

55.8 Animal Communication

Learning Outcomes

1. Explain the nature of signals used in mate attraction.
2. Explain the role of courtship signals in reproductive isolation.
3. Describe how honeybees communicate information about the location of new food sources.

Communication is central to species recognition and reproductive isolation, and to the interactions that are essential to social behavior. Much research in behavior analyzes the nature of communication signals, determining how they are produced and received, and identifies their ecological roles and evolutionary origins. Communication involves several signal modalities, including visual, acoustic, chemical, electric, and vibrational signals.

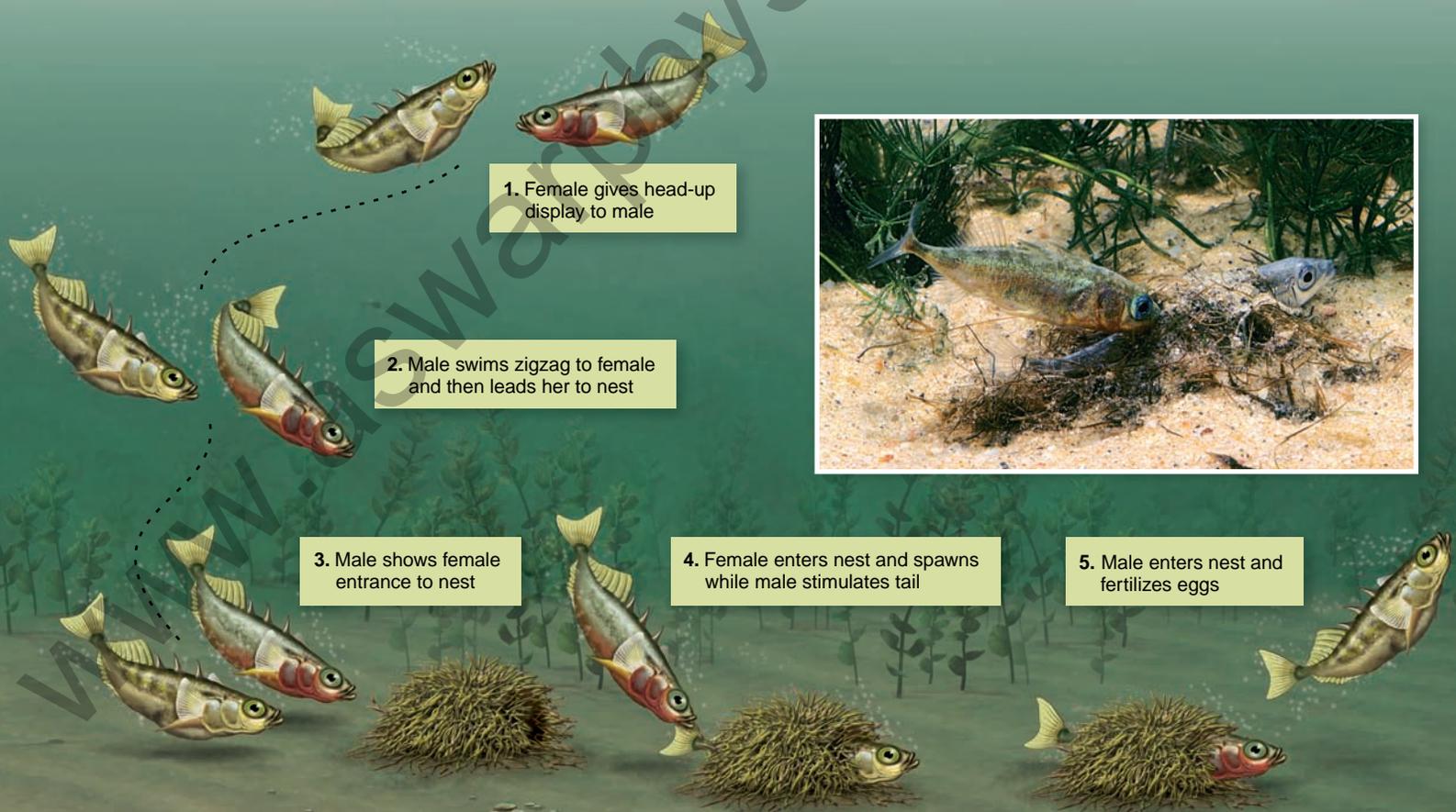
We know relatively little about how other migrating animals navigate. For instance, green sea turtles migrate from Brazil halfway across the Atlantic Ocean to Ascension Island, where the females lay their eggs. How do they find this tiny island in the middle of the ocean, which they haven't seen for perhaps 30 years? How do the young that hatch on the island know how to find their way to Brazil? Newly hatched turtles use wave action as a cue to head to sea. Some sea turtles use the Earth's magnetic field to maintain position in the North Atlantic, but turtle migration is still largely a mystery.

Learning Outcomes Review 55.7

Migration is the long-distance movement of a population, often in a cyclic way. Orientation refers to following a bearing or a direction; navigation involves setting a bearing or direction based on some sort of map or memory. Many species use celestial navigation; they may also be able to detect magnetic fields when those cues are absent. The precision of animal migration remains a mystery in many species.

- **Animals as diverse as butterflies and birds migrate over long distances. Would you expect them to use different navigation systems? Why or why not?**

Figure 55.18 A stimulus–response chain. Stickleback courtship involves a sequence of behaviors leading to the fertilization of eggs.



Successful reproduction depends on appropriate signals and responses

During courtship, animals produce signals to communicate with potential mates and with other members of their own sex. A stimulus–response chain sometimes occurs, in which the behavior of the male in turn releases a behavior in the female, resulting in mating (figure 55.18). These signals are usually highly species-specific. Many studies on communication involve designing experiments to determine which key stimuli associated with an animal’s visual appearance, sounds, or odors convey information about the nature of the signals produced by the sender. One classical study analyzed territorial defense and courtship communication in stickleback fish (figure 55.19).

Finding a mate: Communicating information about species identity

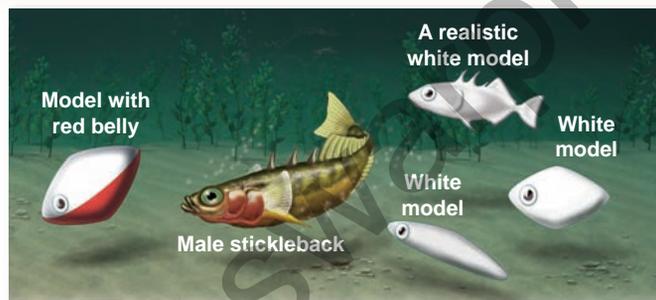
Courtship signals often restrict communication to members of the same species and in doing so serve a key function in reproductive isolation (see chapter 22). The flashes of fireflies (which are actually beetles) are species-specific signals: females recognize conspecific males by their flash pattern (figure 55.20), and

SCIENTIFIC THINKING

Hypothesis: The red underside of male stickleback is the key stimulus that releases an aggressive response by a territory-holding male.

Prediction: Models with red coloration will trigger an attack by a resident male.

Test: Construct plastic models, some of which accurately resemble a stickleback male, but lack the red underside. Construct other models that vary in their fishlike appearance, but have red-colored undersides. Expose a territorial male to the models one at a time, and record the number of attacks.



Result: Realistic models lacking red elicit no response. Odd-shape models trigger an attack if they have red undersides, even if they poorly resemble fish.

Conclusion: The red underside of a male stickleback is the key stimulus that triggers aggressive behavior.

Further Experiments: How would you determine if the color of a male stickleback was a releaser of aggressive behavior? How would you know if sound was important? Could you determine if stimuli have additive effects? How? Why do you think the color red is important in territorial defense? Might it also be a courtship signal? What information might the color red encode for a female looking for a mate? (see also figure 55.18)

Figure 55.19 Key stimulus in stickleback fish.

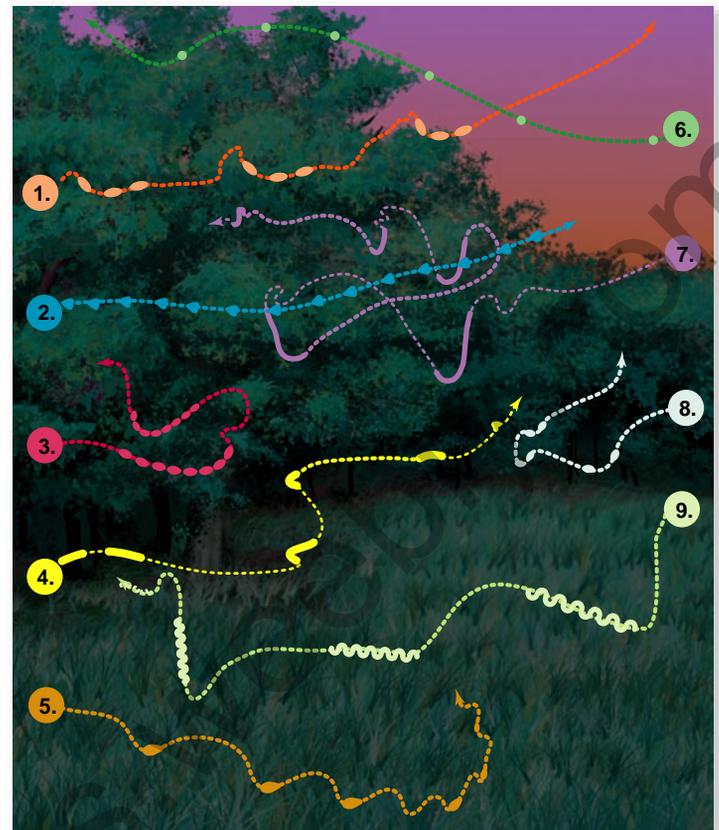


Figure 55.20 Firefly fireworks. The bioluminescent displays of these lampyrid beetles are species-specific and serve as behavioral mechanisms of reproductive isolation. Each number represents the flash pattern of a male of a different species.

males recognize conspecific females by their flash response. This series of reciprocal responses provides a continuous “check” on the species identity of potential mates.

Pheromones, chemical messengers used for communication between individuals of the same species, serve as sex attractants in many animals. Female silk moths (*Bombyx mori*) produce a sex pheromone called bombykol in a gland associated with the reproductive system. The male’s antennae contain numerous highly sensitive sensory receptors, and neurophysiological studies show they specifically detect bombykol. In some moth species, males can detect extremely low concentrations of sex pheromone and locate females from as far as 7 km away!

Many insects, amphibians, and birds produce species-specific acoustic signals to attract mates. Bullfrog males call by inflating and discharging air from their vocal sacs, located beneath the lower jaw. Females can distinguish a conspecific male’s call from those of other frogs that may be in the same habitat and calling at the same time. As mentioned earlier, male birds sing to advertise their presence and to attract females. In many species, variations in the males’ songs identify individual males in a population. In these species, the song is individually specific as well as species-specific. Vibrations, like sound signals, are a form of mechanical communication used by insects, amphibians, and other animals.

Courtship behaviors play a major role in sexual selection, which we discuss later in this chapter.



Figure 55.21 Alarm calling by a prairie dog (*Cynomys ludovicianus*). When a prairie dog sees a predator, it stands on its hind legs and gives an alarm call, which causes other prairie dogs to rapidly return to their burrows.

Communication enables information exchange among group members

Many insects, fish, birds, and mammals live in social groups in which information is communicated between group members. For example, some individuals in mammalian societies serve as sentinels, vigilantly on the lookout for danger. When a predator appears, they give an alarm call, and group members respond by seeking shelter (figure 55.21). Social insects such as ants and honeybees produce alarm pheromones that trigger attack behavior. Ants also deposit trail pheromones between the nest and a food source to lead other colony members to food. Honeybees have an extremely complex dance language that directs hivesmates to nectar sources.

The dance language of the honeybee

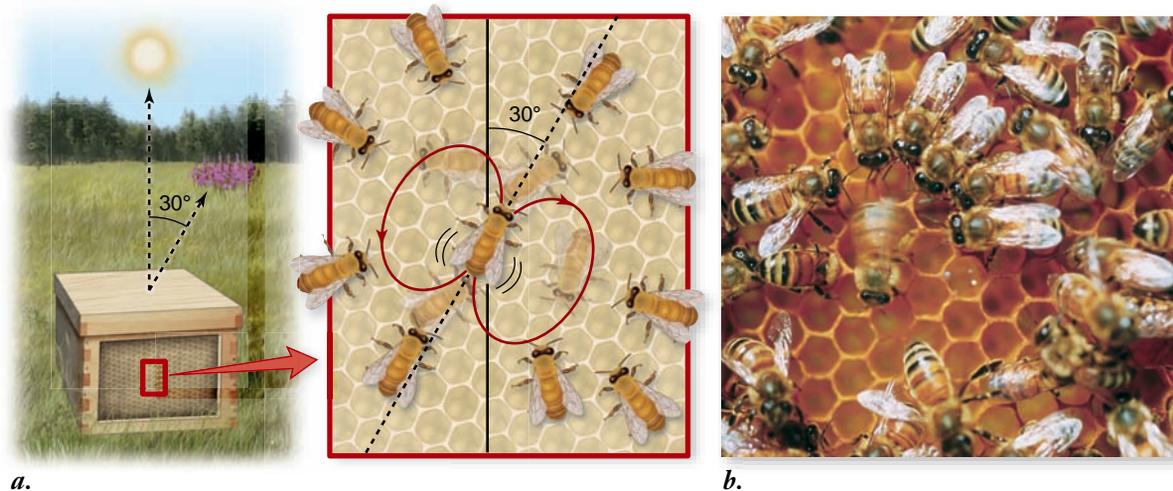
The European honeybee lives in colonies of tens of thousands of individuals whose behaviors are integrated into a complex,

cooperative society. Worker bees may forage miles from the hive, collecting nectar and pollen from a variety of plants and switching between plant species depending on their energetic rewards. Food sources used by bees tend to occur in patches, and each patch offers much more food than a single bee can transport to the hive. A colony is able to exploit the resources of a patch because of the behavior of scout bees, which locate patches and communicate their location to hivesmates through a dance language. Over many years, Nobel laureate Karl von Frisch (who shared the 1973 prize with Tinbergen and Lorenz), together with generations of students and colleagues, was able to unravel the details of dance language communication.

When a scout bee returns after finding a distant food source, she performs a remarkable behavior pattern called a waggle dance on a vertical comb in the darkness of the hive. The path of the bee during the dance resembles a figure-eight. On the straight part of the path (indicated with dashes in figure 55.22), the bee vibrates (“waggles”) her abdomen while producing bursts of sound. The bee may stop periodically to give her hivesmates a sample of the nectar carried in her crop. As she dances, she is followed closely by other bees, which soon appear at the new food source to assist in collecting food.

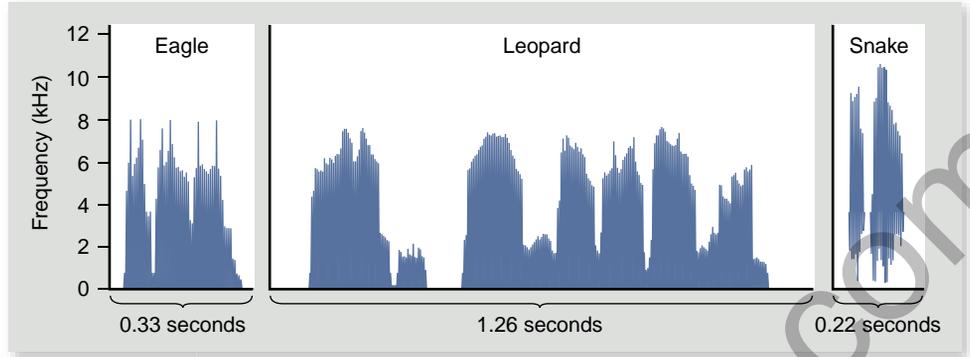
Von Frisch and his colleagues performed experiments to show that hivesmates use information in the waggle dance to locate new food sources. The scout bee indicates the direction of the food source by representing the angle between the food source, the hive, and the Sun as the deviation from vertical of the straight run of the dance performed on the hive comb. Thus if the bee danced with the straight run pointing directly up, then the food source would be in the direction of the Sun. If the food is at a 30° angle to the right of the Sun’s position, then the straight run would be oriented upward at a 30° angle to the right of vertical (figure 55.22a). The distance to the food source is indicated by the duration of the straight run. One ingenious experiment designed to show that the bees actually use the information in the dance tricked bees that were unaware of the location of food into misinterpreting the directions given by the scout bee’s dance. Computer-controlled robot bees have also been used to give hivesmates incorrect information, again demonstrating that bees use the directions coded in the dance!

Figure 55.22 The waggle dance of honeybees (*Apis mellifera*). *a.* The angle between the food source, the nest, and the Sun is represented by a dancing bee as the angle between the straight part of the dance and vertical. The food is 30° to the right of the Sun, and the straight part of the bee’s dance on the hive is 30° to the right of vertical. *b.* A scout bee dances on a comb in the hive.





a.



b.

Figure 55.23 Primate semantics. Vervet monkeys (*Cercopithecus aethiops*) give different alarm calls (a) when troop members sight an eagle, leopard, or snake. b. Each distinctive call elicits a different and adaptive escape behavior.

Language in nonhuman primates and humans

Evolutionary biologists have sought the origins of human language in the communication systems of monkeys and apes. Some nonhuman primates have a “vocabulary” that allows individuals to signal the identity of specific predators. Different vocalizations of African vervet monkeys, for example, indicate eagles, leopards, or snakes, among other threats (figure 55.23).

The complexity of human language would at first appear to defy biological explanation, but closer examination suggests that the differences are in fact superficial—all languages share many basic similarities. All of the roughly 3000 languages draw from the same set of 40 consonant and vowel sounds (English uses two dozen of them), and humans of all cultures can acquire and learn them. Researchers believe these similarities reflect the way our brains handle abstract information. The discovery of *FoxP2*, the so-called “language gene,” supports the idea that human language has a hereditary basis.

Learning Outcomes Review 55.8

Animal communication involves production and reception of signals, in the form of sounds, chemicals, or movements, that primarily have an ecological function. Courtship signals are highly species-specific and serve as a mechanism of reproductive isolation. Animals living in social groups, such as honeybees, may use complex systems of communication to exchange information about food and predators.

- Two species of moth use the same sex pheromone to locate mates. Explain how these species could nevertheless be reproductively isolated.

55.9 Behavioral Ecology

Learning Outcomes

- Describe behavioral ecology.
- Discuss the economic analysis of behaviors.

Niko Tinbergen pioneered the study of the adaptive function of behavior. Stated simply, this is how behavior allows an animal to stay alive and keep its offspring alive. For example, Tinbergen observed that after gull nestlings hatch, the parents remove the eggshells from the nest. To understand why (ultimate causation), he painted chicken eggs to resemble gull eggs (figure 55.24), which had camouflage coloration to allow them

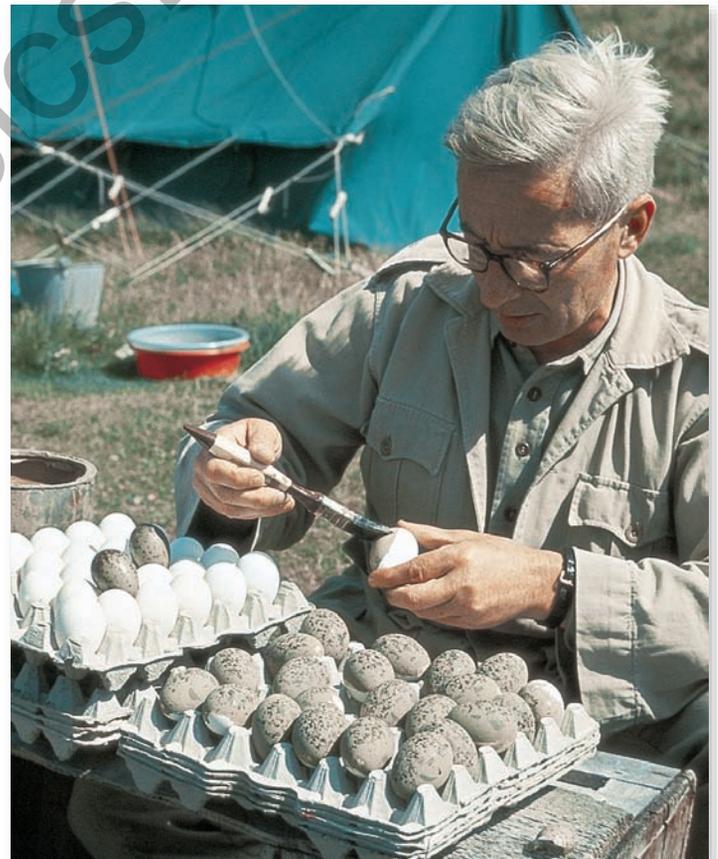


Figure 55.24 The adaptive value of egg coloration.

Niko Tinbergen, a winner of the 1973 Nobel Prize in physiology or medicine, painted chicken eggs to resemble the mottled brown camouflage of gull eggs. The eggs were used to test the hypothesis that camouflaged eggs are more difficult for predators to find and thus increase the young’s chances of survival.

to be inconspicuous against the natural background. He distributed them throughout the area in which the gulls were nesting, placing broken eggshells with their prominent white interiors next to some of the eggs. As a control, he left other camouflaged eggs alone without eggshells. He then noted which eggs were found more easily by crows. Because the crows could use the white interior of a broken eggshell as a cue, they ate more of the camouflaged eggs that were near eggshells. Tinbergen concluded that eggshell removal behavior is adaptive: it reduces predation and thus increases the offspring's chances of survival.

Tinbergen is credited with being one of the founders of **behavioral ecology**, the study of how natural selection shapes behavior. This branch of ecology examines the adaptive significance of behavior, or how behavior may increase survival and reproduction. Current research in behavioral ecology focuses on how behavior contributes to an animal's reproductive success, or fitness. As we saw in section 55.3, differences in behavior among individuals often result from genetic differences. Therefore, natural selection operating on behavior has the potential to produce evolutionary change.

Consequently, the field of behavioral ecology is concerned with two questions. First, is behavior adaptive? Although it is tempting to assume that behavior must in some way represent an adaptive response to the environment, this need not be the case. As you saw in chapter 20, traits can appear for many reasons other than natural selection, such as genetic drift, gene flow, or the correlated consequences of selection on other traits. Moreover, traits may be present in a population because they evolved as adaptations in the past, but are no longer useful. These possibilities hold true for behavioral traits as much as for any other kind of trait.

If behavior is adaptive, the next question is: How is it adaptive? Although the ultimate criterion is reproductive success, behavioral ecologists are interested in how behavior can lead to greater reproductive success. Does a behavior enhance energy intake, thus increasing the number of offspring produced? Does it increase mating success? Does it decrease the chance of predation? The job of a behavioral ecologist is to determine the effect of a behavioral trait—for example, foraging efficiency—on each of these activities and then to discover whether increases translate into increased fitness. Benefits and costs of behaviors, estimated in terms of energy or offspring, are often used to analyze the adaptive nature of behavior.

Foraging behavior can directly influence energy intake and individual fitness

A useful way to understand the approach of behavioral ecology is by focusing on foraging behavior. For many animals, food comes in a variety of sizes. Larger foods may contain more energy but may be harder to capture and less abundant. In addition, animals may forage for some types of food that are farther away than other types. For these animals foraging involves a trade-off between a food's energy content and the cost of obtaining it. The net energy (estimated in calories or joules) gained by feeding on prey of each size is simply the energy content of the prey minus the energy costs of pursuing and handling it. According to

optimal foraging theory, natural selection favors individuals whose foraging behavior is as energetically efficient as possible. In other words, animals tend to feed on prey that maximize their net energy intake per unit of foraging time.

A number of studies have demonstrated that foragers do prefer prey that maximize energy return. Shore crabs, for example, tend to feed primarily on intermediate-sized mussels, which provide the greatest energy return; larger mussels yield more energy, but also take considerably more energy to crack open (figure 55.25).

This optimal foraging approach assumes natural selection will favor behavior that maximizes energy acquisition if the increased energy reserves lead to increases in reproductive success. In both Colombian ground squirrels and captive zebra finches, a direct relationship exists between net energy intake and the number of offspring raised; similarly, the reproductive success of orb-weaving spiders is related to how much food they can capture.

Animals have other needs besides energy, however, and sometimes these needs conflict. One obvious need is the avoidance of predators: Often, the behavior that maximizes energy intake is not the one that minimizes predation risk. In this case, the behavior that maximizes fitness often may reflect a trade-off between obtaining the most energy at the least risk of being eaten. Not surprisingly, many studies have shown that a wide variety of animal species alter their foraging behavior—becoming less active, spending more time watching for predators, or staying nearer to cover—when predators are present. Compromises, in this case a trade-off between vigilance and feeding, may thus be made during foraging.

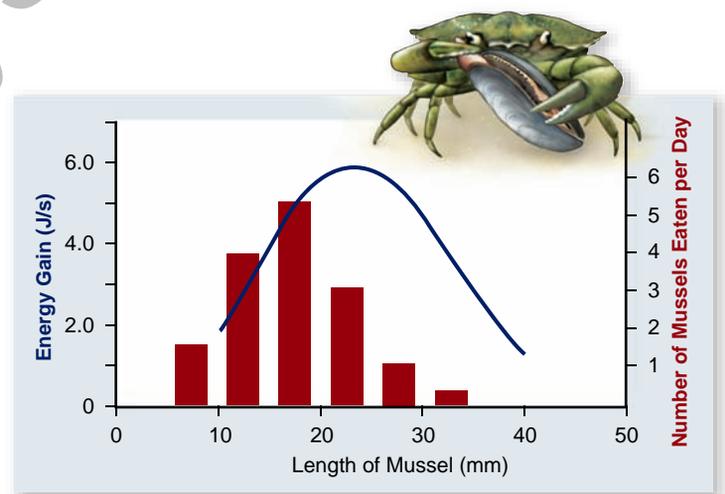


Figure 55.25 Optimal diet. The shore crab selects a diet of energetically profitable prey. The curve describes the net energy gain (equal to energy gained minus energy expended) derived from feeding on different sizes of mussels. The bar graph shows the numbers of mussels of each size in the diet. Shore crabs tend to feed on those mussels that provide the most energy.

Inquiry question

? What factors might be responsible for the slight difference in peak prey length relative to the length optimal for maximum energy gain?

Optimal foraging theory assumes that energy-maximizing behavior has evolved by natural selection. Therefore, it must have a genetic basis. For example, female zebra finches particularly successful in maximizing net energy intake tend to have similarly successful offspring. In this study, young birds were removed from their mothers before they were able to leave the nest, so this similarity indicates that foraging behavior probably has a genetic component. Studies on other animals show that age, experience, and learning are also important to the development of efficient foraging.

Territorial behavior evolves if the benefits of holding a territory exceed the costs

Animals often move over a large area, or home range, during their course of activity. In many species, the home range of several individuals overlaps in time or in space, but each individual defends a portion of its home range and uses it and its resources exclusively. This behavior is called **territoriality** (figure 55.26).

The defining characteristic of territorial behavior is defense against intrusion and resource use by other individuals. Territories are defended by displays advertising that territories are occupied, and by overt aggression. A bird sings from its perch within a territory to prevent take-over by a neighboring bird. If a potential usurper is not deterred by the song, the territory owner may attack and try to drive it away. But territorial defense has its costs. Singing is energetically expensive, and attacks can lead to injury. Using a signal (a song or visual display) to advertise occupancy can reveal a bird's position to a predator.

Why does an animal bear the costs of territorial defense? Energetic benefits of territoriality may take the form of increased food intake due to exclusive use of resources, access to mates, or access to refuges from predators. Studies of nectar-feeding birds such as hummingbirds and sunbirds provide an example (figure 55.27). A bird benefits from having the exclusive use of a patch of flowers because it can efficiently harvest the nectar the flowers produce. To maintain exclusive use, the bird

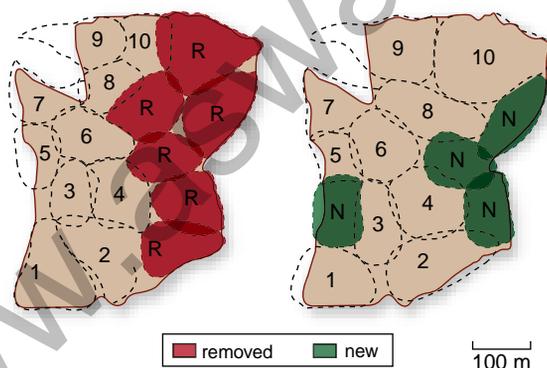


Figure 55.26 Competition for space. Territory size in birds is adjusted according to the number of competitors. When six pairs of great tits (*Parus major*) were removed from their territories (indicated by R in the left figure), their territories were taken over by other birds in the area and by four new pairs (indicated by N in the right figure). Numbers correspond to the birds present before and after.



Figure 55.27 The benefit of territoriality. Sunbirds (on the left), found in Africa and ecologically similar to New World hummingbirds (on the right), protect their food source by attacking other sunbirds that approach flowers in their territory.

must actively defend the patch. The benefits of exclusive use outweigh the costs of defense only under certain conditions.

Sunbirds, for example, expend 3000 calories per hour chasing intruders from a territory. Whether the benefit of defending a territory will exceed this cost depends on the amount of nectar in the flowers and how efficiently the bird can collect it. When flowers are very scarce or nectar levels are very low, a nectar-feeding bird may not gain enough energy to balance the energy used in defense. Under these conditions, it is not energetically advantageous to be territorial. Similarly, when flowers are very abundant, a bird can efficiently meet its daily energy requirements without behaving territorially and adding the costs of defense. Again, from an energetic standpoint, defending abundant resources isn't worth the cost, either. Territoriality therefore only occurs at intermediate levels of flower availability and nectar production, when the benefits of defense outweigh the costs.

In many species, access to females is a more important determinant of territory size for males than is food availability. In some lizards, for example, males maintain enormous territories during the breeding season. These territories, which encompass the territories of several females, are much larger than would be required to supply enough food, and they are defended vigorously. In the nonbreeding season, by contrast, male territory size decreases dramatically, as does aggressive territorial behavior.

Learning Outcomes Review 55.9

Behavioral ecology is the study of the adaptive significance of behavior—that is, how it affects survival and reproductive success. An economic approach estimates the energy benefits and costs of a behavior and assumes that animals gain more from a behavior than they expend, obtaining a fitness advantage. Foraging behavior and defense of a territory can be analyzed in this way. Apart from energy gains, considerations such as avoiding predators are also important to fitness.

- **The Hawaiian honeycreeper, a nectar-feeding bird, fails to defend flowers that are either infrequently encountered or very abundant. Why?**

55.10 Reproductive Strategies and Sexual Selection

Learning Outcomes

1. Explain parental investment and the prediction it makes about mate choice.
2. Describe how sexual selection leads to the evolution of secondary sexual characteristics.
3. Explain why some species are generally monogamous and other are polygynous.

During the breeding season, animals make several important life-history “decisions” concerning their choice of mates, how many mates to have, and how much time and energy to devote to rearing offspring. These decisions are all aspects of an animal’s **reproductive strategy**, a set of behaviors that presumably have evolved to maximize reproductive success. Energetic costs of reproduction appear to have been critically important to behavioral differences between females and males. Ecological factors such as the way food resources, nest sites, and members of the opposite sex are spatially distributed in the environment, as well as disease, are important in the evolution of reproductive decisions.

The sexes often have different reproductive strategies

Males and females have the common goal of improving the quantity and quality of offspring they produce, but usually

differ in the way they attempt to maximize fitness. Such a difference in reproductive behavior is clearly seen in mate choice. Darwin was the first to observe that females often do not mate with the first male they encounter, but instead seem to evaluate a male’s quality and then decide whether to mate. Peahens prefer to mate with peacocks that have more eyespots on their elaborate tail feathers (figure 55.28*b, c*). Similarly, female frogs prefer to mate with males having more acoustically complex, and thus attractive, calls. This behavior, called mate choice, is well known in many invertebrate and vertebrate species.

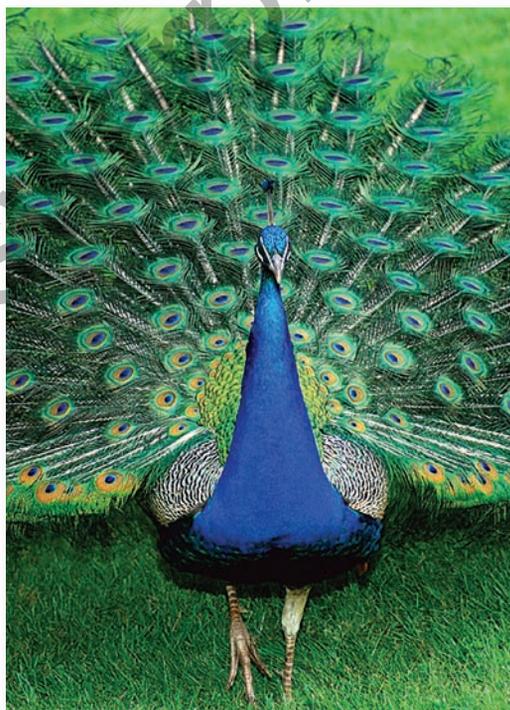
Males are selective in choosing a mate much less frequently than females. Why should this be? Many of the differences in reproductive strategies between the sexes can be understood by comparing the parental investment made by males and females. **Parental investment** refers to the energy and time each sex makes (“invests”) in producing and rearing offspring; it is, in effect, an estimate of the energy expended by males and females in each reproductive event.

Numerous studies have shown that females generally have a higher parental investment. One reason is that eggs are much larger than sperm—195,000 times larger in humans! Eggs contain proteins and lipids in the yolk and other nutrients for the developing embryo, but sperm are little more than mobile DNA packages. In some groups of animals (mammals, for example), females are responsible for gestation and lactation, costly reproductive functions only they can carry out.

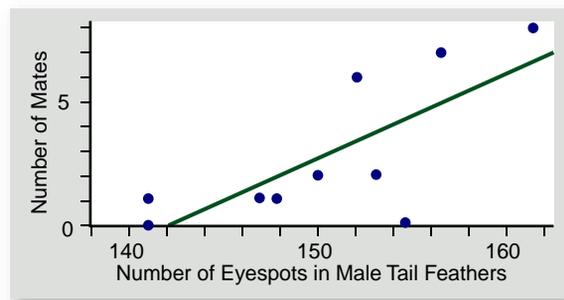
The consequence of such inequalities in reproductive investment is that the sexes face very different selective pressures. Because any single reproductive event is relatively inexpensive for males, they can best increase their fitness by mating with as many females as possible. This is because



a.



b.



c.

Figure 55.28 Products of sexual selection.

Attracting mates with long feathers is common in bird species such as (a) the African paradise whydah (*Vidua paradisaea*), and (b) the peacock (*Pavo cristatus*) which show pronounced sexual dimorphism. c. Female peahens prefer to mate with males having greater numbers of eyespots in their tail feathers.

Inquiry question



Why do females prefer males with more spots?

male fitness is likely limited by the amount of sperm they can produce. By contrast, each reproductive event for females is much more costly, and the number of eggs that can be produced often limits reproductive success. For this reason, a female should be choosy, trying to pick the male that can provide the greatest benefit to her offspring and thus improve her fitness.

These conclusions hold only when female reproductive investment is much greater than that of males. In species with biparental care, males may contribute equally to the cost of raising young; in this case, the degree of mate choice should be more equal between the sexes.

In some cases, male investment exceeds that of females. For example, male Mormon crickets transfer a protein-containing packet (a spermatophore) to females during mating. Almost 30% of a male's body weight is made up by the spermatophore, which provides nutrition for the female and helps her develop her eggs. As we might expect from our model of mate choice, in this case it is the females that compete with one another for access to males, which are the choosy sex. Indeed, males are quite selective, favoring heavier females. Heavier females have more eggs; thus, males that choose larger females leave more offspring (figure 55.29).

Males care for eggs and developing young in many species, including seahorses and a number of birds and insects. As with Mormon crickets, these males are often choosy, and females compete for mates.

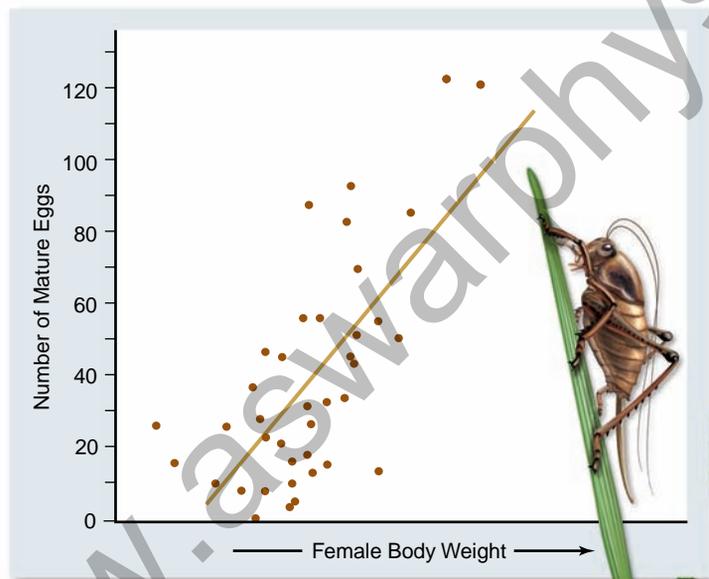


Figure 55.29 The advantage of male mate choice. Male Mormon crickets (*Anabrus simplex*) choose heavier females as mates, and larger females have more eggs. Thus, male mate selection increases fitness.

Inquiry question



Is there a benefit to females for mating with large males?

Sexual selection occurs through mate competition and mate choice

As discussed in chapter 20, the reproductive success of an individual is determined by how long the individual lives, how frequently it mates, and how many offspring it produces per mating. The second of these factors, competition for mates, is termed **sexual selection**. Some people consider sexual selection to be distinctive from natural selection, but others see it as a subset of natural selection, just one of the many factors affecting an organism's fitness.

Sexual selection involves both **intrasexual selection**, or competitive interactions between members of one sex (“the power to conquer other males in battle,” as Darwin put it), and **intersexual selection**, which is another name for mate choice (“the power to charm”). Sexual selection leads to the evolution of structures used in combat with other males, such as a deer's antlers and a ram's horns, as well as ornaments used to “persuade” members of the opposite sex to mate, such as long tail feathers and bright plumage (see figure 55.28*a, b*). These traits are called **secondary sexual characteristics**.

Selection strongly favors any trait that confers greater ability in mate competition. Larger body size is a great advantage if dominance is important, as it is in territorial species. Males may thus be considerably larger than females. Such differences between the sexes are referred to as sexual dimorphism. In other species, structures used for fighting, such as horns, antlers, and large canine teeth, have evolved to be larger in males because of the advantage they give in intrasexual competition.

Sometimes **sperm competition** occurs between the sperm of different males if females mate with multiple males. This type of competition, which occurs after mating, has selected for sperm-transfer organs designed to remove the sperm of a prior mating, large testes to produce more sperm per mating, and sperm that hook themselves together to swim more rapidly. These traits enhance the likelihood of fertilizing an egg.

Intrasexual selection

In many species, individuals of one sex—usually males—compete with one another for the opportunity to mate. Competition can occur for a territory in which females feed or bear young. Males may also directly compete for the females themselves. A few successful males may engage in an inordinate number of matings, while most males do not mate at all. For example, elephant seal males control territories on breeding beaches and a few dominant males do most of the breeding (figure 55.30). On one beach, for example, eight males impregnated 348 females, while the remaining males mated rarely, if at all.

Intersexual selection

Intersexual selection concerns the active choice of a mate. Mate choice has both direct and indirect benefits.

Direct benefits of mate choice. In some cases, the benefits of mate choice are obvious. If males help raise offspring, females benefit by choosing the male that can provide the best



Figure 55.30 Female defense polygyny in northern elephant seals (*Mirounga angustirostris*). Male elephant seals fight with one another for possession of territories. Only the largest males can hold territories, which contain many females.

care—the better the parent, the more offspring she is likely to rear. In other species, males provide no care, but maintain territories that provide food, nesting sites, and predator refuges. In red deer, males that hold territories with the highest quality grasses mate with the most females. In this case, there is a direct benefit of a female mating with such a territory owner: She feeds with little disturbance on quality food.

Indirect benefits of mate choice. In many species, however, males provide no direct benefits of any kind to females. In such cases, it is not intuitively obvious what females have to gain by being “choosy.” Moreover, what could be the possible benefit of choosing a male with an extremely long tail or a complex song?

