involves learning. To test this hypothesis, diagrammatic pictures of gull heads were painted on small cards, and then eggs were collected in the field. The eggs were hatched in a dark incubator to eliminate visual stimuli before the test. On the day of hatching, each chick was allowed to make about a dozen pecks at the model. The chicks were returned to the nest, and then each was retested. The tests showed that on the average, only one-third of the pecks by a newly hatched chick strike the model. But one day after hatching, more than half of the pecks are accurate, and two days after hatching, the accuracy reaches a level of more than 75%. Investigators concluded that improvement in motor skills, as well as visual experience, strongly affect development of chick begging behavior.

Imprinting

Imprinting is considered a form of learning. Imprinting was first observed in birds when chicks, ducklings, and goslings followed the first moving object they saw after hatching. This object is ordinarily their mother. Imprinting in the wild, rather than in the laboratory, has survival value and leads to reproductive success, because it leads to being able to recognize one's species and, therefore, an appropriate mate.

But in the laboratory, investigators found that birds can seemingly be imprinted on any object—a human or a red ball—if it is the first moving object they see during a sensitive period of two to three days after hatching. The term *sensitive period* means that the behavior develops only during this time.

A chick imprinted on a red ball follows it around and chirps whenever the ball is moved out of sight. Social interactions between parent and offspring during the sensitive period seem key to normal imprinting. For example, female mallards cluck during the entire time imprinting is occurring, and it could be that vocalization before and after hatching is necessary to normal imprinting.

Goslings imprinted on an investigator

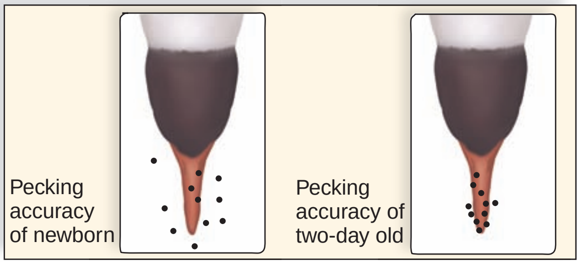
Social Interactions and Learning

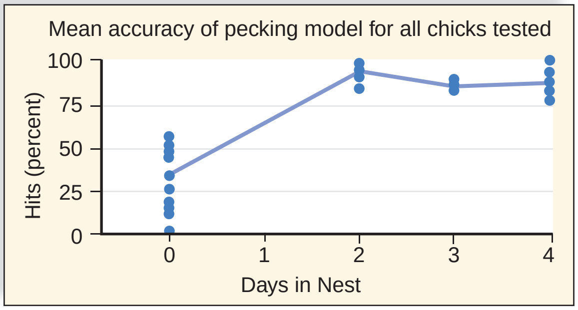
White-crowned sparrows sing a species-specific song, but males of a particular region have their own dialect. Birds were caged in order to test the hypothesis that young white-crowned sparrows learn how to sing from older members of their species.

Three groups of birds were tested. Birds in the first group *heard no songs at all.* When grown, these birds sang a song, but it was not fully developed. Birds in the second group *heard tapes of white-crowns singing.* When grown, they sang in that dialect, as long as the tapes had been played during a sensitive period from about age 10–50 days. White-crowned sparrows' dialects (or other species' songs) played before or after this sensitive period had no effect on the birds. Birds in a third group did not hear tapes and instead were *given an adult tutor.* These birds sang a song of a different species—no matter when the tutoring began—showing that social interactions apparently assist learning in birds.

FIGURE 43.4 Pecking behavior in laughing gulls.

At about three days, a laughing gull chick grasps the red bill of a parent, stroking it downward, and the parent then regurgitates food. *Right:* The top diagrams show the accuracy of a chick when striking a test probe, painted red. The bottom diagram shows chick-pecking accuracy graphically. Note from these diagrams that a chick markedly improves its ability (within only two days) to peck a bill, a behavior that normally causes a parent to regurgitate food.





Associative Learning

A change in behavior that involves an association between two events is termed **associative learning.** For example, birds that get sick after eating a monarch butterfly no longer prey on monarch butterflies, even though they may be readily available. Or the smell of fresh baked bread may entice you, even though you may have just eaten. If so, perhaps you associate the taste of bread with a pleasant memory, such as being at home. Both classical conditioning and operant conditioning are examples of associative learning.

Classical Conditioning

In **classical conditioning,** the paired presentation of two different types of stimuli (at the same time) causes an animal to form an association between them. The best-known laboratory example of classical conditioning is that of an experiment done by the Russian psychologist Ivan Pavlov. First, Pavlov observed that dogs salivate when presented with food. Then, he rang a bell whenever the dogs were fed. Eventually, the dogs would salivate whenever the bell was rung, regardless of whether food was present (Fig. 43.5).

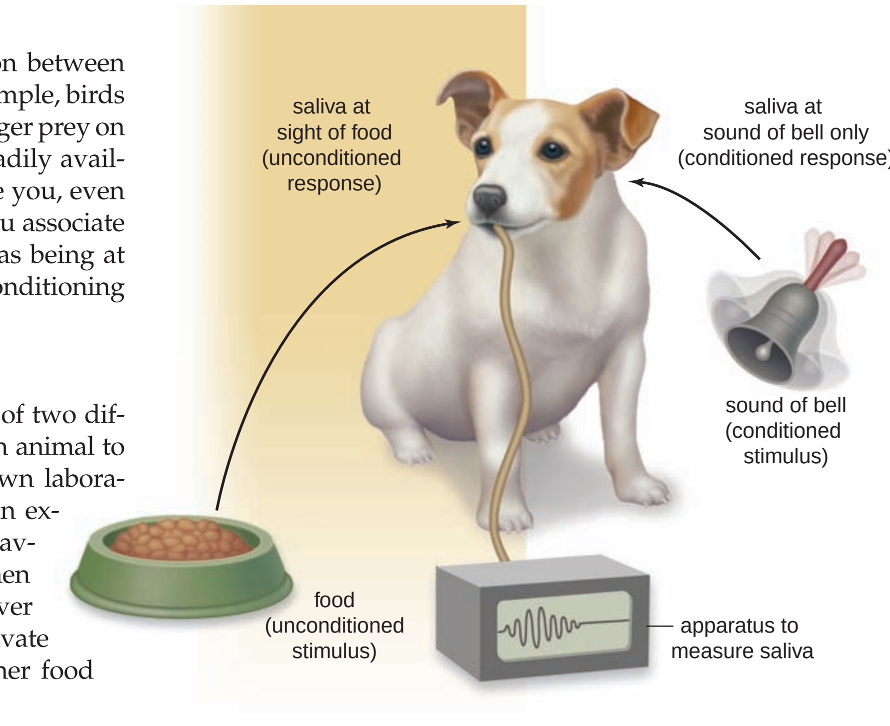


FIGURE 43.5 Classical conditioning.

Ivan Pavlov discovered classical conditioning by performing this experiment with dogs. A bell is rung when a dog is fed food. Salivation is noted. Eventually, the dog salivates when the bell is rung, even though no food is presented. Food is an unconditioned stimulus, and the sound of the bell is a conditioned stimulus that brings about the response—that is, salivation.

Classical conditioning suggests that an organism can be trained—that is, conditioned—to associate any response to any stimulus. Unconditioned responses are those that occur naturally, as when salivation follows the presentation of food. Conditioned responses are those that are learned, as when a dog learns to salivate when it hears a bell. Advertisements attempt to use classical conditioning to sell products. Why do commercials pair attractive people with a product being advertised? The hope is that viewers will associate attractiveness with the product. This pleasant association may cause them to buy the product.

Some types of classical conditioning can be helpful. For example, it's been suggested that you hold a child on your lap when reading to them. Why? Because the child will associate a pleasant feeling with reading.

Operant Conditioning

During **operant conditioning,** a stimulus-response connection is strengthened. Most people know that it is helpful to give an animal an award, such as food or affection, when teaching it a trick. When we go to an animal show, it is quite obvious that trainers use operant conditioning. They present a stimulus, say, a hoop, and then give a reward (food) for the proper response (jumping through the hoop). Sometimes the reward need not be immediate. In latent operant conditioning, an animal makes an association without the immediate reward, as when squirrels make a mental map of where they have hidden nuts.

B. F. Skinner is well known for studying this type of learning in the laboratory. In the simplest type of experiment performed by Skinner, a caged rat happens to press a lever and is rewarded with sugar pellets, which it avidly consumes. Thereafter, the rat regularly presses the lever whenever it wants a sugar pellet. In more sophisticated experiments, Skinner even taught pigeons to play Ping-Pong by reinforcing desired responses to stimuli.

As an example in child rearing again, it's been suggested that parents who give a positive reinforcement for good behavior will be more successful than parents who punish behaviors they believe are undesirable.

Orientation and Migratory Behavior

Migration is long-distance travel from one location to another. Loggerhead sea turtles hatch on a Florida beach and then travel across the Atlantic Ocean to the Mediterranean Sea, which offers an abundance of food. After several years, pregnant females return to the same beaches to lay their eggs. Every year, monarch butterflies fly from North America to Mexico where they can continue breeding because milkweed plants are still available there to serve as a source of food for their larvae.

At the very least, migration requires **orientation,** the ability to travel in a particular direction, such as south in the winter and north in the spring. Most of the work regarding orientation has been done in birds. Many birds can use the sun during the day or the stars at night to orient themselves. The sun moves across the sky during the day, but the birds are able to compensate for this because they have a sense of time. They are presumed to have a biological clock that

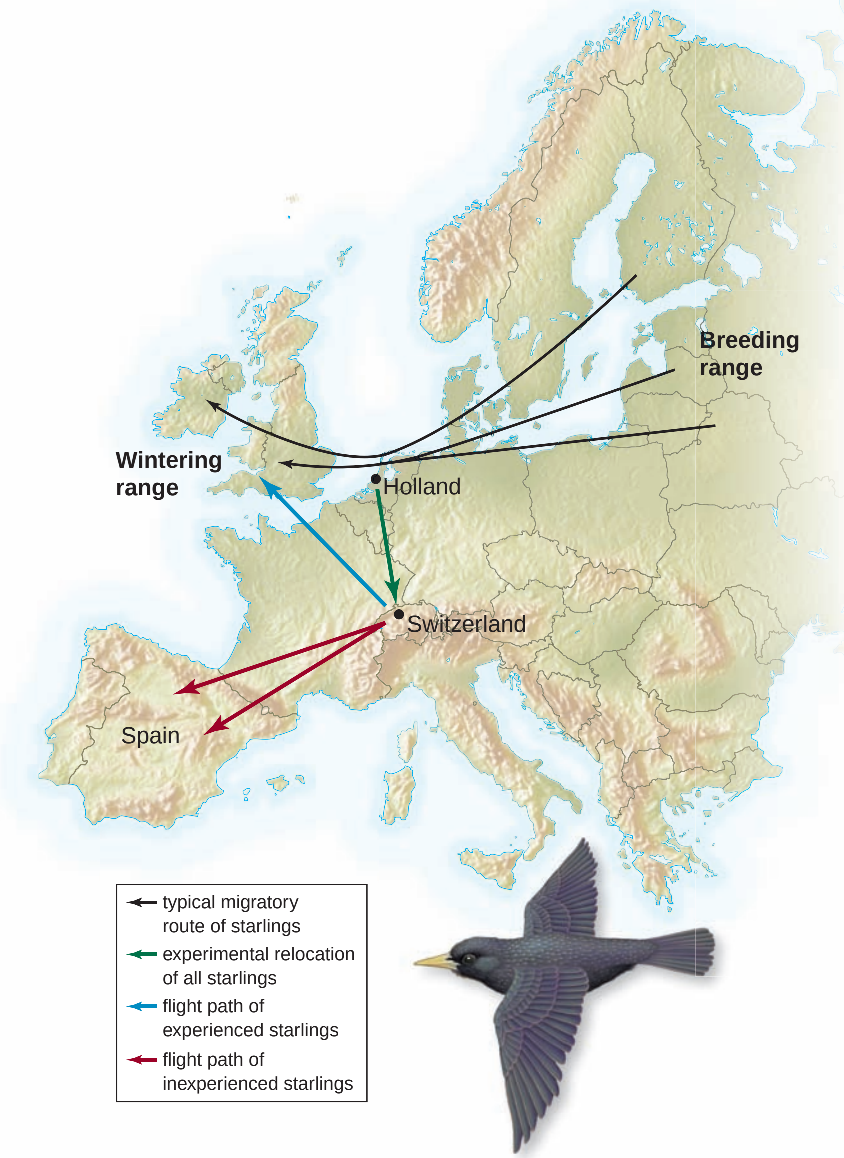


FIGURE 43.6 Starling migratory experiment.

Starlings, *Sturnus vulgaris,* on their way from the Baltics to Great Britain were captured and released in Switzerland. Inexperienced birds kept flying in the same direction and ended up in Spain. Experienced birds had learned to navigate, as witnessed by the fact that they still arrived in Great Britain.

allows them to know where the sun will be in relation to the way they should be going any time of the day.

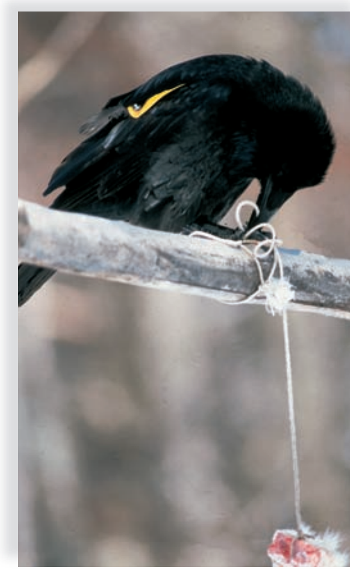
Experienced birds can also **navigate.** They are able to change their direction in response to other environmental clues that tell them they are currently headed in the wrong direction. These clues are apt to come from the Earth's magnetic field. Figure 43.6 shows a study that was done with starlings, which typically migrate from the Baltics to Great Britain and return. Test starlings were captured in Holland and transported to Switzerland. Experienced birds corrected their flight pattern and still got to Great Britain. Young, inexperienced birds ended up in Spain instead of Great Britain!

Migratory behavior has a proximate cause and an ultimate cause. The proximate cause is due to environmental stimuli that tell the birds it is time to travel. The ultimate cause is due to the possibility of reaching a more favorable environment for survival and reproduction. Is the benefit worth the cost—the dangers of the journey? It must be, or else the behavior would not have arisen.

Cognitive Learning

In addition to the modes of learning already discussed, animals may learn through imitation and insight. Many organisms learn through observation and imitation. For example, Japanese macaques learn to wash sweet potatoes before eating them by imitating others.

