

26

Animal Behavior

Concept Outline

26.1 Ethology focuses on the natural history of behavior.

Approaches to the Study of Behavior. Field biologists focus on evolutionary aspects of behavior.

Behavioral Genetics. At least some behaviors are genetically determined.

26.2 Comparative psychology focuses on how learning influences behavior.

Learning. Association plays a major role in learning.

The Development of Behavior. Parent-offspring interactions play a key role in the development of behavior.

The Physiology of Behavior. Hormones influence many behaviors, particularly reproductive ones.

Behavioral Rhythms. Many behaviors are governed by innate biological clocks.

26.3 Communication is a key element of many animal behaviors.

Courtship. Animals use many kinds of signals to court one another.

Communication in Social Groups. Bees and other social animals communicate in complex ways.

26.4 Migratory behavior presents many puzzles.

Orientation and Migration. Animals use many cues from the environment to navigate during migrations.

26.5 To what degree animals “think” is a subject of lively dispute.

Animal Cognition. It is not clear to what degree animals “think.”



FIGURE 26.1

Rearing offspring involves complex behaviors. Living in groups called prides makes lions better mothers. Females share the responsibilities of nursing and protecting the pride's young, increasing the probability that the youngsters will survive into adulthood.

Organisms interact with their environment in many ways. To understand these interactions, we need to appreciate both the internal factors that shape the way an animal behaves, as well as aspects of the external environment that affect individuals and organisms. In this chapter, we explore the mechanisms that determine an animal's behavior (figure 26.1), as well as the ways in which behavior develops in an individual. In the next chapter, we will consider the field of behavioral ecology, which investigates how natural selection has molded behavior through evolutionary time.

26.1 Ethology focuses on the natural history of behavior.

Approaches to the Study of Behavior

During the past two decades, the study of animal behavior has emerged as an important and diverse science that bridges several disciplines within biology. Evolution, ecology, physiology, genetics, and psychology all have natural and logical linkages with the study of behavior, each discipline adding a different perspective and addressing different questions.

Research in animal behavior has made major contributions to our understanding of nervous system organization, child development, and human communication, as well as the process of speciation, community organization, and the mechanism of natural selection itself. The study of the behavior of nonhuman animals has led to the identification of general principles of behavior, which have been applied, often controversially, to humans. This has changed the way we think about the origins of human behavior and the way we perceive ourselves.

Behavior can be defined as the way an organism responds to stimuli in its environment. These stimuli might be as simple as the odor of food. In this sense, a bacterial cell “behaves” by moving toward higher concentrations of sugar. This behavior is very simple and well-suited to the life of bacteria, allowing these organisms to live and reproduce. As animals evolved, they occupied different environments and faced diverse problems that affected their survival and reproduction. Their nervous systems and behavior concomitantly became more complex. Nervous systems perceive and process information concerning environmental stimuli and trigger adaptive motor responses, which we see as patterns of behavior.

When we observe animal behavior, we can explain it in two different ways. First, we might ask *how* it all works, that is, how the animal’s senses, nerve networks, or internal state provide a physiological basis for the behavior. In this way, we would be asking a question of **proximate causation**. To analyze the proximate cause of behavior, we might measure hormone levels or record the impulse activity of neurons in the animal. We could also ask *why* the behavior evolved, that is, what is its adaptive value? This is a question concerning **ultimate causation**. To study the ultimate cause of a behavior, we would attempt to determine how it influenced the animal’s survival or reproductive success. Thus, a male songbird may sing during the breeding season because it has a level of the steroid sex hormone, testosterone, which binds to hormone receptors in the brain and triggers the production of song; this would be the proximate cause of the male bird’s song. But the male sings to defend a territory from

other males and to attract a female to reproduce; this is the ultimate, or evolutionary, explanation for the male’s vocalization.

The study of behavior has had a long history of controversy. One source of controversy has been the question of whether behavior is determined more by an individual’s genes or its learning and experience. In other words, is behavior the result of nature (instinct) or nurture (experience)? In the past, this question has been considered an “either/or” proposition, but we now know that instinct and experience both play significant roles, often interacting in complex ways to produce the final behavior. The scientific study of instinct and learning, as well as their interrelationship, has led to the growth of several scientific disciplines, including ethology, behavioral genetics, behavioral neuroscience, and comparative psychology.

Ethology

Ethology is the study of the natural history of behavior. Early ethologists (figure 26.2) were trained in zoology and evolutionary biology, fields that emphasize the study of animal behavior under natural conditions. As a result of this training, they believed that behavior is largely instinctive, or innate—the product of natural selection. Because behavior is often **stereotyped** (appearing in the same way in different individuals of a species), they argued that it must be based on preset paths in the nervous system. In their view, these paths are structured from genetic blueprints and cause animals to show a relatively complete behavior the first time it is produced.

The early ethologists based their opinions on behaviors such as egg retrieval by geese. Geese incubate their eggs in a nest. If a goose notices that an egg has been knocked out of the nest, it will extend its neck toward the egg, get up, and roll the egg back into the nest with a side-to-side motion of its neck while the egg is tucked beneath its bill. Even if the egg is removed during retrieval, the goose completes the behavior, as if driven by a program released by the initial sight of the egg outside the nest. According to ethologists, egg retrieval behavior is triggered by a **sign stimulus** (also called a **key stimulus**), the appearance of an egg out of the nest; a component of the goose’s nervous system, the **innate releasing mechanism**, provides the neural instructions for the motor program, or **fixed action pattern** (figure 26.3). More generally, the sign stimulus is a “signal” in the environment that triggers a behavior. The innate releasing mechanism is the sensory mechanism that detects the signal, and the fixed action pattern is the stereotyped act.



FIGURE 26.2

The founding fathers of ethology: Karl von Frisch, Konrad Lorenz, and Niko Tinbergen pioneered the study of behavioral science. In 1973, they received the Nobel Prize in Physiology or Medicine for their path-making contributions. Von Frisch led the study of honeybee communication and sensory biology. Lorenz focused on social development (imprinting) and the natural history of aggression. Tinbergen examined the functional significance of behavior and was the first behavioral ecologist.

Similarly, a frog unfolds its long, sticky tongue at the sight of a moving insect, and a male stickleback fish will attack another male showing a bright red underside. Such responses certainly appear to be programmed and instinctive, but what evidence supports the ethological view that behavior has an underlying neural basis?

Behavior as a Response to Stimuli in the Environment

In the example of egg retrieval behavior in geese, a goose must first perceive that an egg is outside of the nest. To respond to this stimulus, it must convert one form of energy which is an input to its visual system—the energy of photons of light—into a form of energy its nervous system can understand and use to respond—the electrical energy of a nerve impulse. Animals need to respond to other stimuli in the environment as well. For an animal to orient from a food source back to its nest, it might rely on the position of the sun. To find a mate, an animal might use a particular chemical scent. The electromagnetic energy of light and the chemical energy of an odor must be converted to the electrical energy of a nerve impulse. This is done through **transduction**, the conversion of energy in the environment to an action potential, and the first step in the processing of stimuli perceived by the senses. For example, rhodopsin is responsible for the transduction of visual stimuli. Rhodopsin is made of *cis*-retinal and the protein opsin. Light is absorbed by the visual pigment *cis*-retinal causing it



FIGURE 26.3

Lizard prey capture. The complex series of movements of the tongue this chameleon uses to capture an insect represents a fixed action pattern.

to change its shape to *trans*-retinal (see chapter 55). This in turn changes the shape of the companion protein opsin, and induces the first step in a cascade of molecular events that finally triggers a nerve impulse. Sound, odor, and tastes are transduced to nerve impulses by similar processes.

Ethologists study behavior from an evolutionary perspective, focusing on the neural basis of behaviors.

Behavioral Genetics

In a famous experiment carried out in the 1940s, Robert Tryon studied the ability of rats to find their way through a maze with many blind alleys and only one exit, where a reward of food awaited. Some rats quickly learned to zip right through the maze to the food, making few incorrect turns, while other rats took much longer to learn the correct path (figure 26.4). Tryon bred the fast learners with one another to establish a “maze-bright” colony, and he similarly bred the slow learners with one another to establish a “maze-dull” colony. He then tested the offspring in each colony to see how quickly they learned the maze. The offspring of maze-bright rats learned even more quickly than their parents had, while the offspring of maze-dull parents were even poorer at maze learning. After repeating this procedure over several generations, Tryon was able to produce two behaviorally distinct types of rat with very different maze-learning abilities. Clearly the ability to learn the maze was to some degree hereditary, governed by genes passed from parent to offspring. Furthermore, those genes were specific to this behavior, as the two groups of rats did not differ in their ability to perform other behavioral tasks, such as running a completely different kind of maze. Tryon’s research demonstrates how a study can reveal that behavior has a heritable component.

Further support for the genetic basis of behavior has come from studies of hybrids. William Dilger of Cornell University has examined two species of lovebird (genus *Agapornis*), which differ in the way they carry twigs, paper, and other materials used to build a nest. *A. personata* holds nest material in its beak, while *A. roseicollis* carries material tucked under its flank feathers (figure 26.5). When Dilger crossed the two species to produce hybrids, he found that the hybrids carry nest material in a way that seems intermediate between that of the parents: they repeatedly shift material between the bill and the flank feathers. Other studies conducted on courtship songs in crickets and tree frogs also demonstrate the intermediate nature of hybrid behavior.