A number of theories have been proposed to explain the evolution of such preferences. One idea is that females choose the male that is the healthiest or oldest. Large males, for example, have probably been successful at living long, acquiring a lot of food, and resisting parasites and disease. In other species, features other than size may indicate a male’s condition. In guppies and some birds, the brightness of a male’s color reflects the quality of his diet and overall health. Females may gain two benefits from mating with the healthiest males. First, healthy males are less likely to be carrying diseases, which might be transmitted to the female during mating. Second, to the extent that the males’ success in living long and prospering is the re-

sult of his genetic makeup, the female will be ensuring that her offspring receive good genes from their father.

Several experimental studies in fish and moths have examined whether female mate choice leads to greater reproductive success. In these experiments, females in one group were allowed to choose males, whereas males were randomly mated to a different group of females. Offspring of females that chose their mates were more vigorous and survived better than offspring from females given no choice, which suggests that females preferred males with a better genetic makeup.

A variant of this theory goes one step further. In some cases, females prefer mates with traits that appear to be detrimental to survival (see figure 55.28c). The long tail of the peacock is a hindrance in flying and makes males more vulnerable to predators. Why should females prefer males with such traits? The **handicap hypothesis** states that only genetically superior mates can survive with such a handicap. By choosing a male with the largest handicap, the female is ensuring that her offspring will receive these quality genes. Of course, the male offspring will also inherit the genes for the handicap. For this reason, evolutionary biologists are still debating the merit of this hypothesis.

Alternative theories about the evolution of mate choice.

Some courtship displays appear to have evolved from a predisposition in the female’s sensory system to respond to certain stimuli. For example, females may be better able to detect particular colors or sounds at a certain frequency, and thus be attracted to such signals. **Sensory exploitation** involves the evolution in males of a signal that “exploits” these preexisting biases. For example, if females are particularly adept at detecting red objects, then red coloration may evolve in males as part of a courtship display.

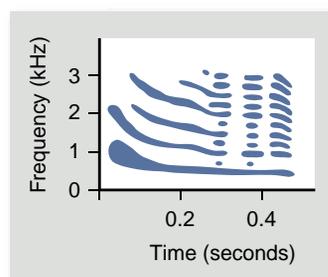
To understand the evolution of courtship calls, consider the vocalizations of the Túngara frog (figure 55.31). Unlike related species, males include a short burst of sound, termed a “chuck,” at the end of their calls. Recent research suggests that not only are females of this species particularly attracted to calls of this sort, but so are females of related species, even though males of these species do not produce “chucks.”

A great variety of other hypotheses have been proposed to explain the evolution of mating preferences. Many of these hypotheses may be correct in some circumstances, but none seems capable of explaining all of the variation in mating behavior in the animal world. This is an area of vibrant research, with new discoveries appearing regularly.

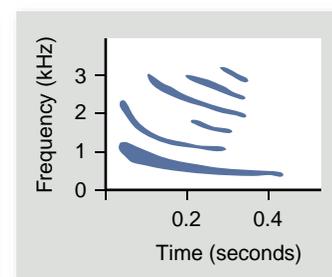
Figure 55.31 Male Túngara frog (*Physalaemus pustulosus*) calling. Female frogs of several species in the genus *Physalaemus* prefer males that include a “chuck” in their call. However, only males of the Túngara frog (a) produce such calls (b); males of other species do not (c).



a.



b.



c.

Mating systems reflect the ability of parents to care for offspring and are influenced by ecology

The number of individuals with which an animal mates during the breeding season varies among species. Mating systems include monogamy (one male mates with one female), polygyny (one male mates with more than one female; see figure 55.30), and polyandry (one female mates with more than one male). Only monogamous mating includes a pair bond (like prairie voles). Like mate choice, mating systems have evolved to allow females and males to maximize fitness.

The option of having more than one mate may be constrained by the need for offspring care. If females and males are able to care for young, then the presence of both parents may be necessary for young to be reared successfully. Monogamy may thus be favored. Generally this is the case for birds, in which over 90% of all species appear to be monogamous. A male may either remain with his mate and provide care for the offspring or desert that mate to search for others; both strategies may increase his fitness. The strategy that natural selection will favor depends on the requirement for male assistance in feeding or defending the offspring. In some species (like humans!), offspring are **altricial**—they require prolonged and extensive care. In these species, the need for care by two parents reduces the tendency for the male to desert his mate and seek other matings. In species in which the young are **precocial** (requiring little parental care), males may be more likely to be polygynous because the need for their parenting is lower. In mammals, only females lactate, freeing males from feeding offspring. It follows that most mammals are polygynous.

Mating systems are strongly influenced by ecology. A male may defend a territory that holds nest sites or food sources sufficient for more than one female. If territories vary in quality or quantity of resources, a female's fitness is maximized if she mates with a male holding a high-quality territory, even if he has mated. Although a male may already have a mate, it is still more advantageous for the female to breed with a mated male holding a high-quality territory than with an unmated male holding a low-quality territory. This favors the evolution of polygyny.

Polyandry is relatively rare, but the evolution of multiple mating by females is becoming better understood. It is best known in birds like spotted sandpipers and jacanas living in highly productive environments such as marshes and wetlands. Here, females take advantage of the increased resources available to rear offspring by laying clutches of eggs with more than one male. Males provide all incubation and parenting, and females mate and leave eggs with two or more males.

Females may also mate with several males to genetically diversify their offspring, which in turn increases disease resistance. This appears to be the case in honey bees, for example, in which a queen may mate with many males.

Extra-pair copulations

The “monogamy” of many bird species has been re-evaluated as DNA fingerprinting (see chapter 15) has become commonly used to determine paternity and precisely quantify the reproductive success of individual males (figure 55.32a). In red-winged blackbirds (figure 55.32b), researchers established that

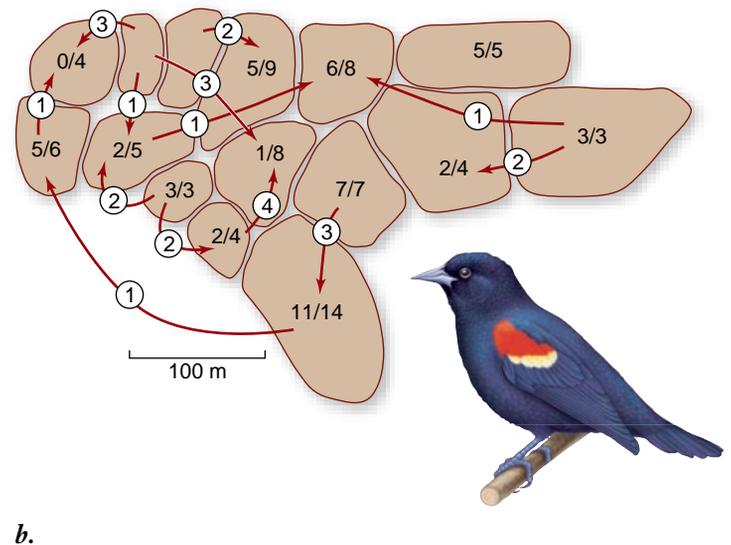
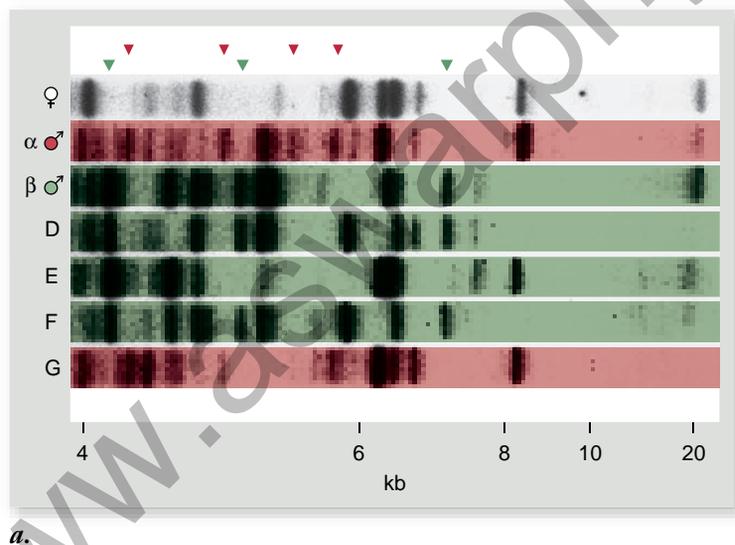


Figure 55.32 The study of paternity. *a.* A DNA fingerprinting gel from the dunnock (*Prunella modularis*). The bands represent fragments of DNA of different lengths. The four nestlings (D–G) were in the nest of the female. By comparing the bands present in the two males and the female, we can determine which male fathered which offspring. The triangles point to the bands that are diagnostic for one male and not the other. In this case, the β -male fathered three (D, E, F, but not G) of the four offspring. *b.* Results of a DNA fingerprinting study in red-winged blackbirds (*Agelaius phoeniceus*). Fractions indicate the proportion of offspring fathered by the male in whose territory the nest occurred. Arrows indicate how many offspring were fathered by particular males outside of each territory. Nests on some territories were not sampled.

55.11 Altruism

Learning Outcomes

1. Explain altruism and its benefits.
2. Explain kin selection and inclusive fitness.
3. Discuss how haplodiploidy influences kin selection in eusocial insects.

half of all nests contained at least one hatchling fertilized by a male other than the territory owner; overall, 20% of the offspring were the result of such **extra-pair copulations (EPCs)**.

What is the evolutionary advantage of EPCs? For males, the answer is obvious: increased reproductive success. Females, on the other hand, may mate with genetically superior individuals even if already paired with a male, thus enhancing the genes passed on to their offspring. The female doesn't produce more offspring, but offspring of better genetic quality. In some birds and other animals, EPCs may help females increase the amount of care they get from males to raise their offspring. This is exactly what happens in a common English bird, the dunnock. Females mate not only with the territory owner, but also with subordinate males that hang around the edge of the territory. If these subordinates mate a sufficient number of times with a female, they will help raise her young, presumably because they may have fathered some of these young.

Alternative mating strategies

Natural selection has led to the evolution of many ways of increasing reproductive success. For example, in many species of fish, there are two genetic classes of males. One group is large and defends territories to obtain matings. The other group is small and adopts a completely different strategy. These males do not maintain territories, but loiter at the edge of the territories of large males. Just at the end of a male's courtship, when the female is laying her eggs and the territorial male is depositing sperm, the smaller male darts in and releases its own sperm into the water, thus fertilizing some of the eggs. If this strategy is successful, natural selection will favor the evolution of these two different male reproductive strategies.

Similar patterns are seen in other organisms. In some dung beetles, territorial males have large horns that they use to guard the chambers in which females reside, whereas genetically small males don't have horns. Instead, the smaller males dig side tunnels and attempt to intercept the female inside her chamber. In Isopods, there are three genetic size classes. The medium-sized males pass for females and enter a large male's territory in this way; the smallest class are so tiny, they are able to sneak in completely undetected.

This is just a glimpse of the rich diversity in mating systems and mating tactics that have evolved. The bottom line is: If there is a way of increasing reproductive success, natural selection will favor its evolution.

Learning Outcomes Review 55.10

The sex that invests more in reproduction (parental investment) tends to exhibit mate choice. Females or males can be selective, depending on the energy and time they devote to parental care. Sexual selection governs evolution of secondary sex characteristics in that mates are chosen on the basis of phenotype and competitive success. Reproductive success influences whether males and females mate monogamously or with multiple partners.

- *Pipefish males incubate young in a brood pouch. Which sex would you expect to show mate choice? Why?*

Understanding the evolution of altruism has been a particular challenge to evolutionary biologists, including Darwin himself. Why should an individual decrease his or her own fitness to help another? How could genes for altruism be favored by natural selection, given that the frequency of such genes should decrease in populations through time?

In fact, there can be great benefits to being an altruist, even if the altruism leads an individual to forego reproduction or even sacrifice its own life. Let's examine how this can work.

Altruism is behavior that benefits another individual at a cost to the actor. Humans sacrificing themselves in times of war or placing themselves in jeopardy to help their children are examples, but altruism also has been described in an extraordinary variety of organisms. In many bird species, for example, there are "helpers at the nest"—birds other than parents who assist in raising their young. In both mammals and birds, individuals that spy a predator may give an alarm call, alerting other members of their group to allow them to escape, even though such an act might call the predator's attention to the caller. And in social insects like ants, workers are sterile offspring that help their mother, the colony's queen, to reproduce.

A number of explanations have been put forward to explain the evolution of altruism. Once it was thought that altruism evolved for the "good of the species." Individuals that fail to mate, for example, have been called "altruists" because their lack of success in competition has been misinterpreted as a willingness to forego reproduction so that the population or species does not increase in size, exhaust its resources, and go extinct. This group selection explanation (selection acting on a population or species) is simply incorrect because individuals that fail to secure mates and not breed will not leave any offspring. Therefore, their "altruism" would not be favored by selection.

Current studies of altruism note that seemingly altruistic acts are in fact selfish. For example, helpers at the nest are often young birds that gain valuable parenting experience by assisting established breeders; this may give them an advantage when they breed. Moreover, they may have limited opportunities to reproduce on their own, and by hanging around breeding pairs, may inherit the territory when established breeders die.

Reciprocity theory explains altruism between unrelated individuals

One explanation of altruism proposes that genetically unrelated individuals may form "partnerships" in which mutual exchanges of altruistic acts occur because they benefit both participants.

Partners are willing to give aid at one time and delay “repayment” for the good deed to a time in the future when they themselves are in need. In **reciprocal altruism**, the partnerships are stable because “cheaters” (nonreciprocators) are discriminated against and do not receive future aid. According to this hypothesis, if the altruistic act is relatively inexpensive, the small benefit a cheater receives by not reciprocating is far outweighed by the potential cost of not receiving future aid. Under these conditions, cheating behavior should be eliminated by selection.

Vampire bats roost in hollow trees, caves, and mines in groups of 8 to 12 individuals (figure 55.33). Because bats have a high metabolic rate, individuals that have not fed recently may die. Bats that have found a host imbibe a great deal of blood, so giving up a small amount to keep a roostmate from starvation presents no great energy cost to the donor. Vampire bats tend to share blood with past reciprocators that are not necessarily relatives. If an individual fails to give blood to a bat from which it received blood in the past, it will be excluded from future bloodsharing. Reciprocity routinely occurs in many primates, including humans (obviously!).

Kin selection theory proposes a direct genetic advantage to altruism

The great population geneticist J. B. S. Haldane once passionately said in a pub that he would willingly lay down his life for two brothers or eight first cousins.

Evolutionarily speaking, this sacrifice makes sense, because for each allele Haldane received from his parents, his brothers each had a 50% chance of receiving the same allele (figure 55.34). Statistically, it is expected that two of his brothers would pass on as many of Haldane’s particular combination



Figure 55.33 Truth is stranger than fiction: Reciprocal altruism in vampire bats (*Desmodus rotundus*). Vampire bats do feed on the blood of large mammals, but they don’t transform into people and sleep in coffins. Vampires live in groups and share blood meals. They remember which bats have provided them with blood in the past and are more likely to share with those bats that have shared with them previously. The bats here are feeding on cattle in Brazil.

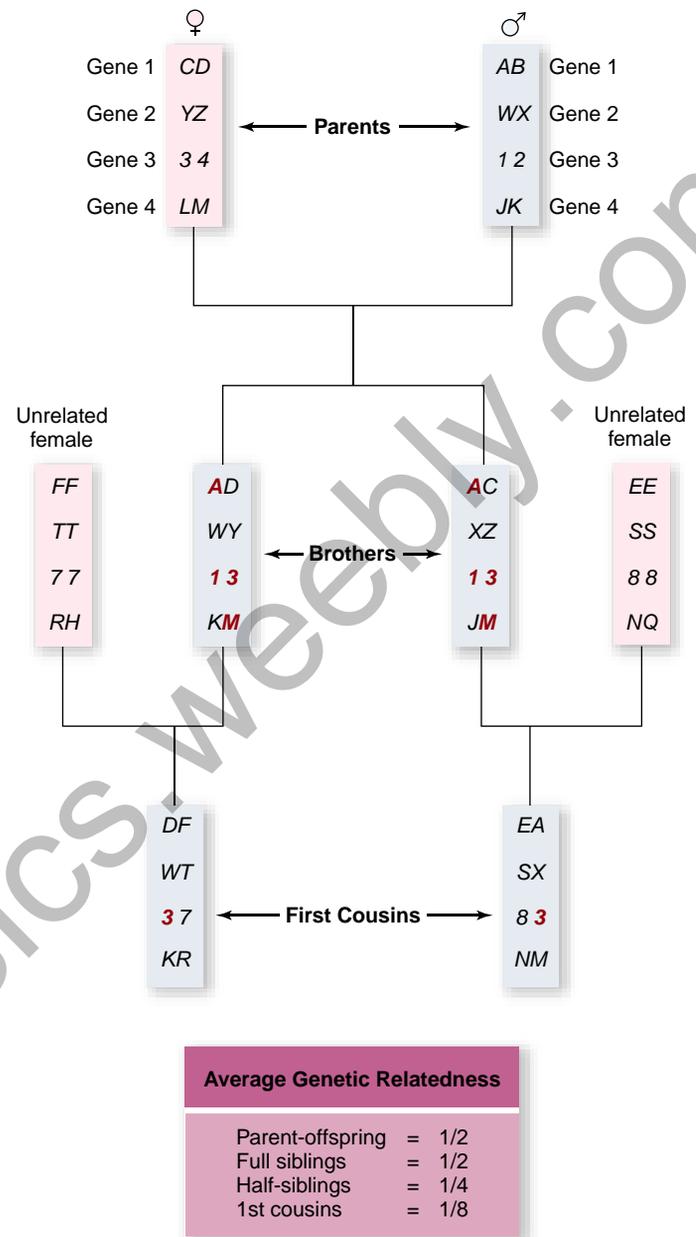


Figure 55.34 Hypothetical example of genetic relationships. On average, full siblings share half of their alleles. By contrast, cousins only share one-eighth of their alleles on average. Each letter and number represents a different allele.

of alleles to the next generation as Haldane himself would. Similarly, Haldane and a first cousin would share an eighth of their alleles (see figure 55.34). Their parents, who are siblings, would each share half their alleles, and each of their children would receive half of these, of which half on the average would be in common: $1/2 \times 1/2 \times 1/2 = 1/8$. Eight first cousins would therefore pass on as many of those alleles to the next generation as Haldane himself would.

The most compelling explanation for the kin-related origin of altruism was presented by one of the most influential evolutionary biologists of our time, William D. Hamilton, in 1964. Hamilton understood Haldane’s point: Natural selection will favor any behavior, including the sacrifice of life, that increases the propagation of an individual’s alleles.

Hamilton mathematically showed that by directing aid toward close genetic relatives, an altruist may increase the reproductive success of its relatives enough to not only compensate for the reduction in its own fitness, but even increase its fitness beyond what would be possible without assisting relatives. Because the altruist's behavior increases the propagation of alleles in relatives, it will be favored by natural selection. Selection that favors altruism directed toward relatives is called kin selection. Although the behaviors are altruistic, the genes are actually "behaving selfishly," because they encourage the organism to favor the success of copies of themselves in relatives. In other words, if an individual has a dominant allele that causes altruism, any action that increases the frequency of this allele in future generations will be favored, even if that action is detrimental to the actor.

Hamilton then defined reproductive success with a new concept—inclusive fitness. Inclusive fitness considers gene propagation through both direct (personal fitness) and indirect (the fitness of relatives) reproduction. Hamilton's kin selection model predicts that altruism is likely to be directed toward close relatives. The more closely related two individuals are, the greater the potential genetic payoff, and the greater inclusive fitness. This is described by Hamilton's rule, which states that altruistic acts are favored when $rb > c$. In this expression, b and c are the benefits and costs of the altruistic act, respectively, and r is the coefficient of relatedness, the proportion of alleles shared by two individuals through common descent. For example, an individual should be willing to have one less child ($c = 1$) if such actions allow a half-sibling, which shares one-quarter of its genes ($r = 0.25$), to have five or more additional offspring ($b = 5$).

Haplodiploidy and altruism in ants, bees, and wasps

The relationship between genetic relatedness, kin selection, and altruism can be best understood using social insects as an example. A hive of honeybees consists of a single queen, who is the sole egg-layer, and tens of thousands of her offspring, female workers with nonfunctional ovaries (figure 55.35). Honeybees are eusocial ("truly" social): their societies are defined by reproductive division of labor (only the queen reproduces), cooperative care of the brood (workers nurse, clean, and forage), and overlap of generations (the queen lives with several generations of her offspring).

Darwin was perplexed by eusociality. How could natural selection favor the evolution of sterile workers that left no offspring? It remained for Hamilton to explain the origin of eusociality in hymenopterans (bees, wasps, and ants) using his kin selection model. In these insects, males are haploid (produced from unfertilized eggs) and females are diploid. This system of sex determination and parthenogenesis, called haplodiploidy, leads to unusual genetic relatedness among colony members. If the queen is fertilized by a single male, then all female offspring will inherit exactly the same alleles from their father (because he is haploid and has only one copy of each allele). Female offspring (workers and future queens) will also share among themselves, on average, half of the alleles they get from their mother, the queen. Consequently, they will share, on average, 75% of their alleles with each sister (to verify this, rework figure 55.34, but allow the father to only have one allele for each gene).

Now recall Haldane's statement of commitment to family while you read this section. If a worker should have offspring of



Figure 55.35 Reproductive division of labor in honeybees. The queen (center) is the sole egg-layer. Her daughters are sterile workers.

her own, she would share only half of her alleles with her young (the other half would come from their father). Thus, because of this close genetic relatedness due to haplodiploidy, workers would propagate more of their own alleles by giving up their own reproduction to assist their mother in rearing their sisters, some of whom will be new queens, start new colonies, and reproduce.

In this way, the unusual haplodiploid system may have set the "genetic stage" for the evolution of eusociality. Indeed, eusociality has evolved at least 12 separate times in the Hymenoptera. One wrinkle in this theory, however, is that eusocial systems have evolved in other insects (thrips, weevils, and termites), and mammals (naked mole rats). Although thrips are also haplodiploid, termites and naked mole rats are not. Thus, although haplodiploidy may have facilitated the evolution of eusociality, other factors can influence social evolution.

Other examples of kin selection

Kin selection may explain altruism in other animals. Belding's ground squirrels give alarm calls when they spot a predator such as a coyote or a badger. Such predators may attack a calling squirrel, so giving the signal places the caller at risk. A ground squirrel colony consists of a female and her daughters, sisters, aunts, and nieces. When males mature, they disperse long distances from where they are born, so adult males in the colony are not genetically related to the females. By marking all squirrels in a colony with an individual dye pattern on their fur and by recording which individuals gave calls and the social circumstances of their calling, researchers found that females who have relatives living nearby are more likely to give alarm calls than females with no kin nearby. Males tend to call much less frequently, as would be expected because they are not related to most colony members.

Another example of kin selection is provided by the white-fronted bee-eater, a bird which lives along river banks in Africa in colonies of 100 to 200 individuals (figure 55.36). In contrast to ground squirrels, the male bee-eaters usually remain in the colony in which they were born, and the females disperse to join new colonies. Many bee-eaters do not raise their own offspring, but instead help others. Most helpers are young birds,



Figure 55.36 Kin selection in the white-fronted bee-eater (*Merops bullockoides*). Bee-eaters are small insectivorous birds that live in Africa in large colonies. Bee-eaters often help others raise their young; helpers usually choose to help close relatives.

but older birds whose nesting attempts have failed may also be helpers. The presence of a single helper, on average, doubles the number of offspring that survive. Two lines of evidence support the idea that kin selection is important in determining helping behavior in this species. First, helpers are normally males, which are usually related to other birds in the colony, and not females, which are not related. Second, when birds have the choice of helping different parents, they almost invariably choose the parents to which they are most closely related.

Learning Outcomes Review 55.11

Genetic and ecological factors have contributed to evolution of altruism, a behavior that benefits another individual at a cost to the actor. Individuals may benefit directly if cooperative acts are reciprocated among unrelated interactants. Kin selection explains how altruistic acts directed toward relatives, which share alleles, increase an individual's inclusive fitness. Haplodiploidy has resulted in eusociality among some insects by increasing genetic relatedness; it is not found in vertebrates.

- Imagine that you witness older group members rescuing infants in a troupe of monkeys when a predator appears. How would you test whether the altruistic act you see is reciprocity or kin selection?

55.12 The Evolution of Group Living and Animal Societies

Learning Outcomes

1. Explain the possible advantages of group living.
2. Contrast the nature of insect and vertebrate societies.
3. Discuss social organization in African weaver birds and how it is influenced by ecology.

Organisms from cnidarians and insects to fish, whales, chimpanzees, and humans live in social groups. To encompass the

wide variety of social phenomena, we can broadly define a society as a group of organisms of the same species that are organized in a cooperative manner.

Why have individuals in some species given up a solitary existence to become members of a group? One hypothesis is that individuals in groups benefit directly from social living. For example, a bird in a flock may be better protected from predators. As flock size increases, the risk of predation decreases because there are more individuals to scan the environment for predators (figure 55.37).

A member of a flock may also increase its feeding success if it can acquire information from other flock members about the location of new, rich food sources. In some predators, hunting in groups can increase success and allow the group to tackle prey too large for any one individual.

Insect societies form efficient colonies containing specialized castes

We've already discussed the origin of eusociality in the insect order Hymenoptera (ants, bees, and wasps). Additionally, all termites (order Isoptera) are also eusocial, and a few other insect and arthropod species are eusocial. Social insect colonies are composed of different *castes*, groups of individuals that differ in reproductive ability (queens vs. workers), size, and morphology and perform different tasks. Workers nurse, maintain the nest, and forage; soldiers are large and have powerful jaws specialized for defense.

The structure of an insect society is illustrated by leaf-cutters, which form colonies of as many as several million individuals. These ants cut leaves and use it to grow crops of fungi beneath the ground. Workers divide the tasks of leaf cutting, defense, mulching the fungus garden, and implanting fungal hyphae according to their body size (figure 55.38).

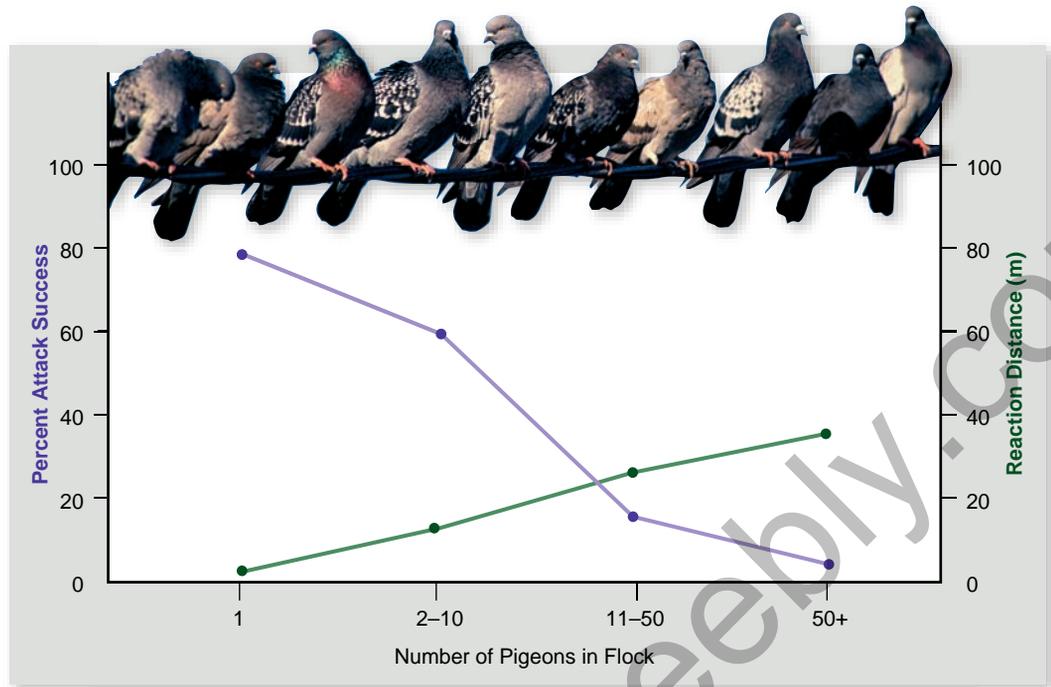
The structure of a vertebrate society is related to ecology

In contrast to the highly structured and integrated insect societies and their remarkable forms of altruism, vertebrate social

Figure 55.37 Flocking behavior decreases predation.

When more pigeons are present in the flock, they can detect hawks at greater distances, thus allowing more time for the pigeons to escape. As a result, as the size of a pigeon flock increases, hawks are less successful at capturing pigeons.

Inquiry question
? How would living in a flock affect the time available for foraging by individual pigeons?



groups are usually less rigidly organized and less cohesive. It seems paradoxical that vertebrates, which have larger brains and are capable of more complex behaviors, are generally less altruistic than insects (the exception, of course, is humans). Reciprocity and kin-selected altruism are common in vertebrate societies, although there is often more conflict and aggression among group members. Conflicts generally center on access to food and mates and occur because a vertebrate society is a made up of individuals striving to improve their own fitness.

Social groups of vertebrates have a size, stability of members, number of breeding males and females, and type of mating system characteristic of a given species. Diet and predation

are important factors in shaping social groups. For example, meerkats take turns watching for predators while other group members forage for food (figure 55.39).

African weaver birds, which construct nests from vegetation, provide an excellent example of the relationship between ecology and social organization. Their roughly 90 species can be divided according to the type of social group they form. One group of species lives in the forest and builds camouflaged, solitary nests. Males and females are monogamous; they forage for insects to feed their young. The second group of species nests in colonies in trees on the savanna. They are polygynous and feed in flocks on seeds.

The feeding and nesting habits of these two groups of species are correlated with their mating systems. In the forest, insects are hard to find, and both parents must cooperate in feeding the young. The camouflaged nests do not call the attention of predators to their brood. On the open savanna, building a hidden nest is not an option. Rather, savanna-dwelling weaver birds protect their young from predators by nesting in trees, which are not very abundant. This shortage of safe nest sites means that birds must nest together in colonies. Because seeds occur abundantly, a female can acquire all the food needed to rear young without a male's help. The male, free from the duties of parenting, spends his time courting many females—a polygynous mating system.

One exception to the general rule that vertebrate societies are not organized like those of insects is the naked mole rat, a small, hairless rodent that lives in and near East Africa. Unlike other kinds of mole rats, which live alone or in small family groups, naked mole rats form large underground colonies with a far-ranging system of tunnels and a central nesting area. It is not unusual for a colony to contain 80 individuals.

Naked mole rats feed on bulbs, roots, and tubers, which they locate by constant tunneling. As in insect societies, there is a division of labor among the colony members, with some individuals working as tunnelers while others perform different



Figure 55.38 Castes of ants. These leaf-cutter ants are members of different castes. The large ant is a worker carrying leaves to the nest, whereas the smaller ants are protecting the worker from attack.



Figure 55.39 Foraging and predator avoidance. A meerkat sentinel on duty. Meerkats (*Suricata suricata*) are a species of highly social mongoose living in the semiarid sands of the Kalahari Desert in southern Africa. This meerkat is taking its turn to act as a lookout for predators. Under the security of its vigilance, the other group members can focus their attention on foraging.

tasks, depending on the size of their bodies. Large mole rats defend the colony and dig tunnels.

Naked mole rat colonies have a reproductive division of labor similar to the one normally associated with the eusocial insects. All of the breeding is done by a single female, or “queen,” who has one or two male consorts. The workers, consisting of both sexes, keep the tunnels clear and forage for food.

Learning Outcomes Review 55.12

Advantages of group living include protection from predators and increased feeding success. Eusocial insects form complex, highly altruistic societies that increase the fitness of the colony. The members of vertebrate societies exhibit more conflict and competition, but also cooperate and behave altruistically, especially toward kin. African weaver birds have developed different types of societies depending on the ecology of their habitat, particularly the safety of nesting sites.

- What are the benefits and costs associated with living in social groups?
- Why is altruism directed toward kin considered to be selfish behavior?
- Is a human army more like an insect society or a vertebrate society? Explain your answer.



Chapter Review

55.1 The Natural History of Behavior

Behavior can be analyzed in terms of mechanisms (cause) and evolutionary origin (adaptive nature).

Proximate causation refers to the mechanisms of behavior. Ultimate causation examines a behavior’s evolutionary significance.

Ethology emphasizes the study of instinct and its origins.

Innate, or instinctive, behavior is a response to an environmental stimulus or trigger that does not require learning (see figure 55.1).

55.2 Nerve Cells, Neurotransmitters, Hormones, and Behavior

Instinctive behaviors are accomplished by neural circuits, which develop under genetic control. Hormones and neurotransmitters can act to regulate behavior.

55.3 Behavioral Genetics

Artificial selection and hybrid studies link genes and behavior.

Breeding fast-learning and slow-learning rats among each other for several generations produced two distinct behavioral populations (see figure 55.3).

Some behaviors appear to be controlled by a single gene.

55.4 Learning

Learning mechanisms include habituation and association.

Habituation, a form of nonassociative learning, is a decrease in response to repeated nonessential stimuli. Associative learning is a change in behavior by association of two stimuli or of a behavior and a response (conditioning).

Classical (Pavlovian) conditioning occurs when two stimuli are associated with each other. Operant conditioning occurs when an animal associates a behavior with reward or punishment.

Instinct governs learning preparedness.

What an animal can learn is biologically influenced—that is, learning is possible only within the boundaries set by evolution.

55.5 The Development of Behavior

Parent–offspring interactions influence how behavior develops.

In imprinting, a young animal forms an attachment to other individuals or develops preferences that influence later behavior.

Instinct and learning may interact as behavior develops.

Animals may have an innate genetic template that guides their learning as behavior develops, such as song development in birds.

Studies on twins reveal a role for both genes and environment in human behavior.

55.6 Animal Cognition

Some animals exhibit cognitive behavior and can respond to novel situations using logic (see figures 55.12, 55.13).

55.7 Orientation and Migratory Behavior

Migration often involves populations moving large distances.

Migrating animals must be capable of orientation and navigation (see figure 55.16).

Orientation is the mechanism by which animals move by tracking environmental stimuli such as celestial clues or Earth's magnetic field. Navigation is following a route based on orientation and some sort of “map.” The nature of the map in animals is not known.

55.8 Animal Communication

Successful reproduction depends on appropriate signals and responses.

Courtship signals are usually species-specific and help to ensure reproductive isolation (see figure 55.19).

Communication enables information exchange among group members (see figures 55.20, 55.21).

55.9 Behavioral Ecology

Foraging behavior can directly influence energy intake and individual fitness.

Natural selection favors optimal foraging strategies in which energy acquisition (cost) is minimized and reproductive success (benefit) is maximized.

Territorial behavior evolves if the benefits of holding a territory exceed the costs.

55.10 Reproductive Strategies and Sexual Selection

The sexes often have different reproductive strategies.

One sex may be choosier than the other, and which one often depends on the degree of parental investment.

Sexual selection occurs through mate competition and mate choice.

Intrasexual selection involves competition among members of the same sex for the chance to mate. Intersexual selection is one sex choosing a mate.

Mate choice may provide direct benefits (increased resource availability or parental care) or indirect benefits (genetic quality of the mate).

Mating systems reflect the ability of parents to care for offspring and are influenced by ecology.

Mating systems include monogamy, polygyny, and polyandry; they are influenced by ecology and constrained by needs of offspring.

55.11 Altruism

Reciprocity theory explains altruism between unrelated individuals.

Mutual exchanges benefit both participants; a participant that does not reciprocate would not receive future aid.

Kin selection theory proposes a direct genetic advantage to altruism.

Kin selection increases the reproductive success of relatives and increased frequency of alleles shared by kin, and thus increases an individual's inclusive fitness.

Ants, bees, and wasps have haplodiploid reproduction, and therefore high degree of gene sharing.

55.12 The Evolution of Group Living and Animal Societies

A social system is a group organized in a cooperative manner.

Insect societies form efficient colonies containing specialized castes (see figure 55.38).

Social insect societies are composed of different castes that are specialized to reproduce or to perform certain colony maintenance tasks.

The structure of a vertebrate society is related to ecology.

Vertebrate social systems are less rigidly organized and cohesive and are influenced by food availability and predation.



Review Questions

UNDERSTAND

1. A key stimulus, innate releasing mechanism, and fixed action pattern
 - a. are mechanisms associated with behaviors that are learned.
 - b. are components of behaviors that are innate.
 - c. involve behaviors that cannot be explained in terms of ultimate causation.
 - d. involve behaviors that are not subject to natural selection.
2. In operant conditioning
 - a. an animal learns that a particular behavior leads to a reward or punishment.
 - b. an animal associates an unconditioned stimulus with a conditioned response.
 - c. learning is unnecessary.
 - d. habituation is required for an appropriate response.

3. The study of song development in sparrows showed that
 - a. the acquisition of a species-specific song is innate.
 - b. there are two components to this behavior: a genetic template and learning.
 - c. song acquisition is an example of associative learning.
 - d. All of these are correct.
4. The difference between following a set of driving directions given to you by somebody on the street (for example “. . . take a right at the next light, go four blocks and turn left . . .”) and using a map to find your destination is
 - a. the difference between navigation and orientation, respectively.
 - b. the difference between learning and migration, respectively.
 - c. the difference between orientation and navigation, respectively.
 - d. why birds are not capable of orientation.
5. In courtship communication
 - a. the signal itself is always species-specific.
 - b. the sign communicates species identity.
 - c. it involves a stimulus–response chain.
 - d. courtship signals are produced only by males.
6. Behavioral ecology assumes
 - a. that all behavioral traits are innate.
 - b. learning is the dominant determinant of behavior.
 - c. behavioral traits are subject to natural selection.
 - d. behavioral traits do not affect fitness.
7. According to optimal foraging theory
 - a. individuals minimize energy intake per unit of time.
 - b. energy content of a food item is the only determinant of a forager’s food choice.
 - c. time taken to capture a food item is the only determinant of a forager’s food choice.
 - d. a higher energy item might be less valuable than a lower energy item if it takes too much time to capture the larger item.
8. The elaborate tail feathers of a male peacock evolved because they
 - a. improve reproductive success of males and females.
 - b. improve male survival.
 - c. reduce survival.
 - d. None of the above.
9. From the perspective of females, extra-pair copulations (EPCs)
 - a. are always disadvantageous to females.
 - b. can be associated with receiving male aid.
 - c. are too rare to affect female fitness.
 - d. can only be of benefit if the EPC male has elaborate secondary sexual traits.
10. In the haplodiploidy system of sex determination, males are
 - a. haploid.
 - b. diploid.
 - c. sterile.
 - d. not present because bees exist as single-sex populations.
11. According to kin selection, saving the life of your ____ would do the least for increasing your inclusive fitness.

a. mother	c. sister-in-law
b. brother	d. niece
12. Altruism
 - a. is only possible through reciprocity.
 - b. is only possible through kin selection.

- c. can only be explained by group selection.
- d. will only occur when the fitness benefit of a given act is greater than the fitness cost.

APPLY

1. Refer to figure 55.25. Data on size of mussels eaten by shore crabs suggest they eat sizes smaller than expected by an optimal foraging model. Suggest a hypothesis for why and describe an experiment to test your hypothesis.
2. Refer to figure 55.26. Six pairs of birds were removed but only four pairs moved in. Where did the new pairs come from? Additionally, it appears that many of the birds that were not removed expanded their territories and that the new residents ended up with smaller territories than the pairs they replaced. Explain.
3. Refer to figure 55.28. Peahens prefer to mate with peacocks that have more eyespots in their tail feathers (that is, longer tail feathers). It has also been suggested that the longer the tail feathers, the more impaired the flight of the males. One possible hypothesis to explain such a preference by females is that the males with the longest tail feathers experience the most severe handicap, and if they can nevertheless survive, it reflects their “vigor.” Suggest some studies that would allow you to test this idea. Your description should include the kinds of traits that you would measure and why.
4. An altruistic act is defined as one that benefits another individual at a cost to the actor. There are two theories to explain how such behavior evolves: reciprocity and kin selection. How would you distinguish between the two in a field study? In the context of natural selection, is an altruistic act “costly” to an individual who performs it?

