Behavioral Ecology

17

CHAPTER 17

Chapter Outline

Key Concepts	Applications
Understand that behavior has evolutionary and ecological significance.	• Describe why the behavioral evolution of social animals is different from that of nonsocial animals. • Appreciate that territoriality and dominance hierarchies allocate resources. • State the adaptive value of specific behaviors such as communication, food storage, navigation, a time sense, care of the young, and hibernation in particular ecological settings.
Know the characteristics of instinctive and learned behaviors.	• Recognize that there are different kinds of learning. • Recognize that instinctive behaviors are inherited and can be very complicated. • Recognize that most animals show both learned and instinctive behaviors. • Describe various human behaviors that illustrate instinct, habituation, imprinting, conditioning, and insight.

17.1 The Adaptive Nature of Behavior

Behavior is how an animal acts, what it does, and how it does it. When we observe behavior, we must keep in mind that behavior is adaptive just like any other characteristic displayed by an animal. Behaviors are important for survival and appropriate for the environment in which an animal lives. As with the highly adaptive structural characteristics we see in animals, behaviors are the result of a long evolutionary process.

Both plants and animals must solve the same kinds of problems. For example, they must obtain nutrients, avoid being eaten, and reproduce. While behaviors are important for animals, plants, for the most part, must rely on structures, physiological changes, or chance to accomplish the same ends. Animals use many kinds of behaviors (searching, flying, walking, chewing) to find and process the food they need, while plants can only obtain nutrients that happen to be located near their roots. A rabbit can run away from a predator, a plant cannot. But plants may have thorns or toxic compounds in their leaves that discourage animals from eating them. Animals engage in elaborate courtship behaviors to identify the species and sex of a potential mate. Most plants rely on a much more random method for transferring male gametes to the female plant.

Before we go much further, we need to discuss how animals generate specific behaviors and the two major kinds of behaviors: instinctive and learned. Both instinct and learning are involved in the behavior patterns of most organisms. We recognize **instinctive behavior** as behavior that is inborn, automatic, and inflexible; whereas **learned behavior** requires experience, produces new behaviors, and can be changed. Most animals have a high proportion of instinctive behavior and very little learning; some, like many birds and mammals, are able to demonstrate a great deal of learned behavior in addition to many instinctive behaviors. Since the majority of the behaviors of most animals are instinctive, inherited behaviors, they evolved just like the structures of animals. In this respect, behavioral characteristics are no different from structural characteristics. However, the evolution of behavior is much more difficult to study, because behavior is temporary and it is difficult to find fossils that allow us to follow the development of behavior the way fossils allow us to follow changes in structures. Fossils of footprints, and nests, and the presence of specific structures like grinding teeth, do tell us something about the behavior of extinct animals, but these represent only a few fragments of the total behavior that must have been a part of the life of extinct animals. When we compare the behavior of closely related animals living today, it is often possible to see inherited behaviors that are slightly different from one another, just as the wings of different species of birds are slightly different but based on the same pattern.

17.2 Interpreting Behavior

When you watch a bird or squirrel or any other animal, its activities appear to have a purpose. Birds search for food, take flight as you approach, and build nests in which to raise young. Usually the nests are inconspicuous or placed in difficult-to-reach spots. Likewise, squirrels collect and store nuts and acorns, "scold" you when you get too close, and learn to visit sites where food is available. All of these activities are adaptive and contribute to the success of the species. Birds that do not take flight at the approach of another animal will be eaten by predators. Squirrels that do not find deposits of food will be less likely to survive, and birds that build obvious nests on the ground will be more likely to lose their young to predators. However, we need to take care not to attach too much meaning to what animals do. They may not have the same "thoughts" and "motivations" we do.

Why are most people afraid of snakes? Is this a behavior we are born with or do we learn it? It appears that fear of snakes is a learned behavior in humans because little children do not react to snakes any differently than to other small moving objects. Fear of snakes can certainly be a valuable behavior since many common kinds of snakes are poisonous. Why do you blink when an object rapidly approaches your face? The automatic blinking of eyes is a reflexive behavior that is programmed into your nervous system. The behavior serves to protect the eye from injury. Why do you find it more difficult to communicate with someone on the phone or by computer than face-to-face? You probably find it more difficult to communicate when you cannot see the person because you rely on facial expression and gestures to communicate part of the message.

It is not always easy to identify the significance of a behavior without careful study of the behavior pattern and the impact it has on other organisms (How Science Works 17.1). For example, a hungry baby herring gull pecks at a red spot on its parent's bill. What possible value can this behavior have for either the chick or the parent? If we watch, we see that when the chick pecks at the spot, the parent regurgitates food onto the ground, and the chick feeds (figure 17.1). This looks like a simple behavior, but there is more to it than meets the eye. Why did the chick peck to begin with? How did it "know" to peck at that particular spot? Why did the pecking cause the parent to regurgitate food? These questions are not easy to answer. Many people assume that the actions have the same motivation and direction as similar human behaviors, but this is not necessarily a correct assumption. For example, when a human child points to a piece of candy and makes appropriate noises, it is indicating to its parent that it wants some candy. Is that what the herring gull chick is doing? We don't know. Although both kinds of young may get food, we don't know what the baby gull is thinking because we can't ask it.

HOW SCIENCE WORKS 17.1

Observation and Ethology

Ethology is the study of the behavior of animals in their natural environment. Such studies do not lend themselves easily to experimentation because it is difficult to manipulate conditions to fit the criteria of an experimental design. Therefore, most studies of the behavior of wild animals involve careful, extended observation to determine the significance of specific animal behaviors. Often the meaning of behaviors can be understood only if the observer is able to identify the individuals involved. For most of us, all robins, raccoons, and opossums look alike, making it difficult for us to understand behaviors we see between individuals.

Ethologists have used various techniques to allow easy identification of individuals. Some animals have individual variations that allow identification. Wild horses differ in size and color patterns, whales have differently shaped tails, and gorillas have size, color, and facial differences. It is the observational skill of the scientist that allows recognition of unique features. One scientist observing chipmunks was able to identify many individuals by specific characteristics of the tail, such as the shape and size of the tail, how the tail was carried, and minor differences in color.

In studies of bird behavior, scientists have placed colored bands on birds' legs that can be viewed through powerful binoculars. This allows investigators to determine which birds in a group are dominant, how they move through their environment, or how long they live. The attachment of small radio transmitters to animals as small as pigeons and as large as bears and sea turtles has allowed investigators to locate and follow individuals over large areas.

Regardless of the technique used to identify individuals, the ingenious mind of the investigator is still required to decipher meaning from the behaviors observed.

Figure 17.1

Animal Behavior
A baby herring gull causes its parent to regurgitate food onto the ground by pecking at the red spot on its parent's bill. The parent then picks up the food and feeds it to the baby.

17.3 The Problem of Anthropomorphism

Poets, composers, and writers have often described birdsong as the act of a joyful songster. But is that bird singing on a warm, sunny spring day making that beautiful sound because it is so happy? Students of animal behavior do not accept this idea and have demonstrated that a bird sings to tell other birds to keep out of its territory. The barbed stinger of a honeybee remains in your skin after you are stung, and the bee tears the stinger out of its body when it flies away. The damage to its body is so great that it dies. Has the bee performed a noble deed of heroism and self-sacrifice? Was it defending its hive from you? We need to know a great deal more about the behavior of bees to understand the value of such behavior to the success of the bee species. The fact that bees are social animals like us makes it particularly tempting to think that they are doing things for the same reasons we are.

The idea that we can ascribe human feelings, meanings, and emotions to the behavior of animals is called **anthropomorphism.** But we cannot crawl inside the brain of another animal and see what it is thinking so we need to avoid these anthropomorphic assumptions when attempting to understand the behavior of nonhuman animals. The fable of the grasshopper and the ant is another example of inappropriately crediting animals with human qualities. The ant is pictured as an animal that, despite temptations, works hard from morning until night, storing away food for the winter (figure 17.2). The grasshopper, on the other hand, is represented as a lazy good-for-nothing that fools away the summer singing, when it really ought to be saving up for the tough times ahead. If one is looking for analogies to human behavior, these are pretty good illustrations. But they really are not accurate statements about the lives of the animals from an ecological point of view. Ant colonies may live through the winter on stored food and all the grasshoppers may die. However, the grasshopper has left eggs in sheltered spots and these will hatch the next spring. Both the ant and

Figure 17.2

The Fable of the Ant and the Grasshopper
In many ways we give human meaning to the actions of animals. The ant is portrayed as an industrious individual that prepares for the future, and the grasshopper as a lazy fellow that sits in the sun and sings all day. This view of animal behavior is anthropomorphic.

the grasshopper are very successful organisms, but each has a different way of satisfying its needs and ensuring that some of its offspring will be able to provide another generation of organisms. One method of survival is not necessarily better than another, as long as both animals are successful. This is what the study of behavior is all about—looking at the activities of an organism during its entire life and determining the value of the behavior in the ecological niche of the organism. The scientific study of the nature of behavior and its ecological and evolutionary significance in its natural setting is known as **ethology.**

17.4 Instinct and Learning

Instinctive and learned behaviors have already been defined, but a more complete understanding of these two kinds of behaviors is necessary to better understand how the behavior of an animal fits with its environment and how differences in behavior relate to the evolutionary history of an animal.