The role of genetics can also be seen in humans by comparing the behavior of identical twins. Identical twins are, as their name implies, genetically identical. However, most sets of identical twins are raised in the same environment, so it is not possible to determine whether similarities in behavior result from their genetic similarity or from experiences shared as they grew up (the classic nature versus nurture debate). However, in some cases, twins have been separated at birth. A recent study of 50 such sets of twins revealed many similarities in personality, temperament, and even leisure-time activities, even though the twins were often raised in very different environments. These similarities indicate that genetics plays a role in determining behavior even in humans, although the relative importance of genetics versus environment is still hotly debated.

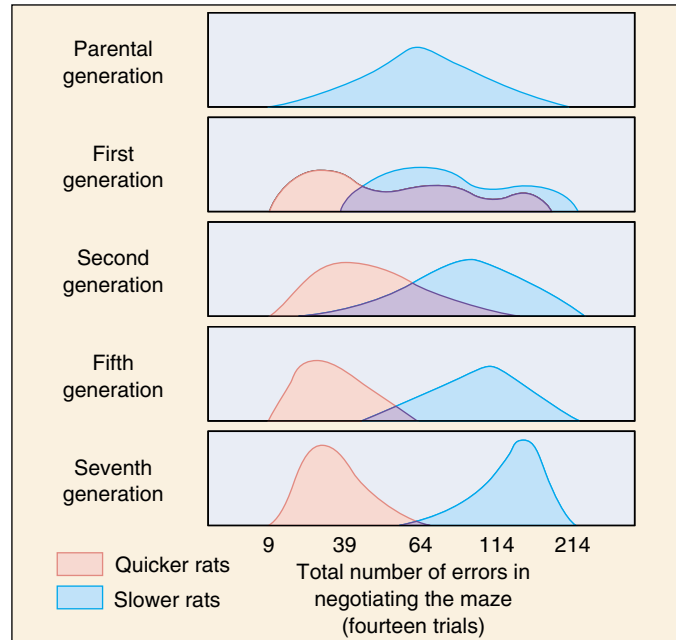


FIGURE 26.4

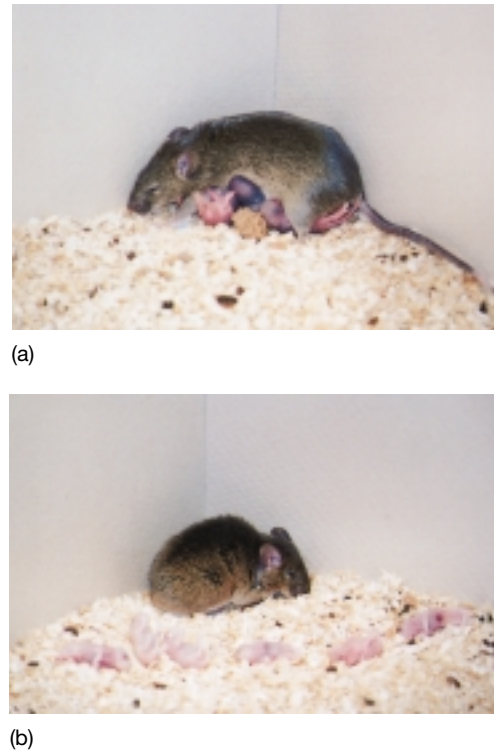
The genetics of learning. Tryon selected rats for their ability to learn to run a maze and demonstrated that this ability is influenced by genes. He tested a large group of rats, selected those that ran the maze in the shortest time, and let them breed with one another. He then tested their progeny and again selected those with the quickest maze-running times for breeding. After seven generations, he had succeeded in halving the average time an inexperienced rat required to negotiate the maze. Parallel “artificial selection” for slow running time more than doubled the average running time.



FIGURE 26.5

Genetics of lovebird behavior. Lovebirds inherit the tendency to carry nest material, such as these paper strips, under their flank feathers.

FIGURE 26.6
Genetically caused defect in maternal care. (a) In mice, normal mothers take very good care of their offspring, retrieving them if they move away and crouching over them. (b) Mothers with the mutant *fosB* allele perform neither of these behaviors, leaving their pups exposed. (c) Amount of time female mice were observed crouching in a nursing posture over offspring. (d) Proportion of pups retrieved when they were experimentally moved.



Single Gene Effects on Behavior

The maze-learning, hybrid, and identical twins studies just described suggest genes play a role in behavior, but recent research has provided much greater detail on the genetic basis of behavior. In the fruit fly *Drosophila*, and in mice, many mutations have been associated with particular behavioral abnormalities.

In fruit flies, for example, individuals that possess alternative alleles for a single gene differ greatly in their feeding behavior as larvae; larvae with one allele move around a great deal as they eat, whereas individuals with the alternative allele move hardly at all. A wide variety of mutations at other genes are now known in *Drosophila* which affect almost every aspect of courtship behavior.

The ways in which genetic differences affect behavior have been worked out for several mouse genes. For example, some mice with one mutation have trouble remembering information that they learned two days earlier about where objects are located. This difference appears to result because the mutant mice do not produce the enzyme α -calcium-calmodulin-dependent kinase II, which plays an important role in the functioning of a part of the brain, the hippocampus, that is important for spatial learning.

Modern molecular biology techniques allow the role of genetics in behavior to be investigated with ever greater precision. For example, male mice genetically engineered (as “knock-outs”) to lack the ability to synthesize nitric oxide, a brain neurotransmitter, show increased aggressive behavior.

A particularly fascinating breakthrough occurred in 1996, when scientists using the knock-out technique discovered a new gene, *fosB*, that seems to determine whether or not female mice will nurture their young. Females with both *fosB* alleles knocked out will initially investigate their newborn babies, but then ignore them, in stark contrast to the caring and protective maternal behavior provided by normal females (figure 26.6).

The cause of this inattentiveness appears to result from a chain reaction. When mothers of new babies initially inspect them, information from their auditory, olfactory, and tactile senses are transmitted to the hypothalamus, where *fosB* alleles are activated, producing a particular protein, which in turn activates other enzymes and genes that affect the neural circuitry within the hypothalamus. These modifications within the brain cause the female to react maternally toward her offspring. In contrast, in mothers lacking the *fosB* alleles, this reaction is stopped midway. No protein is activated, the brain’s neural circuitry is not rewired, and maternal behavior does not result.

As these genetic techniques are becoming used more widely, the next few years should see similar dramatic advances in our knowledge of how genes affect behavior in many varieties of humans.

The genetic basis of behavior is supported by artificial selection experiments, hybridization studies, and studies on the behavior of mutants. Research has also identified specific genes that control behavior.

26.2 Comparative psychology focuses on how learning influences behavior.

Learning

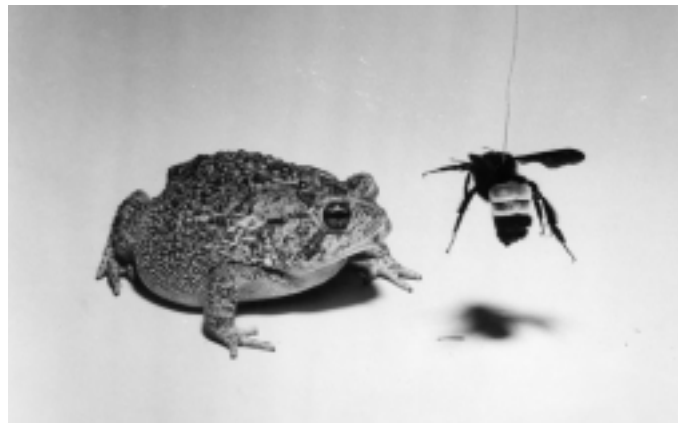
While ethologists were attempting to explain behavior as an instinctive process, **comparative psychologists** focused heavily on learning as the major element that shapes behavior. These behavioral scientists, working primarily on rats in laboratory settings, identified the ways in which animals learn. Learning is any modification of behavior that results from experience rather than maturation.

The simplest type of learning, **nonassociative learning**, does not require an animal to form an association between two stimuli or between a stimulus and a response. One form of nonassociative learning is **habituation**, which can be defined as a decrease in response to a repeated stimulus that has no positive or negative consequences (that is, no *reinforcement*). In many cases, the stimulus evokes a strong response when it is first encountered, but the magnitude of the response gradually declines with repeated exposure. For example, young birds see many types of objects moving overhead. At first, they may respond by crouching down and remaining still. Some of the objects, like falling leaves or members of their own species flying by, are seen very frequently and have no positive or negative consequence to the nestlings. Over time, the young birds may habituate to such stimuli and stop responding. Thus, habituation can be thought of as learning *not* to respond to a stimulus. Being able to ignore unimportant stimuli is critical to an animal confronting a barrage of stimuli in a complex environment. Another form of nonassociative learning is **sensitization**, characterized by an increased responsiveness to a stimulus. Sensitization is essentially the opposite of habituation.

A change in behavior that involves an association between two stimuli or between a stimulus and a response is termed **associative learning** (figure 26.7). The behavior is modified, or **conditioned**, through the association. This form of learning is more complex than habituation or sensitization. The two major types of associative learning are called **classical conditioning** and **operant conditioning**; they differ in the way the associations are established.