SYNTHESIZE

1. Insects that sting or contain toxic chemicals often have black and yellow coloration and consequentially are not eaten by predators. How could you determine if a predator has an innate avoidance of insects that are colored this way, or if the avoidance is learned? If avoidance is learned, how would you determine the learning mechanism involved? How would you measure the adaptive significance of the black and yellow coloration to the prey insect?
2. Behavioral genetics has made great advances from detailed studies of a single animal such as the fruit fly as a model system to develop general principles of how genes regulate behavior. What are advantages and disadvantages of this “model system” approach? How would you determine how broadly applicable the results of such studies are to other animals?
3. If a female bird chooses to live in the territory of a particular male, why might she mate with a male other than the territory owner?

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Ecology of Individuals and Populations

Chapter Outline

- 56.1** The Environmental Challenges
- 56.2** Populations: Groups of a Single Species in One Place
- 56.3** Population Demography and Dynamics
- 56.4** Life History and the Cost of Reproduction
- 56.5** Environmental Limits to Population Growth
- 56.6** Factors That Regulate Populations
- 56.7** Human Population Growth

Introduction

Ecology, the study of how organisms relate to one another and to their environments, is a complex and fascinating area of biology that has important implications for each of us. In our exploration of ecological principles, we first consider how organisms respond to the abiotic environment in which they exist and how these responses affect the properties of populations, emphasizing population dynamics. In chapter 57, we discuss communities of coexisting species and the interactions that occur among them. In subsequent chapters, we discuss the functioning of entire ecosystems and of the biosphere, concluding with a consideration of the problems facing our planet and our fellow species.

56.1 The Environmental Challenges

Learning Outcomes

1. List some challenges that organisms face in their environments.
2. Describe ways in which individuals respond to environmental changes.
3. Explain how species adapt to environmental conditions.

The nature of the physical environment in large measure determines which organisms live in a particular climate or region. Key elements of the environment include:

Temperature. Most organisms are adapted to live within a relatively narrow range of temperatures and will not thrive if temperatures are colder or warmer. The growing season of plants, for example, is importantly influenced by temperature.

Water. All organisms require water. On land, water is often scarce, so patterns of rainfall have a major influence on life.





Figure 56.1 Meeting the challenge of obtaining moisture. On the dry sand dunes of the Namib Desert in southwestern Africa, the fog-basking beetle (*Onymacris unguicularis*) collects moisture from the fog by holding its abdomen up at the crest of a dune to gather condensed water; water condenses as droplets and trickles down to the beetle's mouth.

Sunlight. Almost all ecosystems rely on energy captured by photosynthesis; the availability of sunlight influences the amount of life an ecosystem can support, particularly below the surface in marine communities.

Soil. The physical consistency, pH, and mineral composition of the soil often severely limit terrestrial plant growth, particularly the availability of nitrogen and phosphorus.

An individual encountering environmental variation may maintain a “steady-state” internal environment, a condition known as *homeostasis*. Many animals and plants actively employ physiological, morphological, or behavioral mechanisms to maintain homeostasis. The beetle in figure 56.1 is using a behavioral mechanism to cope with drastic changes in water availability. Other animals and plants are known as conformers because they conform to the environment in which they find themselves, their bodies adopting the temperature, salinity, and other physical aspects of their surroundings.

Responses to environmental variation can be seen over both the short and the long term. In the short term, spanning periods of a few minutes to an individual's lifetime, organisms have a variety of ways of coping with environmental change. Over longer periods, natural selection can operate to make a population better adapted to the environment.

Organisms are capable of responding to environmental changes that occur during their lifetime

During the course of a day, a season, or a lifetime, an individual organism must cope with a range of living conditions. They do so through the physiological, morphological, and behavioral abilities they possess. These abilities are a product of natural selection acting in a particular environmental setting over time, which explains why an individual organism that is moved to a different environment may not survive.



TABLE 56.1		Physiological Changes at High Elevation
Increased rate of breathing		
Increased erythrocyte production, raising the amount of hemoglobin in the blood		
Decreased binding capacity of hemoglobin, increasing the rate at which oxygen is unloaded in body tissues		
Increased density of mitochondria, capillaries, and muscle myoglobin		

Physiological responses

Many organisms are able to adapt to environmental change by making physiological adjustments. For example, you sweat when it is hot, increasing evaporative heat loss and thus preventing overheating. Similarly, people who visit high altitudes may initially experience altitude sickness—the symptoms of which include heart palpitations, nausea, fatigue, headache, mental impairment, and in serious cases, pulmonary edema—because of the lower atmospheric pressure and consequent lower oxygen availability in the air. After several days, however, the same people usually feel fine, because a number of physiological changes have increased the delivery of oxygen to their body tissues (table 56.1).

Some insects avoid freezing in the winter by adding glycerol “antifreeze” to their blood; others tolerate freezing by converting much of their glycogen reserves into alcohols that protect their cell membranes from freeze damage.

Morphological capabilities

Animals that maintain a constant internal temperature (endotherms) in a cold environment have adaptations that tend to minimize energy expenditure. For example, many mammals grow thicker coats during the winter, their fur acting as insulation to retain body heat. In general, the thicker the fur, the greater the insulation (figure 56.2). Thus, a wolf's fur is about three times thicker in winter than in summer and insulates more than twice as well.

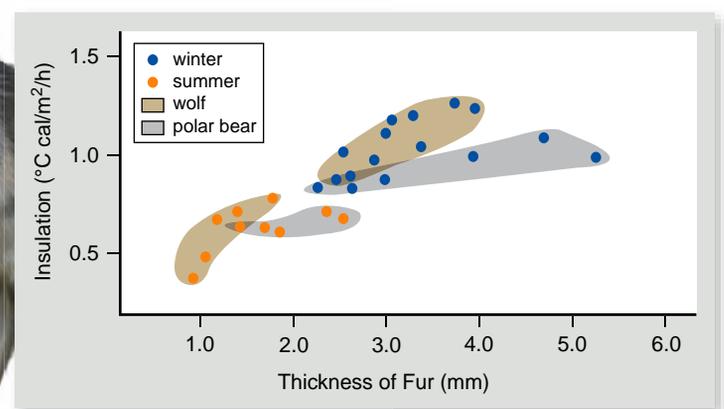


Figure 56.2 Morphological adaptation. Fur thickness in North American mammals has a major effect on the degree of insulation the fur provides.

Behavioral responses

Many animals deal with variation in the environment by moving from one patch of habitat to another, avoiding areas that are unsuitable. The tropical lizard in figure 56.3 manages to maintain a fairly uniform body temperature in an open habitat by basking in patches of sunlight and then retreating to the shade when it becomes too hot. By contrast, in shaded forests, the same lizard does not have the opportunity to regulate its body temperature through behavioral means. Thus, it becomes a conformer and adopts the temperature of its surroundings.

Behavioral adaptations can be extreme. Spadefoot toads (genus *Scaphiopus*), which live in the deserts of North America, can burrow nearly a meter below the surface and remain there for as long as nine months of each year, their metabolic rates greatly reduced as they live on fat reserves. When moist, cool conditions return, the toads emerge and breed. The young toads mature rapidly and burrow underground.

Natural selection leads to evolutionary adaptation to environmental conditions

The ability of an individual to alter its physiology, morphology, or behavior is itself an evolutionary adaptation, the result of natural selection. The results of natural selection can also be detected by comparing closely related species that live in different environments. In such cases, species often have evolved striking adaptations to the particular environment in which they live.

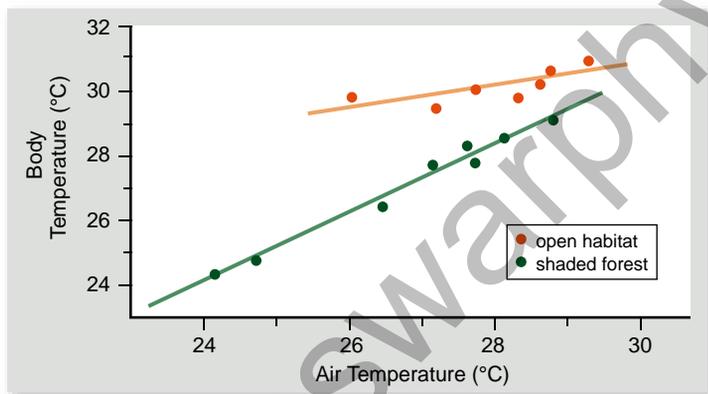
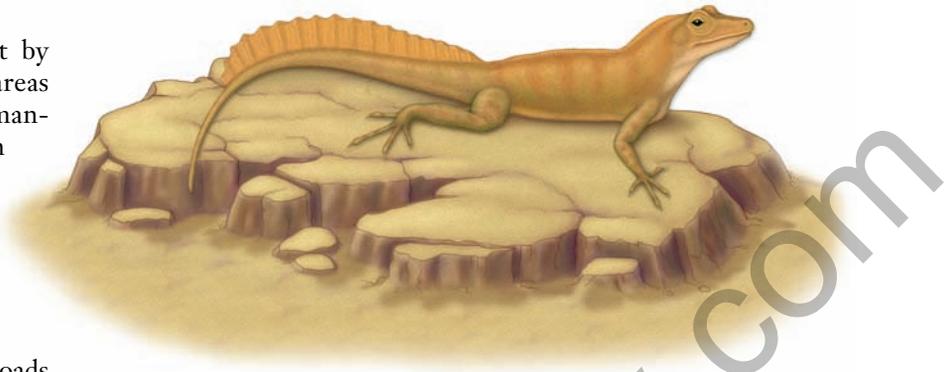


Figure 56.3 Behavioral adaptation. In open habitats, the Puerto Rican crested lizard (*Anolis cristatellus*) maintains a relatively constant temperature by seeking out and basking in patches of sunlight; as a result, it can maintain a relatively high temperature even when the air is cool. In contrast, in shaded forests, this behavior is not possible, and the lizard's body temperature conforms to that of its surroundings.

Inquiry question

When given the opportunity, lizards regulate their body temperature to maintain a temperature optimal for physiological functioning. Would lizards in open habitats exhibit different escape behaviors from lizards in shaded forest?



For example, animals that live in different climates show many differences. Mammals from colder climates tend to have shorter ears and limbs—a phenomenon termed *Allen's rule*—which reduces the surface area across which animals lose heat. Lizards that live in different climates exhibit physiological adaptations for coping with life at different temperatures. Desert lizards are unaffected by high temperatures that would kill a lizard from northern Europe, but the northern lizards are capable of running, capturing prey, and digesting food at cooler temperatures at which desert lizards would be completely immobilized.

Many species also exhibit adaptations to living in areas where water is scarce. Everyone knows of the camel and other desert animals that can go extended periods without drinking water. Another example of desert adaptation is seen in frogs. Most frogs have moist skins through which water permeates readily. Such animals could not survive in arid climates because they would rapidly dehydrate and die. However, some frogs have solved this problem by evolving a greatly reduced rate of water loss through the skin. One species, for example, secretes a waxy substance from specialized glands that waterproofs its skin and reduces rates of water loss by 95%.

Adaptation to different environments can also be studied experimentally. For example, when strains of *E. coli* were grown at high temperatures (42°C), the speed at which the bacteria utilized resources improved through time. After 2000 generations, this ability increased 30% over what it had been when the experiment started. The means by which efficiency of resource use increased is unknown and is the focus of current research.

Learning Outcomes Review 56.1

Environmental conditions include temperature, water and light availability, and soil characteristics. When the environment changes, individual organisms use a variety of physiological, morphological, and behavioral mechanisms to adjust. Over time, adaptations to different environments may evolve in populations.

- How might a species respond if its environment grew steadily warmer over time?

56.2 Populations: Groups of a Single Species in One Place

Learning Outcomes

1. Distinguish between a population and a metapopulation.
2. Understand what causes a species' geographic ranges to change through time.

Organisms live as members of populations, groups of individuals that occur together at one place and time. In the rest of this chapter, we consider the properties of populations, focusing on factors that influence whether a population grows or shrinks, and at what rate. The explosive growth of the world's human population in the last few centuries provides a focus for our inquiry.

The term *population* can be defined narrowly or broadly. This flexibility allows us to speak in similar terms of the world's human population, the population of protists in the gut of a termite, or the population of deer that inhabit a forest. Sometimes the boundaries defining a population are sharp, such as the edge of an isolated mountain lake for trout, and sometimes they are fuzzier, as when deer readily move back and forth between two forests separated by a cornfield.

Three characteristics of population ecology are particularly important: (1) population range, the area throughout which a population occurs; (2) the pattern of spacing of individuals within that range; and (3) how the population changes in size through time.

A population's geographic distribution is termed its range

No population, not even one composed of humans, occurs in all habitats throughout the world. Most species, in fact, have relatively limited geographic ranges, and the range of some species is miniscule. For example, the Devil's Hole pupfish lives in a single spring in southern Nevada (figure 56.4), and the Socorro isopod (*Thermosphaeroma thermophilus*) is known from a single spring system in New Mexico. At the other extreme, some species are widely distributed. The common dolphin (*Delphinus delphis*), for example, is found throughout all the world's oceans.

As discussed earlier, organisms must be adapted for the environment in which they occur. Polar bears are exquisitely adapted to survive the cold of the Arctic, but you won't find them in the tropical rain forest. Certain prokaryotes can live in the near-boiling waters of Yellowstone's geysers, but they do not occur in cooler streams nearby. Each population has its own requirements—temperature, humidity, certain types of food, and a host of other factors—that determine where it can live and reproduce and where it can't. In addition, in places that are otherwise suitable, the presence of predators, competitors, or parasites may prevent a population from occupying an area, a topic we will take up in chapter 57.



Figure 56.4 The Devil's Hole pupfish (*Cyprinodon diabolis*). This fish has the smallest range of any vertebrate species in the world.

Ranges undergo expansion and contraction

Population ranges are not static but change through time. These changes occur for two reasons. In some cases, the environment changes. As the glaciers retreated at the end of the last ice age, approximately 10,000 years ago, many North American plant and animal populations expanded northward. At the same time, as climates warmed, species experienced shifts in the elevation at which they could live (figure 56.5).

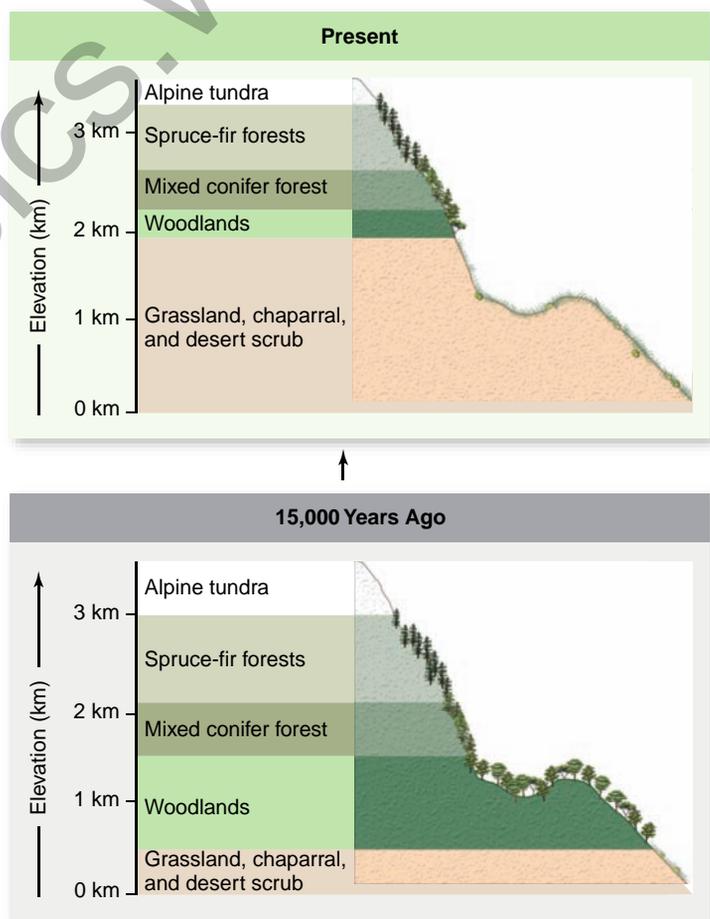


Figure 56.5 Altitude shifts in altitudinal distributions of trees in the mountains of southwestern North America.

During the glacial period 15,000 years ago, conditions were cooler than they are now. As the climate warmed, tree species that require colder temperatures shifted their range upward in altitude so that they live in the climatic conditions to which they are adapted.

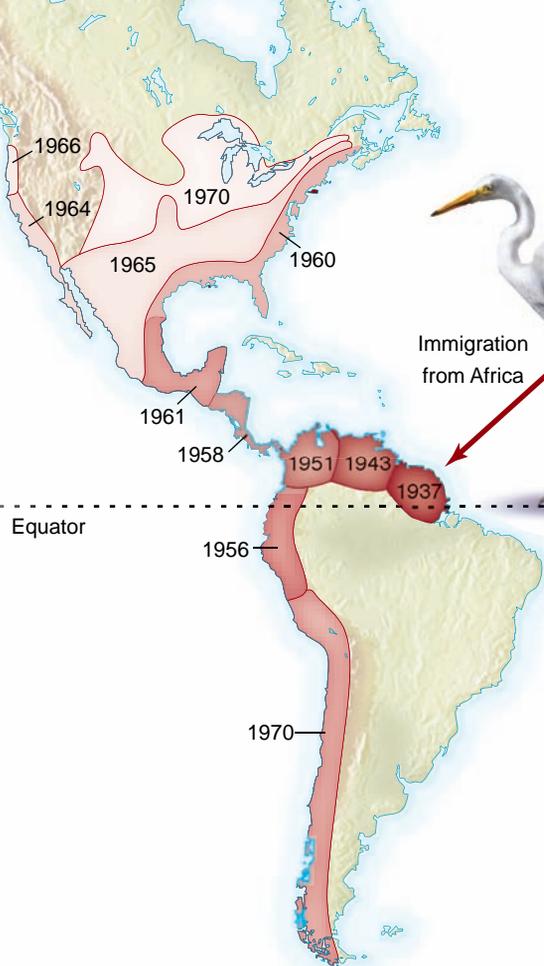


Figure 56.6 Range expansion of the cattle egret (*Bubulcus ibis*). The cattle egret—so named because it follows cattle and other hoofed animals, catching any insects or small vertebrates it disturbs—first arrived in South America from Africa in the late 1800s. Since the 1930s, the range expansion of this species has been well documented, as it has moved northward into much of North America, as well as southward along the western side of the Andes to near the southern tip of South America.

In addition, populations can expand their ranges when they are able to circumvent inhospitable habitat to colonize suitable, previously unoccupied areas. For example, the cattle egret is native to Africa. Some time in the late 1800s, these birds appeared in northern South America, having made the nearly 3500-km transatlantic crossing, perhaps aided by strong winds. Since then, they have steadily expanded their range and now can be found throughout most of the United States (figure 56.6).

The human effect

By altering the environment, humans have allowed some species, such as coyotes, to expand their ranges and move into areas they previously did not occupy. Moreover, humans have served as an agent of dispersal for many species. Some of these transplants have been widely successful, as is discussed in greater detail in chapter 60. For example, 100 starlings were introduced into New York City in 1896 in a misguided attempt to establish every species of bird mentioned by Shakespeare. Their population steadily spread so

that by 1980, they occurred throughout the United States. Similar stories could be told for countless plants and animals, and the list increases every year. Unfortunately, the success of these invaders often comes at the expense of native species.

Dispersal mechanisms

Dispersal to new areas can occur in many ways. Lizards have colonized many distant islands, as one example, probably due to individuals or their eggs floating or drifting on vegetation. Bats are the only mammals on many distant islands because they can fly to them.

Seeds of plants are designed to disperse in many ways (figure 56.7). Some seeds are aerodynamically designed to be blown long distances by the wind. Others have structures that stick to the fur or feathers of animals, so that they are carried long distances before falling to the ground. Still others are enclosed in fleshy fruits. These seeds can pass through the digestive systems of mammals or birds and then germinate where they are defecated. Finally, seeds of mistletoes (*Arceuthobium*) are violently propelled from the base of the fruit in an explosive discharge. Although the probability of long-distance dispersal events leading to successful establishment of new populations is low, over millions of years, many such dispersals have occurred.

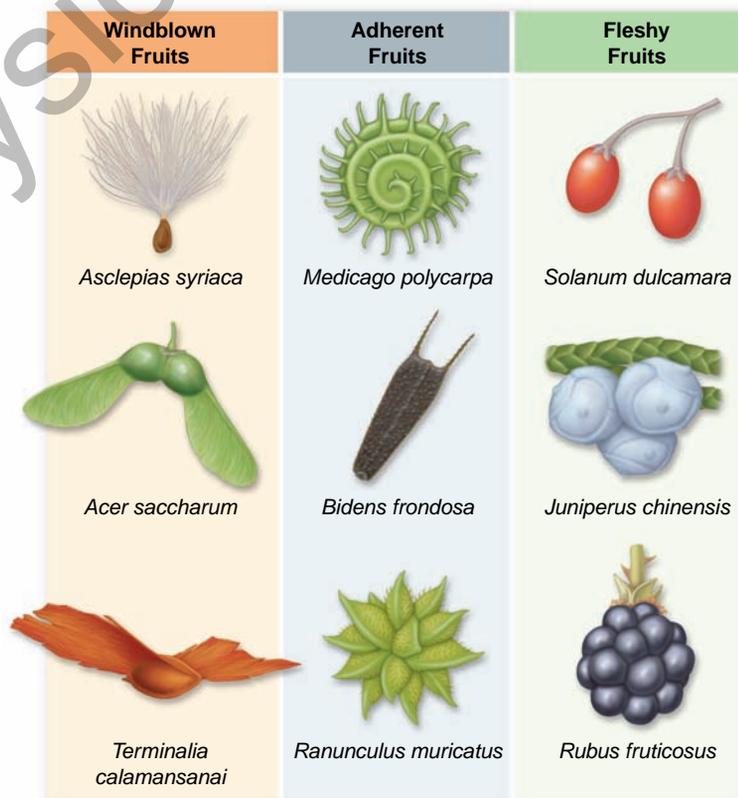


Figure 56.7 Some of the many adaptations of seeds.

Seeds have evolved a number of different means of facilitating dispersal from their maternal plant. Some seeds can be transported great distances by the wind, whereas seeds enclosed in adherent or fleshy fruits can be transported by animals.

Individuals in populations exhibit different spacing patterns

Another key characteristic of population structure is the way in which individuals of a population are distributed. They may be randomly spaced, uniformly spaced, or clumped.

Random spacing

Random spacing of individuals within populations occurs when they do not interact strongly with one another and when they are not affected by nonuniform aspects of their environment. Random distributions are not common in nature. Some species of trees, however, appear to exhibit random distributions in Panamanian rain forests.

Uniform spacing

Uniform spacing within a population may often, but not always, result from competition for resources. This spacing is accomplished, however, in many different ways

In animals, uniform spacing often results from behavioral interactions, as described in chapter 55. In many species, individuals of one or both sexes defend a territory from which other individuals are excluded. These territories provide the owner with exclusive access to resources, such as food, water, hiding refuges, or mates, and tend to space individuals evenly across the habitat. Even in nonterritorial species, individuals often maintain a defended space into which other animals are not allowed to intrude.

Among plants, uniform spacing is also a common result of competition for resources. Closely spaced individual plants compete for available sunlight, nutrients, or water. These contests can be direct, as when one plant casts a shadow over another, or indirect, as when two plants compete by extracting nutrients or water from a shared area. In addition, some plants, such as the creosote bush, produce chemicals in the surrounding soil that are toxic to other members of their species. In all of these cases, only plants that are spaced an adequate distance from each other will be able to coexist, leading to uniform spacing.

Clumped spacing

Individuals clump into groups or clusters in response to uneven distribution of resources in their immediate environments. Clumped distributions are common in nature because individual animals, plants, and microorganisms tend to occur in habitats defined by soil type, moisture, or other aspects of the environment to which they are best adapted.

Social interactions also can lead to clumped distributions. Many species live and move around in large groups, which go by a variety of names (for example, flock, herd, pride). These groupings can provide many advantages, including increased awareness of and defense against predators, decreased energy cost of moving through air and water, and access to the knowledge of all group members.

On a broader scale, populations are often most densely populated in the interior of their range and less densely distributed toward the edges. Such patterns usually result from the manner in which the environment changes in different areas.

Populations are often best adapted to the conditions in the interior of their distribution. As environmental conditions

change, individuals are less well adapted, and thus densities decrease. Ultimately, the point is reached at which individuals cannot persist at all; this marks the edge of a population's range.

A metapopulation comprises distinct populations that may exchange members

Species often exist as a network of distinct populations that interact with one another by exchanging individuals. Such networks, termed **metapopulations**, usually occur in areas in which suitable habitat is patchily distributed and is separated by intervening stretches of unsuitable habitat.

Dispersal and habitat occupancy

The degree to which populations within a metapopulation interact depends on the amount of dispersal; this interaction is often not symmetrical: Populations increasing in size tend to send out many dispersers, whereas populations at low levels tend to receive more immigrants than they send off. In addition, relatively isolated populations tend to receive relatively few arrivals.

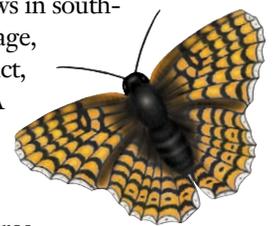
Not all suitable habitats within a metapopulation's area may be occupied at any one time. For a number of reasons, some individual populations may become extinct, perhaps as a result of an epidemic disease, a catastrophic fire, or the loss of genetic variation following a population bottleneck (see chapter 60). Dispersal from other populations, however, may eventually recolonize such areas. In some cases, the number of habitats occupied in a metapopulation may represent an equilibrium in which the rate of extinction of existing populations is balanced by the rate of colonization of empty habitats.

Source-sink metapopulations

A species may also exhibit a metapopulation structure in areas in which some habitats are suitable for long-term population maintenance, but others are not. In these situations, termed **source-sink metapopulations**, the populations in the better areas (the sources) continually send out dispersers that bolster the populations in the poorer habitats (the sinks). In the absence of such continual replenishment, sink populations would have a negative growth rate and would eventually become extinct.

Metapopulations of butterflies have been studied particularly intensively. In one study, researchers sampled populations of the Glanville fritillary butterfly at 1600 meadows in southwestern Finland (figure 56.8). On average, every year, 200 populations became extinct, but 114 empty meadows were colonized. A variety of factors seemed to increase the likelihood of a population's extinction, including small population size, isolation from sources of immigrants, low resource availability (as indicated by the number of flowers on a meadow), and lack of genetic variation within the population.

The researchers attribute the greater number of extinctions than colonizations to a string of very dry summers. Because none of the populations is large enough to survive on its own, continued survival of the species in southwestern Finland would appear to require the continued existence of a metapopulation network in which new populations are continually



56.3 Population Demography and Dynamics

Learning Outcomes

1. Define demography.
2. Describe the factors that influence a species' demography.
3. Explain the significance of survivorship curves.

The dynamics of a population—how it changes through time—are affected by many factors. One important factor is the age distribution of individuals—that is, what proportion of individuals are adults, juveniles, and young.

Demography is the quantitative study of populations. How the size of a population changes through time can be studied at two levels: as a whole or broken down into parts. At the most inclusive level, we can study the whole population to determine whether it is increasing, decreasing, or remaining constant. Put simply, populations grow if births outnumber deaths and shrink if deaths outnumber births. Understanding these trends is often easier, however, if we break the population into smaller units composed of individuals of the same age (for example, 1-year-olds) and study the factors affecting birth and death rates for each unit separately.

Sex ratio and generation time affect population growth rates

Population growth can be influenced by the population's sex ratio. The number of births in a population is usually directly related to the number of females; births may not be as closely related to the number of males in species in which a single male can mate with several females. In many species, males compete for the opportunity to mate with females, as you learned in the preceding chapter; consequently, a few males have many matings, and many males do not mate at all. In such species, the sex ratio is female-biased and does not affect population growth rates; reduction in the number of males simply changes the identities of the reproductive males without reducing the number of births. By contrast, among monogamous species, pairs may form long-lasting reproductive relationships, and a reduction in the number of males can then directly reduce the number of births.

Generation time is the average interval between the birth of an individual and the birth of its offspring. This factor can also affect population growth rates. Species differ greatly in generation time. Differences in body size can explain much of this variation—mice go through approximately 100 generations during the course of one elephant generation (figure 56.9). But small size does not always mean short generation time. Newts, for example, are smaller than mice, but have considerably longer generation times.

In general, populations with short generations can increase in size more quickly than populations with long generations. Conversely, because generation time and life span are

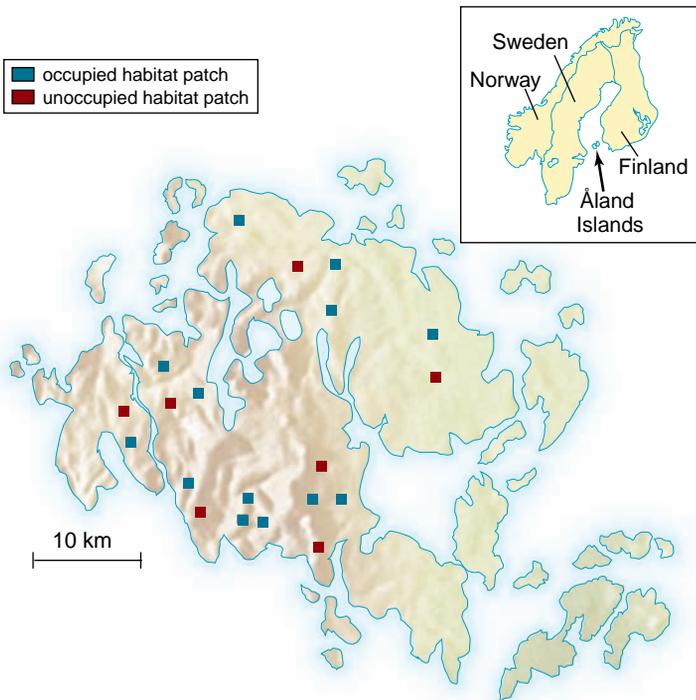


Figure 56.8 Metapopulations of butterflies.

The Glanville fritillary butterfly (*Melitaea cinxia*) occurs in metapopulations in southwestern Finland on the Åland Islands. None of the populations is large enough to survive for long on its own, but continual immigration of individuals from other populations allows some populations to survive. In addition, continual establishment of new populations tends to offset extinction of established populations, although in recent years, extinctions have outnumbered colonizations.

created and existing populations are supplemented by immigrants. Continued bad weather thus may doom the species, at least in this part of its range.

Metapopulations, where they occur, can have two important implications for the range of a species. First, through continuous colonization of empty patches, metapopulations prevent long-term extinction. If no such dispersal existed, then each population might eventually perish, leading to disappearance of the species from the entire area. Moreover, in source-sink metapopulations, the species occupies a larger area than it otherwise might, including marginal areas that could not support a population without a continual influx of immigrants. For these reasons, the study of metapopulations has become very important in conservation biology as natural habitats become increasingly fragmented.

Learning Outcomes Review 56.2

A population is a group of individuals of a single species existing together in an area. A population's range, the area it occupies, changes over time. Populations, in turn, may form a network, or metapopulation, connected by individuals that move from one group to another. Within a population, the distribution of individuals can be random, uniform, or clumped, and the distribution is determined in part by the availability of resources.

- How might the geographic range of a species change if populations could not exchange individuals with each other?

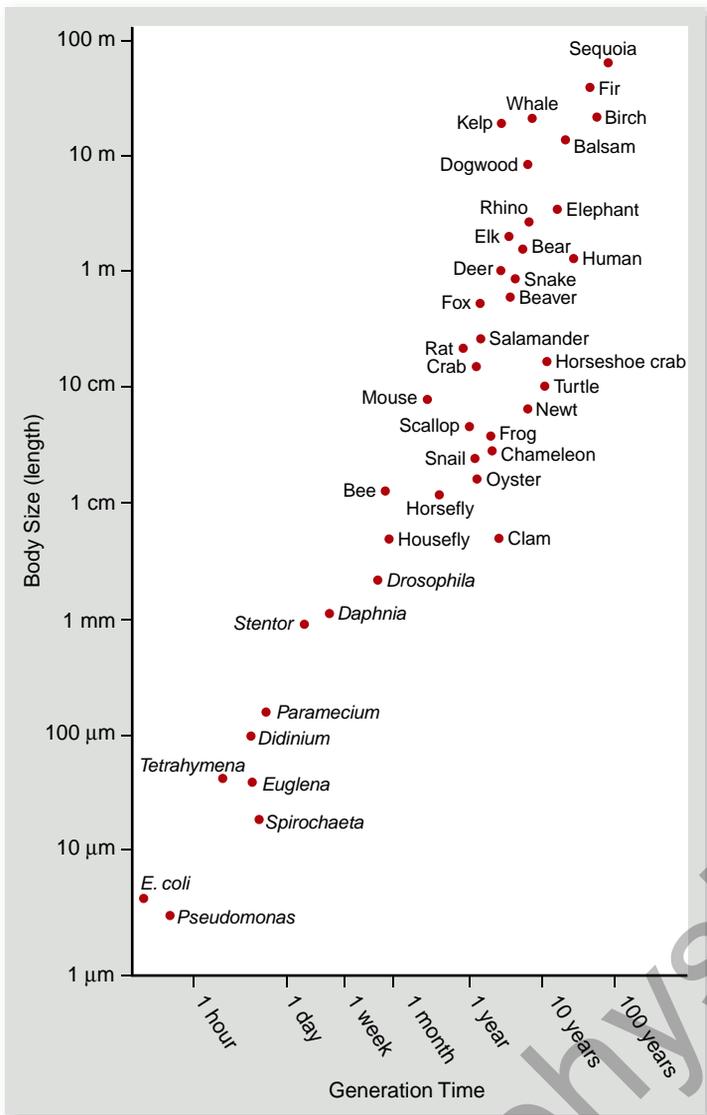


Figure 56.9 The relationship between body size and generation time. In general, larger organisms have longer generation times, although there are exceptions.

Inquiry question

? If resources became more abundant, would you expect smaller or larger species to increase in population size more quickly?

usually closely correlated, populations with short generation times may also diminish in size more rapidly if birth rates suddenly decrease.

Age structure is determined by the numbers of individuals in different age groups

A group of individuals of the same age is referred to as a cohort. In most species, the probability that an individual will reproduce or die varies through its life span. As a result, within

a population, every cohort has a characteristic birth rate, or **fecundity**, defined as the number of offspring produced in a standard time (for example, per year), and death rate, or **mortality**, the number of individuals that die in that period.

The relative number of individuals in each cohort defines a population's **age structure**. Because different cohorts have different fecundity and death rates, age structure has a critical influence on a population's growth rate. Populations with a large proportion of young individuals, for example, tend to grow rapidly because an increasing proportion of their individuals are reproductive. Human populations in many developing countries are an example, as will be discussed later in this chapter. Conversely, if a large proportion of a population is relatively old, populations may decline. This phenomenon now characterizes Japan and some countries in Europe.

Life tables show probability of survival and reproduction through a cohort's life span

To assess how populations in nature are changing, ecologists use a **life table**, which tabulates the fate of a cohort from birth until death, showing the number of offspring produced and the number of individuals that die each year. Table 56.2 shows an example of a life table analysis from a study of the meadow grass *Poa annua*. This study follows the fate of 843 individuals through time, charting how many survive in each interval and how many offspring each survivor produces.

In table 56.2, the first column indicates the age of the cohort (that is, the number of 3-month intervals from the start of the study). The second and third columns indicate the number of survivors and the proportion of the original cohort still alive at the beginning of that interval. The fifth column presents the **mortality rate**, the proportion of individuals that started that interval alive but died by the end of it. The seventh column indicates the average number of seeds produced by each surviving individual in that interval, and the last column shows the number of seeds produced relative to the size of the original cohort.

Much can be learned by examining life tables. In the case of *P. annua*, we see that both the probability of dying and the number of offspring produced per surviving individual steadily increases with age. By adding up the numbers in the last column, we get the total number of offspring produced per individual in the initial cohort. This number is almost 2, which means that for every original member of the cohort, on average two new individuals have been produced. A figure of 1.0 would be the break-even number, the point at which the population was neither growing nor shrinking. In this case, the population appears to be growing rapidly.

In most cases, life table analysis is more complicated than this. First, except for organisms with short life spans, it is difficult to track the fate of a cohort until the death of the last individual. An alternative approach is to construct a cross-sectional study, examining the fate of cohorts of different ages in a single period. In addition, many factors—such as offspring

TABLE 56.2

Life Table of the Meadow Grass (*Poa annua*) for a Cohort Containing 843 Seedlings

Age (in 3-month intervals)	Number Alive at Beginning of Time Interval	Proportion of Cohort Alive at Beginning of Time Interval (survivorship)	Deaths During Time Interval	Mortality Rate During Time Interval	Seeds Produced During Time Interval	Seeds Produced per Surviving Individual (fecundity)	Seeds Produced per Member of Cohort (fecundity \times survivorship)
0	843	1.000	121	0.143	0	0.00	0.00
1	722	0.857	195	0.271	303	0.42	0.36
2	527	0.625	211	0.400	622	1.18	0.74
3	316	0.375	172	0.544	430	1.36	0.51
4	144	0.171	90	0.626	210	1.46	0.25
5	54	0.064	39	0.722	60	1.11	0.07
6	15	0.018	12	0.800	30	2.00	0.04
7	3	0.004	3	1.000	10	3.33	0.01
8	0	0.000	—		Total = 1665		Total = 1.98

reproducing before all members of their parents' cohort have died—complicate the interpretation of whether populations are growing or shrinking.

Survivorship curves demonstrate how survival probability changes with age

The percentage of an original population that survives to a given age is called its **survivorship**. One way to express some aspects of the age distribution of populations is through a *survivorship curve*. Examples of different survivorship curves are shown in figure 56.10. Oysters produce vast numbers of offspring, only a few of which live to reproduce. However, once they become established and grow into reproductive individuals, their mortality rate is extremely low (type III survivorship curve). Note that in this type of curve, survival and mortality rates are inversely related. Thus, the rapid decrease in the proportion of oysters surviving indicates that few individuals survive, thus producing a high mortality rate. In contrast, the relatively flat line at older ages indicates high survival and low mortality.

In hydra, animals related to jellyfish, individuals are equally likely to die at any age. The result is a straight survivorship curve (type II).

Finally, mortality rates in humans, as in many other animals and in protists, rise steeply later in life (type I survivorship curve).

Of course, these descriptions are just generalizations, and many organisms show more complicated patterns. Examination of the data for *P. annua*, for example, reveals that it is most similar to a type II survivorship curve (figure 56.11).

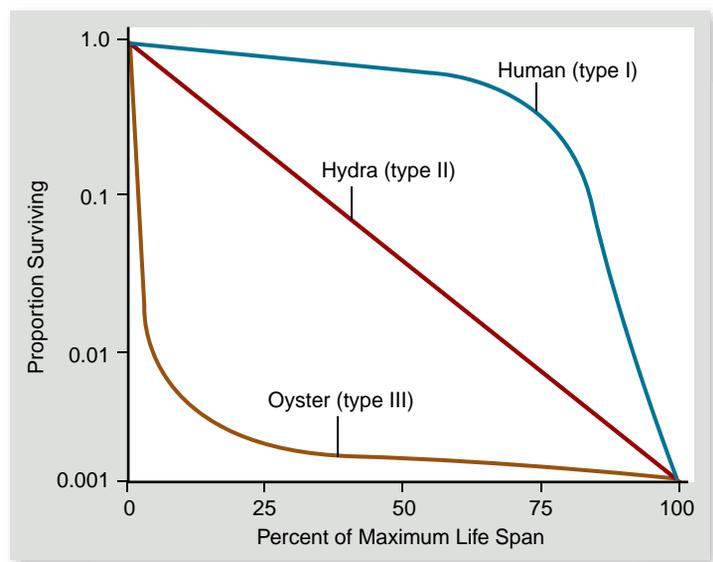
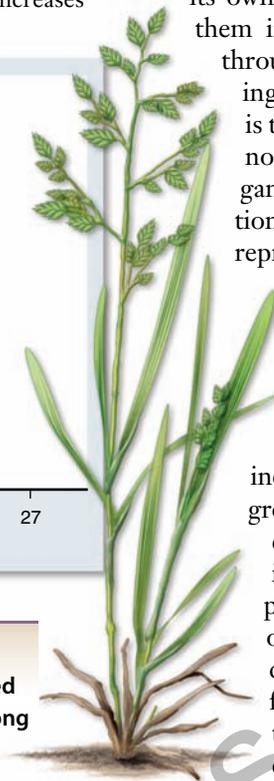
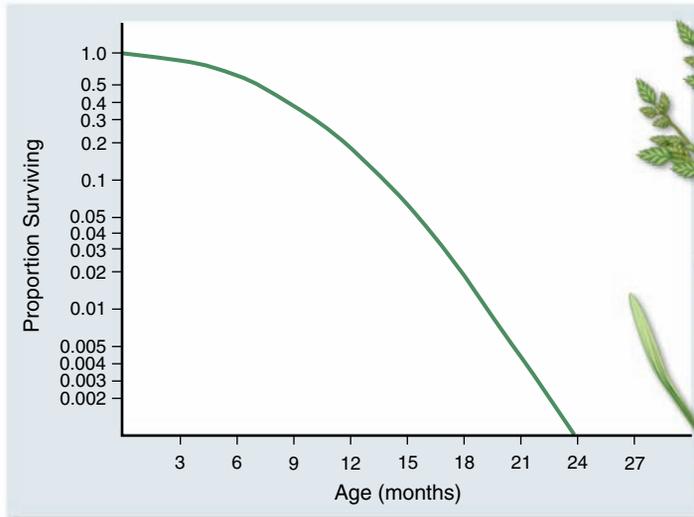


Figure 56.10 Survivorship curves. By convention, survival (the vertical axis) is plotted on a log scale. Humans have a type I life cycle, hydra (an animal related to jellyfish) type II, and oysters type III.