Insight learning occurs when an animal suddenly solves a problem without any prior experience with the situation. The animal appears to call upon prior experience with other circumstances to solve the problem. For example, chimpanzees have been observed stacking boxes to reach bananas in laboratory settings. Other animals too, aside from primates, seem to be able to reason things out. In one experiment, ravens were offered meat that was attached to string hanging from a branch in a confined aviary. The ravens were accustomed to eating meat, but had no knowledge of how strings work. It took several hours but eventually one raven flew to the branch, reached down, grabbed the string with its beak, and pulled the string up over and over again, each time securing the string with its foot. Eventually, the meat was within reach, and the raven was able to grab the meat with its beak. Other ravens were then able to also perform this behavior.



Ravens learn to retrieve food.

Can animals also plan ahead? It seems so. A sea otter saves a particular rock to act as a hard surface against which to bash open clams. A chimpanzee strips leaves off a twig, which it then uses to secure termites from a termite nest.

If animals can think, do they have emotions? This too is an unexplored area that is now an area of interest. The Science Focus reading on page 806 explores the possibility that animals have emotions and they can feel pain.

Check Your Progress 43.2

1. What type of learning occurs when an animal no longer tries to eat bumblebees after being stung by one?
2. Give an example that shows how instinct and learning may interact as behavior develops.
3. Cite evidence that animals have cognitive abilities.

science focus

Do Animals Have Emotions?

In recent years, investigators have become interested in determining whether animals have emotions. The body language of animals can be interpreted to suggest that animals do have feelings. When wolves reunite, they wag their tails to and fro, whine, and jump up and down; elephants vocalize—emit their "greeting rumble"—flay their ears, and spin about. Many young animals play with one another or even with themselves, as when dogs chase their own tails. On the other hand, upon the death of a friend or parent, chimps are apt to sulk, stop eating, and even die. It seems reasonable to hypothesize that animals are "happy" when they reunite, "enjoy" themselves when they play, and are "depressed" over the loss of a close friend or relative. Even people who rarely observe animals usually agree about what an animal must be feeling when it exhibits certain behaviors (Fig. 43A).

In the past, scientists found it expedient to collect data only about observable behavior and to ignore the possible mental state of the animal. Why? Because emotions are personal, and no one can ever know exactly how another animal is feeling. B. F. Skinner, whose research method is described earlier in this chapter, regarded animals as robots that become conditioned to respond automatically to a particular stimulus. He and others never considered that animals might have feelings. But now, some scientists believe they have sufficient data to suggest that at least other vertebrates and/or mammals do have feelings, including fear, joy, embarrassment, jealousy, anger, love, sadness, and grief. And they believe that those who hypothesize otherwise should have to present the opposing data.

Perhaps it would be reasonable to consider the suggestion of Charles Darwin, the father of evolution, who said that animals are different in degree rather than in kind. This means that all animals can, say, feel love, but perhaps not to the degree that humans can. B. Würsig watched the courtship of two baleen whales. They touched, caressed, rolled side-by-side, and eventually swam off together. He wondered if their behavior indicated they felt love for one another. When you think about it, it is unlikely that emotions first appeared in humans with no evolutionary homologies in animals.

Iguanas, but not fish and frogs, tend to stay where it is warm. M. Cabanac has found that warmth makes iguanas experience a rise in body temperature and an increase in heart rate. These are biological responses associated with emotions in humans. Perhaps the ability of animals to feel pleasure and displeasure is a mental state that rises to the level of consciousness.

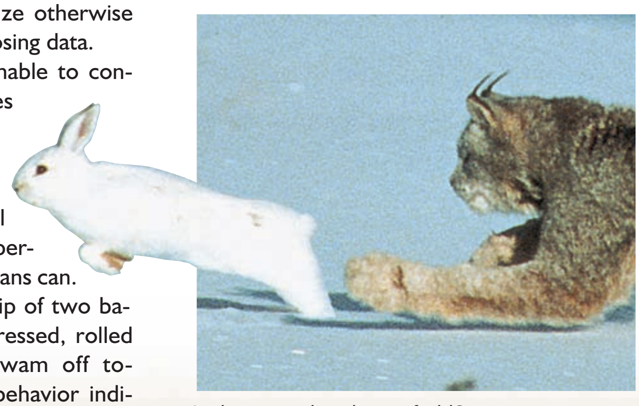
Neurobiological data support the hypothesis that other animals, aside from humans, are capable of enjoying themselves when they perform an activity such as play. Researchers have found a high level of dopamine in the brain when rats play, and the dopamine level increases even when rats anticipate the opportunity to play. Certainly even the staunchest critic is aware that many different species of animals have limbic systems and are capable of fight-or-flight responses to dangerous situations. Can we go further and suggest that animals feel fear even when no physiological response has yet occurred?

Laboratory animals may be too stressed to provide convincing data on emotions; we have to consider that emotions evolved under an animal's normal environmental conditions. This makes field research more useful. It is possible to fit animals with devices that transmit information on heart rate, body temperature, and eye movements as they go about their daily routine. Such information will help researchers learn how animal emotions might correlate with their behavior, just as emotions influence human behavior. One possible definition describes emotion as a psychological phenomenon that helps animals direct and manage their behavior.

M. Bekoff, who is prominent in the field of animal behavior, encourages us to be open to the possibility that animals have emotions. He states:

> By remaining open to the idea that many animals have rich emotional lives, even if we are wrong in some cases, little truly is lost. By closing the door on the possibility that many animals have rich emotional lives, even if they are very different from our own or from those of animals with whom we are most familiar, we will lose great opportunities to learn about the lives of animals with whom we share this wonderous planet.[1]

[1]Bekoff, M. Animal emotions: Exploring passionate natures. October 2000. *Bioscience 50:10*, page 869.



Is the snowshoe hare afraid?

Is the young chimp comforted?

FIGURE 43A Emotions in animals.

43.3 Animal Communication

Animals exhibit a wide diversity of social behaviors. Some animals are largely solitary and join with a member of the opposite sex only for the purpose of reproduction. Others pair, bond, and cooperate in raising offspring. Still others form a **society** in which members of a species are organized in a cooperative manner, extending beyond sexual and parental behavior. We have already mentioned the social groups of naked mole rats, baboons, and red deer (see page 292). Social behavior in these and other animals requires that they communicate with one another.

Communicative Behavior

Communication is an action by a sender that may influence the behavior of a receiver. The communication can be purposeful, but it does not have to be. Bats send out a series of sound pulses and listen for the corresponding echoes to find their way through dark caves and locate food at night. Some moths have an ability to hear these sound pulses, and they begin evasive tactics when they sense that a bat is near. Are the bats purposefully communicating with the moths? No, bat sounds are simply a cue to the moths that danger is near.

Chemical Communication

Chemical signals have the advantage of being effective both night and day. The term **pheromone** [Gk. *phero,* bear, carry, and *monos,* alone] designates chemical signals in low concentration that are passed between members of the same species. Some animals are capable of secreting different pheromones, each with a different meaning. Female moths secrete chemicals from special abdominal glands, which are detected downwind by receptors on male antennae. The antennae are especially sensitive, and this ensures that only male moths of the correct species (not predators) will be able to detect them.

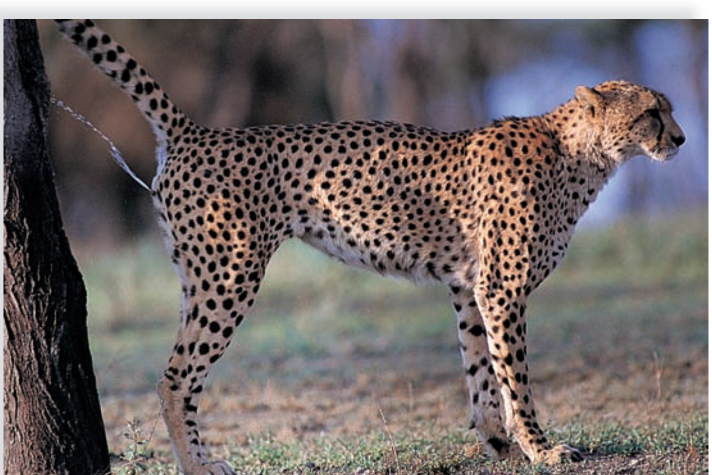


FIGURE 43.7 Use of a pheromone.

This male cheetah is spraying urine onto a tree to mark its territory.

Ants and termites mark their trails with pheromones. Cheetahs and other cats mark their territories by depositing urine, feces, and anal gland secretions at the boundaries (Fig. 43.7). Klipspringers (small antelope) use secretions from a gland below the eye to mark twigs and grasses of their territory. Pheromones are known to control the behavior of social insects, as when workers slavishly care for the offspring produced by a queen.

To what degree do pheromones, in addition to hormones, affect the behavior of mammals, even humans, determining whether they carry out parental care, become agressive, or engage in courtship behavior? Some researchers maintain that human behavior is influenced by undetectable pheromones wafting through the air. They have discovered that like the mouse, humans have an organ in the nose, called the vomeronasal organ (VNO), that can detect not only odors, but also pheromones. The neurons from this organ lead to the hypothalamus, the part of the brain that controls the release of many hormones in the body. One investigator has isolated and plans to market a perfume containing a pheromone released by men that appears to reduce premenstrual nervousness and tension in women.

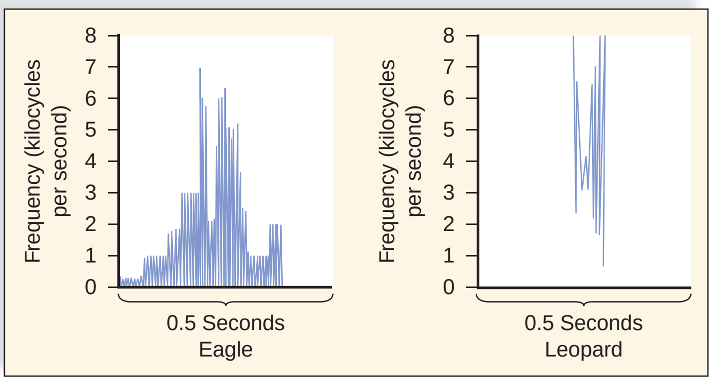
Auditory Communication

Auditory (sound) **communication** has some advantages over other kinds of communication. It is faster than chemical communication, and it too is effective both night and day. Further, auditory communication can be modified not only by loudness but also by pattern, duration, and repetition. In an experiment with rats, a researcher discovered that an intruder can avoid attack by increasing the frequency with which it makes an appeasement sound.

Male crickets have calls, and male birds have songs for a number of different occasions. For example, birds may have one song for distress, another for courting, and still another for marking territories. Sailors have long heard the songs of humpback whales transmitted through the hull of a ship. But only recently has it been shown that the song has six basic themes, each with its own phrases, that can vary in length and be interspersed with sundry cries and chirps. The purpose of the song is probably sexual, serving to advertise the availability of the singer. Bottlenose dolphins have one of the most complex languages in the animal kingdom.

Language is the ultimate auditory communication. Only humans have the biological ability to produce a large number of different sounds and to put them together in many different ways. Nonhuman primates have different vocalizations, each having a definite meaning, such as when vervet monkeys give alarm calls (Fig. 43.8). Although chimpanzees can be taught to use an artificial language, they never progress beyond the capability level of a two-year-old child. It has also been difficult to prove that chimps understand the concept of grammar or can use their language to reason. It still seems as if humans possess a communication ability unparalleled by other animals.

a.



b.

FIGURE 43.8 **Auditory communication.**

a. Vervet monkeys, *Cercopithecus aethiops*, are responding to an alarm call. Vervet monkeys can give different alarm calls according to whether a troop member sights an eagle or a leopard, for example. **b.** The frequency per second of the sound differs for each type call.

FIGURE 43.9 **Male baboon displaying full threat.**

In baboons, males are larger than females and have enlarged canines. Competition involving displaying the canines establishes a dominance hierarchy among males for the distribution of resources and access to females. This is a chacma baboon, *Papio ursinus*.

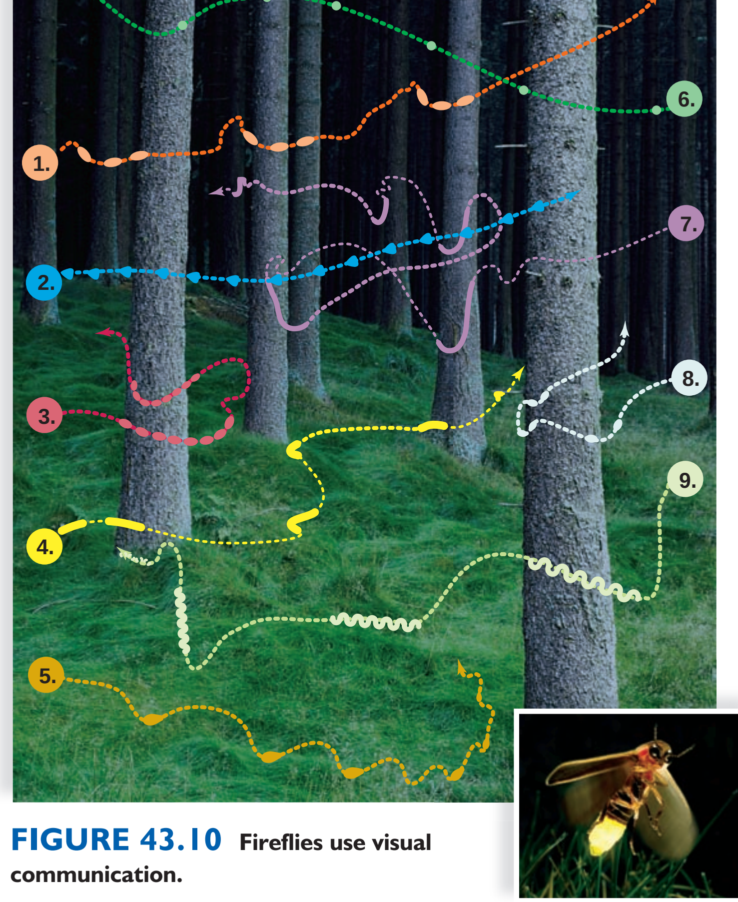


FIGURE 43.10 **Fireflies use visual communication.**

Each number represents the male flash pattern of a different species. The patterns are a behavorial reproductive isolation mechanism.

