on them. Though these upwelling zones make up only a few percent of the ocean's area, they are the source of more than a quarter of all fish caught globally.

Bodies of Water

Ocean currents influence climate along the coasts of continents by heating or cooling overlying air masses that pass across the land. Coastal regions are also generally wetter than inland areas at the same latitude. The cool, misty climate produced by the cold California Current that flows southward along western North America supports a coniferous rain forest ecosystem along much of the continent's Pacific coast and large redwood groves farther south. Conversely, the west coast of northern Europe has a mild climate because the Gulf Stream carries warm water from the equator to the North Atlantic **(Figure 51.5)**. As a result, northwestern Europe is warmer during winter than southeastern Canada, which is farther south but is cooled by the Labrador Current flowing south from the coast of Greenland.

Because of the high specific heat of water (see Concept 3.2), oceans and large lakes tend to moderate the climate of nearby land. During a hot day, when land is warmer than the water, air over the land heats up and rises, drawing a cool breeze from the water across the land **(Figure 51.6)**. In contrast, because temperatures drop more quickly over land than over water at night, air over the now warmer water rises, drawing cooler air from the land back out over the water and replacing it with warmer air from offshore. This local moderation of climate can be limited to the coast itself, however. In southern California and southwestern Australia, cool, dry ocean breezes in summer are warmed when they contact the land, absorbing moisture and creating a hot, arid climate just a few kilometers inland (see Figure 3.5). This climate pattern also occurs around the Mediterranean Sea, which gives it the name *Mediterranean climate*.

Mountains

Like large bodies of water, mountains influence air flow over land. When warm, moist air approaches a mountain, the air rises and cools, releasing moisture on the windward side of the peak (see Figure 51.6). On the leeward side, cooler, dry air descends, absorbing moisture and producing a "rain shadow." Such leeward rain shadows determine where many deserts are found, including the Mojave Desert of western North America and the Gobi Desert of Asia.

Mountains also affect the amount of sunlight reaching an area and thus the local temperature and rainfall. South-facing

▼ Figure 51.5 Global circulation of surface water in the oceans. Water is warmed at the equator and flows north and south toward the poles, where it cools. Note the similarities between the direction of water circulation in the gyres and the direction of the trade winds in Figure 51.3.

