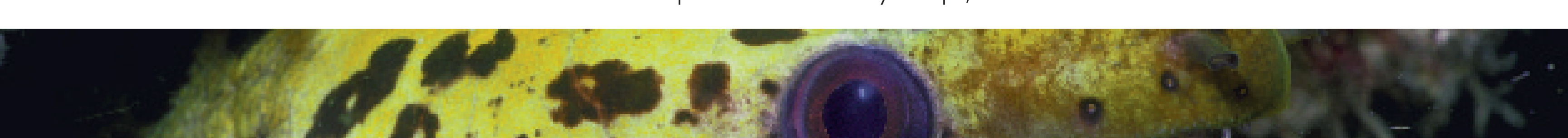
chapter 34

Animal Behavior

1. Behavior refers to the varied activities that an animal performs during its lifetime. Internal physiological conditions, environmental stimuli, and social situations influence specific behavioral responses.
2. Proximate factors that influence the behavior of an animal include genetics, developmental experiences, and the current environment, including photoperiod, season, and temperature. The nervous and endocrine systems of the animal mediate these effects.
3. The ultimate factor that influences the behavior of an animal is natural selection. Animals that possess certain traits are more successful at surviving and reproducing.
4. Two key problems that face each animal are finding food and a place to live.
5. The evolution of various social systems, in which animals live in groups, affects many aspects of their behavior.

This chapter contains evolutionary concepts, which are set off in this font.



Animal behavior refers to the activities animals perform during their lifetime, including locomotion, feeding, breeding, capture of prey, avoidance of predators, and social behavior. Animals send signals, respond to signals or stimuli, carry out maintenance behavior, make choices, and interact with one another. This chapter examines some of these aspects of animal behavior.

Four Approaches To Animal Behavior

Naturalists and philosophers have observed animal behavior for centuries. Only in the last century, however, has there been significant progress in understanding this behavior.

One approach to the study of animal behavior is **comparative psychology.** Comparative psychologists emphasize studies of the genetic, neural, and hormonal bases of animal behavior. Psychologists conduct experimental studies, in both laboratory and field settings, that relate to animal learning and to the development of behavior. They explore how animals receive information, and the processes and nature of the behavior patterns constituting the animals' responses to their surroundings.

Ethology (Gr. *ethologica,* depicting character) is the study of animal behavior that focuses on evolution and the natural environment. The leaders of this approach have been Konrad Lorenz, Niko Tinbergen, and Karl von Frisch, who were awarded the Nobel Prize in Physiology or Medicine in 1973. Ethologists observe the behavior of a variety of animals in their natural environments and study the behavior of closely related species to consider the evolution and origin of certain behavior patterns. Ethologists rarely deal with learning and are interested instead in animal communication, mating behavior, and social behavior.

Behavioral ecology emphasizes the ecological aspects of animal behavior. Predator-prey interactions, foraging strategies, reproductive strategies, habitat selection, intraspecific and interspecific competition, and social behavior are topics of interest to behavioral ecologists.

Sociobiology is the study of the evolution of social behavior. It combines many aspects of ethology and behavioral ecology. Sociobiologists emphasize the importance of natural selection on individuals living in groups.

Proximate and Ultimate Causes

Behavioral scientists frequently ask, "Why do animals do what they do?" More immediate ecological and physiological causes of behavior, such as eating to satisfy hunger, are called proximate causes. Another level of causation in behavior occurs on the evolutionary time scale and is that of ultimate causes. For example, a display not only attracts a mate, but also increases the likelihood of passing genetic information to the next generation.

Anthropomorphism

Anthropomorphism (Gr. *anthropos,* man + *morphe,* form) is the application of human characteristics to anything not human. In observations of animals, assigning human feelings to animal behavior is not likely to be accurate, especially with invertebrate animals. Consider the example of placing an earthworm on a fishhook. Does the fishhook hurt the earthworm, causing it to writhe in pain? Both of the descriptive words, hurt and pain, are based on human experience and conscious awareness. A better explanation that reduces the anthropomorphic interpretation is that placing the earthworm on the hook stimulates certain receptors which generate nerve impulses that travel along reflex neural circuits. The impulses stimulate muscles that allow the worm to wriggle in an attempt to escape from the hook. This explanation more closely describes what has been observed and does not attempt to suggest what the earthworm "feels."

Development of Behavior

Development of a normal behavior pattern requires the genes that code for the formation of the structures and organs involved in the behavior. For example, in vertebrates, normal locomotion movements will not occur without proper development and growth of the limbs. This process requires some interaction with the animal's environment because proper nourishment, water balance, and other factors must be maintained for normal development.