Instinctive Behavior

Instinctive behaviors are automatic, preprogrammed, and genetically determined. Such behaviors are found in a wide range of organisms from simple one-celled protozoans to complex vertebrates. These behaviors are performed correctly the first time without previous experience when the proper stimulus is given. A **stimulus** is some change in the internal or external environment of the organism that causes it to react. The reaction of the organism to the stimulus is called a **response.**

An organism can respond only to stimuli it can recognize. For example, it is difficult for us as humans to appreciate what the world seems like to a bloodhound. The bloodhound is able to identify individuals by smell, whereas we have great difficulty detecting, let alone distinguishing, many odors. Some animals, like dogs, deer, and mice are color-blind and are able to see only shades of gray. Others, such as honeybees, see ultraviolet light, which is invisible to us. Some birds and other animals are able to detect the magnetic field of the Earth. And some, such as rattlesnakes, are able to detect infrared radiation (heat) from distant objects.

In our example of the herring-gull chick, the red spot on the bill of the adult bird serves as a stimulus to the chick. The chick responds to this spot in a genetically programmed way. The behavior is innate—it is done correctly the first time without prior experience. The pecking behavior of the chick is in turn the stimulus for the adult bird to regurgitate food. It is obvious that these behaviors have adaptive value for the gull species because they leave little to chance. The young will get food from the adult automatically. Instinctive behavior has great value to a species because it allows correct, appropriate, and necessary behavior to occur without prior experience.

The drawback of instinctive behavior is that it cannot be modified when a new situation presents itself, but it can be very effective for the survival of a species if it is involved in fundamental, essential activities that rarely require modification. Instinctive behavior is most common in animals that have short life cycles, simple nervous systems, and little contact with parents. Over long periods of evolutionary time, these genetically determined behaviors have been selected for and have been useful to most of the individuals of the species. However, some instances of inappropriate behavior may be generated by unusual stimuli or unusual circumstances in which the stimulus is given. For example, many insects fly toward a source of light. Over the millions of years of insect evolution, this has been a valuable and useful behavior. It allows them to easily find their way to open space. However, the human species invented artificial lights and transparent windows that generate totally inappropriate behavior. You have all seen insects drawn to lights at night or observed insects inside houses constantly flying against window panes through which sunlight is entering. This mindless, mechanical behavior seems incredibly stupid to us but, although *individual* animals die, the behavior is still valuable for the species because the *majority* do not encounter artificial lights or get trapped inside houses, and complete their life cycles normally.

Geese and other birds sit on nests to keep the eggs warm. During this incubation period, eggs may roll out of the nest as the parents get on and off the nest. When this happens, certain species of geese display a behavior that involves rolling eggs back into the nest. If the developing young within the egg are exposed to extremes of heat or cold they will be killed. Thus the egg-rolling behavior has a significant adaptive value. If, however, the egg is taken from the goose when it is in the middle of egg-rolling behavior, the goose will continue its egg rolling until it gets back to the nest, even though there is no egg to roll (figure 17.3).

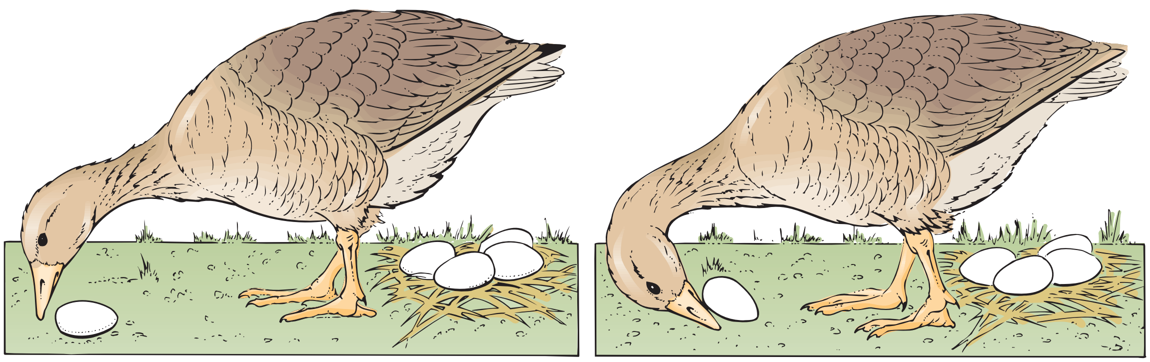

Figure 17.3

Egg-Rolling Behavior in Geese
Geese will use a specific set of head movements to roll any reasonably round object back to the nest. There are several components to this instinctive behavior, including recognition of the object and head-tucking movements. If the egg is removed during the head-tucking movements, the behavior continues as if the egg were still there.

This is typical of the inflexible nature of instinctive behaviors. It was also discovered that many other somewhat egg-shaped structures would generate the same behavior. For example, beer cans and baseballs were good triggers for egg-rolling behavior. So not only was the bird unable to stop the egg-rolling behavior in midstride, but several nonegg objects generated inappropriate behavior because they had approximately the correct shape.

Some activities are so complex that it seems impossible for an organism to be born with such abilities. For example, you have seen spiderwebs in fields, parks, or vacant lots. You may have even watched a spider spin its web. This is not just a careless jumble of silk threads. A web is so precisely made that you can recognize what species of spider made it. But web spinning is not a learned ability. A spider has no opportunity to learn how to spin a web because it never observes others doing it. Furthermore, spiders do not practice several times before they get a proper, workable web. It is as if a "program" for making a particular web is in the spider's "computer" (figure 17.4). Many species of spiders appear to be unable to repair defective webs. When a web is damaged they typically start from the beginning and build an entirely new web. This inability to adapt as circumstances change is a prominent characteristic of instinctive behavior.

Could these behavior patterns be the result of natural selection? It is well established that many kinds of behaviors are controlled by genes. The "computer" in our example is really the DNA of the organism, and the "program" consists of a specific package of genes. Through the millions of years that spiders have been in existence, natural selection has modified the web-making program to refine the process. Certain genes of the program have undergone mutation, resulting in changes in behavior. Imagine various ancestral spiders, each with a slightly different program. The inherited

Figure 17.4

Inflexible Instinctive Behavior
The kind of web constructed by a spider is determined by instinctive behavior patterns. The spider cannot change the fundamental form of the web. If the web is damaged, the spider generally rebuilds it from the beginning rather than repair it.

program that gives the best chance of living long enough to produce a new generation is the program selected for and most likely to be passed on to the next generation.

Learned Behavior

The alternative to preprogrammed, instinctive behavior is learned behavior. **Learning** is a change in behavior as a result of experience. (Your behavior will be different in some way as a result of reading this chapter.)

Learning becomes more significant in long-lived animals that care for their young. Animals that live many years are more likely to benefit from an ability to recognize previously encountered situations and modify their behavior accordingly. Furthermore, because the young spend time with their parents they can imitate their parents and develop behaviors that are appropriate to local conditions. These behaviors take time to develop but have the advantage of adaptability. In order for learning to become a dominant feature of an animal's life, the animal must also have a memory which requires a relatively large brain in which to store the new information it is learning. This is probably why learning is a major part of life for only a few kinds of animals like the vertebrates. In humans, it is clear that nearly all behavior is learned. Even such important behaviors as walking, communicating, feeding oneself, and sexual intercourse must be learned.

17.5 Kinds of Learning

Scientists who study learning recognize that there are different kinds that can be subdivided into several categories: *habituation, association, imprinting,* and *insight.*

Habituation

Habituation is a change in behavior in which an animal ignores an insignificant stimulus after repeated exposure to it. There are many examples of this kind of learning. Typically, wild animals flee from humans. Under many conditions this is a valuable behavior. However, in situations where wild animals frequently encounter humans and never experience negative outcomes, they may "learn" to ignore humans. Many wild animals such as the deer, elk, and bears in parks have been habituated to the presence of humans and behave in a way that would be totally inappropriate in areas near the park where hunting is allowed. Similarly, loud noises will startle humans and other animals. However constant exposure to such sounds results in the individuals ignoring the sound. As a matter of fact, the sound may become so much a part of the environment that the cessation of the sound will evoke a response. This kind of learning is valuable because the animal does not waste time and energy responding to a stimulus that will not have a beneficial or negative impact on the animal. Animals that are continually responding to inconsequential stimuli have less time to feed and may miss other more important stimuli.

Association

Association occurs when an animal makes a connection between a stimulus and an outcome. Associating a particular outcome with a particular stimulus is important to survival because it allows an animal to avoid danger or take advantage of a beneficial event. If this kind of learning allows the animal to get more food, avoid predators, or protect its young more effectively, it will be advantageous to the species. The association of certain shapes, colors, odors, or sounds with danger is especially valuable. There are three common kinds of association learning: *classical conditioning, operant (instrumental) conditioning,* and *observational learning (imitation).*

Classical Conditioning

Classical conditioning occurs when an involuntary, natural, reflexive response to a natural stimulus is transferred from the natural stimulus to a new stimulus. The response produced by the new stimulus is called a **conditioned response.** During the period when learning is taking place, the new stimulus is given *before* or *at the same time as* the normal stimulus.