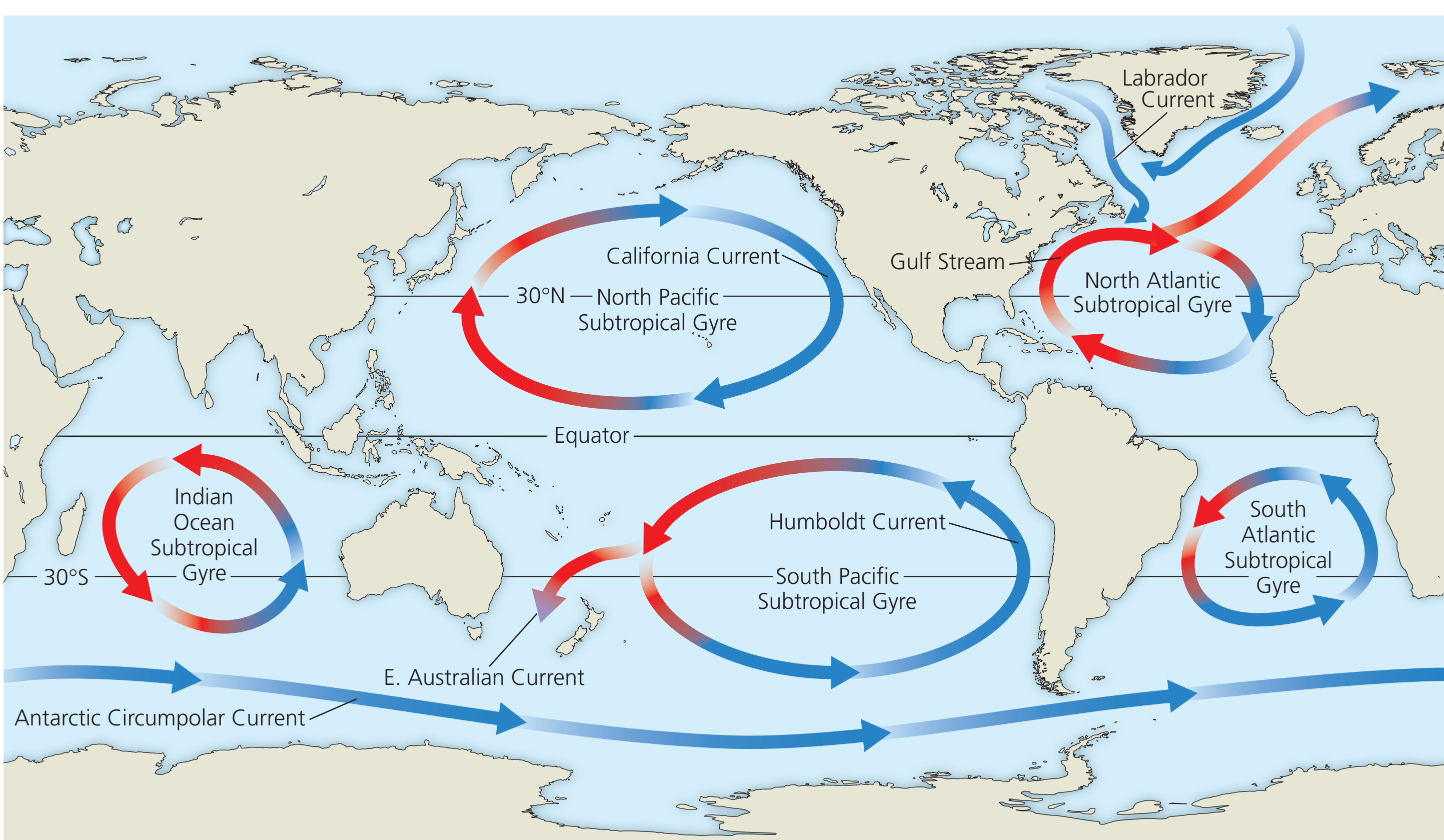
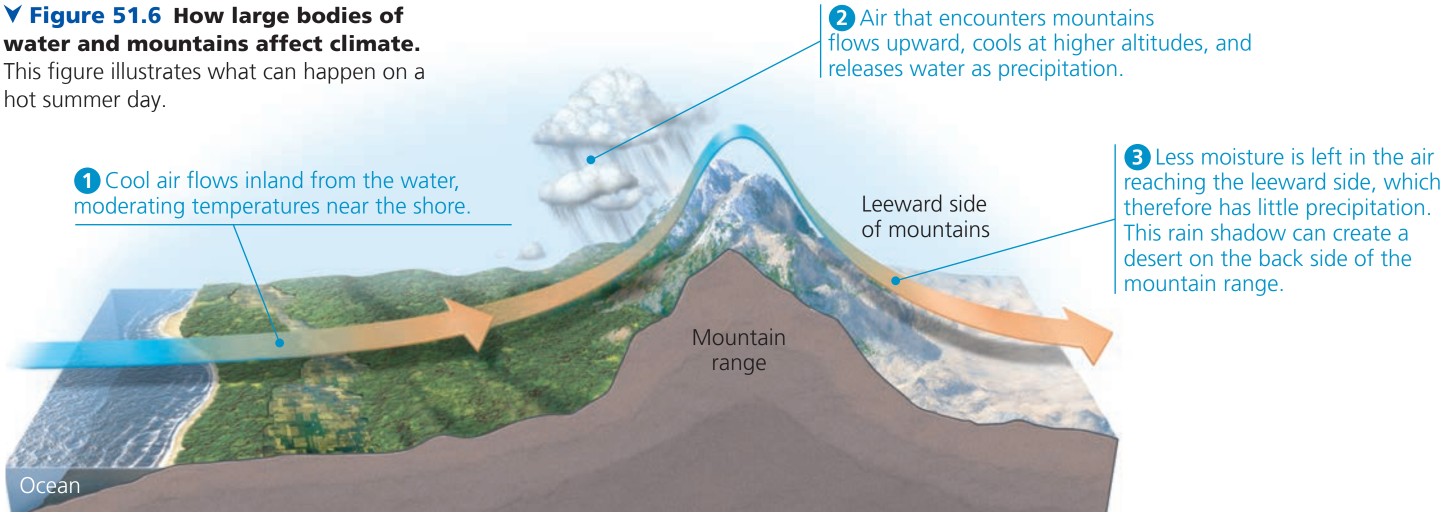