Figure 56.11 Survivorship curve for a cohort of the meadow grass. After several months of age, mortality increases at a constant rate through time.



Inquiry question

? Suppose you wanted to keep meadow grass in your room as a houseplant. Suppose, too, that you wanted to buy an individual plant that was likely to live as long as possible. What age plant would you buy? How might the shape of the survivorship curve affect your answer?

Learning Outcomes Review 56.3

Demography is the quantitative study of populations. Demographic characteristics include age structure, life span, sex ratio, generation time, and birth and mortality rates. The age structure of a population and the manner in which mortality and birth rates vary among different age cohorts, determine whether a population will increase or decrease in size.

- Will populations with higher survivorship rates always have higher population growth rates than populations with lower survivorship rates?

56.4 Life History and the Cost of Reproduction

Learning Outcomes

- Describe reproductive trade-offs in an organism's life history.
- Compare the costs and benefits of allocating resources to reproduction.

Natural selection favors traits that maximize the number of surviving offspring left in the next generation by an individual organism. Two factors affect this quantity: how long an individual lives, and how many young it produces each year.

Why doesn't every organism reproduce immediately after its own birth, produce large families of offspring, care for them intensively, and perform these functions repeatedly throughout a long life, while outcompeting others, escaping predators, and capturing food with ease? The answer is that no one organism can do all of this, simply because not enough resources are available. Consequently, organisms allocate resources either to current reproduction or to increasing their prospects of surviving and reproducing at later life stages.

The complete life cycle of an organism constitutes its life history. All life histories involve significant trade-offs. Because resources are limited, a change that increases reproduction may decrease survival and reduce future reproduction. As one example, a Douglas fir tree that produces more cones increases its current reproductive success—but it also grows more slowly. Because the number of cones produced is a function of how large a tree is, this diminished growth will decrease the number of cones it can produce in the future. Similarly, birds that have more offspring each year have a higher probability of dying during that year or of producing smaller clutches the following year (figure 56.12). Conversely, individuals that delay reproduction may grow faster and larger, enhancing future reproduction.

In one elegant experiment, researchers changed the number of eggs in the nests of a bird, the collared flycatcher (figure 56.13). Birds whose clutch size (the number of eggs produced in one breeding event) was decreased expended less energy raising their young and thus were able to lay more eggs the next year, whereas those given more eggs worked harder and consequently produced fewer eggs the following year. Ecologists refer to the reduction in future reproductive potential resulting from current reproductive efforts as the **cost of reproduction**.

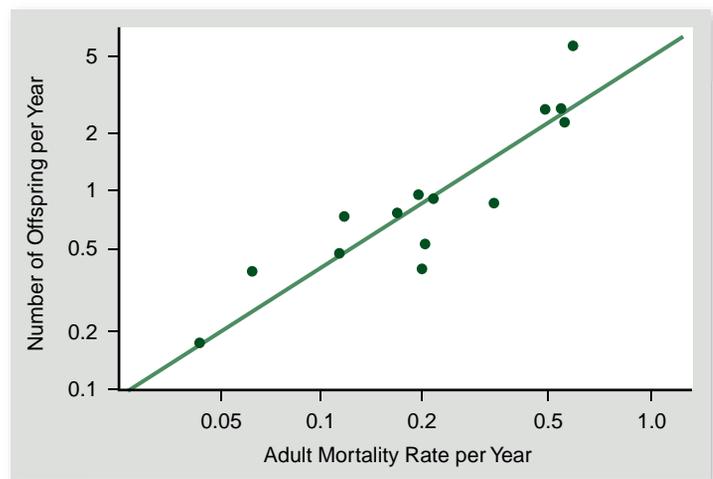


Figure 56.12 Reproduction has a price. Data from many bird species indicate that increased fecundity in birds correlates with higher mortality, ranging from the albatross (lowest) to the sparrow (highest). Birds that raise more offspring per year have a higher probability of dying during that year.

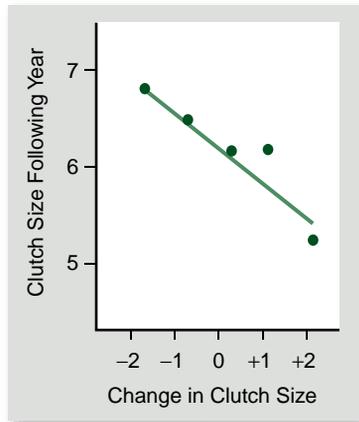


Figure 56.13 Reproductive events per lifetime. Adding eggs to nests of collared flycatchers (*Ficedula albicollis*), which increases the reproductive efforts of the female rearing the young, decreases clutch size the following year; removing eggs from the nest increases the next year's clutch size. This experiment demonstrates the trade-off between current reproductive effort and future reproductive success.

Natural selection favors the life history that maximizes lifetime reproductive success. When the cost of reproduction is low, individuals should produce as many offspring as possible because there is little cost. Low costs of reproduction may occur when resources are abundant and may also be relatively low when overall mortality rates are high. In the latter case, individuals may be unlikely to survive to the next breeding season anyway, so the incremental effect of increased reproductive efforts may have little effect on future survival.

Alternatively, when costs of reproduction are high, lifetime reproductive success may be maximized by deferring or minimizing current reproduction to enhance growth and survival rates. This situation may occur when costs of reproduction significantly affect the ability of an individual to survive or decrease the number of offspring that can be produced in the future.

A trade-off exists between number of offspring and investment per offspring

In terms of natural selection, the number of offspring produced is not as important as how many of those offspring themselves survive to reproduce. Assuming that the amount of energy to be invested in offspring is limited, a balance must be reached between the number of offspring produced and the size of each offspring (figure 56.14). This trade-off has been experimentally demonstrated in the side-blotched lizard, which normally lays between four and five eggs at a time. When some of the eggs are removed surgically early in the reproductive cycle, the female lizard produces only one to three eggs, but supplies each of these eggs with greater amounts of yolk, producing eggs and, subsequently, hatchlings that are much larger than normal (figure 56.15). Alternatively, by removing yolk from eggs, scientists have demonstrated that smaller young would be produced.

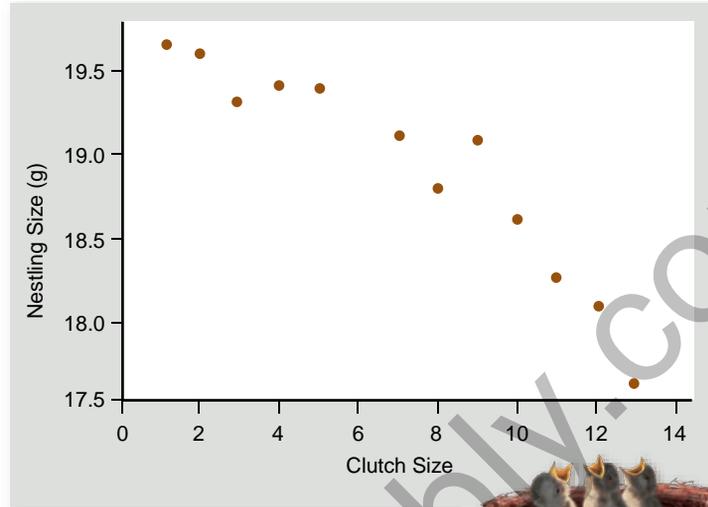


Figure 56.14 The relationship between clutch size and offspring size.

In great tits (*Parus major*), the size of the nestlings is inversely related to the number of eggs laid. The more mouths they have to feed, the less the parents can provide to any one nestling.



Inquiry question



Would natural selection favor producing many small young or a few large ones?



Figure 56.15 Variation in the size of baby side-blotched lizards (*Uta stansburiana*) produced by experimental manipulations. In clutches in which some developing eggs were surgically removed, the remaining offspring were larger (center) than lizards produced in control clutches in which all the eggs were allowed to develop (right). In experiments in which some of the yolk was removed from the eggs, smaller lizards hatched (left).

56.5 Environmental Limits to Population Growth

In the side-blotched lizard and many other species, the size of offspring is critical—larger offspring have a greater chance of survival. Producing many offspring with little chance of survival might not be the best strategy, but producing only a single, extraordinarily robust offspring also would not maximize the number of surviving offspring. Rather, an intermediate situation, in which several fairly large offspring are produced, should maximize the number of surviving offspring.

Reproductive events per lifetime represent an additional trade-off

The trade-off between age and fecundity plays a key role in many life histories. Annual plants and most insects focus all their reproductive resources on a single large event and then die. This life history adaptation is called **semelparity**. Organisms that produce offspring several times over many seasons exhibit a life history adaptation called **iteroparity**.

Species that reproduce yearly must avoid overtaxing themselves in any one reproductive episode so that they will be able to survive and reproduce in the future. Semelparity, or “big bang” reproduction, is usually found in short-lived species that have a low probability of staying alive between broods, such as plants growing in harsh climates. Semelparity is also favored when fecundity entails large reproductive cost, exemplified by Pacific salmon migrating upriver to their spawning grounds. In these species, rather than investing some resources in an unlikely bid to survive until the next breeding season, individuals put all their resources into one reproductive event.

Age at first reproduction correlates with life span

Among mammals and many other animals, longer-lived species put off reproduction longer than short-lived species, relative to expected life span. The advantage of delayed reproduction is that juveniles gain experience before expending the high costs of reproduction. In long-lived animals, this advantage outweighs the energy that is invested in survival and growth rather than reproduction.

In shorter-lived animals, on the other hand, time is of the essence; thus, quick reproduction is more critical than juvenile training, and reproduction tends to occur earlier.

Learning Outcomes Review 56.4

Life history adaptations involve many trade-offs between reproductive cost and investment in survival. These trade-offs take a variety of forms, from laying fewer than the maximum possible number of eggs to putting all energy into a single bout of reproduction. Natural selection favors maximizing reproductive success, but number of offspring produced must be tempered by available resources.

- How might the life histories of two species differ if one was subject to high levels of predation and the other had few predators?

Learning Outcomes

1. Explain exponential growth.
2. Discuss why populations cannot grow exponentially forever.
3. Define carrying capacity.

Populations often remain at a relatively constant size, regardless of how many offspring are born. As you saw in chapter 1, Darwin based his theory of natural selection partly on this seeming contradiction. Natural selection occurs because of checks on reproduction, with some individuals producing fewer surviving offspring than others. To understand populations, we must consider how they grow and what factors in nature limit population growth.

The exponential growth model applies to populations with no growth limits

The rate of population increase, r , is defined as the difference between the birth rate, b , and the death rate, d , corrected for movement of individuals in or out of the population (e , rate of movement out of the area; i , rate of movement into the area). Thus,

$$r = (b - d) + (i - e)$$

Movements of individuals can have a major influence on population growth rates. For example, the increase in human population in the United States during the closing decades of the 20th century was mostly due to immigration.

The simplest model of population growth assumes that a population grows without limits at its maximal rate and also that rates of immigration and emigration are equal. This rate, called the **biotic potential**, is the rate at which a population of a given species increases when no limits are placed on its rate of growth. In mathematical terms, this is defined by the following formula:

$$\frac{dN}{dt} = r_i N$$

where N is the number of individuals in the population, dN/dt is the rate of change in its numbers over time, and r_i is the intrinsic rate of natural increase for that population—its innate capacity for growth.

The biotic potential of any population is exponential (red line in figure 56.16). Even when the *rate* of increase remains constant, the actual *number* of individuals accelerates rapidly as the size of the population grows. The result of unchecked exponential growth is a population explosion.

A single pair of houseflies, laying 120 eggs per generation, could produce more than 5 trillion descendants in a year. In 10 years, their descendants would form a swarm more than 2 m thick over the entire surface of the Earth! In practice, such patterns of unrestrained growth prevail only for short periods, usually when an organism reaches a new habitat with abundant

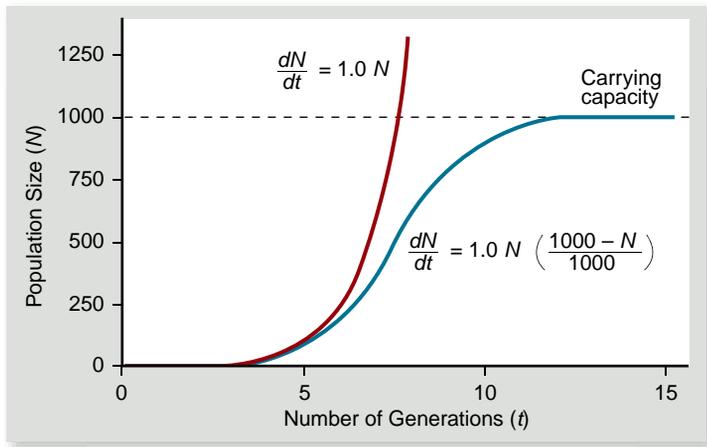


Figure 56.16 Two models of population growth. The red line illustrates the exponential growth model for a population with an r of 1.0. The blue line illustrates the logistic growth model in a population with $r = 1.0$ and $K = 1000$ individuals. At first, logistic growth accelerates exponentially; then, as resources become limited, the death rate increases and growth slows. Growth ceases when the death rate equals the birth rate. The carrying capacity (K) ultimately depends on the resources available in the environment.

resources. Natural examples of such short period of unrestrained growth include dandelions arriving in the fields, lawns, and meadows of North America from Europe for the first time; algae colonizing a newly formed pond; or cats introduced to an island with many birds, but previously lacking predators.

Carrying capacity

No matter how rapidly populations grow, they eventually reach a limit imposed by shortages of important environmental factors, such as space, light, water, or nutrients. A population ultimately may stabilize at a certain size, called the **carrying capacity** of the particular place where it lives. The carrying capacity, symbolized by K , is the maximum number of individuals that the environment can support.

The logistic growth model applies to populations that approach their carrying capacity

As a population approaches its carrying capacity, its rate of growth slows greatly, because fewer resources remain for each new individual to use. The growth curve of such a population, which is always limited by one or more factors in the environment, can be approximated by the following logistic growth equation:

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

In this model of population growth, the growth rate of the population (dN/dt) is equal to its intrinsic rate of natural increase (r multiplied by N , the number of individuals present at any one time), adjusted for the amount of resources available. The adjust-

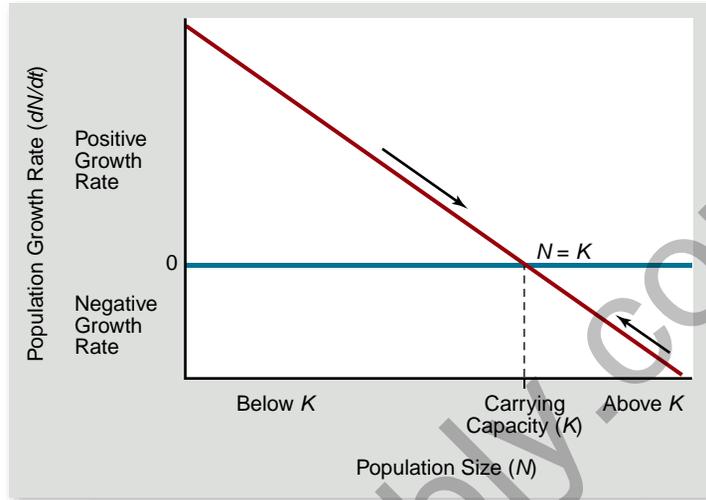


Figure 56.17 Relationship between population growth rate and population size. Populations far from the carrying capacity (K) have high growth rates—positive if the population is below K , and negative if it is above K . As the population approaches K , growth rates approach zero.

Inquiry question

? Why does the growth rate converge on zero?

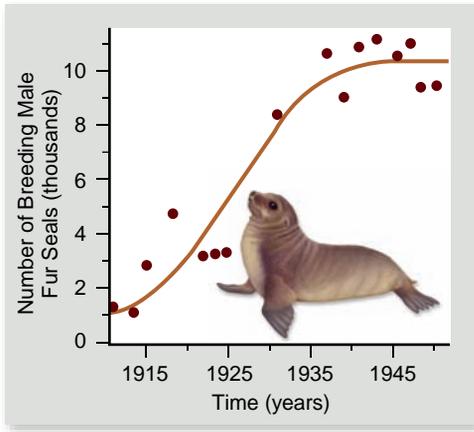
ment is made by multiplying rN by the fraction of K , the carrying capacity, still unused $[(K - N)/K]$. As N increases, the fraction of resources by which r is multiplied becomes smaller and smaller, and the rate of increase of the population declines.

Graphically, if you plot N versus t (time), you obtain a **sigmoidal growth curve** characteristic of many biological populations. The curve is called “sigmoidal” because its shape has a double curve like the letter **S**. As the size of a population stabilizes at the carrying capacity, its rate of growth slows, eventually coming to a halt (blue line in figure 56.16).

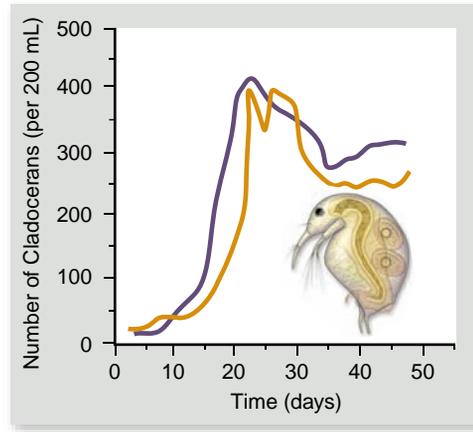
In mathematical terms, as N approaches K , the *rate* of population growth (dN/dt) begins to slow, reaching 0 when $N = K$ (figure 56.17). Conversely, if the population size exceeds the carrying capacity, then $K - N$ will be negative, and the population will experience a negative growth rate. As the population size then declines toward the carrying capacity, the magnitude of this negative growth rate will decrease until it reaches 0 when $N = K$.

Notice that the population tends to move toward the carrying capacity regardless of whether it is initially above or below it. For this reason, logistic growth tends to return a population to the same size. In this sense, such populations are considered to be in equilibrium because they would be expected to be at or near the carrying capacity at most times.

In many cases, real populations display trends corresponding to a logistic growth curve. This is true not only in the laboratory, but also in natural populations (figure 56.18a). In some cases, however, the fit is not perfect (figure 56.18b), and as we shall see shortly, many populations exhibit other patterns.



a.



b.

Figure 56.18 Many populations exhibit logistic growth. *a.* A fur seal (*Callorhinus ursinus*) population on St. Paul Island, Alaska. *b.* Two laboratory populations of the cladoceran *Bosmina longirostris*. Note that the populations first exceeded the carrying capacity, before decreasing to a size that was then maintained.

Learning Outcomes Review 56.5

Exponential growth refers to population growth in which the number of individuals accelerates even when the rate of increase remains constant; it results in a population explosion. Exponential growth is eventually limited by resource availability. The size at which a population in a particular location stabilizes is defined as the carrying capacity of that location for that species. Populations often grow to the carrying capacity of their environment.

- What might cause a population's carrying capacity to change, and how would the population respond?

A number of factors may affect population size through time. Some of these factors depend on population size and are therefore termed *density-dependent*. Other factors, such as natural disasters, affect populations regardless of size; these factors are termed *density-independent*. Many populations exhibit cyclic fluctuations in size that may result from complex interactions of factors.

Density-dependent effects occur when reproduction and survival are affected by population size

The reason population growth rates are affected by population size is that many important processes have **density-dependent effects**. That is, as population size increases, either reproductive rates decline or mortality rates increase, or both, a phenomenon termed *negative feedback* (figure 56.19).

Populations can be regulated in many different ways. When populations approach their carrying capacity, competition for resources can be severe, leading both to a decreased birth rate and an increased risk of death (figure 56.20). In addition, predators often focus their attention on a particularly common prey species, which also results in increasing rates of mortality as populations increase. High population densities can also lead to an accumulation of toxic wastes in the environment.

56.6 Factors That Regulate Populations

Learning Outcomes

1. Compare density-dependent and density-independent factors.
2. Evaluate why the size of some populations cycle.
3. Consider how the life history adaptations of species may differ depending on how often populations are at their carrying capacity.

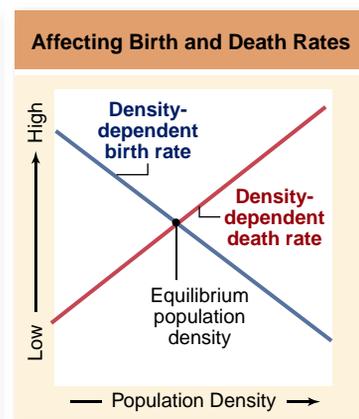
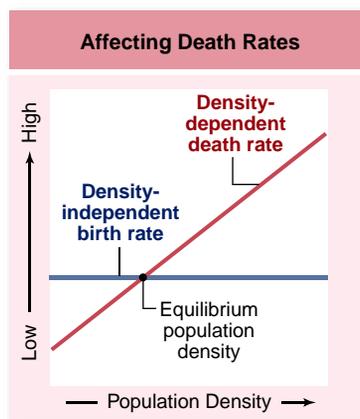
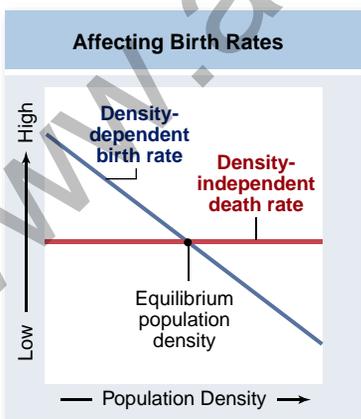


Figure 56.19 Density-dependent population regulation. Density-dependent factors can affect birth rates, death rates, or both.

Inquiry question

? Why might birth rates be density-dependent?

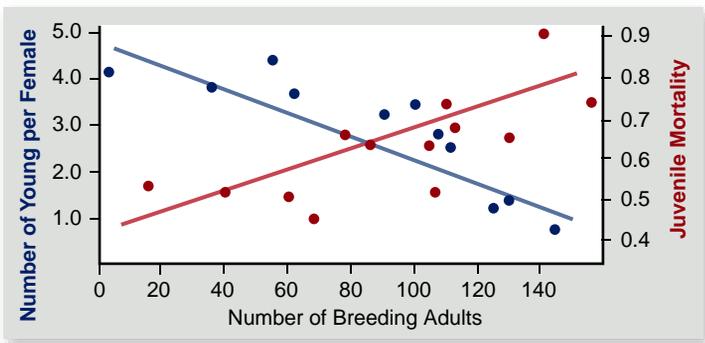


Figure 56.20 Density dependence in the song sparrow (*Melospiza melodia*) on Mandarte Island. Reproductive success decreases and mortality rates increase as population size increases.

Inquiry question

? What would happen if researchers supplemented the food available to the birds?

Behavioral changes may also affect population growth rates. Some species of rodents, for example, become antisocial, fighting more, breeding less, and generally acting stressed-out. These behavioral changes result from hormonal actions, but their ultimate cause is not yet clear; most likely, they have evolved as adaptive responses to situations in which resources are scarce. In addition, in crowded populations, the population growth rate may decrease because of an increased rate of emigration of individuals attempting to find better conditions elsewhere (figure 56.21).

However, not all density-dependent factors are negatively related to population size. In some cases, growth rates increase with population size. This phenomenon is referred to as the **Allee effect** (after Warder Allee, who first described it), and is an example of *positive feedback*. The Allee effect can take several forms. Most obviously, in populations that are too sparsely distributed, individuals may have difficulty finding mates. Moreover, some species may rely on large groups to deter predators or to provide the necessary stimulation for breeding activities. The Allee effect



Figure 56.21 Density-dependent effects. Migratory locusts (*Locusta migratoria*) are a legendary plague of large areas of Africa and Eurasia. At high population densities, the locusts have different hormonal and physical characteristics and take off as a swarm.

is a major threat for many endangered species, which may never recover from decreased population sizes caused by habitat destruction, overexploitation, or other causes (see chapter 60).

Density-independent effects include environmental disruptions and catastrophes

Growth rates in populations sometimes do not correspond to the logistic growth equation. In many cases, such patterns result because growth is under the control of **density-independent effects**. In other words, the rate of growth of a population at any instant is limited by something unrelated to the size of the population.

A variety of factors may affect populations in a density-independent manner. Most of these are aspects of the external environment, such as extremely cold winters, droughts, storms, or volcanic eruptions. Individuals often are affected by these occurrences regardless of the size of the population.

Populations in areas where such events occur relatively frequently display erratic growth patterns in which the populations increase rapidly when conditions are benign, but exhibit large reductions whenever the environment turns hostile (figure 56.22). Needless to say, such populations do not produce the sigmoidal growth curves characteristic of the logistic equation.

Population cycles may reflect complex interactions

In some populations, density-dependent effects lead not to an equilibrium population size but to cyclic patterns of increase and decrease. For example, ecologists have studied cycles in hare

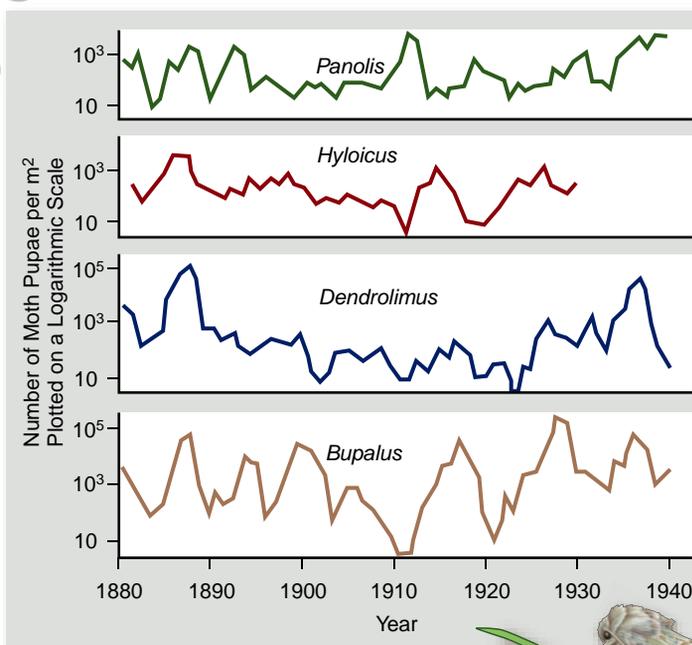


Figure 56.22 Fluctuations in the number of pupae of four moth species in Germany. The population fluctuations suggest that density-independent factors are regulating population size. The concordance in trends through time suggests that the same factors are regulating population size in all four species.

populations since the 1820s. They have found that the North American snowshoe hare (*Lepus americanus*) follows a “10-year cycle” (in reality, the cycle varies from 8 to 11 years). Hare population numbers fall 10-fold to 30-fold in a typical cycle, and 100-fold changes can occur (figure 56.23). Two factors appear to be generating the cycle: food plants and predators.

Food plants. The preferred foods of snowshoe hares are willow and birch twigs. As hare density increases, the quantity of these twigs decreases, forcing the hares to feed on high-fiber (low-quality) food. Lower birthrates, low juvenile survivorship, and low growth rates follow. The hares also spend more time searching for food, an activity that increases their exposure to predation. The result is a precipitous decline in willow and birch twig abundance, and a corresponding fall in hare abundance. It takes 2 to 3 years for the quantity of mature twigs to recover.

Predators. A key predator of the snowshoe hare is the Canada lynx. The Canada lynx shows a “10-year” cycle of abundance that seems remarkably entrained to the hare abundance cycle (see figure 55.23). As hare numbers increase, lynx numbers do too, rising in response to the increased availability of the lynx’s food. When hare numbers fall, so do lynx numbers, their food supply depleted.

Which factor is responsible for the predator–prey oscillations? Do increasing numbers of hares lead to overharvesting of plants (a hare–plant cycle), or do increasing numbers of lynx lead to overharvesting of hares (a hare–lynx cycle)? Field experiments carried out by Charles Krebs and coworkers in 1992 provide an answer.

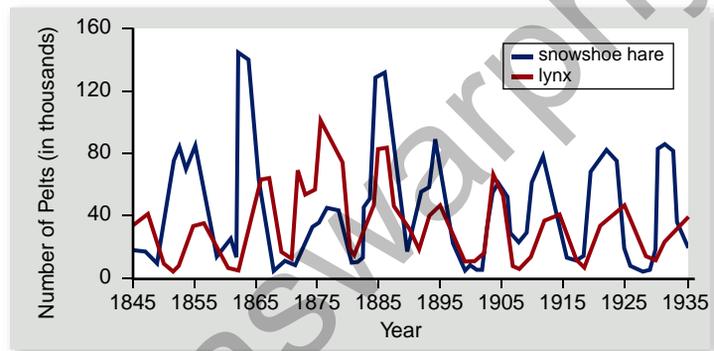


Figure 56.23 Linked population cycles of the snowshoe hare (*Lepus americanus*) and the northern lynx (*Lynx canadensis*). These data are based on records of fur returns from trappers in the Hudson Bay region of Canada. The lynx population carefully tracks that of the snowshoe hare, but lags behind it slightly.

Inquiry question



Suppose experimenters artificially kept the hare population at a high and constant level; what would happen to the lynx population? Conversely, if experimenters artificially kept the lynx population at a high and constant level, what would happen to the hare population?

In Canada’s Yukon, Krebs set up experimental plots that contained hare populations. If food is added (no food shortage effect) and predators are excluded (no predator effect) in an experimental area, hare numbers increase 10-fold and stay there—the cycle is lost. However, the cycle is retained if either of the factors is allowed to operate alone: exclude predators but don’t add food (food shortage effect alone), or add food in the presence of predators (predator effect alone). Thus, both factors can affect the cycle, which in practice seems to be generated by the interaction between the two.

Population cycles traditionally have been considered to occur rarely. However, a recent review of nearly 700 long-term (25 years or more) studies of trends within populations found that cycles were not uncommon; nearly 30% of the studies—including birds, mammals, fish, and crustaceans—provided evidence of some cyclic pattern in population size through time, although most of these cycles are nowhere near as dramatic in amplitude as the hare–lynx cycles. In some cases, such as that of the snowshoe hare and lynx, density-dependent factors may be involved, whereas in other cases, density-independent factors, such as cyclic climatic patterns, may be responsible.

Resource availability affects life history adaptations

As you have seen, some species usually maintain stable population sizes near the carrying capacity, whereas in other species population sizes fluctuate markedly and are often far below carrying capacity. The selective factors affecting such species differ markedly. Individuals in populations near their carrying capacity may face stiff competition for limited resources; by contrast, individuals in populations far below carrying capacity have access to abundant resources.

We have already described the consequences of such differences. When resources are limited, the cost of reproduction often will be very high. Consequently, selection will favor individuals that can compete effectively and utilize resources efficiently. Such adaptations often come at the cost of lowered reproductive rates. Such populations are termed **K-selected** because they are adapted to thrive when the population is near its carrying capacity (K). Table 56.3 lists some of the typical features of K -selected populations. Examples of K -selected species include coconut palms, whooping cranes, whales, and humans.

By contrast, in populations far below the carrying capacity, resources may be abundant. Costs of reproduction are low, and selection favors those individuals that can produce the maximum number of offspring. Selection here favors individuals with the highest reproductive rates; such populations are termed **r-selected**. Examples of organisms displaying r -selected life history adaptations include dandelions, aphids, mice, and cockroaches.

Most natural populations show life history adaptations that exist along a continuum ranging from completely r -selected traits to completely K -selected traits. Although these tendencies hold true as generalities, few populations are purely r - or K -selected and show all of the traits listed in table 56.3. These attributes should be treated as generalities, with the recognition that many exceptions exist.

TABLE 56.3
***r*-Selected and *K*-Selected Life History Adaptations**

Adaptation	<i>r</i> -Selected Populations	<i>K</i> -Selected Populations
Age at first reproduction	Early	Late
Life span	Short	Long
Maturation time	Short	Long
Mortality rate	Often high	Usually low
Number of offspring produced per reproductive episode	Many	Few
Number of reproductions per lifetime	Few	Many
Parental care	None	Often extensive
Size of offspring or eggs	Small	Large

Learning Outcomes Review 56.6

Density-dependent factors such as resource availability come into play particularly when population size is larger; density-independent factors such as natural disasters operate regardless of population size. Population density may be cyclic due to complex interactions such as resource cycles and predator effects. Populations with density-dependent regulation often are near their carrying capacity; in species with populations well below carrying capacity, natural selection may favor high rates of reproduction when resources are abundant.

- Can a population experience both positive and negative density-dependent effects?

56.7 Human Population Growth

Learning Outcomes

1. Explain how the rate of human population growth has changed through time.
2. Describe the effects of age distribution on future growth.
3. Evaluate the relative importance of rapid population growth and resource consumption as threats to the biosphere and human welfare.

Humans exhibit many *K*-selected life history traits, including small brood size, late reproduction, and a high degree of parental care. These life history traits evolved during the early history of hominids, when the limited resources available from the environment controlled population size. Throughout most of

human history, our populations have been regulated by food availability, disease, and predators. Although unusual disturbances, including floods, plagues, and droughts, no doubt affected the pattern of human population growth, the overall size of the human population grew slowly during our early history.

Two thousand years ago, perhaps 130 million people populated the Earth. It took a thousand years for that number to double, and it was 1650 before it had doubled again, to about 500 million. In other words, for over 16 centuries, the human population was characterized by very slow growth. In this respect, human populations resembled many other species with predominantly *K*-selected life history adaptations.

Human populations have grown exponentially

Starting in the early 1700s, changes in technology gave humans more control over their food supply, enabled them to develop superior weapons to ward off predators, and led to the development of cures for many diseases. At the same time, improvements in shelter and storage capabilities made humans less vulnerable to climatic uncertainties. These changes allowed humans to expand the carrying capacity of the habitats in which they lived and thus to escape the confines of logistic growth and re-enter the exponential phase of the sigmoidal growth curve.

Responding to the lack of environmental constraints, the human population has grown explosively over the last 300 years. Although the birth rate has remained unchanged at about 30 per 1000 per year over this period, the death rate has fallen dramatically, from 20 per 1000 per year to its present level of 13 per 1000 per year. The difference between birth and death rates meant that the population grew as much as 2% per year, although the rate has now declined to 1.2% per year.

A 1.2% annual growth rate may not seem large, but it has produced a current human population of nearly 7 billion people (figure 56.24). At this growth rate, 78 million people would be added to the world population in the next year, and the human population would double in 58 years. Both the current human population level and the projected growth rate have potentially grave consequences for our future.

Population pyramids show birth and death trends

Although the human population as a whole continues to grow rapidly at the beginning of the 21st century, this growth is not occurring uniformly over the planet. Rather, most of the population growth is occurring in Africa, Asia, and Latin America (figure 56.25). By contrast, populations are actually decreasing in some countries in Europe.

The rate at which a population can be expected to grow in the future can be assessed graphically by means of a **population pyramid**, a bar graph displaying the numbers of people in each age category (figure 56.26). Males are conventionally shown to the left of the vertical age axis, females to the right. A human population pyramid thus displays the age composition of a population by sex. In most human population pyramids, the number of older females is disproportionately large compared with the

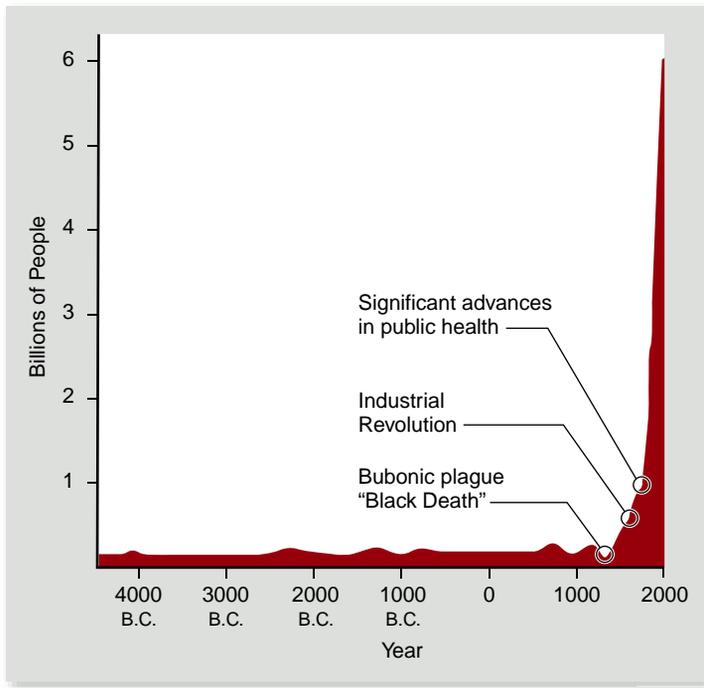


Figure 56.24 History of human population size.

Temporary increases in death rate, even a severe one such as that occurring during the Black Death of the 1300s, have little lasting effect. Explosive growth began with the Industrial Revolution in the 1800s, which produced a significant, long-term lowering of the death rate. The current world population is 6.9 billion, and at the present rate, it will double in 58 years.

Inquiry question

? Based on what we have learned about population growth, what do you predict will happen to human population size?

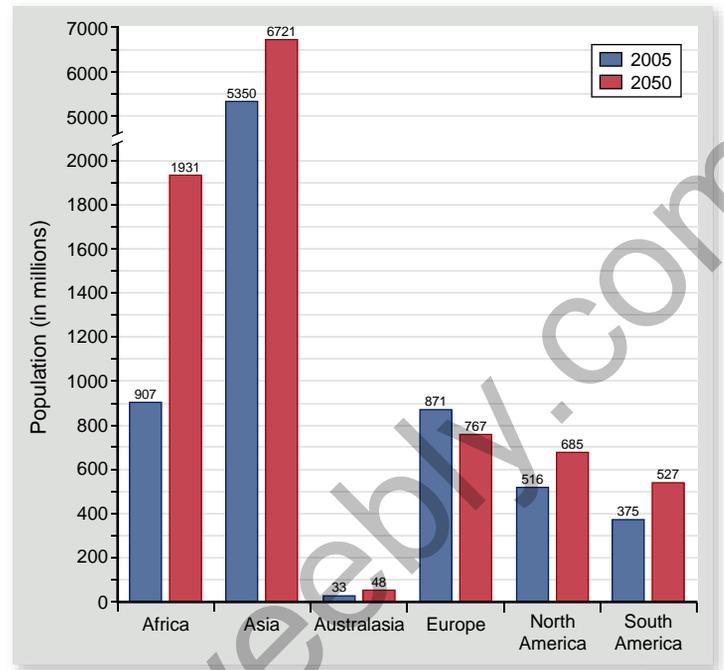


Figure 56.25 Projected population growth in 2050.

Developed countries are predicted to grow little; almost all of the population increase will occur in less-developed countries.

number of older males, because females in most regions have a longer life expectancy than males.