A Russian physiologist, Ivan Pavlov (1849–1936), was investigating the physiology of digestion when he discovered that dogs can transfer a normal response to a new stimulus. He was studying the production of saliva by dogs and he knew that a natural stimulus, such as the presence or smell of food, would cause the dogs to start salivating. Then he rang a bell just prior to the presentation of the food. After a training period, the dogs would begin to salivate when the bell was rung even though no food was presented. The natural response (salivating) was transferred from the natural stimulus (smell or taste of food) to the new stimulus (the sound of a bell). Animals can also be conditioned unintentionally. Many pets anticipate their mealtimes because their owners go through a certain set of behaviors, such as going to a cupboard or opening a can of pet food prior to putting food in the dish. It is doubtful that this kind of learning is a common occurrence in wild animals, because it is hard to imagine such tightly controlled sets of stimuli in nature.

Operant Conditioning

Operant (instrumental) conditioning also involves the association of a particular outcome with a specific stimulus, but differs from classical conditioning in several ways. First, during operant conditioning the animal learns to repeat acts that bring good results and avoid those that bring bad results. Second, a reward or punishment is received *after* the animal has engaged in a particular behavior. Third, the response is typically a more complicated behavior than a simple reflex. A reward that encourages a behavior is known as positive reinforcement and a punishment that discourages a behavior is known as negative reinforcement. The training of many kinds of animals involves this kind of conditioning. If a dog being led on a chain is given the command "heel" and is then vigorously jerked into the correct position by its master it eventually associates the word "heel" with assuming the correct position at the knee. This is negative reinforcement because the animal avoids the unpleasantness of being jerked about if it assumes the correct position. Similarly, petting or giving food to a dog when it has done something correctly will positively reinforce the desired behavior. For example, pushing the dog into the sitting position on the command "sit" and rewarding the dog when it performs the behavior on command is positive reinforcement.

Wild animals have many opportunities to learn through positive or negative reinforcement. As animals encounter the same stimulus repeatedly there is an opportunity to associate the stimulus with a particular outcome. For example, many kinds of birds eat berries and other small fruits. If a distinctly colored berry has a good flavor, birds will return repeatedly and feed from that source. Pigeons in cities have learned to associate food with people in parks. They can even identify specific individuals who regularly feed them. Their behavior is reinforced by being fed. Many birds in urban areas have associated automobiles with food, and are seen picking smashed insects from the grills and bumpers of cars. When a car drives into the area it is immediately examined for food.

In some of our national parks, bears have associated backpacks with food. In some cases, attempts have been made to use negative reinforcement to condition these bears to avoid humans. Bears that are repeat offenders are often killed. Conversely, in areas where bears are hunted they have generally been conditioned to avoid contact with humans. If certain kinds of fruits or insects have unpleasant tastes, animals will learn to associate the bad tastes with the colors and shapes of the offending objects and avoid them in the future (figure 17.5). Each species of animal has a distinctive smell. If a deer or rabbit has several bad experiences with a predator that has a particular smell, it can avoid places where the smell of the predator is present.

Animals also engage in trial-and-error learning which involves elements of conditioning. When confronted with a particular problem, they will try one option after another until they achieve a positive result. Once they have solved the problem, they can use the same solution repeatedly. For example, if a squirrel has a den in a hollow tree on one side of a stream and is attracted to a source of food on the other side, it may explore several routes to get across the stream. It may jump from a tree on one side of the stream to another on the opposite side. It may run across a log that spans the stream. It may wade a shallow portion of the stream. Once it has found a good pathway, it is likely to use the same pathway repeatedly. Many hummingbirds visit many different flowers during the course of a day. When they have found a series of nectar-rich flowers, they will follow a particular route and visit the same flowers several times a day.

Observational Learning

In animals that participate in social groups, imitation is possible. **Observational learning (imitation)** is a form of associative learning that consists of a complex set of associations formed while watching another animal being rewarded or punished after performing a particular behavior. In this case, the animal is not receiving the reward or punishment itself but is observing the "fruits" of the behavior of other animals. Subsequently, the observer may show the same behavior. It is likely that conditioning is involved in imitation, since when an animal imitates a beneficial behavior it is rewarded. Observing a negative outcome to another animal is also beneficial because it allows the observer to avoid negative consequences. Many kinds of young birds and mammals follow their parents and sample the same kinds of foods their parents eat. If the foods taste good, they are positively reinforced. They may also observe warning and avoidance behaviors associated with particular predators and mimic these behaviors when the predator is present. For example, crows will "mob" predators such as hawks and owls. As young birds observe older crows cawing loudly and chasing an owl, the young crows learn to perform the same behavior. They associate a certain kind of behavior ("mobbing") with a certain kind of stimulus (owls or hawks).

(a)

(b)

Figure 17.5

Associative Learning
Many animals learn to associate unpleasant experiences with the color or shape of offensive objects and thus avoid them in the future. The blue jay is eating a monarch butterfly. These butterflies contain a chemical that makes the blue jay sick. After one or two such experiences, blue jays learn not to eat the monarch.

Exploratory Learning

Animals are constantly moving about and sampling their environment. Since they have a memory, it is possible for animals to store information about their surroundings as they wander about. In some cases, the new information may have immediate value. For example, in the spring of the year a queen bumblebee will fly about examining holes in the ground. Eventually she will find a hole in which she will lay eggs and begin to raise her first brood of young. Once she has selected a site she must learn to recognize that particular spot so she can return to it each time she leaves to find food, or her young will die. In similar fashion, the exploratory behavior of birds and mammals allows them to find sources of food to which they can return repeatedly. When you put up a bird feeder, it does not take very long before many birds are visiting the feeder on a regular basis.

In other cases, the information learned may not be used immediately but could be of use in the future. If an animal has an inventory of its environment, it can call on the inventory to solve problems later in life. Many kinds of animals hide food items when food is plentiful and are able to find these hidden sources later when food is needed. Even if they don't remember exactly where the food is hidden, if they always hide food in a particular kind of place they are likely to be able to find it at a later date. (For example, if you need to drive a car that you have never seen before, you would know that you need to use the key and you would search in a particular place in the car for the place to insert the key.) Having a general knowledge of its environment is very useful to an animal.

Many kinds of small mammals such as mice and ground squirrels avoid predators by scurrying under logs or other objects or into holes in the ground. Experiments with mice and owl predators show that mice that have developed a familiarity with their surroundings are more likely to escape predators than are those that are unfamiliar with their surroundings.

Imprinting

Imprinting is a special kind of irreversible learning in which a very young animal is genetically primed to learn a specific behavior in a very short period during a specific time in its life. The time during which the learning is possible is known as the **critical period.** This type of learning was originally recognized by Konrad Lorenz (1903–1989) in his experiments with geese and ducks. He determined that, shortly after hatching, a duckling would follow an object if the object was fairly large, moved, and made noise. In one of his books, Lorenz described himself as squatting on the lawn one day, waddling and quacking, followed by newly hatched ducklings (figure 17.6). He was being a "mother duck." He was surprised to see a group of tourists on the other side of the fence watching him in amazement. They couldn't see the ducklings hidden by the tall grass. All they could see was this strange performance by a big man with a beard!

Figure 17.6

Imprinting
Imprinting is a special kind of irreversible learning that occurs during a very specific part of the life of an animal. These geese have been imprinted on Konrad Lorenz and exhibit the "following response" typical of this type of behavior.

Ducklings will follow only the object on which they were originally imprinted. Under normal conditions, the first large, noisy, moving object newly hatched ducklings see is their mother. Imprinting ensures that the immature birds will follow her and learn appropriate feeding, defensive tactics, and other behaviors by example. Because they are always near their mother, she can also protect them from enemies or bad weather. If animals imprint on the wrong objects, they are not likely to survive. Since these experiments by Lorenz in the early 1930s, we have discovered that many young animals can be imprinted on several types of stimuli and that there are responses other than following.

The way song sparrows learn their song appears to be a kind of imprinting. It has been discovered that the young birds must hear the correct song during a specific part of their youth or they will never be able to perform the song correctly as adults. This is true even if later in life they are surrounded by other adult song sparrows that are singing the correct song. Furthermore, the period of time when they learn the song is prior to the time they begin singing. Recognizing and performing the correct song is important because it has particular meaning to other song sparrows. For males, it conveys the information that a male song sparrow has a space reserved for himself. For females, the male's song is an announcement of the location of a male of the correct species that could be a possible mate.

Mother sheep and many other kinds of mammals imprint on the odor of their offspring. They are able to identify their offspring among a group of lambs and will allow only their own lambs to suck milk. Shepherds have known for centuries that they can sometimes get a mother that has lost her lambs to accept an orphan lamb if they place the skin of the mother's dead lamb over the orphan.

Many fish appear to imprint on odors in the water. Salmon are famous for their ability to return to the freshwater streams where they were hatched. They will jump waterfalls and use specially constructed fish ladders to get around dams. Fish that are raised in artificial hatcheries can be imprinted on minute amounts of special chemicals and be induced to return to any stream that contains the chemical.