Classical Conditioning

In classical conditioning, the paired presentation of two different kinds of stimuli causes the animal to form an association between the stimuli. Classical conditioning is also called **Pavlovian conditioning**, after Russian psychologist Ivan Pavlov, who first described it. Pavlov presented meat powder, an *unconditioned stimulus*, to a dog and noted that the dog responded by salivating, an *unconditioned response*. If an unrelated stimulus, such as the ringing of a bell, was



(a)



(b)



(c)

FIGURE 26.7

Learning what is edible. Associative learning is involved in predator-prey interactions. (a) A naive toad is offered a bumblebee as food. (b) The toad is stung, and (c) subsequently avoids feeding on bumblebees or any other insects having their black-and-yellow coloration. The toad has associated the appearance of the insect with pain, and modifies its behavior.

presented at the same time as the meat powder, over repeated trials the dog would salivate in response to the sound of the bell *alone*. The dog had learned to associate the unrelated sound stimulus with the meat powder stimulus. Its response to the sound stimulus was, therefore, conditioned, and the sound of the bell is referred to as a *conditioned stimulus*.

Operant Conditioning

In operant conditioning, an animal learns to associate its behavioral response with a reward or punishment. American psychologist B. F. Skinner studied operant conditioning in rats by placing them in an apparatus that came to be called a “Skinner box.” As the rat explored the box, it would occasionally press a lever by accident, causing a pellet of food to appear. At first, the rat would ignore the lever, eat the food pellet, and continue to move about. Soon, however, it learned to associate pressing the lever (the behavioral response) with obtaining food (the reward). When it was hungry, it would spend all its time pressing the lever. This sort of trial-and-error learning is of major importance to most vertebrates.

Comparative psychologists used to believe that any two stimuli could be linked in classical conditioning and that animals could be conditioned to perform any learnable behavior in response to any stimulus by operant conditioning. As you will see below, this view has changed. Today, it is thought that instinct guides learning by determining what type of information can be learned through conditioning.

Instinct

It is now clear that some animals have innate predispositions toward forming certain associations. For example, if a rat is offered a food pellet at the same time it is exposed to X rays (which *later* produces nausea), the rat will remember the taste of the food pellet but not its size. Conversely, if a rat is given a food pellet at the same time an electric shock is delivered (which *immediately* causes pain), the rat will remember the size of the pellet but not its taste. Similarly, pigeons can learn to associate *food* with colors but not with sounds; on the other hand, they can associate *danger* with sounds but not with colors.

These examples of **learning preparedness** demonstrate that what an animal can learn is biologically influenced—that is, learning is possible only within the boundaries set by instinct. Innate programs have evolved because they underscore adaptive responses. Rats, which forage at night and have a highly developed sense of smell, are better able to identify dangerous food by its odor than by its size or color. The seed a pigeon eats may have a distinctive color that the pigeon can see, but it makes no sound the pigeon can hear. The study of learn-



FIGURE 26.8

The Clark's nutcracker has an extraordinary memory. A Clark's nutcracker can remember the locations of up to 2000 seed caches months after hiding them. After conducting experiments, scientists have concluded that the birds use features of the landscape and other surrounding objects as spatial references to memorize the locations of the caches.

ing has expanded to include its ecological significance, so that we are now able to consider the “evolution of learning.” An animal's ecology, of course, is key to understanding what an animal is capable of learning. Some species of birds, like Clark's nutcracker, feed on seeds. Birds store seeds in caches they bury when seeds are abundant so they will have food during the winter. Thousands of seed caches may be buried and then later recovered. One would expect the birds to have an extraordinary spatial memory, and this is indeed what has been found (figure 26.8). Clark's nutcracker, and other seed-hoarding birds, have an unusually large hippocampus, the center for memory storage in the brain (see chapter 54).

Habituation and sensitization are simple forms of learning in which there is no association between stimuli and responses. In contrast, associative learning (classical and operant conditioning) involves the formation of an association between two stimuli or between a stimulus and a response.

The Development of Behavior

Behavioral biologists now recognize that behavior has both genetic and learned components, and the schools of ethology and psychology are less polarized than they once were. Thus far in this chapter we have discussed the influence of genes and learning separately. As we will see, these factors interact during development to shape behavior.

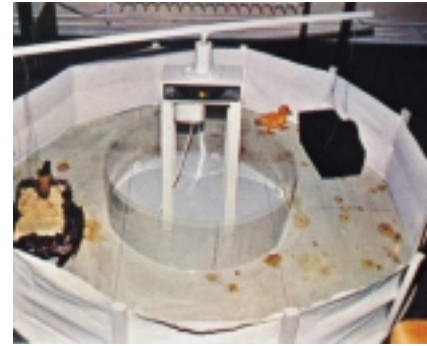
Parent-Offspring Interactions

As an animal matures, it may form social attachments to other individuals or form preferences that will influence behavior later in life. This process, called **imprinting**, is sometimes considered a type of learning. In **filial imprinting**, social attachments form between parents and offspring. For example, young birds of some species begin to follow their mother within a few hours after hatching, and their following response results in a bond between mother and young. However, the young birds' initial experience determines how this imprint is established. The German ethologist Konrad Lorenz showed that birds will follow the first object they see after hatching and direct their social behavior toward that object. Lorenz raised geese from eggs, and when he offered himself as a model for imprinting, the goslings treated him as if he were their parent, following him dutifully (figure 26.9). Black boxes, flashing lights, and watering cans can also be effective imprinting objects (figure 26.10). Imprinting occurs during a **sensitive phase**, or a **critical period** (roughly 13 to 16 hours after hatching in geese), when the success of imprinting is highest.

Several studies demonstrate that the social interactions that occur between parents and offspring during the critical period are key to the normal development of behavior. The psychologist Harry Harlow gave orphaned rhesus monkey infants the opportunity to form social attachments with two surrogate “mothers,” one made of soft cloth covering a wire frame and the other made only of wire. The infants chose to spend time with the cloth mother, even if only the wire mother provided food, indicating that texture and tactile contact, rather than providing food, may be among the key qualities in a mother that promote infant social attachment. If infants are deprived of normal social contact, their development is abnormal. Greater degrees of deprivation lead to greater abnormalities in social behavior during



FIGURE 26.9
An unlikely parent. The eager goslings following Konrad Lorenz think he is their mother. He is the first object they saw when they hatched, and they have used him as a model for imprinting.



(a)



(b)

FIGURE 26.10
How imprinting is studied. Ducklings will imprint on the first object they see, even (a) a black box or (b) a white sphere.

childhood and adulthood. Studies on orphaned human infants suggest that a constant “mother figure” is required for normal growth and psychological development.

Recent research has revealed a biological need for the stimulation that occurs during parent-offspring interactions early in life. Female rats lick their pups after birth, and this stimulation inhibits the release of an endorphin (see chapter 56) that can block normal growth. Pups that receive normal tactile stimulation also have more brain receptors for glucocorticoid hormones, longer-lived brain neurons, and a greater tolerance for stress. Premature human infants who are massaged gain weight rapidly. These studies indicate that the need for normal social interaction is based in the brain and that touch and other aspects of contact between parents and offspring are important for physical as well as behavioral development.

Sexual imprinting is a process in which an individual learns to direct its sexual behavior at members of its own species. **Cross-fostering** studies, in which individuals of one species are raised by parents of another species, reveal that this form of imprinting also occurs early in life. In most species of birds, these studies have shown that the fostered bird will attempt to mate with members of its foster species when it is sexually mature.

Interaction between Instinct and Learning

The work of Peter Marler and his colleagues on the acquisition of courtship song by white-crowned sparrows provides an excellent example of the interaction between instinct and learning in the development of behavior. Courtship songs are sung by mature males and are species-specific. By rearing male birds in soundproof incubators provided with speakers and microphones, Marler could control what a bird heard as it matured and record the song it produced as an adult. He found that white-crowned sparrows that heard no song at all during development, or that heard only the song of a different species, the song sparrow, sang a poorly developed song as adults (figure 26.11). But birds that heard the song of their own species, or that heard the songs of *both* the white-crowned sparrow and the song sparrow, sang a fully developed, white-crowned sparrow song as adults. These results suggest that these birds have a **genetic template**, or instinctive program, that guides them to learn the appropriate song. During a critical period in development, the template will accept the correct song as a model. Thus, song acquisition depends on learning, but only the song of the correct species can be learned. The genetic template for learning is *selective*. However, learning plays a prominent role as well. If a young white-crowned sparrow is surgically deafened *after* it hears its species' song during the critical period, it will also sing a poorly developed song as an adult. Therefore, the bird must “practice” listening to himself sing, matching what he hears to the model his template has accepted.

Although this explanation of song development stood unchallenged for many years, recent research has shown that white-crowned sparrow males *can* learn another species' song under certain conditions. If a live male strawberry finch is placed in a cage next to a young male sparrow, the young sparrow will learn to sing the strawberry finch's song! This finding indicates that social stimuli may be more effective than a tape-recorded song in overriding the innate program that guides song development. Furthermore, the males of some bird species have no opportunity to hear the song of their own species. In such cases, it appears that the males instinctively “know” their own species' song. For example, cuckoos are brood parasites; females lay their eggs in the nest of another species of bird, and the young that hatch are reared by the foster parents (figure 26.12). When the cuckoos become adults, they sing the song of their own species rather than that of their foster parents. Because male brood parasites would most likely hear the song of their host species during development, it is adaptive for them to ignore such “incorrect” stimuli. They hear no adult males of their own species singing, so no correct song models are available. In these species, natural selection has programmed the male with a genetically guided song.