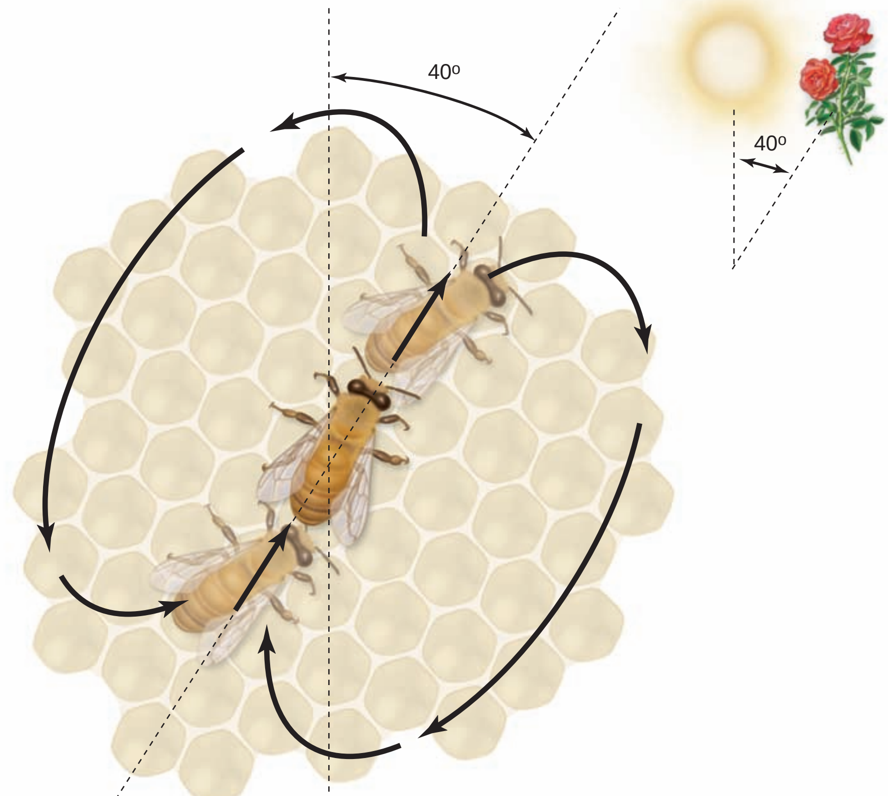
Visual Communication

Visual signals are most often used by species that are active during the day. Contests between males make use of threat postures and possibly prevent outright fighting, a behavior that might result in reduced fitness. A male baboon displaying full threat is an awesome sight that establishes his dominance and keeps peace within the baboon troop (Fig. 43.9). Hippopotamuses perform territorial displays that include mouth opening.

Many animals use complex courtship behaviors and displays. The plumage of a male Raggiana Bird of Paradise allows him to put on a spectacular courtship dance to attract a female, giving her a basis on which to select a mate. Defense and courtship displays are exaggerated and always performed in the same way so that their meaning is clear. Fireflies use a flash pattern to signal females of the same species (Fig. 43.10).

Visual communication allows animals to signal others of their intentions without the need to provide any auditory or chemical messages. The body language of students during a lecture provides an example. Some students lean forward in their seats and make eye contact with the instructor. They want the instructor to know they are interested and find the material of value. Others lean back in their chairs and look at the floor or doodle. These students indicate they are not interested in the material. Teachers can use students' body language to determine if they are effectively presenting the material and make changes accordingly.

a.



b.

FIGURE 43.11 Communication among bees.

a. Honeybees do a waggle dance to indicate the direction of food. **b.** If the dance is done outside the hive on a horizontal surface, the straight run of the dance will point to the food source. If the dance is done inside the hive on a vertical surface, the angle of the straightaway to that of the direction of gravity is the same as the angle of the food source to the sun.

Other human behaviors also send visual clues to others. The hairstyle and dress of a person or the way he or she walks and talks are ways to send messages to others. Some studies have suggested that women are apt to dress in an appealing manner and be sexually inviting when they are ovulating. People who dress in black, move slowly, fail to make eye contact, and sit alone may be telling others that they are unhappy. Psychologists have long tried to understand how visual clues can be used to better understand human emotions and behavior. Similarly, body language in animals is being used by researchers to suggest that they, as well as humans, have emotions.

Tactile Communication

Tactile communication occurs when one animal touches another. For example, laughing gull chicks peck at the parent's bill to induce the parent to feed them (see Fig. 43.4). A male leopard nuzzles the female's neck to calm her and to stimulate her willingness to mate. In primates, grooming—one animal cleaning the coat and skin of another—helps cement social bonds within a group.

Honeybees use a combination of communication methods, but especially tactile ones, to impart information about the environment. When a foraging bee returns to the hive, it performs a waggle dance that indicates the distance and the direction of a food source (Fig. 43.11). As the bee moves between the two loops of a figure 8, it buzzes noisily and shakes its entire body in so-called waggles. Outside the hive, the dance is done on a horizontal surface, and the straight run indicates the direction of the food. Inside the hive, the angle of the straight run to that of the direction of gravity is the same as the angle of the food source with the sun. In other words, a 40° angle to the left of vertical means that food is 40° to the left of the sun.

Bees can use the sun as a compass to locate food because they have a biological clock, which allows them to compensate for the movement of the sun in the sky. A biological clock is an internal means of telling time. Today, we know that the ticking of the clock, in both insects and mammals (including humans), requires alterations in the expression of a gene called *period.*

Check Your Progress 43.3

1. Give evidence that communication is meant to affect the behavior of the receiver.
2. Give an advantage and disadvantage to each type of communication discussed.
3. State the human receptor for each type of communication discussed.

43.4 Behaviors That Increase Fitness

Behavioral ecology assumes that behavior is subject to natural selection. We have established that behavior has a genetic basis, and we would expect that certain behaviors more than others will lead to increased survival and number of offspring. Therefore, the behavior of organisms we can observe today must have adaptive value. These types of behaviors in particular have been studied for their adaptive value.

Territoriality and Fitness

In order to gather food, animals often have a particular home range where they can be found during the course of the day. One portion of the range can be defended for their exclusive use and other members of their species are not welcome there. This portion of the home range is called their **territory** and the behavior is called **territoriality.** An animal's territory may have a good food source and/or may be the area in which they will reproduce.

For example, gibbons live in the tropical rain forest of South and Southeast Asia. Normally, their home range can be covered in about 3–4 days, and they are also monogamous and territorial. Territories are maintained by loud singing (Fig. 43.12). Males sing just before sunrise, and mated pairs sing duets during the morning. Males, but not females, show evidence of fighting to defend their territory in the form of broken teeth and scars. Obviously, defense of a territory has a certain cost; it takes energy to sing and fight off others. Also, you might get hurt. So, what is the adaptive value of being territorial? Chief among the benefits of territoriality are to ensure a source of food, exclusive rights to one or more females, and to have a place to rear young and possibly to protect yourself from predators. The territory has to be the right size for the animal. Too large a territory cannot be defended, and too small a territory may not contain enough food. Cheetahs require a large territory in order to hunt for their prey and, therefore, they use means of marking their territory that will last for a while. As shown in Figure 43.7, cheetahs, like many dogs, use urine to mark their territory. Hummingbirds are known to defend a very small territory because they depend on only a small patch of flowers as their food source.

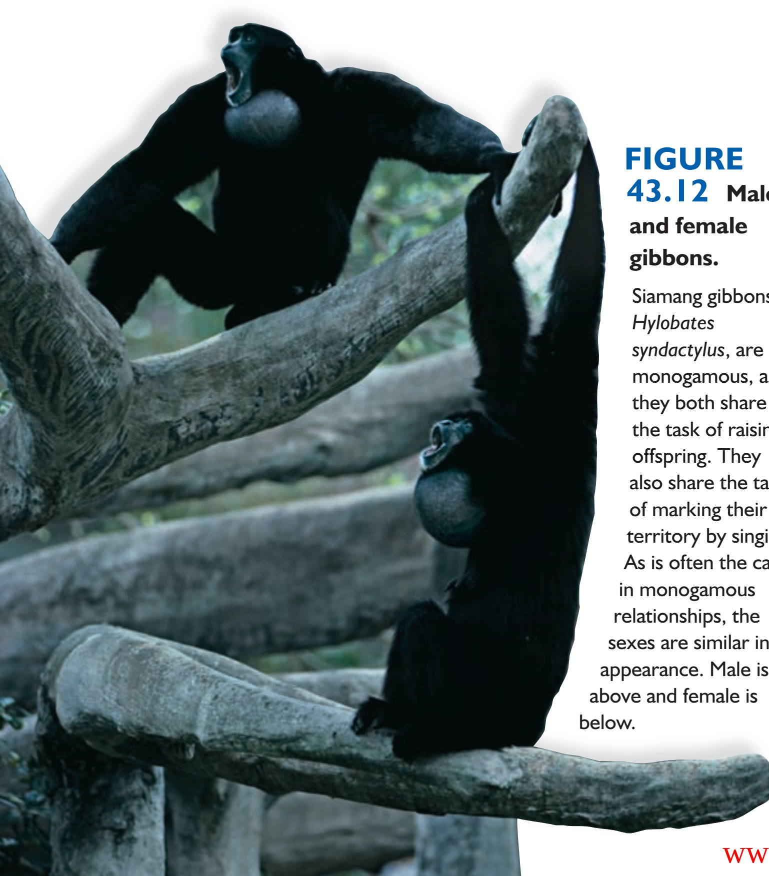


FIGURE 43.12 Male and female gibbons. Siamang gibbons, *Hylobates syndactylus*, are monogamous, and they both share the task of raising offspring. They also share the task of marking their territory by singing. As is often the case in monogamous relationships, the sexes are similar in appearance. Male is above and female is below.

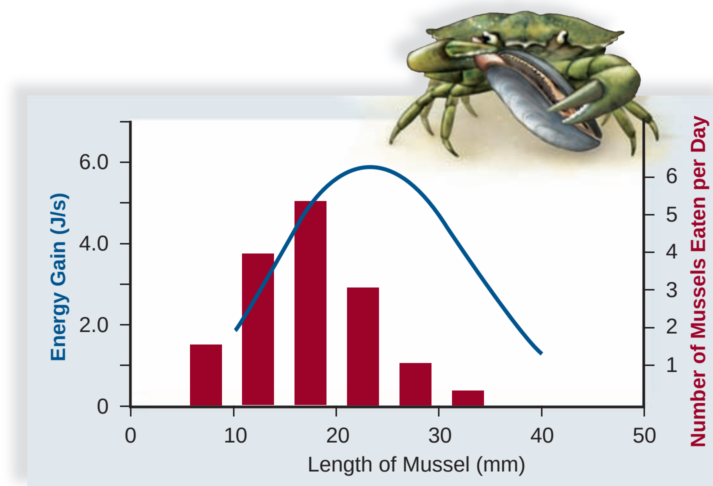


FIGURE 43.13 Foraging for food.

When offered a choice of an equal number of each size of mussel, the shore crab, *Carcinus maenas*, prefers the intermediate size. Their size provides the highest rate of net energy return. Net energy is determined by the yield per time used in breaking open the shell.

Territoriality is more likely to occur during times of reproduction. Seabirds have very large home ranges consisting of hundreds of kilometers of open ocean, but when they reproduce they become fiercely territorial. Each bird has a very small territory consisting of only a small patch of beach where they place their nest.

Foraging for Food

Food gathering is technically called foraging for food. A concern for an animal is to acquire a food source that will provide more energy than the effort of acquiring the food. In one study, it was shown that shore crabs eat intermediate-sized mussels because the net energy gain was more than if they ate larger-sized mussels (Fig. 43.13). The large mussels take too much energy to open per the amount of energy they provide. The **optimal foraging model** states that it is adaptive for foraging behavior to be as energetically efficient as possible.

Even though it can be shown that animals that take in more energy are the ones that are likely to have more offspring, animals often have to consider other factors such as escaping from predation. If an animal is killed and eaten, it has no chance at all of having offspring. Animals often face trade-offs that cause them to modify their behavior or even stop foraging for a while.

FIGURE 43.14 Hamadryas baboons.

Among Hamadryas baboons, *Papio hamadryas,* a male, which is silver-white and twice the size of a female, keeps and guards a harem of females with whom he mates exclusively.

FIGURE 43.15 Competition.

During the mating season, bull elk, *Cervus elaphus,* males may find it necessary to engage in antler wrestling in order to have sole access to females in a territory.

Reproductive Strategies and Fitness

Usually, primates are **polygamous,** and males monopolize multiple females. Because of gestation and lactation, females invest more in their offspring than do males and may not always be available for mating. Under these circumstances, it is adaptive for females to be concerned with a good food source. When food sources are clumped, females congregate in small groups. Because only a few females are expected to be receptive at a time, males will likely be able to defend these few from other males. Males are expected to compete with other males for the limited number of receptive females available (Fig. 43.14).

A limited number of primates are **polyanthrus.** Tamarins are squirrel-sized New World monkeys that live in Central or South America. Tamarins live together in groups of one or more families in which one female mates with more than one male. The female normally gives birth to twins of such a large size that the fathers, and not the mother, carry it about. This may be the reason these animals are polyanthrus. Polyandry also occurs when the environment does not have sufficient resources to support several young at a time.

We have already mentioned the reproductive strategy of gibbons. They are **monogamous,** which means that they pair bond, and both male and female help with the rearing of the young. Males are active fathers, frequently grooming and handling infants. Monogamy is relatively rare in primates, which includes prosimians, monkeys, and apes (only about 18% are monogamous). In primates, monogamy occurs when males have limited mating opportunities, territoriality exists, and the male is fairly certain the offspring are his. In gibbons, females are evenly distributed in the environment, most likely because they are aggressive to one another. Investigators note that females do attack a speaker when it plays female sounds in their territory.

Sexual Selection

Sexual selection is a form of natural selection that favors features that increase an animal's chances of mating. In other words, these features are adaptive in the sense that they lead to increased fitness.

Sexual selection often results in female choice and male competition. Because females produce only one egg a month, it is adaptive for them to be choosy about their mate. If they choose a mate that passes on features to a male offspring that will cause him to be chosen by females, their fitness has increased. Whether females choose features that are adaptive to the environment is in question. For example, peahens are likely to choose peacocks that have the most elaborate tails. Such a fancy tail could otherwise be detrimental to the male and make him more likely to be captured by a predator. In one study, an extra ornament was attached to a father zebra finch and the daughters of this bird underwent the process of imprinting (see page 803). Now, these females were more likely to choose a mate that also had the same artificial ornament.