Viewing such a pyramid, we can predict demographic trends in births and deaths. In general, a rectangular pyramid is characteristic of countries whose populations are stable, neither growing nor shrinking. A triangular pyramid is characteristic of a country that will exhibit rapid future growth because most of

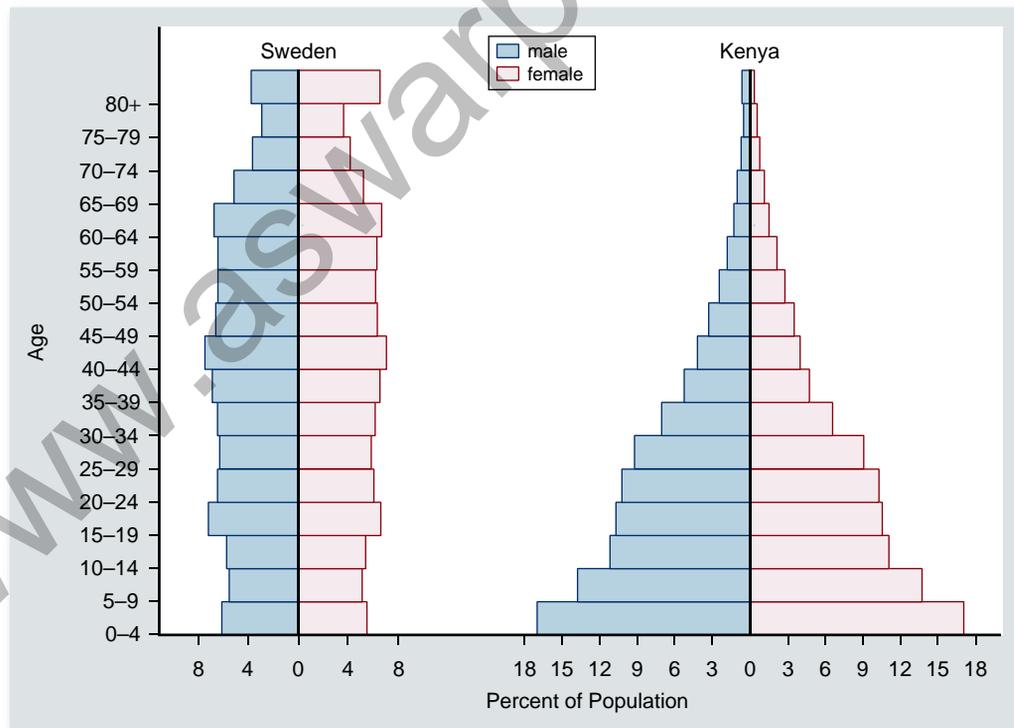


Figure 56.26 Population pyramids from 2008.

Population pyramids are graphed according to a population's age distribution. Kenya's pyramid has a broad base because of the great number of individuals below childbearing age. When the young people begin to bear children, the population will experience rapid growth. The Swedish pyramid exhibits a slight bulge among middle-aged Swedes, the result of the "baby boom" that occurred in the middle of the 20th century, and many postreproductive individuals resulting from Sweden's long average life span.

Inquiry question

? What will the population distributions look like in 20 years?

its population has not yet entered the childbearing years. Inverted triangles are characteristic of populations that are shrinking, usually as a result of sharply declining birth rates.

Examples of population pyramids for Sweden and Kenya in 2008 are shown in figure 56.26. The two countries exhibit very different age distributions. The nearly rectangular population pyramid for Sweden indicates that its population is not expanding because birth rates have decreased and average life span has increased. The very triangular pyramid of Kenya, by contrast, results from relatively high birth rates and shorter average life spans, which can lead to explosive future growth. The difference is most apparent when we consider that only 16% of Sweden's population is less than 15 years old, compared with nearly half of all Kenyans. Moreover, the fertility rate (offspring per woman) in Sweden is 1.7; in Kenya, it is 4.7. As a result, Kenya's population could double in less than 35 years, whereas Sweden's will remain stable.

Humanity's future growth is uncertain

Earth's rapidly growing human population constitutes perhaps the greatest challenge to the future of the biosphere, the world's interacting community of living things. Humanity is adding 78 million people a year to its population—over a million every 5 days, 150 every minute! In more rapidly growing countries, the resulting population increase is staggering (table 56.4). India, for example, had a population of 1.05 billion in 2002; by 2050, its population likely will exceed 1.6 billion.

A key element in the world's population growth is its uneven distribution among countries. Of the billion people added to the world's population in the 1990s, 90% live in developing countries (figure 56.27). The fraction of the world's population that lives in industrialized countries is therefore diminishing. In 1950, fully one-third of the world's population lived in industrialized countries; by 1996, that proportion had fallen to one-quarter; and in 2020, the proportion will have fallen to one-sixth.

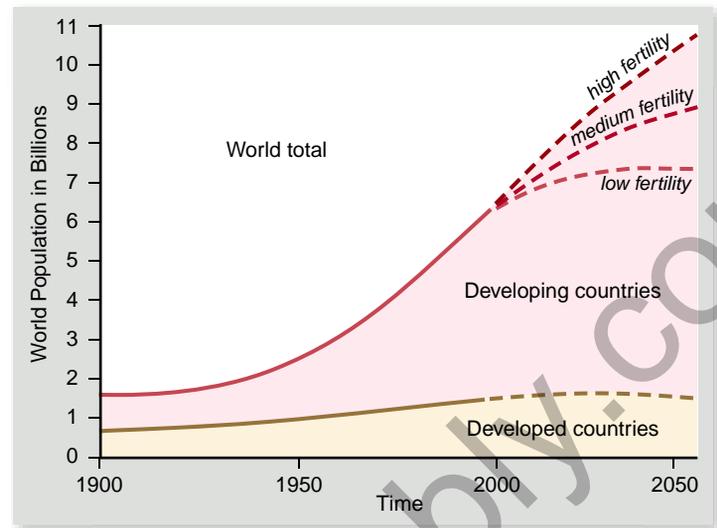


Figure 56.27 Distribution of population growth. Most of the worldwide increase in population since 1950 has occurred in developing countries. The age structures of developing countries indicate that this trend will increase in the near future. World population in 2050 likely will be between 7.3 and 10.7 billion, according to a recent United Nations study. Depending on fertility rates, the population at that time will either be increasing rapidly or slightly, or in the best case, declining slightly.

In the future, the world's population growth will be centered in the parts of the world least equipped to deal with the pressures of rapid growth.

Rapid population growth in developing countries has had the harsh consequence of increasing the gap between rich and poor. Today, the 19% of the world's population that lives in the industrialized world have a per capita income of \$22,060, but 81% of the world's population lives in developing countries and has a per capita income of only \$3,580. Furthermore, of the

TABLE 56.4	A Comparison of 2005 Population Data in Developed and Developing Countries		
	United States (highly developed)	Brazil (moderately developed)	Ethiopia (poorly developed)
Fertility rate	2.1	1.9	5.3
Doubling time at current rate (years)	75	65	29
Infant mortality rate (per 1000 births)	6.5	30	95
Life expectancy at birth (years)	78	72	49
Per capita GDP (U.S. \$)*	\$40,100	\$8100	\$800
Population < 15 years old (%)	21	26	44

*GDP, gross domestic product.

people in the developing world, about one-quarter of the population gets by on \$1 per day. Eighty percent of all the energy used today is consumed by the industrialized world, but only 20% is used by developing countries.

No one knows whether the world can sustain today's population of 6.9 billion people, much less the far greater numbers expected in the future. As chapter 58 outlines, the world ecosystem is already under considerable stress. We cannot reasonably expect to expand its carrying capacity indefinitely, and indeed we already seem to be stretching the limits.

Despite using an estimated 45% of the total biological productivity of Earth's landmasses and more than one-half of all renewable sources of fresh water, between one-fourth and one-eighth of all people in the world are malnourished. Moreover, as anticipated by Thomas Malthus in his famous 1798 work, *Essay on the Principle of Population*, death rates are beginning to rise in some areas. In sub-Saharan Africa, for example, population projections for the year 2025 have been scaled back from 1.33 billion to 1.05 billion (21%) because of the effect of AIDS. Similar decreases are projected for Russia as a result of higher death rates due to disease.

If we are to avoid catastrophic increases in the death rate, birth rates must fall dramatically. Faced with this grim dichotomy, significant efforts are underway worldwide to lower birth rates.

The population growth rate has declined

The world population growth rate is declining, from a high of 2.0% in the period 1965–1970 to 1.2% in 2008. Nonetheless, because of the larger population, this amounts to an increase of 78 million people per year to the world population, compared with 53 million per year in the 1960s.

The United Nations attributes the growth rate decline to increased family planning efforts and the increased economic power and social status of women. The United States has led the world in funding family planning programs abroad, but some groups oppose spending money on international family planning. The opposition believes that money is better spent on improving education and the economy in other countries, leading to an increased awareness and lowered fertility rates. The U.N. certainly supports the improvement of education programs in developing countries, but interestingly, it has reported increased education levels *following* a decrease in family size as a result of family planning.

Most countries are devoting considerable attention to slowing the growth rate of their populations, and there are genuine signs of progress. For example, from 1984 to 2008, family planning programs in Kenya succeeded in reducing the fertility rate from 8.0 to 4.7 children per couple, thus lowering the population growth rate from 4.0% per year to 2.8% per year. Because of these efforts, the global population may stabilize at about 8.9 billion people by the middle of the current century. How many people the planet can support sustainably depends on the quality of life that we want to achieve; there are already more people than can be sustainably supported with current technologies.

Consumption in the developed world further depletes resources

Population size is not the only factor that determines resource use; per capita consumption is also important. In this respect, we in the industrialized world need to pay more attention to lessening the impact each of us makes because, even though the vast majority of the world's population is in developing countries, the overwhelming percentage of consumption of resources occurs in the industrialized countries. Indeed, the wealthiest 20% of the world's population accounts for 86% of the world's consumption of resources and produces 53% of the world's carbon dioxide emissions, whereas the poorest 20% of the world is responsible for only 1.3% of consumption and 3% of carbon dioxide emissions. Looked at another way, in terms of resource use, a child born today in the industrialized world will consume many more resources over the course of his or her life than a child born in the developing world.

One way of quantifying this disparity is by calculating what has been termed the **ecological footprint**, which is the amount of productive land required to support an individual at the standard of living of a particular population through the course of his or her life. This figure estimates the acreage used for the production of food (both plant and animal), forest products, and housing, as well as the area of forest required to absorb carbon dioxide produced by the combustion of fossil fuels. As figure 56.28 illustrates, the

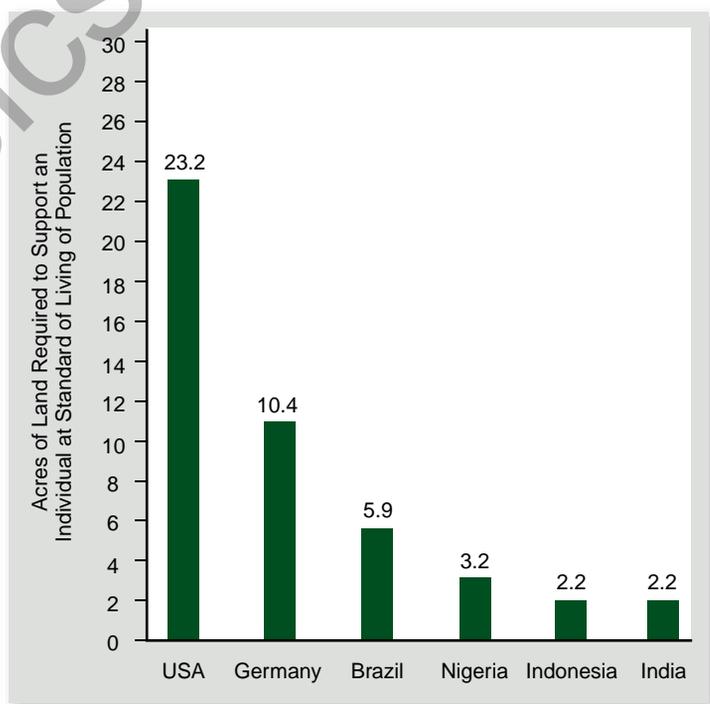


Figure 56.28 Ecological footprints of individuals in different countries. An ecological footprint calculates how much land is required to support a person through his or her life, including the acreage used for production of food, forest products, and housing, in addition to the forest required to absorb the carbon dioxide produced by the combustion of fossil fuels.

Inquiry question



Which is a more important cause of resource depletion, overpopulation or overconsumption?

ecological footprint of an individual in the United States is more than 10 times greater than that of someone in India.

Based on these measurements, researchers have calculated that resource use by humans is now one-third greater than the amount that nature can sustainably replace. Moreover, consumption is increasing rapidly in parts of the developing world; if all humans lived at the standard of living in the industrialized world, two additional planet Earths would be needed.

Building a sustainable world is the most important task facing humanity's future. The quality of life available to our children will depend to a large extent on our success in limiting both population growth and the amount of per capita resource consumption.

Learning Outcomes Review 56.7

For most of its history, the K -selected human population increased gradually. In the last 400 years, with resource control, the human population has grown exponentially; at the current rate, it would double in 58 years. A population pyramid shows the number of individuals in different age categories. Pyramids with a wide base are undergoing faster growth than those that are uniform from top to bottom. Growth rates overall are declining, but consumption per capita in the developed world is still a significant drain on resources.

- Which is more important, reducing global population growth or reducing resource consumption levels in developed countries?

Chapter Review

56.1 The Environmental Challenges

Key environmental factors include temperature, water, sunlight, and soil type. Individuals seek to maintain internal homeostasis.

Organisms are capable of responding to environmental changes that occur during their lifetime.

Most individuals can cope with variations in their natural habitat, such as short-term changes in temperature and water availability.

Natural selection leads to evolutionary adaptation to environmental conditions.

Over evolutionary time, physiological, morphological, or behavioral adaptations evolve that make organisms better suited to the environment in which they live.

56.2 Populations: Groups of a Single Species in One Place

A population's geographic distribution is termed its range.

Ranges undergo expansion and contraction.

Most populations have limited geographic ranges that can expand or contract through time as the environment changes.

Dispersal mechanisms may allow some species to cross a barrier and expand their range. Human actions have led to range expansion of some species, often with detrimental effects.

Individuals in populations exhibit different spacing patterns.

Within a population, individuals are distributed randomly, uniformly, or are clumped. Nonrandom distributions may reflect resource distributions or competition for resources.

A metapopulation comprises distinct populations that may exchange members.

The degree of exchange between populations in a metapopulation is highest when populations are large and more connected.

Metapopulations may act as a buffer against extinction by permitting recolonization of vacant areas or marginal areas.

56.3 Population Demography and Dynamics

Sex ratio and generation time affect population growth rates.

Abundant females, a short generation time, or both can be responsible for more rapid population growth.

Age structure is determined by the numbers of individuals in different age groups.

Every age cohort has a characteristic fecundity and death rate, and so the age structure of a population affects growth.

Life tables show probability of survival and reproduction through a cohort's life span.

Survivorship curves demonstrate how survival probability changes with age (see figures 56.11, 56.12).

In some populations, survivorship is high until old age, whereas in others, survivorship is lowest among the youngest individuals.

56.4 Life History and the Cost of Reproduction

Because resources are limited, reproduction has a cost. Resources allocated toward current reproduction cannot be used to enhance survival and future reproduction (see figure 56.13).

A trade-off exists between number of offspring and investment per offspring.

When reproductive cost is high, fitness can be maximized by deferring reproduction, or by producing a few large-sized young that have a greater chance of survival.

Reproductive events per lifetime represent an additional trade-off.

Semelparity is reproduction once in a single large event. Iteroparity is production of offspring several times over many seasons.

Age at first reproduction correlates with life span.

Longer-lived species delay first reproduction longer compared with short-lived species, in which time is of the essence.

56.5 Environmental Limits to Population Growth

The exponential growth model applies to populations with no growth limits.

The rate of population increase, r , is defined as the difference between birth rate, b , and death rate, d .

Exponential growth occurs when a population is not limited by resources or by other species (see figure 56.16).

The logistic model applies to populations that approach their carrying capacity.

Logistic growth is observed as a population reaches its carrying capacity. Usually, a population's growth rate slows to a plateau. In some cases the population overshoots and then drops back to the carrying capacity.

56.6 Factors That Regulate Populations

Density-dependent effects occur when reproduction and survival are affected by population size.

Density-dependent factors include increased competition and disease. To stabilize a population size, birth rates must decline, death rates must increase, or both.

Density-independent effects include environmental disruptions and catastrophes.

Density-independent factors are not related to population size and include environmental events that result in mortality.

Population cycles may reflect complex interactions.

In some cases, population size is cyclic because of the interaction of factors such as food supply and predation (see figure 56.23).

Resource availability affects life history adaptations.

Populations at carrying capacity have adaptations to compete for limited resources; populations well below carrying capacity exhibit a high reproductive rate to use abundant resources.

56.7 Human Population Growth

Human populations have grown exponentially.

Technology and other innovations have simultaneously increased the carrying capacity and decreased mortality in the past 300 years.

Population pyramids show birth and death trends.

Populations with many young individuals are likely to experience high growth rates as these individuals reach reproductive age.

Humanity's future growth is uncertain.

The human population is unevenly distributed. Rapid growth in developing countries has resulted in poverty, whereas most resources are utilized by the industrialized world.

The population growth rate has declined.

Even at lower growth rates, the number of individuals on the planet is likely to plateau at 7 to 10 billion.

Consumption in the developed world further depletes resources.

Resource consumption rates in the developed world are very high; a sustainable future requires limits both to population growth and to per capita resource consumption.



Review Questions

UNDERSTAND

- Source-sink metapopulations are distinct from other types of metapopulations because
 - exchange of individuals only occurs in the former.
 - populations with negative growth rates are a part of the former.
 - populations never go extinct in the former.
 - all populations eventually go extinct in the former.
- The potential for social interactions among individuals should be maximized when individuals
 - are randomly distributed in their environment.
 - are uniformly distributed in their environment.
 - have a clumped distribution in their environment.
 - None of the above
- When ecologists talk about the cost of reproduction they mean
 - the reduction in future reproductive output as a consequence of current reproduction.
 - the amount of calories it takes for all the activity used in successful reproduction.
 - the amount of calories contained in eggs or offspring.
 - None of the above
- A life history trade-off between clutch size and offspring size
 - means that as clutch size increases, offspring size increases.
 - means that as clutch size increases, offspring size decreases.
 - means that as clutch size increases, adult size increases.
 - means that as clutch size increases, adult size decreases.
- The difference between exponential and logistic growth rates is
 - exponential growth depends on birth and death rates and logistic does not.
 - in logistic growth, emigration and immigration are unimportant.
 - that both are affected by density, but logistic growth is slower.
 - that only logistic growth reflects density-dependent effects on births or deaths.
- The logistic population growth model, $dN/dt = rN[(K - N)/K]$, describes a population's growth when an upper limit to growth is assumed. As N approaches (numerically) the value of K
 - dN/dt increases rapidly.
 - dN/dt approaches 0.
 - dN/dt increases slowly.
 - the population becomes threatened by extinction.

7. Which of the following is an example of a density-dependent effect on population growth?
- An extremely cold winter
 - A tornado
 - An extremely hot summer in which cool burrow retreats are fewer than number of individuals in the population
 - A drought

APPLY

- If the size of a population is reduced due to a natural disaster such as a flood
 - population growth rates may increase because the population is no longer near its carrying capacity.
 - population growth rates may decrease because individuals have trouble finding mates.
 - both effects a. and b. may occur and whether population rates increase or decrease cannot be predicted.
 - All of the above
- In populations subjected to high levels of predation
 - individuals should invest little in reproduction so as to maximize their survival.
 - individuals should produce few offspring and invest little in any of them.
 - individuals should invest greatly in reproduction because their chance of surviving to another breeding season is low.
 - individuals should stop reproducing altogether.
- In a population in which individuals are uniformly distributed
 - the population is probably well below its carrying capacity.
 - natural selection should favor traits that maximize the ability to compete for resources.
 - immigration from other populations is probably keeping the population from going extinct.
 - None of the above
- The elimination of predators by humans
 - will cause its prey to experience exponential growth until new predators arrive or evolve.
 - will lead to an increase in the carrying capacity of the environment.

- may increase the population size of a prey species if that prey's population was being regulated by predation from the predator.
- will lead to an Allee effect.

SYNTHESIZE

- Refer to figure 56.8. What are the implications for evolutionary divergence among populations that are part of a metapopulation versus populations that are independent of other populations?
- Refer to figure 56.13. Given a trade-off between current reproductive effort and future reproductive success (the so-called cost of reproduction), would you expect old individuals to have the same “optimal” reproductive effort as young individuals?
- Refer to figure 56.14. Because the number of offspring that a parent can produce is often a trade-off with the size of individual offspring, many circumstances lead to an intermediate number and size of offspring being favored. If the size of an offspring was completely unrelated to the quality of that offspring (its chances of surviving until it reaches reproductive age), would you expect parents to fall on the left or right side of the x -axis (clutch size)? Explain.
- Refer to figure 56.26. Would increasing the mean generation time have the same kind of effect on population growth rate as reducing the number of children that an individual female has over her lifetime? Which effect would have a bigger influence on population growth rate? Explain.

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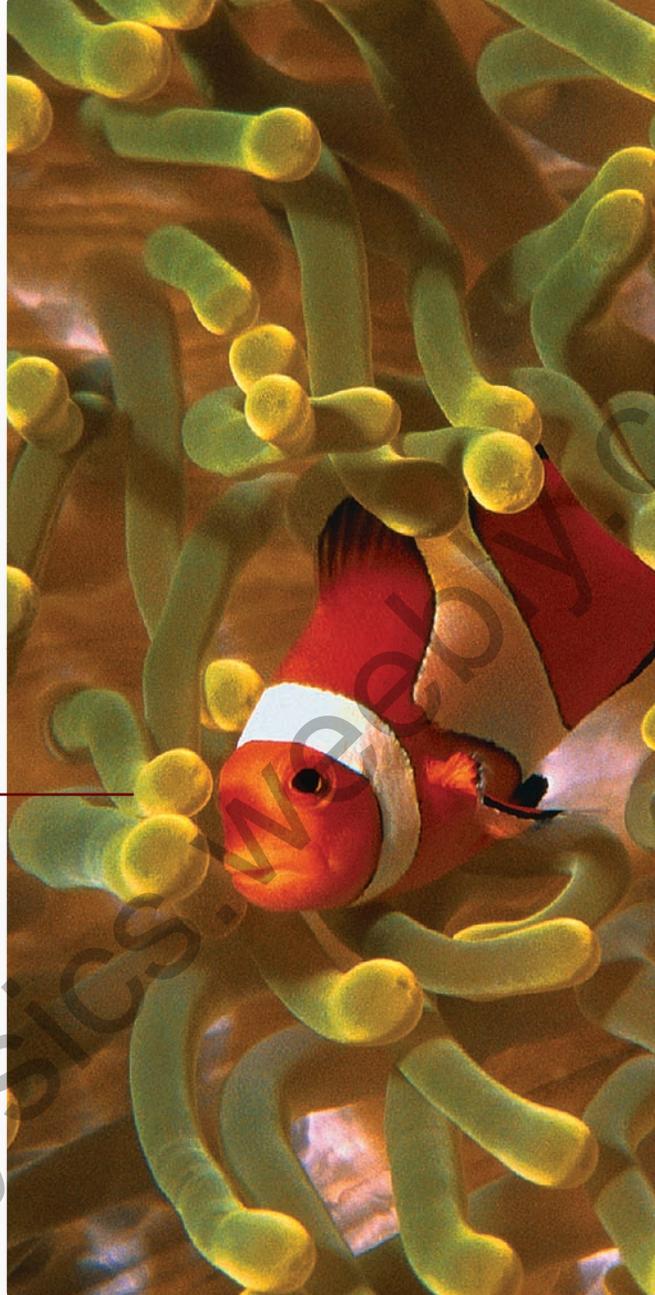
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Chapter 57

Community Ecology

Chapter Outline

- 57.1** Biological Communities: Species Living Together
- 57.2** The Ecological Niche Concept
- 57.3** Predator–Prey Relationships
- 57.4** The Many Types of Species Interactions
- 57.5** Ecological Succession, Disturbance, and Species Richness



Introduction

All the organisms that live together in a place are members of a community. The myriad of species that inhabit a tropical rain forest are a community. Indeed, every inhabited place on Earth supports its own particular array of organisms. Over time, the different species that live together have made many complex adjustments to community living, evolving together and forging relationships that give the community its character and stability. Both competition and cooperation have played key roles; in this chapter, we look at these and other factors in community ecology.

Biological Communities: Species Living Together

Learning Outcomes

1. Define community.
2. Describe how community composition may change across a geographic landscape.

Almost any place on Earth is occupied by species, sometimes by many of them, as in the rain forests of the Amazon, and sometimes by only a few, as in the near-boiling waters of Yellowstone's geysers (where a number of microbial species live). The term **community** refers to the species that occur at any particular locality (figure 57.1). Communities can be characterized either by their constituent species or by their properties, such as **species richness** (the number of species present) or **primary productivity** (the amount of energy produced).

Interactions among community members govern many ecological and evolutionary processes. These interactions, such as predation and mutualism, affect the population biology of particular species—whether a population increases or decreases in abundance, for example—as well as the ways in which energy and nutrients cycle through the ecosystem. Moreover, the community context affects the patterns of natural selection faced by a species, and thus the evolutionary course it takes.

Scientists study biological communities in many ways, ranging from detailed observations to elaborate, large-scale experiments. In some cases, studies focus on the entire community, whereas in other cases only a subset of species that are likely to

interact with one another are studied. Although scientists sometimes refer to such subsets as communities (for example, the “spider community”), the term **assemblage** is more appropriate to connote that the species included are only a portion of those present within the entire community.

Communities have been viewed in different ways

Two views exist on the structure and functioning of communities. The *individualistic concept* of communities holds that a community is simply an aggregation of species that happen to occur together at one place.

By contrast, the **holistic concept** of communities views communities as an integrated unit. In this sense, the community could be viewed as a superorganism whose constituent species have coevolved to the extent that they function as part of a greater whole, just as the kidneys, heart, and lungs all function together within an animal's body. In this view, then, a community would amount to more than the sum of its parts.

These two views make differing predictions about the integrity of communities across space and time. If, as the individualistic view implies, communities are nothing more than a combination of species that occur together, then moving geographically across the landscape or back through time, we would not expect to see the same community. That is, species should appear and disappear independently, as a function of each species' own unique ecological requirements. By contrast, if a community is an integrated whole, then we would make the opposite prediction: Communities should stay the same through space or time, until being replaced by completely different communities when environmental differences are sufficiently great.

Figure 57.1 An African savanna community. A community consists of all the species—plants, animals, fungi, protists, and prokaryotes—that occur at a locality, in this case Etosha National Park in Namibia.



Communities change over space and time

Most ecologists today favor the individualistic concept. For the most part, species seem to respond independently to changing environmental conditions. As a result, community composition changes gradually across landscapes as some species appear and become more abundant, while others decrease in abundance and eventually disappear.

A famous example of this pattern is the abundance of tree species in the Santa Catalina Mountains of Arizona along a geographic gradient running from very dry to very moist. Figure 57.2 shows that species can change abundance in patterns that are for the most part independent of one another. As a result, tree communities at different localities in these mountains fall on a continuum, one merging into the next, rather than representing discretely different sets of species.

Similar patterns through time are seen in paleontological studies. For example, a very good fossil record exists for the trees and small mammals that occurred in North America over the past 20,000 years. Examination of prehistoric communities shows little similarity to those that occur today. Many species that occur together today were never found together in the past. Conversely, species that used to occur in the same communities often do not overlap in their geographic ranges today. These findings suggest that as climate has changed during the waxing and waning of the Ice Ages, species have responded independently, rather than shifting their distributions together, as would be expected if the community were an integrated unit.

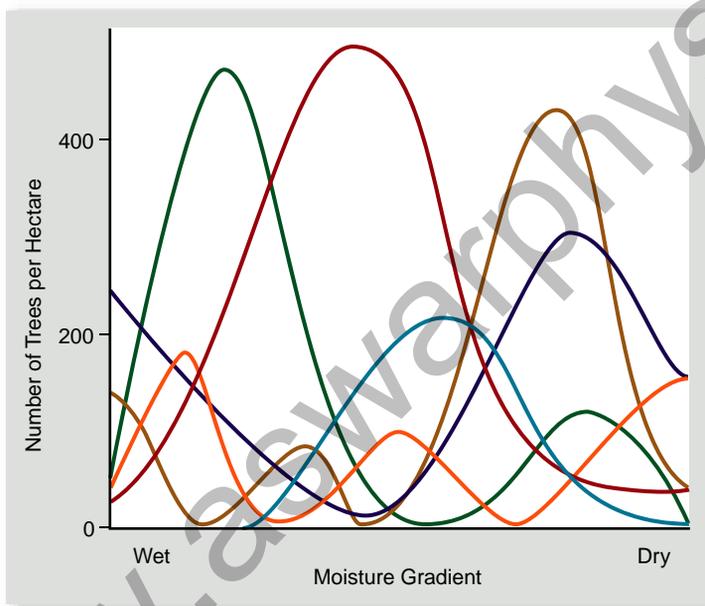


Figure 57.2 Abundance of tree species along a moisture gradient in the Santa Catalina Mountains of southeastern Arizona. Each line represents the abundance of a different tree species. The species' patterns of abundance are independent of one another. Thus, community composition changes continually along the gradient.

Inquiry question

? Why do species exhibit different patterns of response to change in moisture?

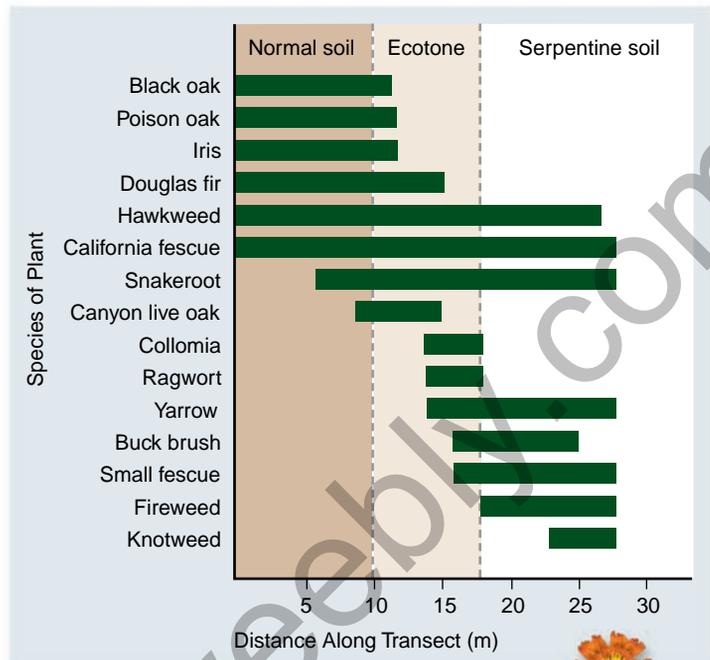


Figure 57.3 Change in community composition across an ecotone. The plant assemblages on normal and serpentine soils are greatly different, and the transition from one community to another occurs over a short distance.



Inquiry question

? Why is there a sharp transition between the two community types?

Nonetheless, in some cases the abundance of species in a community does change geographically in a synchronous pattern. Often, this occurs at **ecotones**, places where the environment changes abruptly. For example, in the western United States, certain patches of habitat have serpentine soils. This soil differs from normal soil in many ways—for example, high concentrations of nickel, chromium, and iron; low concentrations of copper and calcium. Comparison of the plant species that occur on different soils shows that distinct communities exist on each type, with an abrupt transition from one to the other over a short distance (figure 57.3). Similar transitions are seen wherever greatly different habitats come into contact, such as at the interface between terrestrial and aquatic habitats or where grassland and forest meet.

Learning Outcomes Review 57.1

A community comprises all species that occur at one site. In most cases, the abundance of community members appears to vary independently across space and through time. Community composition also changes gradually depending on environmental factors when moving from one location to another, such as from a very dry area to a very moist area.

- In a community, would you expect greater variation over time in abundance of animal life or plant life? Why?

57.2 The Ecological Niche Concept

Learning Outcomes

1. Define niche and resource partitioning.
2. Differentiate between fundamental and realized niches.
3. Explain how the presence of other species can affect a species' realized niche.

Each organism in a community confronts the challenge of survival in a different way. The **niche** an organism occupies is the total of all the ways it uses the resources of its environment. A niche may be described in terms of space utilization, food consumption, temperature range, appropriate conditions for mating, requirements for moisture, and other factors.

Sometimes species are not able to occupy their entire niche because of the presence or absence of other species. Species can interact with one another in a number of ways, and these interactions can either have positive or negative effects. One type of interaction, **interspecific competition**, occurs when two species attempt to use the same resource and there is not enough of the resource to satisfy both. Physical interactions over access to resources—such as fighting to defend a territory or displacing an individual from a particular location—are referred to as **interference competition**; consuming the same resources is called **exploitative competition**.

Fundamental niches are potential; realized niches are actual

The entire niche that a species is capable of using, based on its physiological tolerance limits and resource needs, is called the

fundamental niche. The actual set of environmental conditions, including the presence or absence of other species, in which the species can establish a stable population is its **realized niche**. Because of interspecific interactions, the realized niche of a species may be considerably smaller than its fundamental niche.

Competition between species for niche occupancy

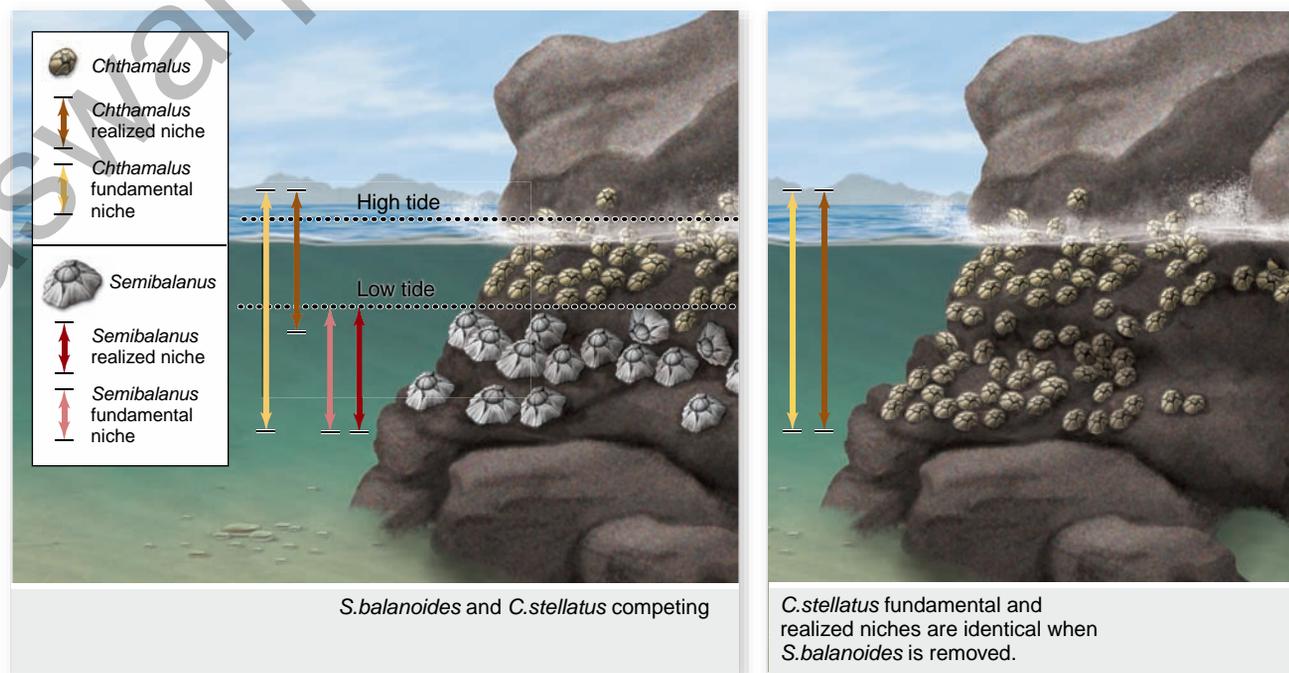
In a classic study, Joseph Connell of the University of California, Santa Barbara, investigated competitive interactions between two species of barnacles that grow together on rocks along the coast of Scotland. Of the two species Connell studied, *Chthamalus stellatus* lives in shallower water, where tidal action often exposes it to air, and *Semibalanus balanoides* (called *Balanus balanoides* prior to 1995) lives lower down, where it is rarely exposed to the atmosphere (figure 57.4). In these areas, space is at a premium. In the deeper zone, *S. balanoides* could always outcompete *C. stellatus* by crowding it off the rocks, undercutting it, and replacing it even where it had begun to grow, an example of interference competition.

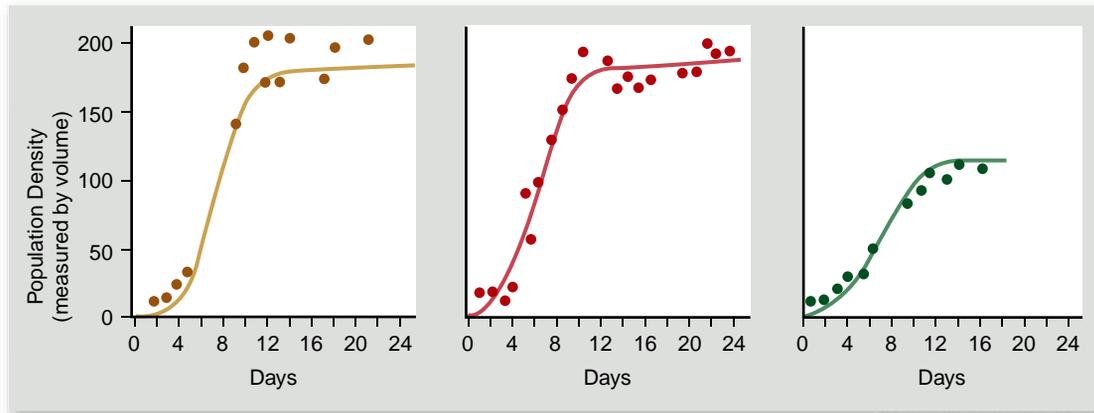
When Connell removed *S. balanoides* from the area, however, *C. stellatus* was easily able to occupy the deeper zone, indicating that no physiological or other general obstacles prevented it from becoming established there. In contrast, *S. balanoides* could not survive in the shallow-water habitats where *C. stellatus* normally occurs; it does not have the physiological adaptations to warmer temperatures that allow *C. stellatus* to occupy this zone. Thus, the fundamental niche of *C. stellatus* includes both shallow and deeper zones, but its realized niche is much narrower because *C. stellatus* can be outcompeted by *S. balanoides* in parts of its fundamental niche. By contrast, the realized and fundamental niches of *S. balanoides* appear to be identical.

Other causes of niche restriction

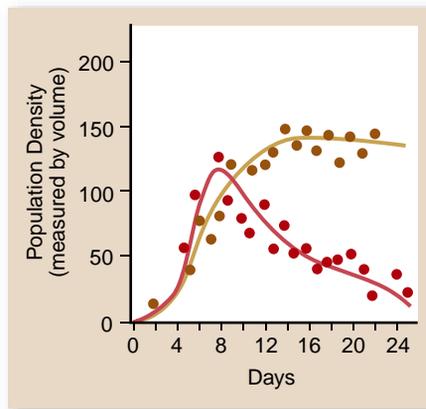
Processes other than competition can also restrict the realized niche of a species. For example, the plant St. John's wort (*Hypericum perforatum*) was introduced and became widespread in

Figure 57.4
Competition among two species of barnacles. The fundamental niche of *Chthamalus stellatus* includes both deep and shallow zones, but *Semibalanus balanoides* forces *C. stellatus* out of the part of its fundamental niche that overlaps the realized niche of *Semibalanus*.

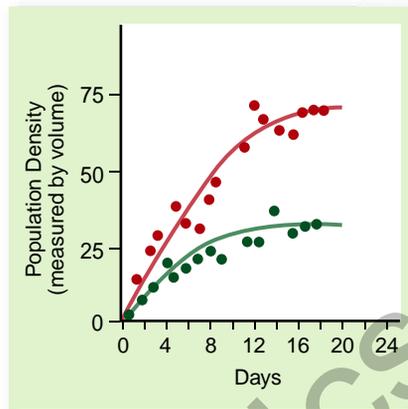




a.



b.



c.

● *Paramecium caudatum*
● *Paramecium aurelia*
● *Paramecium bursaria*

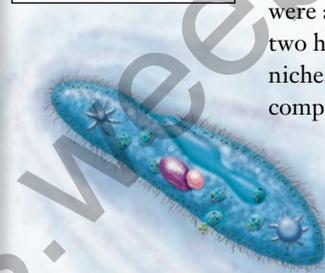


Figure 57.5 Competitive exclusion among three species of *Paramecium*.