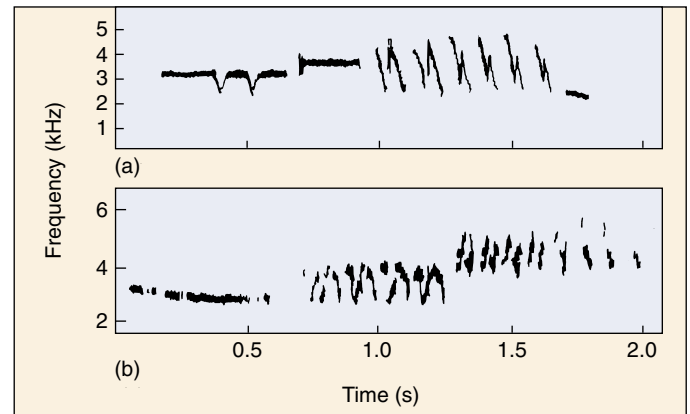


FIGURE 26.11

Song development in birds. (a) The sonograms of songs produced by male white-crowned sparrows that had been exposed to their own species' song during development are different from (b) those of male sparrows that heard no song during rearing. This difference indicates that the genetic program itself is insufficient to produce a normal song.



FIGURE 26.12

Brood parasite. Cuckoos lay their eggs in the nests of other species of birds. Because the young cuckoos (large bird to the right) are raised by a different species (like this meadow pipit, smaller bird to the left), they have no opportunity to *learn* the cuckoo song; the cuckoo song they later sing is innate.

Interactions that occur during sensitive phases of imprinting are critical to normal behavioral development. Physical contact plays an important role in the development of psychological well-being and growth.

The Physiology of Behavior

The early ethologists' emphasis on instinct sometimes overlooked the internal factors that control behavior. If asked why a male bird defends a territory and sings only during the breeding season, they would answer that a bird sings when it is in the right *motivational state* or *mood* and has the appropriate *drive*. But what do these phrases mean in terms of physiological control mechanisms?

Part of our understanding of the physiological control of behavior has come from the study of reproductive behavior. Animals show reproductive behaviors such as courtship only during the breeding season. Research on lizards, birds, rats, and other animals has revealed that hormones play an important role in these behaviors. Changes in day length trigger the secretion of gonadotropin-releasing hormone by the hypothalamus, which stimulates the release of the gonadotropins, follicle-stimulating hormone (FSH) and luteinizing hormone, by the anterior pituitary gland. These hormones cause the development of reproductive tissues to ready the animal for breeding. The gonadotropins, in turn, stimulate the secretion of the steroid sex hormones, estrogens and progesterone in females and testosterone in males. The sex hormones act on the brain to trigger behaviors associated with reproduction. For example, birdsong and territorial behavior depend upon the level of testosterone in the male, and the receptivity of females to male courtship depends upon estrogen levels.

Hormones have both organizational and activational effects. In the example of birdsong given above, estrogen in the male causes the development of the song system, which is composed of neural tissue in the forebrain and its connections to the spinal cord and the syrinx (a structure like our larynx that allows the bird to sing). Early in a male's development, the gonads produce estrogen, which stimulates neuron growth in the brain. In the mature male, the testes produce testosterone, which activates song. Thus, the development of the neural systems that are responsible for behavior is first organized, then activated by hormones.

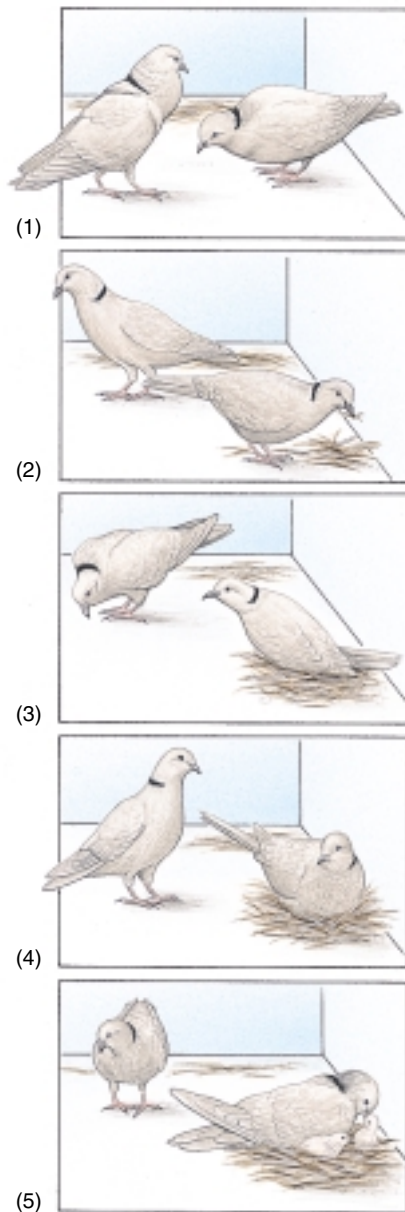


FIGURE 26.13
Hormonal control of reproductive behavior. Reproduction in the ring dove involves a sequence of behaviors regulated by hormones: (1) courtship and copulation; (2) nest building; (3) egg laying; (4) incubation; and (5) feeding crop milk to the young after they hatch.

Research on the physiology of reproductive behavior shows that there are important interactions among hormones, behavior, and stimuli in both the physical and social environments of an individual. Daniel Lehrman's work on reproduction in ring doves provides an excellent example of how these factors interact (figure 26.13). Male courtship behavior is controlled by testosterone and related steroid hormones. The male's behavior causes the release of FSH in the female, and FSH promotes the growth of the ovarian follicles (see chapter 59). The developing follicles release estrogens, which affect other reproductive tissues. Nest construction follows after one or two days. The presence of the nest then triggers the secretion of progesterone in the female, initiating incubation behavior after the egg is laid. Feeding occurs once the eggs hatch, and this behavior is also hormonally controlled.

The research of Lehrman and his colleagues paved the way for many additional investigations in **behavioral endocrinology**, the study of the hormonal regulation of behavior. For example, male *Anolis* lizards begin courtship after a seasonal rise in temperature, and the male's courtship is needed to stimulate the growth of ovarian follicles in the female. These and other studies demonstrate the interactive effects of the physical environment (for example, temperature and day length) and the social environment (such as the presence of a nest and the courtship display of a mate) on the hormonal condition of an animal. Hormones are, therefore, a proximate cause of behavior. To control reproductive behavior, they must be released when the conditions are most favorable for the growth of young. Other behaviors, such as territoriality and dominance behavior, also have hormonal correlates.

Hormones may interact with neurotransmitters to alter behavior. Estrogen affects the neurotransmitter serotonin in female mice, and may be in part responsible for the "mood swings" experienced by some human females during the menstrual cycle.

Hormones have important influences on reproductive and social behavior.

Behavioral Rhythms

Many animals exhibit behaviors that vary at regular intervals of time. Geese migrate south in the fall, birds sing in the early morning, bats fly at night rather than during the day, and most humans sleep at night and are active in the daytime. Some behaviors are timed to occur in concert with lunar or tidal cycles (figure 26.14). Why do regular repeating patterns of behavior occur, and what determines when they occur? The study of questions like these has revealed that rhythmic animal behaviors are based on both **endogenous** (internal) **rhythms** and **exogenous** (external) **timers**.

Most studies of behavioral rhythms have focused on behaviors that appear to be keyed to a daily cycle, such as sleeping. Rhythms with a period of about 24 hours are called **circadian** (“about a day”) **rhythms**. Many of these behaviors have a strong endogenous component, as if they were driven by a **biological clock**. Such behaviors are said to be *free-running*, continuing on a regular cycle even in the absence of any cues from the environment. Almost all fruit fly pupae hatch in the early morning, for example, even if they are kept in total darkness throughout their week-long development. They keep track of time with an internal clock whose pattern is determined by a single gene, called the *per* (for *period*) gene. Different mutations of the *per* gene shorten or lengthen the daily rhythm. The *per* gene produces a protein in a regular 24-hour cycle in the brain, serving as the fly’s pacemaker of activity. The protein probably affects the expression of other genes that ultimately regulate activity. As the *per* protein accumulates, it seems to turn off the gene. In mice, the *clock* gene is responsible for regulating the animal’s daily rhythm.

Most biological clocks do not exactly match the rhythms of the environment. Therefore, the behavioral rhythm of an individual deprived of external cues gradually drifts out of phase with the environment. Exposure to an environmental cue resets the biological clock and keeps the behavior properly synchronized with the environment. Light is the most common cue for resetting circadian rhythms.

The most obvious circadian rhythm in humans is the sleep-activity cycle. In controlled experiments, humans have lived for months in underground apartments, where all light is artificial and there are no external cues whatsoever indicating day length. Left to set their own schedules, most of these people adopt daily activity patterns (one phase of activity plus one phase of sleep) of about 25 hours, although there is considerable variation. Some individuals exhibit 50-hour clocks, active for as long as 36 hours during each period! Under normal circumstances, the day-night cycle resets an individual’s free-running clock every day to a cycle period of 24 hours.