Insight

Insight is a special kind of learning in which past experiences are reorganized to solve new problems. When you are faced with a new problem, whether it is a crossword puzzle, a math problem, or any one of a hundred other everyday problems, you sort through your past experiences and locate those that apply. You may not even realize that you are doing it, but you put these past experiences together in a new way that may give the solution to your problem. Because this process is internal and can be demonstrated only through some response, it is very difficult to understand exactly what goes on during insight learning. Behavioral scientists have explored this area for many years, but the study of insight learning is still in its infancy.

Insight learning is particularly difficult to study because it is impossible to know for sure whether a novel solution to a problem is the result of "thinking it through" or an accidental occurrence. For example, a small group of Japanese macaques (monkeys) was studied on an island. They were fed by simply dumping food, such as sweet potatoes or wheat, onto the beach. Eventually, one of the macaques discovered that she could get the sand off the sweet potato by washing it in a nearby stream. She also discovered that she could sort the wheat from the sand by putting the mixture into water because the wheat would float. Are these examples of insight learning? We will probably never know, but it is tempting to think so. In addition, in the colony of macaques the other individuals soon began to display the same behavior, probably because they were imitating the female that first made the discovery.

Table 17.1 summarizes the significance of each of the kinds of learning.

17.6 Instinct and Learning in the Same Animal

It is important to recognize that all animals have both learned and instinctive behaviors and that one behavior may have elements that are both instinctive and learned. For example, biologists have raised young song sparrows in the absence of any adult birds so there was no song for the young birds to imitate. These isolated birds would sing a series of notes similar to the normal song of the species, but not exactly correct. Birds from the same nest that were raised with their parents developed a song nearly identical to that of their parents. If bird songs were totally instinctive, there would be no difference between these two groups. It appears that the basic melody of the song was inherited by the birds and that the refinements of the song were the result of experience. Therefore, the characteristic song of that species was partly learned behavior (a change in behavior as a result of experience) and partly unlearned (instinctive). This is probably true of the behavior of many organisms; they show complex behaviors that are a combination of instinct and learning. It is important to note that many kinds of birds learn most of their songs with very few innate components. Mockingbirds are very good at imitating the songs of a wide variety of bird species found in their local region.

This mixture of learned and instinctive behavior is not the same for all species. Many invertebrate animals rely on instinct for the majority of their behavior patterns, whereas many of the vertebrates (particularly birds and mammals) make use of a great deal of learning (figure 17.7).

Typically the learned components of an animal's behavior have particular value for the animal's survival. Most of the behavior of a honeybee is instinctive, but it is able to learn new routes to food sources. The style of nest built by a bird is instinctive, but the skill with which it builds may improve with experience. The food-searching behavior of birds is probably instinctive, but the ability to modify the behavior to exploit unusual food sources such as bird feeders is learned. On the other hand, honeybees cannot be taught to make products other than honey and beeswax, a robin will not build a nest in a birdhouse, and most insect-eating birds will not learn to visit bird feeders. Table 17.2 compares instinctive behaviors and learned behaviors.

17.7 What About Human Behavior?

We tend to think of ourselves as being different from other animals, and we are. However, it is important to recognize that we are different only in the degree to which we employ these different kinds of behavior. Humans have few behaviors that can be considered instincts. We certainly have reflexes that cause us to respond appropriately without

Table 17.1

THE SIGNIFICANCE OF VARIOUS KINDS OF LEARNING

Kind of Learning	Defining Characteristic	Ecological Significance	Example
Habituation	An animal ignores a stimulus to which it is continually subjected.	An animal does not waste time or energy by responding to unimportant stimuli.	Wild animals raised in the presence of humans "lose their fear" of humans.
Association	An animal learns that a particular outcome is connected with a particular stimulus.	An animal can avoid danger or anticipate beneficial events by connecting a particular outcome with a specific stimulus when that stimulus is frequently tied to a particular outcome.	
Classical conditioning	A new stimulus is presented with a natural stimulus. The animal transfers its response from the natural stimulus to the new stimulus.		Pets can anticipate when they will be fed because food-preparing behavior of their owner occurs before food is presented.
Operant conditioning	A new stimulus elicits a response. The animal is rewarded or punished following its response. Eventually the animal associates the reward or punishment with the stimulus and responds appropriately to the stimulus.		Dogs can be trained to respond to a spoken or hand signal by being rewarded when they perform correctly or being punished when they perform incorrectly.
Observational learning (imitation)	An animal imitates the behaviors of others.		Young animals run when their mothers do or feed on the food their parents do.
Exploratory learning	An animal moves through and observes elements of its environment.	Information stored in memory may be valuable later.	Awareness of hiding places could allow an animal to escape a predator.
Imprinting	An animal learns specific predetermined activity at a specific time in life.	The animal gains a completely developed behavior that has immediate value to survival.	Many kinds of newborn animals will follow their mothers.
Insight	An animal understands the connection between things it had no way of experiencing previously.	Information stored in an animal's memory can be used to solve new problems.	Tools are use by humans and some other primates.

thinking. Touching a hot object and rapidly pulling your hand away is a good example. Newborns grasp objects and hang on tightly with both their hands and feet. This kind of grasping behavior in our primitive ancestors would have allowed the child to hang onto its mother's hair as the mother and child traveled from place to place. But do we have more complicated instinctive behaviors? Although nearly all behavior other than reflexes is learned, newborn infants display several behaviors that could be considered instinctive. If you stroke the side of an infant's face, the child will turn its head toward the side touched and begin sucking movements. This is not a simple reflex behavior but rather requires the coordination of several sets of muscles and certainly involves the brain. It is hard to see how this could be a learned behavior because the child does the behavior without prior experience. Therefore it is probably instinctive. This behavior may be associated with nursing, because carrying the baby on its back would place the cheek of the child against the breast of the mother. Other mammals, even those whose eyes do not open for several days

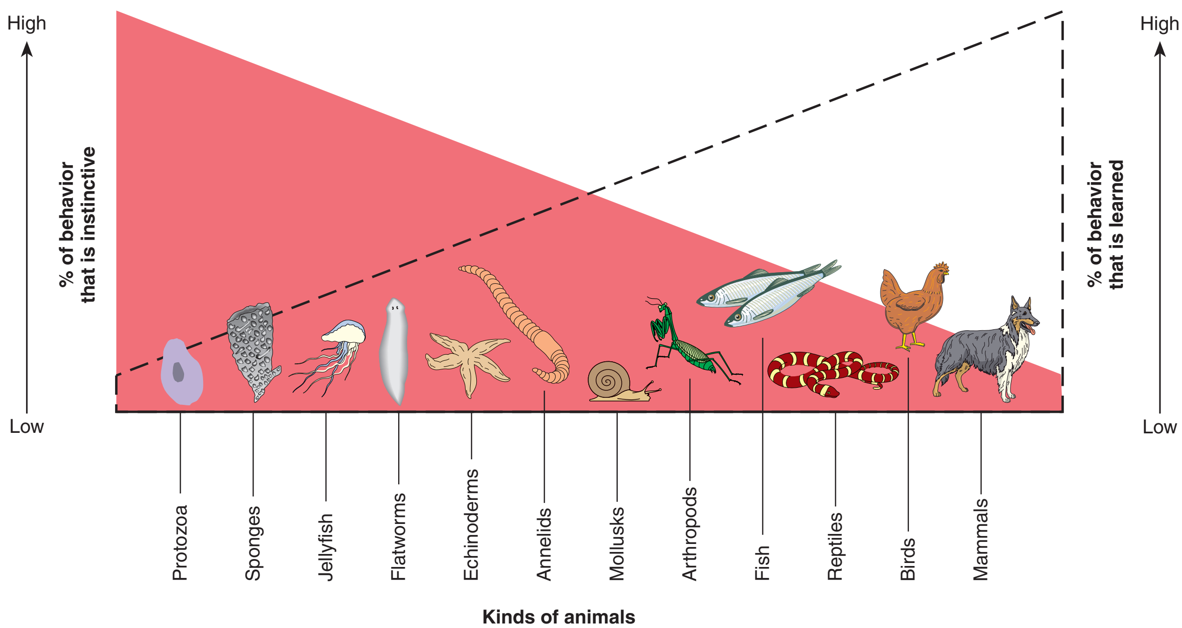

Figure 17.7

The Distribution of Learned and Instinctive Behaviors
Different groups of animals show different proportions of instinctive and learned behavior in their behavior patterns.

Table 17.2

A COMPARISON OF INSTINCT AND LEARNING

Instinct	Learning
Animal is born with the behavior.	Animal is not born with the behavior.
Instinctive behavior is genetically determined.	Learned behavior is not genetically determined but the way in which learning occurs is at least partly hereditary.
No experience is required; behavior is done correctly the first time.	Performance improves with experience; behavior requires practice.
Behavior cannot be changed.	Behavior can be changed.
Memory is not important.	Memory is important.
Instinctive behavior can evolve as gene frequencies change.	Changes in learned behaviors are not the result of genetic changes.
Instinct is typical of simple animals that have short lives and little contact with their parents.	Learning is typical of more complex animals that have long lives and extensive contact with parents.
Instinctive behaviors can only be passed from parent of offspring by genetic means.	Learning allows acquired behaviors to be passed from parent to offspring by cultural means.

following birth, are able to find nipples and begin nursing shortly after birth.

