5 Biodiversity, Species Interactions, and Population Control

CORE CASE STUDY Southern Sea Otters: Are They Back from the Brink of Extinction?

Southern sea otters (Figure 5-1, top left) live in giant kelp forests (Figure 5-1, right) in shallow waters along part of the Pacific coast of North America. Most remaining members of this endangered species are found between the U.S. state of California's coastal cities of Santa Cruz and Santa Barbara.

Southern sea otters are fast and agile swimmers that dive to the ocean bottom looking for shellfish and other prey. These tool-using marine mammals use stones to pry shellfish off rocks under water. When they return to the surface they break open the shells while swimming on their backs, using their bellies as a table (Figure 5-1, top left). Each day a sea otter consumes about a fourth of its weight in clams, mussels, crabs, sea urchins, abalone, and about 40 other species of bottom-dwelling organisms.

Historically, between 16,000 and 17,000 southern sea otters are believed to have populated the waters along their habitat area of the California coast before fur traders began killing them for their thick, luxurious fur. For that reason, and because the otters competed with humans for valuable abalone and other shellfish, the species was hunted almost to extinction in this region by the early 1900s.

However, between 1938 and 2007 the population of southern sea otters off California's coast increased from about 50 to almost 3,026. This partial recovery was helped when, in 1977, the U.S. Fish and Wildlife Service declared the species endangered in most of its range. But this species has a long way to go before its population increases enough to allow removing it from the endangered species list.

Why should we care about this species? One reason is that people love to look at these charismatic, cute, and cuddly animals as they play in the water. As a result, they help to generate millions of dollars a year in tourism income in coastal areas where they are found. Another reason is *ethical.* Some people believe it is wrong to cause the premature extinction of any species.

A third reason to care about otters—and a key reason in our study of environmental science—is that biologists classify them as a *keystone species* (p. 95), which play an important ecological role through its interactions with other species. The otters help to keep sea urchins and other kelp-eating species from depleting highly productive and rapidly growing kelp forests, which provide habitats for a number of species in offshore coastal waters, as discussed in more detail later in this chapter. Without southern sea otters, sea urchins would probably destroy the kelp forests and much of the rich biodiversity associated with them.

Biodiversity, an important part of the earth's natural capital, is the focus of one of the four **scientific principles of sustainability** (see back cover). One of its components is species diversity (Figure 4-2, p. 79), which is affected by how species interact with one another and, in the process, help control each others' population sizes.

Tom and Pat Leeson, Ardea London Ltd

Bruce Coleman USA

Figure 5-1 An endangered southern sea otter in Monterey Bay, California (USA), uses a stone to crack the shell of a clam (top left). It lives in a giant kelp bed near San Clemente Island, California (right). Scientific studies indicate that the otters act as a keystone species in a kelp forest system by helping to control the populations of sea urchins and other kelp-eating species.

Key Questions and Concepts

5-1 How do species interact?

CONCEPT 5-1 Five types of species interactions—competition, predation, parasitism, mutualism, and commensalism—affect the resource use and population sizes of the species in an ecosystem.

5-2 How can natural selection reduce competition between species?

CONCEPT 5-2 Some species develop adaptations that allow them to reduce or avoid competition with other species for resources.

5-3 What limits the growth of populations?

CONCEPT 5-3 No population can continue to grow indefinitely because of limitations on resources and because of competition among species for those resources.

5-4 How do communities and ecosystems respond to changing environmental conditions?

CONCEPT 5-4 The structure and species composition of communities and ecosystems change in response to changing environmental conditions through a process called ecological succession.

Note: Supplements 2 (p. S4), 4 (p. S20), 5 (p. S31), 6 (p. S39), and 13 (p. S78) can be used with this chapter.

In looking at nature, never forget that every single organic being around us may be said to be striving to increase its numbers.

CHARLES DARWIN, 1859

5-1 How Do Species Interact?

CONCEPT 5-1 Five types of species interactions—competition, predation, parasitism, mutualism, and commensalism—affect the resource use and population sizes of the species in an ecosystem.

Species Interact in Five Major Ways

Ecologists identify five basic types of interactions between species that share limited resources such as food, shelter, and space:

- **Interspecific competition** occurs when members of two or more species interact to gain access to the same limited resources such as food, light, or space.
- **Predation** occurs when a member of one species (the *predator*) feeds directly on all or part of a member of another species (the *prey*).
- **Parasitism** occurs when one organism (the *parasite*) feeds on the body of, or the energy used by, another organism (the *host*), usually by living on or in the host.
- **Mutualism** is an interaction that benefits both species by providing each with food, shelter, or some other resource.
- **Commensalism** is an interaction that benefits one species but has little, if any, effect on the other.

These interactions have significant effects on the resource use and population sizes of the species in an ecosystem (**Concept 5-1**). Interactions that help to limit population size illustrate one of the four **scientific principles of sustainability** (see back cover). These interactions also influence the abilities of the interacting species to survive and reproduce; thus the interactions serve as agents of natural selection (**Concept 4-2B**, p. 80).

SUSTAINABILITY

CONCEPT LINK

Most Species Compete with One Another for Certain Resources

The most common interaction between species is *competition* for limited resources. While fighting for resources does occur, most competition involves the ability of one species to become more efficient than another species in acquiring food or other resources.

Recall that each species plays a unique role in its ecosystem called its *ecological niche* (p. 91). Some species are generalists with broad niches and some are specialists with narrow niches. When two species compete with one another for the same resources such as food, light, or space, their niches overlap (Figure 4-11, p. 91).

The greater this overlap the more intense their competition for key resources.

Although different species may share some aspects of their niches, no two species can occupy exactly the same ecological niche for very long—a concept known as the *competitive exclusion principle.* When there is intense competition between two species for the same resources, both species suffer harm by having reduced access to important resources. If one species can take over the largest share of one or more key resources, the other competing species must migrate to another area (if possible), shift its feeding habits or behavior through natural selection to reduce or alter its niche, suffer a sharp population decline, or become extinct in that area.

Humans compete with many other species for space, food, and other resources. As our ecological footprints grow and spread (Figure 1-10, p. 15) and we convert more of the earth's land, aquatic resources, and net primary productivity (Figure 3-16, p. 64) to our uses, we are taking over the habitats of many other species and depriving them of resources they need to survive.

> **THINKING ABOUT**
> **Humans and the Southern Sea Otter**
> CORE CASE STUDY
> What human activities have interfered with the ecological niche of the southern sea otter (**Core Case Study**)?

Most Consumer Species Feed on Live Organisms of Other Species

All organisms must have a source of food to survive. Recall that members of producer species, such as plants and floating phytoplankton, make their own food, mostly through photosynthesis (p. 58). Other species are consumers that interact with some species by feeding on them. Some consumers feed on live individuals of other species. They include herbivores that feed on plants, carnivores that feed on the flesh of other animals, and omnivores that feed on plants and animals. Other consumers, such as detritus feeders and decomposers, feed on the wastes or dead bodies of organisms.

In **predation,** a member of one species (the **predator**) feeds directly on all or part of a living organism of another plant or animal species (the **prey**) as part of a food web (**Concept 3-4A**, p. 61). Together, the two different species, such as lions (the predator or hunter) and zebras (the prey or hunted), form a **predator–prey relationship.** Such relationships are shown in Figures 3-13 (p. 62) and 3-14 (p. 63).

CONCEPT LINK

Herbivores, carnivores, and omnivores are predators. However, detritus feeders and decomposers, while they do feed on other organisms after they have died, are not considered predators because they do not feed on live organisms.

Sometimes predator–prey relationships can surprise us. During the summer months, the grizzly bears of the Greater Yellowstone ecosystem in the western United States eat huge amounts of army cutworm moths, which huddle in masses high on remote mountain slopes. One grizzly bear can dig out and lap up as many as 40,000 of these moths in a day. Consisting of 50–70% fat, the moths offer a nutrient that the bear can store in its fatty tissues and draw on during its winter hibernation.

In giant kelp forest ecosystems, sea urchins prey on giant kelp, a form of seaweed (**Core Case Study**, Figure 5-1, right). However, as keystone species, southern sea otters (Figure 5-1, top left) prey on the sea urchins and help to keep them from destroying the kelp forest ecosystems (Science Focus, p. 104).

CORE CASE STUDY

Predators have a variety of methods that help them capture prey. *Herbivores* can simply walk, swim, or fly up to the plants they feed on. For example, sea urchins (Science Focus, Figure 5-A, p. 104) can move along the ocean bottom to feed on the base of giant kelp plants. *Carnivores* feeding on mobile prey have two main options: *pursuit* and *ambush.* Some, such as the cheetah, catch prey by running fast; others, such as the American bald eagle, can fly and have keen eyesight; still others, such as wolves and African lions, cooperate in capturing their prey by hunting in packs.

Other predators use *camouflage* to hide in plain sight and ambush their prey. For example, praying mantises (Figure 3-A, right, p. 54) sit in flowers of a similar color and ambush visiting insects. White ermines (a type of weasel) and snowy owls hunt in snow-covered areas. People camouflage themselves to hunt wild game and use camouflaged traps to ambush wild game.

Some predators use *chemical warfare* to attack their prey. For example, spiders and poisonous snakes use venom to paralyze their prey and to deter their predators.

Prey species have evolved many ways to avoid predators, including abilities to run, swim, or fly fast, and highly developed senses of sight or smell that alert them to the presence of predators. Other avoidance adaptations include protective shells (as on armadillos and turtles), thick bark (giant sequoia), spines (porcupines), and thorns (cacti and rosebushes). Many lizards have brightly colored tails that break off when they are attacked, often giving them enough time to escape.

Other prey species use the camouflage of certain shapes or colors or the ability to change color (chameleons and cuttlefish). Some insect species have shapes that make them look like twigs (Figure 5-2a), bark, thorns, or even bird droppings on leaves. A leaf insect can be almost invisible against its background (Figure 5-2b), as can an arctic hare in its white winter fur.

Chemical warfare is another common strategy. Some prey species discourage predators with chemicals that are *poisonous* (oleander plants), *irritating* (stinging nettles and bombardier beetles, Figure 5-2c), *foul smelling* (skunks, skunk cabbages, and stinkbugs), or *bad tast-*

ing (buttercups and monarch butterflies, Figure 5-2d). When attacked, some species of squid and octopus emit clouds of black ink, allowing them to escape by confusing their predators.