Maturation

Some behavior patterns appear only after a specific developmental stage or time. During **maturation,** performance of the behavior pattern improves as parts of the nervous system and other structures complete development. A classic example is tail movement in frog embryos that are near hatching. While still in the egg membranes, they start moving their tails as they would if they were swimming, and movement coordination improves with time. These improved movements are due to maturation, not practice or experience.

Instinct/Learning Interactions

In recent years, many behavioral scientists have concluded that both instinct and learning are important in animal behavior. Interaction of inherited (i.e., instinctive) and learned components shapes a number of behavior patterns. For example, young bobcats raised in isolation without the chance to catch live prey did not attack a white rat placed with them, unless the rat tried to escape. At first, their attacks were not efficient, but after some experience, they were seizing prey by the neck and rapidly killing them. Apparently, learning refines inherited components of this behavior.

Under normal conditions, the learning or experiences occur during play with littermates.

Another example involving instinctive and learned components to behavior is the nut-cracking behavior of squirrels. Squirrels gnaw and pry to open a nut. Inexperienced squirrels are not efficient; they gnaw and pry at random on the nut. Experienced squirrels, however, gnaw a furrow on the broad side, then wedge their lower incisors into the furrow and crack the nut open.

Imprinting

During **imprinting,** a young animal develops an attachment toward another animal or object (figure 34.1*a*). The attachment usually forms only during a specific critical period soon after hatching or birth and is not reversible (figure 34.1*b*). Imprinting is a rapid learning process that apparently occurs without reinforcement.

Konrad Lorenz (1903–1989) conducted experiments with geese in which he allowed the geese to imprint on him. The goslings followed him as though he was their mother. In nature, many species of birds in which the young follow the parent soon after birth use imprinting so that the young can identify with or recognize their parent(s). They can then be led successfully to the nest or to water. Both visual and auditory cues are important in imprinting systems.

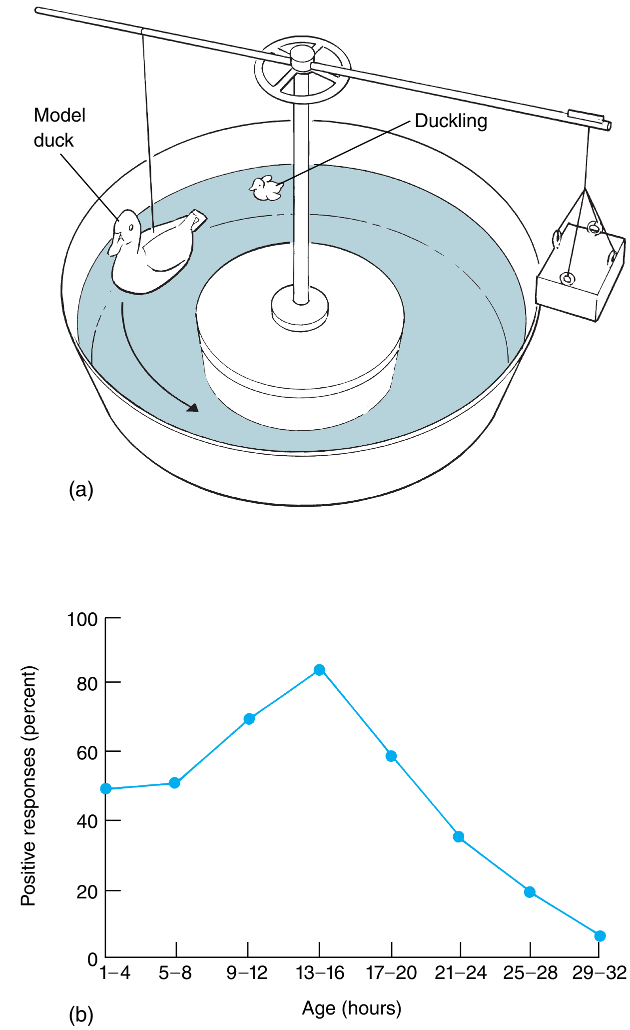


Figure 34.1

Imprinting in Young Birds. *(a)* Circular arena apparatus for imprinting the young duckling on its "mother" (a stuffed model). *(b)* The critical period for imprinting is most likely 13 to 16 hours after hatching.

Learning

Learning produces changes in the behavior of an individual that are due to experience. Learning is adaptive because it allows an animal to respond quickly to changes in its environment. Once an animal learns something, its behavioral choices increase.