What constitutes an animal’s biological clock? In some insects, the clock is thought to be located in the optic lobes of the brain, and timekeeping appears to be based on hormones. In mammals, including humans, the biological



FIGURE 26.14
Tidal rhythm. Oysters open their shells for feeding when the tide is in and close them when the tide is out.

clock lies in a specific region of the hypothalamus called the **suprachiasmatic nucleus (SCN)**. The SCN is a self-sustaining oscillator, which means it undergoes spontaneous, cyclical changes in activity. This oscillatory activity helps the SCN to act as a pacemaker for circadian rhythms, but in order for the rhythms to be entrained to external light-dark cycles, the SCN must be influenced by light. In fact, there are both direct and indirect neural projections from the retina to the SCN.

The SCN controls circadian rhythms by regulating the secretion of the hormone **melatonin** by the **pineal gland**. During the daytime, the SCN suppresses melatonin secretion. Consequently, more melatonin is secreted over a 24-hour period during short days than during long days. Variations in melatonin secretion thus serve as an indicator of seasonal changes in day length, and these variations participate in timing the seasonal reproductive behavior of many mammals. Disturbances in melatonin secretion may be partially responsible for the “jet-lag” people experience when air travel suddenly throws their internal clocks out of register with the day-night cycle.

Many important behavioral rhythms have cycle periods longer than 24 hours. For example, **circannual behaviors** such as breeding, hibernation, and migration occur on a yearly cycle. These behaviors seem to be largely timed by hormonal and other physiological changes keyed to exogenous factors such as day length. The degree to which endogenous biological clocks underlie circannual rhythms is not known, as it is very difficult to perform constant-environment experiments of several years’ duration. The mechanism of the biological clock remains one of the most tantalizing puzzles in biology today.

Endogenous circadian rhythms have free-running cycle periods of approximately 24 hours; they are entrained to a more exact 24-hour cycle period by environmental cues.

26.3 Communication is a key element of many animal behaviors.

Much of the research in animal behavior is devoted to analyzing the nature of communication signals, determining how they are perceived, and identifying the ecological roles they play and their evolutionary origins.

Courtship

During courtship, animals produce signals to communicate with potential mates and with other members of their own sex. A **stimulus-response chain** sometimes occurs, in which the behavior of one individual in turn releases a behavior by another individual (figure 26.15).

Courtship Signaling

A male stickleback fish will defend the nest it builds on the bottom of a pond or stream by attacking *conspecific* males (that is, males of the same species) that approach the nest. Niko Tinbergen studied the social releasers responsible for this behavior by making simple clay models. He found that a model's shape and degree of resemblance to a fish were

unimportant; any model with a red underside (like the underside of a male stickleback) could release the attack behavior. Tinbergen also used a series of clay models to demonstrate that a male stickleback recognizes a female by her abdomen, swollen with eggs.

Courtship signals are often *species-specific*, limiting communication to members of the same species and thus playing a key role in reproductive isolation. The flashes of fireflies (which are actually beetles) are such species-specific signals. Females recognize conspecific males by their flash pattern (figure 26.16), and males recognize conspecific females by their flash response. This series of reciprocal responses provides a continuous “check” on the species identity of potential mates.

Visual courtship displays sometimes have more than one component. The male *Anolis* lizard extends and retracts his fleshy and often colorful dewlap while perched on a branch in his territory (figure 26.17). The display thus involves both color and movement (the extension of the dewlap as well as a series of lizard “push-ups”). To which component of the display does the female respond? Experiments in which the dewlap color is altered with ink show that color is unimportant for some species; that is, a female can be courted successfully by a male with an atypically colored dewlap.

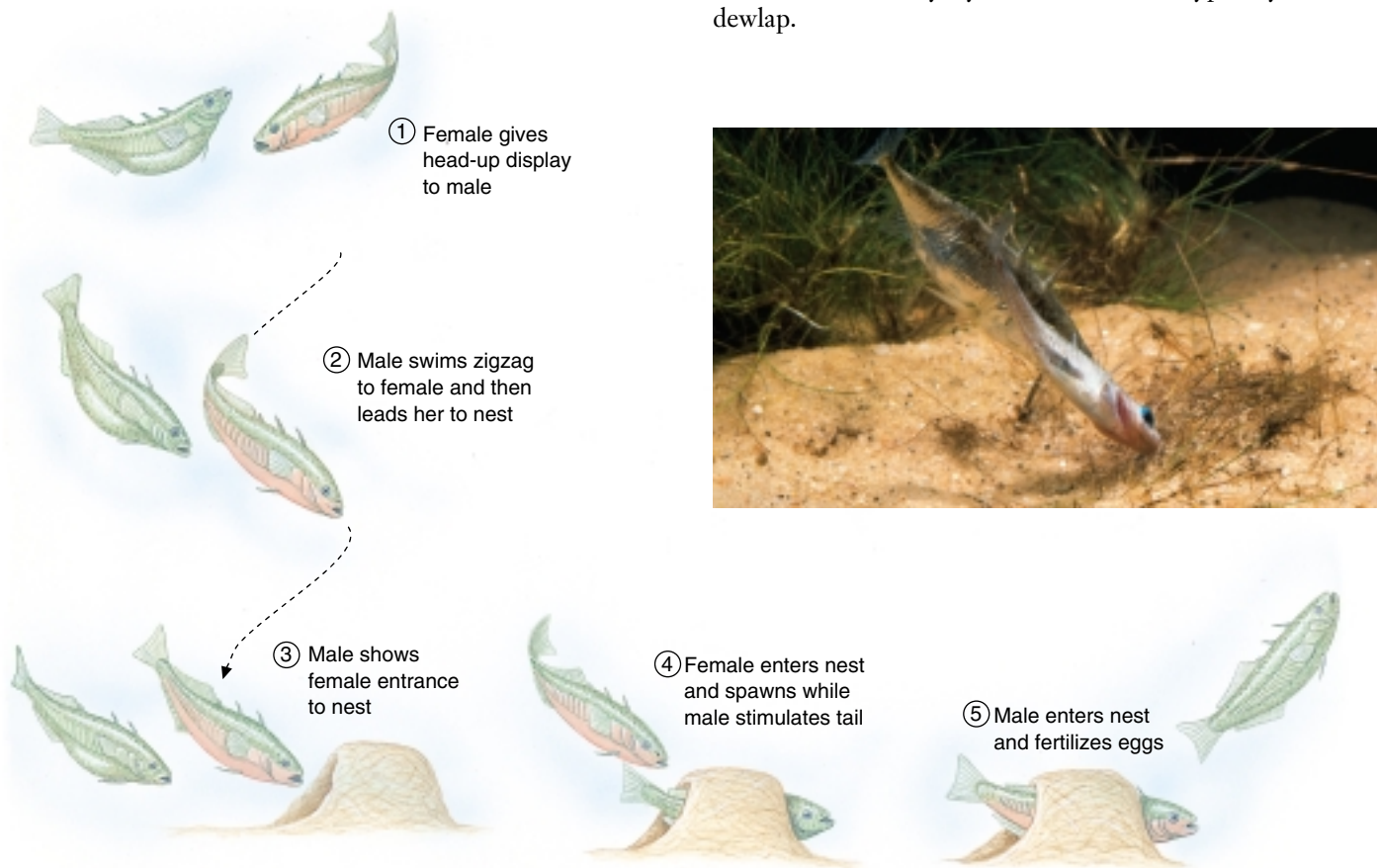


FIGURE 26.15
A stimulus-response chain. Stickleback courtship involves a sequence of behaviors leading to the fertilization of eggs.

Pheromones

Chemical signals also mediate interactions between males and females. **Pheromones**, chemical messengers used for communication between individuals of the same species, serve as sex attractants among other functions in many animals. Even the human egg produces a chemical attractant to communicate with sperm! Female silk moths (*Bombyx mori*) produce a sex pheromone called *bombykol* in a gland associated with the reproductive system. Neurophysiological studies show that the male's antennae contain numerous sensory receptors specific for bombykol. These receptors are extraordinarily sensitive, enabling the male to respond behaviorally to concentrations of bombykol as low as one molecule in 10^{17} molecules of oxygen in the air!

Many insects, amphibians, and birds produce species-specific acoustic signals to attract mates. Bullfrog males call to females by inflating and discharging air from their vocal sacs, located beneath the lower jaw. The female can distinguish a conspecific male's call from the call of other frogs that may be in the same habitat and mating at the same time. Male birds produce songs, complex sounds composed of notes and phrases, to advertise their presence and to attract females. In many bird species, variations in the males' songs identify *particular* males in a population. In these species, the song is individually specific as well as species-specific.

Level of Specificity

Why should different signals have different levels of specificity? The **level of specificity** relates to the function of the signal. Many courtship signals are species-specific to help animals avoid making errors in mating that would produce inviable hybrids or otherwise waste reproductive effort. A male bird's song is individually specific because it allows his presence (as opposed to simply the presence of an unidentifiable member of the species) to be recognized by neighboring birds. When territories are being established, males may sing and aggressively confront neighboring conspecifics to defend their space. Aggression carries the risk of injury, and it is energetically costly to sing. After territorial borders have been established, intrusions by neighbors are few because the outcome of the contests have already been determined. Each male then "knows" his neighbor by the song he sings, and also "knows" that male does not constitute a threat because they have already settled their territorial contests. So, all birds in the population can lower their energy costs by identifying their neighbors through their individualistic songs. In a similar way, mammals mark their territories with pheromones that signal individual identity, which may be encoded as a blend of a number of chemicals. Other signals, such as the mobbing and alarm calls of birds, are anonymous, conveying no information about the identity of the sender. These signals may permit communication about the presence of a predator common to several bird species.