Many bad-tasting, bad-smelling, toxic, or stinging prey species have evolved *warning coloration,* brightly colored advertising that enables experienced predators to recognize and avoid them. They flash a warning: "Eating me is risky." Examples are brilliantly colored poisonous frogs (Figure 5-2e); and foul-tasting monarch butterflies (Figure 5-2d). For example, when a bird such as a blue jay eats a monarch butterfly it usually vomits and learns to avoid them.

Biologist Edward O. Wilson gives us two rules, based on coloration, for evaluating possible danger from an unknown animal species we encounter in nature. *First,* if it is small and strikingly beautiful, it is probably poisonous. *Second,* if it is strikingly beautiful and easy to catch, it is probably deadly.

Some butterfly species, such as the nonpoisonous viceroy (Figure 5-2f), gain protection by looking and acting like the monarch, a protective device known as *mimicry.* Other prey species use *behavioral strategies* to avoid predation. Some attempt to scare off predators by puffing up (blowfish), spreading their wings (peacocks), or mimicking a predator (Figure 5-2h). Some moths have wings that look like the eyes of much larger animals (Figure 5-2g). Other prey species gain some protection by living in large groups such as schools of fish and herds of antelope.

THINKING ABOUT
Predation and the Southern Sea Otter

CORE CASE STUDY

Describe a trait possessed by the southern sea otter (**Core Case Study**) that helps it **(a)** catch prey and **(b)** avoid being preyed upon?

At the individual level, members of the predator species benefit and members of the prey species are harmed. At the population level, predation plays a role in evolution by natural selection (**Concept 4-2B**, p. 80). Animal predators, for example, tend to kill the sick, weak, aged, and least fit members of a population because they are the easiest to catch. This leaves behind individuals with better defenses against predation. Such individuals tend to survive longer and leave more offspring with adaptations that can help them avoid predation. Thus, predation can help increase biodiversity by promoting natural selection in which species evolve with the ability to share limited resources by reducing their niche overlap.

CONCEPT LINK

Some people tend to view certain animal predators with contempt. When a hawk tries to capture and feed on a rabbit, some root for the rabbit. Yet the hawk, like all predators, is merely trying to get enough food for itself and its young. In doing so, it plays an important ecological role in controlling rabbit populations.

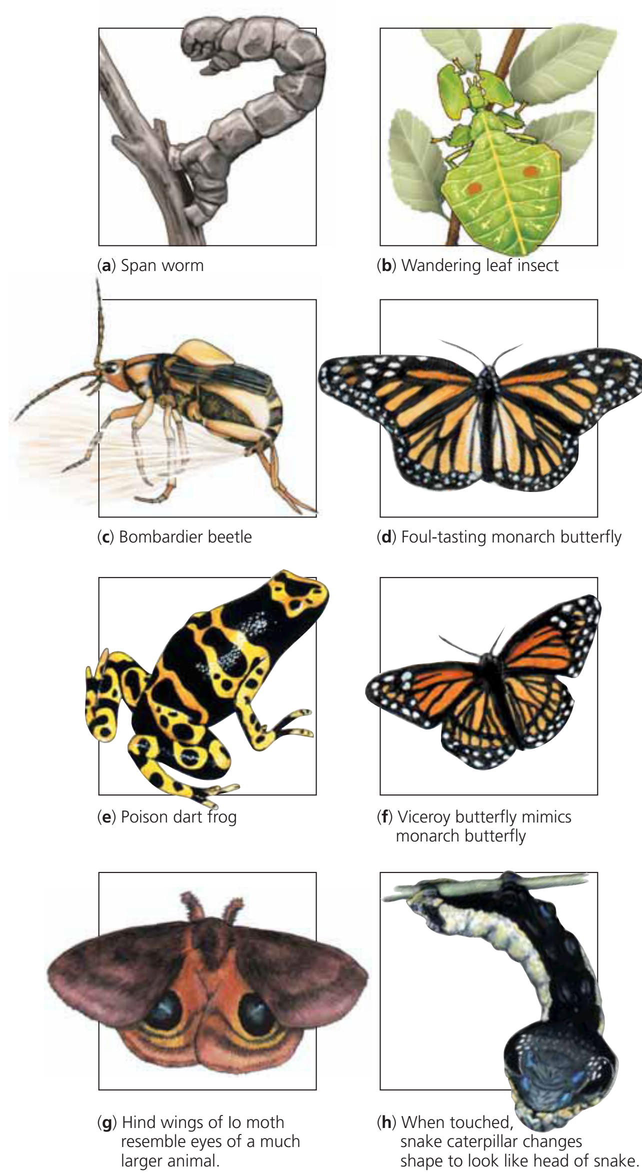


Figure 5-2 Some ways in which prey species avoid their predators: **(a, b)** *camouflage,* **(c–e)** *chemical warfare,* **(d, e)** *warning coloration,* **(f)** *mimicry,* **(g)** *deceptive looks,* and **(h)** *deceptive behavior.*

Predator and Prey Species Can Drive Each Other's Evolution

To survive, predators must eat and prey must avoid becoming a meal. As a result, predator and prey populations exert intense natural selection pressures on one another. Over time, as prey develop traits that make them more difficult to catch, predators face selection

SCIENCE FOCUS

Why Should We Care about Kelp Forests?

A kelp forest is a forest of seaweed called giant kelp whose large blades grow straight to the surface (Figure 5-1, right) (**Core Case Study**). CORE CASE STUDY The dependence of these plants on photosynthesis restricts their growth to cold, nutrient-rich, and fairly shallow coastal waters, which are found in various areas of the world, such as off the coast of northern California (USA).

Giant kelp is one of the world's fastest growing plants. Under good conditions, its blades can grow 0.6 meter (2 feet) a day. Each blade is held up by a gas-filled bladder at its base. The blades are very flexible and can survive all but the most violent storms and waves.

Kelp forests are one of the most biologically diverse ecosystems found in marine waters, supporting large numbers of marine plants and animals. These forests help reduce shore erosion by blunting the force of incoming waves and helping to trap outgoing sand. People harvest kelp as a renewable resource, extracting a substance called algin from its blades. We use this substance in toothpaste, cosmetics, ice cream, and hundreds of other products.

Sea urchins and pollution are major threats to kelp forests. Large populations of sea urchins (Figure 5-A) can rapidly devastate a kelp forest because they eat the base of young kelp. Male southern sea otters, a keystone species, help to control populations of sea urchins. An adult male southern sea otter (Figure 5-1, top left) can eat up to 50 sea urchins a day—equivalent to a 68-kilogram (150-pound) person eating 160 quarter-pound hamburgers a day. Without southern sea otters, giant kelp forest ecosystems would collapse and reduce aquatic biodiversity.

Deborah Meeks/SuperStock

Figure 5-A Purple sea urchin in coastal waters of the U.S. state of California.

A second threat to kelp forests is polluted water running off of the land into the coastal waters where kelp forests grow. The pollutants in this runoff include pesticides and herbicides, which can kill kelp plants and other kelp forest species and upset the food webs in these forests. Another runoff pollutant is fertilizer whose plant nutrients (mostly nitrates) can cause excessive growth of algae and other plants. These growths block some of the sunlight needed to support the growth of giant kelp, and thus upset these aquatic ecosystems.

A third looming threat is global warming. Giant kelp forests require fairly cool water, where the temperature stays between 28–36 °C (50–65 °F). If coastal waters warm up as projected during this century, many—perhaps most—of the world's giant kelp forests will disappear and along with them the southern sea otter and many other species.

Critical Thinking

What are three ways to protect giant kelp forests and southern sea otters?

pressures that favor traits that increase their ability to catch prey. Then prey must get better at eluding the more effective predators.

When populations of two different species interact in this way over a such long period of time, changes in the gene pool of one species can lead to changes in the gene pool of the other species. Such changes can help both sides to become more competitive or can help to avoid or reduce competition. Biologists call this process **coevolution.**

Consider the species interaction between bats (the predator) and certain species of moths (the prey). Bats like to eat moths, and they hunt at night (Figure 5-3) and use echolocation to navigate and to locate their prey, emitting pulses of extremely high-frequency and high-intensity sound. They capture and analyze the returning echoes and create a sonic "image" of their prey. (We have copied this natural technology by using sonar to detect submarines, whales, and schools of fish.)

As a countermeasure to this effective prey-detection system, certain moth species have evolved ears that are especially sensitive to the sound frequencies that bats use to find them. When the moths hear the bat frequencies, they try to escape by dropping to the ground or flying evasively.

Some bat species evolved ways to counter this defense by changing the frequency of their sound pulses. In turn, some moths have evolved their own high-frequency clicks to jam the bats' echolocation systems. Some bat species then adapted by turning off their echolocation systems and using the moths' clicks to locate their prey.

Coevolution is like an arms race between interacting populations of different species. Sometimes the predators surge ahead; at other times the prey get the upper hand. Coevolution is one of nature's ways of maintaining long-term sustainability through population control (see back cover and **Concept 1-6**, p. 23), and it can promote biodiversity by increasing species diversity. CONCEPT LINK

However, we should not think of coevolution as a process with which species can design strategies to increase their survival chances. Instead, it is a prime example of populations responding to changes in environmental conditions as part of the process of evolution by natural selection. And, unlike a human arms race, each step in this process takes hundreds to thousands of years.

Some Species Feed off Other Species by Living on or in Them

Parasitism occurs when one species (the *parasite*) feeds on the body of, or the energy used by, another organism (the *host*), usually by living on or in the host. In this relationship, the parasite benefits and the host is harmed but not immediately killed.

Unlike the typical predator, a parasite usually is much smaller than its host and rarely kills its host. Also, most parasites remain closely associated with their hosts, draw nourishment from them, and may gradually weaken them over time.

Some parasites, such as tapeworms and some disease-causing microorganisms (pathogens), live *inside* their hosts. Other parasites attach themselves to the *outsides* of their hosts. Examples of the latter include mosquitoes, mistletoe plants (Figure 5-4, left), and sea lampreys, which use their sucker-like mouths to attach themselves to fish and feed on their blood (Figure 5-4, right). Some parasites move from one host to another, as fleas and ticks do; others, such as tapeworms, spend their adult lives with a single host.

Some parasites have little contact with their hosts. For example, North American cowbirds take over the nests of other birds by laying their eggs in them and then letting the host birds raise their young.

From the host's point of view, parasites are harmful. But at the population level, parasites can promote biodiversity by increasing species richness, and they help to keep their hosts' populations in check.