While females can always be sure an offspring is theirs, males do not have this certainty. However, males produce a plentiful supply of sperm. The best strategy for males to increase their fitness, therefore, is to have as many offspring as possible. Competition may be required for them to gain access to females, and ornaments, such as antlers, can enhance a male's ability to fight (Fig. 43.15). When bull elk compete, they issue a loud number of screams that gives way to a series of grunts. If still necessary, the two bulls walk in parallel to show each other their physique. If this doesn't convince one or the other to back off, the pair resorts to ramming each other with their antlers. Rarely is either bull actually hurt. Whereas a peacock cannot shed his tail, elk shed their antlers as soon as mating season is over.

science focus

Sexual Selection in Male Bowerbirds

At the start of the breeding season, male bowerbirds use small sticks and twigs to build elaborate display areas called bowers (Fig. 43B). They clear the space around the bower and decorate the area with fresh flowers, fruits, pebbles, shells, bits of glass, tinfoil, and any bright baubles they can find. The Satin Bowerbird of eastern Australia prefers blue objects, a color that harmonizes with the male's glossy blue-back plumage. Males collect blue parrot feathers, flowers, berries, ballpoint pens, clothespins, and even toothbrushes from researchers' cabins.

After the bower is complete, a male bowerbird spends most of his time near this bower, calling to females, renewing his decorations, and guarding his work against possible raids by other males. After inspecting many bowers and their owners, a female approaches one, and the male begins a display. He faces her, fluffs up his feathers, and flaps his wings to the beat of a call. The female enters the bower, and if she crouches, the two mate.

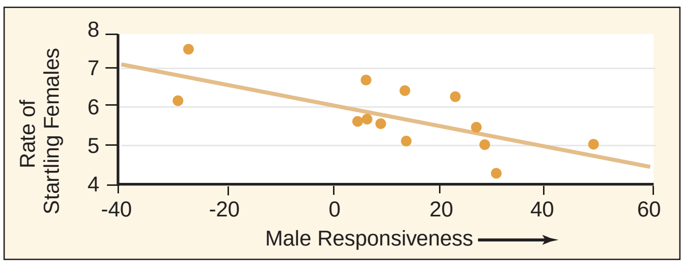
Female bowerbirds build their own nests and raise the young without help from their mates, so attractive males can mate with multiple females. The reproductive advantage gained by attractive male bowerbirds is quite large; the most attractive males may mate with up to 25 females per year, but most males mate rarely or not at all. As already discussed, Dr. [Gerald] Borgia found that the males most often chosen by females have well-built bowers with well-decorated platforms. In addition, it is possible that the ability of a male bowerbird to respond appropriately to the female during courtship might influence his success. I [Gail Patricelli] and my colleagues studied this interactive component of Satin Bowerbird mating behavior as part of my doctoral dissertation research at the University of Maryland, in collaboration with Dr. Borgia, my graduate advisor.

Male bowerbirds are not gaudy in appearance, but their displays are highly intense and aggressive. Their courting displays are similar to those used by males to intimidate each other in aggressive encounters—with males puffing their feathers, rapidly extending their wings, and running, while making a loud, buzzing vocalization. Analysis of natural courtships has shown that males must display

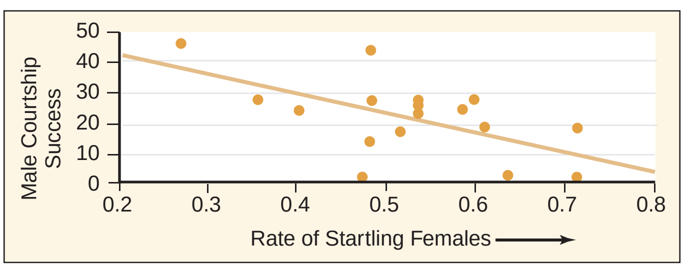
FIGURE 43B Male and female bowerbird.
Among Satin Bowerbirds, Ptilonorhynchus violaceus, *the male bowerbird (right) has prepared this bower and decorated its platform with particularly blue objects. A female bowerbird (left) has entered the bower and a male courtship display will now begin.*

intensely to be attractive, *but males that are too intense too soon can startle females*. Females may benefit from preferentially mating with the most intensely displaying males (e.g., if these displays indicate male health or vigor), but when females are startled repeatedly by male displays, they may not be able to efficiently assess male traits. Thus both sexes can maximize the potential benefits of intense male courtship displays—and minimize the potential costs—by communicating. Indeed, a female behavior (degree of crouching) reflects the level of display intensity that the female will tolerate without being startled. By giving higher-intensity displays only when females increase their crouching, males could increase their courtship success by displaying intensely enough to be attractive without threatening females with displays more intense than they are ready to tolerate.

With this information in mind, we specifically tested the hypothesis that males respond to female crouching signals by adjusting their intensity, and that a particular male's ability to respond to female signals is related to his success in courtship. A male's ability to modify his courtship display according to the rapidity with which the female crouches was difficult



a.



b.

FIGURE 43C Courtship success of males.
Some males have more courtship success than others. This experiment may explain why. ***a.*** *An experimenter using a remote control (photograph) can regulate the crouch rate of a robotic female. Some males are better able than others to vary the intensity of their courtship depending on the crouch rate of the robotic female (top graph). In other words, only if the robotic female crouches more do they respond more. Therefore, they are predicted to startle females less.* ***b.*** *Experimenters found that males who respond best under experimental conditions do startle live females less and do have better courtship success.*

to measure in natural courtships, since it was not clear whether males were responding to females, or vice versa. To solve this problem, we collaborated with an engineer to develop robotic female bowerbirds, which used tiny servo motors to mimic female movements (Fig. 43C *right*).

Using these "fembots," we were able to control female signals and measure male response in experimental courtships. During the bowerbird mating season at our field site in Wallaby Creek, Australia, we worked with student volunteers to test each male in our population with robots that crouched at four different rates: no crouch, slow, moderate, and fast. These experiments showed that male Satin Bowerbirds in general modulate their displays in response to robotic female crouching (Fig. 43C*a*). This supports the prediction that males are able to respond to female signals by giving their highest-intensity courtship displays for females who crouched the fastest and are least likely to be startled.

Utilizing automatically triggered video cameras that monitor behaviors at bowers, it was possible to measure each male's courtship/mating success with no difficulty. We found that males who modulate their displays more effectively in response to robotic female signals startle real females less often in natural courtships, and are thus more successful in courting females (Fig. 43C*b*).

Our results suggest that females prefer intensely displaying males as mates, but that successful males do not always display at maximum intensity; they modulate their intensity in response to female signals, thus producing displays attractive to females without threatening them.

Male responsiveness to female signals may be an important part of successful courtship in many species—even if males do not dance aggressively during courtship like male bowerbirds. For instance, when females choose their mates based on bright coloration, successful males may respond to female signals by altering their position relative to the sun, their distance from the female, or the way they shake their tail when displaying their colors. So, along with extreme male traits—such as gaudy colors and aggressive dances—sexual selection may favor the ability of males to read female signals and adjust courtship displays accordingly.

Courtesy of Gail Patricelli
University of Maryland

Societies and Fitness

The principles of evolutionary biology can be applied to the study of social behavior in animals. Sociobiologists hypothesize that living in a society has a greater reproductive benefit than reproductive cost. A cost-benefit analysis can help determine if this hypothesis is supported.

Group living does have its benefits. It can help an animal avoid predators, rear offspring, and find food. A group of impalas is more likely to hear an approaching predator than a solitary one. Many fish moving rapidly in many directions might distract a would-be predator. Weaver birds form giant colonies that help protect them from predators, but the birds may also share information about food sources. Primate members of the same baboon troop signal to one another when they have found an especially bountiful fruit tree. Lions working together are able to capture large prey, such as zebra and buffalo.

Group living also has its disadvantages. When animals are crowded together into a small area, disputes can arise over access to the best feeding places and sleeping sites. Dominance hierarchies are one way to apportion resources, but this puts subordinates at a disadvantage. Among red deer, sons are preferable because, as a harem master, sons will result in a greater number of grandchildren. However, sons, being larger than daughters, need to be nursed more frequently and for a longer period of time. Subordinate females do not have access to enough food resources to adequately nurse sons and, therefore, they tend to rear daughters, not sons. Still, like the subordinate males in a baboon troop, subordinate females in a red deer harem may be better off in terms of fitness if they stay with a group, despite the cost involved.

Living in close quarters exposes individuals to illness and parasites that can easily pass from one animal to another. Social behavior helps to offset some of the proximity disadvantages. For example, baboons and other types of social primates invest much time in grooming one another, and this most likely helps them remain healthy. Humans use extensive medical care to help offset the health problems that arise from living in the densely populated cities of the world.

Altruism Versus Self-Interest

Altruism [L. *alter,* the other] is a behavior that has the potential to decrease the lifetime reproductive success of the altruist, while benefiting the reproductive success of another member of the society. In insect societies, especially, reproduction is limited to only one pair, the queen and her mate. For example, among army ants, the queen is inseminated only during her nuptial flight, and thereafter she spends her time reproducing (Fig. 43.16). The society has three different sizes of sterile female workers. The smallest workers (3 mm), called the nurses, take care of the queen and larvae, feeding them and keeping them clean. The intermediate-sized workers, constituting most of the population, go out on raids to collect food. The soldiers (14 mm), with huge heads and powerful jaws, run along the sides and rear of raiding parties and protect the column of ants from attack by intruders. While rare in mammals, the introduction to this chapter describes how mole rats have a similar type of societal structure.

Can the altruistic behavior of sterile workers be explained in terms of fitness, which is judged by reproductive success? Genes are passed from one generation to the next in two quite different ways. The first way is direct: A parent can pass a gene directly to an offspring. The second way is indirect: A relative that reproduces can pass the gene to the next generation. *Direct selection* is adaptation to the environment due to the reproductive success of an individual. *Indirect selection,* called **kin selection,** is adaptation to the environment due to the reproductive success of the individual's relatives. The **inclusive fitness** of an individual includes

FIGURE 43.16 Queen ant.

A queen ant, *Solenopsis geminata,* has a large abdomen for egg production and is cared for by small ants, called nurses. The idea of inclusive fitness suggests that relatives, in addition to offspring, increase an individual's reproductive success. Therefore, sterile nurses are being altruistic when they help the queen produce offspring to whom they are closely related.

personal reproductive success and the reproductive success of relatives.

Among social bees, social wasps, and ants, the queen is diploid (2n), but her mate is haploid (n). If the queen has had only one mate, sister workers are more closely related to each other. They share, on average, 75% of their genes because they inherit 100% of their father's alleles. Their potential offspring would share, on average, only 50% of their genes with the queen. Therefore, a worker can achieve a greater inclusive fitness by helping her mother (the queen) produce additional sisters than by directly reproducing. Under these circumstances, behavior that appears altruistic is more likely to evolve.

Indirect selection can also occur among animals whose offspring receive only a half set of genes from both parents. Consider that your brother or sister shares 50% of your genes, your niece or nephew shares 25%, and so on. Therefore, the survival of two nieces (or nephews) is worth the survival of one sibling, assuming they both go on to reproduce.

Among chimpanzees in Africa, a female in estrus frequently copulates with several members of the same group, and the males make no attempt to interfere with each other's matings. How can they be acting in their own self-interest? Genetic relatedness appears to underlie their apparent altruism. Members of a group share more than 50% of their genes in common because members never leave the territory in which they are born.

Reciprocal Altruism

In some bird species, offspring from a previous clutch of eggs may stay at the nest to help parents rear the next batch of offspring. In a study of Florida scrub jays, the number of fledglings produced by an adult pair doubled when they had helpers. Mammalian offspring are also observed to help their parents (Fig. 43.17). Among jackals in Africa, solitary pairs managed to rear an average of 1.4 pups, whereas pairs with helpers reared 3.6 pups. What are the benefits of staying behind to help? First, a helper is contributing to the survival of its own kin. Therefore, the helper actually gains a fitness benefit. Second, a helper is more likely than a nonhelper to inherit a parental territory—including other helpers. Helping, then, involves making a minimal, short-term reproductive sacrifice in order to maximize future reproductive potential. Therefore, helpers at the nest are also practicing a form of **reciprocal altruism.** Reciprocal altruism also occurs in animals that are not necessarily closely related. In this event, an animal helps or cooperates with another animal with no immediate benefit. However, the animal that was helped will repay the debt at some later time. Reciprocal altruism usually occurs in groups of animals that are mutually dependent. Cheaters in reciprocal altruism are recognized and not reciprocated in future events. Reciprocal altruism occurs in vampire bats that live in the tropics. Bats returning to the roost after a feeding activity share their blood meal with other bats in the roost. If a bat fails to share blood with one that had previously shared blood with it, the cheater bat will be excluded from future blood sharing.

FIGURE 43.17 Inclusive fitness.

A meerkat is acting as a babysitter for its young sisters and brothers while their mother is away. Researchers point out that the helpful behavior of the older meerkat can lead to increased inclusive fitness.

Check Your Progress 43.4

1. In what way is territoriality related to foraging for food?
2. In what way is an animal's reproductive strategy related to sexual selection.
3. Why can it be said that altruistic behavior is probably in the self-interest of the animal.

Connecting the Concepts

Birds build nests, dogs bury bones, cats chase quick-moving objects, and snakes bask in the sun. All animals, including humans, behave—they respond to stimuli, both from the physical environment and from other individuals of the same or different species. It can be shown that behaviors have a genetic basis and yet behaviors can be modified by experience. Regardless, behaviorists use an evolutionary approach to generate hypotheses that can be tested to better understand how the behavior increases individual fitness (i.e., the capacity to produce surviving offspring).

Inheritance produces the behavioral variations that are subject to natural selection, resulting in the most adaptive responses to stimuli. Still, behaviorists concede that both nature and nurture determine behavior. Genetics determines, for example, that hawks hunt by using vision rather than smell, and that cats, not dogs, climb trees. Songbirds are born with the ability to sing, but which song or dialect they sing is strongly dependent on the songs they hear from their parents and siblings. A new chimpanzee mother naturally cares for her young, but she is a better mother if she has observed other females in her troop raising young.

A behavior such as territoriality or foraging has its trade-offs, but this behavior would not have evolved unless the benefit outweighed the cost. Sexual selection explains much about mating behavior. Males are apt to compete and females to choose because this type of behavior is most apt to lead to reproductive success. Also, there is survival value, after all, in the ability of male baboons to react aggressively when the troop is under attack. There is a cost to certain behaviors. Why should older offspring help younger offspring? The evolutionary answer is that, in the end, there are benefits that outweigh the costs. Otherwise, the behavior would not continue. Similarly, group living in which animals communicate must have some benefits. The evolutionary approach to studying behavior has proved fruitful in helping us understand why birds sing their melodious songs, dolphins frolic in groups, and wondrous male Raggiana Birds of Paradise display to females.

summary

43.1 Inheritance Influences Behavior

Investigators have long been interested in the degree to which nature (genetics) or nurture (environment) influences behavior. Studies with birds, snakes, humans, snails, and mice have been done, among many others. Hybrid studies with lovebirds produce results consistent with the hypothesis that behavior has a genetic basis. Garter snake experiments indicate that the nervous system controls behavior. Twin studies in humans show that certain types of behavior are apparently inherited. *Aplysia* DNA studies indicate that the endocrine system also controls behavior.