An animal's ability to learn may correlate with the predictability of certain characteristics of its environment. Where certain changes in the habitat occur regularly and are predictable, the animal may rapidly respond to a stimulus with an unmodified instinctive behavior. An animal would not necessarily benefit from learning in this situation. However, where certain environmental changes are unpredictable and cannot be anticipated, an animal may modify its behavioral responses through learning or experience. This modification is adaptive because it allows an animal to not only change its response to fit a given situation, but also to improve its response to subsequent, similar environmental changes.

Several different categories of learning have been identified, ranging from habituation (the simplest form of learning) to insight learning (the most complex form) that involves cognitive processes.

Habituation

Habituation is the simplest and perhaps most common type of behavior in many different animals. Habituation involves a waning or decrease in response to repeated or continuous stimulation. Simply, an animal learns not to respond to stimuli in its environment that are constant and probably relatively unimportant. By habituating to unimportant stimuli, an animal conserves energy and time that are better spent on other important functions. For example, after time, birds learn to ignore scarecrows that previously caused them to flee. Squirrels in a city park adjust to the movements of humans and automobiles. If the stimulus is withheld, then the response returns rapidly. Habituation does not involve any conditioning. Habituation is believed to be controlled through the central nervous system and should be distinguished from sensory adaptation. Sensory adaptation involves repeated

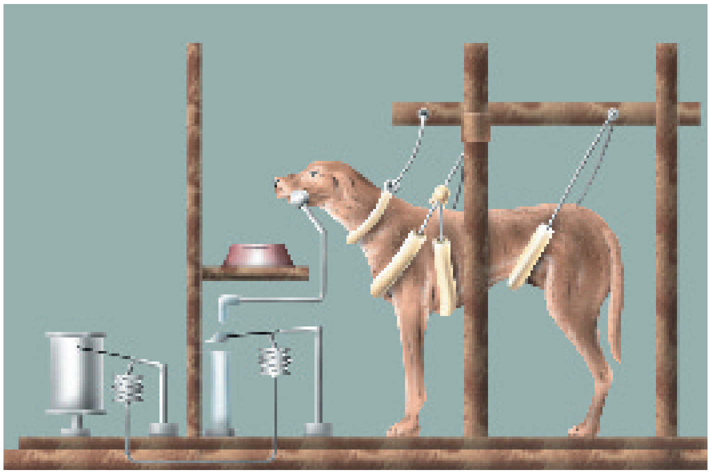


FIGURE 34.2

Apparatus Pavlov Used to Demonstrate Classical Conditioning. If a bell rings just before a dog is given food, the dog soon begins to associate the stimulus with the food and becomes conditioned to salivate with the ringing of the bell alone. From Benjamin B. Lahey, *Psychology: An Introduction*, 3d ed. New York, McGraw-Hill. Reprinted by permission of The McGraw-Hill Companies.

stimulation of receptors until they stop responding. For example, if you enter a room with an unusual odor, your olfactory sense organs soon stop responding to these odors.

Classical Conditioning

Classical conditioning is a type of learning documented by Russian physiologist, Ivan Pavlov (1849–1936). In his classic experiment on the salivary reflex in dogs, Pavlov presented food right after the sound of a bell (figure 34.2). After a number of such presentations, the dogs were conditioned—they associated the sound of the bell with food. It was then possible to elicit the dog's usual response to food—salivation—with just the sound of the bell. The food was a positive reinforcement for salivating behavior, but responses could also be conditioned using negative reinforcement.

Classical conditioning is very common in the animal kingdom. For example, birds learn to avoid certain brightly colored caterpillars that have a noxious taste. Because birds associate the color pattern with the bad taste, they may also avoid animals with a similar color pattern.

Instrumental Conditioning

In **instrumental conditioning** (also known as trial-and-error learning), the animal learns while carrying out certain searching actions, such as walking and moving about. For example, if the animal finds food during these activities, the food reinforces the behavior, and the animal associates the reward with the behavior. If this association is repeated several times, the animal learns that the behavior leads to reinforcement.

A classic example of instrumental conditioning is that of a rat in a "Skinner box," developed by B. F. Skinner (1904–1990), a prominent psychologist. When placed in the box, the rat begins to explore. It moves all about the box and, by accident, eventually presses a lever and is rewarded with a food pellet. Because food rewards are provided each time the rat presses the lever, the rat associates the reward with the behavior. Through repetition, the rat learns to press the lever right away to receive the reward. In this type of learning, the animal is instrumental in providing its own reinforcement.