Figure 51.6 How large bodies of water and mountains affect climate. This figure illustrates what can happen on a hot summer day.



slopes in the Northern Hemisphere receive more sunlight than north-facing slopes and are therefore warmer and drier. These physical differences influence species distributions locally. On many mountains in western North America, spruce and other conifers grow on the cooler north-facing slopes, but shrubby, drought-resistant plants inhabit the south-facing slopes. In addition, every 1,000-m increase in elevation produces an average temperature drop of 6°C, equivalent to that produced by an 880-km increase in latitude. This is one reason that high-elevation communities near the equator, for example, can be similar to lower-elevation communities that are far from the equator.

Microclimate

At an even smaller scale is the **microclimate**, very fine, localized patterns in climatic conditions. Many features in the environment influence microclimate by casting shade, altering evaporation from soil, or changing wind patterns. For example, forest trees often moderate the microclimate below them. Cleared areas therefore typically experience greater temperature extremes than the forest interior because of greater solar radiation and wind currents that arise from the rapid heating and cooling of open land. Within a forest, low-lying ground is usually wetter than higher ground and tends to be occupied by different tree species. A log or large stone can shelter organisms such as salamanders, worms, and insects, buffering them from the extremes of temperature and moisture.

Every environment on Earth is characterized by a mosaic of small-scale differences in chemical and physical attributes, such as temperature, light, water, and nutrients. Later in this chapter, we'll examine how these **abiotic**, or nonliving, factors influence the distribution and abundance of organisms. Similarly, all of the **biotic**, or living, factors—the other organisms that are part of an individual's environment—also influence the distribution and abundance of life on Earth.

Global Climate Change

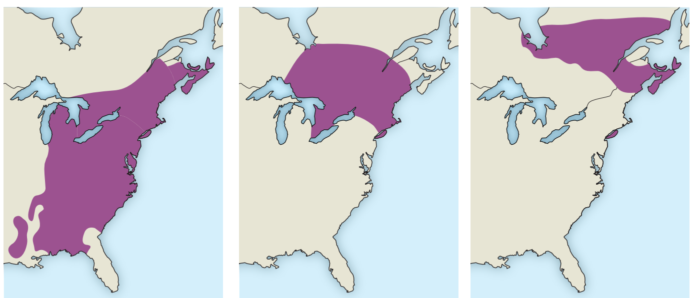
Because climatic variables affect the geographic ranges of most plants and animals, any large-scale change in Earth's climate profoundly affects the biosphere. In fact, such a large-scale climate "experiment" is already under way: The burning of fossil fuels and deforestation are increasing the concentrations of carbon dioxide and other greenhouse gases in the atmosphere. This has caused **climate change**, a directional change to the global climate that lasts three decades or more (as opposed to short-term changes in the weather). As we'll explore in more detail in Concept 56.4, Earth has warmed an average of 0.9°C (1.6°F) since 1900 and is projected to warm 1–6°C (2–11°F) more by the year 2100. The climate is changing in other ways as well: Wind and precipitation patterns are shifting, and extreme weather events (such as droughts and storms) are occurring more frequently.