43.2 The Environment Influences Behavior

Even behaviors formerly thought to be fixed action patterns (FAPs), or otherwise inflexible, sometimes can be modified by learning. The red bill of laughing gulls initiates chick begging behavior. However, with experience, chick begging behavior improves and the chicks demonstrate an increased ability to recognize parents.

Other studies suggest that learning is involved in behaviors. Imprinting in birds, during a sensitive period, causes them to follow the first moving object they see. Song learning in birds involves various elements—including the existence of a sensitive period, during which an animal is primed to learn—and the positive benefit of social interactions.

Associative learning includes classical conditioning and operant conditioning. In classical conditioning, the pairing of two different types of stimuli causes an animal to form an association between them. In this way, dogs will salivate at the sound of a bell. In operant conditioning, animals learn behaviors because they are rewarded when they perform them.

Orientation and migratory behavior occur in several groups of animals. Orientation is the ability to move in a certain direction, but migration can require navigation, and is a learned ability to change direction if need be. Animals use the sun, stars, and the Earth's magnetic field in order to migrate.

Imitation and insight learning does occur in animals. Insight learning has occurred when an animal can solve a new and different problem without prior experience.

43.3 Animal Communication

Communication is an action by a sender that affects the behavior of a receiver. Chemical, auditory, visual, and tactile signals are forms of communication that foster cooperation that benefits both the sender and the receiver. Pheromones are chemical signals that are passed between members of the same species. Auditory communication includes language, which may occur between other types of animals and not just humans. Visual communication allows animals to signal others without the need of auditory or chemical messages. Tactile communication is especially associated with sexual behavior.

43.4 Behaviors That Increase Fitness

Traits that promote reproductive success are expected to be advantageous overall, despite any possible disadvantage. Some animals are territorial and defend a territory where they have food resources and can reproduce. When animals choose those foods that return the most net energy, they have more energy left over for reproduction.

Reproductive strategies include monogamy, polygamy, and polyandry. Which strategy is employed depends on the animal and its environment. Sexual selection is a form of natural selection that selects for traits that increase an animal's fitness. Males produce many sperm and are expected to compete to inseminate females. Females produce few eggs and are expected to be selective about their mates.

Living in a social group can have its advantages (e.g., ability to avoid predators, raise young, and find food). It also has disadvantages (e.g., tension between members, spread of illness and parasites, and reduced reproductive potential). When animals live in groups, the benefits must outweigh the costs or the behavior would not exist.

In most instances, the individuals of a society act to increase their own fitness (ability to produce surviving offspring). In this context, it is necessary to consider inclusive fitness, which includes personal reproductive success and the reproductive success of relatives, also. Sometimes, animals perform altruistic acts, as when individuals help their parents rear siblings. Social insects help their mother reproduce, but this behavior seems reasonable when we consider that siblings share 75% of their genes. Among mammals, a parental helper may be likely to inherit the parent's territory. In reciprocal altruism, animals aid one another for future benefits.

understanding the terms

altruism 814	monogamous 811
associative learning 804	navigate 805
auditory communication 807	operant conditioning 804
behavior 800	optimal foraging model 810
behavioral ecology 810	orientation 804
classical conditioning 804	pheromone 807
communication 807	polyanthrus 811
fixed action pattern (FAP) 802	polygamous 811
imprinting 803	reciprocal altruism 815
inclusive fitness 814	sexual selection 811
insight learning 805	society 807
kin selection 814	tactile communication 809
learning 802	territoriality 810
migration 804	territory 810
	visual communication 808

Match the terms to these definitions:

a. _______________ Behavior related to defending a particular area, which is often used for the purpose of feeding, mating, and caring for young.

b. _______________ Social interaction that benefits others and has the potential to decrease the lifetime reproductive success of the member exhibiting the behavior.

c. _______________ Signal by a sender that may influence the behavior of a receiver.

d. _______________ Chemical substance secreted into the environment by one organism that may influence the behavior of another.

reviewing this chapter

1. Describe two studies that suggest behavior has a genetic basis. 800–801
2. Describe two studies that show that behavior has a genetic basis. 801–2
3. How does an experiment with laughing gull chicks support the hypothesis that environment (nurture) influences behavior? 802–3
4. Describe two types of associative learning. 804
5. Give examples of the different types of communication among members of a social group. 807–9
6. What is territoriality, and how might it increase fitness? 810
7. Name three types of reproductive strategies, and describe how they can be related to the environment. 811
8. What is sexual selection, and why does it foster female choice and male competition during mating? 811
9. Give examples of behaviors that appear to be altruistic but actually increase the inclusive fitness of an individual. 814–15

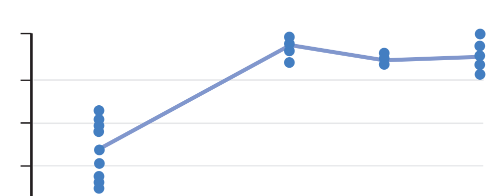
testing yourself

Choose the best answer for each question.
For questions 1–4, match the type of learning in the key with its description. Answers may be used more than once.

KEY:

a. classical conditioning
b. insight learning
c. imprinting
d. migration

1. Ducks follow the first moving object they see after hatching.
2. A dog salivates when a bell is rung.
3. Starlings fly between the Balkins and Great Britain in the fall and spring.
4. Chimpanzees pile up boxes to reach bananas.
5. Behavior is
   a. any action that is learned.
   b. all responses to the environment.
   c. any action that can be observed and described.
   d. all activity that is controlled by hormones.
   e. unique to birds and humans.
6. A behaviorist would most likely study which one of the following items?
   a. the flow of energy through an ecosystem
   b. the way a bird digests seeds
   c. the number of times a fiddler crab flashes its claw to attract a mate
   d. the structure of a horse's leg
   e. All of the above are correct.
7. Which one of the following is considered, by behaviorists, to control (in part or in whole) animal behavior?
   a. circulatory and respiratory systems
   b. respiratory and digestive systems
   c. digestive and nervous systems
   d. nervous and endocrine systems
   e. All systems of the body control behavior.
8. Which of the following is not an example of a genetically based behavior?
   a. Inland garter snakes do not eat slugs, while coastal populations do.
   b. One species of lovebird carries nesting strips one at a time, while another carries several.
   c. One species of warbler migrates, while another one does not.
   d. Snails lay eggs in response to egg-laying hormone.
   e. Wild foxes raised in captivity are not capable of hunting for food.
9. How would the following graph differ if pecking behavior in laughing gulls was a fixed action pattern?
   a. It would be a diagonal line with an upward incline.
   b. It would be a diagonal line with a downward incline.
   c. It would be a horizontal line.
   d. It would be a vertical line.
   e. None of these is correct.



10. Egg-laying hormone causes snails to lay eggs, implicating which system in this behavior?
    a. digestive
    b. endocrine
    c. nervous
    d. lymphatic
    e. respiratory
11. Using treats to train a dog to do a trick is an example of
    a. imprinting.
    b. tutoring.
    c. vocalization.
    d. operant conditioning.

12. The benefits of imprinting generally outweigh the costs because
    a. an animal that has been imprinted on the wrong object can be reimprinted on the mother.
    b. imprinting behavior never lasts more than a few months.
    c. animals in the wild rarely imprint on anything other than their mother.
    d. animals that imprint on the wrong object generally die before they pass their genes on.
13. In white-crowned sparrows, social experience exhibits a very strong influence over the development of singing patterns. What observation led to this conclusion?
    a. Birds only learned to sing when they were trained by other birds.
    b. The window in which birds learn from other birds is wider than that when birds learn from tape recordings.
    c. Birds can learn different dialects only from other birds.
    d. Birds that learned to sing from a tape recorder could change their song when they listened to another bird.
14. Which of the following best describes classical conditioning?
    a. The gradual strengthening of stimulus-response connections that seemingly are unrelated.
    b. A type of associative learning in which there is no contingency between response and reinforcer.
    c. The learning behavior in which an organism follows the first moving object it encounters.
    d. The learning behavior in which an organism exhibits a fixed action pattern from the time of birth.
15. The observation that male bowerbirds decorate their nests with blue objects favored by females can best be associated with
    a. insight learning.
    b. imprinting.
    c. sexual selection.
    d. altruism
16. Foraging
    a. is best done at night.
    b. should result in net energy to the animal.
    c. is an unnecessary activity.
    d. is a part of sexual selection.
17. Migratory behavior
    a. has a higher cost than a benefit.
    b. affects the reproductive strategy.
    c. pertains only to birds.
    d. involves the ability to navigate.

For problems 18–22, match the type of communication in the key with its description. Answers may be used more than once.

KEY:

a. chemical communication
b. auditory communication
c. visual communication
d. tactile communication

18. Aphids (insects) release an alarm pheromone when they sense they are in danger.
19. Male peacocks exhibit an elaborate display of feathers to attract females.
20. Ground squirrels give an alarm call to warn others of the approach of a predator.
21. Male silk moths are attracted to females by a sex attractant released by the female moth.
22. Sage grouses perform an elaborate courtship dance.
23. After migrating south, birds usually
    a. reproduce.
    b. fight to win the right to mate.
    c. learn a new song.
    d. All of these are correct.
24. Bees that do a waggle dance are teaching other bees
    a. how to dance.
    b. where to find food.
    c. how to find and use the sun for navigation.
    d. how to use auditory communication.

thinking scientifically

1. Meerkats are said to exhibit altruistic behavior because certain members of a population act as sentries. How would you test the hypothesis that sentries are engaged in altruistic behavior?
2. You are testing the hypothesis that human infants instinctively respond to higher-pitched voices. Your design is to record head turns toward speakers when they play voices in different pitches. When you do the experiment using several different infants, your data support your hypothesis. However, prior learning by infants is still a serious criticism. What is the basis of this criticism?

bioethical issue

Putting Animals in Zoos

Is it ethical to keep animals in zoos, where they are not free to behave as they would in the wild? If we keep animals in zoos, are we depriving them of their freedom? Some point out that freedom is never absolute. Even an animal in the wild is restricted in various ways by its abiotic and biotic environment. Many modern zoos keep animals in habitats that nearly match their natural ones so that they have some freedom to roam and behave naturally. Perhaps, too, we should consider the education and enjoyment of the many thousands of human visitors to a zoo compared to the freedom lost by a much smaller number of animals kept in a zoo.

Today, reputable zoos rarely go out and capture animals in the wild—they usually get their animals from other zoos. Most people feel it is not a good idea to take animals from the wild except for very serious reasons. Certainly, zoos should not be involved in the commercial and often illegal trade of wild animals that still goes on today. Many zoos today are involved in the conservation of animals. They provide the best home possible while animals are recovering from injury or increasing their numbers until they can be released to the wild. Can we perhaps look at zoos favorably if they show that they are keeping animals under good conditions and are also involved in preserving animals? What is your opinion?

Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

http://www.mhhe.com/maderbiology10

44

Population Ecology

Elephants attain a large size, are social, live a long time, even up to 70 years, and produce few offspring. Females live in social family units, and the much larger males visit them only during breeding season. Females give birth about every five years to a single calf that is well cared for and has a good chance of meeting the challenges of its lifestyle. Normally, an elephant population exists at the carrying capacity of the environment.

Elephants are currently threatened because of human population growth, and because males, in preference to females, are killed for their ivory tusks. A moratorium on killing male elephants has increased the estimate of their numbers. So, the hope is that we do have enough time to learn what factors are most critical for elephants to sustain a healthy population before it is too late. This chapter previews the principles of population ecology, a field that is extremely important to the preservation of species and the maintenance of the diversity of life on Earth.

Social unit of female elephants, *Loxodonta africana.*

concepts

44.1 Scope of Ecology

In 1866, the German zoologist Ernst Haeckel coined the word *ecology* from two Greek roots [Gk. *oikos,* home, house, and *-logy,* "study of" from *logikos,* rational, sensible]. He said that **ecology** is the study of the interactions among all organisms and with their physical environment. Haeckel also pointed out that ecology and evolution are intertwined because ecological interactions are selection pressures that result in evolutionary change, which in turn affects ecological interactions.

Ecology, like so many biological disciplines, is wide-ranging. At one of its lowest levels, ecologists study how the individual organism is adapted to its environment. For example, they study how a fish is adapted to and survives in its **habitat** (the place where the organism lives) (Fig. 44.1). Most organisms do not exist singly; rather, they are part of a population, the functional unit that interacts with the environment and on which natural selection operates. A **population** is defined as all the organisms belonging to the same species within an area at the same time. At this level of study, ecologists are interested in factors that affect the growth and regulation of population size.

A **community** consists of all the various populations of multiple species interacting at a locale. In a coral reef, there are numerous populations of algae, corals, crustaceans, fishes, and so forth. At this level, ecologists want to know how interactions such as predation and competition affect the organization of a community. An **ecosystem** contains a community of populations and also the abiotic environment (e.g., the availability of sunlight for plants). Energy flow and chemical cycling are significant aspects of understanding how an ecosystem functions. Ecosystems rarely have distinct boundaries and are not totally self-sustaining. Usually, a transition zone called an ecotone, which has a mixture of organisms from adjacent ecosystems, exists between ecosystems. The **biosphere** encompasses the zones of the Earth's soil, water, and air where living organisms are found. Table 44.1 summarizes the levels of biological study.