In instrumental conditioning, providing the reinforcement (food) whenever the animal comes close to the lever and continuing to supply reinforcement when the animal touches the lever "shapes" the behavior. Finally, the animal learns to press the lever to obtain food.

Young animals' attempts to learn new motor patterns often involve instrumental conditioning. A young bird learning to fly or a young mammal at play may improve coordination of certain movements or behavior patterns by practice during these activities.

Latent Learning

Latent learning, sometimes called exploratory learning, involves making associations without immediate reinforcement or reward. The reward is not obvious. An animal is apparently motivated, however, to learn about its surroundings. For example, if a rat is placed in a maze that has no food or reward, it explores the maze, although rather slowly. If food or another reward is provided, the rat quickly runs the maze. Apparently, previous learning of the maze had occurred but remained latent, or hidden, until an obvious reinforcement was provided. Latent learning allows an animal to learn about its surroundings as it explores. Knowledge about an animal's home area may be important for its survival, perhaps enabling it to escape from a predator or capture prey.

Insight Learning

In **insight learning,** the animal uses cognitive or mental processes to associate experiences and solve problems. The classic example is the work of Wolfgang Kohler (1887–1967) on chimpanzees that were trained to use tools to obtain food rewards (figure 34.3*a*). One chimpanzee was given some bamboo poles that could be joined to make a longer pole, and some bananas were hung from the ceiling. Once the chimp formed the longer pole, it used the pole to knock the bananas to the cage floor. Kohler believed that the animal used insight learning to get the bananas.

In addition, Jane van Lawick-Goodall (1934–) has observed chimpanzees in the wild using tools to accomplish various tasks. For example, they use crumpled leaves as a sponge for drinking water (figure 34.3*b*).

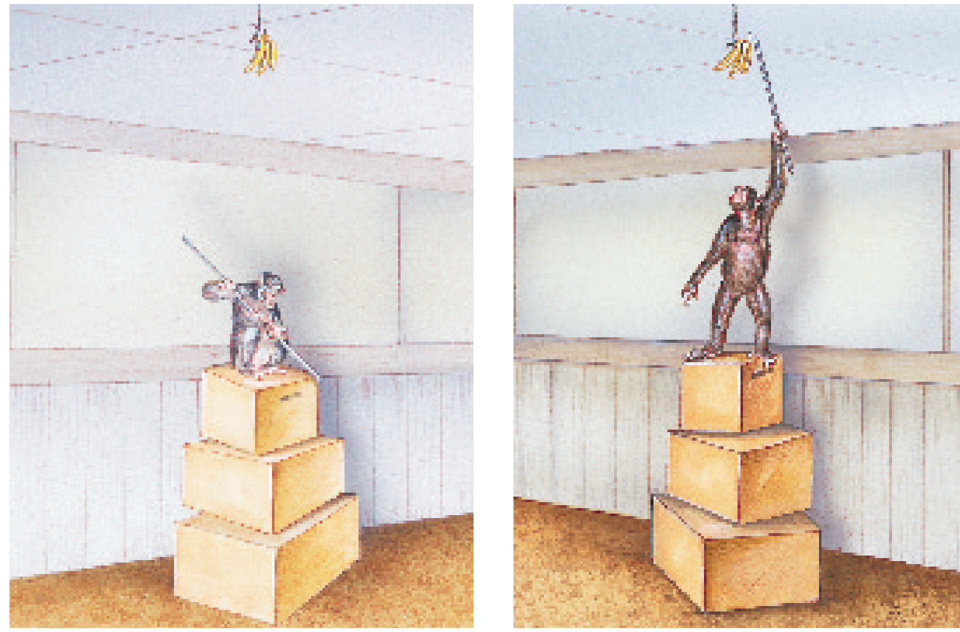


FIGURE 34.3

Insight Learning in Chimpanzees. This chimpanzee *(Pan troglodytes)* puts two sticks together and stands on stacked boxes to reach the bananas suspended from the ceiling.

CONTROL OF BEHAVIOR

Internal mechanisms (proximate causes) that include the nervous system and the endocrine system regulate animal behavior. These systems receive information from the external environment via the sensory organs, process that information involving the brain and the endocrine glands, and initiate responses in terms of motor patterns or changes in the operations of internal organs. In general, the nervous system mediates more specific and rapid responses, while the endocrine system monitors slower, more general responses.