In the microscopic world, *Paramecium* is a ferocious predator that preys on smaller protists. **a.** In his experiments, Gause found that three species of *Paramecium* grew well alone in culture tubes. **b.** However, *P. caudatum* declined to extinction when grown with *P. aurelia* because they shared the same realized niche, and *P. aurelia* outcompeted *P. caudatum* for food resources. **c.** *P. caudatum* and *P. bursaria* were able to coexist because the two have different realized niches and thus avoided competition.

open rangeland habitats in California until a specialized beetle was introduced to control it. Population size of the plant quickly decreased, and it is now only found in shady sites where the beetle cannot thrive. In this case, the presence of a predator limits the realized niche of a plant.

In some cases, the absence of another species leads to a smaller realized niche. Many North American plants depend on insects for pollination; indeed, the value of insect pollination for American agriculture has been estimated as more than \$2 billion per year. However, pollinator populations are currently declining for several reasons. Conservationists are concerned that if these insects disappear from some habitats, the realized niche of many plant species will decrease or even disappear entirely. In this case, the absence—rather than the presence—of another species will be the cause of a relatively small realized niche.

Competitive exclusion can occur when species compete for limited resources

In classic experiments carried out in 1934 and 1935, Russian ecologist Georgii Gause studied competition among three species of *Paramecium*, a tiny protist. Each of the three species grew well in culture tubes by themselves, preying on bacteria and yeasts that fed on oatmeal suspended in the culture fluid (figure 57.5a). However, when Gause grew *P. aurelia* together

with *P. caudatum* in the same culture tube, the numbers of *P. caudatum* always declined to extinction, leaving *P. aurelia* the only survivor (figure 57.5b). Why did this happen? Gause found that *P. aurelia* could grow six times faster than its competitor *P. caudatum* because it was able to better utilize the limited available resources, an example of exploitative competition.

From experiments such as this, Gause formulated what is now called the principle of **competitive exclusion**. This principle states that if two species are competing for a limited resource such as food or water, the species that uses the resource more efficiently will eventually eliminate the other locally. In other words, no two species with the same niche can coexist when resources are limiting.

Niche overlap and coexistence

In a revealing experiment, Gause challenged *Paramecium caudatum*—the defeated species in his earlier experiments—with a third species, *P. bursaria*. Because he expected these two species to also compete for the limited bacterial food supply, Gause thought one would win out, as had happened in his previous experiments. But that's not what happened. Instead, both species survived in the culture tubes, dividing the food resources.

The explanation for the species' coexistence is simple. In the upper part of the culture tubes, where the oxygen concentration and bacterial density were high, *P. caudatum* dominated because it was better able to feed on bacteria. In the lower part

of the tubes, however, the lower oxygen concentration favored the growth of a different potential food, yeast, and *P. bursaria* was better able to eat this food. The fundamental niche of each species was the whole culture tube, but the realized niche of each species was only a portion of the tube. Because the realized niches of the two species did not overlap too much, both species were able to survive. However, competition did have a negative effect on the participants (figure 57.5c). When grown without a competitor, both species reached densities three times greater than when they were grown with a competitor.

Competitive exclusion refined

Gause's principle of competitive exclusion can be restated as: No two species can occupy the same niche *indefinitely* when resources are limiting. Certainly species can and do coexist while competing for some of the same resources. Nevertheless, Gause's hypothesis predicts that when two species coexist on a long-term basis, either resources must not be limited or their niches will always differ in one or more features; otherwise, one species will outcompete the other, and the extinction of the second species will inevitably result.

Competition may lead to resource partitioning

Gause's competitive exclusion principle has a very important consequence: If competition for a limited resource is intense, then either one species will drive the other to extinction, or natural selection will reduce the competition between them.

When the ecologist Robert MacArthur studied five species of warblers, small insect-eating forest songbirds, he discovered that they appeared to be competing for the same resources. But when he studied them more carefully, he found that each species actually fed in a different part of spruce trees and so ate different subsets of insects. One species fed on insects near the tips of branches, a second within the dense foliage, a third on the lower branches, a fourth high on the trees, and a fifth at the very apex of the trees. Thus, each species of warbler had evolved so as to utilize a different portion of the spruce tree resource. They had *subdivided the niche* to avoid direct competition with one another. This niche subdivision is termed **resource partitioning**.

Resource partitioning is often seen in similar species that occupy the same geographic area. Such sympatric species often avoid competition by living in different portions of the habitat or by using different food or other resources (figure 57.6). This pattern of resource partitioning is thought to result from the process of natural selection causing initially similar species to diverge in resource use to reduce competitive pressures.

Whether such evolutionary divergence occurs can be investigated by comparing species whose ranges only partially overlap. Where the two species occur together, they often tend to exhibit greater differences in morphology (the form and structure of an organism) and resource use than do allopatric populations of the same species that do not occur with the other species. Called *character displacement*, the differences evident between sympatric species are thought to have been favored by

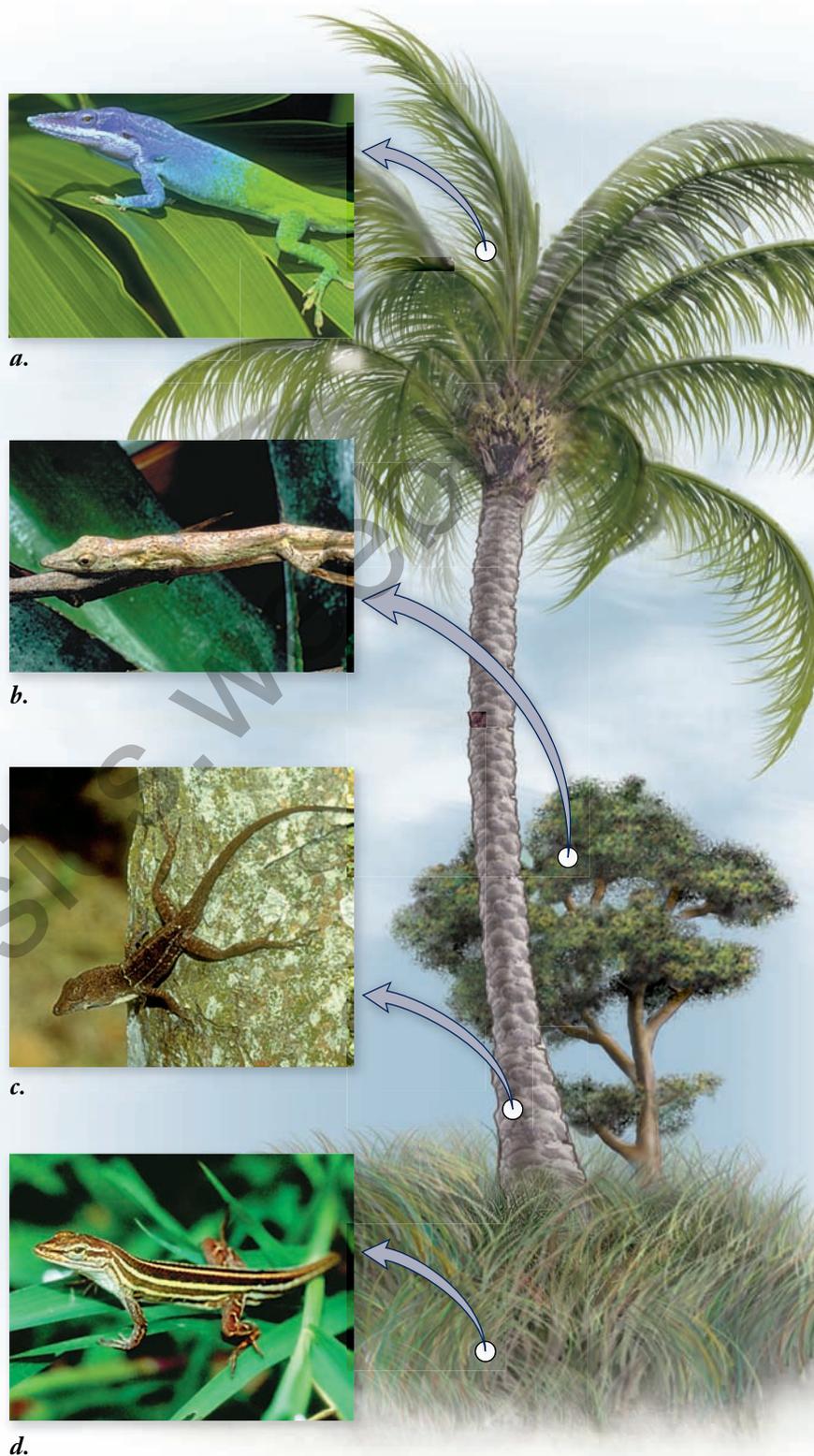


Figure 57.6 Resource partitioning among sympatric lizard species. Species of *Anolis* lizards on Caribbean islands partition their habitats in a variety of ways. *a.* Some species occupy leaves and branches in the canopy of trees, *(b)* others use twigs on the periphery, and *(c)* still others are found at the base of the trunk. In addition, *(d)* some use grassy areas in the open. When two species occupy the same part of the tree, they either utilize different-sized insects as food or partition the thermal microhabitat; for example, one might only be found in the shade, whereas the other would only bask in the sun.

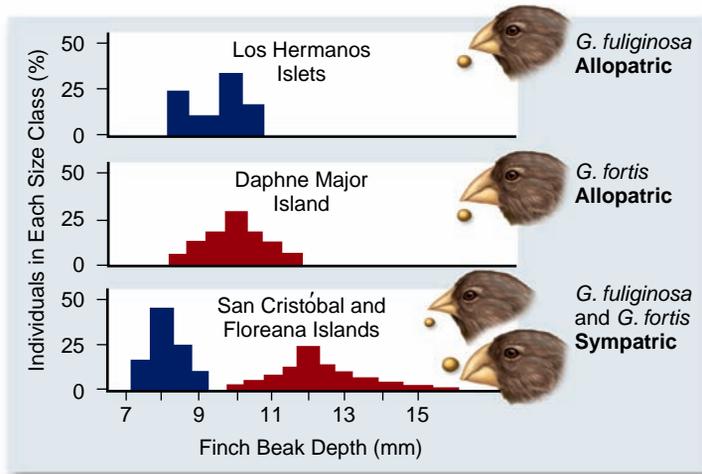


Figure 57.7 Character displacement in Darwin's finches. These two species of finches (genus *Geospiza*) have beaks of similar size when allopatric, but different size when sympatric.

natural selection as a means of partitioning resources and thus reducing competition.

As an example, the two Darwin's finches in figure 57.7 have bills of similar size where the finches are allopatric (that is, each living on an island where the other does not occur). On islands where they are sympatric (that is, occur together), the two species have evolved beaks of different sizes, one adapted to larger seeds and the other to smaller ones. Character displacement such as this may play an important role in adaptive radiation, leading new species to adapt to different parts of the environment, as discussed in chapter 22.

Detecting interspecific competition can be difficult

It is not simple to determine when two species are competing. The fact that two species use the same resources need not imply competition if that resource is not in limited supply. Even if the population sizes of two species are negatively correlated, such that where one species has a large population, the other species has a small population and vice versa, the two species may not be competing for the same limiting resource. Instead, the two species might be independently responding to the same feature of the environment—perhaps one species thrives best in warm conditions and the other where it's cool.

Experimental studies of competition

Some of the best evidence for the existence of competition comes from experimental field studies. By setting up experiments in which two species occur either alone or together, scientists can determine whether the presence of one species has a negative effect on a population of the second species.

For example, a variety of seed-eating rodents occur in North American deserts. In 1988, researchers set up a series of 50-m × 50-m enclosures to investigate the effect of kangaroo rats on smaller, seed-eating rodents. Kangaroo rats were removed from half of the enclosures, but not from the others. The walls of all of the enclosures had holes that allowed rodents to come and go, but in the plots in which the kangaroo

rats had been removed, the holes were too small to allow the kangaroo rats to reenter.

Over the course of the next 3 years, the researchers monitored the number of the smaller rodents present in the plots. As figure 57.8 illustrates, the number of other rodents was substantially higher in the absence of kangaroo rats, indicating that kangaroo rats compete with the other rodents and limit their population sizes.

A great number of similar experiments have indicated that interspecific competition occurs between many species of plants and animals. The effects of competition can be seen in aspects of population biology other than population size, such

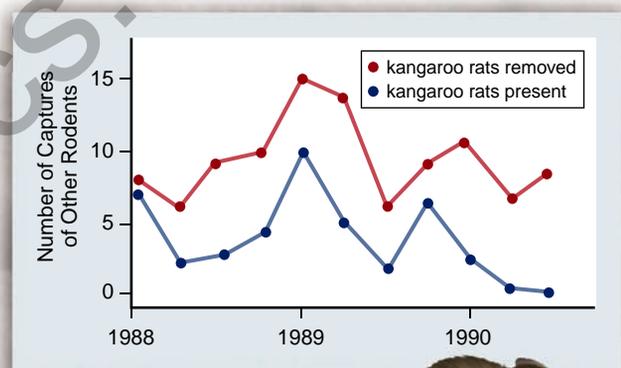
SCIENTIFIC THINKING

Question: Does interspecific interaction occur between rodent species?

Hypothesis: The larger kangaroo rat will have a negative effect on other species.

Experiment: Build large cages in desert areas. Remove kangaroo rats from some cages, leaving them present in others.

Result: In the absence of kangaroo rats, the number of other rodents increases quickly and remains higher than in the control cages throughout the course of the experiment.



Interpretation: Why do you think population sizes rise and fall in synchrony in the two cages?

Figure 57.8 Detecting interspecific competition.

This experiment tested how removal of kangaroo rats affected the population size of other rodents. Immediately after kangaroo rats were removed, the number of other rodents increased relative to the enclosures that still contained kangaroo rats. Notice that population sizes (as estimated by number of captures) changed in synchrony in the two treatments, probably reflecting changes in the weather.

Inquiry question

? Why are there more individuals of other rodent species when kangaroo rats are excluded?

57.3 Predator–Prey Relationships

Learning Outcomes

1. Define predation.
2. Describe the effects predation can have on a population.

as behavior and individual growth rates. For example, two species of *Anolis* lizards occur on the Caribbean island of St. Maarten. When one of the species, *A. gingivinus*, is placed in 12-m × 12-m enclosures without the other species, individual lizards grow faster and perch lower than do lizards of the same species when placed in enclosures in which *A. pogus*, a species normally found near the ground, is also present.

Limitations of experimental studies

Experimental studies are a powerful means of understanding interactions between coexisting species and are now commonly conducted by ecologists. Nonetheless, they have their limitations.

First, care is necessary in interpreting the results of field experiments. Negative effects of one species on another do not automatically indicate the existence of competition. For example, many similarly sized fish have a negative effect on one another, but it results not from competition, but from the fact that adults of each species prey on juveniles of the other species.

In addition, the presence of one species may attract predators or parasites, which then also prey on the second species. In this case, even if the two species are not competing, the second species may have a lower population size in the presence of the first species due to predators or parasites. Indeed, we can't rule out this possibility with the results of the kangaroo rat exclusion study just mentioned, although the close proximity of the enclosures (they were adjacent) would suggest that the same predators and parasites were present in all of them. Thus, experimental studies are most effective when combined with detailed examination of the ecological mechanisms causing the observed effect of one species on another.

Second, experimental studies are not always feasible. For example, the coyote population has increased in the United States in recent years concurrently with the decline of the grey wolf. Is this trend an indication that the species compete? Because of the size of the animals and the large geographic areas occupied by each individual, manipulative experiments involving fenced areas with only one or both species—with each experimental treatment replicated several times for statistical analysis—are not practical. Similarly, studies of slow-growing trees might require many centuries to detect competition between adult trees. In such cases, detailed studies of the ecological requirements of each species are our best bet for understanding interspecific interactions.

Learning Outcomes Review 57.2

A niche comprises the total number of ways in which an organism utilizes resources in its environment. A fundamental niche is the entire niche possible to a species; a realized niche is the niche a species actually utilizes. If resources are limiting, two species cannot occupy the same niche indefinitely without competition driving one to local extinction. Resource partitioning allows two sympatric species to occupy a niche, reducing competition between them and also lessening the size of the realized niche.

- Under what circumstances can two species with identical niches coexist indefinitely?

Predation is the consuming of one organism by another. In this sense, predation includes everything from a leopard capturing and eating an antelope, to a deer grazing on spring grass.

When experimental populations are set up under simple laboratory conditions, as illustrated in figure 57.9 with the predatory protist *Didinium* and its prey *Paramecium*, the predator often exterminates its prey and then becomes extinct itself, having nothing left to eat. If refuges are provided for the *Paramecium*, however, its population drops to low levels but not to extinction. Low prey population levels then provide inadequate food for the *Didinium*, causing the predator population to decrease. When this occurs, the prey population can recover.

Predation strongly influences prey populations

In nature, predators often have large effects on prey populations. As the previous example indicates, however, the interaction is a two-way street: prey can also affect the dynamics of predator populations. The outcomes of such interactions are complex and depend on a variety of factors.

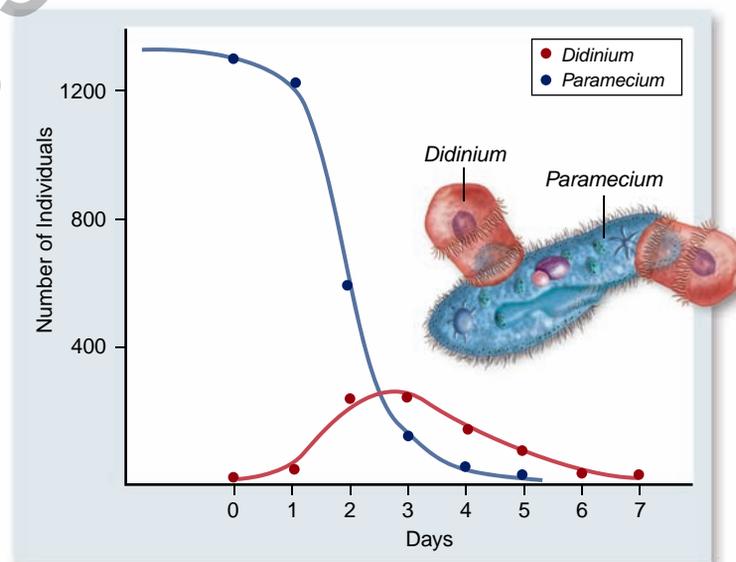


Figure 57.9 Predator–prey in the microscopic world.

When the predatory *Didinium* is added to a *Paramecium* population, the numbers of *Didinium* initially rise, and the numbers of *Paramecium* steadily fall. When the *Paramecium* population is depleted, however, the *Didinium* individuals also die.

Inquiry question



Can you think of any ways this experiment could be changed so that *Paramecium* might not go extinct?

Prey population explosions and crashes

Some of the most dramatic examples of the interconnection between predators and their prey involve situations in which humans have either added or eliminated predators from an area. For example, the elimination of large carnivores from much of the eastern United States has led to population explosions of white-tailed deer, which strip the habitat of all edible plant life within their reach. Similarly, when sea otters were hunted to near extinction on the western coast of the United States, populations of sea urchins, a principal prey item of the otters, exploded.

Conversely, the introduction of rats, dogs, and cats to many islands around the world has led to the decimation of native fauna. Populations of Galápagos tortoises on several islands are endangered by introduced rats, pigs, dogs, and cats, which eat the eggs and the young tortoises. Similarly, in New Zealand, several species of birds and reptiles have been eradicated by rat predation and now only occur on a few offshore islands that the rats have not reached. On Stephens Island, near New Zealand, every individual of the now-extinct Stephens Island wren was killed by a single lighthouse keeper's cat.

A classic example of the role predation can play in a community involves the introduction of prickly pear cactus to Australia in the 19th century. In the absence of predators, the cactus spread rapidly, so that by 1925 it occupied 12 million hectares of rangeland in an impenetrable morass of spines that made cattle ranching difficult. To control the cactus, a predator from its natural habitat in Argentina, the moth *Cactoblastis cactorum*, was introduced, beginning in 1926. By 1940, cactus populations had been greatly reduced and it now usually occurs in small populations.

Predation and coevolution

Predation provides strong selective pressures on prey populations. Any feature that would decrease the probability of capture should be strongly favored. In turn, the evolution of such features causes natural selection to favor counteradaptations in predator populations. The process by which these adaptations are selected in lockstep fashion in two or more interacting species is termed **coevolution**. A coevolutionary “arms race” may ensue in which predators and prey are constantly evolving better defenses and better means of circumventing these defenses. In the sections that follow, you'll learn more about these defenses and responses.

Plant adaptations defend against herbivores

Plants have evolved many mechanisms to defend themselves from herbivores. The most obvious are morphological defenses: Thorns, spines, and prickles play an important role in discouraging large plant eaters, and plant hairs, especially those that have a glandular, sticky tip, deter insect herbivores. Some plants, such as grasses, deposit silica in their leaves, both strengthening and protecting themselves. If enough silica is present, these plants are simply too tough to eat.

Chemical defenses

As significant as morphological adaptations are, the chemical defenses that occur so widely in plants are even more widespread. Plants exhibit some amazing chemical adaptations to combat herbivores. For example, recent work demonstrates

that when attacked by caterpillars, wild tobacco plants emit a chemical into the air that attracts a species of bug that feeds on that caterpillar (discussed in greater detail in chapter 40).

The best known and perhaps most important of the chemical defenses of plants against herbivores are *secondary chemical compounds*. These chemicals are distinguished from primary compounds, which are the components of a major metabolic pathway, such as respiration. Many plants, and apparently many algae as well, contain structurally diverse secondary compounds that are either toxic to most herbivores or disturb their metabolism greatly, preventing, for example, the normal development of larval insects. Consequently, most herbivores tend to avoid the plants that possess these compounds.

The mustard family (Brassicaceae) produces a group of chemicals known as mustard oils. These substances give the pungent aromas and tastes to plants such as mustard, cabbage, watercress, radish, and horseradish. The flavors we enjoy indicate the presence of chemicals that are toxic to many groups of insects. Similarly, plants of the milkweed family (Asclepiadaceae) and the related dogbane family (Apocynaceae) produce a milky sap that deters herbivores from eating them. In addition, these plants usually contain cardiac glycosides, molecules that can produce drastic deleterious effects on the heart function of vertebrates.

The coevolutionary response of herbivores

Certain groups of herbivores are associated with each family or group of plants protected by a particular kind of secondary compound. These herbivores are able to feed on these plants without harm, often as their exclusive food source.

For example, cabbage butterfly caterpillars (subfamily Pierinae) feed almost exclusively on plants of the mustard and caper families, as well as on a few other small families of plants that also contain mustard oils (figure 57.10). Similarly, caterpillars of

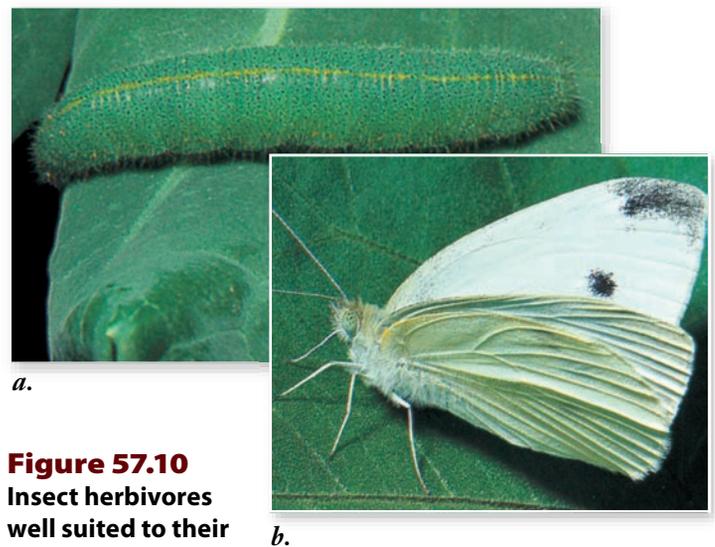


Figure 57.10
Insect herbivores well suited to their plant hosts. *a.* The

green caterpillars of the cabbage white butterfly (*Pieris rapae*) are camouflaged on the leaves of cabbage and other plants on which they feed. Although mustard oils protect these plants against most herbivores, the cabbage white butterfly caterpillars are able to break down the mustard oil compounds. *b.* An adult cabbage white butterfly.

monarch butterflies and their relatives (subfamily Danainae) feed on plants of the milkweed and dogbane families. How do these animals manage to avoid the chemical defenses of the plants, and what are the evolutionary precursors and ecological consequences of such patterns of specialization?

We can offer a potential explanation for the evolution of these particular patterns. Once the ability to manufacture mustard oils evolved in the ancestors of the caper and mustard families, the plants were protected for a time against most or all herbivores that were feeding on other plants in their area. At some point, certain groups of insects—for example, the cabbage butterflies—evolved the ability to break down mustard oils and thus feed on these plants without harming themselves. Having developed this new capability, the butterflies were able to use a new resource without competing with other herbivores for it. As we saw in chapter 22, exposure to an underutilized resource often leads to evolutionary diversification and adaptive radiation.

Animal adaptations defend against predators

Some animals that feed on plants rich in secondary compounds receive an extra benefit. For example, when the caterpillars of monarch butterflies feed on plants of the milkweed family, they do not break down the cardiac glycosides that protect these plants from herbivores. Instead, the caterpillars concentrate and store the cardiac glycosides in fat bodies; they then pass them through the chrysalis stage to the adult and even to the eggs of the next generation.

The incorporation of cardiac glycosides protects all stages of the monarch life cycle from predators. A bird that eats a monarch butterfly quickly regurgitates it (figure 57.11) and in the future avoids the conspicuous orange-and-black pattern that characterizes the adult monarch. Some bird species have



Figure 57.11 A blue jay learns not to eat monarch butterflies. *a.* This cage-reared jay had never seen a monarch butterfly before it tried eating one. *b.* The same jay regurgitated the butterfly a few minutes later. This bird will probably avoid trying to capture all orange-and-black insects in the future.



Figure 57.12 Vertebrate chemical defenses. Frogs of the family Dendrobatidae, abundant in the forests of Central and South America, are extremely poisonous to vertebrates; 80 different toxic alkaloids have been identified from different species in this genus. Dendrobatids advertise their toxicity with bright coloration. As a result of either instinct or learning, predators avoid such brightly colored species that might otherwise be suitable prey.

evolved the ability to tolerate the protective chemicals; these birds eat the monarchs.

Chemical defenses

Animals also manufacture and use a startling array of defensive substances. Bees, wasps, predatory bugs, scorpions, spiders, and many other arthropods use chemicals to defend themselves and to kill their own prey. In addition, various chemical defenses have evolved among many marine invertebrates, as well as a variety of vertebrates, including frogs, snakes, lizards, fishes, and some birds.

The poison-dart frogs of the family Dendrobatidae produce toxic alkaloids in the mucus that covers their brightly colored skin; these alkaloids are distasteful and sometimes deadly to animals that try to eat the frogs (figure 57.12). Some of these toxins are so powerful that a few micrograms will kill a person if injected into the bloodstream. More than 200 different alkaloids have been isolated from these frogs, and some are playing important roles in neuromuscular research. Similarly intensive investigations of marine animals, venomous reptiles, algae, and flowering plants are underway in search of new drugs to fight cancer and other diseases, or to use as sources of antibiotics.

Defensive coloration

Many insects that feed on milkweed plants are brightly colored; they advertise their poisonous nature using an ecological strategy known as warning coloration.

Showy coloration is characteristic of animals that use poisons and stings to repel predators; organisms that lack specific chemical defenses are seldom brightly colored. In fact, many have cryptic coloration—color that blends with the surroundings and thus hides the individual from predators (figure 57.13). Camouflaged animals usually do not live together in groups because a predator that discovers one individual gains a valuable clue to the presence of others.



Figure 57.13 **Cryptic coloration and form.** An inchworm caterpillar (*Nacophora quernaria*) closely resembles the twig on which it is hanging.

Mimicry allows one species to capitalize on defensive strategies of another

During the course of their evolution, many species have come to resemble distasteful ones that exhibit warning coloration. The mimic gains an advantage by looking like the distasteful model. Two types of mimicry have been identified: Batesian mimicry and Müllerian mimicry.

Batesian mimicry

Batesian mimicry is named for Henry Bates, the British naturalist who first brought this type of mimicry to general attention in 1857. In his journeys to the Amazon region of South America, Bates discovered many instances of palatable insects that resembled brightly colored, distasteful species. He reasoned that the mimics would be avoided by predators, who would be fooled by the disguise into thinking the mimic was the distasteful species.

Many of the best-known examples of Batesian mimicry occur among butterflies and moths. Predators of these insects must use visual cues to hunt for their prey; otherwise, similar color patterns would not matter to potential predators. Increasing evidence indicates that Batesian mimicry can involve non-visual cues, such as olfaction, although such examples are less obvious to humans.

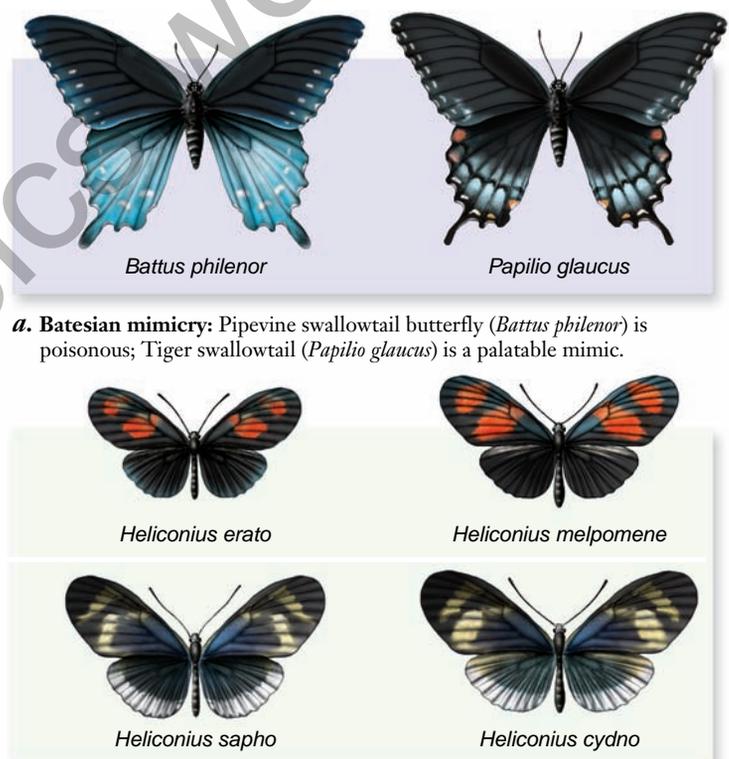
The kinds of butterflies that provide the models in Batesian mimicry are, not surprisingly, members of groups whose caterpillars feed on only one or a few closely related plant families. The plant families on which they feed are strongly protected by toxic chemicals. The model butterflies incorporate the poisonous molecules from these plants into their bodies. The mimic butterflies, in contrast, belong to groups in which the feeding habits of the caterpillars are not so restricted. As caterpillars, these butterflies feed on a number of different plant families that are unprotected by toxic chemicals.

One often-studied mimic among North American butterflies is the tiger swallowtail, whose range occurs throughout the eastern United States and into Canada (figure 57.14a). In areas in which the poisonous pipevine swallowtail occurs, female tiger swallowtails are polymorphic and one color form is extremely similar in appearance to the pipevine swallowtail.

The caterpillars of the tiger swallowtail feed on a variety of trees, including tulip, aspen, and cherry, and neither caterpillars nor adults are distasteful to birds. Interestingly, the Batesian mimicry seen in the adult tiger swallowtail butterfly does not extend to the caterpillars: Tiger swallowtail caterpillars are camouflaged on leaves, resembling bird droppings, but the pipevine swallowtail's distasteful caterpillars are very conspicuous.

Müllerian mimicry

Another kind of mimicry, **Müllerian mimicry**, was named for the German biologist Fritz Müller, who first described it in 1878. In Müllerian mimicry, several unrelated but protected animal species come to resemble one another (figure 57.14b). If animals that resemble one another are all poisonous or dangerous, they gain an advantage because a predator will learn more quickly to avoid them. In some cases, predator populations even evolve an innate avoidance of species; such evolution may occur more quickly when multiple dangerous prey look alike.



a. Batesian mimicry: Pipevine swallowtail butterfly (*Battus philenor*) is poisonous; Tiger swallowtail (*Papilio glaucus*) is a palatable mimic.

b. Müllerian mimicry: Two pairs of mimics; all are distasteful.

Figure 57.14 **Mimicry.** **a.** Batesian mimicry. Pipevine swallowtail butterflies (*Battus philenor*) are protected from birds and other predators by the poisonous compounds they derive from the food they eat as caterpillars and store in their bodies. Adult pipevine swallowtails advertise their poisonous nature with warning coloration. Tiger swallowtails (*Papilio glaucus*) are Batesian mimics of the poisonous pipevine swallowtail and are not chemically protected. **b.** Pairs of Müllerian mimics. *Heliconius erato* and *H. melpomene* are sympatric, and *H. sapho* and *H. cydno* are sympatric. All of these butterflies are distasteful. They have evolved similar coloration patterns in sympatry to minimize predation; predators need only learn one pattern to avoid.

In both Batesian and Müllerian mimicry, mimic and model must not only look alike but also act alike. For example, the members of several families of insects that closely resemble wasps behave surprisingly like the wasps they mimic, flying often and actively from place to place.

Learnings Outcomes Review 57.3

Predation is the consuming of one organism by another. High predation can drive prey populations to extinction; conversely, in the absence of predators, prey populations often explode and exhaust their resources. Defensive adaptations may evolve in prey species, such as becoming distasteful or poisonous, or having defensive structures, appearance, or capabilities.

- A nonpoisonous scarlet king snake has red, black, and yellow bands of color similar to that of the poisonous eastern coral snake. What type of mimicry is being exhibited?

57.4 The Many Types of Species Interactions

Learning Outcomes

1. Explain the different forms of symbiosis.
2. Describe how coevolution occurs between mutualistic partners.
3. Explain how the occurrence of one ecological process may affect the outcome of another occurring at the same time.

The plants, animals, protists, fungi, and prokaryotes that live together in communities have changed and adjusted to one another continually over millions of years. We have already discussed competition and predation, but other types of ecological interactions commonly occur. For example, many features of flowering plants have evolved in relation to the dispersal of the plant's gametes by animals (figure 57.15). These animals, in turn, have evolved a number of special traits that enable them to obtain food or other resources efficiently from the plants they visit, often from their flowers. While doing so, the animals pick up pollen, which they may deposit on the next plant they visit, or seeds, which may be left elsewhere in the environment, sometimes a great distance from the parent plant.

Symbiosis involves long-term interactions

In symbiosis, two or more kinds of organisms interact in often elaborate and more-or-less permanent relationships. All symbiotic relationships carry the potential for coevolution between the organisms involved, and in many instances the results of this coevolution are fascinatingly complex.

Examples of symbiosis include lichens, which are associations of certain fungi with green algae or cyanobacteria. Another important example are mycorrhizae, associations between fungi and the roots of most kinds of plants. The fungi expedite the plant's absorption of certain nutrients, and the plants in



Figure 57.15 Pollination by a bat. Many flowers have coevolved with other species to facilitate pollen transfer. Insects are widely known as pollinators, but they're not the only ones: birds, bats, and even small marsupials and lizards serve as pollinators for some species. Notice the cargo of pollen on the bat's snout.

turn provide the fungi with carbohydrates (both mycorrhizae and lichens are discussed in greater detail in chapter 31). Similarly, root nodules that occur in legumes and certain other kinds of plants contain bacteria that fix atmospheric nitrogen and make it available to their host plants.

In the tropics, leaf-cutter ants are often so abundant that they can remove a quarter or more of the total leaf surface of the plants in a given area in a single year (see figure 31.18). They do not eat these leaves directly; rather, they take them to underground nests, where they chew them up and inoculate them with the spores of particular fungi. These fungi are cultivated by the ants and brought from one specially prepared bed to another, where they grow and reproduce. In turn, the fungi constitute the primary food of the ants and their larvae. The relationship between leaf-cutter ants and these fungi is an excellent example of symbiosis. Recent phylogenetic studies using DNA and assuming a molecular clock (see chapter 23) suggest that these symbioses are ancient, perhaps originating more than 50 MYA.

The major kinds of symbiotic relationships include (1) commensalism, in which one species benefits and the other neither benefits nor is harmed; (2) mutualism, in which both participating species benefit; and (3) **parasitism**, in which one species benefits but the other is harmed. Parasitism can also be viewed as a form of predation, although the organism that is preyed on does not necessarily die.

Commensalism benefits one species and is neutral to the other

In commensalism, one species benefits and the other is neither hurt nor helped by the interaction. In nature, individuals of one species are often physically attached to members of another. For example, epiphytes are plants that grow on the branches of other plants. In general, the host plant is unharmed, and the epiphyte that grows on it benefits. An example is Spanish moss, which hangs on trees in the southern United States. This plant and other members of its genus, which is in the pineapple family, grow on trees to gain access to sunlight; they generally do not harm the trees (figure 57.16).

Similarly, various marine animals, such as barnacles, grow on other, often actively moving sea animals, such as whales, and thus are carried passively from place to place. These “passengers” presumably gain more protection from predation than they would if they were fixed in one place, and they also reach new sources of food. The increased water circulation that these animals receive as their host moves around may also be of great importance, particularly if the passengers are filter feeders. Unless the number of these passengers gets too large, the host species is usually unaffected.

When commensalism may not be commensalism

One of the best known examples of symbiosis involves the relationships between certain small tropical fishes (clownfish) and sea anemones, shown in the first figure of this chapter. The fish have evolved the ability to live among the stinging tentacles of sea anemones, even though these tentacles would quickly paralyze other fishes that touched them. The clownfish feed on food particles left from the meals of the host anemone, remaining uninjured under remarkable circumstances.

On land, an analogous relationship exists between birds called oxpeckers and grazing animals such as cattle or ante-

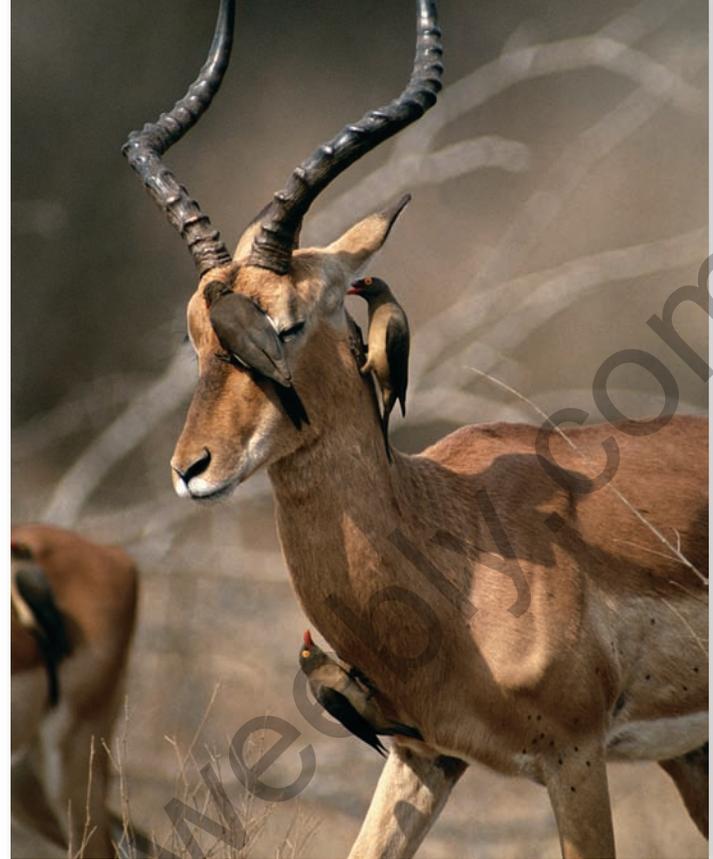


Figure 57.17 Commensalism, mutualism, or parasitism?