Habituation is a common experience. We readily ignore sounds that are continuous such as the sound of air conditioning equipment or the background music typical of shopping malls. Teachers recognize that it is important to change activities regularly if they are going to keep the attention of their students.

Associative learning is extremely common in humans. We associate smells with certain kinds of food, sirens with emergency vehicles, and words with their meanings. Much of the learning that we do is by association. We also often use positive and negative reinforcement as ways to change behavior. We seek to reward appropriate behavior and punish inappropriate behavior. Much of the positive and negative reinforcement can be accomplished without having the actual experience because we can visualize possible consequences of our behavior. Adults routinely describe consequences for children so that children will not experience particularly harmful effects. "If you don't study for your biology exam you will probably fail it."

Imprinting in humans is more difficult to demonstrate, but there are some instances in which imprinting may be taking place. Bonding between mothers and infants is thought to be an important step in the development of the mother-child relationship. Most mothers form very strong emotional attachments to their children and, likewise, the children are attached to their mothers, sometimes literally, as they seek to maintain physical contact with their mothers. However, it is very difficult to show what is actually happening at this early time in the life of a child.

Another interesting possibility is the language development of children. All children learn whatever languages are spoken where they grow up. If multiple languages are spoken they will learn them all and they learn them easily. However, adults have more difficulty learning new languages, and they often find it impossible to "unlearn" previous languages, so they speak new languages with an accent. This appears to meet the definition of imprinting. Learning takes place at a specific time in life (critical period), the kind of learning is preprogrammed, and what is learned cannot be unlearned. Recent research using tomographic images of the brain shows that those who learned a second language as adults use two different parts of the brain for language—one part for the native language or languages they learned as children and a different part for their second language.

Insight is what our species prides itself on. We are thinking animals. **Thinking** is a mental process that involves memory, a concept of self, and an ability to reorganize information. We come up with new solutions to problems. We invent new objects, new languages, new culture, and new challenges to solve. However, how much of what we think is really completely new, and how much is imitation? As mentioned earlier, association is a major core of our behavior, but we also are able to use past experiences, stored in our large brains, to provide clues to solving new problems.

17.8 Selected Topics in Behavioral Ecology

Of the examples used so far in this chapter, some involved laboratory studies, some were field studies, and some included aspects of both. Often these studies overlap with the field of psychology. This is particularly true for many of the laboratory studies. You can see that the science of animal behavior is a broad one that draws on information from several fields of study and can be used to explore many kinds of questions. The topics that follow avoid the field of psychology and concentrate on the significance of behavior from an ecological and an evolutionary point of view.

Now that we have some understanding of how organisms generate behavior, we can look at a variety of behaviors in several kinds of animals and see how they are useful to the animals in their ecological niches.

Reproductive Behavior

Reproductive behavior of many kinds of animals has been studied a great deal. Although each species of animal has its own specific behaviors, there are certain components of reproductive behavior that are common to nearly all kinds of animals. In order for an animal to reproduce, several events must occur—a suitable mate must be located, mating and fertilization must take place, and the young must be provided for.

Finding Each Other

In order to reproduce, an animal must find individuals of the same species that are of the opposite sex. Several techniques are used for this purpose. Different species of animals employ different methods, but most involve the production of signals that can be interpreted by others of the same species. Depending on the species, any of the senses (sound, sight, touch, smell, or taste) may be used to identify the species, sex, and sexual receptiveness of another animal. For instance, different species of frogs produce distinct calls. The call is a code system that delivers a very private message because it is meant for only one species. It is, however, meant for any member of that species near enough to hear. The call produced by male frogs, which both male and female frogs can receive by hearing, results in frogs of both sexes congregating in a limited area. Once they gather in a small pond, it is much easier to have the further communication necessary for mating to take place.

Many other animals including most birds, insects like crickets, reptiles like alligators, and some mammals produce sounds that are important for bringing individuals together for mating.

Chemicals can also serve to attract animals. **Pheromones** are chemicals produced by animals and released into the environment that trigger behavioral or developmental changes in other animals of the same species. They have the same effect as sounds made by frogs or birds; they are just using a different code system. The classic example of a pheromone is the chemical that female moths release into the air. The large, fuzzy antennae of the male moths can receive the chemical in unbelievably tiny amounts. The male then changes his direction of flight and flies upwind to the source of the pheromone, which is the female (figure 17.8). Some of these sex-attractant pheromones have been synthesized in the

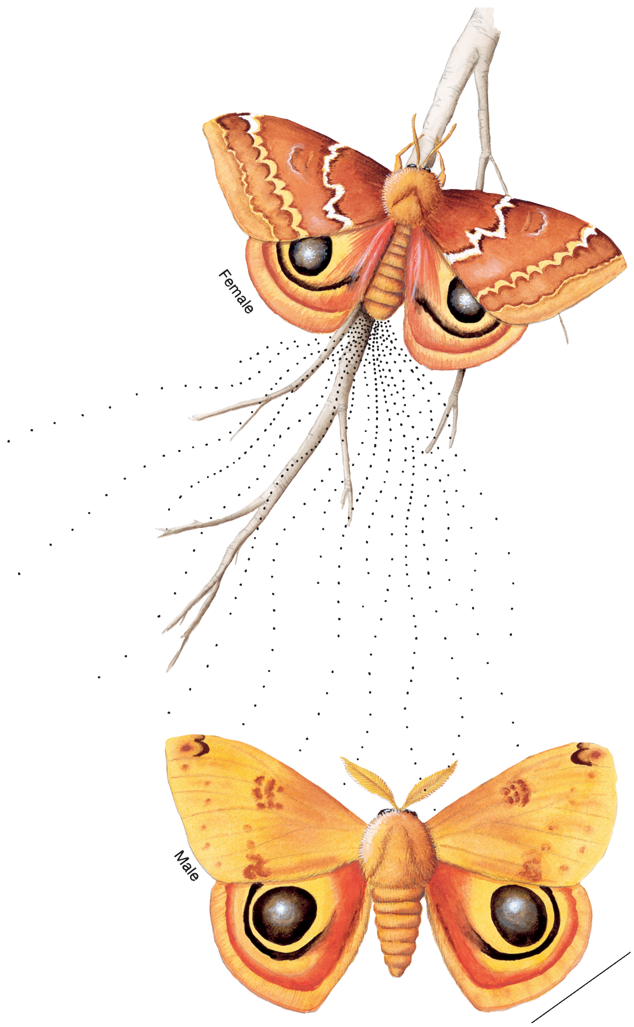

Figure 17.8

Communication
The female moth signals her readiness to mate and attracts males by releasing a pheromone that attracts males from long distances downwind.

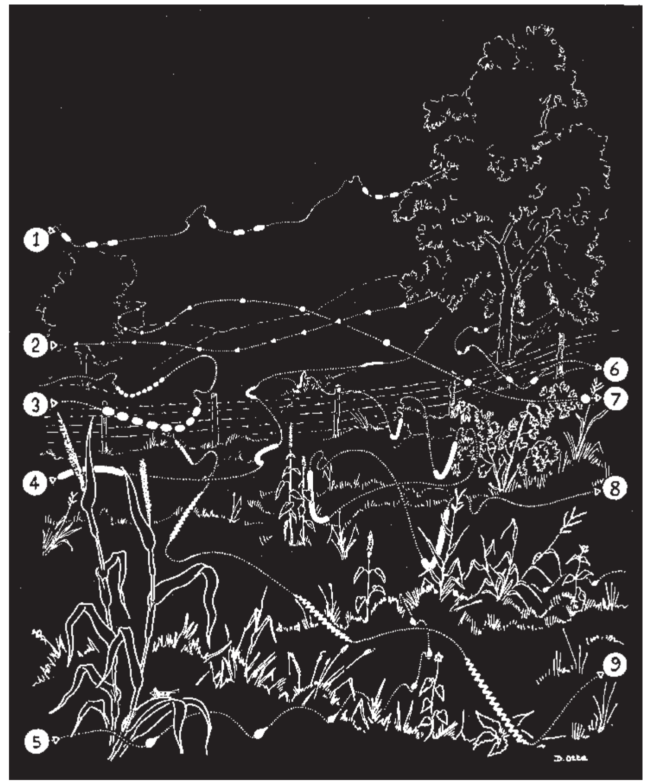

Figure 17.9

Firefly Communication
The pattern of light flashes, the location of light flashes, and the duration of light flashes all help fireflies identify members of the opposite sex who are of the appropriate species.

laboratory. One of these, called Disparlure, is widely used to attract and trap male gypsy moths. Because gypsy moths cause considerable damage to trees by feeding on the leaves, the sex attractant is used to estimate population size so that control measures can be taken to prevent large population outbreaks.

Most mammals rely on odors. Females typically produce distinct odors when they are in breeding condition. When males happen on such an odor trail, they follow it to the female. Many reptiles also produce distinctive odors.

Visual cues are also important for many species. Brightly colored birds, insects, fish, and many other animals often use specific patches of color for species identification. Conspicuous movements may also be used to attract the attention of a member of the opposite sex.

