CHAPTER 5

Species Interactions, Ecological Succession, and Population Control

> 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**

Key Questions

5.1 How do species interact?

5.2 How do communities and ecosystems respond to changing environmental conditions?

5.3 What limits the growth of populations?

A clownfish gains protection by living among sea anemones and helps protect the anemones from some of their predators.

Morrison/Dreamstime.com

Core Case Study

The Southern Sea Otter: A Species in Recovery

Southern sea otters (Figure 5.1, left) live in giant kelp forests (Figure 5.1, right) in shallow waters along parts of the Pacific coast of North America. Most of the remaining members of this endangered species are found off the California coast between the cities of Santa Cruz and Santa Barbara.

Fast and agile swimmers, the otters dive to the ocean bottom looking for shellfish and food. They swim on their backs on the ocean surface and use their bellies as a table to eat their prey (Figure 5.1, left). Each day, a sea otter consumes 20–35% of its weight in clams, mussels, crabs, sea urchins, abalone, and 40 other species of bottom-dwelling organisms. Their incredibly dense fur traps air bubbles and keeps them warm.

At one time, an estimated 13,000 to 20,000 southern sea otters lived in California's coastal waters. By the early 1900s, they had been hunted almost to extinction by fur traders who killed them for their luxurious fur. Commercial fishers also killed otters, viewing them as competitors in the hunt for valuable abalone and other shellfish.

The otter population grew from a low of 50 in 1938 to 1,850 in 1977 when the U.S. Fish and Wildlife listed the species as endangered. Since then, it has continued to make a slow recovery to 3,054 individuals in 2015, which is below the size needed for it to be removed from the endangered species list.

Why should we care about the southern sea otters of California? One reason is ethical: Many people believe it is wrong to allow human activities to cause the extinction of a species. Another reason is that people love to look at these appealing and highly intelligent animals as they play in the water. As a result, otters help to generate millions of dollars a year in tourism revenues. A third reason—and a key reason in our study of environmental science—is that biologists classify the southern sea otter as a *keystone species* (see p. 83). Scientists hypothesize that in the absence of southern sea otters, sea urchins and other kelp-eating species would probably destroy the Pacific coast kelp forests and much of the rich biodiversity they support.

Biodiversity is an important part of the earth's natural capital and is the focus of one of the three **scientific principles of sustainability**. In this chapter, we look at how species interact and help control one another's population sizes. We also explore how communities, ecosystems, and populations of species respond to changes in environmental conditions.

FIGURE 5.1 An endangered southern sea otter in Monterey Bay, California (USA) uses a stone to crack the shells of the clams that it feeds on (left). It lives in a bed of seaweed called *giant kelp* (right).

Left: Kirsten Wahlquist/Dreamstime.com. Right: Paul Whitted/Shutterstock.com.

5.1 HOW DO SPECIES INTERACT?

CONCEPT 5.1 Five types of interactions among species—interspecific competition, predation, parasitism, mutualism, and commensalism—affect the resource use and population sizes of species.

Competition for Resources

Ecologists have identified five basic types of interactions among species as they share limited resources such as food, shelter, and space. These types of interactions are called *interspecific competition*, *predation*, *parasitism*, *mutualism*, and *commensalism*. These interactions affect the population sizes of the species in an ecosystem and their use of resources (**Concept 5.1**).

Competition is the most common interaction among species. It occurs when members of one or more species interact to use the same limited resources such as food, water, light, and space. Competition between different species is called **interspecific competition**. It plays a larger role in most ecosystems than *intraspecific competition*—competition among members of the same species.

When two species compete with one another for the same resources, their niches (p. 82) overlap. The greater this overlap, the more they compete for key resources. For example, if species A takes over the largest share of one or more key resources, then competing species B must move to another area (if possible) or suffer a population decline.

Given enough time for natural selection to occur, populations can develop adaptations that enable them to reduce or avoid competition with other species. An example is **resource partitioning**, which occurs when different species competing for similar scarce resources evolve specialized traits that allow them to share the same resources. This can involve using parts of the resources or using the resources at different times or in different ways. Figure 5.2 shows resource partitioning by insect-eating bird species. Adaptations allow the birds to reduce competition by feeding in different portions of certain spruce trees and by feeding on different insect species.

Another example of resource partitioning through natural selection involves birds called *honeycreepers* that live in the U.S. state of Hawaii (Figure 5.3). Figure 4.10 (p. 83) shows how the evolution of specialized feeding niches has reduced competition for resources among bird species in a coastal wetland.

Predation

In **predation**, a member of one species is a **predator** that feeds directly on all or part of a member of another species, the **prey**. A brown bear (the predator) and a salmon (the prey) are engaged in a **predator–prey relationship** (Figure 5.4). Such a relationship (between a lion and a zebra) is also shown in Figure 3.6, p. 53. This type of species interaction has a strong effect on population sizes and other factors in many ecosystems.

FIGURE 5.2 *Sharing the wealth:* Resource partitioning among five species of insect-eating warblers in the spruce forests of the U.S. state of Maine. Each species spends at least half its feeding time in its associated yellow-highlighted areas of these spruce trees.

After R. H. MacArthur, "Population Ecology of Some Warblers in Northeastern Coniferous Forests," Ecology 36:533–536, 1958.

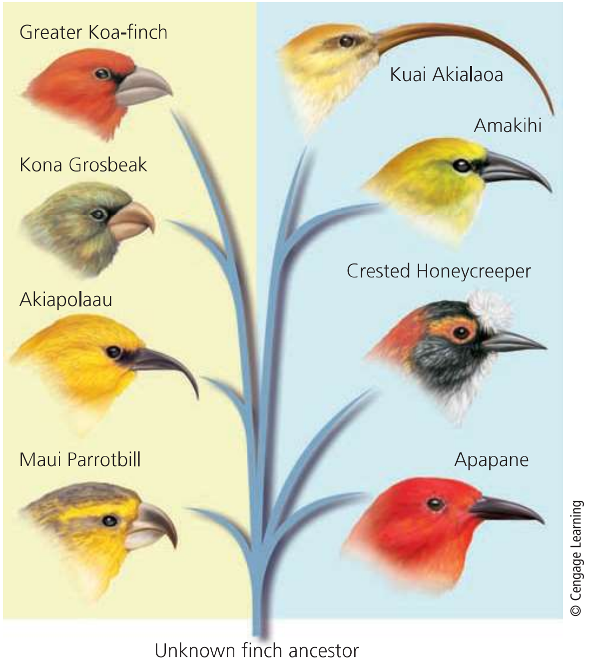


FIGURE 5.3 *Specialist species of honeycreepers:* Through natural selection, different species of honeycreepers have shared resources by evolving specialized beaks to take advantage of certain types of food such as insects, seeds, fruits, and nectar from certain flowers. ***Question:*** Look at each bird's beak and take a guess at what sort of food that bird might eat.

FIGURE 5.4 *Predator–prey relationship:* This brown bear (the predator) in the U.S. state of Alaska has captured and will feed on this salmon (the prey).

CONSIDER THIS . . .

CONNECTIONS Grizzly Bears and Moths

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. In this predator–prey interaction, one grizzly bear can dig out and lap up as many as 40,000 cutworm 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 a giant kelp forest ecosystem, sea urchins prey on kelp, a type of seaweed (Science Focus 5.1). As a keystone species, southern sea otters (**Core Case Study**) prey on the sea urchins and prevent them from destroying the kelp forests. An adult southern sea otter can eat as many as 1,500 sea urchins a day.

Predators use a variety of ways to help them capture prey. *Herbivores* can walk, swim, or fly to the plants they feed on. Many *carnivores*, such as cheetahs, use speed to chase down and kill prey, such as zebras. Eagles and hawks can fly and have keen eyesight to find prey. Some predators such as female African lions work in groups to capture large or fast-running prey.

