and function of behavior.

Comparative psychology originated primarily in America. Until the past several decades, most psychologists generally worked under controlled laboratory conditions. Much of their research was carried out on small rodents, particularly the domesticated rat. Comparative psychologists placed primary emphasis on proximate issues—the "how" questions of the physiological and developmental mechanisms underlying observed behavior patterns. Dewsbury's history of comparative psychology (1984) provides many details regarding the development of concepts and theories in this field and many insights into the individuals responsible for the experimental and theoretical work. Dewsbury defines comparative psychology as the attempt to make comparisons across species in order to develop principles of generality regarding animal behavior. He examines the course of development that characterizes this field since 1900 and notes the many myths that have been associated with what scientists and nonscientists alike have come to believe a comparative psychologist is.

Animal behavior is now a unified discipline with a broad synthetic approach: much of the research conducted by animal or comparative psychologists today is indistinguishable from that of other animal behaviorists with different backgrounds. These research endeavors include explorations of the genetic aspects of food-searching behavior in blowflies (McGuire and Tully 1986), the effects of aversive conditioning on learning behavior of honeybees (Abramson 1986), the role of hormonal factors in infanticidal behavior in rats (R. E. Brown 1986), and the role of the brain in budgerigars' interpreting acoustic information from contact calls (S. D. Brown et al. 1988).

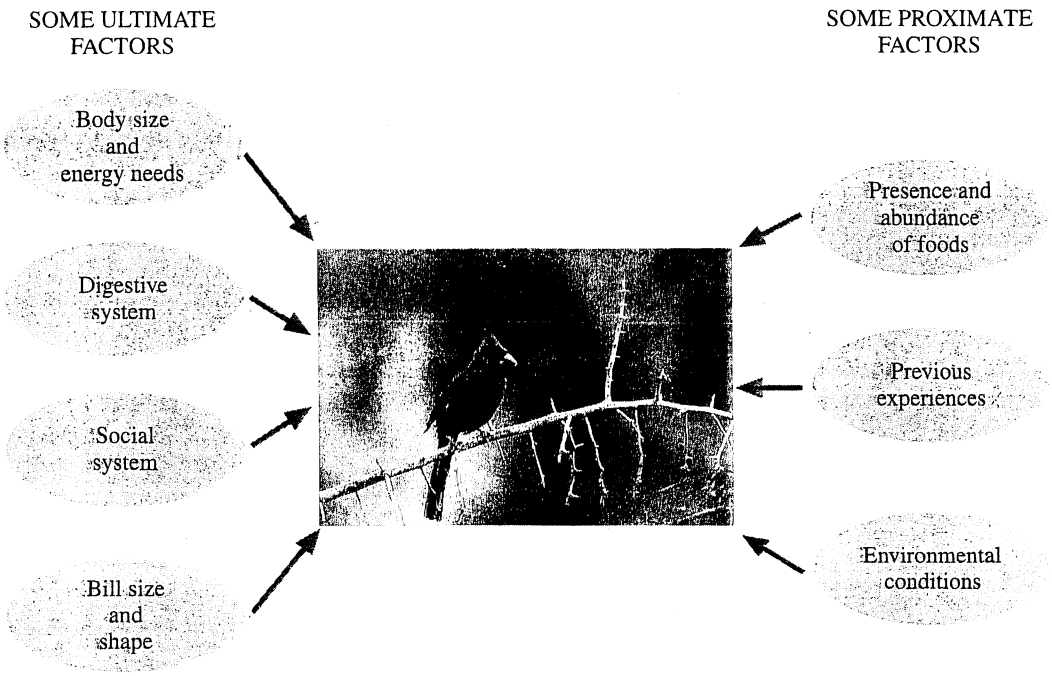

FIGURE 2.6 Factors affecting the feeding behavior of northern cardinals.
Constraints that have arisen through evolution establish the limits on the dietary habits for the cardinal. Past experience and current environmental conditions influence the immediate choices made by the animal as it forages.
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Behavioral Ecology and Sociobiology

In the past five decades, a third approach to the study of animal behavior has emerged. **Behavioral ecology** and **sociobiology,** with origins in zoology, examine the ways in which animals interact with their environments and the survival value of behavior (Morse 1980; Krebs and Davies 1993, 1997). "Environment" as used here includes animals of the same species (conspecifics), other animals within the same ecological community, plants, and inorganic physical features of the habitat.

Behavioral ecologists are concerned with both ultimate and proximate questions about behavior. Suppose we are interested in the feeding habits of the northern cardinal (*Cardinalis cardinalis*), living in a variety of places in the North American countryside (figure 2.6). Ultimate constraints affecting the cardinal would include its body size and related energy needs; the type of bill, which affects the foods it can consume; the digestive system, with regard to what foods the bird can process; and the social system of the species, which could influence the partitioning of available food resources. Proximate factors influencing feeding would include the presence and relative abundance of specific foods; past experiences of the bird in searching for and handling particular foods; and the season of the year, with particular regard to variations in energy needs due, for example, to reproduction or cold winter weather. Ultimate factors establish the limits, and proximate factors affect the behavior of an animal within those limits.