How will such changes in climate affect the distribution of organisms? One way to answer this question is to look back at the changes that have occurred since the last ice age ended. Until about 16,000 years ago, continental glaciers covered much of North America and Eurasia. As the climate warmed and the glaciers retreated, tree species distributions expanded northward. A detailed record of these changes is captured in fossilized pollen deposits that have been discovered in lakes and ponds. These fossilized pollen data show that while some species moved northward rapidly, others moved more slowly. For species that moved more slowly, the expansion of their ranges lagged several thousand years behind the shift in suitable habitat.

Will plants and other species be able to keep up with the much more rapid warming projected for this century? Consider the American beech, *Fagus grandifolia*. Ecological models predict that the northern limit of the beech's range may move 700–900 km northward in the next century, and its southern range limit will shift even more. The current and

Figure 51.7 Current range and predicted ranges for the American beech under two climate-change scenarios.

American beech (*Fagus grandifolia*)



(a) Current range **(b) 4.5°C warming over next century** **(c) 6.5°C warming over next century**

? *The predicted range in each scenario is based on climate factors alone. What other factors might alter the distribution of this species?*

MB **Interview with Margaret Davis: Using fossil pollen to track tree species migration**

Figure 51.8 The rusty-patched bumblebee (*Bombus affinis*). This species has not been able to expand its range and is now endangered.

predicted geographic ranges of this species under two different climate-change scenarios are illustrated in **Figure 51.7**. If these predictions are even approximately correct, the beech's range must shift 7–9 km northward per year to keep pace with the warming climate. However, since the end of the last ice age, the beech has moved at a rate of only 0.2 km per year. Without human help in moving to new habitats, species such as the American beech may have much smaller ranges or even become extinct.

In fact, the climate change that has *already* occurred has affected the geographic ranges of hundreds of terrestrial, marine, and freshwater organisms. For example, as the climate has warmed, 22 of 35 European butterfly species studied have shifted their ranges farther north by 35–240 km in recent decades. In western North America, nearly 200 plant species have moved to lower elevations, most likely in response to decreased rain and snow at higher elevations. Other research shows that a Pacific diatom species, *Neodenticula seminae*, recently colonized the Atlantic Ocean for the first time in 800,000 years. In these and many other such cases, when climate change enables or causes a species to expand its range into a new geographic area, other organisms living there may be harmed (see Figure 56.30).

Furthermore, as the climate changes, some species are facing a shortage of suitable replacement habitat, while others cannot migrate quickly enough. For example, a 2015 study found that on average, the geographic ranges of 67 bumblebee species in the Northern Hemisphere were shrinking: The bumblebees were retreating from the southern edges of their distributions, but failing to expand their ranges to the north **(Figure 51.8)**. Overall, climate change is causing the populations of many species to decrease in size or even disappear (see Figure 1.12). In the next section, we'll continue to examine the importance of climate in determining species distributions around the world.

CONCEPT CHECK 51.1

1. Explain how the sun's unequal heating of Earth's surface results in deserts near 30° north and south of the equator.
2. What are some of the differences in microclimate between an unplanted agricultural field and a nearby stream corridor with trees?
3. **WHAT IF?** ➤ Changes in Earth's climate at the end of the last ice age happened gradually, taking centuries to thousands of years. If the current global warming happens very quickly, as predicted, how may this rapid climate change affect the evolution of long-lived trees compared with that of annual plants, which have much shorter generation times?
4. **MAKE CONNECTIONS** ➤ Focusing just on the effects of temperature, would you expect the global distribution of C_4 plants to expand or contract as Earth becomes warmer? Why? (See Concept 11.4.)

For suggested answers, see Appendix A.