Like predator–prey interactions, parasite–host interactions can lead to coevolutionary change. For example, malaria is caused by a parasite spread by the bites of a certain mosquito species. The parasite invades red blood cells, which are destroyed every few days when they are swept into the spleen. However, through coevolution, the malaria parasite developed an adaptation that keeps it from being swept into the spleen. The parasite produces a sticky protein nodule that attaches the cell it has infected to the wall of a blood vessel.

However, the body's immune system detects the foreign protein on the blood vessel wall and sends antibodies to attack it. Through coevolution, the malaria parasite has in turn developed a defense against this attack. It produces thousands of different versions of the sticky protein that keep it attached to the blood vessel wall. By the time the immune system recognizes and attacks one type of the protein, the parasite has switched to another type.

ullstein-Nill/Peter Arnold, Inc.

Figure 5-3 *Coevolution.* A Langohrfledermaus bat hunting a moth. Long-term interactions between bats and their prey such as moths and butterflies can lead to coevolution, as the bats evolve traits that increase their chances of getting a meal and the moths evolve traits that help them avoid being eaten.

PhotoAlto/SuperStock

U.S. Fish and Wildlife Service Photo

Figure 5-4 *Parasitism:* **(a)** Healthy tree on the left and an unhealthy one on the right, which is infested with parasitic mistletoe. **(b)** Blood-sucking parasitic sea lampreys attached to an adult lake trout from the Great Lakes (USA).

(a) Oxpeckers and black rhinoceros **(b)** Clownfish and sea anemone

Figure 5-5 Examples of *mutualism.* **(a)** Oxpeckers (or tickbirds) feed on parasitic ticks that infest large, thick-skinned animals such as the endangered black rhinoceros. **(b)** A clownfish gains protection and food by living among deadly stinging sea anemones and helps protect the anemones from some of their predators. (Oxpeckers and black rhinoceros: Joe McDonald/Tom Stack & Associates; clownfish an sea anemone: Fred Bavendam/Peter Arnold, Inc.)

In Some Interactions, Both Species Benefit

In **mutualism,** two species behave in ways that benefit both by providing each with food, shelter, or some other resource. For example, honeybees, caterpillars, butterflies, and other insects feed on a male flower's nectar, picking up pollen in the process, and then pollinating female flowers when they feed on them.

Figure 5-5 shows two examples of mutualistic relationships that combine *nutrition* and *protection.* One involves birds that ride on the backs of large animals like African buffalo, elephants, and rhinoceroses (Figure 5-5a). The birds remove and eat parasites and pests (such as ticks and flies) from the animal's body and often make noises warning the larger animals when predators approach.

A second example involves the clownfish species (Figure 5-5b), which live within sea anemones, whose tentacles sting and paralyze most fish that touch them. The clownfish, which are not harmed by the tentacles, gain protection from predators and feed on the detritus left from the anemones' meals. The sea anemones benefit because the clownfish protect them from some of their predators.

In *gut inhabitant mutualism,* vast armies of bacteria in the digestive systems of animals help to break down (digest) their hosts' food. In turn, the bacteria receive a sheltered habitat and food from their host. Hundreds of millions of bacteria in your gut secrete enzymes that help digest the food you eat. Cows and termites are able to digest the cellulose in plant tissues they eat because of the large number of microorganisms, mostly bacteria, that live in their guts.

It is tempting to think of mutualism as an example of cooperation between species. In reality, each species benefits by unintentionally exploiting the other as a result of traits they obtained through natural selection.

Luiz C. Marigo/Peter Arnold, Inc.

Figure 5-6 In an example of *commensalism,* this bromeliad—an epiphyte, or air plant, in Brazil's Atlantic tropical rain forest—roots on the trunk of a tree, rather than in soil, without penetrating or harming the tree. In this interaction, the epiphyte gains access to water, other nutrient debris, and sunlight; the tree apparently remains unharmed.

In Some Interactions, One Species Benefits and the Other Is Not Harmed

Commensalism is an interaction that benefits one species but has little, if any, effect on the other. For example, in tropical forests certain kinds of silverfish insects move along with columns of army ants to share the food obtained by the ants in their raids. The army ants receive no apparent harm or benefit from the silverfish.

Another example involves plants called *epiphytes* (such as certain types of orchids and bromeliads), which attach themselves to the trunks or branches of large trees in tropical and subtropical forests (Figure 5-6). These *air plants* benefit by having a solid base on which to grow. They also live in an elevated spot that gives them better access to sunlight, water from the humid air and rain, and nutrients falling from the tree's upper leaves and limbs. Their presence apparently does not harm the tree.

CENGAGE**NOW**™ Review the way in which species can interact and see the results of an experiment on species interaction at CengageNOW™.

5-2 How Can Natural Selection Reduce Competition between Species?

▶ **CONCEPT 5-2 Some species develop adaptations that allow them to reduce or avoid competition with other species for resources.**

Some Species Evolve Ways to Share Resources

Over a time scale long enough for natural selection to occur, populations of some species competing for the same resources develop adaptations through natural selection that allow them to reduce or avoid such competition (**Concept 5-2**). In other words, some species evolve to reduce niche overlap. One way this happens is through **resource partitioning.** It occurs when species competing for similar scarce resources evolve specialized traits that allow them to use shared resources at different times, in different ways, or in different places. For example, through natural selection, the fairly broad and overlapping niches of two competing species (Figure 5-7, top) can reduce their niche overlap by becoming more specialized (Figure 5-7, bottom).

Figure 5-8 shows resource partitioning by some insect-eating bird species. In this case, their adaptations allow them to reduce competition by feeding in different portions of the same tree species and by feeding on different insect species. Figure 4-13 (p. 93) shows how bird species in a coastal wetland have

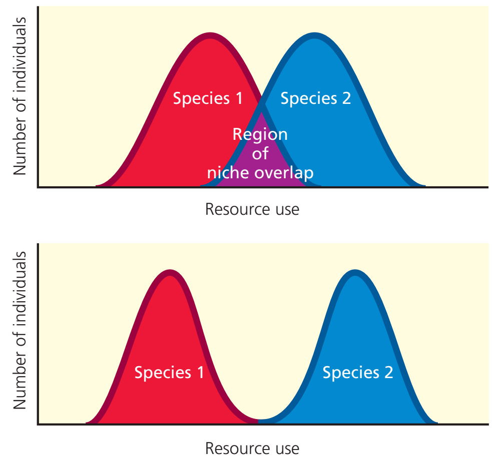


Figure 5-7 Competing species can evolve to reduce niche overlap. The top diagram shows the overlapping niches of two competing species. The bottom diagram shows that through natural selection, the niches of the two species become separated and more specialized (narrower) as the species develop adaptations that allow them to avoid or reduce competition for the same resources.

Figure 5-8 *Sharing the wealth: resource partitioning* of five species of insect-eating warblers in the spruce forests of the U.S. state of Maine. Each species minimizes competition for food with the others by spending at least half its feeding time in a distinct portion (shaded areas) of the spruce trees, and by consuming different insect species. (After R. H. MacArthur, "Population Ecology of Some Warblers in Northeastern Coniferous Forests," *Ecology* 36 (1958): 533–536.)

evolved specialized feeding niches, thereby reducing their competition for resources.

Another example of resource partitioning through natural selection involves birds called honeycreepers that live in the U. S. state of Hawaii. Long ago these birds started from a single ancestor species. But because of evolution by natural selection, there are now numerous honeycreeper species. Each has a different type of beak specialized to feed on certain food sources, such as specific types of insects, nectar from particular types of flowers, and certain types of seeds and fruit (Figure 5-9). This is an example of a process called *evolutionary divergence.*

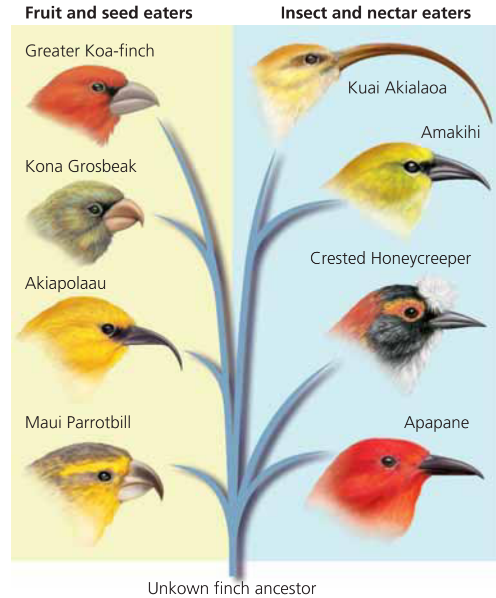


Figure 5-9 *Specialist species of honeycreepers.* Evolutionary divergence of honeycreepers into species with specialized ecological niches has reduced competition between these species. Each species has evolved a beak specialized to take advantage of certain types of food resources.

5-3 What Limits the Growth of Populations?

CONCEPT 5-3 No population can continue to grow indefinitely because of limitations on resources and because of competition among species for those resources.

Populations Have Certain Characteristics

Populations differ in factors such as their *distribution, numbers, age structure* (proportions of individuals in different age groups), and *density* (number of individuals in a certain space). **Population dynamics** is a study of how these characteristics of populations change in response to changes in environmental conditions. Examples of such conditions are temperature, presence of disease organisms or harmful chemicals, resource availability, and arrival or disappearance of competing species.

Studying the population dynamics of southern sea otter populations (**Core Case Study**) and their interactions with other species has helped us understand the ecological importance of this keystone species. Let's look at some of the characteristics of populations in more detail.

CORE CASE STUDY

Most Populations Live Together in Clumps or Patches

Let's begin our study of population dynamics with how individuals in populations are distributed or dispersed within a particular area or volume. Three general patterns of *population distribution* or *dispersion* in a habitat are *clumping, uniform dispersion,* and *random dispersion* (Figure 5-10).

In most populations, individuals of a species live together in clumps or patches (Figure 5-10a). Examples are patches of desert vegetation around springs, cottonwood trees clustered along streams, wolf packs, flocks of birds, and schools of fish. The locations and sizes of these clumps and patches vary with the availability of resources. Southern sea otters (Figure 5-1, top left), for example, are usually found in groups known as rafts or pods ranging in size from a few to several hundred animals.

Why clumping? Several reasons: *First,* the resources a species needs vary greatly in availability from place to place, so the species tends to cluster where the resources are available. *Second,* individuals moving in groups have a better chance of encountering patches or clumps of resources, such as water and vegetation, than they would searching for the resources on their own. *Third,* living in groups protects some animals from predators. *Fourth,* hunting in packs gives some predators a better chance of finding and catching prey. *Fifth,* some species form temporary groups for mating and caring for young.