Other predators use *camouflage* to hide in plain sight and ambush their prey. For example, praying mantises (see Figure 4.4, right, p. 78) sit on flowers or plants of a color similar to their own and ambush visiting insects. White ermines (a type of weasel), snowy owls, and arctic foxes (Figure 5.5) hunt their prey in snow-covered areas. People camouflage themselves to hunt wild game and use camouflaged traps to capture wild animals. Some predators use *chemical warfare* to attack their prey. For example, some spiders and poisonous snakes use venom to paralyze their prey and to deter their predators.

Prey species have evolved many ways to avoid predators. Some can run, swim, or fly fast and some have highly developed senses of sight, sound, or smell that alert them to the presence of predators. Other adaptations include protective shells (abalone and turtles), thick bark (giant sequoia trees), spines (porcupines), and thorns (cacti and rose bushes).

Other prey species use camouflage to blend into their surroundings. Some insect species have shapes that look like twigs (Figure 5.6a), or bird droppings on leaves. A leaf insect can be almost invisible against its background (Figure 5.6b), as can an arctic hare in its white winter fur.

Prey species also use *chemical warfare*. Some discourage predators by containing or emitting chemicals that are *poisonous* (oleander plants), *irritating* (stinging nettles and bombardier beetles, Figure 5.6c), *foul smelling* (skunks and stinkbugs), or *bad tasting* (buttercups and monarch butterflies, Figure 5.6d). 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 flash a warning coloration that eating them is risky.

SCIENCEFOCUS 5.1

Threats to Kelp Forests

A kelp forest contains large concentrations of seaweed called *giant kelp*. Anchored to the ocean floor, its long blades grow toward the sunlit surface waters (Figure 5.1, right). Under good conditions, the blades can grow 0.6 meter (2 feet) in a day and the plant can grow as tall as a 10-story building. The blades are flexible and can survive all but the most violent storms and waves.

Kelp forests support many marine plants and animals and are one of the most biologically diverse marine ecosystems. These forests also reduce shore erosion by blunting the force of incoming waves and trapping some of the outgoing sand.

Sea urchins (Figure 5.A) prey on kelp plants. Large populations of these predators can rapidly devastate a kelp forest because they eat the bases of young kelp plants. Scientific studies by biologists, including James Estes of the University of California at Santa Cruz, indicate that the southern sea otter is a keystone species that helps to sustain kelp forests by controlling populations of sea urchins.

Polluted water running off the land also threatens kelp forests. The pollutants in this runoff include pesticides and herbicides that can kill kelp plants and other species and upset the food webs in these aquatic forests. Another runoff pollutant is fertilizer. Its plant nutrients (mostly nitrates) can cause excessive growth of algae and other aquatic plants. This growth blocks some of the sunlight needed to support the growth of giant kelp.

Some scientists warn that the warming of the world's oceans is a growing threat to kelp forests, which require cool water. If coastal waters get warmer during this century, as projected by climate models, many or most of California's coastal kelp forests could disappear.

Kokhanchikov/Shutterstock.com

FIGURE 5.A The purple sea urchin inhabits the coastal waters of the U.S. state of California and feeds on kelp.

CRITICAL THINKING

List three ways in which we could reduce the degradation of giant kelp forest ecosystems.

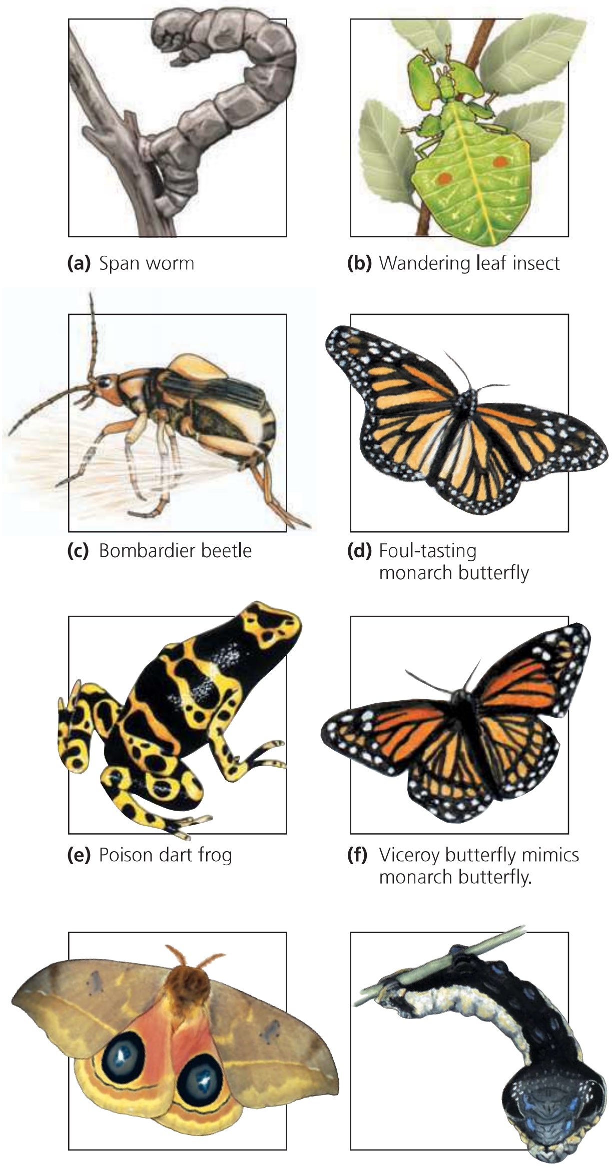
Examples are the brilliantly colored, foul-tasting monarch butterflies (Figure 5.6d) and poisonous frogs (Figure 5.6e). When a bird eats a monarch butterfly, it usually vomits and learns to avoid monarchs.

Some butterfly species gain protection by looking and acting like other, more dangerous species, a protective device known as *mimicry*. The nonpoisonous viceroy butterfly (Figure 5.6f) mimics the monarch butterfly. 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 5.6h). Some moths have wings that look like the eyes of much larger animals (Figure 5.6g). Other prey species gain some protection by living in large groups such as schools of fish and herds of antelope.

Biologist Edward O. Wilson proposed two criteria for evaluating the dangers posed by various brightly colored animal species. *First*, if they are small and strikingly beautiful, they are probably poisonous. *Second*, if they are strikingly beautiful and easy to catch, they are probably deadly.

Paul Nicklen/National Geographic Creative

FIGURE 5.5 A white arctic fox hunts its prey by blending into its snowy background to avoid being detected.



(a) Span worm
(b) Wandering leaf insect
(c) Bombardier beetle
(d) Foul-tasting monarch butterfly
(e) Poison dart frog
(f) Viceroy butterfly mimics monarch butterfly.
(g) Hind wings of Io moth resemble eyes of a much larger animal.
(h) When touched, snake caterpillar changes shape to look like head of snake.

FIGURE 5.6 These prey species have developed specialized ways to avoid their predators: (a, b) *camouflage*, (c, d, e) *chemical warfare*, (d, e, f) *warning coloration*, (f) *mimicry*, (g) *deceptive looks*, and (h) *deceptive behavior*.

Coevolution

At the individual level, members of predator species benefit from their predation and members of prey species are harmed. At the population level, predation plays a role in natural selection. Animal predators tend to kill the sick, weak, aged, and least fit members of a prey population because they are the easiest to catch. Individuals with better defenses against predation thus tend to survive longer and leave more offspring with adaptations that can help them avoid predation. Over time, as a prey species develops traits that make it more difficult to catch, its predators face selection pressures that favor traits increasing their ability to catch their prey. Then the prey species must get better at eluding the more effective predators.

This back-and-forth adaptation is called **coevolution**, a natural selection process in which changes in the gene pool of one species leads to changes in the gene pool of another species. It can play an important role in controlling population growth of predator and prey species. When populations of two species interact as predator and prey over a long time, genetic changes occur in both species that help them to become more competitive or to avoid or reduce competition.

For example, coevolution can be observed between bats and certain species of moths they feed on. Bats prey on certain species of moths that they hunt at night using echolocation. They emit pulses of high-frequency sound that bounce off their prey. Then they capture the returning echoes that tell them where their prey is located. Over time, certain moth species have evolved ears that are sensitive to the sound frequencies that bats use to find them. When they hear these frequencies, they drop to the ground or fly evasively. Some bat species evolved ways to counter this defense by changing the frequency of their sound pulses. In turn, some moths 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.