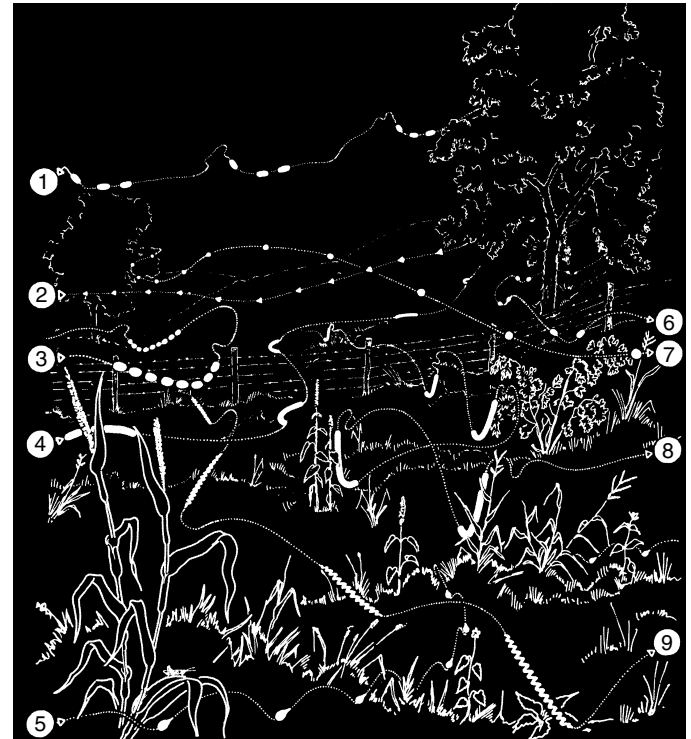


FIGURE 26.16

Firefly fireworks. The bioluminescent displays of these lampyrid beetles are species-specific and serve as behavioral mechanisms of reproductive isolation. Each number represents the flash pattern of a male of a different species.



FIGURE 26.17

Dewlap display of a male *Anolis* lizard. Under hormonal stimulation, males extend their fleshy, colored dewlaps to court females. This behavior also stimulates hormone release and egg-laying in the female.

Courtship behaviors are keyed to species-specific visual, chemical, and acoustic signals.

Communication in Social Groups

Many insects, fish, birds, and mammals live in social groups in which information is communicated between group members. For example, some individuals in mammalian societies serve as “guards.” When a predator appears, the guards give an **alarm call**, and group members respond by seeking shelter. Social insects, such as ants and honeybees, produce **alarm pheromones** that trigger attack behavior. Ants also deposit **trail pheromones** between the nest and a food source to induce cooperation during foraging (figure 26.18). Honeybees have an extremely complex **dance language** that directs nestmates to rich nectar sources.

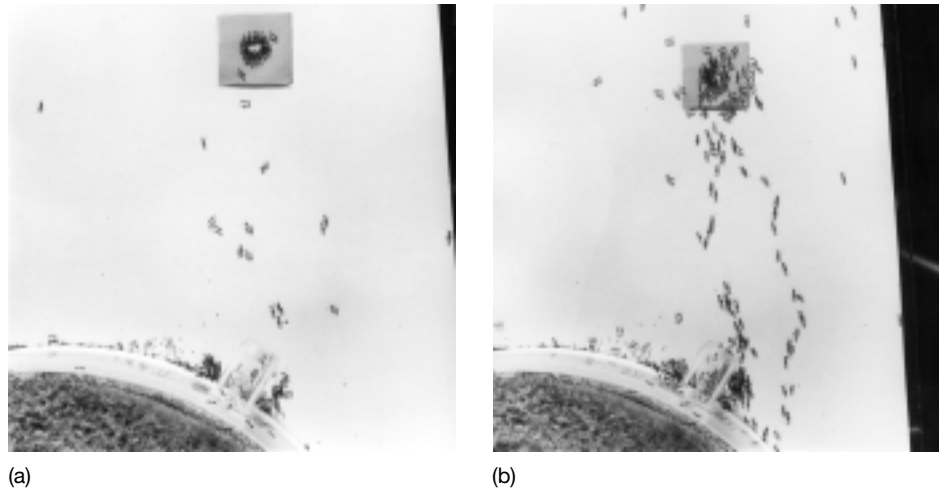


FIGURE 26.18

The chemical control of fire ant foraging. Trail pheromones, produced in an accessory gland near the fire ant’s sting, organize cooperative foraging. The trails taken by the first ants to travel to a food source (a) are soon followed by most of the other ants (b).

The Dance Language of the Honeybee

The European honeybee, *Apis mellifera*, lives in hives consisting of 30,000 to 40,000 individuals whose behaviors are integrated into a complex colony. Worker bees may forage for miles from the hive, collecting nectar and pollen from a variety of plants and switching between plant species and populations on the basis of how energetically rewarding their food is. The food sources used by bees tend to occur in patches, and each patch offers much more food than a single bee can transport to the hive. A colony is able to exploit the resources of a patch because of the behavior of scout bees, which locate patches and communicate their location to hivemates through a *dance language*. Over many years, Nobel laureate Karl von Frisch was able to unravel the details of this communication system.

After a successful scout bee returns to the hive, she performs a remarkable behavior pattern called a *waggle dance* on a vertical comb (figure 26.19). The path of the bee during the dance resembles a figure-eight. On the straight part of the path, the bee vibrates or waggles her abdomen while producing bursts of sound. She may stop periodically to give her hivemates a sample of the nectar she has carried back to the hive in her crop. As she dances, she is followed closely by other bees, which soon appear as foragers at the new food source.

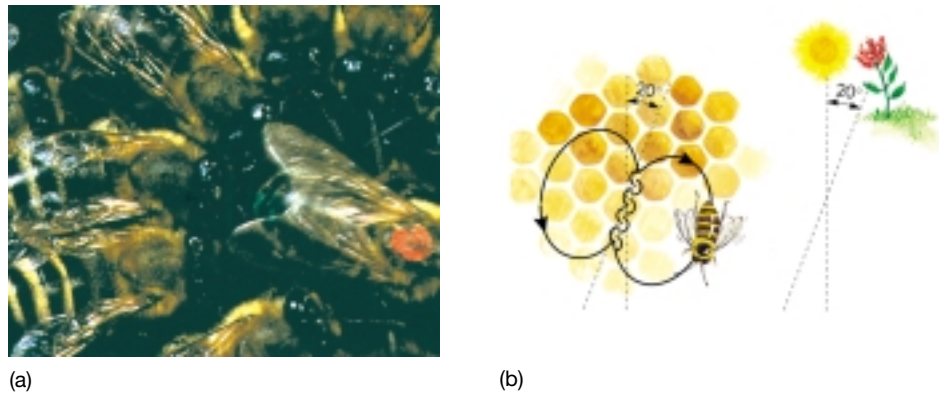


FIGURE 26.19

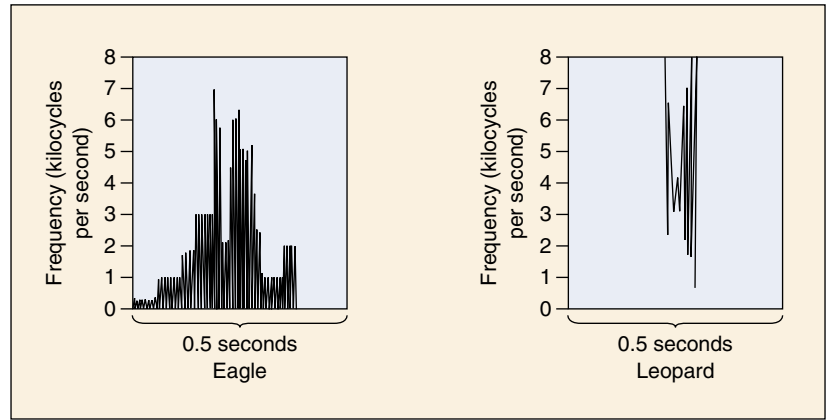
The waggle dance of honeybees. (a) A scout bee dances on a comb in the hive. (b) The angle between the food source and the nest is represented by a dancing bee as the angle between the straight part of the dance and vertical. The food is 20° to the right of the sun, and the straight part of the bee’s dance on the hive is 20° to the right of vertical.

Von Frisch and his colleagues claimed that the other bees use information in the waggle dance to locate the food source. According to their explanation, the scout bee indicates the *direction* of the food source by representing the angle between the food source and the hive in reference to the sun as the angle between the straight part of the dance and vertical in the hive. The *distance* to the food source is indicated by the tempo, or degree of vigor, of the dance.

Adrian Wenner, a scientist at the University of California, did not believe that the dance language communicated anything about the location of food, and he challenged von Frisch’s explanation. Wenner maintained that flower odor was the most important cue allowing recruited bees to arrive at a new food source. A heated controversy ensued as



(a)



(b)

FIGURE 26.20

Primate semantics. (a) Predators, like this leopard, attack and feed on vervet monkeys. (b) The monkeys give different alarm calls when eagles, leopards, and snakes are sighted by troupe members. Each distinctive call elicits a different and adaptive escape behavior.

the two groups of researchers published articles supporting their positions.