(a) Clumped (elephants) **(b)** Uniform (creosote bush) **(c)** Random (dandelions)

Figure 5-10 Generalized *dispersion patterns* for individuals in a population throughout their habitat. The most common pattern is *clumps* of members of a population scattered throughout their habitat, mostly because resources are usually found in patches. **Question:** Why do you think the creosote bushes are uniformly spaced while the dandelions are not?

THINKING ABOUT
Population Distribution

Why do you think living in packs would help some predators to find and kill their prey?

Some species maintain a fairly constant distance between individuals. Because of its sparse distribution pattern, creosote bushes in a desert (Figure 5-10b) have better access to scarce water resources. Organisms with a random distribution (Figure 5-10c) are fairly rare. The living world is mostly clumpy and patchy.

Populations Can Grow, Shrink, or Remain Stable

Over time, the number of individuals in a population may increase, decrease, remain about the same, or go up and down in cycles in response to changes in environmental conditions. Four variables—*births, deaths, immigration,* and *emigration*—govern changes in population size. A population increases by birth and immigration (arrival of individuals from outside the population) and decreases by death and emigration (departure of individuals from the population):

$$\text{Population change} = (\text{Births} + \text{Immigration}) - (\text{Deaths} + \text{Emigration})$$

In natural systems, species that are able to move can leave or *emigrate* from an area where their habitat has been degraded or destroyed and *immigrate* to another area where resources are more plentiful.

A population's **age structure**—the proportions of individuals at various ages—can have a strong effect on how rapidly it increases or decreases in size. Age structures are usually described in terms of organisms not mature enough to reproduce (the *pre-reproductive age*), those capable of reproduction (the *reproductive stage*), and those too old to reproduce (the *post-reproductive stage*).

The size of a population will likely increase if it is made up mostly of individuals in their reproductive stage or soon to enter this stage. In contrast, a population dominated by individuals past their reproductive stage will tend to decrease over time. Excluding emigration and immigration, the size of a population with a fairly even distribution among these three age groups tends to remain stable because reproduction by younger individuals will be roughly balanced by the deaths of older individuals.

No Population Can Grow Indefinitely: J-Curves and S-Curves

Species vary in their **biotic potential** or capacity for population growth under ideal conditions. Generally, populations of species with large individuals, such as elephants and blue whales, have a low biotic potential while those of small individuals, such as bacteria and insects, have a high biotic potential.

The **intrinsic rate of increase (*r*)** is the rate at which the population of a species would grow if it had unlimited resources. Individuals in populations with a high intrinsic rate of growth typically *reproduce early in life, have short generation times* (the time between successive generations), *can reproduce many times,* and *have many offspring each time they reproduce.*

Some species have an astounding biotic potential. With no controls on population growth, a species of bacteria that can reproduce every 20 minutes would generate enough offspring to form a layer 0.3 meter (1 foot) deep over the entire earth's surface in only 36 hours!

Fortunately, this is not a realistic scenario. Research reveals that no population can grow indefinitely because of limitations on resources and competition with populations of other species for those resources (**Concept 5-3**). In the real world, a rapidly growing population reaches some size limit imposed by one or more *limiting factors,* such as light, water, space, or nutrients, or by exposure to too many competitors, predators, or infectious diseases. *There are always limits to population growth in nature.* This is one of nature's four **scientific principles of sustainability** (see back cover and **Concept 1-6**, p. 23). Sea otters, for example, face extinction because of low biotic potential and other factors (Science Focus, p. 110).

SCIENCE FOCUS

Why Are Protected Sea Otters Making a Slow Comeback?

The southern sea otter (**Core Case Study**) does not have a high biotic potential for several reasons. Female southern sea otters reach sexual maturity between 2 and 5 years of age, can reproduce until age 15, and typically each produce only one pup a year.

CORE CASE STUDY

The population size of southern sea otters has fluctuated in response to changes in environmental conditions. One such change has been a rise in populations of orcas (killer whales) that feed on them. Scientists hypothesize that orcas feed more on southern sea otters when populations of their normal prey, sea lions and seals, decline.

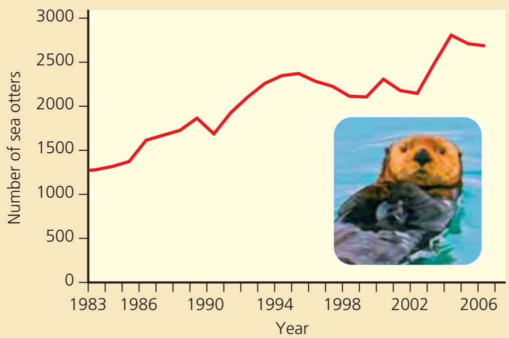


Figure 5-B Population size of southern sea otters off the coast of the U.S. state of California, 1983–2007. According to the U.S. Fish and Wildlife Service, the sea otter population would have to reach about 8,400 animals before it can be removed from the endangered species list. (Data from U.S. Geological Survey)

Another factor may be deaths from parasites known to breed in cats. Scientists hypothesize that some sea otters may be dying because California cat owners flush used cat litter containing these parasites down their toilets or dump it in storm drains that empty into coastal waters.

Thorny-headed worms from seabirds are also known to be killing sea otters, as are toxic algae blooms triggered by urea, a key ingredient in fertilizer that washes into coastal waters. Toxins such as PCBs and other toxic chemicals released by human activities accumulate in the tissues of the shellfish on which otters feed and prove fatal to otters. The facts that sea otters feed at high trophic levels and live close to the shore makes them vulnerable to these and other pollutants in coastal waters. In other words, sea otters are *indicator species* that warn us of the condition of coastal waters in their habitat.

Some southern sea otters also die when they encounter oil spilled from ships. The entire California southern sea otter population could be wiped out by a large oil spill from a single tanker off the state's central coast. These factors plus a fairly low reproductive rate have hindered the ability of the endangered southern sea otter to rebuild its population (Figure 5-B).

Critical Thinking

How would you design a controlled experiment to test the hypothesis that parasites contained in cat litter that is flushed down toilets may be killing sea otters?

Environmental resistance is the combination of all factors that act to limit the growth of a population. Together, biotic potential and environmental resistance determine the **carrying capacity (*K*):** the maximum population of a given species that a particular habitat can sustain indefinitely without being degraded. The growth rate of a population decreases as its size nears the carrying capacity of its environment because resources such as food, water, and space begin to dwindle.

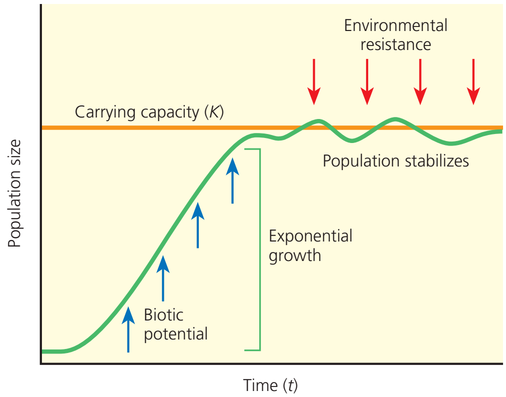
A population with few, if any, limitations on its resource supplies can grow exponentially at a fixed rate such as 1% or 2% per year. *Exponential* or *geometric growth* (Figure 1-1, p. 5) starts slowly but then accelerates as the population increases, because the base size of the population is increasing. Plotting the number of individuals against time yields a J-shaped growth curve (Figure 5-11, left half of curve).

Logistic growth involves rapid exponential population growth followed by a steady decrease in population growth until the population size levels off (Figure 5-11, right half of curve). This slowdown occurs as the population encounters environmental resistance from declining resources and other environmental factors and approaches the carrying capacity of its environment. After leveling off, a population with this type of growth typically fluctuates slightly above and below the carrying capacity. The size of such a population may also increase or decrease as the carrying capacity changes because of short- or long-term changes in environmental conditions.

A plot of the number of individuals against time yields a sigmoid, or S-shaped, logistic growth curve (the whole curve in Figure 5-11). Figure 5-12 depicts such a curve for sheep on the island of Tasmania, south of Australia, in the 19th century.

CENGAGENOW™ Learn how to estimate a population of butterflies and see a mouse population growing exponentially at CengageNOW.

Sometimes a species whose population has been kept in check mostly by natural predators is deliberately or accidentally transferred to a different ecosystem where it has few if any predators. For example, the *brown tree snake* is native to the Solomon Islands,



CENGAGENOW™ **Active Figure 5-11** No population can continue to increase in size indefinitely. *Exponential growth* (left half of the curve) occurs when resources are not limiting and a population can grow at its *intrinsic rate of increase* (*r*) or *biotic potential.* Such exponential growth is converted to *logistic growth,* in which the growth rate decreases as the population becomes larger and faces environmental resistance. Over time, the population size stabilizes at or near the *carrying capacity* (*K*) of its environment, which results in a sigmoid (S-shaped) population growth curve. Depending on resource availability, the size of a population often fluctuates around its carrying capacity, although a population may temporarily exceed its carrying capacity and then suffer a sharp decline or crash in its numbers. *See an animation based on this figure at* CengageNOW. **Question:** What is an example of environmental resistance that humans have not been able to overcome?

New Guinea, and Australia. After World War II, a few of these snakes stowed away on military planes going to the island of Guam. With no enemies or rivals in Guam, they have multiplied exponentially for several decades and have wiped out 8 of Guam's 11 native forest bird species. Their venomous bites have also sent large numbers of people to emergency rooms. Sooner or later the brown tree snake will use up most of its food supply in Guam and will then decline in numbers, but meanwhile they are causing serious ecological and economic damage. They may also end up on islands such as those in Hawaii, where they could devastate bird populations.

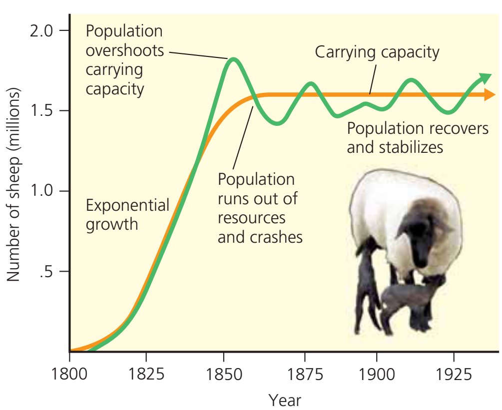


Figure 5-12 *Logistic growth* of a sheep population on the island of Tasmania between 1800 and 1925. After sheep were introduced in 1800, their population grew exponentially, thanks to an ample food supply. By 1855, they had overshot the land's carrying capacity. Their numbers then stabilized and fluctuated around a carrying capacity of about 1.6 million sheep.