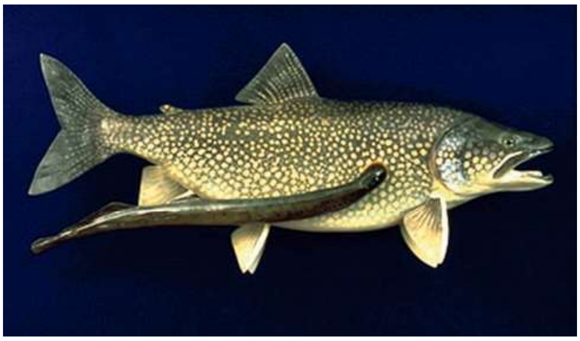
CONSIDER THIS . . .

LEARNING FROM NATURE

Bats and dolphins use echolocation to navigate and locate prey in the darkness of night and in the ocean's murky water. Scientists are studying how they do this to improve our sonar systems, sonic imaging tools for detecting underground mineral deposits, and medical ultrasound imaging systems.

Parasitism, Mutualism, and Commensalism

Parasitism occurs when one species (the *parasite*) lives in or on another organism (the *host*). The parasite benefits by extracting nutrients from the host. A parasite weakens its host but rarely kills it, since doing so would eliminate the source of its benefits. For example, tapeworms are parasites that live part of their life cycle inside their hosts. Others such as mistletoe plants and blood-sucking sea lampreys (Figure 5.7) attach themselves to the outsides of their hosts. Some parasites (such as fleas and ticks) move from one host to another whereas others (such as certain protozoa) spend their adult lives within a single host. Parasites help keep their host populations in check.



Great Lakes Fishery Commission

FIGURE 5.7 *Parasitism:* This blood-sucking, parasitic sea lamprey has attached itself to an adult lake trout from one of the Great Lakes (USA, Canada).

In **mutualism**, two species interact in ways that benefit both by providing each with food, shelter, or some other resource. An example is pollination of flowering plants by species such as honeybees, hummingbirds, and butterflies (see Chapter 4 opening photo, pp. 74–75) that feed on the nectar of flowers. Figure 5.8 shows an example of a mutualistic relationship that combines *nutrition* and *protection*. It involves birds that ride on the backs or heads of large animals such as elephants, rhinoceroses, and impalas. The birds remove and eat parasites and pests (such as ticks and flies) from the animals' bodies and often make noises warning the animals when predators are approaching.

Another example of mutualism involves clownfish, which usually live within sea anemones (see chapter-opening photo), 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 waste matter left from the anemones' meals. The sea anemones benefit because the clownfish protect them from some of their predators and parasites.

Mutualism might appear to be a form of cooperation between species. However, each species is concerned only for its own survival.

Commensalism is an interaction that benefits one species but has little, if any, beneficial or harmful effect on the other. One example involves plants called *epiphytes* (air plants), which attach themselves to the trunks or branches of trees (Figure 5.9) in tropical and subtropical forests. The plants gain access to sunlight, water from the humid air and rain, and nutrients falling from the tree's upper leaves

Villiers Steyn/Dreamstime.com

FIGURE 5.8 *Mutualism:* Oxpeckers feed on parasitic ticks that infest animals such as this impala and warn of approaching predators.

parinyabinsuk/Shutterstock.com

FIGURE 5.9 *Commensalism:* This pitcher plant is attached to a branch of a tree without penetrating or harming the tree. This carnivorous plant feeds on insects that become trapped inside it.

and limbs, but their presence apparently does not harm the tree. Similarly, birds benefit by nesting in trees, generally without harming them.

5.2 HOW DO COMMUNITIES AND ECOSYSTEMS RESPOND TO CHANGING ENVIRONMENTAL CONDITIONS?

CONCEPT 5.2 The species composition of a community or ecosystem can change in response to changing environmental conditions through a process called *ecological succession*.

Ecological Succession Creates and Changes Ecosystems

The types and numbers of species in biological communities and ecosystems change in response to changing environmental conditions. The normally gradual change in species composition in a given terrestrial area or aquatic system is called **ecological succession** (**Concept 5.2**). Ecologists recognize two major types of ecological succession, depending on the conditions present at the beginning of the process.

Primary ecological succession involves the gradual establishment of communities of different species in lifeless areas. This type of succession begins where there is no soil in a terrestrial ecosystem or no bottom sediment in an aquatic ecosystem. Examples include bare rock exposed by a retreating glacier (Figure 5.10), newly cooled lava from a volcanic eruption, an abandoned highway or parking lot, and a newly created shallow pond or lake (Figure 5.11). Primary succession usually takes hundreds to thousands of years because of the need to build up fertile soil or aquatic sediments to provide the nutrients needed to establish a plant community.

Species such as lichens and mosses that quickly colonize the newly exposed rocks are called **pioneer species**. They often have seeds or spores that can travel long distances and quickly spread over the exposed rock (Figure 5.10). As lichens grow and spread, they release

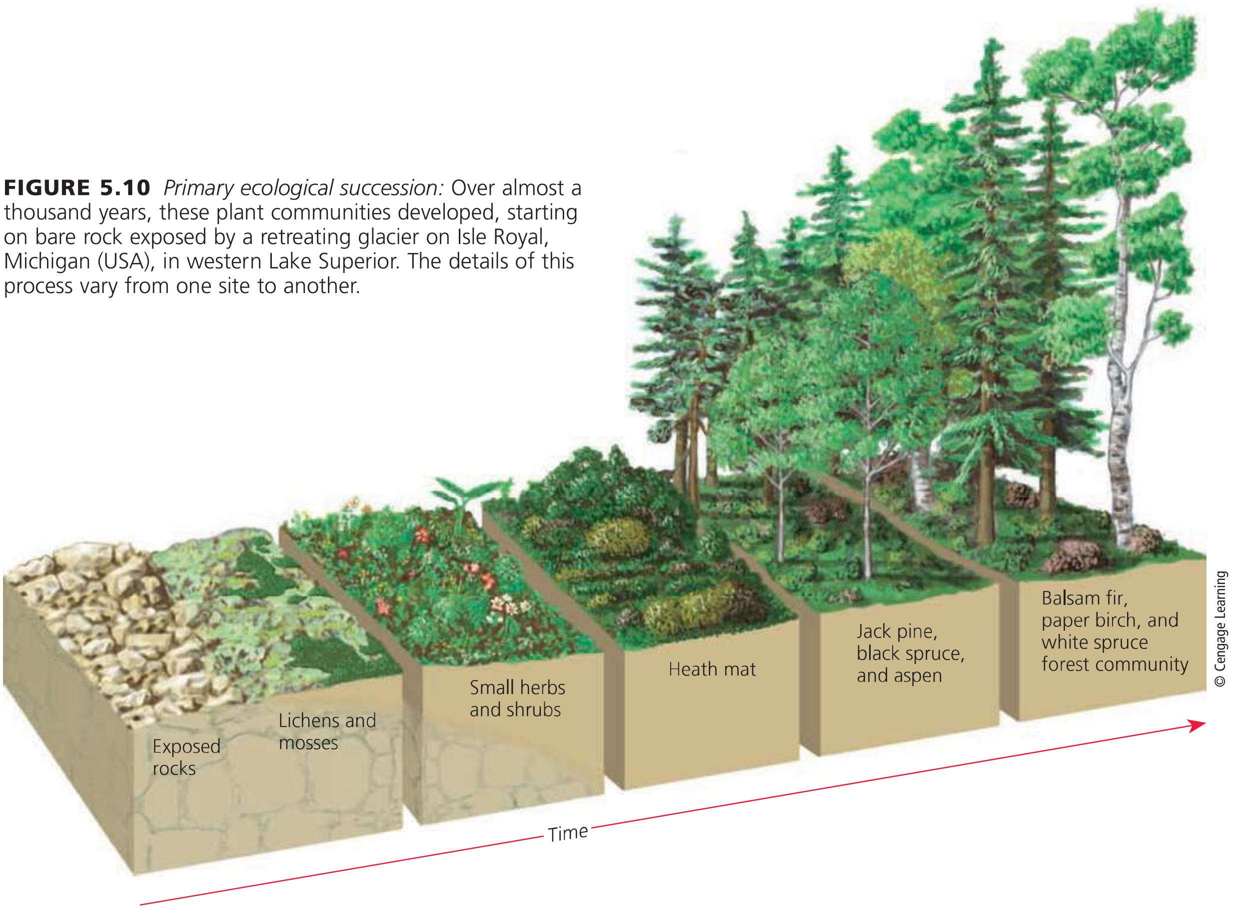


FIGURE 5.10 *Primary ecological succession:* Over almost a thousand years, these plant communities developed, starting on bare rock exposed by a retreating glacier on Isle Royal, Michigan (USA), in western Lake Superior. The details of this process vary from one site to another.