The firefly is probably the most familiar organism that uses light signals to bring males and females together. Several different species may live in the same area, but each species flashes its own code. The code is based on the length of the flashes, their frequency, and their overall pattern (figure 17.9). There is also a difference between the signals given by males and those given by females. For the most part, males are attracted to and mate with females of their own species. Once male and female animals have attracted one another's attention, the second stage in successful reproduction takes place. However, in one species of firefly, the female has the remarkable ability to signal the correct answering code to species other than her own. After she has mated with a male of her species, she will continue to signal to passing males of other species. She is not hungry for sex, she is just hungry. The luckless male who responds to her "come-on" is going to be her dinner.

Assuring Fertilization

The second important activity in reproduction is fertilizing eggs. Many marine organisms simply release their gametes into the sea simultaneously and allow fertilization and further development to take place without any input from the parents. Sponges, jellyfishes, and many other marine animals fit this category. Other aquatic animals congregate so that the chances of fertilization are enhanced by the male and female being near one another as the gametes are shed. This is typical of many fish and some amphibians, such as frogs. Internal fertilization, in which the sperm are introduced into the reproductive tract of the female, occurs in most terrestrial animals. Some spiders and other terrestrial animals produce packages of sperm that the female picks up with her reproductive structures. Many of these mating behaviors require elaborate, species-specific communication prior to the mating act. Several examples were given in the previous paragraphs.

Raising the Young

A third element in successful reproduction is providing the young with the resources they need to live to adulthood. Many invertebrate animals spend little energy on the care of the young, leaving them to develop on their own. Usually the young become free-living larvae that eat and grow rapidly. In some species, females make preparations for the young by laying their eggs in suitable sites. Many insects lay their eggs on the particular species of plant that the larva will use as food as it develops. Parasitic species seek out the required host in which to lay their eggs. The eggs of others may be placed in spots that provide safety until the young hatch from the egg. Turtles, many fish, and some insects fit this category. In most of these cases, however, the female lays large numbers of eggs, and most of the young die before reaching adulthood. This is an enormously expensive process: the female invests considerable energy in the production of the eggs but has a low success rate.

An alternative to this “wasteful” loss of potential young is to produce fewer young but invest large amounts of energy in their care. This is typical of birds and mammals. Parents build nests, share in the feeding and protection of the young, and often assist the young in learning appropriate behaviors. Many insects, such as bees, ants, and termites, have elaborate social organizations in which one or a few females produce large numbers of young that are cared for by sterile offspring of the fertile females. Some of the female’s offspring will be fertile, reproducing individuals.

The activity of caring for the young involves many complex behavior patterns. It appears that most animals that feed and raise young are able to recognize their own young from those of other nearby families and may even kill the young of another family unit. Elaborate greeting ceremonies are usually performed when animals return to the nest or the den. Perhaps this has something to do with being able to identify individual young. Often this behavior is shared among adults as well. This is true for many colonial nesting birds, such as gulls and penguins, and for many carnivorous mammals, such as wolves, dogs, and hyenas.

Territorial Behavior

One kind of behavior pattern that is often tied to successful reproduction is territorial behavior. A **territory** is the space used for food, mating, or other purposes, that an animal defends against others of the same species. The behaviors involved in securing and defending the territory are called **territorial behaviors.** A territory has great importance because it reserves exclusive rights to the use of a certain space for an individual.

When territories are first being established, there is much conflict between individuals. This eventually gives way to the use of a series of signals that define the territory and communicate to others that the territory is occupied. The male redwing blackbird has red shoulder patches, but the female does not. The male will perch on a high spot, flash his red shoulder patches, and sing to other males that happen to venture into his territory. Most other males get the message and leave his territory; those that do not leave, he attacks. He will also attack a stuffed, dead male redwing blackbird in his territory, or even a small piece of red cloth. Clearly, the spot of red is the characteristic that stimulates the male to defend his territory. Once the initial period of conflict is over, the birds tend to respect one another’s boundaries. All that is required is to frequently announce that the territory is still occupied. This is accomplished by singing from some conspicuous position in the territory. After the territorial boundaries are established, little time is required to prevent other males from venturing close. Thus the animal may spend a great deal of time and energy securing the territory initially, but doesn’t need to expend much to maintain it.

Not all male redwing blackbirds are successful in obtaining territories. During the initial period, when fighting is common, some birds regularly win and maintain their territories. Some lose and must choose a less favorable territory or go without. Therefore, territorial behavior is a way to distribute a resource that is in short supply. Because females choose which male’s territory they will build their nest in, males that do not have territories are much less likely to fertilize females.

With many kinds of animals the possession of a territory is often a requirement for reproductive success. In a way, then, territorial behavior has the effect of allocating breeding space and limiting population size to that which the ecosystem can support. This kind of behavior is widespread in the animal kingdom and can be seen in such diverse groups as insects, spiders, fish, reptiles, birds, and mammals.

Many seabird colonies have extremely small nest territories. Each territory is just beyond the reach of the bills of the neighbors (figure 17.10). Trespassers are severely punished. Within a gull colony, each nest is in a territory of about 1 square meter. When one gull walks or lands on the

Figure 17.10

Territorial Behavior
Colonial nesting seabirds typically have very small nest territories. Each territory is just out of pecking range of the neighbors.

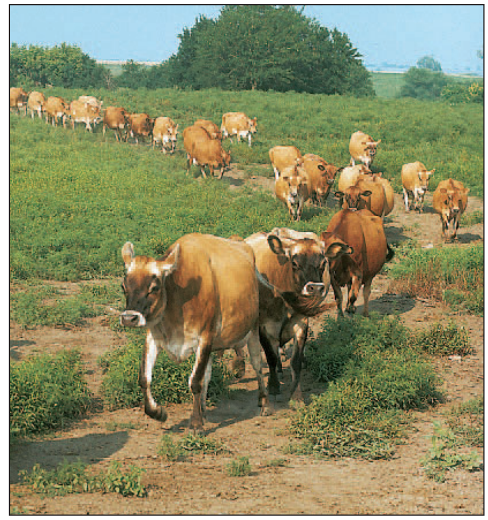

Figure 17.11

A Dominance Hierarchy
Many animals maintain order within their groups by establishing a dominance hierarchy. For example, whenever you see a group of cows or sheep walking in single file, it is likely that the dominant animal is at the head of the line and the lowest-ranking individual is at the end.

territory of another, the defender walks toward the other in the upright threat posture. The head is pointed down with the neck stretched outward and upward. The folded wings are raised slightly as if to be used as clubs. The upright threat posture is one of a number of movements that signal what an animal is likely to do in the near future. The bird is communicating an intention to do something, to fight in this case, but it may not follow through. If the invader shows no sign of retreating, then one or both gulls may start pulling up the grass very vigorously with their beaks. This seems to make no sense. The gulls were ready to fight one moment; the next moment they apparently have forgotten about the conflict and are pulling grass. But the struggle has not been forgotten: pulling grass is an example of redirected aggression. In **redirected aggression,** the animal attacks something other than the natural opponent. If the intruding gull doesn't leave at this point, there will be an actual battle. (A person who pounds the desk during an argument is showing redirected aggression. Look for examples of this behavior in your neighborhood cats and dogs—maybe even in yourself!)

Many carnivorous mammals like foxes, weasels, cougars, coyotes, and wolves use urine or other scents to mark the boundaries of their territories. One of the primary values of the territory for these animals is the food contained within the large space they defend. These territories may include several square kilometers of land. Many other kinds of animals are territorial but use other signaling methods to maintain ownership of their territories. For example, territorial fish use color patterns and threat postures to defend their territories. Crickets use sound and threat postures. Male bullfrogs engage in shoving matches to displace males who invade their small territories along the shoreline.

Dominance Hierarchy

Another way of allocating resources is by the establishment of a **dominance hierarchy,** in which a relatively stable, mutually understood order of priority within the group is maintained. A dominance hierarchy is often established in animals that form social groups. One individual in the group dominates all others. A second-ranking individual dominates all but the highest-ranking individual, and so forth, until the lowest-ranking individual must give way to all others within the group. This kind of behavior is seen in barnyard chickens, where it is known as a *pecking order.* Figure 17.11 shows a dominance hierarchy; the lead animal has the highest ranking and the last animal has the lowest ranking.

A dominance hierarchy allows certain individuals to get preferential treatment when resources are scarce. The dominant individual will have first choice of food, mates, shelter, water, and other resources because of its position. Animals low in the hierarchy may be malnourished or fail to mate in times of scarcity. In many social animals, like wolves, usually only the dominant male and female reproduce. This ensures that the most favorable genes will be passed on to the next generation. Poorly adapted animals with low rank may never reproduce. Once a dominance hierarchy is established, it results in a more stable social unit with little conflict, except perhaps for an occasional altercation that reinforces the knowledge of which position an animal occupies in the hierarchy. Such a hierarchy frequently results in low-ranking individuals emigrating from the area. Such migrating individuals are often subject to heavy predation. Thus the dominance hierarchy serves as a population-control mechanism and a way of allocating resources.