Changes in the population sizes of keystone species such as the southern sea otter (**Core Case Study**) and the American alligator (Chapter 4 Core Case Study, p. 77) can alter the species composition and biodiversity of an ecosystem. For example, a decline in the population of the southern sea otter caused a decline in the populations of species dependent on them, including the giant kelp. This reduced species diversity of the kelp forest and altered its functional biodiversity by upsetting its food webs and reducing energy flows and nutrient cycling within the forest.

CORE CASE STUDY

THINKING ABOUT
Southern Sea Otters

CORE CASE STUDY

Name two species whose populations will likely decline if the population of southern sea otters in kelp beds declines sharply. Name a species whose population would increase if this happened.

When a Population Exceeds Its Habitat's Carrying Capacity, Its Population Can Crash

Some species do not make a smooth transition from exponential growth to logistic growth. Such populations use up their resource supplies and temporarily *overshoot,* or exceed, the carrying capacity of their environment. This occurs because of a *reproductive time lag*—the period needed for the birth rate to fall and the death rate to rise in response to resource overconsumption.

In such cases, the population suffers a *dieback,* or *crash,* unless the excess individuals can switch to new resources or move to an area with more resources. Such a crash occurred when reindeer were introduced onto a small island in the Bering Sea (Figure 5-13, p. 112).

The carrying capacity of an area or volume is not fixed. The carrying capacity of some areas can increase or decrease seasonally and from year to year because of variations in weather and other factors, including an abundance of predators and competitors. For example, a drought can decrease the amount of vegetation growing in an area supporting deer and other herbivores, and this would decrease the normal carrying capacity for those species.

Sometimes when a population exceeds the carrying capacity of an area, it causes damage that reduces the area's carrying capacity. For example, overgrazing by cattle on dry western lands in the United States has reduced grass cover in some areas. This has allowed sagebrush—which cattle cannot eat—to move in, thrive, and replace grasses, reducing the land's carrying capacity for cattle.

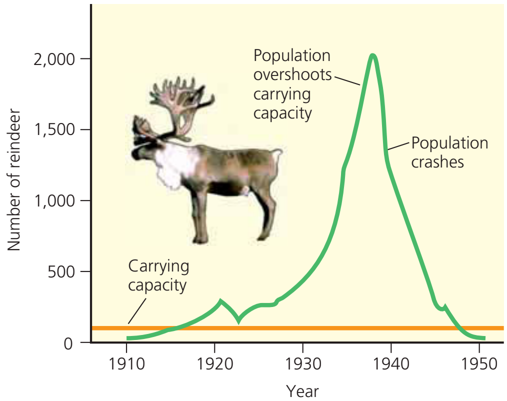


Figure 5-13 Exponential growth, overshoot, and population crash of reindeer introduced to the small Bering Sea island of St. Paul. When 26 reindeer (24 of them female) were introduced in 1910, lichens, mosses, and other food sources were plentiful. By 1935, the herd size had soared to 2,000, overshooting the island's carrying capacity. This led to a population crash, when the herd size plummeted to only 8 reindeer by 1950. **Question:** Why do you think this population grew fast and crashed, unlike the sheep in Figure 5-12?

THINKING ABOUT
Population Overshoot and Human Ecological Footprints

Humanity's ecological footprint is about 25% larger than the earth's ecological capacity (Figure 1-10, bottom, p. 15) and is growing rapidly. If this keeps up, is the curve for future human population growth more likely to resemble Figure 5-12 or Figure 5-13? Explain.

Species Have Different Reproductive Patterns

Species have different reproductive patterns that can help enhance their survival. Species with a capacity for a high rate of population increase (*r*) are called **r-selected species** (Figure 5-14). These species have many, usually small, offspring and give them little or no parental care or protection. They overcome typically massive losses of offspring by producing so many offspring that a few will likely survive to reproduce many more offspring to begin this reproductive pattern again. Examples include algae, bacteria, rodents, frogs, turtles, annual plants (such as dandelions), and most insects.

Such species tend to be *opportunists.* They reproduce and disperse rapidly when conditions are favorable or when a disturbance opens up a new habitat or niche for invasion. Environmental changes caused by disturbances, such as fires, clear-cutting, and volcanic eruptions, can allow opportunist species to gain a foothold. However, once established, their populations may crash because of unfavorable changes in environmental conditions or invasion by more competitive species. This helps to explain why most opportunist species go through irregular and unstable boom-and-bust cycles in their population sizes.

At the other extreme are *competitor* or **K-selected species** (Figure 5-14). They tend to reproduce later in life and have a small number of offspring with fairly long life spans. Typically, for K-selected mammals, the offspring develop inside their mothers (where they are safe), are born fairly large, mature slowly, and are cared for and protected by one or both parents, and in some cases by living in herds or groups, until they reach reproductive age. This reproductive pattern results in a few big and strong individuals that can compete for resources and reproduce a few young to begin the cycle again.

Such species are called K-selected species because they tend to do well in competitive conditions when their population size is near the carrying capacity (*K*) of their environment. Their populations typically follow a logistic growth curve (Figure 5-12).

Most large mammals (such as elephants, whales, and humans), birds of prey, and large and long-lived plants (such as the saguaro cactus, and most tropical rain forest trees) are K-selected species. Ocean fish such as orange roughy and swordfish, which are now being depleted by overfishing, are also K-selected. Many of these species—especially those with long times between generations and low reproductive rates like elephants, rhinoceroses, and sharks—are prone to extinction.

Most organisms have reproductive patterns between the extremes of r-selected and K-selected species. In agriculture we raise both r-selected species (crops) and K-selected species (livestock). Individuals of species with different reproductive strategies tend to have different *life expectancies,* or expected lengths of life.

THINKING ABOUT
r-Selected and K-selected Species

If the earth experiences significant warming during this century as projected, is the resulting climate change likely to favor r-selected or K-selected species? Explain.

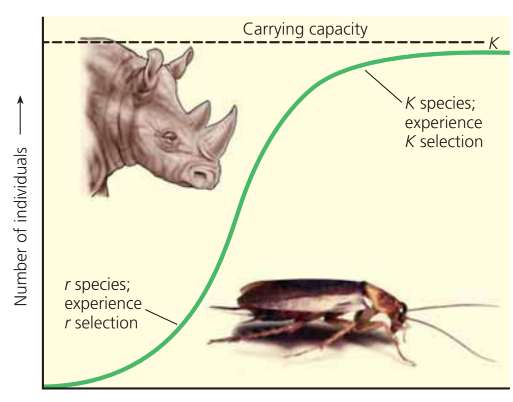


Figure 5-14 Positions of *r-selected* and *K-selected* species on the sigmoid (S-shaped) population growth curve.

Genetic Diversity Can Affect the Size of Small Populations

In most large populations, genetic diversity is fairly constant and the loss or addition of some individuals has little effect on the total gene pool. However, several genetic factors can play a role in the loss of genetic diversity and the survival of small, isolated populations.

One such factor, called the *founder effect,* can occur when a few individuals in a population colonize a new habitat that is geographically isolated from other members of the population (Figure 4-8, p. 87). In such cases, limited genetic diversity or variability may threaten the survival of the colonizing population.

Another factor is a *demographic bottleneck.* It occurs when only a few individuals in a population survive a catastrophe such as a fire or hurricane, as if they had passed through the narrow neck of a bottle. Lack of genetic diversity may limit the ability of these individuals to rebuild the population. Even if the population is able to increase in size, its decreased genetic diversity may lead to an increase in the frequency of harmful genetic diseases.

A third factor is *genetic drift.* It involves random changes in the gene frequencies in a population that can lead to unequal reproductive success. For example, some individuals may breed more than others do and their genes may eventually dominate the gene pool of the population. This change in gene frequency could help or hinder the survival of the population. The founder effect is one cause of genetic drift.

A fourth factor is *inbreeding.* It occurs when individuals in a small population mate with one another. This can occur when a population passes through a demographic bottleneck. This can increase the frequency of defective genes within a population and affect its long-term survival.

Conservation biologists use the concepts of founder effects, demographic bottleneck, genetic drift, inbreeding, and island biogeography (Science Focus, p. 90) to estimate the *minimum viable population size* of rare and endangered species: the number of individuals such populations need for long-term survival.

Under Some Circumstances Population Density Affects Population Size

Population density is the number of individuals in a population found in a particular area or volume. Some factors that limit population growth have a greater effect as a population's density increases. Examples of such *density-dependent population controls* include predation, parasitism, infectious disease, and competition for resources.

Higher population density may help sexually reproducing individuals find mates, but it can also lead to increased competition for mates, food, living space, water, sunlight, and other resources. High population density can help to shield some members from predators, but it can also make large groups such as schools of fish vulnerable to human harvesting methods. In addition, close contact among individuals in dense populations can increase the transmission of parasites and infectious diseases. When population density decreases, the opposite effects occur. Density-dependent factors tend to regulate a population at a fairly constant size, often near the carrying capacity of its environment.

Some factors—mostly abiotic—that can kill members of a population are *density independent.* In other words, their effect is not dependent on the density of the population. For example, a severe freeze in late spring can kill many individuals in a plant population or a population of monarch butterflies (Figure 3-A, left, p. 54), regardless of their density. Other such factors include floods, hurricanes, fire, pollution, and habitat destruction, such as clearing a forest of its trees or filling in a wetland.

Several Different Types of Population Change Occur in Nature

In nature, we find four general patterns of variation in population size: *stable, irruptive, cyclic,* and *irregular.* A species whose population size fluctuates slightly above and below its carrying capacity is said to have a fairly stable population size (Figure 5-12). Such stability is characteristic of many species found in undisturbed tropical rain forests, where average temperature and rainfall vary little from year to year.

For some species, population growth may occasionally explode, or *irrupt,* to a high peak and then crash to a more stable lower level or in some cases to a very low level. Many short-lived, rapidly reproducing species such as algae and many insects have irruptive population cycles that are linked to seasonal changes in weather or nutrient availability. For example, in temperate climates, insect populations grow rapidly during the spring and summer and then crash during the hard frosts of winter.