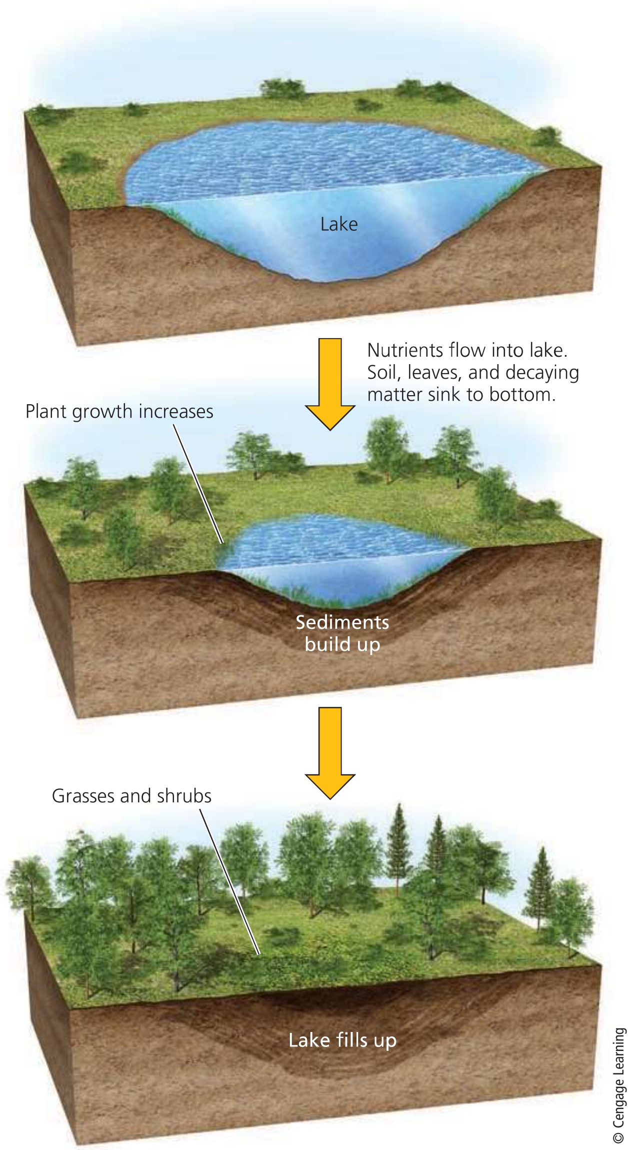


FIGURE 5.11 *Primary ecological succession* in a lake basin in which sediments and plants have been gouged out by a glacier. When the glacier melts, the lake basin begins accumulating sediments and plant and animal life. Over hundreds to thousands of years, the lake can fill with sediments and become a terrestrial habitat.

acids that can breakdown the rock and start the soil formation process (see Figure 3.10, p. 56). As the soil slowly forms, small plants, insects, and worms invade and add more nutrients that build up the soil. Each successive wave of new organisms changes the environmental conditions in ways that provide more nutrients, habitats, and favorable environmental conditions for future arrivals.

The other, more common type of ecological succession is **secondary ecological succession**, in which a series of terrestrial communities or ecosystems with different species develop in places containing soil or bottom sediment. This type of 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 (Figure 5.12), burned or cut forests, heavily polluted streams, and flooded land. Because some soil or sediment is present, new vegetation can begin to grow, usually within a few weeks. On land, growth begins with the germination of seeds already in the soil and seeds imported by wind or in the droppings of birds and other animals.

Ecological succession is an important ecosystem service that can enrich the biodiversity of communities and ecosystems by increasing species diversity and interactions among species. Such interactions enhance sustainability by promoting population control and increasing the complexity of food webs. Primary and secondary ecological succession are examples of *natural ecological restoration*.

Ecologists have identified three factors that affect how and at what rate ecological succession occurs. One is *facilitation*, in which one set of species makes an area suitable for species with different niche requirements, and often less suitable for itself. For example, as lichens and mosses gradually build up soil on a rock in primary succession, herbs and grasses can move in and crowd out the lichens and mosses (Figure 5.10).

A second factor is *inhibition*, in which some species hinder the establishment and growth of other species. For example, needles dropping off some pine trees make the soil beneath the trees too acidic for most other plants to grow there. A third factor is *tolerance*, in which plants in the late stages of succession succeed because they are not in direct competition with other plants for key resources. Shade-tolerant plants, for example, can live in shady forests because they do not need as much sunlight as the trees above them do (Figure 5.12).

Is There a Balance of Nature?

According to the traditional view, ecological succession proceeds in an orderly sequence along an expected path until a certain stable type of *climax community* (Figures 5.10 and 5.12), which is assumed to be in balance with its environment, occupies an area. 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 based on ecological research. There is a general tendency for succession to lead to more complex, diverse, and presumably more resilient ecosystems that can withstand changes in environmental conditions if the changes are