Behavioral ecologists, trained primarily in zoology, ecology, and related fields, are also greatly influenced by the methods of comparative animal psychology. Behavioral ecologists often begin a field investigation and define questions about, for example, population regulation or predator-prey relations. Does the predator maximize its energy intake by utilizing some form of optimal foraging strategy? Certain aspects of the overall investigation (what are the most important features of the prey for predator recognition and detection?) may require experiments more systematic than those that can be done in the field setting. Thus, as behavioral ecologists, we might bring specific, testable hypotheses into the laboratory or controlled outdoor setting where the experiments are conducted. Attempts can then be made to relate laboratory findings to what is known about the animal in its natural field setting.

For an example of an investigation using the behavioral ecology approach, consider the prey-catching behavior of the shore crab (*Carcinus maenas*). When these animals are given their choice of what sized mussel to consume (figure 2.7), they select the size that provides them with the highest rate of energy return (Elner and Hughes 1978). Notice that although the crabs do eat mussels in a variety of sizes, they may avoid the larger mussels because of the extra time and energy needed to crack open the shells. The wide size range that the crabs eat may represent a compromise: lots of time spent searching for just the right sized mussel would be inefficient. Thus, we see that both the time it takes to find food and the ability of the predator to handle the prey can influence prey selection. We will explore these and other aspects of feeding in chapter 15. We'll look at similar factors that influence choices and selection of the most efficient pattern for animal habitat selection in chapter 14.

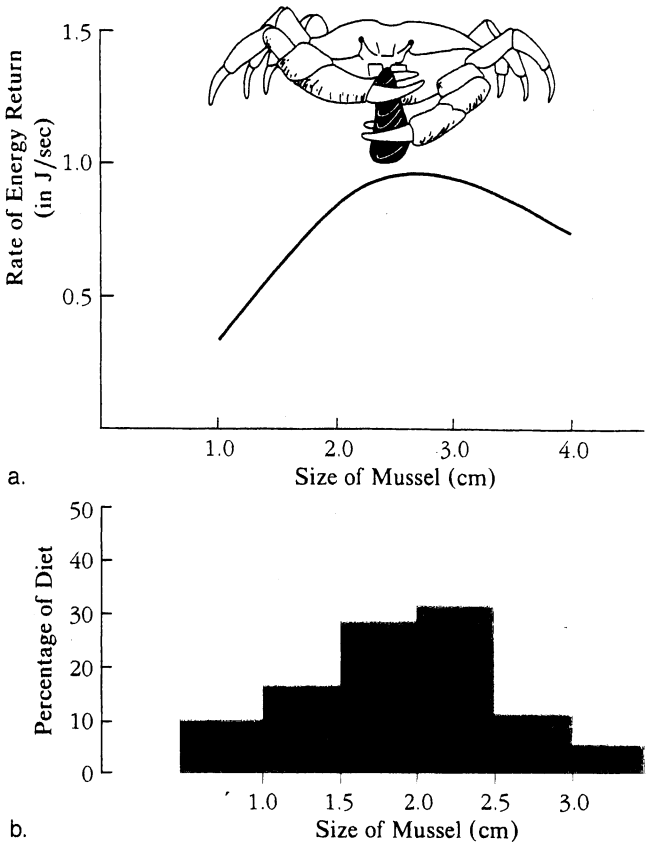

FIGURE 2.7 Shore crabs select mussels for food.
(a)Shore crabs select those sizes of mussels that provide the best rate of energy return more often than other sizes, though (b)they do eat mussels of a variety of sizes.

Source: Data from R.W. Elner and R.N. Hughes, "Energy Maximization in the Diet of the Shore Crab, *Carcinus maenas*," in *Journal of Animal Ecology*, 47:103–16, copyright 1978 by Blackwell Scientific Publications Ltd., Oxford.

Among the investigations in behavior ecology, those of Emlen (1952a,b) on bird behavior and energy budgets, Davis (1951) on population biology of rats, and King (1955) on the relationship of prairie dog social behavior to habitat, were notable for the way they established topical areas for research work within the developing discipline. In more recent years, topics that have received particular attention by investigators include foraging strategy (Stephens and Krebs 1986; Vander Wall 1990; Bell 1991; Ydenberg and Hurd 1998), proximate mechanisms in behavioral ecology (Real 1994; Braude et al. 1999), predator-prey systems and predation risk (Haskins et al. 1997; Randall and Matocq 1997), the ecology of sex and strategies of reproduction (Askenmo 1984; Clutton-Brock 1988), and social systems in relation to ecology (Thornhill and Alcock 1983; Christenson 1984; Hill 1998). The last two topics are indicative of the joint nature of the approach involving behavioral ecology and sociobiology.