A third type of fluctuation consists of regular *cyclic fluctuations,* or *boom-and-bust cycles,* of population size over a time period. Examples are lemmings, whose populations rise and fall every 3–4 years, and lynx and snowshoe hare, whose populations generally rise and fall in a 10-year cycle. Ecologists distinguish between *top-down population regulation,* through predation, and *bottom-up population regulation,* in which the size of predator and prey populations is controlled by the scarcity of one or more resources (Figure 5-15, p. 114).

Finally, some populations appear to have *irregular* changes in population size, with no recurring pattern. Some scientists attribute this irregularity to chaos in

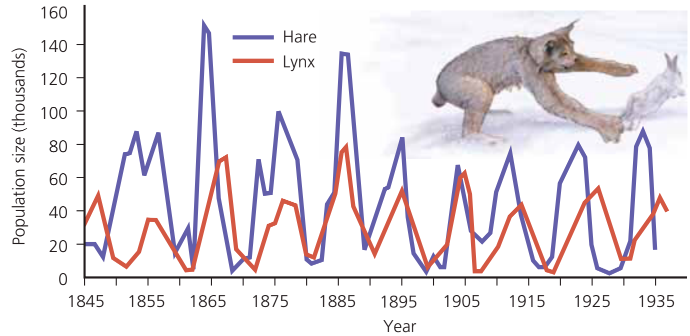


Figure 5-15 Population cycles for the snowshoe hare and Canada lynx. At one time, scientists believed these curves provided circumstantial evidence that these predator and prey populations regulated one another. More recent research suggests that the periodic swings in the hare population are caused by a combination of *top-down population control*—through predation by lynx and other predators—and *bottom-up population control,* in which changes in the availability of the food supply for hares help determine hare population size, which in turn helps determine the lynx population size. (Data from D. A. MacLulich)

such systems. Others scientists contend that it may represent fluctuations in response to periodic catastrophic population crashes due to severe winter weather.

Humans Are Not Exempt from Nature's Population Controls

Humans are not exempt from population overshoot and dieback. Ireland experienced a population crash after a fungus destroyed the potato crop in 1845. About 1 million people died from hunger or diseases related to malnutrition, and 3 million people migrated to other countries, mostly the United States.

During the 14th century the *bubonic plague* spread through densely populated European cities and killed at least 25 million people. The bacterium causing this disease normally lives in rodents. It was transferred to humans by fleas that fed on infected rodents and then bit humans. The disease spread like wildfire through crowded cities, where sanitary conditions were poor and rats were abundant.

Currently, the world is experiencing a global epidemic of eventually fatal AIDS, caused by infection with the human immunodeficiency virus (HIV). Between 1981 and 2007, AIDS killed more than 25 million people (584,000 in the United states) and claims another 2.1 million lives each year—an average of four deaths per minute.

So far, technological, social, and other cultural changes have extended the earth's carrying capacity for the human species. We have increased food production and used large amounts of energy and matter resources to occupy normally uninhabitable areas. As humans spread into larger areas, they interact with and attempt to control the populations of other species such as alligators (Chapter 4 Core Case Study, p. 77) and white-tailed deer in the United States (Case Study, at right), as these two case studies reveal.

Some say we can keep expanding our ecological footprint indefinitely, mostly because of our technological ingenuity. Others say that sooner or later, we will reach the limits that nature always imposes on populations.

HOW WOULD YOU VOTE?

Can we continue to expand the earth's carrying capacity for humans? Cast your vote online at **academic.cengage.com/biology/miller**.

THINKING ABOUT
The Human Species

If the human species were to suffer a sharp population decline, name three types of species that might move in to occupy part of our ecological niche.

■ CASE STUDY

Exploding White-Tailed Deer Populations in the United States

By 1900, habitat destruction and uncontrolled hunting had reduced the white-tailed deer population in the United States to about 500,000 animals. In the 1920s and 1930s, laws were passed to protect the remaining deer. Hunting was restricted and predators such as wolves and mountain lions that preyed on the deer were nearly eliminated.

These protections worked, and some suburbanites and farmers say perhaps they worked too well. Today there are 25–30 million white-tailed deer in the United States. During the last 50 years, large numbers of Americans have moved into the wooded habitat of deer and provided them with flowers, garden crops, and other plants they like to eat.

Deer like to live in the woods for security and go to nearby fields, orchards, lawns, and gardens for food. Border areas between two ecosystems such as forests and fields are called *edge* habitat, and suburbanization has created an all-you-can-eat edge paradise for deer. Their populations in such areas have soared. In some forests, they are consuming native ground cover vegetation and allowing nonnative weed species to take over. Deer also spread Lyme disease (carried by deer ticks) to humans.

In addition, in deer–vehicle collisions, deer accidentally kill and injure more people each year in the United

States than do any other wild animals. Each year, these 1.5 million accidents injure at least 14,000 people and kill at least 200 (up from 101 deaths in 1993).

There are no easy answers to the deer population problem in the suburbs. Changing hunting regulations to allow killing of more female deer cuts down the overall deer population. But these actions have little effect on deer in suburban areas because it is too dangerous to allow widespread hunting with guns in such populated communities. Some areas have hired experienced and licensed archers who use bows and arrows to help reduce deer numbers. To protect nearby residents the archers hunt from elevated tree stands and shoot their arrows only downward. However, animal activists strongly oppose killing deer on ethical grounds, arguing that this is cruel and inhumane treatment.

Some communities spray the scent of deer predators or rotting deer meat in edge areas to scare off deer. Others use electronic equipment that emits high-frequency sounds, which humans cannot hear, for the same purpose. Some homeowners surround their gardens and yards with a high black plastic mesh fencing that is invisible from a distance. Such deterrents may protect one area, but cause the deer to seek food in someone else's yard or garden.

Deer can also be trapped and moved from one area to another, but this is expensive and must be repeated whenever deer move back into an area. Also, there are questions concerning where to move the deer and how to pay for such programs.

Should we put deer on birth control? Darts loaded with a contraceptive could be shot into female deer to hold down their birth rates. But this is expensive and must be repeated every year. One possibility is an experimental single-shot contraceptive vaccine that causes females to stop producing eggs for several years. Another approach is to trap dominant males and use chemical injections to sterilize them. Both these approaches will require years of testing.

Meanwhile, suburbanites can expect deer to chow down on their shrubs, flowers, and garden plants unless they can protect their properties with high, deer-proof fences or other methods. Deer have to eat every day just as we do. Suburban dwellers might consider not planting their yards with plants that deer like to eat.

THINKING ABOUT
White-Tailed Deer

Some blame the white-tailed deer for invading farms and suburban yards and gardens to eat food that humans have made easily available to them. Others say humans are mostly to blame because they have invaded deer territory, eliminated most of the predators that kept their populations under control, and provided the deer with plenty to eat in their lawns and gardens. Which view do you hold? Do you see a solution to this problem?

5-4 How Do Communities and Ecosystems Respond to Changing Environmental Conditions?

▶ **CONCEPT 5-4 The structure and species composition of communities and ecosystems change in response to changing environmental conditions through a process called ecological succession.**

Communities and Ecosystems Change over Time: Ecological Succession

We have seen how changes in environmental conditions (such as loss of habitat) can reduce access to key resources and how invasions by competing species can lead to increases or decreases in species population sizes. Next, we look at how the types and numbers of species in biological communities change in response to changing environmental conditions such as a fires, climate change, and the clearing of forests to plant crops.

Mature forests and other ecosystems do not spring up from bare rock or bare soil. Instead, they undergo changes in their species composition over long periods of time. The gradual change in species composition in a given area is called **ecological succession,** during which, some species colonize an area and their populations become more numerous, while populations of other species decline and may even disappear. In this process, *colonizing* or *pioneer species* arrive first. As environmental conditions change, they are replaced by other species, and later these species may be replaced by another set of species.

Ecologists recognize two main types of ecological succession, depending on the conditions present at the beginning of the process. **Primary succession** involves the gradual establishment of biotic communities in lifeless areas where there is no soil in a terrestrial ecosystem or no bottom sediment in an aquatic ecosystem. The other more common type of ecological succession is called **secondary succession,** in which a series of communities or ecosystems with different species develop in places containing soil or bottom sediment. As part of the earth's natural capital, both types of succession are examples of *natural ecological restoration,* in which various forms life adapt to changes in environmental conditions, resulting in changes to the species composition, population size, and biodiversity in a given area.

Some Ecosystems Start from Scratch: Primary Succession

Primary succession begins with an essentially lifeless area where there is no soil in a terrestrial system (Figure 5-16) or bottom sediment in an aquatic system. Examples include bare rock exposed by a retreating glacier or severe soil erosion, newly cooled lava from a volcanic eruption, an abandoned highway or parking lot, and a newly created shallow pond or reservoir.

Primary succession usually takes a long time because there is no fertile soil to provide the nutrients needed to establish a plant community. Over time, bare rock *weathers* by crumbling into particles and releasing nutrients. Physical weathering occurs when a rock is fragmented, as water in its cracks freezes and expands. Rocks also undergo chemical weathering, reacting with substances in the atmosphere or with precipitation, which can break down the rock's surface material.

The slow process of soil formation begins when *pioneer* or *early successional species* arrive and attach themselves to inhospitable patches of the weathered rock. Examples are lichens and mosses whose seeds or spores are distributed by the wind and carried by animals. A lichen consists of an alga and a fungus interacting in a mutualistic relationship. The fungi in the lichens provide protection and support for the algae, which, through photosynthesis, provide sugar nutrients for both of the interacting species.

These tough *early successional plant species* start the long process of soil formation by trapping wind-blown soil particles and tiny pieces of detritus, and adding their own wastes and dead bodies. They also secrete mild acids that further fragment and break down the rock. As the lichens spread over the rock, drought-resistant and sun-loving mosses start growing in cracks. As the mosses spread, they form a mat that traps moisture, much like a sponge. When the lichens and mosses die, their decomposing remains add to the growing thin layer of nutrients.

After hundreds to thousands of years, the soil may be deep and fertile enough to store the moisture and nutrients needed to support the growth of *midsuccessional plant species* such as herbs, grasses, and low shrubs. As the shrubs grow and create shade, the lichens and mosses die and decay from lack of sunlight. Next, trees that need lots of sunlight and are adapted to the area's climate and soil usually replace the grasses and shrubs.