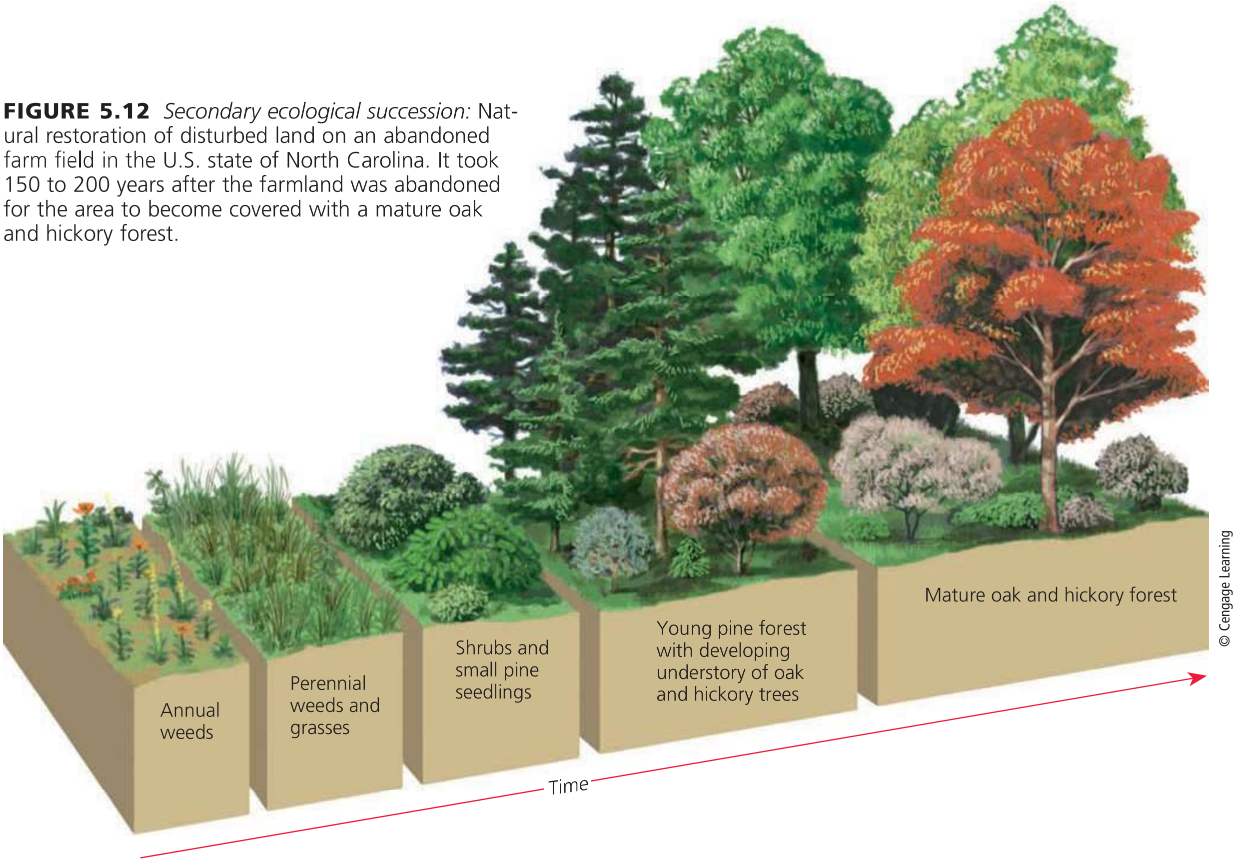


FIGURE 5.12 *Secondary ecological succession:* Natural restoration of disturbed land on an abandoned farm field in the U.S. state of North Carolina. It took 150 to 200 years after the farmland was abandoned for the area to become covered with a mature oak and hickory forest.

not too large or too sudden. However, the current scientific view is that we cannot predict a given course of succession or view it as inevitable progress toward an ideally adapted climax plant community or ecosystem. Rather, ecological succession reflects the ongoing struggle by different species for enough light, water, nutrients, food, space, and other key resources.

Living Systems Are Sustained through Constant Change

All living systems, from a cell to the biosphere, constantly change in response to changing environmental conditions. Living systems have complex processes that interact to provide some degree of stability, or sustainability. This stability, or the capacity to withstand external stress and disturbance, is maintained by constant change in response to changing environmental conditions. 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.

Ecologists distinguish between two aspects of stability or sustainability in ecosystems. One, called **inertia**, or **persistence**, is the ability of an ecosystem to survive moderate disturbances. A second factor, **resilience**, is the ability of an ecosystem to be restored through secondary ecological succession after a severe disturbance.

Evidence suggests that some ecosystems have one of these properties but not the other. Tropical rain forests have high species diversity and high inertia and thus are resistant to low levels of change or damage. But once a large tract of tropical rain forest is cleared or severely damaged, the resilience of the degraded forest ecosystem may be so low that the degradation reaches an ecological tipping point. Beyond that point, the forest might not be restored by secondary ecological succession. One reason is that most of the nutrients in a tropical rain forest are stored in its vegetation, not in the topsoil. Once the nutrient-rich vegetation is gone, frequent rains on a large cleared area of land can remove most of the remaining soil nutrients and thus prevent the return of a tropical rain forest to such an area.

By contrast, grasslands are much less diverse than most forests. Thus, they have low inertia and can burn easily. Because most of their plant matter is stored in underground roots, these ecosystems have high resilience and can recover quickly after a fire because 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.

FIGURE 5.13 A population, or *school*, of Anthias fish on coral in Australia's Great Barrier Reef.

iStockphoto.com/Rich Carey

5.3 WHAT LIMITS THE GROWTH OF POPULATIONS?

CONCEPT 5.3 No population can grow indefinitely because of limitations on resources and because of competition among species for those resources.

Populations Can Grow, Shrink, or Remain Stable

A **population** is a group of interbreeding individuals of the same species (Figure 5.13). **Population size** is the number of individual organisms in a population at a given time. The size of a population may increase, decrease, go up and down in cycles, or remain roughly the same in response to changing environmental conditions.

Scientists use sampling techniques to estimate the sizes of large populations of species such as oak trees that are spread over a large area and squirrels that move around and are hard to count. Typically, they count the number of individuals in one or more small sample areas and use this information to estimate the number of individuals in a larger area.

Populations of different species vary in their distribution over their habitats, or *dispersion*, as shown in Figure 5.14. Most populations live together in *clumps* or *groups* such as packs of wolves, schools of fish (Figure 5.13), and flocks of birds. Southern sea otters (**Core Case Study**), for example, are usually found in groups known as rafts or pods ranging in size from a few to several hundred animals.

Living in groups allows organisms to cluster where resources are available. Group living also provides some protection from predators, and gives some predator species a better chance of getting a meal.

Four variables—*births*, *deaths*, *immigration*, and *emigration*—govern changes in population size. A population increases through birth and immigration (arrival of individuals from outside the population). Populations decrease through death and emigration (departure of individuals from the population):

$$\text{Population change} = \text{Individuals added} - \text{Individuals lost}$$

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

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

FIGURE 5.14 Three general habitat *dispersion patterns* for individuals in a population.

Left: EcoPrint/Shutterstock.com. Center: kenkistler/Shutterstock.com. Right: Nataly Lukhanina/Shutterstock.com.

Several Factors Can Limit Population Size

Each population in an ecosystem has a **range of tolerance**—a range of variations in its physical and chemical environment under which it can survive. For example, a trout population may do best within a narrow band of temperatures (*optimum level* or *range*), but a few individuals can survive above and below that band (Figure 5.15). If the water becomes too hot or too cold, none of the trout can survive.

Individuals within a population may also have slightly different tolerance ranges for temperature, other physical factors, or chemical factors. These occur because of small differences in their genetic makeup, health, and age. Such differences allow for evolution through natural selection. The individuals that have a wider tolerance for change in some factor such as temperature are more likely to survive such a change and produce offspring that can tolerate it.

Various physical or chemical factors can determine the number of organisms in a population and how fast a population grows or declines. Sometimes one or more factors, known as **limiting factors**, are more important than other factors in regulating population growth.

On land, precipitation often is the limiting factor. Low precipitation levels in desert ecosystems limit desert plant growth. Lack of key soil nutrients limits the growth of plants, which in turn limits populations of animals that eat plants, and animals that feed on such plant-eating animals.

Limiting physical factors for populations in *aquatic systems* include water temperature (Figure 5.15) and water depth and clarity (allowing for more or less sunlight). Other important factors are nutrient availability, acidity, salinity, and the level of oxygen gas in the water (dissolved oxygen content).

An additional factor that can limit the sizes of some populations is **population density**, the number of individuals in a population found within a defined area or volume. It is a measure of how crowded the members of a population are.

Density-dependent factors are variables that become more important as a population's density increases. For example, in a dense population, parasites and diseases can spread more easily, resulting in higher death rates. On the other hand, a higher population density helps sexually reproducing individuals to find mates more easily to produce offspring. Other factors such as flood, fires, landslides, drought, and climate change are considered *density-independent factors*, because any effects they have on a population's size are not related to its density.

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

Some species have an incredible ability to increase their numbers and grow exponentially (see p. 15). Plotting these numbers against time yields a J-shaped curve of exponential growth when a population increases by a fixed percentage each year (Figure 5.16, left). Members of such populations typically reproduce at an early age, have many offspring each time they reproduce, and reproduce many times with short intervals between generations.