Modern ecology is not just descriptive, it is predictive. It analyzes levels of organization and develops models and hypotheses that can be tested. A central goal of modern ecology is to develop models that explain and predict the distribution and abundance of organisms. Ultimately, ecology considers not one particular area, but the distribution and abundance of

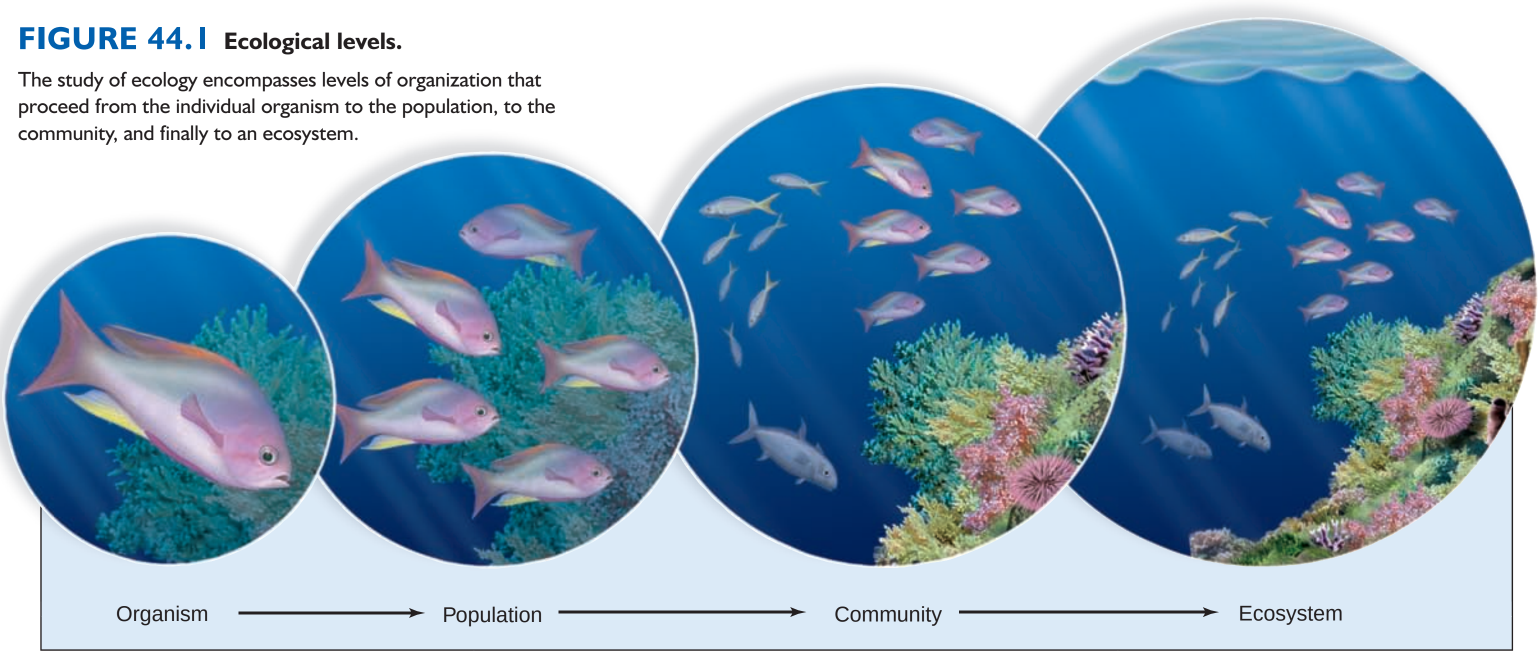
TABLE 44.1

Ecological Terms

Term	*Definition*
Ecology	Study of the interactions of organisms with each other and with the physical environment
Population	All the members of the same species that inhabit a particular area
Community	All the populations found in a particular area
Ecosystem	A community and its physical environment, including both nonliving (abiotic) and living (biotic) components
Biosphere	All the communities on Earth whose members exist in air and water and on land

FIGURE 44.1 Ecological levels.

The study of ecology encompasses levels of organization that proceed from the individual organism to the population, to the community, and finally to an ecosystem.



populations in the biosphere. For example, what factors have selected for the mix of plants and animals in a tropical rain forest at one latitude and in a desert at another? While modern ecology is useful in and of itself, it also has unlimited application possibilities, including the proper management of plants and wildlife, the identification of and efficient use of renewable and nonrenewable resources, the preservation of habitats and natural cycles, the maintenance of food resources, and the ability to predict the impact and course of a disease such as malaria or AIDS.

Check Your Progress 44.1

1. What is the difference between a population and a community?
2. What is a central goal of modern ecological studies today?
3. What is meant by the "abiotic environment"?

44.2 Demographics of Populations

Demography is the statistical study of a population, such as its density, its distribution, and its rate of growth, which is dependent on such factors as its mortality pattern and age distribution.

Density and Distribution

Population density is the number of individuals per unit area, such as there are 73 persons per square mile in the United States. Population density figures make it seem as if individuals are uniformly distributed, but this often is not the case. For example, we know full well that most people in the United States live in cities, where the number of people per unit area is dramatically higher than in the country. And even within a city, more people live in particular neighborhoods than others, and such distributions can change over time. Therefore, basing ecological models solely on population density, as has often been done in the past, can lead to misleading results.

Population distribution is the pattern of dispersal of individuals across an area of interest. The availability of resources can affect where populations live. **Resources** are nonliving (abiotic) and living (biotic) components of an environment that support living organisms. Light, water, space, mates, and food are some important resources for populations. **Limiting factors** are those environmental aspects that particularly determine where an organism lives. For example, trout live only in cool mountain streams, where the oxygen content is high, but carp and catfish are found in rivers near the coast because they can tolerate warm waters, which have a low concentration of oxygen. The timberline is the limit of tree growth in mountainous regions or in high latitudes. Trees cannot grow above the high timberline because of low temperatures and the fact that water remains frozen most of the year. The distribution of organisms can also be due to biotic factors. In Australia, the red kangaroo does not live outside arid inland areas because it is adapted to feeding on the grasses that grow there.

Three descriptions—*clumped, random,* and *uniform*—are often used to characterize observed patterns of distribution. Suppose you considered the distribution of a species across its full range. A range is that portion of the globe where the species can be found; red kangaroos live in Australia. On that scale, you would expect to find a clumped distribution. However, organisms are located in areas suitable to their adaptations; as mentioned, red kangaroos live in grasslands, and catfish live in warm river water near the coast.

Within a smaller area such as a single body of water or a single forest, the availability of resources again influences which of the patterns of distribution is common for a particular population. For example, a study of the distribution of hard clams in a bay on the south shore of Long Island, New York, showed that clam abundance is associated with sediment shell content. Investigators hope to use this information to transform areas that have few clams into high-abundance areas. Distribution patterns need not be constant. In a study of desert shrubs, it was found that the distribution changed from clumped to random to a uniform distribution pattern as the plants matured. As time passed, it was found that competition for belowground resources caused the distribution pattern to become uniform (Fig. 44.2).

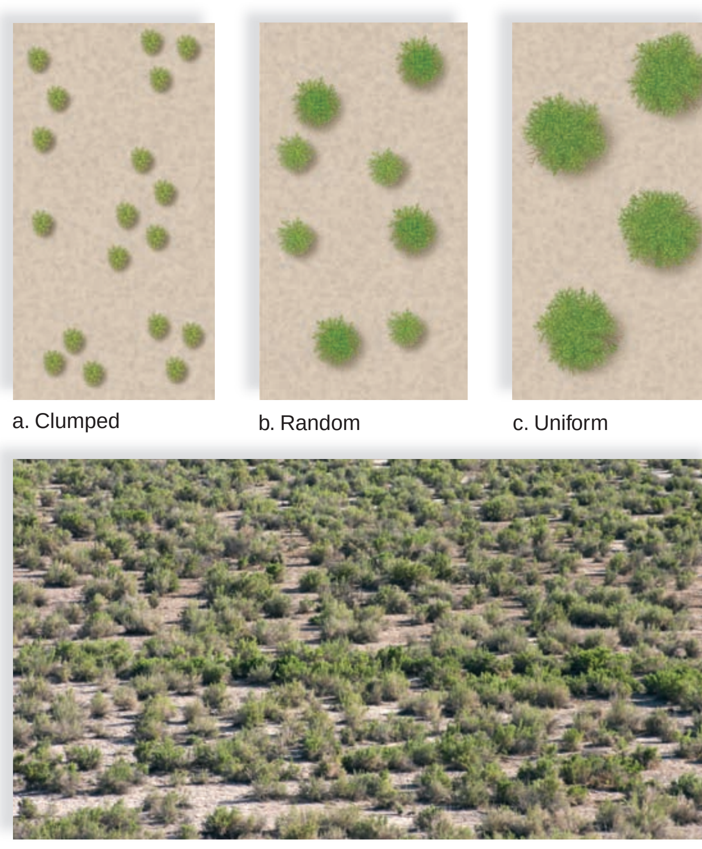


FIGURE 44.2 Distribution patterns of the creosote bush.

a. Young, small desert shrubs are clumped. **b.** Medium shrubs are randomly distributed. **c.** Mature shrubs are uniformly distributed. **d.** Photograph of mature shrub distribution.

a.

b.

FIGURE 44.3 Biotic potential.

A population's maximum growth rate under ideal conditions—that is, its biotic potential—is greatly influenced by the number of offspring produced in each reproductive event. **a.** Pigs, which produce many offspring that quickly mature to produce more offspring, have a much higher biotic potential than (**b**) the rhinoceros, which produces only one or two offspring per infrequent reproductive event.

Other factors besides resource availability can influence distribution patterns. Breeding golden eagles, like many other birds, exhibit territoriality, and this behavioral characteristic discourages a clumped distribution at this time. On the other hand, cedar trees tend to be clumped near the parent plant because seeds are not widely dispersed.

Population Growth

The **rate of natural increase (*r*),** which for our purposes is the same as the growth rate, is dependent on the number of individuals born each year and the number of individuals that die each year. Usually it is possible to assume that immigration and emigration are equal and need not be considered in the calculation of the growth rate. Populations grow when the number of births exceeds the number of deaths. If the number of births is 30 per year and the number of deaths is 10 per year per 1,000 individuals, the growth rate would be:

$$(30 - 10)/1{,}000 = 0.02 = 2.0\%$$

The highest possible rate of natural increase for a population when resources are unlimited is called its **biotic potential** (Fig. 44.3). Whether the biotic potential is high or low depends on characteristics of the population that reduce or slow its potential reproduction, such as the following:

- Usual number of offspring per reproductive event
- Chances of survival until age of reproduction
- How often each individual reproduces
- Age at which reproduction begins

Mortality Patterns

Population growth patterns assume that populations are made up of identical individuals. Actually the individuals of a population are in different stages of their life span. A **cohort** is all the members of a population born at the same time. Some investigators study population dynamics and construct life tables that show how many members of a cohort are still alive after certain intervals of time. For example, Table 44.2 is a life table for a bluegrass cohort. The cohort contains 843 individuals. The table tells us that after three months, 121 individuals have died, and therefore the mortality rate is 0.143 per capita. Another way to express this same statistic, however, is to consider that 722 individuals are still alive—have survived—after three months. **Survivorship** is the probability of newborn individuals of a cohort surviving to particular ages. If we plot the number surviving at each age, a survivorship curve is produced (see Fig. 44.4*b*). The results of such investigations show that each species tends to have one of the typical survivorship curves.

TABLE 44.2

A Life Table for a Bluegrass Cohort

Age (months)	*Number Observed Alive*	*Number Dying*	*Mortality Rate per Capita*	*Avg. Number of Seeds per Individual*
0–3	843	121	0.143	0
3–6	722	195	0.271	300
6–9	527	211	0.400	620
9–12	316	172	0.544	430
12–15	144	95	0.626	210
15–18	54	39	0.722	60
18–21	15	12	0.800	30
21–24	3	3	1.000	10
24	0	—	—	—

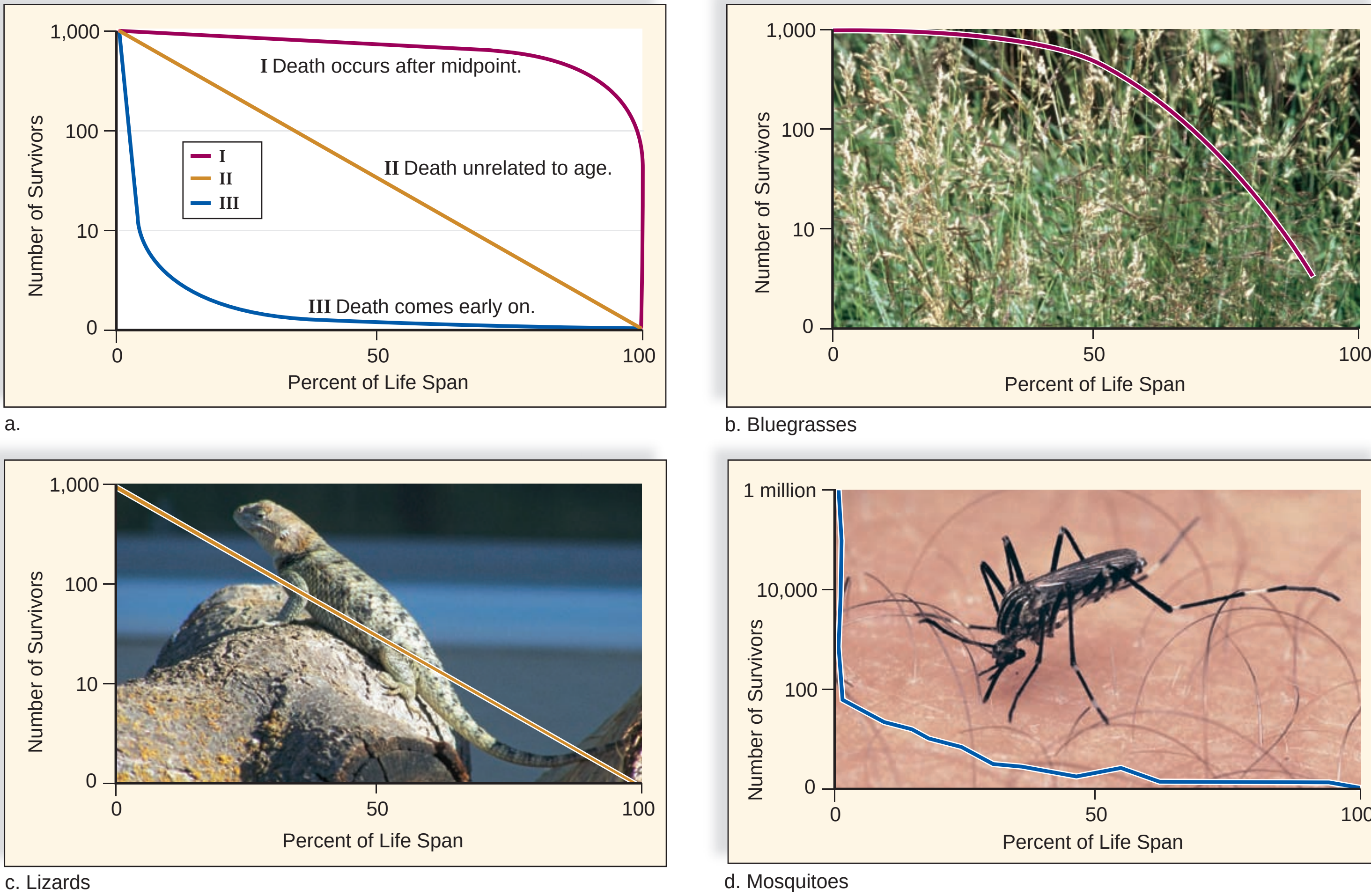


FIGURE 44.4 Survivorship curves.