Avoiding Periods of Scarcity

Resource allocation becomes most critical during periods of scarcity. In some areas, the dry part of the year is the most stressful. In temperate areas, winter reduces many sources of food and forces organisms to adjust. Animals have several ways of coping with seasonal stress. Some animals simply avoid the stress. In areas where drought occurs, many animals become inactive until water becomes available. Frogs, toads, and many insects remain inactive (estivate) underground during long periods and emerge to mate when it rains. Hibernation in warm-blooded animals is a response to cold, seasonal temperatures in which the body temperature drops and there is a physiological slowing of all body processes that allows an animal to survive on food it has stored within its body. Hibernation is typical of bats, marmots, and some squirrels. Similarly cold-blooded animals have their activities slowed because a drop in air temperature causes a corresponding drop in body temperature.

Other animals have built-in behavior patterns that cause them to store food during seasons of plenty for periods of scarcity. These behaviors are instinctive and are seen in a variety of animals. Squirrels bury nuts, acorns, and other seeds. (They also plant trees because they never find all the seeds they bury.) Chickadees stash seeds in cracks and crevices when the food is plentiful and spend many hours during the winter exploring similar places for food. Some of the food they find is food they stored. Honeybees store honey, which allows them to live through the winter when nectar is not available. This requires a rather complicated set of behaviors that coordinates the activities of thousands of bees in the hive.

Navigation and Migration

Because animals move from place to place to meet their needs it is useful to be able to return to a nest, water hole, den, or favorite feeding spot. This requires some sort of memory of their surroundings (a mental map) and a way of determining direction. Often it is valuable to have information about distance as well. Direction can be determined by such things as magnetic fields, identifying landmarks, scent trails, or reference to the Sun or stars. If the Sun or stars are used for navigation, some sort of time sense is also needed because these bodies move in the sky.

In honeybees, navigation also involves communication among the various individuals that are foraging for nectar. The bees are able to communicate information about the direction and distance of the nectar source from the hive. If the source of nectar is some distance from the hive, the scout bee performs a "wagging dance" in the hive. The bee walks in a straight line for a short distance, wagging its rear end from side to side. It then circles around back to its starting position and walks the same path as before (figure 17.12). This dance is repeated many times. The direction of the straight-path portion of the dance indicates the direction of the nectar relative to the position of the Sun. For instance, if the bee walks straight upward on a vertical surface in the hive, that tells the other bees to fly directly toward the Sun. If the path is 30 degrees to the right of vertical, the source of the nectar is 30 degrees to the right of the Sun's position.

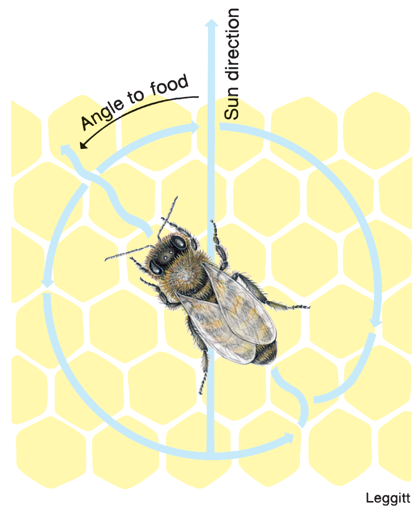

Figure 17.12

Honeybee Communication and Navigation
The direction of the straight, tail-wagging part of the dance of the honeybee indicates the direction to a source of food. The angle that this straight run makes with the vertical is the same angle the bee must fly in relation to the Sun to find the food source. The length of the straight run and the duration of each dance cycle indicate the flying time necessary to reach the food source.

The duration of the entire dance and the number of waggles in the straight-path portion of the dance are positively correlated with the length of time the bee must fly to get to the nectar source. So the dance is able to communicate the duration of flight as well as the direction. Because the recruited bees have picked up the scent of the nectar source from the dancer, they also have information about the kind of flower to visit when they arrive at the correct spot. Because the Sun is not stationary in the sky, the bee must constantly adjust its angle to the Sun. It appears that they do this with some kind of internal clock. Bees that are prevented from going to the source of nectar or from seeing the Sun will still fly in the proper direction sometime later, even though the position of the Sun is different.

The ability to sense changes in time is often used by animals to prepare for seasonal changes. In areas away from the equator, the length of the day changes as the seasons change. The length of the day is called the **photoperiod.** Many birds prepare for migration and have their migration direction determined by the changing photoperiod. For example, in the fall of the year many birds instinctively change their behavior, store up fat, and begin to migrate from northern areas to areas closer to the equator. This seasonal migration allows them to avoid the harsh winter conditions signaled by the shortening of days. The return migration in the spring is triggered by the lengthening photoperiod. This migration certainly requires a lot of energy, but it allows many birds to exploit temporary food resources in the north during the summer months.

Like honeybees, some daytime-migrating birds use the Sun to guide them. We need two instruments to navigate by the Sun—an accurate clock and a sextant for measuring the angle between the Sun and the horizon. Can a bird perform such measurements without instruments when we, with our much bigger brains, need these instruments to help us? It is unquestionably true! For nighttime migration, some birds use the stars to help them find their way. In one interesting experiment, warblers, which migrate at night, were placed in a planetarium. The pattern of stars as they appear at any season could be projected onto a large domed ceiling. During autumn, when these birds would normally migrate southward, the stars of the autumn sky were shown on the ceiling. The birds responded with much fluttering activity at the south side of the cage, as if they were trying to migrate southward. Then the experimenters tried projecting the stars of the spring sky, even though it was autumn. Now the birds tended to try to fly northward, although there was less unity in their efforts to head north; the birds seemed somewhat confused. Nevertheless, the experiment showed that the birds recognized star patterns and were influenced by them.

There is evidence that some birds navigate by compass direction—that is, they fly as if they had a compass in their heads. They seem to be able to sense magnetic north. Their ability to sense magnetic fields was proven at the U.S. Navy's test facility in Wisconsin. The weak magnetism radiated from this test site has changed the flight pattern of migrating birds, but it is yet to be proved that birds use the magnetism of the Earth to guide their migration. Homing pigeons are famous for their ability to find their way home. They make use of a wide variety of clues, but it has been shown that one of the clues they use involves magnetism. Birds with tiny magnets glued to the sides of their heads were very poor navigators; others with nonmagnetic objects attached to the sides of their heads did not lose their ability to navigate.

Biological Clocks

As mentioned earlier, bees, birds, and probably most other animals have internal clocks. In the case of bees, the clock allows them to predict the position of the Sun. In the case of birds and mammals, the changing length of day allows them to time their migration, mating, food-storing behavior, or time for entering hibernation. So some clocks are annual clocks, whereas others are daily clocks. For instance, you have a daily clock. Travelers who fly partway around the world by nonstop jet plane need some time to recover from "jet lag." Their digestion, sleep, or both, may be upset. Their discomfort is not caused by altitude, water, or food, but by having rapidly crossed several time zones. There is a great difference in the time as measured by the Sun or local clocks and that measured by the body; the body's clock adjusts more slowly.

There are many examples of animal behaviors that are timed, some of which show a great deal of precision. In the animal world, mating is the most obviously timed event. In the Pacific Ocean, off some of the tropical islands, lives a marine worm known as the *palolo worm.* Its habit of making a well-timed brief appearance in enormous swarms is a striking example of a biological clock phenomenon. At mating time, these worms swarm into the shallows of the islands and discharge sperm and eggs. There are so many worms that the sea looks like noodle soup. The people of the islands find this an excellent time to change their diets. They dip up the worms much as North Americans dip up smelt or other small fish that are making a spawning run. The worms appear around the third quarter of the Moon in October or November, the time varying somewhat according to local environmental conditions. It appears that they have an annual cycle for mating but that a monthly, or lunar, cycle is superimposed on the annual cycle. Because these animals are marine worms it is unclear whether they are responding to the Moon or the tidal effects of the Moon or something else entirely.

Social Behavior

Many species of animals are characterized by interacting groups called **societies,** in which there is division of labor. Societies differ from simple collections of organisms by the greater specialization and division of labor in the roles displayed by the individuals in the group. The individuals performing one function cooperate with others having different special abilities. As a result of specialization and cooperation, the society has characteristics not found in any one member of the group: the whole is more than the sum of its parts. But if cooperation and division of labor are to occur, there must be communication among individuals and coordination of effort.

Honeybees, for example, have an elaborate communication system and are specialized for specific functions. A few individuals known as *queens* and *drones* specialize in reproduction, whereas large numbers of *worker* honeybees are involved in collecting food, defending the hive, and caring for the larvae. These roles are rigidly determined by inherited behavior patterns. Each worker honeybee has a specific task, and all tasks must be fulfilled for the group to survive and prosper. As they age, the worker honeybees move through a series of tasks over a period of weeks. When they first emerge from their wax cells, they clean the cells.

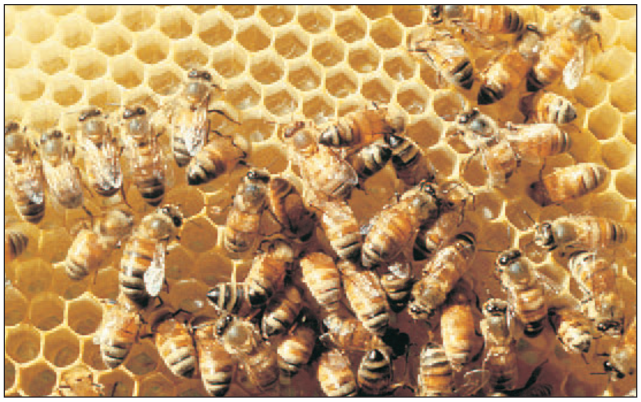

Figure 17.13

Honeybee Society
Within the hive the queen lays eggs that the sterile workers care for. The workers also clean and repair the hive and forage for food.