In this symbiotic relationship, oxpeckers definitely receive a benefit in the form of nutrition from the ticks and other parasites they pick off their host (in this case, an impala, *Aepyceros melampus*). But the effect on the host is not always clear. If the ticks are harmful, their removal benefits the host, and the relationship is mutually beneficial. If the oxpeckers also pick at scabs, causing blood loss and possible infection, the relationship may be parasitic. If the hosts are unharmed by either the ticks or the oxpeckers, the relationship may be an example of commensalism.

lopes (figure 57.17). The birds spend most of their time clinging to the animals, picking off parasites and other insects, carrying out their entire life cycles in close association with the host animals.

No clear-cut boundary exists between commensalism and mutualism; in each of these cases, it is difficult to be certain whether the second partner receives a benefit or not. A sea anemone may benefit by having particles of food removed from its tentacles because it may then be better able to catch other prey. Similarly, although often thought of as commensalism, the association of grazing mammals and gleaning birds is actually an example of mutualism. The mammal benefits by having parasites and other insects removed from its body, but the birds also benefit by gaining a dependable source of food.

On the other hand, commensalism can easily transform itself into parasitism. Oxpeckers are also known to pick not only parasites, but also scabs off their grazing hosts. Once the scab is picked, the birds drink the blood that flows from the wound. Occasionally, the cumulative effect of persistent attacks can greatly weaken the herbivore, particularly when conditions are not favorable, such as during droughts.



Figure 57.16 An example of commensalism. Spanish moss (*Tillandsia usneoides*) benefits from using trees as a substrate, but the trees generally are not affected positively or negatively.

Mutualism benefits both species

Mutualism is a symbiotic relationship between organisms in which both species benefit. Mutualistic relationships are of fundamental importance in determining the structure of biological communities.

Mutualism and coevolution

Some of the most spectacular examples of mutualism occur among flowering plants and their animal visitors, including insects, birds, and bats. During the course of flowering-plant evolution, the characteristics of flowers evolved in relation to the characteristics of the animals that visit them for food and, in the process, spread their pollen from individual to individual. At the same time, characteristics of the animals have changed, increasing their specialization for obtaining food or other substances from particular kinds of flowers.

Another example of mutualism involves ants and aphids. Aphids are small insects that suck fluids from the phloem of living plants with their piercing mouthparts. They extract a certain amount of the sucrose and other nutrients from this fluid, but they excrete much of it in an altered form through their anus. Certain ants have taken advantage of this—in effect, domesticating the aphids. Like ranchers taking cattle to fresh fields to graze, the ants carry the aphids to new plants and then consume as food the “honeydew” that the aphids excrete.

Ants and acacias: A prime example of mutualism

A particularly striking example of mutualism involves ants and certain Latin American tree species of the genus *Acacia*. In these species, certain leaf parts, called stipules, are modified as paired, hollow thorns. The thorns are inhabited by stinging ants of the genus *Pseudomyrmex*, which do not nest anywhere else (figure 57.18). Like all thorns that occur on plants, the acacia thorns serve to deter herbivores.

At the tip of the leaflets of these acacias are unique, protein-rich bodies called Beltian bodies, named after the 19th-century British naturalist Thomas Belt. Beltian bodies do not occur in species of *Acacia* that are not inhabited by ants, and their role is clear: they serve as a primary food for the ants. In addition, the plants secrete nectar from glands near the bases of their leaves. The ants consume this nectar as well, feeding it and the Beltian bodies to their larvae.

Obviously, this association is beneficial to the ants, and one can readily see why they inhabit acacias of this group. The ants and their larvae are protected within the swollen thorns, and the trees provide a balanced diet, including the sugar-rich nectar and the protein-rich Beltian bodies. What, if anything, do the ants do for the plants?

Whenever any herbivore lands on the branches or leaves of an acacia inhabited by ants, the ants, which continually patrol the acacia's branches, immediately attack and devour the herbivore. The ants that live in the acacias also help their hosts compete with other plants by cutting away any encroaching branches that touch the acacia in which they are living. They create, in effect, a tunnel of light through which the acacia can grow, even in the lush tropical rain forests of lowland Central America. In fact, when an ant colony is experimentally removed



Figure 57.18 Mutualism: Ants and acacias. Ants of the genus *Pseudomyrmex* live within the hollow thorns of certain species of acacia trees in Latin America. The nectaries at the bases of the leaves and the Beltian bodies at the ends of the leaflets provide food for the ants. The ants, in turn, supply the acacias with organic nutrients and protect the acacias from herbivores and shading from other plants.

from a tree, the acacia is unable to compete successfully in this habitat. Finally, the ants bring organic material into their nests. The parts they do not consume, together with their excretions, provide the acacias with an abundant source of nitrogen.

When mutualism may not be mutualism

As with commensalism, however, things are not always as they seem. Ant-acacia associations also occur in Africa; in Kenya, several species of acacia ants occur, but only a single species is found on any one tree. One species, *Crematogaster nigriceps*, is competitively inferior to two of the other species. To prevent invasion by these other ant species, *C. nigriceps* prunes the branches of the acacia, preventing it from coming into contact with branches of other trees, which would serve as a bridge for invaders.

Although this behavior is beneficial to the ant, it is detrimental to the tree because it destroys the tissue from which flowers are produced, essentially sterilizing the tree. In this case, what initially evolved as a mutualistic interaction has instead become a parasitic one.

Parasitism benefits one species at the expense of another

Parasitism is harmful to the prey organism and beneficial to the parasite. In many cases, the parasite kills its host, and thus the ecological effects of parasitism can be similar to those of predation. In the past parasitism was studied mostly in terms of its effects on individuals and the populations in which they live, but in recent years researchers have realized that parasitism can be an important factor affecting community structure.

External parasites

Parasites that feed on the exterior surface of an organism are external parasites, or ectoparasites (figure 57.19). Many instances of external parasitism are known in both plants and animals. **Parasitoids** are insects that lay eggs in or on living hosts. This behavior is common among wasps, whose larvae feed on the body of the unfortunate host, often killing it.

Internal parasites

Parasites that live within the body of their hosts, termed **endoparasites**, occur in many different phyla of animals and protists. Internal parasitism is generally marked by much more extreme specialization than external parasitism, as shown by the many protist and invertebrate parasites that infect humans.

The more closely the life of the parasite is linked with that of its host, the more its morphology and behavior are likely to have been modified during the course of its evolution (the same is true of symbiotic relationships of all sorts). Conditions within the body of an organism are different from those encountered outside and are apt to be much more constant. Consequently, the structure of an internal parasite is often simplified, and unnecessary armaments and structures are lost as it evolves (for example, see descriptions of tapeworms in chapter 33).

Parasites and host behaviors

Many parasites have complex life cycles that require several different hosts for growth to adulthood and reproduction. Recent research has revealed the remarkable adaptations of certain parasites that alter the behavior of the host and thus facilitate transmission from one host to the next. For example, many parasites cause their hosts to behave in ways that make them more vulnerable to their predators; when the host is ingested, the parasite is able to infect the predator.



Figure 57.19 An external parasite. The yellow vines are the flowering plant dodder (*Cuscuta*), a parasite that has lost its chlorophyll and its leaves in the course of its evolution. Because it is heterotrophic (unable to manufacture its own food), dodder obtains its food from the host plants it grows on.

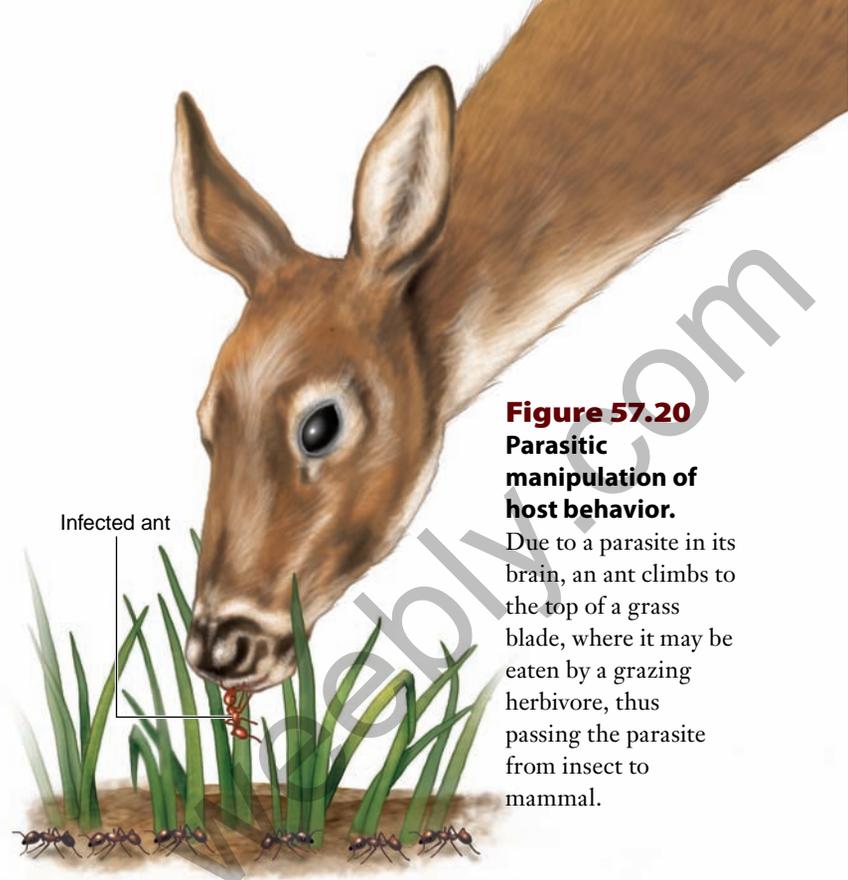


Figure 57.20 Parasitic manipulation of host behavior.

Due to a parasite in its brain, an ant climbs to the top of a grass blade, where it may be eaten by a grazing herbivore, thus passing the parasite from insect to mammal.

One of the most famous examples involves a parasitic flatworm, *Dicrocoelium dendriticum*, which lives in ants as an intermediate host, but reaches adulthood in large herbivorous mammals such as cattle and deer. Transmission from an ant to a cow might seem difficult because cows do not normally eat insects. The flatworm, however, has evolved a remarkable adaptation. When an ant is infected, one of the flatworms migrates to the brain and causes the ant to climb to the top of vegetation and lock its mandibles onto a grass blade at the end of the day, just when herbivores are grazing (figure 57.20). The result is that the ant is eaten along with the grass, leading to infection of the grazer.

Ecological processes have interactive effects

We have seen the different ways in which species can interact with one another. In nature, however, more than one type of interaction often occurs at the same time. In many cases, the outcome of one type of interaction is modified or even reversed when another type of interaction is also occurring.

Predation reduces competition

When resources are limiting, a superior competitor can eliminate other species from a community through competitive exclusion. However, predators can prevent or greatly reduce exclusion by lowering the numbers of individuals of competing species.

A given predator may often feed on two, three, or more kinds of plants or animals in a given community. The predator's choice depends partly on the relative abundance of the prey options. In other words, a predator may feed on species A when it is abundant and then switch to species B when A is rare. Similarly, a given prey species may become a primary source of food for increasing numbers of species as it becomes more abundant. In this way, superior competitors may be prevented from competitively excluding other species.

Such patterns are often characteristic of communities in marine intertidal habitats. For example, in preying selectively on bivalves, sea stars prevent bivalves from monopolizing a habitat, opening up space for many other organisms (figure 57.21). When sea stars are removed from a habitat, species diversity falls precipitously, and the seafloor community comes to be dominated by a few species of bivalves.

Predation tends to reduce competition in natural communities, so it is usually a mistake to attempt to eliminate a major predator, such as wolves or mountain lions, from a community. The result may be a decrease in biological diversity.

Parasitism may counter competition

Parasites may affect sympatric species differently and thus influence the outcome of interspecific interactions. One classic experiment investigated interactions between two sympatric flour beetles, *Tribolium castaneum* and *T. confusum*, with and without a parasite, *Adelina*. In the absence of the parasite, *T. castaneum* is dominant, and *T. confusum* normally becomes extinct. When the parasite is present, however, the outcome is reversed, and *T. castaneum* perishes.

Similar effects of parasites in natural systems have been observed in many species. For example, in the *Anolis* lizards of St. Maarten mentioned previously, the competitively inferior species is resistant to lizard malaria (a disease related to human

malaria), whereas the other species is highly susceptible. In places where the parasite occurs, the competitively inferior species can hold its own and the two species coexist; elsewhere, the competitively dominant species outcompetes and eliminates it.

Indirect effects

In some cases, species may not directly interact, yet the presence of one species may affect a second by way of interactions with a third. Such effects are termed indirect effects.

The desert rodents described earlier in the experiment with kangaroo rats eat seeds, and so do the ants in their community; thus, we might expect them to compete with each other. But when all rodents were removed from experimental enclosures and not allowed back in (unlike the previous experiment, no holes were placed in the enclosure walls), ant populations first increased but then declined (figure 57.22).

The initial increase was the expected result of removing a competitor. Why did it then reverse? The answer reveals the intricacies of natural ecosystems. Rodents prefer large seeds, whereas ants prefer smaller ones. Furthermore, in this system, plants with large seeds are competitively superior to plants with small seeds. The removal of rodents therefore led to an increase in the number of plants with large seeds, which reduced the number of small seeds available to ants, which in turn led to a decline in ant populations. In summary, the effect

SCIENTIFIC THINKING

Question: Does predation affect the outcome of interspecific competitive interactions?

Hypothesis: In the absence of predators, prey populations will increase until resources are limiting, and some species will be competitively excluded.

Experiment: Remove predatory sea stars (*Pisaster ochraceus*) from some areas of rocky intertidal shoreline and monitor populations of species the sea stars prey upon. In control areas, pick up sea stars, but replace them where they were found.



a.

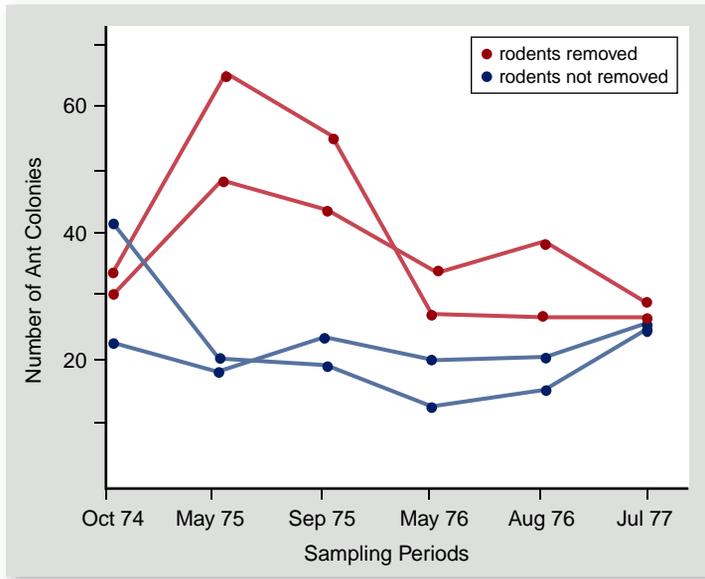


b.

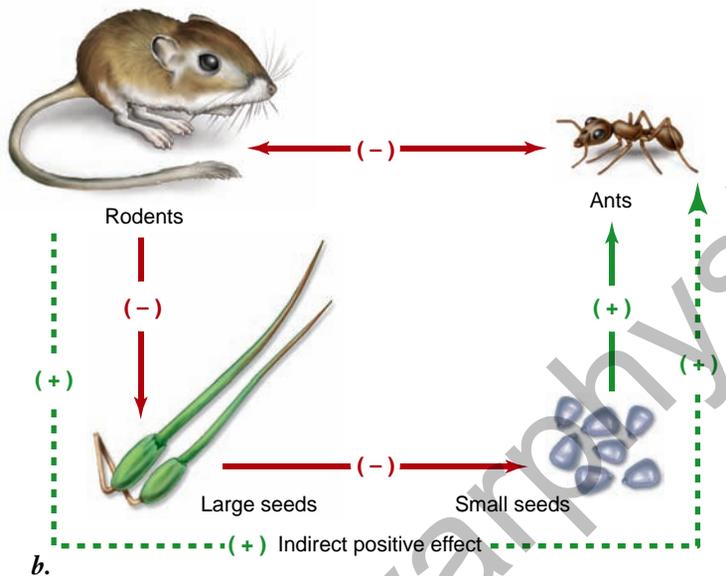
Result: In the absence of sea stars, the population of the mussel *Mytilus californianus* exploded, occupying all available space and eliminating many other species from the community.

Interpretation: What would happen if sea stars were returned to the experimental plots?

Figure 57.21 Predation reduces competition. a. In a controlled experiment in a coastal ecosystem, Robert Paine of the University of Washington removed a key predator, sea stars (*Pisaster*). b. In response, fiercely competitive mussels, a type of bivalve mollusk, exploded in population growth, effectively crowding out seven other indigenous species.



a.



b.

Figure 57.22 Direct and indirect effects in an ecological community. *a.* In the enclosures in which kangaroo rats had been removed, ants initially increased in population size relative to the ants in the control enclosures, but then these ant populations declined. *b.* Rodents and ants both eat seeds, so the presence of rodents has a direct negative effect on ants, and vice versa. However, the presence of rodents has a negative effect on large seeds. In turn, the presence of plants with large seeds has a negative effect on plants that produce small seeds, which the ants eat. Hence, the presence of rodents should increase the number of small seeds. In turn, the number of small seeds has a positive effect on ant populations. Thus, indirectly, the presence of rodents has a positive effect on ant population size.

Inquiry question

? How would you test the hypothesis that plant competition mediates the positive effect of kangaroo rats on ants?

of rodents on ants is complicated: a direct, negative effect of resource competition and an indirect, positive effect mediated by plant competition.

Keystone species have major effects on communities

Species whose effects on the composition of communities are greater than one might expect based on their abundance are termed **keystone species**. Predators, such as the sea star described earlier, can often serve as keystone species by preventing one species from outcompeting others, thus maintaining high levels of species richness in a community.

A wide variety of other types of keystone species also exist. Some species manipulate the environment in ways that create new habitats for others. Beavers, for example, change running streams into small impoundments, altering the flow of water and flooding areas (figure 57.23). Similarly, alligators excavate deep holes at the bottoms of lakes. In times of drought, these holes are the only areas where water remains, thus allowing aquatic species that otherwise would perish to persist until the drought ends and the lake refills.

Learning Outcomes Review 57.4

The types of symbiosis include mutualism, in which both participants benefit; commensalism, in which one benefits and the other is neutrally affected; and parasitism, in which one benefits at the expense of the other. Mutualistic species often undergo coevolution, such as the shape of flowers and the features of animals that feed on and pollinate them. Ecological interactions can affect many processes in a community; for example, predation and parasitism may lessen resource competition.

- How could the presence of a predator positively affect populations of a species on which it preys?

Figure 57.23 Example of a keystone species. Beavers, by constructing dams and transforming flowing streams into ponds, create new habitats for many plant and animal species.



57.5 Ecological Succession, Disturbance, and Species Richness

Learning Outcomes

1. Define succession and distinguish primary versus secondary.
2. Describe how early colonizers may affect subsequent occurrence of other species.
3. Explain how disturbance can either positively or negatively affect species richness.

Even when the climate of an area remains stable year after year, communities have a tendency to change from simple to complex in a process known as **succession**. This process is familiar to anyone who has seen a vacant lot or cleared woods slowly become occupied by an increasing number of species.

Succession produces a change in species composition

If a wooded area is cleared or burned and left alone, plants will slowly reclaim the area. Eventually, all traces of the clear-

ing will disappear, and the area will again be woods. This kind of succession, which occurs in areas where an existing community has been disturbed but organisms still remain, is called **secondary succession**.

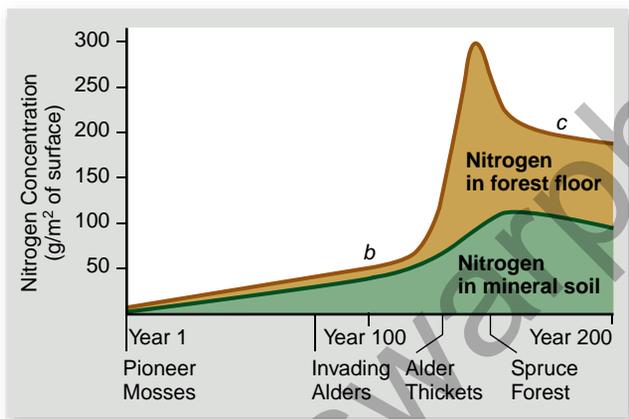
In contrast, **primary succession** occurs on bare, lifeless substrate, such as rocks, or in open water, where organisms gradually move into an area and change its nature. Primary succession occurs in lakes and on land exposed after the retreat of glaciers, and on volcanic islands that rise from the sea (figure 57.24).

Primary succession on glacial moraines provides an example (see figure 57.24). On the bare, mineral-poor ground exposed when glaciers recede, soil pH is basic as a result of carbonates in the rocks, and nitrogen levels are low. Lichens are the first vegetation able to grow under such conditions. Acidic secretions from the lichens help break down the substrate and reduce the pH, as well as adding to the accumulation of soil. Mosses then colonize these pockets of soil, eventually building up enough nutrients in the soil for alder shrubs to take hold. Over a hundred years, the alders, which have symbiotic bacteria that fix atmospheric nitrogen (described in chapter 28), increase soil nitrogen levels, and their acidic leaves further lower soil pH. Eventually, spruce trees grow above the alders and shade them, crowding them out entirely and forming a dense spruce forest.

In a similar example, an *oligotrophic* lake—one poor in nutrients—may gradually, by the accumulation of organic matter, become *eutrophic*—rich in nutrients. As this occurs, the composition of communities will change, first increasing in species richness and then declining.

Why succession happens

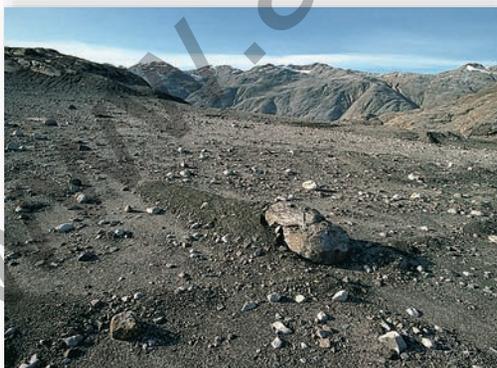
Succession happens because species alter the habitat and the resources available in it in ways that favor other species. Three dynamic concepts are of critical importance in the process: establishment, facilitation, and inhibition.



a.

Figure 57.24 Primary succession at Alaska's Glacier Bay.

a. Initially, the glacial moraine at Glacier Bay, Alaska, had little soil nitrogen **b.** The first invaders of these exposed sites are pioneer moss species with nitrogen-fixing, mutualistic microbes. **c.** Within 20 years, young alder shrubs take hold. Rapidly fixing nitrogen, they soon form dense thickets. **d.** Eventually spruce overgrow the mature alders, forming a forest.



b.



c.



d.

- 1. Establishment.** Early successional stages are characterized by weedy, r -selected species that are tolerant of the harsh, abiotic conditions in barren areas (the preceding chapter discussed r -selected and K -selected species).
- 2. Facilitation.** The weedy early successional stages introduce local changes in the habitat that favor other, less weedy species. Thus, the mosses in the Glacier Bay succession convert nitrogen to a form that allows alders to invade (see figure 57.24). Similarly, the nitrogen build-up produced by the alders, though not necessary for spruce establishment, leads to more robust forests of spruce better able to resist attack by insects.
- 3. Inhibition.** Sometimes the changes in the habitat caused by one species, while favoring other species, also inhibit the growth of the original species that caused the changes. Alders, for example, do not grow as well in acidic soil as the spruce and hemlock that replace them.

Over the course of succession, the number of species typically increases as the environment becomes more hospitable. In some cases, however, as ecosystems mature, more K -selected species replace r -selected ones, and superior competitors force out other species, leading ultimately to a decline in species richness.

Succession in animal communities

The species of animals present in a community also change through time in a successional pattern. As the vegetation changes during succession, habitat disappears for some species and appears for others.

A particularly striking example occurred on the Krakatau islands, which were devastated by an enormous volcanic eruption in 1883. Initially composed of nothing but barren ash-fields, the three islands of the group experienced rapid successional change as vegetation became reestablished. A few blades of grass appeared the next year, and within 15 years the coastal vegetation was well established and the interior was covered with dense grasslands. By 1930, the islands were almost entirely forested (figure 57.25).

The fauna of Krakatau changed in synchrony with the vegetation. Nine months after the eruption, the only animal found was a single spider, but by 1908, 200 animal species were found in a 3-day exploration. For the most part, the first animals were grassland inhabitants, but as trees became established, some of these early colonists, such as the zebra dove and the long-tailed shrike (a type of predatory bird), disappeared and were replaced by forest-inhabiting species, such as fruit bats and fruit-eating birds.

Although patterns of succession of animal species have typically been caused by vegetational succession, changes in the composition of the animal community in turn have affected plant occurrences. In particular, many plant species that are animal-dispersed or pollinated could not colonize Krakatau until their dispersers or pollinators had become established. For example, fruit bats were slow to colonize Krakatau, and until they appeared, few bat-dispersed plant species were present.

Disturbances can play an important role in structuring communities

Traditionally, many ecologists considered biological communities to be in a state of equilibrium, a stable condition that resisted change and fairly quickly returned to its original state if disturbed by humans or natural events. Such stability was usually attributed to the process of interspecific competition.

In recent years, this viewpoint has been reevaluated. Increasingly, scientists are recognizing that communities are constantly changing as a result of climatic changes, species invasions, and disturbance events. As a result, many ecologists now invoke nonequilibrium models that emphasize change, rather than stability. A particular focus of ecological research concerns the role that disturbances play in determining the structure of communities.

Disturbances can be widespread or local. Severe disturbances, such as forest fires, drought, and floods, may affect large areas. Animals may also cause severe disruptions. Gypsy moths can devastate a forest by consuming all of the leaves on its trees. Unregulated deer populations may grow explosively, the deer

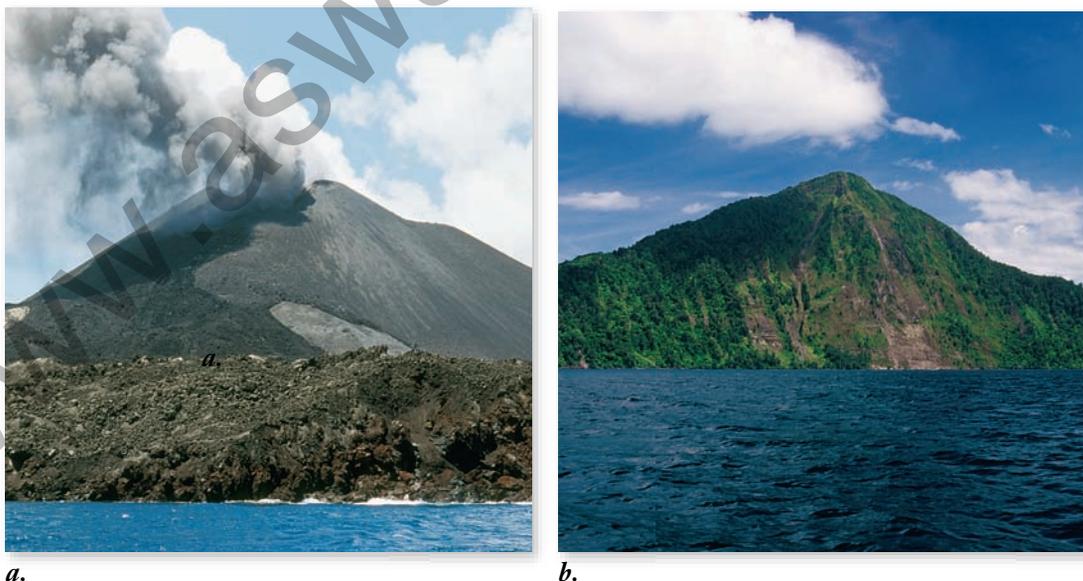


Figure 57.25 Succession after a volcanic eruption.

A major volcanic explosion in 1883 on the island of Krakatau destroyed all life on the island. **a.** This photo shows a later, much less destructive eruption of the volcano. **b.** Krakatau, forested and populated by animals.

overgrazing and so destroying the forest in which they live. On the other hand, local disturbances may affect only a small area, as when a tree falls in a forest or an animal digs a hole and uproots vegetation.

Intermediate disturbance hypothesis

In some cases, disturbance may act to increase the species richness of an area. According to the *intermediate disturbance hypothesis*, communities experiencing moderate amounts of disturbance will have higher levels of species richness than communities experiencing either little or great amounts of disturbance.

Two factors could account for this pattern. First, in communities where moderate amounts of disturbance occur, patches of habitat exist at different successional stages. Within the area as a whole, then, species diversity is greatest because the full range of species—those characteristic of all stages of succession—are present. For example, a pattern of intermittent episodic disturbance that produces gaps in the rain forest (as when a tree falls) allows invasion of the gap by other species (figure 57.26). Eventually, the species inhabiting the gap will go through a successional sequence, one tree replacing another, until a canopy tree species comes again to occupy the gap. But if there are many gaps of different ages in the forest, many different species will be coexisting, some in young gaps and others in older ones.

Second, moderate levels of disturbance may prevent communities from reaching the final stages of succession, in which a few dominant competitors eliminate most of the other species. In contrast, too much disturbance might leave the community continually in the earliest stages of succession, when species richness is relatively low.

Ecologists are increasingly realizing that disturbance is common, rather than exceptional, in many communities. As a result, the idea that communities inexorably move along a successional trajectory culminating in the development of a predictable end-state, or “climax,” community is no longer widely accepted. Rather, predicting the state of a community in the future may be difficult because the unpredictable occurrence of disturbances will often counter successional changes. Understanding the role that disturbances play in structuring communities is currently an important area of investigation in ecology.



Figure 57.26 Intermediate disturbance. A single fallen tree created a small light gap in the tropical rain forest of Panama. Such gaps play a key role in maintaining the high species diversity of the rain forest. In this case, a sunlight-loving plant is able to sprout up among the dense foliage of trees in the forest.

Learning Outcomes Review 57.5

Communities change through time by a process termed succession. Primary succession occurs on bare, lifeless substrate; secondary succession occurs where an existing community has been disturbed. Early-arriving species alter the environment in ways that allow other species to colonize, and new colonizers may have negative effects on species already present. Sometimes, moderate levels of disturbance can lead to increased species richness because species characteristic of all levels of succession may be present.

- *From a community point of view, would clear-cutting a forest be better than selective harvest of individual trees? Why or why not?*

Chapter Review

57.1 Biological Communities: Species Living Together

A community is a group of different species that occupy a given location.

Communities have been viewed in different ways.

The individualistic concept of a community is a random assemblage of species that happen to occur in a given place. The holistic concept

of a community is an integrated unit composed of species that work together as part of a functional whole.

Communities change over space and time.

In accordance with the individualistic view, species generally respond independently to environmental conditions, and community composition gradually changes over space and time. However, in locations where conditions rapidly change, species composition may change greatly over short distances.

57.2 The Ecological Niche Concept

Fundamental niches are potential; realized niches are actual.

A niche is the total of all the ways a species uses environmental resources. The fundamental niche is the entire niche a species is capable of using if there are no intervening factors. The realized niche is the set of actual environmental conditions that allow establishment of a stable population.

Realized niches are usually smaller than fundamental niches because interspecific interactions limit a species' use of some resources.

Competitive exclusion can occur when species compete for limited resources.

The principle of competitive exclusion states that if resources are limiting, two species cannot simultaneously occupy the same niche; rather, one species will be eliminated.

Competition may lead to resource partitioning.

By using different resources (partitioning), sympatric species can avoid competing with each other and can coexist with reduced realized niches.

Detecting interspecific competition can be difficult.

Although experimentation is a powerful means of testing the hypothesis that species compete, practical limitations exist. Detailed knowledge of the ecology of species is important to evaluate the results of experiments and possible interactions.

57.3 Predator–Prey Relationships

Predation strongly influences prey populations.

Predation is the consuming of one organism by another, and includes not only one animal eating another, but also an animal eating a plant.

Natural selection strongly favors adaptations of prey species to prevent predation. In turn, sometimes predators evolve counter-adaptations, leading to an evolutionary “arms race.”

Plant adaptations defend against herbivores.

Plants produce secondary chemical compounds that deter herbivores. Sometimes the herbivores evolve an ability to ingest the compounds and use them for their own defense.

Animal adaptations defend against predators.

Animal adaptations include chemical defenses and defensive coloration such as warning coloration or camouflage.

Mimicry allows one species to capitalize on defensive strategies of another.

In Batesian mimicry, a species that is edible or nontoxic evolves warning coloration similar to that of an inedible or poisonous species.

In Müllerian mimicry, two species that are both toxic evolve similar warning coloration.

57.4 The Many Types of Species Interactions

Symbiosis involves long-term interactions.

Many symbiotic species have coevolved and have permanent relationships.

Commensalism benefits one species and is neutral to the other.

Examples of commensal relationships include epiphytes growing on large plants and barnacles growing on sea animals.

Mutualism benefits both species.

One example is the case of ants and acacias, in which *Acacia* plants provide a home and food for a species of stinging ants that protect them from herbivores.

Parasitism benefits one species at the expense of another.

Many organisms have parasitic lifestyles, living on or inside one or more host species and causing damage or disease as a result.

Ecological processes have interactive effects.

Because many processes may occur simultaneously, species may affect one another not only through direct interactions but also through their effects on other species in the community.

Keystone species have major effects on communities.

Keystone species are those that maintain a more diverse community by reducing competition between species or by altering the environment to create new habitats.

57.5 Ecological Succession, Disturbance, and Species Richness

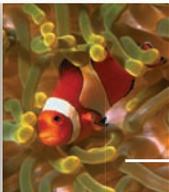
Succession produces a change in species composition.

Primary succession begins with a barren, lifeless substrate, whereas secondary succession occurs after an existing community is disrupted by fire, clearing, or other events.

Disturbances can play an important role in structuring communities.

Community composition changes as a result of local and global disturbances that “reset” succession.

Intermediate levels of such disturbance may maximize species richness in two ways: by creating a patchwork of different habitats harboring different species, and by preventing communities from reaching the final stage of succession, which may be dominated by only a few, competitively superior species.



Review Questions

UNDERSTAND

- Studies that demonstrate that species living in an ecological community change independently of one another in space and time
 - support the individualistic concept of ecological communities.
 - support the holistic concept of ecological communities.
 - suggest species interactions are the sole determinant of which species coexist in a community.
 - None of the above
- If two species have very similar realized niches and are forced to coexist and share a limiting resource indefinitely,
 - both species would be expected to coexist.
 - both species would be expected to go extinct.
 - the species that uses the limiting resource most efficiently should drive the other species extinct.
 - both species would be expected to become more similar to one another.

3. According to the idea of coevolution between predator and prey, when a prey species evolves a novel defense against a predator
 - a. the predator is expected to always go extinct.
 - b. the prey population should increase irreversibly out of control of the predator.
 - c. the predator population should increase.
 - d. evolution of a predator response should be favored by natural selection.
4. In order for mimicry to be effective in protecting a species from predation, it must
 - a. occur in a palatable species that looks like a distasteful species.
 - b. have cryptic coloration.
 - c. occur such that mimics look and act like models.
 - d. occur in only poisonous or dangerous species.
5. Which of the following is an example of commensalism?
 - a. A tapeworm living in the gut of its host
 - b. A clownfish living among the tentacles of a sea anemone
 - c. An acacia tree and acacia ants
 - d. Bees feeding on nectar from a flower
6. A species whose effect on the composition of a community is greater than expected based on its abundance can be called a
 - a. predator.
 - b. primary succession species.
 - c. secondary succession species.
 - d. keystone species.
7. When a predator preferentially eats the superior competitor in a pair of competing species
 - a. the inferior competitor is more likely to go extinct.
 - b. the superior competitor is more likely to persist.
 - c. coexistence of the competing species is more likely.
 - d. None of the above
8. Species that are the first colonists in a habitat undergoing primary succession
 - a. are usually the fiercest competitors.
 - b. help maintain their habitat constant so their persistence is ensured.
 - c. may change their habitat in a way that favors the invasion of other species.
 - d. must first be successful secondary succession specialists.
- c. results in the fundamental and realized niches being the same.
- d. is more common in herbivores than carnivores.
4. Parasitism differs from predation because
 - a. the presence of parasitism doesn't lead to selection for defensive adaptations in parasitized species.
 - b. parasites and the species they parasitize never engage in an evolutionary "arms race."
 - c. parasites don't have strong effects on the populations of the species they parasitize.
 - d. None of the above
5. The presence of one species (A) in a community may benefit another species (B) if
 - a. a commensalistic relationship exists between the two.
 - b. The first species (A) preys on a predator of the second species (B).
 - c. The first species (A) preys on a species that competes with a species that is eaten by the second species (B).
 - d. All of the above

SYNTHESIZE

1. Competition is traditionally indicated by documenting the effect of one species on the population of another. Are there alternative ways to study the potential effects of competition on organisms that are impractical to study with experimental manipulations because they are too big or live too long?
2. Refer to figure 57.9. If the single prey species of *Paramecium* was replaced by several different potential prey species that varied in their palatability or ease of subduing by the predator (leading to different levels of preference by the predator) what would you expect the dynamics of the system to look like; that is, would the system be more or less likely to go to extinction?
3. Refer to figure 57.22. Are there alternative hypotheses that might explain the increase followed by the decrease in ant colony numbers subsequent to rodent removal in the experiment described in figure 57.22? If so, how would you test the mechanism hypothesized in the figure?
4. Refer to figure 57.7. Examine the pattern of beak size distributions of two species of finches on the Galápagos Islands. One hypothesis that can be drawn from this pattern is that character displacement has taken place. Are there other hypotheses? If so, how would you test them?
5. Is it possible that some species function together as an integrated, holistic community, whereas other species at the same locality behave more individually? If so, what factors might determine which species function in which way?

APPLY

1. Which of the following can cause the realized niche of a species to be smaller than its fundamental niche?
 - a. Predation
 - b. Competition
 - c. Parasitism
 - d. All of the above
2. The presence of a predatory species
 - a. always drives a prey species to extinction.
 - b. can positively affect a prey species by having a detrimental effect on competing species.
 - c. indicates that the climax stage of succession has been reached.
 - d. None of the above
3. Resource partitioning by sympatric species
 - a. always occurs when species have identical niches.
 - b. may not occur in the presence of a predator, which reduces prey population sizes.

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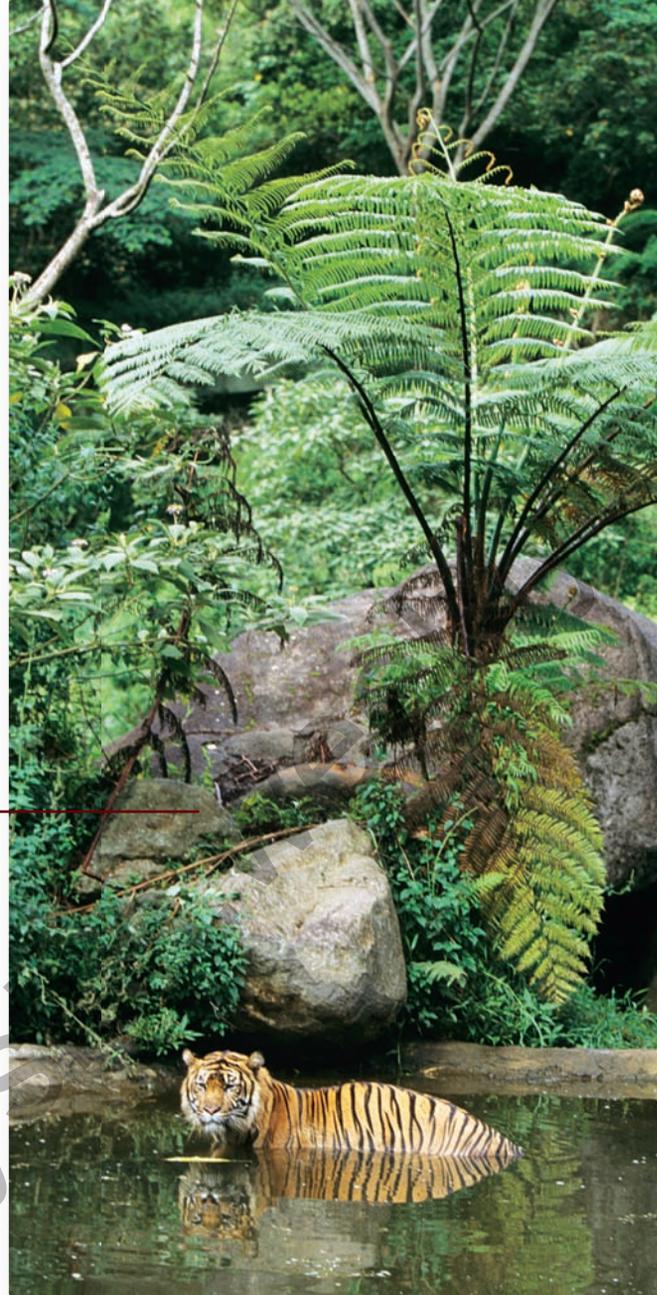
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Chapter 58

Dynamics of Ecosystems

Chapter Outline

- 58.1 Biogeochemical Cycles
- 58.2 The Flow of Energy in Ecosystems
- 58.3 Trophic-Level Interactions
- 58.4 Biodiversity and Ecosystem Stability
- 58.5 Island Biogeography



Introduction

The Earth is a relatively closed system with respect to chemicals. It is an open system in terms of energy, however, because it receives energy at visible and near-visible wavelengths from the Sun and steadily emits thermal energy to outer space in the form of infrared radiation. The organisms in ecosystems interact in complex ways as they participate in the cycling of chemicals and as they capture and expend energy. All organisms, including humans, depend on the specialized abilities of other organisms—plants, algae, animals, fungi, and prokaryotes—to acquire the essentials of life, as explained in this chapter. In chapters 58 and 59, we consider the many different types of ecosystems that constitute the biosphere and discuss the threats to the biosphere and the species it contains.