Survivorship curves show the number of individuals of a cohort that are still living over time. **a.** Three generalized survivorship curves. **b.** The survivorship curve for bluegrasses seems to be a combination of the type I and type II curves. **c.** The survivorship curve for lizards fits the type II curve somewhat. **d.** The survivorship curve for mosquitoes is a type III curve.

Three types of idealized survivorship curves, numbered I, II, and III, are usually recognized (Fig. 44.4*a*). The type I curve is characteristic of a population in which most individuals survive well past the midpoint of the life span, and death does not come until near the end of the life span. Animals that have this type of survivorship curve include large mammals and humans in more-developed countries. On the other hand, the type III curve is typical of a population in which most individuals die very young. This type of survivorship curve occurs in many invertebrates, fishes, and humans in less-developed countries. In the type II curve, survivorship decreases at a constant rate throughout the life span. In many songbirds and small mammals, death is usually unrelated to age; thus they represent a type II survivorship curve.

The survivorship curves of natural populations do not fit these three idealized curves exactly. In a bluegrass cohort, as shown in Table 44.2 for example, most individuals survive till six to nine months, and then the chances of survivorship diminish at an increasing rate (Fig. 44.4*b*). Statistics for a lizard cohort are close enough to classify the survivorship curve in the type II category (Fig. 44.4*c*), while a mosquito cohort has a type III curve (Fig. 44.4*d*).

Much can be learned about the life history of a species by studying its life table and the survivorship curve that can be constructed based on this table. Would you predict that natural selection would favor the most or the fewest members of a population with a type III survivorship curve to contribute offspring to the next generation? Obviously, since death comes early for most members, only a few are living long enough to reproduce. What about the other two types of survivorship curves?

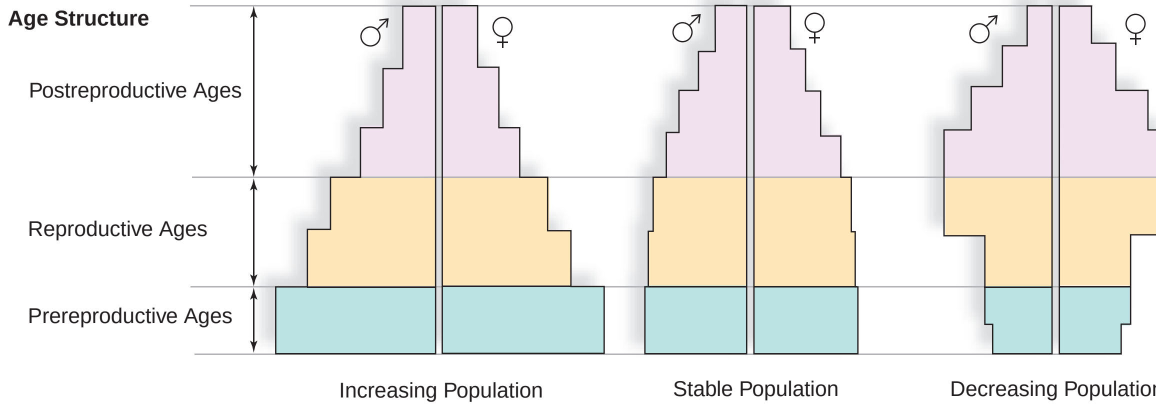
Other types of information are also available from studying life tables. Look again at Table 44.2, the bluegrass life table. It tells us that per capita seed production increases as plants mature, and then seed production drops off. How do you predict this would compare to a cohort of human beings?

Age Distribution

When the individuals in a population reproduce repeatedly, several generations may be alive at any given time. From the perspective of population growth, a population contains three major age groups: prereproductive, reproductive, and postreproductive. Populations differ according to what proportion of the population falls in each age group. At least three **age structure diagrams** are possible (Fig. 44.5).

FIGURE 44.5 Age structure diagrams.

Typical age structure diagrams for hypothetical populations that are increasing, stable, or decreasing. Different numbers of individuals in each age class create these distinctive shapes. In each diagram, the left half represents males while the right half represents females.



When the prereproductive group is the largest of the three groups, the birthrate is higher than the death rate, and a pyramid-shaped diagram is expected. Under such conditions, even if the growth for that year were matched by the deaths for that year, the population would continue to grow in the following years. Why? Because there are more individuals entering than leaving the reproductive years. Eventually, as the size of the reproductive group equals the size of the prereproductive group, a bell-shaped diagram will result. The postreproductive group will still be the smallest, however, because of mortality. If the birthrate falls below the death rate, the prereproductive group will become smaller than the reproductive group. The age structure diagram will then be urn-shaped, because the postreproductive group is now the largest.

The age distribution reflects the past and future history of a population. Because a postwar baby boom occurred in the United States between 1946 and 1964, the postreproductive group will soon be the largest group.

Check Your Progress 44.2

1. Describe the difference between population density and population distribution.
2. Describe the differences among type I, II, and III survivorship curves.
3. Why does a bell-shaped age pyramid indicate a growing population?

44.3 Population Growth Models

Based on observation and natural selection principles, ecologists have developed two working models for population growth. In the pattern called **semelparity** [Gk. *seme,* once, and L. *parous,* to bear or bring forth], the members of the population have only a single reproductive event in their lifetime. When the time for reproduction draws near, the mature adults cease to grow and expend all their energy in reproduction, and then die. Many insects, such as winter moths, and annual plants, such as zinnias, follow this pattern of reproduction growth. They produce a resting stage of development such as eggs or seeds that survive unfavorable conditions and resume growth the next favorable season. In other words, semelparity is an adaptation to an unstable environment. In the pattern called **iteroparity** [Gk. *itero,* repeat], members of the population experience many reproductive events throughout their lifetime. They continue to invest energy in their future survival and this increases their chances of reproducing again. Iteroparity is an adaptation to a stable environment when the offsprings' chances of survival are relatively high. Most vertebrates, shrubs, and trees have this pattern of reproduction.

Figure 44.6 exemplifies that reproduction does not always fit these two patterns. However, ecologists have found it useful to develop mathematical models of

a. b.

FIGURE 44.6 Patterns of reproduction.

Although we can assume that members of populations either have a single sacrificial reproductive event, or they reproduce repeatedly, actually both are simplifications. **a.** Aphids reproduce repeatedly by asexual reproduction during the summer and then reproduce sexually only once, right before the onset of winter. Therefore, aphids use both patterns of reproduction. **b.** The offspring of annual plants can germinate several seasons later. Under these circumstances, population size of these organisms could fluctuate according to environmental conditions.

population growth based on these two very different patterns of reproduction. Although the mathematical models we will be describing are simplifications, they still may predict how best to control the distribution and abundance of organisms, or how to predict the responses of populations when their environment is altered in some way. Testing predictions permits the development of new hypotheses that can then be tested.

Exponential Growth

As an example of semelparous reproduction, we will consider a population of insects in which females reproduce only once a year and then the adult population dies. Each female produces on the average 2.4 eggs per generation that will survive the winter and become offspring the next year. In the next generation, each female will again produce 2.4 eggs. In the case of discrete breeding, R = net reproductive rate.[1] Why net reproductive rate? Because it is the observed rate of natural increase after deaths have occurred.

Figure 44.7*a* shows how the population would grow year after year for ten years, assuming that R stays constant from generation to generation. This growth is equal to the size of the population because all members of the previous generation have died. Mayflies, featured in Figure 44.7, have one reproductive event usually in the spring—hence their name—and then development of the next generation requires as many as 50 molts during the winter. Figure 44.7*b* shows the growth curve for such a population. This growth curve, which has a J shape, depicts exponential growth. With **exponential growth,** the number of individuals added each generation increases as the total number of females increases.

Notice that the curve has these phases:

Lag phase During this phase, growth is slow because the population is small.

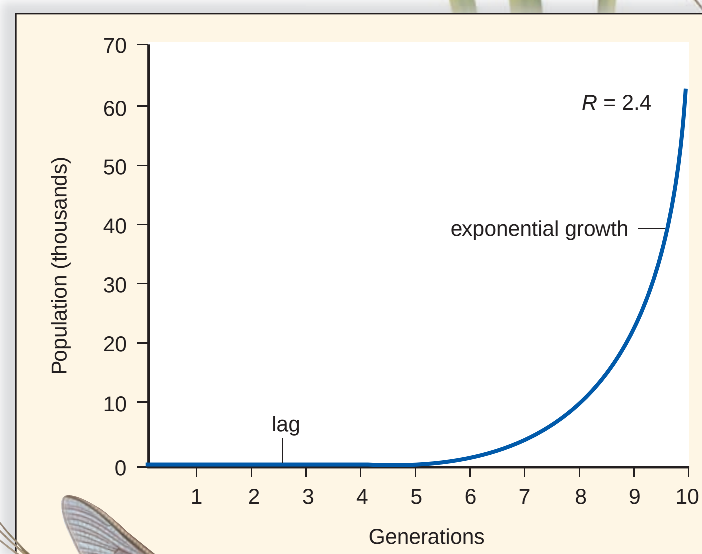
Exponential growth phase During this phase, growth is accelerating.

Figure 44.7*c* gives the mathematical equation that allows you to calculate growth and size for any population that has discrete (nonoverlapping) generations. In other words, as discussed, all members of the previous generation die off before the new generation appears. To use this equation to determine future population size, it is necessary to know R, which is the net reproductive rate determined after gathering mathematical data regarding past population increases. Notice that even though R remains constant, growth is exponential because the number of individuals added each year is increasing. Therefore, the growth of the population is accelerating.

For exponential growth to continue unchecked, each member of the population has to have unlimited resources. Plenty of room, food, shelter, and any other requirements necessary to sustain growth must be available. But in reality, environmental conditions prevent exponential growth. Eventually, any further growth is impossible because the food supply runs out and waste products begin to accumulate. Also, as the population increases in size so do the effects of competition between members, predation, parasites, and disease.

Generation	Population Size
0	10.0
1	24.0
2	57.6
3	138.2
4	331.7
5	796.1
6	1,910.6
7	4,585.4
8	11,005.0
9	26,412.0
10	63,388.8

a.



b.

To calculate population size from year to year, use this formula:

$$N_{t+1} = RN_t$$

N_t = number of females already present

R = net reproductive rate

N_{t+1} = population size the following year

c.

FIGURE 44.7 Model for exponential growth.

When the data for discrete reproduction in (**a**) are plotted, the exponential growth curve in (**b**) results. **c.** This formula produces the same results as (**a**) and generates the same graph.

[1] The change of *r* to *R* is simply customary in discrete breeding calculations; both coefficients deal with the same thing (birth minus death).

Logistic Growth

What type of growth curve results when environmental factors opposing growth come into play? In 1930, Raymond Pearl developed a method for estimating the number of yeast cells accruing every two hours in a laboratory culture vessel. His data are shown in Figure 44.8*a*. When the data are plotted, the growth curve has the appearance shown in Figure 44.8*b*. This type of growth curve is a sigmoidal (S) or S-shaped curve.

Notice that this so-called **logistic growth** has these phases:

Lag phase During this phase, growth is slow because the population is small.
Exponential growth phase During this phase, growth is accelerating.
Deceleration phase During this phase, growth slows down.
Stable equilibrium phase During this phase, there is little if any growth because births and deaths are about equal.

Figure 44.8*c* gives the mathematical equation that allows us to calculate logistic growth (so-called because the exponential portion of the curve would produce a straight line if the log of N were plotted). The entire equation for logistic growth is:

$$\frac{N}{t} = rN\frac{(K-N)}{K}$$

but let's consider each portion of the equation separately.

Because the population has repeated reproductive events, we need to consider growth as a function of change in time (Δ):

$$\frac{\Delta N}{\Delta t} = rN$$

If the change in time is very small, then we can turn to differential calculus, and the instantaneous population growth (d) is given by:

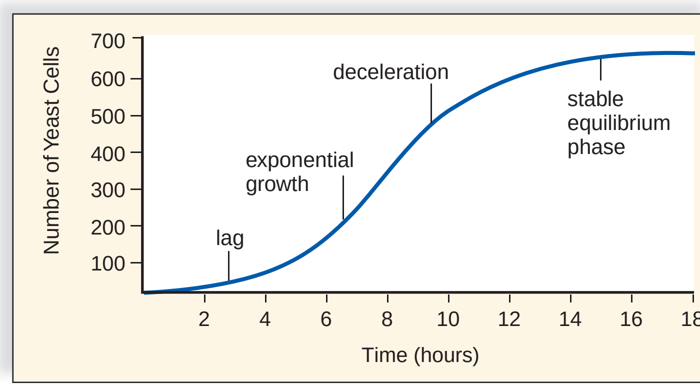
$$\frac{dN}{dt} = rN$$

This portion of the equation applies to the first two phases of growth—the lag phase and the exponential growth phase. Here, also, we do not expect exponential growth to continue. Charles Darwin calculated that a single pair of elephants could have over 19 million live descendants after 750 years. Others have calculated that a single female housefly could produce over 5 trillion flies in one year! Such explosive growth does not occur because environmental conditions, both abiotic and biotic, cause population growth to slow. The yeast population was grown in a vessel in which food could run short and waste products could accumulate. These environmental conditions prevent exponential growth from continuing. Look again at Figure 44.8. Following exponential growth, a population is expected to enter a deceleration phase and then a stable equilibrium phase of the logistic growth curve. Now the population is at the carrying capacity of the environment.

Growth of Yeast Cells in Laboratory Culture

Time (t) (hours)	Number of individuals (N)	Number of individuals added per 2-hour period $\left(\frac{\Delta N}{\Delta t}\right)$
0	9.6	0
2	29.0	19.4
4	71.1	42.1
6	174.6	103.5
8	350.7	176.1
10	513.3	162.6
12	594.4	81.1
14	640.8	46.4
16	655.9	15.1
18	661.8	5.9

a.



b.

To calculate population growth as time passes, use this formula:

$$\frac{N}{t} = rN\left(\frac{K-N}{K}\right)$$

N = population size

N/t = change in population size

r = rate of natural increase

K = carrying capacity

$\frac{K-N}{K}$ = effect of carrying capacity on population growth

c.

FIGURE 44.8 Model for logistic growth.

When the data for repeated reproduction (**a**) are plotted, the logistic growth curve in (**b**) results. **c.** This formula produces the same results as (**a**) and generates the same graph.