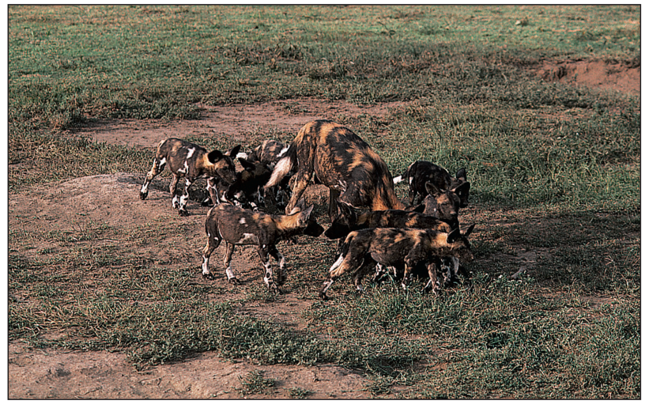

Figure 17.14

African Wild Dog Society
African wild dogs hunt in groups and share food that they bring back to the den. Only the dominant male and female mate and raise offspring.

Several days later, their job is to feed the larvae. Next they build cells. Later they become guards that challenge all insects that land near the entrance to the hive. Finally they become foragers who find and bring back nectar and pollen to feed the other bees in the hive. Foraging is usually the last job before the worker honeybee dies. Although this progression of tasks is the usual order, workers can shift from their main task to others if there is a need. Both the tasks performed and the progression of tasks are instinctively (genetically) determined (figure 17.13).

A hive of bees may contain thousands of individuals, but under normal conditions only the queen bee and the male drones are capable of reproduction. None of the thousands of workers who are also females will reproduce. This does not seem to make sense because they appear to be giving up their chance to reproduce and pass their genes on to the next generation. Is this some kind of self-sacrifice (altruistic behavior) on the part of the workers, or is there another explanation? In general, the workers in the hive are the daughters or sisters of the queen and therefore share a large number of her genes. This means that they are really helping a portion of their genes get to the next generation by assisting in the raising of their own sisters, some of whom will become new queens. This argument has been used to partially explain behaviors in societies that might be bad for the individual but advantageous for the society as a whole.

Animal societies exhibit many levels of complexity and types of social organization differ from species to species. Some societies show little specialization of individuals other than that determined by sexual differences or differences in physical size and endurance. The African wild dog illustrates such a flexible social organization. These animals are nomadic and hunt in packs. Although an individual wild dog can kill prey about its own size, groups are able to kill fairly large animals if they cooperate in the chase and the kill, which often involves a chase of several kilometers. When the dogs are young, they do not follow the pack. When adults return from a successful hunt, they regurgitate food if the proper begging signal is presented to them (figure 17.14). Therefore, the young and the adults that remained behind to guard the young are fed by the hunters. The young are the responsibility of the entire pack, which cooperates in their feeding and protection. During the time that the young are at the den site, the pack must give up its nomadic way of life. Therefore, the young are born during the time of year when prey are most abundant. Only one or two of the females in the pack have young each year. If every female had young, the pack couldn't feed them all. At about two months of age, the young begin to travel with the pack, and the pack can return to its nomadic way of life.

In many ways honeybee and African wild dog societies are similar. Not all females reproduce, the raising of young is a shared responsibility, and there is some specialization of roles. The analysis and comparison of animal societies has led to the thought that there may be fundamental processes that shape all societies. The systematic study of all forms of social behavior, both human and nonhuman, is called **sociobiology.**

How did various types of societies develop? What selective advantage does a member of a social group have? In what ways are social groups better adapted to their environment than nonsocial organisms? How does social organization affect the way populations grow and change? These are difficult questions because, although evolution occurs at the population level, it is individual organisms that are selected. Thus we need new ways of looking at evolutionary processes when describing the evolution of social structures.

The ultimate step is to analyze human societies according to sociobiological principles. Such an analysis is difficult and controversial, however, because humans have a much greater ability to modify behavior than do other animals. However, when we look at human social behavior we see some clear parallels between human and nonhuman behaviors. This implies that there are certain fundamental similarities among social organisms regardless of their species. Do we see territorial behavior in humans? "No trespassing" signs and fences between neighboring houses seem to be clear indications of territorial behavior in our social species. Do groups of humans have dominance hierarchies? Most business, government, and social organizations have a clear dominance hierarchy in which those at the top get more resources (money, prestige) than those lower in the organization. Do human societies show division of labor? Our societies clearly benefit from the specialized skills of certain individuals. Do humans treat their own children differently from other children? Studies of child abuse indicate that abuse is more common between stepparents and their nongenetic stepchildren than between parents and their biological children. Although these few examples do not prove that human societies follow certain rules typical of other animal societies, it bears further investigation. Sociobiology will continue to explore the basis of social organization and behavior and will continue to be an interesting and controversial area of study.

SUMMARY

Behavior is how an organism acts, what it does, and how it does it. The kinds of responses that organisms make to environmental changes (stimuli) may be simple reflexes, very complex instinctive behavior patterns, or learned responses.

From an evolutionary viewpoint, behaviors represent adaptations to the environment. They increase in complexity and variety the more highly specialized and developed the organism is. All organisms have inborn or instinctive behavior, but higher animals also have one or more ways of learning. These include habituation, association, exploration, imprinting, and insight. Communication for purposes of courtship and mating is accomplished by sounds, visual displays, touch, and chemicals like pheromones. Many animals have special behavior patterns that are useful in the care and raising of the young.

Territorial behavior is used to obtain exclusive use of an area and its resources. Both dominance hierarchies and territorial behavior are involved in the allocation of scarce resources. To escape from seasonal stress, some animals estivate or hibernate, others store food, and others migrate. Migration to avoid seasonal extremes involves a timing sense and some way of determining direction. Animals navigate by means of sound, celestial light cues, and magnetic fields.

Societies consist of groups of animals in which individuals specialize and cooperate. Sociobiology attempts to analyze all social behavior in terms of evolutionary principles, ecological principles, and population dynamics.

THINKING CRITICALLY

If you were going to teach an animal to communicate a message new to that animal, what message would you select? How would you teach the animal to communicate the message at the appropriate time?

CONCEPT MAP TERMINOLOGY

Construct a concept map to show relationships among the following concepts.

association
imprinting
insight
instinctive behavior
learning
response
stimulus
territorial behavior
thinking

KEY TERMS

anthropomorphism
association
behavior
classical conditioning
conditioned response
critical period
dominance hierarchy
ethology
habituation
imprinting
insight
instinctive behavior
learned behavior
learning
observational learning (imitation)
operant (instrumental) conditioning
pheromone
photoperiod
redirected aggression
response
society
sociobiology
stimulus
territorial behavior
territory
thinking

e—LEARNING CONNECTIONS *www.mhhe.com/enger10*

Topics	Questions	Media Resources
17.1 The Adaptive Nature of Behavior	1. Why do students of animal behavior reject the idea that a singing bird is happy?	**Quick Overview** • Behaviors **Key Points** • The adaptive nature of behavior **Experience This!** • Observing types of behavior
17.2 Interpreting Behavior	2. Briefly describe an example of unlearned behavior in an animal. Explain why you know it is unlearned. Name the animal.	**Quick Overview** • Usefulness of behaviors **Key Points** • Interpreting behavior
17.3 The Problem of Anthropomorphism		**Quick Overview** • That looks how I feel **Key Points** • The problem of anthropomorphism
17.4 Instinct and Learning	3. Briefly describe an example of learned behavior in an animal. Explain why you know it is learned. Name the animal.	**Quick Overview** • How are they different? the same? **Key Points** • Instinct and learning
17.5 Kinds of Learning	4. Give an example of a conditioned response. Can you describe one that is not mentioned in this chapter? 5. What is imprinting, and what value does it have to the organism? 6. How are classical conditioning and operant conditioning different?	**Quick Overview** • Kinds of learning **Key Points** • Kinds of learning
17.6 Instinct and Learning in the Same Animal		**Quick Overview** • Similarities **Key Points** • Instinct and learning in the same animal
17.7 What About Human Behavior?		**Quick Overview** • Our behavior in a different light **Key Points** • What about human behavior?
17.8 Selected Topics in Behavioral Ecology	7. Name three behaviors typically associated with reproduction. 8. How do territorial behavior and dominance hierarchies help allocate scarce resources? 9. How do animals use chemicals, light, and sound to communicate? 10. What is sociobiology? Ethology? Anthropomorphism? 11. Describe how honeybees communicate the location of a nectar source.	**Quick Overview** • Selected topics in behavioral ecology **Key Points** • Selected topics in behavioral ecology **Animations and Review** • Navigation • Communication • Aggression • Altruism and sociality