Sociobiology came of age in 1975 with the publication of E. O. Wilson's *Sociobiology: The New Synthesis.* Sociobiology applies the principles of evolutionary biology to the study of social behavior in animals. Sociobiology is a hybrid of behavioral biology (from the ethological perspective, with an emphasis on ultimate questions) and the study of social organization (with an ecological perspective) (Wittenberger 1981; Trivers 1985). As we shall see later, sociobiology relies heavily on the comparative method. Diverse groups of animals, living in a wide variety of habitats, are examined to find similarities and differences in their social systems. These examinations reveal if any general patterns explain the social behavior of a species. Thus, for example, we note that in some species of birds, young born in one year may not breed the second year, but help their parents rear the second year's brood. In other instances, adult birds that have lost their mate (or their clutch) may help close relatives rear young. These social systems that involve helping at the nest occur, for example, in Florida scrub jays (Woolfenden 1975), African white-fronted bee-eaters (Emlen 1984), acorn woodpeckers in the western United States (Koenig et al. 1984), and Seychelles warblers (Komdeur 1992; Komdeur et al. 1995). Investigations of these and similar social systems in birds reveal that nests with helpers are more successful—the number of young fledged is higher. Helping behavior would appear to be using energy to assist in rearing of offspring that are not the helper's own progeny. How can such behavior evolve? Sociobiologists are interested in exactly that question and also what the advantages are for the individual bird if it helps versus the advantages if it does not help.

The various theories and concepts that constitute sociobiology have their roots in many earlier works. Among the most significant are the writings of Williams (1966) on natural selection and the concept of adaptation, Trivers (1971, 1972) on the evolutionary aspects of altruism and parental behavior, and Hamilton (1964, 1971) on the genetic theory underlying the evolution of social behavior. Studies conducted under the general heading of sociobiology include, for example, those on altruism in ground squirrels (Sherman 1977), on strategies for reproduction in damselflies and other insects (Waage 1979; 1997), on parental investment in water bugs (Smith 1997), and on mate choice in American kestrels (Duncan and Bird 1989). In recent years, a major topic for investigators using the sociobiological approach has involved sexual selection and various factors influencing mate choice (Andersson 1994; Gowaty 1995; Eberhard 1996).

Since the mid-1970s, sociobiology has had a significant influence on research in animal behavior. Faced with the challenge of devising new research questions and new methods to test aspects of sociobiological theory, investigators have reexamined older data in light of new predictions. One area of prediction and hypothesis—and the source of considerable controversy—is the application of sociobiology to *Homo sapiens.* Some sociobiologists argue that the principles used to investigate the social behavior of animals can be applied to investigate the social behavior of humans. Other individuals argue that sociobiology is merely a form of biological determinism. A complete resolution of this controversy is probably impossible.

SUMMARY

Archeological evidence indicates that early humans had a practical knowledge of the behavior of animals, particularly of those animals that were potential food sources or predators. By Greek and Roman times, writers like Aristotle and Pliny recorded extensive observations about and deductions from natural phenomena.

Three developments of the last half of the nineteenth century contributed to the emergence of animal behavior as a scientific discipline. First, Darwin and Wallace, each working from his own data and from ideas of previous investigators, independently put forth the theory of evolution by natural selection. Second, Romanes pioneered the development of the comparative method and used it initially to study mental evolution. Third, with Mendel's work on inheritance and the rediscovery and development of his findings at the turn of the century, modern theories of genetics and evolution emerged.

Derived from these diverse beginnings, three major approaches characterize current studies of animal behavior. Investigations of the mechanisms controlling behavior have historically been conducted primarily by comparative animal psychologists and physiologists. Although much of the early psychological research relied heavily on introspection and inference, these methods were later replaced by systematic, objective observations and replicable experiments. Modern animal psychologists explore such areas as physiological control of behavior, sensation and perception, learning processes, and behavior genetics.

Ethology encompasses studies of the functional significance and evolution of behavior. Behavioral traits, like physical or physiological traits, are viewed in evolutionary terms and are thus subject to natural selection. Traditionally, ethologists have made many of their research observations in a natural setting. The research objectives and methods of modern ethologists range from observational studies and field experiments conducted to assess the function of behavior patterns, to investigations of the physiological bases of behavior.

Behavioral ecology and sociobiology generate studies that examine biological relationships between an organism and its environment and the evolutionary selection pressures that influence social systems. The questions are asked from an ecological and sometimes evolutionary viewpoint, and investigations conducted in both field and laboratory settings utilize systematic, controlled experimentation. Investigators using this approach are concerned with both proximate and ultimate factors influencing behavior.