NERVOUS SYSTEM

Chapter 24 provides details of the structure of the nervous systems found in animals, and how the various parts function. The goal here is to examine the ways in which the nervous system is involved in behavior. One key role for the nervous system is to act as a **stimulus filter.** Stimuli from many sources continuously bombard each organism. The sensory organs and central nervous system of the animal block incoming stimuli that are unimportant or irrelevant. The information that passes through the sensory filters is then sorted and processed within the nervous system to ensure appropriate responses.

The manner in which blowflies feed illustrates how the nervous system mediates behavior. The blowfly has special sensory receptors on its feet. As the fly moves around and encounters different substrates, the receptors can detect the presence of certain sugars. The information from the feet is processed in the fly's nervous system and results in the extension of the proboscis, which, in turn, stimulates the oral taste receptors, and the fly begins to feed. How does the fly know when to stop feeding? Without some feedback mechanism, the fly could continue to consume the sugar solution until it burst! Receptors in the blowfly's foregut (the first stop for the incoming food in the fly's digestive system), send a message to the fly's brain when the foregut swells sufficiently. The message is relayed to the nerves that control the feeding response, halting further intake of the sugar solution.

Another example of how the nervous system regulates behavior concerns the control of aggressive behavior in rhesus monkeys. In one study, researchers identified the dominant male monkey in a group of four to six animals and then surgically implanted electrodes into the monkey's brain regions involved in either eliciting or inhibiting aggressive behavior. Mild electrical stimulation to the monkey's brain produced either aggressive or passive behaviors, depending on which electrode sent the message. The other monkeys in the group also could be trained to press a lever whenever the dominant monkey became aggressive. Pressing the lever sent a message to the brain of the dominant male that inhibited his aggression.

ENDOCRINE SYSTEM

In animals, the endocrine system is closely interrelated with the nervous system. Many receptors located on neurons in the brain or central nervous system are specialized for receiving input from hormones. In addition, the brain communicates with the endocrine system via neurons, such as the connections between the hypothalamus and pituitary gland of vertebrates *(see chapter 25)*. Other endocrine glands (e.g., the adrenals and gonads) are located throughout the body of the organism. **Hormones,** the products from the endocrine glands, affect behavior in two major ways: organizational effects and activational effects.

Organizational effects of hormones occur during development and are particularly important for sex differentiation. These effects involve the presence of hormones and critical time periods during which the developmental pathways for specific brain regions and developing gonadal tissues are influenced to become either female- or malelike. The major effect is such that at about the middle of gestation in most male mammalian embryos (e.g., guinea pigs, monkeys), the testes produce a surge of male hormone (testosterone). This organizes both other developing tissues and certain regions of the brain. In the absence of a testosterone surge, female embryos develop more femalelike characteristics in terms of external anatomy and brain regions important for sex differences. Genes normally turn on the production and release of testosterone in the tissues of the developing animal, but sometimes, the testosterone comes from an external source.

In cattle, a female embryo is masculinized if her twin is a male fetus. When his system turns on and releases testosterone during gestation, some of that hormone crosses over to affect the developing female. The result is a freemartin, a sterile heifer that exhibits a number of malelike behavior patterns. In humans, some hormone treatments that used to be given to pregnant women who were in danger of losing their fetus resulted in masculinization of female embryos because the hormones injected as a medical treatment were converted to and acted like testosterone within the embryo.

Activational effects of hormones occur when an external stimulus triggers a hormonally mediated response by the organism. Many male fishes change color patterns when their territory boundary is threatened; the color change is a prelude to potentially aggressive behavior to defend the territory. Many animals, including domestic cats, roosters, and mice, lose their aggressive fighting ability after castration (removal of the gonads). The gonads are the source of testosterone, which stimulates particular brain receptors to produce aggression.

COMMUNICATION

Communication is the transfer of information from one animal to another. It requires a sender and receiver that are mutually adapted to each other. The animal acting as the sender must send a clear signal to the receiver. Communication can occur within species (intraspecific) or between species (interspecific). Intraspecific communication in animals is especially important for reproductive success. Examples of interspecific communication include warning signals, such as the rattle of a rattlesnake's tail and the skunk's presentation of its hindquarters and tail.

Animals use a variety of modalities for communication, including visual, auditory, tactile, and chemical signals. Natural selection has influenced the characteristics of a signal system. Animals have evolved combinations of signals that may be more effective than any single signal.

Visual Communication

Visual communication is important to many animals because a large amount of information can be conveyed in a short time. Most animals (e.g., cephalopod molluscs, arthropods, and most vertebrates other than mammals) with well-developed eyes have color vision. Many fishes, reptiles, and birds exhibit brilliant color patterns that usually have a signaling function. Most mammals have plain, darker colors and lack color vision because they are nocturnal, as were their probable ancestors—nocturnal insectivores. Primates are a notable exception in that they have both color vision and colorful displays.