58.1 Biogeochemical Cycles

Learning Outcomes

1. Define ecosystem.
2. List four chemicals whose cyclic interactions are critical to organisms.
3. Describe how human activities disrupt these cycles.

An ecosystem includes all the organisms that live in a particular place, plus the abiotic (nonliving) environment in which they live—and with which they interact—at that location. Ecosystems are intrinsically dynamic in a number of ways, including their processing of matter and energy. We start with matter.

The atomic constituents of matter cycle within ecosystems

During the biological processing of matter, the atoms of which it is composed, such as the atoms of carbon or oxygen, maintain their integrity even as they are assembled into new compounds and the compounds are later broken down. The Earth has an essentially fixed number of each of the types of atoms of biological importance, and the atoms are recycled.

Each organism assembles its body from atoms that previously were in the soil, the atmosphere, other parts of the abiotic environment, or other organisms. When the organism dies, its atoms are released unaltered to be used by other organisms or returned to the abiotic environment. Because of the cycling of the atomic constituents of matter, your body is likely during

your life to contain a carbon or oxygen atom that once was part of Julius Caesar's body or Cleopatra's.

The atoms of the various chemical elements are said to move through ecosystems in biogeochemical cycles, a term emphasizing that the cycles of chemical elements involve not only biological organisms and processes, but also geological (abiotic) systems and processes. Biogeochemical cycles include processes that occur on many spatial scales, from cellular to planetary, and they also include processes that occur on multiple time-scales, from seconds (biochemical reactions) to millennia (weathering of rocks).

Biogeochemical cycles usually cross the boundaries of ecosystems to some extent, rather than being self-contained within individual ecosystems. For example, one ecosystem might import or export carbon to others.

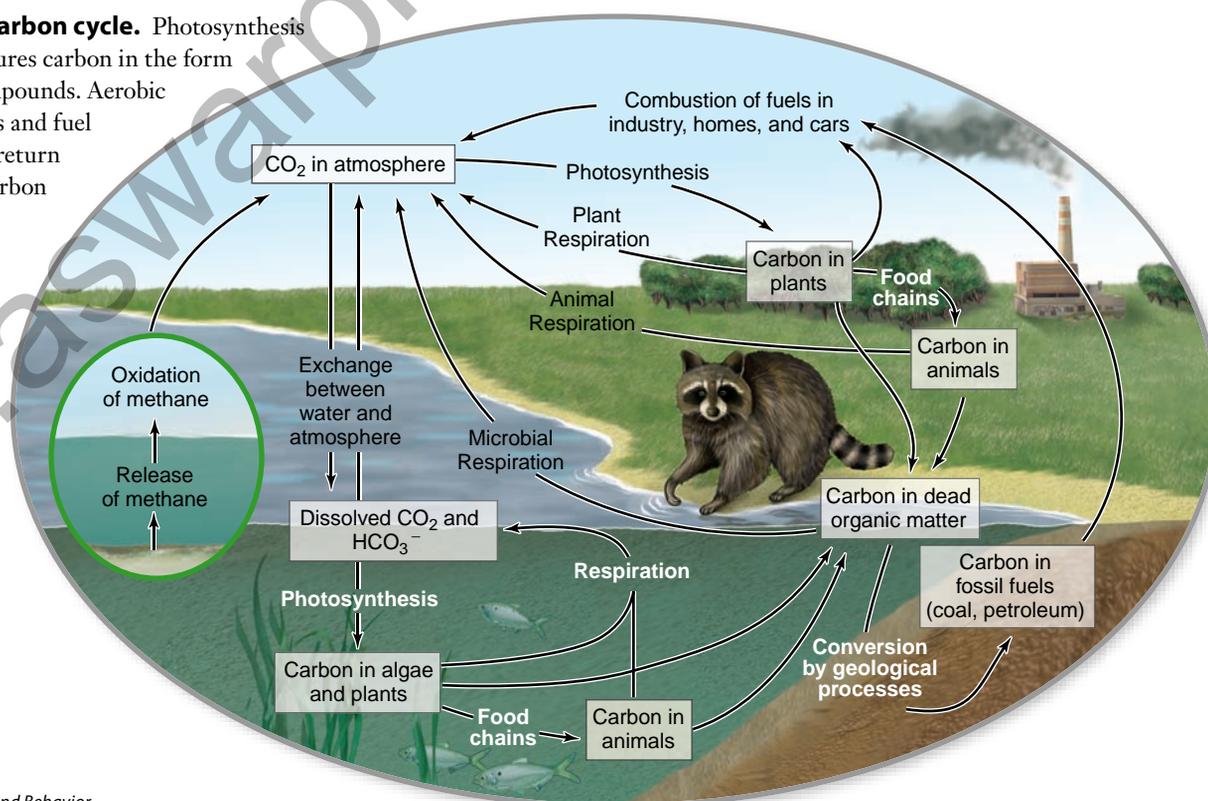
In this section, we consider the cycles of some major elements along with the compound water. We also present an example of biogeochemical cycles in a forest ecosystem.

Carbon, the basis of organic compounds, cycles through most ecosystems

Carbon is a major constituent of the bodies of organisms because carbon atoms help form the framework of all organic compounds (see chapter 3); almost 20% of the weight of the human body is carbon. From the viewpoint of the day-to-day dynamics of ecosystems, carbon dioxide (CO_2) is the most significant carbon-containing compound in the abiotic environments of organisms. It makes up 0.03% of the volume of the atmosphere, meaning the atmosphere contains about 750 billion metric tons of carbon. In aquatic ecosystems, CO_2 reacts spontaneously with the water to form bicarbonate ions (HCO_3^-).

Figure 58.1 The carbon cycle. Photosynthesis

by plants and algae captures carbon in the form of organic chemical compounds. Aerobic respiration by organisms and fuel combustion by humans return carbon to the form of carbon dioxide (CO_2) or bicarbonate (HCO_3^-). Microbial methanogens living in oxygen-free microhabitats, such as the mud at the bottom of the pond, might produce methane (CH_4), a gas that would enter the atmosphere and then gradually be oxidized abiotically to carbon dioxide (shown in green circled inset).



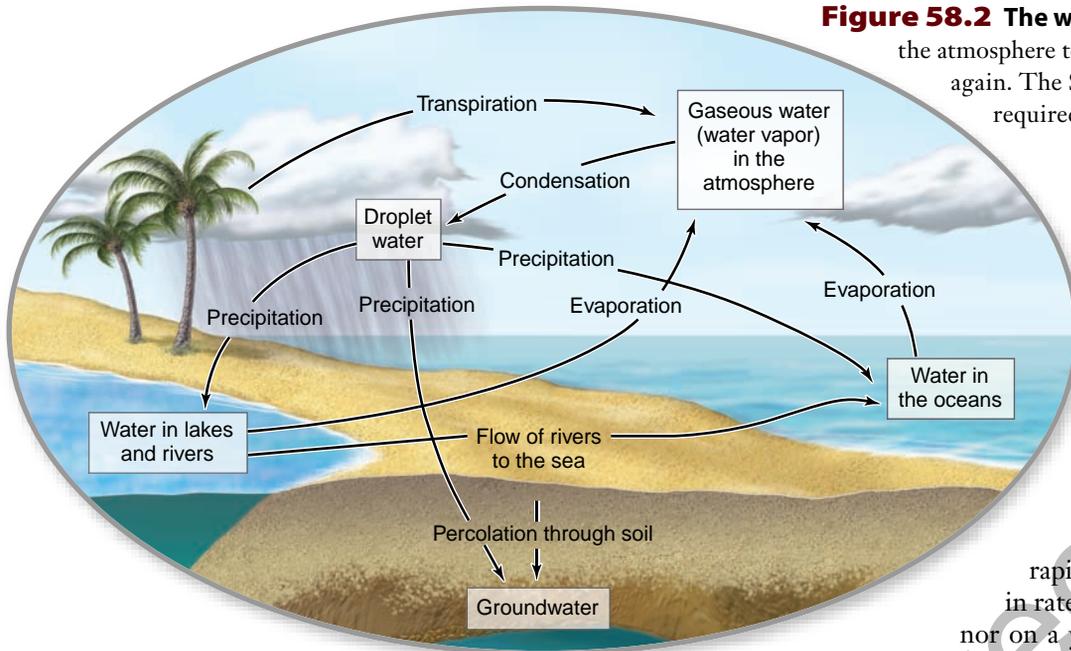


Figure 58.2 The water cycle. Water circulates from the atmosphere to the surface of the Earth and back again. The Sun provides much of the energy required for evaporation.

The basic carbon cycle

The carbon cycle is straightforward, as shown in figure 58.1. In terrestrial ecosystems, plants and other photosynthetic organisms take in CO_2 from the atmosphere and use it in photosynthesis to synthesize the carbon-containing organic compounds of which they are composed (see chapter 8). The process is sometimes called *carbon fixation*; fixation refers to metabolic reactions that make nongaseous compounds from gaseous ones.

Animals eat the photosynthetic organisms and build their own tissues by making use of the carbon atoms in the organic compounds they ingest. Both the photosynthetic organisms and the animals obtain energy during their lives by breaking down some of the organic compounds available to them, through aerobic cellular respiration (see chapter 7). When they do this, they produce CO_2 . Decaying organisms also produce CO_2 . Carbon atoms returned to the form of CO_2 are available once more to be used in photosynthesis to synthesize new organic compounds.

In aquatic ecosystems, the carbon cycle is fundamentally similar, except that inorganic carbon is present in the water not only as dissolved CO_2 , but also as HCO_3^- ions, both of which act as sources of carbon for photosynthesis by algae and aquatic plants.

Methane producers

Microbes that break down organic compounds by anaerobic cellular respiration (see chapter 7) provide an additional dimension to the global carbon cycle. Methanogens, for example, are microbes that produce methane (CH_4) instead of CO_2 . One major source of CH_4 is wetland ecosystems, where methanogens live in the oxygen-free sediments. Methane that enters the atmosphere is oxidized abiotically to CO_2 , but CH_4 that remains isolated from oxygen can persist for great lengths of time.

The rise of atmospheric carbon dioxide

Another dimension of the global carbon cycle is that over long stretches of time, some parts of the cycle may proceed more

rapidly than others. These differences in rate have ordinarily been relatively minor on a year-to-year basis; in any one year, the amount of CO_2 made by breakdown of organic compounds almost matches the amount of CO_2 used to synthesize new organic compounds.

Small mismatches, however, can have large consequences if continued for many years. The Earth's present reserves of coal were built up over geologic time. Organic compounds such as cellulose accumulated by being synthesized faster than they were broken down, and then they were transformed by geological processes into the fossil fuels. Most scientists believe that the world's petroleum reserves were created in the same way.

Human burning of fossil fuels today is creating large contemporary imbalances in the carbon cycle. Carbon that took millions of years to accumulate in the reserves of fossil fuels is being rapidly returned to the atmosphere, driving the concentration of CO_2 in the atmosphere upward year by year and helping to spur fears of global warming (see chapter 59).

The availability of water is fundamental to terrestrial ecosystems

The water cycle, seen in figure 58.2, is probably the most familiar of all biogeochemical cycles. All life depends on the presence of water; even organisms that can survive without water in resting states require water to regain activity. The bodies of most organisms consist mainly of water. The adult human body, for example, is about 60% water by weight. The amount of water available in an ecosystem often determines the nature and abundance of the organisms present, as illustrated by the difference between forests and deserts (see chapter 59).

Each type of biogeochemical cycle has distinctive features. A distinctive feature of the water cycle is that water is a compound, not an element, and thus it can be synthesized and broken down. It is synthesized during aerobic cellular respiration (see chapter 7) and chemically split during photosynthesis (see chapter 8). The rates of these processes are ordinarily about equal, and therefore a relatively constant amount of water cycles through the biosphere.

The basic water cycle

One key part of the water cycle is that liquid water from the Earth's surface evaporates into the atmosphere. The change of water from a liquid to a gas requires a considerable addition of thermal energy, explaining why evaporation occurs more rapidly when solar radiation beats down on a surface.

Evaporation occurs directly from the surfaces of oceans, lakes, and rivers. In terrestrial ecosystems, however, approximately 90% of the water that reaches the atmosphere passes through plants. Trees, grasses, and other plants take up water from soil via their roots, and then the water evaporates from their leaves and other surfaces through a process called transpiration (see chapter 38).

Evaporated water exists in the atmosphere as a gas, just like any other atmospheric gas. The water can condense back into liquid form, however, mostly because of cooling of the air. Condensation of gaseous water (water vapor) into droplets or crystals causes the formation of clouds, and if the droplets or crystals are large enough, they fall to the surface of the Earth as precipitation (rain or snow).

Groundwater

Less obvious than surface water, which we see in rivers and lakes, is water under ground—termed groundwater. Groundwater occurs in **aquifers**, which are permeable, underground layers of rock, sand, and gravel that are often saturated with water. Groundwater is the most important reservoir of water on land in many parts of the world, representing over 95% of all fresh water in the United States, for example.

Groundwater consists of two subparts. The upper layers of the groundwater constitute the water table, which is unconfined in the sense that it flows into streams and is partly accessible to the roots of plants. The lower, confined layers of the groundwater are generally out of reach to streams and plants, but can be tapped by wells. Groundwater is recharged by water that percolates downward from above, such as from precipitation. Water in an aquifer flows much more slowly than surface water, anywhere from a few millimeters to a meter or so per day.

In the United States, groundwater provides about 25% of the water used by humans for all purposes, and it supplies about 50% of the population with drinking water. In the Great Plains states, the deep Ogallala Aquifer is tapped extensively as a water source for agricultural and domestic needs. The aquifer is being depleted faster than it is recharged—a local imbalance in the water cycle—posing an ominous threat to the agricultural production of the area. Similar threats exist in many of the drier portions of the globe.

Changes in ecosystems brought about by changes in the water cycle

Water is so crucial for life that changes in its supply in an ecosystem can radically alter the nature of the ecosystem. Such changes have occurred often during the Earth's geological history.

Consider, for example, the ecosystem of the Serengeti Plain in Tanzania, famous for its seemingly endless grasslands occupied by vast herds of antelopes and other grazing animals. The semiarid grasslands of today's Serengeti were rain forests

25 MYA. Starting at about that time, mountains such as Mount Kilimanjaro rose up between the rain forests and the Indian Ocean, their source of moisture. The presence of the mountains forced winds from the Indian Ocean upward, cooling the air and causing much of its moisture to precipitate before the air reached the rain forests. The land became much drier, and the forests turned to grasslands.

Today, human activities can alter the water cycle so profoundly that major changes occur in ecosystems. Changes in rain forests caused by deforestation provide an example. In healthy tropical rain forests, more than 90% of the moisture that falls as rain is taken up by plants and returned to the air by transpiration. Plants, in a very real sense, create their own rain: The moisture returned to the atmosphere falls back on the forests.

When human populations cut down or burn the rain forests in an area, the local water cycle is broken. Water that falls as rain thereafter drains away in rivers instead of rising to form clouds and fall again on the forests. Just such a transformation is occurring today in many tropical rain forests (figure 58.3). Large areas in Brazil, for example, were transformed in the 20th century from lush tropical forest to semiarid desert, depriving many unique plant and animal species of their native habitat.

The nitrogen cycle depends on nitrogen fixation by microbes

Nitrogen is a component of all proteins and nucleic acids and is required in substantial amounts by all organisms; proteins are 16% nitrogen by weight. In many ecosystems, nitrogen is the chemical element in shortest supply relative to the needs of organisms. A paradox is that the atmosphere is 78% nitrogen by volume.



Figure 58.3 Deforestation disrupts the local water cycle. Tropical deforestation can have severe consequences, such as the extensive erosion in this area in the Amazon region of Brazil.

Nitrogen availability

How can nitrogen be in short supply if the atmosphere is so rich with it? The answer is that the nitrogen in the atmosphere is in its elemental form—molecules of nitrogen gas (N_2)—and the vast majority of organisms, including all plants and animals, have no way to use nitrogen in this chemical form.

For animals, the ultimate source of nitrogen is nitrogen-containing organic compounds synthesized by plants or by algae or other microbes. Herbivorous animals, for example, eat plant or algal proteins and use the nitrogen-containing amino acids in them to synthesize their own proteins.

Plants and algae use a number of simple nitrogen-containing compounds as their sources of nitrogen to synthesize proteins and other nitrogen-containing organic compounds in their tissues. Two commonly used nitrogen sources are ammonia (NH_3) and nitrate ions (NO_3^-). As described in chapter 39, certain prokaryotic microbes can synthesize ammonia and nitrate from N_2 in the atmosphere, thereby constituting a part of the nitrogen cycle that makes atmospheric nitrogen accessible to plants and algae (figure 58.4). Other prokaryotes turn NH_3 and NO_3^- into N_2 , making the nitrogen inaccessible. The balance of the activities of these two sets of microbes determines the accessibility of nitrogen to plants and algae.

Microbial nitrogen fixation, nitrification, and denitrification

The synthesis of nitrogen-containing compounds from N_2 is known as **nitrogen fixation**. The first step in this process is the synthesis of NH_3 from N_2 , and biochemists sometimes use the

term *nitrogen fixation* to refer specifically to this step. After NH_3 has been synthesized, other prokaryotic microbes oxidize part of it to form NO_3^- , a process called **nitrification**.

Certain genera of prokaryotes have the ability to accomplish nitrogen fixation using a system of enzymes known as the nitrogenase complex (the *nif* gene complex; see chapter 28). Most of the microbes are free-living, but on land some are found in symbiotic relationships with the roots of legumes (plants of the pea family, Fabaceae), alders, myrtles, and other plants.

Additional prokaryotic microbes (including both bacteria and archaea) are able to convert the nitrogen in NO_3^- into N_2 (or other nitrogen gases such as N_2O), a process termed **denitrification**. Ammonia can be subjected to denitrification indirectly by being converted first to NO_3^- and then to N_2 .

Nitrogenous wastes and fertilizer use

Most animals, when they break down proteins in their metabolism, excrete the nitrogen from the proteins as NH_3 . Humans and other mammals excrete nitrogen as urea in their urine (see chapter 51); a number of types of microbes convert the urea to NH_3 . The NH_3 from animal excretion can be picked up by plants and algae as a source of nitrogen.

Human populations are radically altering the global nitrogen cycle by the use of fertilizers on lawns and agricultural fields. The fertilizers contain forms of fixed nitrogen that crops can use, such as ammonium (NH_4^+) salts manufactured industrially from atmospheric N_2 . Partly because of the production of fertilizers, humans have already doubled the rate of transfer of N_2 in usable forms into soils and waters.

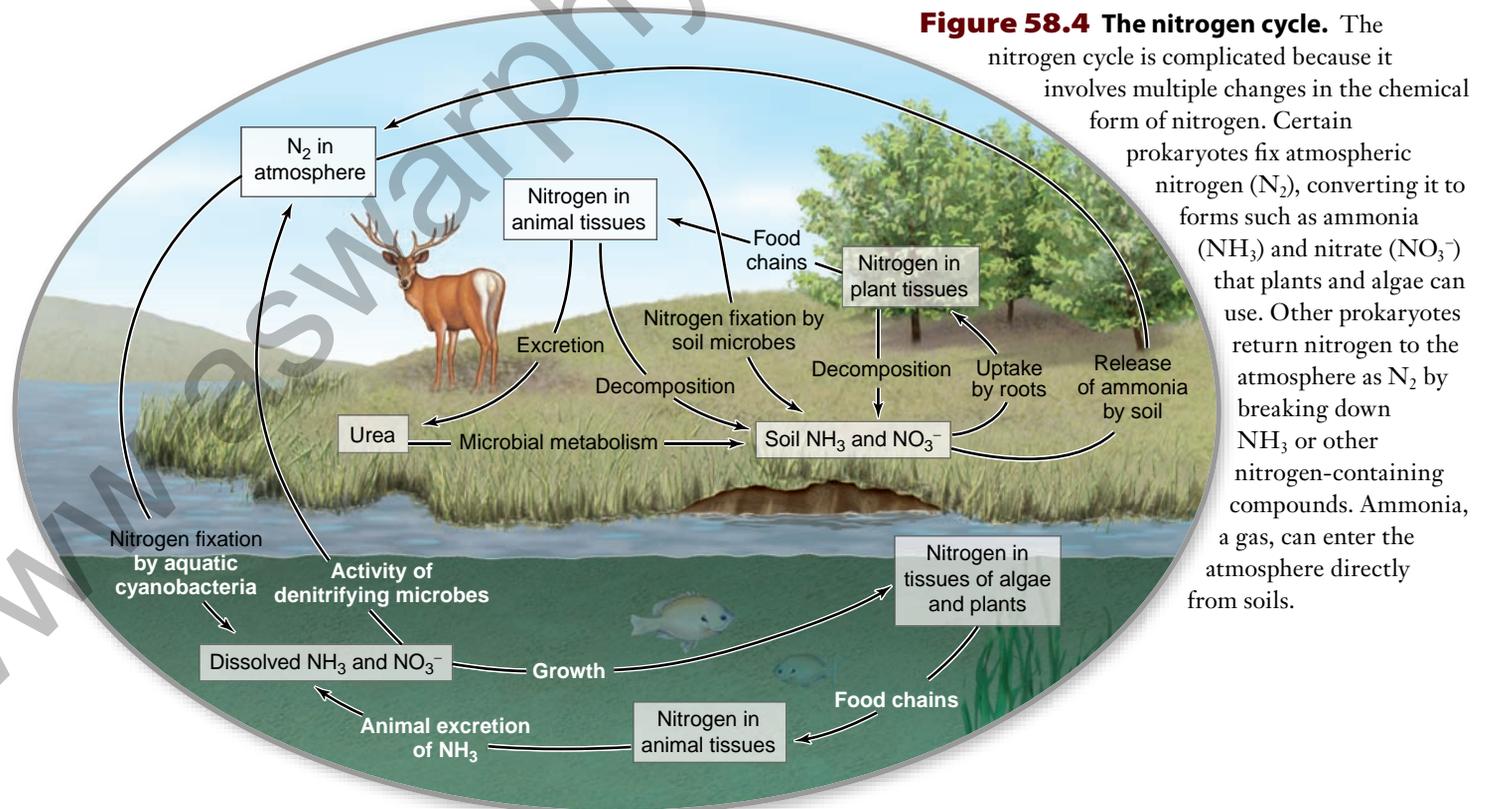
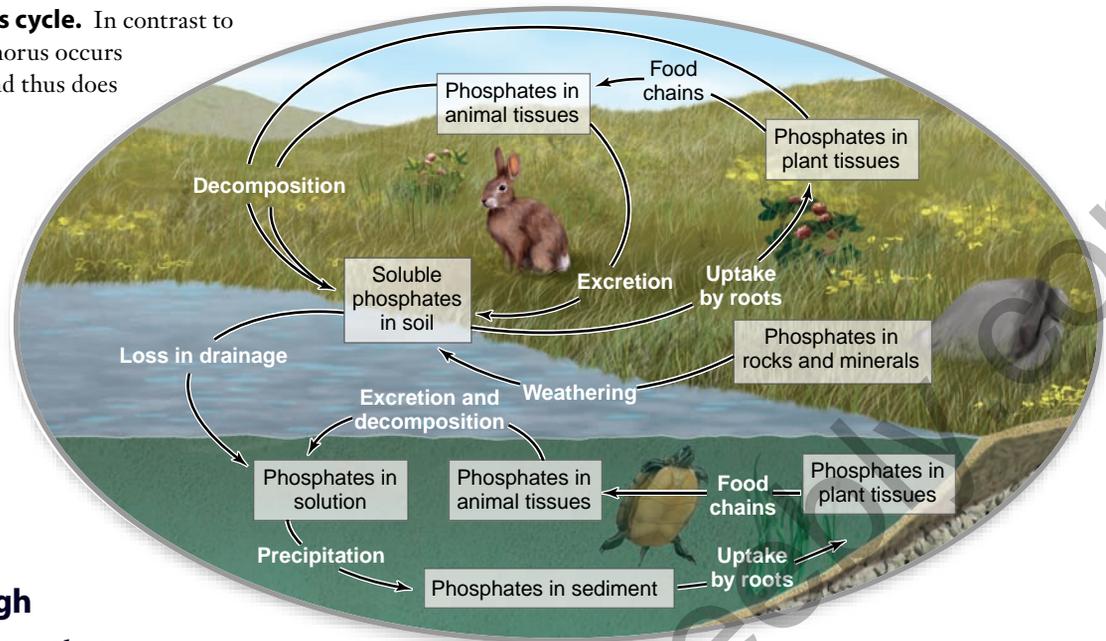


Figure 58.4 The nitrogen cycle. The nitrogen cycle is complicated because it involves multiple changes in the chemical form of nitrogen. Certain prokaryotes fix atmospheric nitrogen (N_2), converting it to forms such as ammonia (NH_3) and nitrate (NO_3^-) that plants and algae can use. Other prokaryotes return nitrogen to the atmosphere as N_2 by breaking down NH_3 or other nitrogen-containing compounds. Ammonia, a gas, can enter the atmosphere directly from soils.

Figure 58.5 The phosphorus cycle. In contrast to carbon, water, and nitrogen, phosphorus occurs only in the liquid and solid states and thus does not enter the atmosphere.



Phosphorus cycles through terrestrial and aquatic ecosystems, but not the atmosphere

Phosphorus is required in substantial quantities by all organisms; it occurs in nucleic acids, membrane phospholipids, and other essential compounds, such as adenosine triphosphate (ATP).

Unlike carbon, water, and nitrogen, phosphorus has no significant gaseous form and does not cycle through the atmosphere (figure 58.5). In this respect, the phosphorus cycle exemplifies the sorts of cycles also exhibited by calcium, silicon, and many other mineral elements. Another feature that greatly simplifies the phosphorus cycle compared with the nitrogen cycle is that phosphorus exists in ecosystems in just a single oxidation state, phosphate (PO_4^{3-}).

Phosphate availability

Plants and algae use free inorganic PO_4^{3-} in the soil or water for synthesizing their phosphorus-containing organic compounds. Animals then tap the phosphorus in plant or algal tissue compounds to build their own phosphorus compounds. When organisms die, decay microbes—in a process called phosphate remineralization—break up the organic compounds in their bodies, releasing phosphorus as inorganic PO_4^{3-} that plants and algae again can use.

The phosphorus cycle includes critical abiotic chemical and physical processes. Free PO_4^{3-} exists in soil in only low concentrations both because it combines with other soil constituents to form insoluble compounds and because it tends to be washed away by streams and rivers. Weathering of many sorts of rocks releases new PO_4^{3-} into terrestrial systems, but then rivers carry the PO_4^{3-} into the ocean basins. There is a large one-way flux of PO_4^{3-} from terrestrial rocks to deep-sea sediments.

Phosphates as fertilizers

Human activities have greatly modified the global phosphorus cycle since the advent of crop fertilization. Fertilizers are typically designed to provide PO_4^{3-} because crops might otherwise be short of it; the PO_4^{3-} in fertilizers is typically derived from crushed phosphate-rich rocks and bones. Detergents are an-

other potential culprit in adding PO_4^{3-} to ecosystems, but laws now mandate low-phosphate detergents in much of the world.

Limiting nutrients in ecosystems are those in short supply relative to need

A chain is only as strong as its weakest link. For the plants and algae in an ecosystem to grow—and to thereby provide food for animals—they need many different chemical elements. The simplest theory is that in any particular ecosystem, one element will be in shortest supply relative to the needs for it by the plants and algae. That element is the limiting nutrient—the weak link—in the ecosystem.

The cycle of a limiting nutrient is particularly important because it determines the rate at which the nutrient is made available for use. We gave the nitrogen and phosphorus cycles close attention precisely because those elements are the limiting nutrients in many ecosystems. Nitrogen is the limiting nutrient in about two-thirds of the oceans and in many terrestrial ecosystems.

Oceanographers have discovered in just the last 15 years that iron is the limiting nutrient for algal populations (phytoplankton) in about one-third of the world's oceans. In these waters, wind-borne soil dust seems often to be the chief source of iron. When wind brings in iron-rich dust, algal populations proliferate, provided the iron is in a usable chemical form. In this way, sand storms in the Sahara Desert, by increasing the dust in global winds, can increase algal productivity in Pacific waters (figure 58.6).

Biogeochemical cycling in a forest ecosystem has been studied experimentally

An ongoing series of studies at the Hubbard Brook Experimental Forest in New Hampshire has yielded much of the available information about the cycling of nutrients in forest ecosystems.

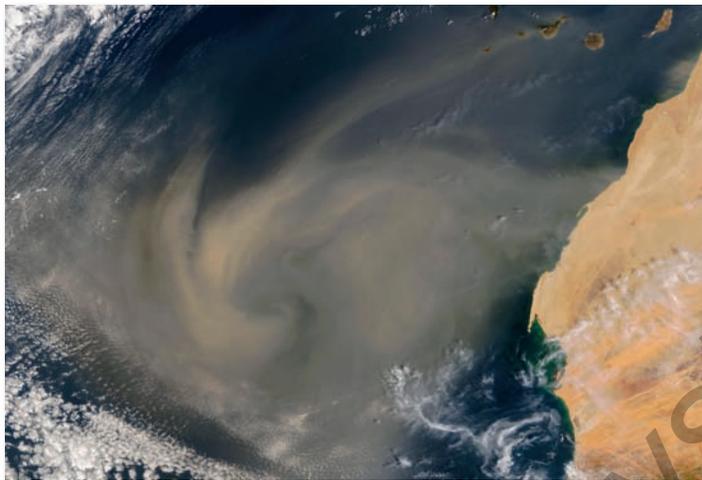
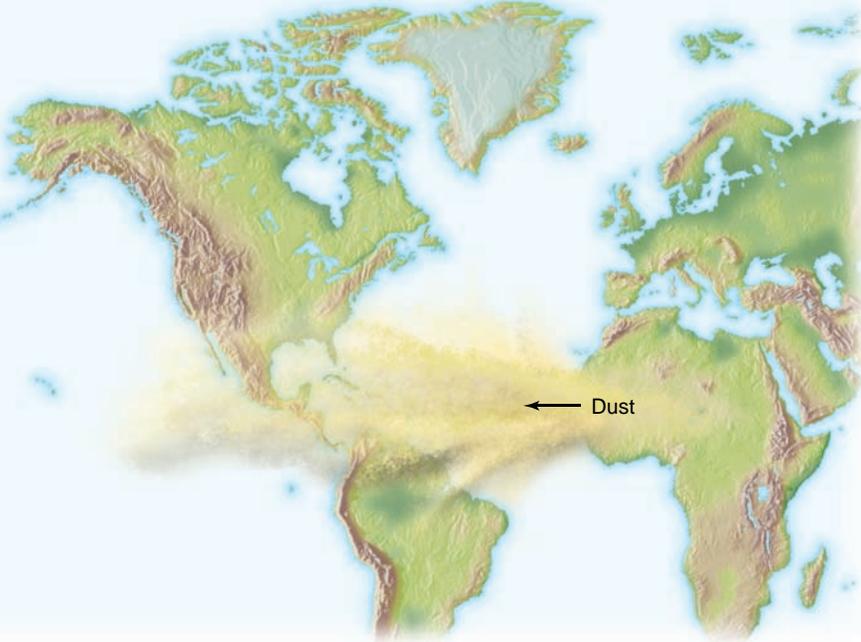


Figure 58.6 One world. Every year, millions of metric tons of iron-rich dust is carried westward by the trade winds from the Sahara Desert and neighboring Sahel area. A working hypothesis of many oceanographers is that this dust fertilizes parts of the ocean, including parts of the Pacific Ocean, where iron is the limiting nutrient. Land use practices in Africa, which are increasing the size of the north African desert, can thus affect ecosystems on the other side of the globe.



a.

Hubbard Brook is the central stream of a large watershed that drains the hillsides of a mountain range covered with temperate deciduous forest. Multiple tributary streams carry water off the hillsides into Hubbard Brook.

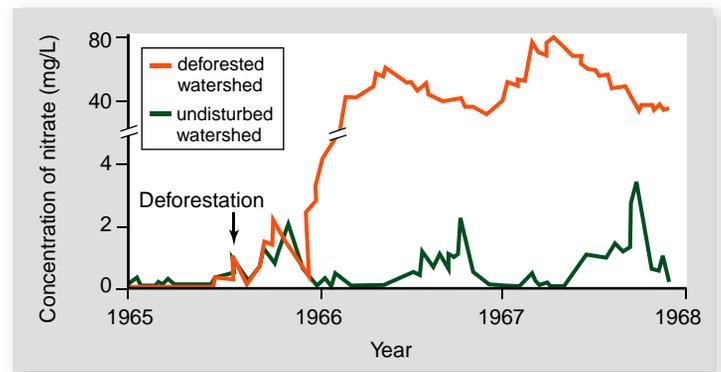
Six tributary streams, each draining a particular valley, were equipped with measurement devices when the study was started. All of the water that flowed out of each valley had to pass through the measurement system, where the flow of water and concentrations of nutrients was quantified.

The undisturbed forests around Hubbard Brook are efficient at retaining nutrients. In a year, only small quantities of nutrients enter a valley from outside, doing so mostly as a result of precipitation. The quantities carried out in stream waters are small also. When we say “small,” we mean the influxes and outfluxes represent just minor fractions of the total amounts of nutrients in the system—about 1% in the case of calcium, for example.

In 1965 and 1966, the investigators felled all the trees and cleared all shrubs in one of the six valleys and prevented regrowth (figure 58.7*a*). The effects were dramatic. The amount of water running out of that valley increased by 40%, indicating that water previously taken up by vegetation and evaporated into the atmosphere was now running off. The amounts of a number of nutrients running out of the system also greatly increased. For example, the rate of loss of calcium increased ninefold. Phosphorus, on the other hand, did not increase in the stream water; it apparently was locked up in insoluble compounds in the soil.

The change in the status of nitrogen in the disturbed valley was especially striking (figure 58.7*b*). The undisturbed forest in this valley had been accumulating NO_3^- at a rate of about 5 kg per hectare per year, but the deforested ecosystem lost NO_3^- at a rate of about 53 kg per hectare per year. The NO_3^- concentration in the stream water rapidly increased. The fertility of the valley decreased dramatically, while the run-off of nitrate generated massive algal blooms downstream, and the danger of downstream flooding greatly increased.

This experiment is particularly instructive at the start of the 21st century because forested land continues to be cleared worldwide (see chapter 59).



b.

Figure 58.7 The Hubbard Brook experiment. *a.* A 38-acre watershed was completely deforested, and the runoff monitored for several years. *b.* Deforestation greatly increased the loss of nutrients in runoff water from the ecosystem. The orange curve shows the nitrate concentration in the runoff water from the deforested watershed; the green curve shows the nitrate concentration in runoff water from an undisturbed neighboring watershed.

Learning Outcomes Review 58.1

An ecosystem consists of the living and nonliving components of a particular place. Biogeochemical cycles describe how elements move between these components. Carbon, nitrogen, and phosphorus cycle in known ways, as does water, which is critical to ecosystems. Human populations disrupt these cycles with artificial fertilization, deforestation, diversion of water, and burning of fossil fuels.

- **Would fertilization with animal manure be less disruptive than fertilization with purified chemicals? Why or why not?**

58.2 The Flow of Energy in Ecosystems

Learning Outcomes

1. Describe the different trophic levels.
2. Distinguish between energy and heat.
3. Explain how energy moves through trophic levels.

The dynamic nature of ecosystems includes the processing of energy as well as that of matter. Energy, however, follows very different principles than does matter. Energy is never recycled. Instead, radiant energy from the Sun that reaches the Earth makes a one-way pass through our planet's ecosystems before being converted to heat and radiated back into space, signifying that the Earth is an open system for energy.

Energy can neither be created nor destroyed, but changes form

Why is energy so different from matter? A key part of the answer is that energy exists in several different forms, such as light, chemical-bond energy, motion, and heat. Although energy is neither created nor destroyed in the biosphere (the First Law of Thermodynamics), it frequently changes form.

A second key point is that organisms cannot convert heat to any of the other forms of energy. Thus, if organisms convert some chemical-bond or light energy to heat, the conversion is one-way; they cannot cycle that energy back into its original form.

Living organisms can use many forms of energy, but not heat

To understand why the Earth must function as an open system with regard to energy, two additional principles need to be recognized. The first is that organisms can use only certain forms of energy. For animals to live, they must have energy specifically as chemical-bond energy, which they acquire from their foods. Plants must have energy as light. Neither animals nor plants (nor any other organisms) can use heat as a source of energy.

The second principle is that whenever organisms use chemical-bond or light energy, some of it is converted to heat; the Second Law of Thermodynamics states that a partial conversion to heat is inevitable. Put another way, animals and plants require chemical-bond energy and light to stay alive, but as they use these forms of energy, they convert them to heat, which they cannot use to stay alive and which they cannot cycle back into the original forms.

Fortunately for organisms, the Earth functions as an open system for energy. Light arrives every day from the Sun. Plants and other photosynthetic organisms use the newly arrived light to synthesize organic compounds and stay alive. Animals then eat the photosynthetic organisms, making use of the chemical-bond energy in their organic molecules to stay alive. Light and chemical-bond energy are partially converted to heat at every step. In fact, the light and chemical-bond energy are ultimately converted completely to heat. The heat leaves the Earth by being radiated into outer space at invisible, infrared wavelengths of the electromagnetic spectrum. For life to continue, new light energy is always required.

The Earth's incoming and outgoing flows of radiant energy must be equal for global temperature to stay constant. One concern is that human activities are changing the composition of the atmosphere in ways that impede the outgoing flow—the so-called *greenhouse effect*, which is described in the following chapter. Heat may be accumulating on Earth, causing global warming (see chapter 59).

Energy flows through trophic levels of ecosystems

In chapter 7, we introduced the concepts of autotrophs (“self-feeders”) and heterotrophs (“fed by others”). **Autotrophs** synthesize the organic compounds of their bodies from inorganic precursors such as CO_2 , water, and NO_3^- using energy from an abiotic source. Some autotrophs use light as their source of energy and therefore are **photoautotrophs**; they are the photosynthetic organisms, including plants, algae, and cyanobacteria. Other autotrophs are **chemoautotrophs** and obtain energy by means of inorganic oxidation reactions, such as the microbes that use hydrogen sulfide available at deep water vents (see chapter 59). All chemoautotrophs are prokaryotic. The photoautotrophs are of greatest importance in most ecosystems, and we focus on them in the remainder of this chapter.

Heterotrophs are organisms that cannot synthesize organic compounds from inorganic precursors, but instead live by taking in organic compounds that other organisms have made. They obtain the energy they need to live by breaking up some of the organic compounds available to them, thereby liberating chemical-bond energy for metabolic use (see chapter 7). Animals, fungi, and many microbes are heterotrophs.

When living in their native environments, species are often organized into chains that eat each other sequentially. For example, a species of insect might eat plants, and then a species of shrew might eat the insect, and a species of hawk might eat the shrew. Food passes through the four species in the sequence: plants \rightarrow insect \rightarrow shrew \rightarrow hawk. A sequence of species like this is termed a food chain.