The “dance language controversy” was resolved (in the minds of most scientists) in the mid-1970s by the creative research of James L. Gould. Gould devised an experiment in which hive members were tricked into misinterpreting the directions given by the scout bee’s dance. As a result, Gould was able to manipulate where the hive members would go if they were using visual signals. If odor were the cue they were using, hive members would have appeared at the food source, but instead they appeared exactly where Gould predicted. This confirmed von Frisch’s ideas.

Recently, researchers have extended the study of the honeybee dance language by building robot bees whose dances can be completely controlled. Their dances are programmed by a computer and perfectly reproduce the natural honeybee dance; the robots even stop to give food samples! The use of robot bees has allowed scientists to determine precisely which cues direct hivemates to food sources.

Primate Language

Some primates have a “vocabulary” that allows individuals to communicate the identity of specific predators. The vocalizations of African vervet monkeys, for example, distinguish eagles, leopards, and snakes (figure 26.20). Chimpanzees and gorillas can learn to recognize a large number of symbols and use them to communicate abstract concepts. The complexity of human language would at first appear to defy biological explanation, but closer examination suggests that the differences are in fact superficial—all languages share many basic structural similarities. All of the roughly 3000 languages draw from the same set of 40 con-

sonant sounds (English uses two dozen of them), and any human can learn them. Researchers believe these similarities reflect the way our brains handle abstract information, a genetically determined characteristic of all humans.

Language develops at an early age in humans. Human infants are capable of recognizing the 40 consonant sounds characteristic of speech, including those not present in the particular language they will learn, while they ignore other sounds. In contrast, individuals who have not heard certain consonant sounds as infants can only rarely distinguish or produce them as adults. That is why English speakers have difficulty mastering the throaty French “r,” French speakers typically replace the English “th” with “z,” and native Japanese often substitute “l” for the unfamiliar English “r.” Children go through a “babbling” phase, in which they learn by trial and error how to make the sounds of language. Even deaf children go through a babbling phase using sign language. Next, children quickly and easily learn a vocabulary of thousands of words. Like babbling, this phase of rapid learning seems to be genetically programmed. It is followed by a stage in which children form simple sentences which, though they may be grammatically incorrect, can convey information. Learning the rules of grammar constitutes the final step in language acquisition.

While language is the primary channel of human communication, odor and other nonverbal signals (such as “body language”) may also convey information. However, it is difficult to determine the relative importance of these other communication channels in humans.

The study of animal communication involves analysis of the specificity of signals, their information content, and the methods used to produce and receive them.

26.4 Migratory behavior presents many puzzles.

Orientation and Migration

Animals may travel to and from a nest to feed or move regularly from one place to another. To do so, they must orient themselves by tracking stimuli in the environment.

Movement toward or away from some stimulus is called **taxis**. The attraction of flying insects to outdoor lights is an example of *positive phototaxis*. Insects that avoid light, such as the common cockroach, exhibit *negative phototaxis*. Other stimuli may be used as orienting cues. For example, trout orient themselves in a stream so as to face against the current. However, not all responses involve a specific orientation. Some animals just become more active when stimulus intensity increases, a responses called **kineses**.

Long-range, two-way movements are known as **migrations**. In many animals, migrations occur circannually. Ducks and geese migrate along flyways from Canada across the United States each fall and return each spring. Monarch butterflies migrate each fall from central and eastern North America to several small, geographically isolated areas of coniferous forest in the mountains of central Mexico (figure 26.21). Each August, the butterflies begin a flight southward to their overwintering sites. At the end of winter, the monarchs begin the return flight to their summer breeding ranges. What is amazing about the migration of the monarch, however, is that two to five generations may be produced as the butterflies fly north. The butterflies that migrate in the autumn to the precisely located overwintering grounds in Mexico have never been there before.

When colonies of bobolinks became established in the western United States, far from their normal range in the Midwest and East, they did not migrate directly to their winter range in South America. Instead, they migrated east to their ancestral range and then south along the original flyway (figure 26.22). Rather than changing the original migration pattern, they simply added a new pattern.

How Migrating Animals Navigate

Biologists have studied migration with great interest, and we now have a good understanding of how these feats of navigation are achieved. It is important to understand the distinction between **orientation** (the ability to follow a bearing) and **navigation** (the ability to set or adjust a bearing, and then follow it). The former is analogous to using a compass, while the latter is like using a compass in conjunction with a map. Experiments on starlings indicate that inexperienced birds migrate by orientation, while older birds that have migrated previously use true navigation (figure 26.23).

Birds and other animals navigate by looking at the sun and the stars. The indigo bunting, which flies during the day and uses the sun as a guide, compensates for the movement of the sun in the sky as the day progresses by reference to the north star, which does not move in the sky. Buntings also use the positions of the constellations and the position of the pole star in the night sky, cues they learn as young birds. Starlings and certain other birds compensate for the sun's apparent movement in the

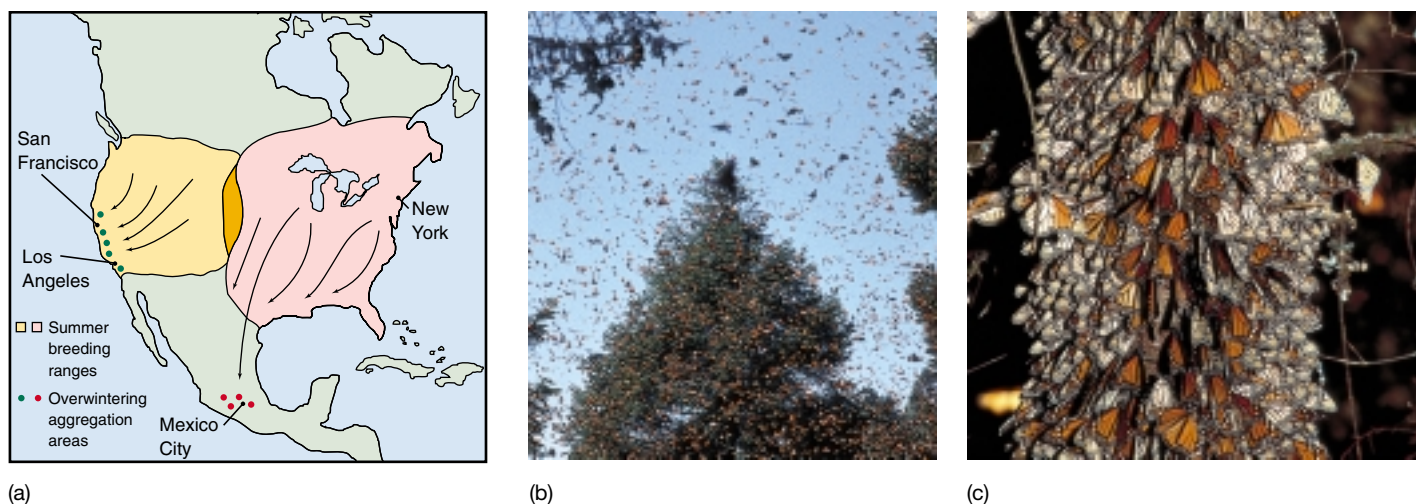
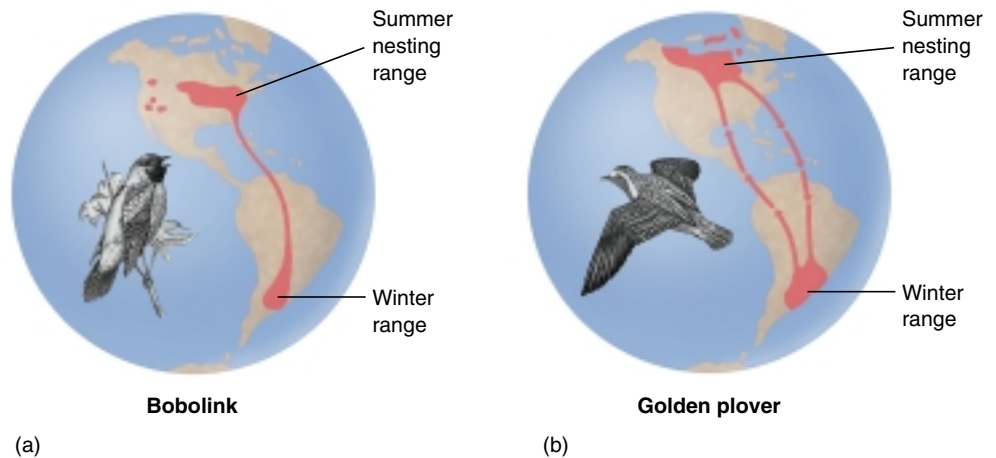


FIGURE 26.21

Migration of monarch butterflies. (a) Monarchs from western North America overwinter in areas of mild climate along the Pacific Coast. Those from the eastern United States and southeastern Canada migrate to Mexico, a journey of over 3000 kilometers that takes from two to five generations to complete. (b) Monarch butterflies arriving at the remote fir forests of the overwintering grounds and (c) forming aggregations on the tree trunks.

FIGURE 26.22

Birds on the move. (a) The summer range of bobolinks recently extended to the far West from their more established range in the Midwest. When they migrate to South America in the winter, bobolinks that nested in the West do not fly directly to the winter range; instead, they fly to the Midwest first and then use the ancestral flyway. (b) The golden plover has an even longer migration route that is circular. These birds fly from Arctic breeding grounds to wintering areas in southeastern South America, a distance of some 13,000 kilometers.



sky by using an internal clock. If such birds are shown an experimental sun in a fixed position while in captivity, they will change their orientation to it at a constant rate of about 15° per hour.