Carrying Capacity

The environmental **carrying capacity** (K) is the maximum number of individuals of a given species the environment can support. The closer population size nears the carrying capacity of the environment, the more likely resources will become scarce and biotic effects such as competition and predation will become evident. The birthrate is expected to decline and the death rate is expected to increase. This will result in a decrease in population growth; eventually, the population stops growing and its size remains stable. Carrying capacity in any given environment can vary throughout time depending on fluctuating conditions, for example, amount of rainfall from one year to the next.

How does our mathematical model for logistic growth take this process into account? To our equation for growth under conditions of exponential growth we add the term:

$$\frac{(K - N)}{K}$$

In this expression, K is the carrying capacity of the environment. The easiest way to understand the effects of this term is to consider two extreme possibilities. First, consider a time at which the population size is well below carrying capacity. Resources are relatively unlimited, and we expect rapid, nearly exponential growth to take place. Does the model predict this? Yes, it does. When N is very small relative to K, the term $(K-N)/K$ is very nearly $(K-0)/K$, or approximately 1. Therefore, $(dN)/(dt)$ = approximately rN.

Similarly, consider what happens when the population reaches carrying capacity. Here, we predict that growth will stop and the population will stabilize. What happens in the model? When $N = K$, the term $(K - N)/K$ declines from nearly 1 to 0, and the population growth slows to zero.

As mentioned, the model we have developed predicts that exponential growth will occur only when population size is much lower than the carrying capacity. So, as a practical matter, if we are using a fish population as a continuous food source, it would be best to maintain the population size in the exponential phase of the logistic growth curve. Biotic potential can have its full effect, and the birthrate is the highest it can be during this phase. If we overfish, the population will sink into the lag phase, and it will be years before exponential growth recurs. On the other hand, if we are trying to limit the growth of a pest, it is best, if possible, to reduce the carrying capacity rather than reduce the population size. Reducing the population size only encourages exponential growth to begin once again. Farmers can reduce the carrying capacity for a pest by alternating rows of different crops rather than growing one type of crop throughout the entire field.

Check Your Progress 44.3

1. What ecological factors might result in iteroparity rather than semelparity?
2. How does carrying capacity (K) limit exponential growth?

44.4 Regulation of Population Size

In a study of winter moth population dynamics, it was discovered that a large proportion of eggs did not survive the winter and exponential growth never occurred. Perhaps the low number of individuals at the start of each season helps prevent the occurrence of exponential growth. This observation raises the question, "How well do the models for exponential and logistic growth predict population growth in natural populations?"

Is it possible, for example, that exponential growth may cause population size to rise above the carrying capacity of the environment, and as a consequence a population crash may occur? For example, in 1911, 4 male and 21 female reindeer were released on St. Paul Island in the Bering Sea off Alaska. St. Paul Island had a completely undisturbed environment—there was little hunting pressure, and there were no predators. The herd grew exponentially to about 2,000 reindeer in 1938, overgrazed the habitat, and then abruptly declined to only 8 animals in 1950 (Fig. 44.9). This pattern of a population explosion eventually followed by a population crash is called irruptive, or Malthusian, growth. It is named in honor of the eighteenth-century economist who had a great influence on Charles Darwin. Populations do not ordinarily undergo Malthusian growth because of factors that regulate population growth.

FIGURE 44.9 Density-dependent effect.

On St. Paul Island, Alaska, reindeer, *Rangifer*, grew exponentially for several seasons and then underwent a sharp decline as a result of overgrazing the available range.

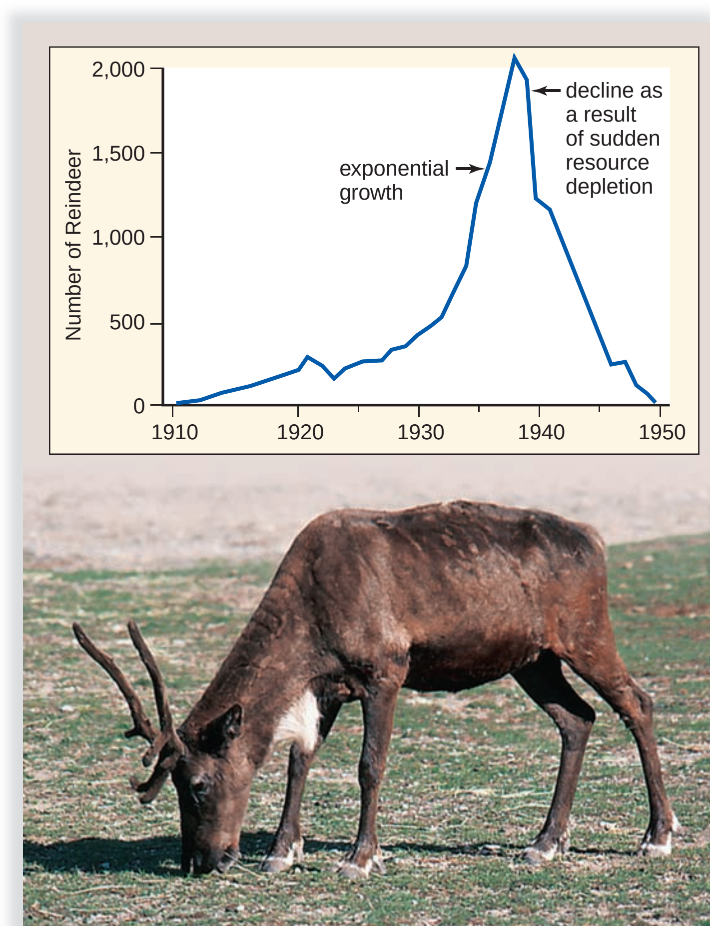


FIGURE 44.10 Density-independent effects.

The impact of a density-independent factor, such as weather or natural disasters, is not influenced by population density. The impact of a flash flood on (**a**) a low-density population (mortality rate of 3/5, or 60%) is similar to the impact on (**b**) a high-density population (mortality rate of 12/20, or 64%).

a. Low density of mice

b. High density of mice

Factors That Regulate Population Growth

Ecologists have long recognized that both abiotic conditions and biotic conditions play an important role in regulating population size in nature.

Density-Independent Factors

Abiotic factors include droughts (lack of rain), freezes, hurricanes, floods, and forest fires. Any one of these natural disasters can cause individuals to die and lead to a sudden and catastrophic reduction in population size. However, such an event does not necessarily kill a larger percentage of a dense population compared to a less dense population. Therefore, an abiotic factor is usually a **density-independent factor,** meaning that the intensity of the effect does not increase with increased population density.

For example, the proportion of a population killed in a flash flood event is independent of density—floods do not necessarily kill a larger percentage of a dense population than of a less dense population. Nevertheless, the larger the population, the greater the number of individuals probably affected. In Figure 44.10, the impact of a flash flood on a low-density population of mice living in a field was 3 out of 5, whereas the impact on a high-density population was 12 out of 20.

Density-Dependent Factors

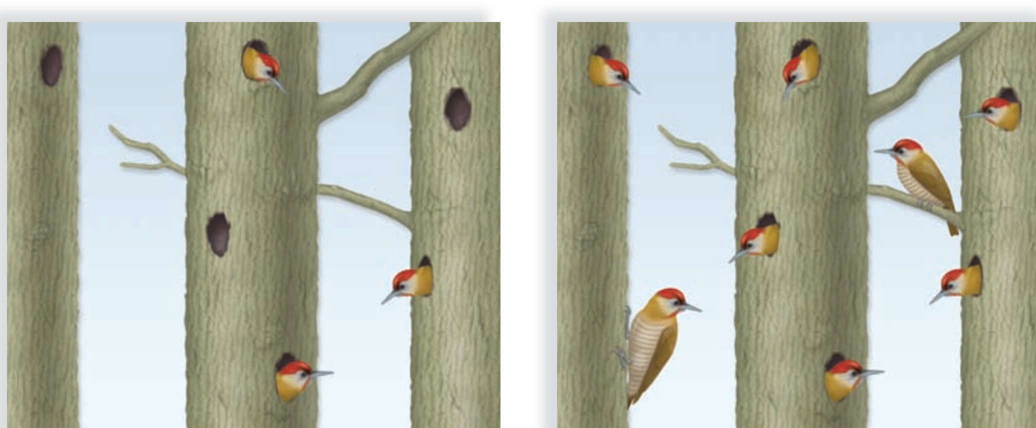
Biotic factors are considered **density-dependent factors** because the percentage of the population affected does increase as the density of the population increases. Competition, predation, and parasitism are all biotic factors that increase in intensity as the density increases.

Competition can occur when members of a species attempt to use resources (such as light, food, space) that are in limited supply. As a result, not all members of the population can have access to the resource to the degree necessary to ensure survival or reproduction or some other aspect of their life history. As an example, let's consider a woodpecker population in which members have to compete for nesting sites. Each pair of birds requires a tree hole to raise offspring. If there are more holes than breeding pairs, each pair can have a hole in which to lay eggs and rear young birds (Fig. 44.11*a*). But if there are fewer holes than there are breeding pairs, then each pair must compete to acquire a nesting site (Fig. 44.11*b*). Pairs that fail to gain access to holes will be unable to contribute new members to the population.

Competition for food also controls population growth. However, resource partitioning among different age groups is a way to reduce competition for food. The life cycle of butterflies includes caterpillars, which require a different food from the adults. The caterpillars graze on leaves, while

FIGURE 44.11 Density-dependent effects—competition.

The impact of competition on a population is directly proportional to the density of the population. When density is low (**a**), every member of the population has access to the resource. But when the density is high (**b**), there is competition between members of the population to gain access to available resources.



a. Low density of birds

b. High density of birds

the adults feed on nectar produced by flowers. Therefore, parents do not compete with their offspring for food.

Predation occurs when one living organism, the predator, eats another, the prey. In the broadest sense, predation can include not only animals such as lions, which kill zebras, but also filter-feeding blue whales, which strain krill from the ocean waters; and even herbivorous deer, which browse on trees and bushes. The effect of predation on a prey population generally increases as the prey population grows denser, because prey is easier to find when hiding places are limited. Consider a field inhabited by a population of mice (Fig. 44.12). Each mouse must have a hole in which to hide to avoid being eaten by a hawk. If there are 100 holes, and a low density of 102 mice, then only 2 mice will be left out in the open. It might be hard for the hawk to find only 2 mice in the field. If neither mouse is caught, then the predation rate is 0/2 = 0%. However, if there are 100 holes, and a high density of 120 mice, then there is a greater chance that the hawk will be able to find some of these 100 mice without holes. If half of the exposed mice are caught, the predation rate is 50/100 = 50%. Therefore, increasing the density of the available prey has increased the proportion of the population preyed upon.

Parasites, such as blood-sucking ticks, are generally much smaller than their host. Although parasites do not always kill their hosts, they do usually weaken them over time. A highly parasitized individual is less apt to produce as many offspring than if it were healthy. In this way, parasitism also plays a role in regulating population size.

Other Considerations

Density-independent and density-dependent factors are extrinsic to the organism. Is it possible that intrinsic factors—those based on the anatomy, physiology, or behavior of the organism—might affect population size and growth rates? Territoriality and dominance hierarchies are behaviors that affect population size and growth rates. Recruitment and migration are other intrinsic social means by which the population sizes of more complex organisms are regulated.

Outside of any regulating factors, it could be that some populations have an innate instability. Ecologists have developed models that predict complex, erratic changes in even simple systems. For example, a computer model of Dungeness crab populations assumed that adults produce many larvae and then die. Most of the larvae do not survive, and those that do stay close to home. Under these circumstances, the model predicted wild fluctuations in population size with no recurring pattern, which is now termed *chaos*.

Population growth regulating factors can serve as selective agents. Some members of a population may possess traits that make it more likely that they, rather than other members of the population, will survive and reproduce when these particular density-independent or density-dependent factors are present in the environment. Therefore, these traits will be more prevalent in the next generation whenever these factors are a part of the environment (see Fig. 15.11).

Check Your Progress 44.4

1. What effect does population density have on competition and predation?
2. Give an example to show that a density-independent factor can be a selective agent.

a. Low density of mice

b. High density of mice

FIGURE 44.12

Density-dependent effects—predation.

The impact of predation on a population is directly proportional to the density of the population. In a low-density population (**a**), the chances of a predator finding the prey are low, resulting in little predation. But in the higher density population (**b**), there is a greater likelihood of the predator locating potential prey, resulting in a greater predation rate.

44.5 Life History Patterns

Populations vary on such particulars as the number of births per reproduction, the age of reproduction, the life span, and the probability of living the entire life span. Such particulars are part of a species' life history. Life histories contain characteristics that can be thought of as trade-offs. Each population is able to capture only so much of the available energy, and how this energy is distributed between its life span (short versus long), reproduction events (few versus many), care of offspring (little versus much), and so forth has evolved over time. Natural selection shapes the final life history of individual species, and therefore it is not surprising that related species, such as frogs and toads, may have different life history patterns, if they occupy different types of environments (Fig. 44.13).

The logistic population growth model has been used to suggest that members of some populations are subject to *r*-selection and members of other populations are subject to *K*-selection. In fluctuating and/or unpredictable environments, density-independent factors will keep populations in the lag or exponential phase of population growth. Population size is low relative to *K*, and ***r*-selection** favors *r*-strategists. As a consequence of this pattern of energy allocation, small individuals that mature early and have a short life span are favored. Most energy goes into producing many relatively small offspring, and no energy goes into parental care. The more offspring, the more likely it is that some of them will survive any future population crash. Because of low population densities, density-dependent mechanisms such as predation and intraspecific competition are unlikely to play a major role in regulating population size

a. Mouth-brooding frog, *Rhinoderma darwinii*

b. Strawberry poison arrow frog, *Dendrobates pumilio*

c. Surinam toad, *Pipa pipa*

d. Wood frog, *Rana sylvatica*

e. Midwife toad, *Alyces obstetricans*

FIGURE 44.13 Parental care among frogs and toads.

a. In mouth-brooding frogs of South America, the male carries the larvae in a vocal pouch (brown area), which elongates the full length of his body before the froglets are released. **b.** In poison arrow frogs of Costa Rica, after the eggs hatch, the tadpoles wiggle onto the parent's back (at white arrow) and are then carried to water. **c.** In the Surinam toads of South America, males fertilize the eggs during a somersaulting bout because the eggs are on the female's back. Each egg develops in a separate pocket, where the tail of the tadpole acts as a placenta to take nourishment from the female's circulatory system. **d.** Wood frogs live mainly in wooded areas, but they breed in temporary ponds arising from spring snowmelt. Toads and any frogs that lay their eggs on land exhibit various forms of parental care. **e.** The midwife toad of Europe carries strings of eggs entwined around his hind legs and takes them to water when they are ready to hatch.