Examples are bacteria and many insect species. For example, with no controls on its population growth, a species of bacteria that can reproduce every 20 minutes would generate enough offspring to form a 0.3-meter-deep (1-foot-deep) layer over the surface of the entire earth in only 36 hours. Such exponential growth occurs in nature

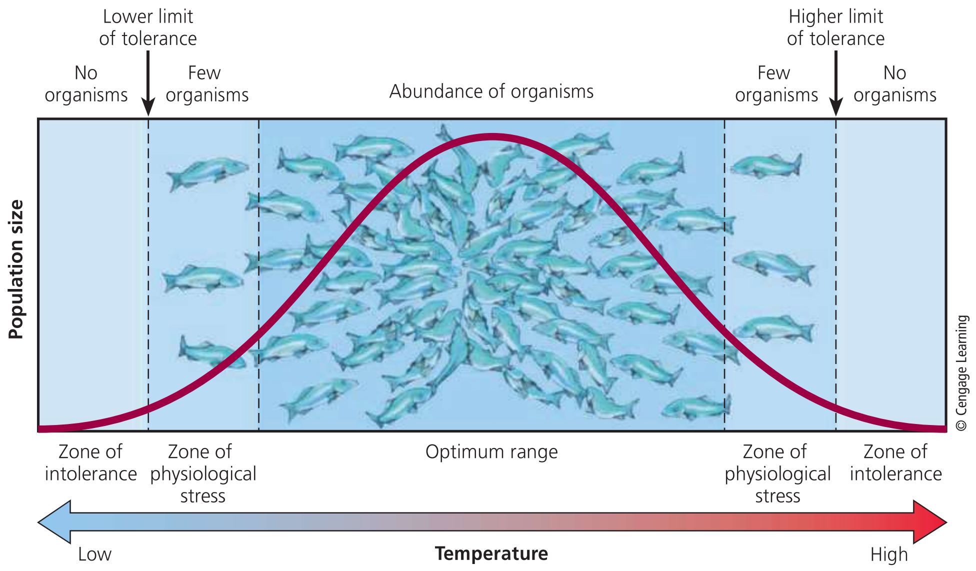


FIGURE 5.15 Range of tolerance for a population of trout to changes in water temperature.

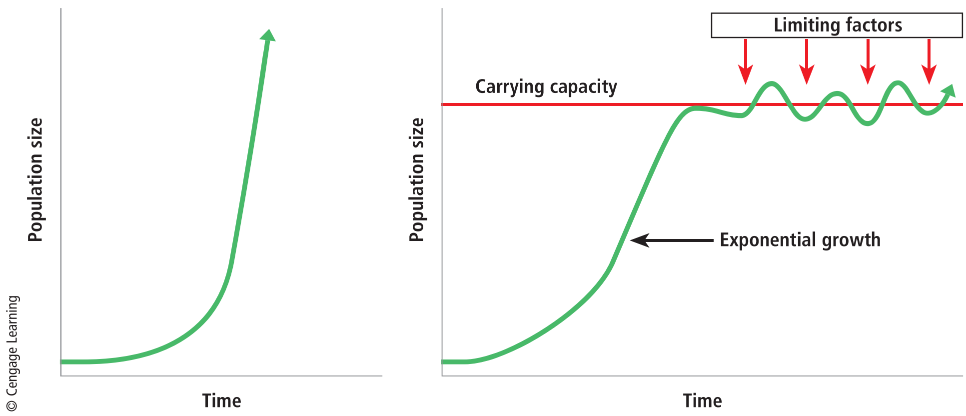


FIGURE 5.16 Populations of species can undergo *exponential growth* represented by a J-shaped curve (left) when resource supplies are plentiful. As resource supplies become limited, a population undergoes *logistic growth*, represented by an S-shaped curve (right), when the size of the population approaches the carrying capacity of its habitat.

when species with a high reproductive potential have few predators, plenty of food and other resources, and little competition from other species for such resources.

However, *there are always limits to population growth in nature*. Research reveals that a rapidly growing population of any species eventually reaches some size limit imposed by limiting factors. These factors include sunlight, water, temperature, space, or nutrients, or exposure to predators or infectious diseases (**Concept 5.3**). **Environmental resistance** is the sum of all such factors in a habitat. Limiting factors largely determine an area's **carrying capacity**, the maximum population of a given species that a particular habitat can sustain indefinitely. The carrying capacity for a population is not fixed and can rise or fall as environmental conditions change the factors that limit the population's growth.

As a population approaches the carrying capacity of its habitat, the J-shaped curve of its exponential growth (Figure 5.16, left) is converted to an S-shaped curve of *logistic growth*, or growth that often fluctuates around the carrying capacity of its habitat (Figure 5.16, right). The population sizes of some species often fluctuate above and below their carrying capacity as shown in the right graph in Figure 5.16.

Some populations do not make a smooth transition from exponential growth to logistic growth. Instead, they use up their resource supplies and temporarily *overshoot*, or exceed, the carrying capacity of their environment. In such cases, the population suffers a sharp decline, called a *dieback*, or **population crash**, unless part of the population can switch to new resources or move to an area that has more resources. Such a crash occurred when reindeer were introduced onto a small island in the Bering Sea in the early 1900s (Figure 5.17).

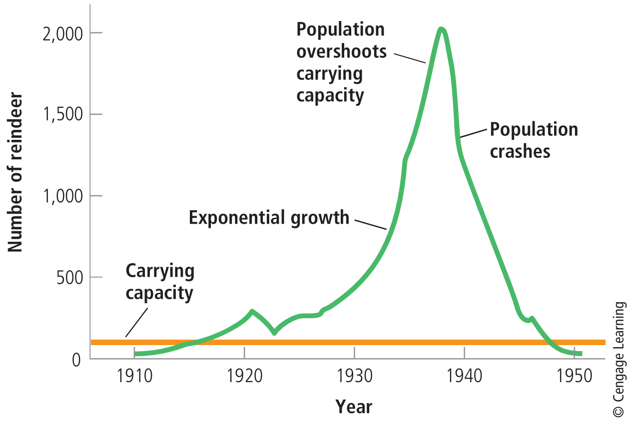


FIGURE 5.17 Exponential growth, overshoot, and population crash of a population of reindeer introduced onto the small Bering Sea island of St. Paul in 1910. ***Data analysis:*** By what percentage did the population of reindeer grow between 1923 and 1940?

Reproductive Patterns

Species vary in their reproductive patterns. Species with a capacity for a high rate of population growth (*r*) (Figure 5.16, left) are called ***r*-selected species**. These species tend to have short life spans and produce many, usually small offspring and give them little or no parental care. As a result, many of the offspring die at an early age. To overcome such losses, *r*-selected species produce large numbers of offspring so that a few will likely survive and have many offspring to sustain the species. Examples of *r*-selected species include algae, bacteria, frogs, most insects, and many fish.

Such species tend to be *opportunists*. They reproduce and disperse rapidly when conditions are favorable or when a disturbance such as a fire or clear-cutting of a forest opens up a new habitat or niches for invasion. Once established, their populations may crash because of unfavorable changes in environmental conditions or invasion by more competitive species. This explains why many opportunist species go through irregular and unstable boom-and-bust cycles in their population sizes.

At the other extreme are ***K*-selected species**. They tend to reproduce later in life, have few offspring, and have long life spans. Typically, the offspring of *K*-selected mammal species develop inside their mothers (where they are safe) and are born relatively large. After birth, they mature slowly and are cared for and protected by one or both parents. In some cases, they live in herds or groups until they reach reproductive age.

Such a species' population size tends to be near the carrying capacity (*K*) of its environment (Figure 5.16, right). Examples of *K*-selected species include 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. Many of these species—especially those with low reproductive rates, such as elephants, sharks, giant redwood trees, and California's southern sea otters (**Core Case Study** and Science Focus 5.2)—are vulnerable to extinction.

Table 5.1 compares typical traits of *r*-selected and *K*-selected species. Most species have reproductive patterns and traits between the extremes of *r*-selected and *K*-selected species.

The reproductive pattern of a species may give it a temporary advantage. However, the key factor in determining the ultimate population size of a species is the availability of suitable habitat with adequate resources.

Changes in habitat or other environmental conditions can reduce the populations of some species while increasing the populations of other species, such as white-tailed deer in the United States (see Case Study that follows).

TABLE 5.1 Typical traits of *r*-selected and *K*-selected species

Trait	*r*-Selected Species	*K*-Selected Species
Reproductive potential	High	Low
Population growth rate	Fast	Slow
Time to reproductive maturity	Short	Long
Number of reproductive cycles	Many	Few
Number of offspring	Many	Few
Size of offspring	Small	Larger
Degree of parental care	Low	High
Life span	Short	Long
Population size	Variable with crashes	Stable, near carrying capacity
Role in environment	Usually prey	Usually predators

CASE STUDY

Exploding White-Tailed Deer Populations in the United States

By 1900, habitat destruction and uncontrolled hunting had reduced the white-tailed deer (Figure 5.18) 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, including wolves and mountain lions that preyed on the deer, were nearly eliminated.