Many migrating birds also have the ability to detect the earth's magnetic field and to orient themselves with respect to it. In a closed indoor cage, they will attempt to move in the correct geographical direction, even though there are no visible external cues. However, the placement of a powerful magnet near the cage can alter the direction in which the birds attempt to move. Magnetite, a magnetized iron ore, has been found in the heads of some birds, but the sensory receptors birds employ to detect magnetic fields have not been identified.

It appears that the first migration of a bird is innately guided by both celestial cues (the birds fly mainly at night) and the earth's magnetic field. These cues give the same information about the general direction of the migration, but the information about direction provided by the stars seems to dominate over the magnetic information when the two cues are experimentally manipulated to give conflicting directions. Recent studies, however, indicate that celestial cues tell northern hemisphere birds to move south when they begin their migration, while magnetic cues give them the direction for the specific migratory path (perhaps a southeast turn the bird must make midroute). In short, these new data suggest that celestial and magnetic cues interact during development to fine-tune the bird's navigation.

We know relatively little about how other migrating animals navigate. For instance, green sea turtles migrate from Brazil halfway across the Atlantic Ocean to Ascension Island, where the females lay their eggs. How do they find this tiny island in the middle of the ocean, which they haven't seen for perhaps 30 years? How do the young that hatch on the island know how to find their way to Brazil? Recent studies suggest that wave action is an important cue.

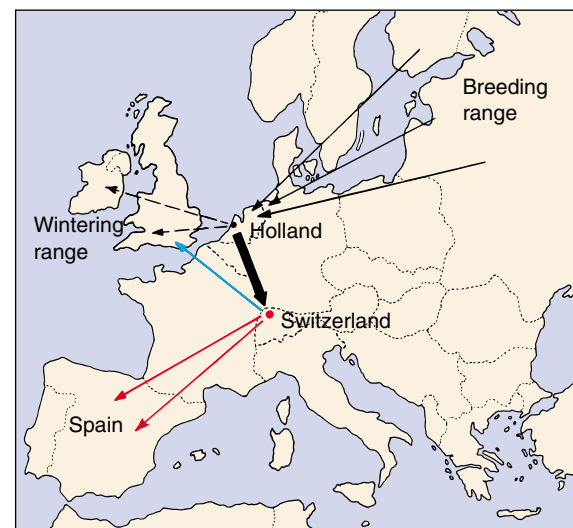


FIGURE 26.23

Migratory behavior of starlings. The navigational abilities of inexperienced birds differ from those of adults who have made the migratory journey before. Starlings were captured in Holland, halfway along their full migratory route from Baltic breeding grounds to wintering grounds in the British Isles; these birds were transported to Switzerland and released. Experienced older birds compensated for the displacement and flew toward the normal wintering grounds (*blue arrow*). Inexperienced young birds kept flying in the same direction, on a course that took them toward Spain (*red arrow*). These observations imply that inexperienced birds fly by orientation, while experienced birds learn true navigation.

Many animals migrate in predictable ways, navigating by looking at the sun and stars, and in some cases by detecting magnetic fields.

26.5 To what degree animals “think” is a subject of lively dispute.

Animal Cognition

It is likely each of us could tell an anecdotal story about the behavior of a pet cat or dog that would seem to suggest that the animal had a degree of reasoning ability or was capable of thinking. For many decades, however, students of animal behavior flatly rejected the notion that nonhuman animals can think. In fact, behaviorist Lloyd Morgan stated that one should never assume a behavior represents conscious thought if there is any other explanation that precludes the assumption of consciousness. The prevailing approach was to treat animals as though they responded to the environment through reflexlike behaviors.

In recent years, serious attention has been given to the topic of animal awareness. The central question is whether animals show **cognitive behavior**—that is, do they process information and respond in a manner that suggests thinking (figure 26.24)? What kinds of behavior would demonstrate cognition? Some birds in urban areas remove the foil caps from nonhomogenized milk bottles to get at the cream beneath, and this behavior is known to

have spread within a population to other birds. Japanese macaques learned to wash potatoes and float grain to separate it from sand. A chimpanzee pulls the leaves off of a tree branch and uses the stick to probe the entrance to a termite nest and gather termites. As we saw earlier, vervet monkeys have a vocabulary that identifies specific predators.

Only a few experiments have tested the thinking ability of nonhuman animals. Some of these studies suggest that animals may give false information (that is, they “lie”). Currently, researchers are trying to determine if some primates deceive others to manipulate the behavior of the other members of their troop. There are many anecdotal accounts that appear to support the idea that deception occurs in some nonhuman primate species such as baboons and chimpanzees, but it has been difficult to devise field-based experiments to test this idea. Much of this type of research on animal cognition is in its infancy, but it is sure to grow and to raise controversy. In any case, there is nothing to be gained by a dogmatic denial of the *possibility* of animal consciousness.



(a)



(b)

FIGURE 26.24

Animal thinking? (a) This chimpanzee is stripping the leaves from a twig, which it will then use to probe a termite nest. This behavior strongly suggests that the chimpanzee is consciously planning ahead, with full knowledge of what it intends to do. (b) This sea otter is using a rock as an “anvil,” against which it bashes a clam to break it open. A sea otter will often keep a favorite rock for a long time, as though it has a clear idea of what it is going to use the rock for. Behaviors such as these suggest that animals have cognitive abilities.

FIGURE 26.25
Problem solving by a chimpanzee. Unable to get the bananas by jumping, the chimpanzee devises a solution.



In any case, some examples, particularly those involving problem-solving, are hard to explain in any way other than as a result of some sort of mental process. For example, in a series of classic experiments conducted in the 1920s, a chimpanzee was left in a room with a banana hanging from the ceiling out of reach. Also in the room were several boxes, each lying on the floor. After unsuccessful attempts to jump up and grab the bananas, the chimpanzee suddenly looks at the boxes and immediately proceeds to move them underneath the banana, stack one on top of another, and climb up to claim its prize (figure 26.25).

Perhaps it is not so surprising to find obvious intelligence in animals as closely related to us as chimpanzees. But recent studies have found that other animals also show evidence of cognition. Ravens have always been considered among the most intelligent of birds. Bernd Heinrich of the University of Vermont recently conducted an experiment using a group of hand-reared crows that lived in an outdoor aviary. Heinrich placed a piece of meat on the end of a string and hung it from a branch in the aviary. The birds liked to eat meat, but had never seen string before and were unable to get at the meat. After several hours, during which time the birds periodically looked at the meat but did nothing else, one bird flew to the branch, reached down, grabbed the string, pulled it up, and placed it under his foot. He then reached down and grabbed another piece of the string, repeating this action over and over, each time bringing the meat closer (figure 26.26). Eventually, the meat was within reach and was grasped. The raven, presented with a completely novel problem, had devised a solution. Eventually, three of the other five ravens also figured out how to get to the meat. Heinrich has conducted other similarly creative experiments that can leave little doubt that ravens have advanced cognitive abilities.

Research on the cognitive behavior of animals is in its infancy, but some examples are compelling.



FIGURE 26.26
Problem solving by a raven. Confronted with a problem it had never previously confronted, the raven figures out how to get the meat at the end of the string by repeatedly pulling up a bit of string and stepping on it.

**Summary****Questions****Media Resources****26.1 Ethology focuses on the natural history of behavior.**

- Behavior is an adaptive response to stimuli in the environment. An animal's sensory systems detect and process information about these stimuli.
1. How does a hybrid lovebird's method of carrying nest materials compare with that of its parents? What does this comparison suggest about whether the behavior is instinctive or learned?

26.2 Comparative psychology focuses on how learning influences behavior.

- Behavior is both instinctive (influenced by genes) and learned through experience. Genes are thought to limit the extent to which behavior can be modified and the types of associations that can be made.
 - The simplest forms of learning involve habituation and sensitization. More complex associative learning, such as classical and operant conditioning, may be due to the strengthening or weakening of existing synapses as well as the formation of entirely new synapses.
 - An animal's internal state influences when and how a behavior will occur. Hormones can change an animal's behavior and perception of stimuli in a way that facilitates reproduction.
2. How does associative learning differ from nonassociative learning? How does classical conditioning differ from operant conditioning?
 3. What is filial imprinting? What is sexual imprinting? Why do some young animals imprint on objects like a moving box?
 4. How does Marler's work on song development in white-crowned sparrows indicate that behavior is shaped by learning? How does it indicate that behavior is shaped by instinct?

26.3 Communication is a key element of many animal behaviors.

- Animals communicate by producing visual, acoustic, and chemical signals. These signals are involved in mating, finding food, defense against predators, and other social situations.
5. How do communication signals participate in reproductive isolation? Give one example of a signal that is species-specific. Why are some signals individually specific?



- On Science Article: Polyandry in Hawks

26.4 Migratory behavior presents many puzzles.

- Animals use cues such as the position of the sun and stars to orient during daily activities and to navigate during long-range migrations.
6. What is the definition of taxis? What are kinesis? What cues do migrating birds use to orient and navigate during their migrations?

26.5 To what degree animals “think” is a subject of lively dispute.

- Many anecdotal accounts point to animal cognition, but research is in its infancy.
7. What evidence would you accept that an animal is “thinking”?