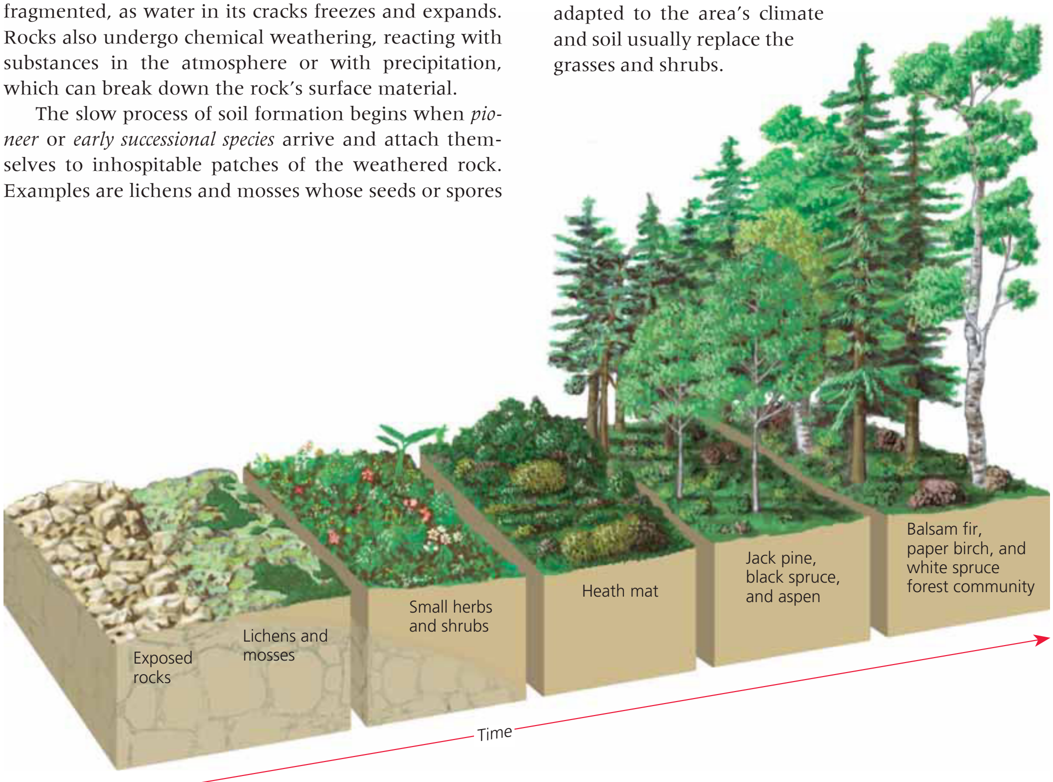


Figure 5-16 *Primary ecological succession.* Over almost a thousand years, plant communities developed, starting on bare rock exposed by a retreating glacier on Isle Royal, Michigan (USA) in northern Lake Superior. The details of this process vary from one site to another. **Question:** What are two ways in which lichens, mosses, and plants might get started growing on bare rock?

As these tree species grow and create shade, they are replaced by *late successional plant species* (mostly trees) that can tolerate shade. Unless fire, flooding, severe erosion, tree cutting, climate change, or other natural or human processes disturb the area, what was once bare rock becomes a complex forest community or ecosystem (Figure 5-16).

Primary succession can also take place in a newly created small pond, starting with an influx of sediments and nutrients in runoff from the surrounding land. This sediment can support seeds or spores of plants carried to the pond by winds, birds, or other animals. Over time, this process can transform the pond first into a marsh and eventually to dry land.

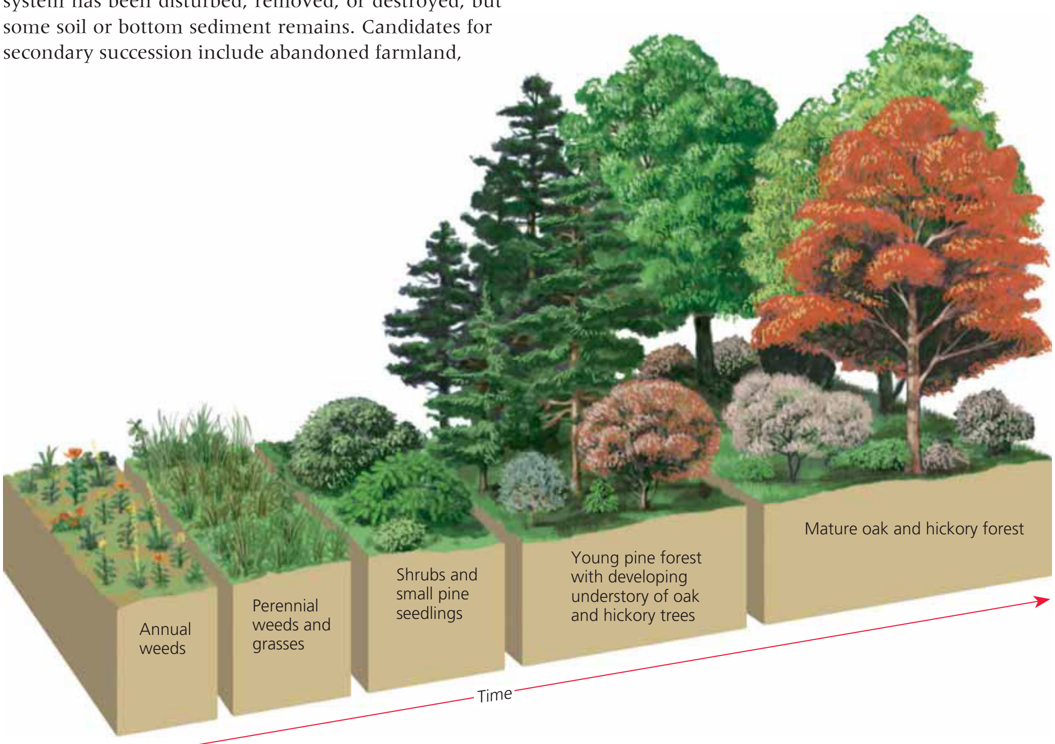
Some Ecosystems Do Not Have to Start from Scratch: Secondary Succession

Secondary succession begins in an area where an ecosystem has been disturbed, removed, or destroyed, but some soil or bottom sediment remains. Candidates for secondary succession include abandoned farmland, burned or cut forests, heavily polluted streams, and land that has been flooded. In the soil that remains on disturbed land systems, new vegetation can germinate, usually within a few weeks, from seeds already in the soil and from those imported by wind, birds, and other animals.

In the central, or Piedmont, region of the U.S. state of North Carolina, European settlers cleared many of the mature native oak and hickory forests and planted the land with crops. Later, they abandoned some of this farmland because of erosion and loss of soil nutrients. Figure 5-17 shows one way in which such abandoned farmland has undergone secondary succession over 150–200 years.

CENGAGENOW™ Explore the difference between primary and secondary succession at CengageNOW.

Descriptions of ecological succession usually focus on changes in vegetation. But these changes in turn affect food and shelter for various types of animals. As a consequence, the numbers and types of animals and



CENGAGENOW™ **Active Figure 5-17** *Natural ecological restoration of disturbed land.* Secondary ecological succession of plant communities on an abandoned farm field in the U.S. state of North Carolina. It took 150–200 years after the farmland was abandoned for the area to become covered with a mature oak and hickory forest. A new disturbance, such as deforestation or fire, would create conditions favoring pioneer species such as annual weeds. In the absence of new disturbances, secondary succession would recur over time, but not necessarily in the same sequence shown here. **Questions:** Do you think the annual weeds (left) would continue to thrive in the mature forest (right)? Why or why not? *See an animation based on this figure at* CengageNOW.

SCIENCE FOCUS

How Do Species Replace One Another in Ecological Succession?

Ecologists have identified three factors that affect how and at what rate succession occurs. One is *facilitation,* in which one set of species makes an area suitable for species with different niche requirements, but less suitable for itself. For example, as lichens and mosses gradually build up soil on a rock in primary succession, herbs and grasses can colonize the site and crowd out the pioneer community of lichens and mosses.

A second factor is *inhibition,* in which some early species hinder the establishment and growth of other species. Inhibition often occurs when plants release toxic chemicals that reduce competition from other plants. For example, pine needles dropped by some species of pines can make the underlying soil acidic and inhospitable to other plant species. Succession then can proceed only when a fire, bulldozer, or other human or natural disturbance removes most of the inhibiting species.

A third factor is *tolerance,* in which late successional plants are largely unaffected by plants at earlier stages of succession because they are not in direct competition with them for key resources. For example, shade tolerant trees and other plants can thrive in the understory of a mature forest (Figure 5-17) because they do not need to compete with the taller species for access to sunlight.

Critical Thinking

Explain how tolerance can increase biodiversity by increasing species diversity and functional diversity (energy flow and chemical cycling) in an ecosystem.

decomposers also change. A key point is that primary succession (Figure 5-16) and secondary succession (Figure 5-17) tend to increase biodiversity and thus the sustainability of communities and ecosystems by increasing species richness and interactions among species. Such interactions in turn enhance sustainability by promoting population control and increasing the complexity of food webs for the energy flow and nutrient cycling that make up the functional component of biodiversity (Figure 4-2, p. 79). Ecologists have been conducting research to find out more about the factors involved in ecological succession (Science Focus, above)

During primary or secondary succession, environmental disturbances such as fires, hurricanes, clear-cutting of forests, plowing of grasslands, and invasions by nonnative species can interrupt a particular stage of succession, setting it back to an earlier stage. For example, the American alligator (Chapter 4 Core Case Study, p. 77) lives in ponds that would normally become filled in through natural selection. The alligator's movements keep bottom vegetation from growing, thus preventing such succession.

Succession Doesn't Follow a Predictable Path

According to traditional view, succession proceeds in an orderly sequence along an expected path until a certain stable type of *climax community* occupies an area. Such a community is dominated by a few long-lived plant species and is in balance with its environment. This equilibrium model of succession is what ecologists once meant when they talked about the *balance of nature.*

Over the last several decades, many ecologists have changed their views about balance and equilibrium in nature. Under the balance-of-nature view, a large terrestrial community or ecosystem undergoing succession eventually became covered with an expected type of climax vegetation such as a mature forest (Figures 5-16 and 5-17). There is a general tendency for succession to lead to more complex, diverse, and presumably stable ecosystems. But a close look at almost any terrestrial community or ecosystem reveals that it consists of an ever-changing mosaic of patches of vegetation at different stages of succession.