These protections worked, and for some suburbanites and farmers, perhaps too well. Today there are over 30 million white-tailed deer in the United States. During the last 50 years, suburbs have expanded and many Americans have moved into the wooded habitat of deer. The gardens and landscaping around their homes provide deer with flowers, shrubs, garden crops, and other plants they like to eat.

Deer prefer to live in the edge areas of forests and woodlots for security and go to nearby fields, orchards, lawns, and gardens for food. A suburban neighborhood can be an all-you-can-eat paradise for white-tailed deer, and their populations in such areas have soared.

In woodlands, deer are consuming native ground-cover vegetation, which has allowed nonnative weed species to take over and upset ecosystem food webs. The deer also help to spread Lyme disease (carried by deer ticks) to humans. In addition, each year about 1 million deer–vehicle collisions injure up to 10,000 Americans and kill at

Roy Toft/National Geographic Creative

FIGURE 5.18 White-tailed deer populations in the United States have been growing.

SCIENCEFOCUS 5.2

The Future of California's Southern Sea Otters

The population of southern sea otters (**Core Case Study**) has fluctuated in response to changes in environmental conditions (Figure 5.B). One change is a rise in populations of the orcas (killer whales) that feed on them. Scientists hypothesize that orcas started feeding more on southern sea otters when populations of their normal prey, sea lions and seals, began declining. In addition, between 2010 and 2012 the number of sea otters killed or injured by sharks increased, possibly because warmer ocean water brought some sharks closer to the shore.

Another factor affecting sea otters may be parasites that breed in the intestines of cats. Scientists hypothesize that some southern sea otters are dying because cat owners flush feces-laden cat litter down their toilets or dump it in storm drains that empty into coastal waters where parasites from the litter can infect otters.

Toxic algae blooms also threaten otters. The algae thrive on urea, a nitrogen-containing ingredient in fertilizer that washes into coastal waters. Other pollutants released by human activities are PCBs and other fat-soluble toxic chemicals. These chemicals can kill otters by accumulating to high levels in the tissues of the shellfish that otters eat. Because southern sea otters feed at high trophic levels and live close to the shore, they are vulnerable to these and other pollutants in coastal waters.

Other threats to otters include oil spills from ships. The entire California southern sea otter population could be wiped out by a large oil spill from a single tanker off the central west coast or by the rupture of an offshore oil well, should drilling for oil be allowed off this coast. Some sea otters die when they are trapped in underwater nets and traps for shellfish. Others are killed by boat strikes and gunshots.

The factors listed here, mostly resulting from human activities, together with a low reproductive rate and a rising mortality rate, have hindered the ability of the endangered southern sea otter to rebuild its population (Figure 5.B). In 2012, the National Geographic Society funded a project led by Nicole Thometz, a biologist at the University of California, Santa Cruz, to learn more about why juvenile sea otters, in particular, were suffering a high mortality rate. Such information could be used to help biologists to refine recovery plans for the southern sea otter.

Since 2012, the sea otter population has increased, possibly because of an increase in the population of sea urchins, their preferred prey. In 2015, the sea otter population was 3,054, the highest it has been since 1985. If the sea otter population exceeds 3,090 for 3 consecutive years, it may be removed from the endangered species list. If this happens, the otters will still be protected under a California state law.

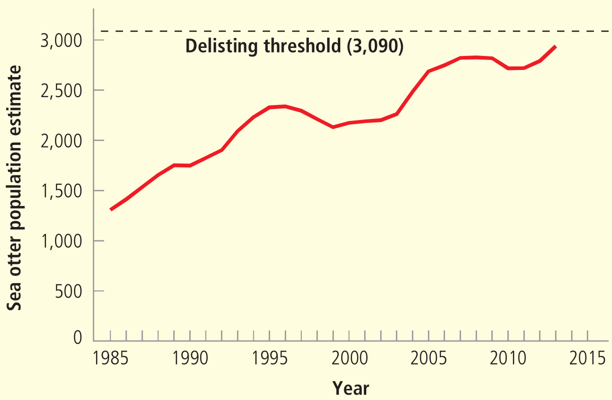


FIGURE 5.B Changes in the population size of southern sea otters off the coast of the U.S. state of California, 1983–2015.

(Compiled by the authors using data from U.S. Geological Survey.)

CRITICAL THINKING

How would you design a controlled experiment to test the hypothesis that cat litter flushed down toilets might be killing southern sea otters?

least 200—the highest human death toll from encounters with any wild animal in the United States.

There are no easy solutions to the deer population problem in the suburbs. Changes in hunting regulations that allow for the killing of more female deer have cut down the overall deer population. However, this has had a limited effect on deer populations 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 only shoot their arrows downward.

Some communities spray the scent of deer predators or of rotting deer meat in edge areas to scare off deer. Others scare off deer by using electronic equipment that emits high-frequency sounds that humans cannot hear. Some homeowners surround their gardens and yards with high, black plastic mesh fencing.

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

Darts loaded with contraceptives can 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 lasts for several years. Another approach is to trap dominant males and use chemical injections to sterilize them. Both of these approaches are costly and 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 fences, repellents, or other methods. Suburban dwellers could also stop planting trees, shrubs, and flowers that attract deer around their homes.

CONSIDER THIS . . .

THINKING ABOUT White-Tailed Deer

Some people 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 deer populations under control, and provided the deer with plenty to eat in their lawns, gardens, and crop fields. Which view do you hold? Why? Do you see a solution to this problem?

Species Vary in Their Life Spans

Individuals of species with different reproductive strategies tend to have different *life expectancies*. This can be illustrated by a **survivorship curve**, which shows the percentages of the members of a population surviving at different ages. There are three generalized types of survivorship curves: late loss, early loss, and constant loss (Figure 5.19). A *late loss* population (*K*-selected species such as elephants and rhinoceroses) typically has high survivorship to a certain age, and then high mortality. A *constant loss* population (such as many songbirds) typically has a constant death rate at all ages. For an *early loss* population (many *r*-selected species and annual plants), survivorship is low early in life. These generalized survivorship curves only approximate the realities of nature.

CONSIDER THIS . . .

THINKING ABOUT Survivorship Curves

Which type of survivorship curve applies to the human species?

Humans Are Not Exempt from Nature's Population Controls

Humans are not exempt from population crashes. In 1845 Ireland experienced such a crash after a fungus destroyed its potato crop. About 1 million people died from hunger or diseases related to malnutrition. Millions more migrated to other countries, sharply reducing the Irish population.

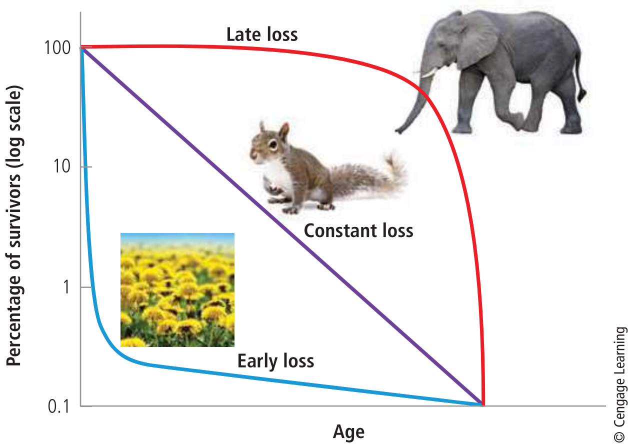


FIGURE 5.19 Survivorship curves for populations of different species, obtained by showing the percentages of the members of a population surviving at different ages.

Top: Gualtiero boffi/Shutterstock.com. Center: IrinaK/Shutterstock.com. Bottom: ultimathule/Shutterstock.com.

During the 14th century, *bubonic plague* spread through densely populated European cities and killed at least 25 million people—one-third of the European population. The bacterium that causes 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. Today several antibiotics can be used to treat bubonic plague.

So far, technological, social, and other cultural changes have expanded the earth's carrying capacity for the human species. We have used large amounts of energy and matter resources to occupy formerly uninhabitable areas. We have expanded agriculture and controlled the populations of other species that compete with us for resources. Some say we can keep expanding our ecological footprint in this way indefinitely because of our technological ingenuity. Others say that at some point, we will reach the limits that nature eventually imposes on any population that exceeds or degrades its resource base. We discuss these issues in Chapter 6.