A visual signal may be present at all times, as are the bright facial markings of a male mandrill. The signal may be hidden or located on a less exposed part of an animal's body, and then suddenly presented. Some lizards, such as green anoles, can actually change their color through activities of pigment cells in the skin.

Visual signals have some disadvantages in that various objects in the environment may block the line of sight, and/or the signals may be difficult to see over a long distance. Also, the signals are usually not effective at night and may be detected by predators.

Acoustic Communication

Arthropods and vertebrates commonly use acoustic or sound communication. These animals must expend energy to produce sounds, but sounds can be used during night or day. Sound waves also have the advantage of traveling around objects, and may be produced or received while an animal is in the open or concealed. Sounds can carry a large amount of information because of the many possible variations in frequency, duration, volume, and tone.

Acoustic communication systems are closely adapted to the environmental conditions in which they are used and the function of the signal. For example, tropical forest birds produce low-frequency calls that pass easily through dense vegetation. Many primates in tropical forests produce sounds that travel over long distances. Other examples include the calls of territorial birds that sit on a high perch to deliver the signal more effectively and the alarm calls of many small species of birds. Some of the more complex acoustic signals that have been studied are birdsong and human speech.

Tactile Communication

Tactile communication refers to the communication between animals in physical contact with each other. The antennae of many invertebrates and the touch receptors in the skin of vertebrates function in tactile communication. Some examples of tactile communication are birds preening the feathers of other birds and primates grooming each other.

Chemical Communication

Chemical communication is another common mode of communication. Unicellular organisms with chemoreceptors can recognize members of their own species. Chemical signals are well-developed in insects, fishes, salamanders, and mammals. Advantages of chemical signals are that they (1) usually provide a simple message that can last for hours or days; (2) are effective night or day; (3) can pass around objects; (4) may be transported over long distances; and (5) take relatively little energy to produce. Disadvantages of chemical signals are that they cannot be changed quickly and are slow to act.

Chemicals that are synthesized by one organism and that affect the behavior of another member of the same species are called **pheromones.** Olfactory receptors in the receiving animal usually detect chemical signals. Many animals mark their territories by depositing odors that act as chemical signals to other animals of the same species. For example, many male mammals mark specific points in their territories with pheromones that warn other males of their presence in the area. The same pheromones may also attract females that are in breeding condition.

Differences in the chemical structure of pheromones may be directly related to their function. Pheromones used for marking territories and attracting mates usually last longer because of their higher molecular weights. Airborne signals have lower molecular weights and disperse easily. For example, the sex attractant pheromones of female moths who are ready to mate are airborne, and males several kilometers away can detect them.

Behavioral Ecology

Behavioral ecologists investigate how animals find their way about (orientation and navigation), how they find a place to live (habitat selection), what foods they select to eat (foraging behavior), and the ways in which behavior can influence population biology.

Habitat Selection

Habitat selection refers to the animal's choice of a place to live. Two types of factors affect where animals of a particular species live. First are the animal's physiological tolerance limits, which are determined by the species evolutionary history and may involve temperature, humidity, water salinity, and other environmental parameters. Within those constraints, a second set of psychological factors are important: Animals make choices about where to reside based on available food resources, nest sites, lack of predators, and past experience. For example, woodland deer mice may be constrained to live in forests rather than fields because they cannot tolerate the high temperatures in the field environment. Within the forest, they may prefer (choose to live in) areas with larger trees (e.g., oak or beech) because these trees provide more food in the form of acorns and beechnuts, in addition to better shelter and more nest sites.

Foraging Behavior

All animals must consume food to survive. For most organisms, a large portion of their daily routine involves finding and consuming food. The process of locating food resources is called **foraging behavior.** Animals face the following choices:

1. What items should be included in the diet?
2. Given that food is not often distributed evenly in the environment, but occurs in patches or clumps, what path should an animal take between patches, and how should it locate new patches of food?
3. As the food in a patch is depleted, when should the animal depart from that location and seek another patch of food?

Hummingbirds and various species of bees that visit clumps of flowers to obtain nectar must make each of these decisions. Owls that forage for small rodents in different habitats, including fields and forests, must make similar decisions.