The current view is that we cannot predict the course of a given succession or view it as preordained progress toward an ideally adapted climax plant community or ecosystem. Rather, succession reflects the ongoing struggle by different species for enough light, nutrients, food, and space. Most ecologists now recognize that mature late-successional ecosystems are not in a state of permanent equilibrium, but rather a state of continual disturbance and change.

Living Systems Are Sustained through Constant Change

All living systems from a cell to the biosphere are dynamic systems that are constantly changing in response to changing environmental conditions. Continents move, the climate changes, and disturbances and succession change the composition of communities and ecosystems.

Living systems contain complex networks of positive and negative feedback loops (Figure 2-11, p. 45, and Figure 2-12, p. 45) that interact to provide some degree of stability, or sustainability, over each system's expected life span. This stability, or capacity to withstand external stress and disturbance, is maintained only by constant change in response to changing environmental conditions. For example, in a mature tropical rain forest, some trees die and others take their places. However, unless the forest is cut, burned, or otherwise destroyed, you would still recognize it as a tropical rain forest 50 or 100 years from now.

It is useful to distinguish among two aspects of stability in living systems. One is **inertia,** or **persistence:** the ability of a living system, such as a grassland or a forest, to survive moderate disturbances. A second factor is **resilience:** the ability of a living system to be restored through secondary succession after a moderate disturbance.

Evidence suggests that some ecosystems have one of these properties but not the other. For example, tropical rain forests have high species diversity and high inertia and thus are resistant to significant alteration or destruction. But once a large tract of tropical rain forest is severely damaged, the resilience of the resulting degraded ecosystem may be so low that the forest may not be restored by secondary ecological succession. One reason for this is that most of the nutrients in a tropical rain forest are stored in its vegetation, not in the soil as in most other terrestrial ecosystems. Once the nutrient-rich vegetation is gone, daily rains can remove most of the other nutrients left in the soil and thus prevent a tropical rain forest from regrowing on a large cleared area.

Another reason for why the rain forest cannot recover is that large-scale deforestation can change an area's climate by decreasing the input of water vapor from its trees into the atmosphere. Without such water vapor, rain decreases and the local climate gets warmer. Over many decades, this can allow for the development of a tropical grassland in the cleared area but not for the reestablishment of a tropical rain forest.

By contrast, grasslands are much less diverse than most forests, and consequently they have low inertia and can burn easily. However, because most of their plant matter is stored in underground roots, these ecosystems have high resilience and can recover quickly after a fire as their root systems produce new grasses. Grassland can be destroyed only if its roots are plowed up and something else is planted in its place, or if it is severely overgrazed by livestock or other herbivores.

Variations among species in resilience and inertia are yet another example of biodiversity—one aspect of natural capital that has allowed life on earth to sustain itself for billions of years.

However, there are limits to the stresses that ecosystems and global systems such as climate can take. As a result, such systems can reach a **tipping point,** where any additional stress can cause the system to change in an abrupt and usually irreversible way that often involves collapse. For example, once a certain number of trees have been eliminated from a stable tropical rain forest, it can crash and become a grassland. And continuing to warm the atmosphere by burning fossil fuels that emit CO_2 and cutting down tropical forests that help remove CO_2 could eventually change the global climate system in ways that could last for thousands of years.

Exceeding a tipping point is like falling off a cliff. There is no way back. One of the most urgent scientific research priorities is to identify these and other tipping points and to develop strategies to prevent natural systems from reaching their tipping points.

REVISITING Southern Sea Otters and Sustainabiliy

CORE CASE STUDY

SUSTAINABILITY

Before the arrival of European settlers on the North American west coast, the sea otter population was part of a complex ecosystem made up of bottom-dwelling creatures, kelp, otters, whales, and other species depending on one another for survival. Giant kelp forests served as food and shelter for sea urchins. Otters ate the sea urchins and other kelp eaters. Some species of whales and sharks ate the otters. And detritus from all these species helped to maintain the giant kelp forests. Each of these interacting populations was kept in check by, and helped to sustain, all others.

When humans arrived and began hunting the otters for their pelts, they probably did not know much about the intricate web of life beneath the ocean surface. But with the effects of overhunting, people realized they had done more than simply take otters. They had torn the web, disrupted an entire ecosystem, and triggered a loss of valuable natural resources and services, including biodiversity.

Populations of most plants and animals depend directly or indirectly on solar energy and each population plays a role in the cycling of nutrients in the ecosystems where they live. In addition, the biodiversity found in the variety of species in different terrestrial and aquatic ecosystems provides alternative paths for energy flow and nutrient cycling and better opportunities for natural selection as environmental conditions change. Disrupt these paths and we can decrease the various components of the biodiversity of ecosystems and the sizes of their populations.

In this chapter, we looked more closely at two **principles of sustainability**: *biodiversity promotes sustainability* and *there are always limits to population growth in nature.* Chapter 6 applies the concepts of biodiversity and population dynamics discussed in this chapter to the growth of the human population and its environmental impacts. Chapters 7 and 8 look more closely at biodiversity in the variety of terrestrial ecosystems (such as deserts, grasslands, and forests) and aquatic ecosystems (such as oceans, lakes, rivers, and wetlands) found on the earth.

We cannot command nature
except by obeying her.

SIR FRANCIS BACON

REVIEW

1. Review the Key Questions and Concepts for this chapter on p. 101. Explain how southern sea otters act as a keystone species in kelp beds. Explain why we should care about protecting this species from extinction. Explain why we should help to preserve kelp forests.

2. Define **interspecific competition, predation, parasitism, mutalism,** and **commensalism** and give an example of each. Explain how each of these species interactions can affect the population sizes of species in ecosystems. Distinguish between a **predator** and a **prey** and give an example of each. What is a **predator–prey relationship?** Describe four ways in which prey species can avoid their predators and four ways in which predators can capture these prey.

3. Define and give an example of **coevolution.**

4. Describe and give an example of **resource partitioning** and explain how it can increase species diversity.

5. What is **population dynamics?** Why do most populations live in clumps?

6. Describe four variables that govern changes in population size and write an equation showing how they interact. What is a population's **age structure** and what are three major age group categories? Distinguish among the **biotic potential, intrinsic rate of increase, exponential growth, environmental resistance, carrying capacity,** and **logistic growth** of a population, and use these concepts to explain why there are always limits to population growth in nature. Why are southern sea otters making a slow comeback and what factors can threaten this recovery? Define and give an example of a **population crash.** Explain why humans are not exempt from nature's population controls.

7. Distinguish between **r-selected species** and **K-selected species** and give an example of each type. Define **population density** and explain how it can affect the size of some but not all populations.

8. Describe the exploding white-tailed deer population problem in the United States and discuss options for dealing with it.

9. What is **ecological succession?** Distinguish between **primary ecological succession** and **secondary ecological succession** and give an example of each. Explain why succession does not follow a predictable path. In terms of stability, distinguish between **inertia (persistence)** and **resilience.** Explain how living systems achieve some degree of stability or sustainability by undergoing constant change in response to changing environmental conditions.

10. Explain how the role of the southern sea otter in its ecosystem (**Core Case Study**) illustrates the population control **principle of sustainability**.

CORE CASE STUDY

SUSTAINABILITY

Note: Key Terms are in **bold** type.

CRITICAL THINKING

1. What difference would it make if the southern sea otter (**Core Case Study**) became prematurely extinct because of human activities? What are three things we could do to help prevent the premature extinction of this species?

CORE CASE STUDY

2. Use the second law of thermodynamics (p. 43) to explain why predators are generally less abundant than their prey.

3. Explain why most species with a high capacity for population growth (high biotic potential) tend to have small individuals (such as bacteria and flies) while those with a low capacity for population growth tend to have large individuals (such as humans, elephants, and whales).

4. List three factors that have limited human population growth in the past that we have overcome. Describe how we overcame each of these factors. List two factors that may limit human population growth in the future.

5. Why are pest species likely to be extreme examples of r-selected species? Why are many endangered species likely to be extreme examples of K-selected species?

6. Given current environmental conditions, if you had a choice, would you rather be an r-strategist or a K-strategist? Explain your answer.

7. Is the southern sea otter an r-strategist or a K-strategist species? Explain. How does this affect our efforts to protect this species from premature extinction?

8. How would you reply to someone who argues that we should not worry about our effects on natural systems because natural succession will heal the wounds of human activities and restore the balance of nature?

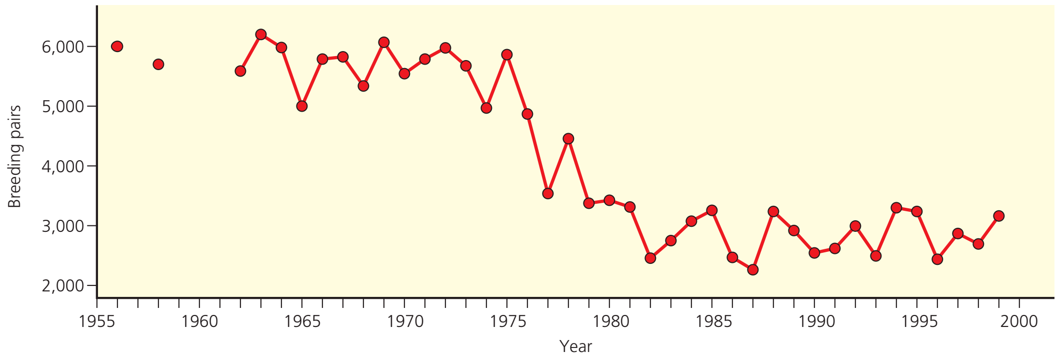
9. In your own words, restate this chapter's closing quotation by Sir Francis Bacon. Do you agree with this notion? Why or why not?

10. List two questions that you would like to have answered as a result of reading this chapter.

Note: See Supplement 13 (p. S78) for a list of Projects related to this chapter.

DATA ANALYSIS

The graph below shows the changes in size of an Emperor Penguin population in terms of breeding pairs on Terre Adelie in the Antarctic. Use the graph to answer the questions below.



Source: Data from *Nature*, May 10, 2001.

1. What was the approximate carrying capacity of the penguin population on the island from 1960 to 1975? (*Hint:* See Figure 5-11, p. 111.) What was the approximate carrying capacity of the penguin population on the island from 1980 to 1999?

2. What is the percentage decline in the penguin population from 1975 to 1999?

LEARNING ONLINE

Log on to the Student Companion Site for this book at **academic.cengage.com/biology/miller**, and choose Chapter 5 for many study aids and ideas for further reading and research. These include flash cards, practice quizzing, Weblinks, information on Green Careers, and InfoTrac® College Edition articles.