BIG IDEAS

- Certain interactions among species affect their use of resources and their population sizes.
- The species composition and population sizes of a community or ecosystem can change in response to changing environmental conditions through a process called *ecological succession*.
- No population can escape natural limiting factors and grow indefinitely.

Tying It All Together

Southern Sea Otters and Sustainability

The sea otters of California are part of a complex ecosystem made up of large underwater kelp forests, bottom-dwelling creatures, and other species that depend on one another for survival. The sea otters act as a keystone species, mostly by feeding on sea urchins and keeping them from destroying the kelp.

fred goldstein/Shutterstock.com

In this chapter, we focused on how biodiversity promotes sustainability, provides a variety of species to restore damaged ecosystems through ecological succession, and limits the sizes of populations. Populations of most plants and animals depend, directly or indirectly, on solar energy, and all populations play roles in the cycling of nutrients in the ecosystems where they live. In addition, the biodiversity in different terrestrial and aquatic ecosystems provides alternative paths for energy flow and nutrient cycling, better opportunities for natural selection as environmental conditions change, and natural population control mechanisms. When we disrupt these paths, we violate the three **scientific principles of sustainability**.

Chapter Review

Core Case Study

1. Explain how southern sea otters act as a keystone species in their environment. Explain why we should care about protecting this species from extinction.

Section 5.1

2. What is the key concept for this section? Define and give an example of **interspecific competition**. How is it different from intraspecific competition? Define and give an example of **resource partitioning** and explain how it can increase species diversity. Define **predation**. Distinguish between a **predator** species and a **prey** species and give an example of each. What is a **predator–prey relationship** and why is it important?

3. Describe three threats to kelp forests and explain why they should be preserved. List three ways in which predators can increase their chances of feeding on their prey and three ways in which prey species can avoid their predators. Define and give an example of **coevolution**.

4. Define **parasitism**, **mutualism**, and **commensalism** and give an example of each. Explain how each of these species interactions, along with predation, can affect the population sizes of species in ecosystems.

Section 5.2

5. What is the key concept for this section? What is **ecological succession**? Distinguish between **primary ecological succession** and **secondary ecological succession** and give an example of each. Define and give an example of a **pioneer species**. Describe three factors that affect how and at what rate succession occurs.

6. Explain why ecological succession does not follow a predictable path and does not necessarily end with a stable climax community. What is the current thinking among ecologists on the concept of a balance of nature? In terms of the stability of ecosystems, distinguish between **inertia (persistence)** and **resilience** and give an example of each.

Section 5.3

7. What is the key concept for this section? Define **population**. Define **population size** and explain how it is estimated, Why do most populations live in clumps? List four variables that govern changes in population size. Write an equation showing how these variables interact. Define **range of tolerance**. Define **limiting factor** and give three examples. Define **population density** and explain how some limiting factors can become more important as a population's density increases.

8. Distinguish between the exponential and logistic growth of a population and describe the nature of their growth curves. Define **environmental resistance**. What is the **carrying capacity** of an environment? Define and give an example of a **population crash**.

9. Describe two different reproductive strategies for species. Distinguish between ***r*-selected species** and ***K*-selected species** and give an example of each. What factors have hindered the recovery of the southern sea otter? Describe the effects of the exploding population of white-tailed deer in the United States and list some possible solutions to this problem. Define **survivorship curve**, describe three types of curves, and for each, give an example of a species that fits that pattern. Explain why humans are not exempt from nature's population controls.

10. What are this chapter's *three big ideas*? Explain how the interactions among plant and animal species in any ecosystem are related to the three **scientific principles of 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 extinct primarily because of human activities? What are three things we could do to help prevent the extinction of this species?

2. Use the second law of thermodynamics (Chapter 2, p. 42) and the concept of food chains and food webs to explain why predators are generally less abundant than their prey.

3. How would you reply to someone who argues that we should not worry about the effects that human activities have on natural systems because ecological succession will repair whatever damage we do?

4. How would you reply to someone who contends that efforts to preserve species and ecosystems are not worthwhile because nature is largely unpredictable?

5. What is the reproductive strategy of most species of insect pests and harmful bacteria? Why does this make it difficult for us to control their populations?

6. If the earth's climate continues to change due to atmospheric warming during this century, as most climate scientists project it will, is this likely to favor *r*-selected or *K*-selected species? Explain.

7. List two factors that may limit human population growth in the future. Do you think that we are close to reaching those limits? Explain.

8. If the human species were to suffer a population crash, name three species that might move in to occupy part of our ecological niche. What are three species that would likely decline as a result? Explain why these other species would decline.

Doing Environmental Science

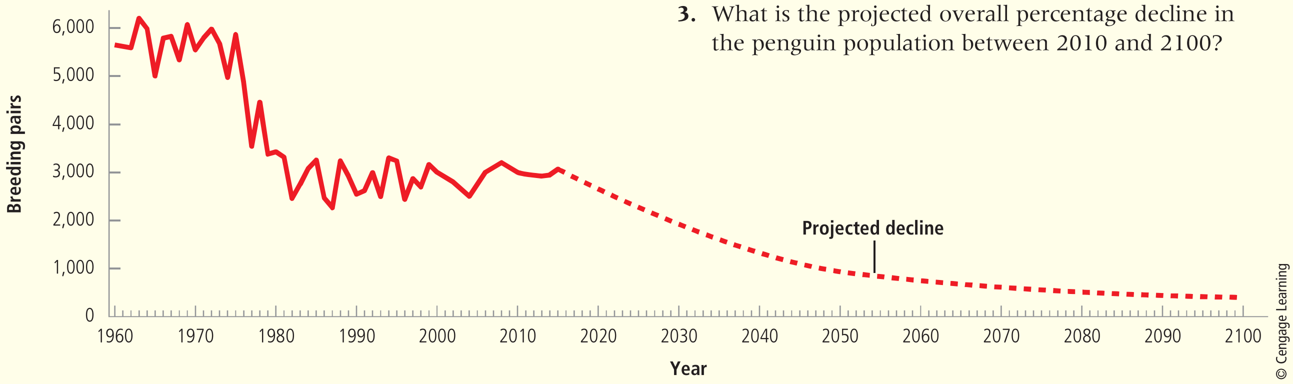
Visit a nearby land area, such as a partially cleared or burned forest, grassland, or an abandoned crop field, and record signs of secondary ecological succession. Take notes on your observations and formulate a hypothesis about what sort of disturbance led to this succession. Include your thoughts about whether this disturbance was natural or caused by humans. Study the area carefully to see whether you can find patches that are at different stages of succession and record your thoughts about what sorts of disturbances have caused these differences. You might want to research the topic of ecological succession in such an area.

Global Environment Watch Exercise

Go to your MindTap course to access the GREENR database. Using the "Basic Search" function at the top of the page, search for *kelp forests* (also sometimes called *kelp beds*), and use the results to find sources of information about how a warmer ocean resulting from climate change might affect California's coastal kelp forests on which the southern sea otters depend (**Core Case Study**). Write a report on what you found. Try to include information on current effects of warmer water on the kelp beds as well as projections about future effects. Also, summarize any information you might find on possible ways to prevent harm to these kelp forests.

Data Analysis

The graph below shows changes in the size of an Emperor penguin population in terms of numbers of breeding pairs on the island of Terre Adelie in the Antarctic. Scientists used this data along with data on the penguins' shrinking ice habitat to project a general decline in the island's Emperor penguin population, to the point where they will be endangered in 2100. Use the graph to answer the following questions.



1. If the penguin population fluctuates around the carrying capacity, what was the approximate carrying capacity of the island for the penguin population from 1960 to 1975? What was the approximate carrying capacity of the island for the penguin population from 1980 to 2010?

2. What was the overall percentage decline in the penguin population from 1975 to 2010?

3. What is the projected overall percentage decline in the penguin population between 2010 and 2100?