Although animals do not calculate their personal energy budgets as they forage, there are energy costs and gains in finding and consuming food. These considerations include energy needed to search for food, energy used to pursue or handle the food, and energy required to digest the food. If the animal is to survive, then the energy gain from digesting a particular set of food items must exceed the costs. Thus, a praying mantis must expend energy to locate a moth, to strike the moth, to remove the moth's wings, to consume the moth's body, and finally, to digest the meal. The mantis will survive if the energy derived from digesting the moth is greater than these costs. This is particularly true if extra energy is needed for searching for a mate or laying eggs.

Specialists and Generalists

Some animals are **specialists** with respect to diet and habitat selection. Evolution has resulted in these animals being very efficient at utilizing a particular resource. The koala, an Australian marsupial, eats the leaves of only certain species of eucalyptus trees. Its digestive system is adapted to derive energy from the leaves of these trees more efficiently than are the digestive systems of other animals. Although being a specialist means successfully exploiting a particular resource, it is also risky. If a plant disease invades and kills trees of the eucalyptus species that form the koalas' diet, koalas may not be able to survive.

At the other end of the continuum are **generalists,** animals capable of eating a variety of foods or living in a variety of habitats. These animals can survive under a wide range of conditions. Humans are a good example of a generalist species. So, too, are some pest species, like European starlings, introduced into the

United States a century ago and now living in almost every available type of habitat. The disadvantage for generalists is that almost everywhere they eat and live, they face competition from other organisms, something that specialists often avoid.

Social Behavior

Social behavior typically refers to any interactions among members of the same species, but it also applies to animals of different species, excluding predator-prey interactions.

Living in Groups

Animal populations are often organized into groups. A group of animals may form an aggregation for some simple purpose, such as feeding, drinking, or mating. Several *Drosophila* flies on a piece of rotting fruit is an example of an aggregation. A true animal **society** is a stable group of individuals of the same species that maintains a cooperative social relationship. This association typically extends beyond the level of mating and taking care of young. Social behavior has evolved independently in many species of animals; invertebrates as well as vertebrates have complex social organizations.

One major benefit of belonging to a group may be that it offers protection against predators (figure 34.4). There is safety in numbers, and predator detection may be enhanced by having several group members on alert to warn against an intruder. Also, cooperative hunting and capture of prey increase the feeding efficiency of predators. Living in social groups is also advantageous in some instances due to the ability to gain protection from the elements (e.g., huddling together in cold weather) and during the processes of mate finding and rearing of young. In many species, most notably the social insects, living in groups has resulted in the evolutionary division of labor, with specific individuals performing specialized tasks (e.g., defense, food procurement, feeding of young).

A disadvantage of group living may be competition for resources. Other disadvantages include the diseases and parasites that may spread more rapidly in group-living animals, and interference between individuals with regard to reproduction and rearing of young. The value of group living depends on the species and behaviors involved.

FIGURE 34.4

Group Living. A flock of birds reacts to a bird of prey by forming a tight group, reducing the chances of the predator singling out any particular individual.

Agonistic Behavior, Territories, and Dominance Hierarchies

A society of animals usually has some maintenance of social structure and spacing of group members. Agonistic behavior, in which one animal is aggressive or attacks another animal, which responds by either returning the aggression or submitting, is often responsible for these patterns. In rare cases, agonistic behavior is lethal, but usually, animals are not killed or even severely injured. In many species, males vent much of their aggression in the form of threat displays. Displays typically involve signals that warn other males of an intention to defend an area or territory. Although agonistic behavior may seem antisocial, it maintains the social order. It is especially important in the maintenance of territories and dominance hierarchies.

A territorial animal uses agonistic behavior to defend a site or area against certain other individuals. The site is known as the animal's **territory,** and competing individuals are excluded from it. Many male birds and mammals occupy a breeding territory for part of the year. A male actively defends his area against other males, so that he can attract a female and court her without interference from other males. In addition to being a location for attracting a mate and rearing young, territories may contain a food supply or provide shelter to avoid predators and unfavorable climate.

In **dominance hierarchies,** a group of animals is organized so that some members of the group have greater access to resources, such as food or mates, than do others. Those near the top of the order have first choice of resources, whereas those near the bottom go last and may do without if resources are in short supply. An example of a dominance hierarchy is the "pecking order" of chickens in a pen. When chickens are placed together, they fight among themselves until a linear hierarchy of dominance is established. Higher-ranked chickens are among the first to eat and may peck lower-ranked chickens. Once the hierarchy is set, peaceful coexistence is possible. Occasional fights will occur if a bird tries to move up in the order.

Dominance hierarchies exist in many vertebrate groups, the most common being in the form of linear relationships, although triangular relationships may form. In baboons, the strongest male is usually highest in the rank order. But sometimes, older males may form coalitions to subdue a stronger male and lead the troop.

Altruism

In **altruism,** an individual gives up or sacrifices some of its own reproductive potential to benefit another individual. For example, one individual of a group of crows gives an alarm call to warn other individuals of the group of an approaching predator, even though the call may attract the predator to the sender of the signal. How did such behavior evolve? Are normal natural selection processes at work here?

To be successful in a biological sense, an animal must produce as many young as possible, thereby passing its genes to succeeding generations. However, genes can be passed on by aiding a relative and its young because they probably share some genes. In terms of reproductive potential or output, an individual may theoretically pass more genes to the next generation by aiding the survival of relatives than it would rearing its own young.

A well-known example of altruism occurs in societies of hymenopteran insects, such as honeybees. The male drones are haploid, and the female workers and queen are diploid, resulting in a genetic asymmetry. Diploid workers share, on the average, three-fourths of their genes with their full sisters. If they reproduced, they would share only half of their genes with hypothetical offspring. Thus, female honeybees may have more genes in common with their sisters than they would with their own offspring. The workers may pass more genes to the next generation by helping their mother produce more full sisters, some of whom may become reproductive queens, than if they produce their own young.

William Hamilton (1936–) proposed the idea of **kin selection** to explain how selection acting on related animals can affect the fitness of an individual. In this way, a gene that a particular individual carries may pass to the next generation through a related animal. An individual's fitness is therefore based on the genes it passes on, as well as those common genes its relatives pass on. A genetically based tendency to be altruistic could therefore be passed on by the individual carrying it or by a relative who also carries it. Obviously, for kin selection to work, individuals of a group must be able to identify relatives, as can small groups of primates and social insects.

Summary

1. Animal behavior includes the many activities of an animal during its lifetime. Four approaches to the study of animal behavior are comparative psychology, ethology, behavioral ecology, and sociobiology.
2. Natural selection influences animal behavior just as it does other animal characteristics. Certain behavioral traits that allow animals to survive and reproduce are favored.
3. Certain behavior patterns require time for maturation, during which performance of the behavior improves as parts of the nervous system and other structures complete development.
4. Many behavior patterns require an interaction of instinctive and learned components for efficient performance. In some instances, an animal may inherit a disposition to learn a specific behavior. Also, an animal may learn certain behavior patterns only during a specific sensitive period early in life.
5. Through learning, an animal can adjust quickly to changes in its environment. Learning is adaptive for animals in an environment where changes are not predictable. The types of learning known to occur in animals include habituation, classical conditioning, instrumental conditioning, latent learning, and insight learning.
6. The nervous system regulates behavior through sensory reception of information from the environment, processing and storing of that information, and mediating appropriate motor responses.
7. Hormonal effects on behavior may either be organizational, affecting developmental processes such as sexual differentiation, or activational, involving more immediate behavioral responses, such as aggression.
8. Communication in animals requires the use of clear signals by one animal and their reception by another. Visual, acoustic, tactile, and chemical signals are important channels in communication systems.
9. Animals have evolved mechanisms for guiding their selection of foods and of habitats in which to live and reproduce.
10. Many animal species live in groups that provide various benefits. Groups range from simple aggregations to more complex social organizations, or societies.
11. Agonistic behavior in the form of attacks or threat displays is important in spacing the members of a species or establishing and defending a territory. In some instances, a dominance hierarchy may rank members in order from the most dominant individual to the most subordinate individual. Once the hierarchy is established, agonistic behavior is reduced in the group.
12. In some societies, one individual sacrifices its reproductive potential to help another individual. Altruism may be a result of kin selection, in which aiding one's relatives enhances the spreading of genes shared with relatives.

Selected Key Terms

behavioral ecology
classical conditioning
comparative psychology
dominance hierarchies
ethology
foraging behavior
habitat selection
habituation
imprinting
insight learning
instrumental conditioning
latent learning
maturation
sociobiology
territory

Critical Thinking Questions

1. How can you distinguish between classical and instrumental conditioning? What are some examples of each that might occur in nature?
2. How is kin selection related to natural selection?
3. Will a seagull incubate an infertile chicken egg placed in her nest? Explain your answer.
4. An advertisement for Boone Trail Nugget Company features a hiker eating a bowl of cereal on a mountaintop. Upon what type of learning does this type of advertisement rely? Explain your answer.
5. What habitat features would a rattlesnake examine when looking for a place to live?