CONCEPT 51.2

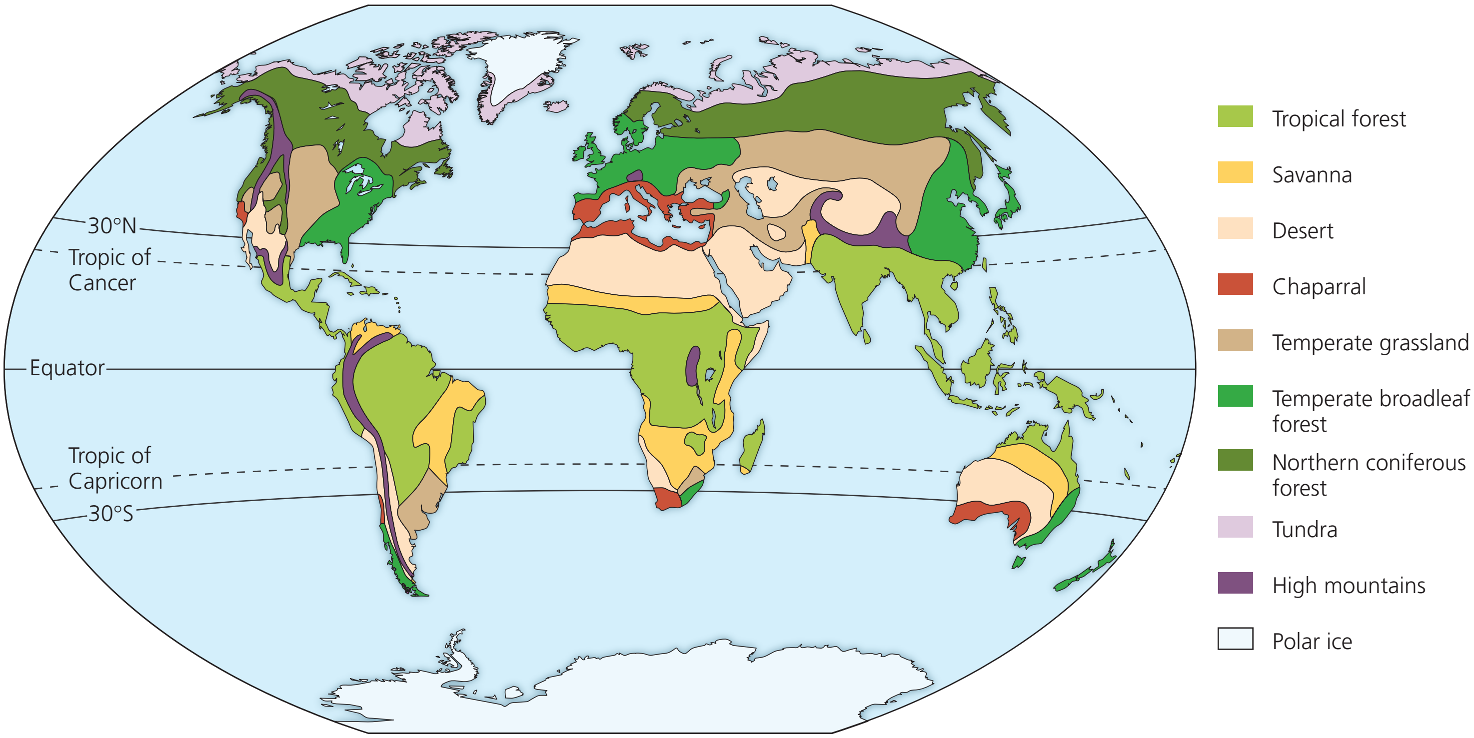
The distribution of terrestrial biomes is controlled by climate and disturbance

Earth's life is distributed on a grand scale in **biomes**, major life zones characterized by vegetation type in terrestrial biomes (or by the physical environment in aquatic biomes, as you'll read in Concept 51.3). What determines where these biomes are located?

Climate and Terrestrial Biomes

Because climate has a strong influence on the distribution of plant species, it is a major factor in determining the locations of terrestrial biomes **(Figure 51.9)**. One way to highlight the importance of climate on the distribution of biomes is to construct a **climograph**, a plot of the annual mean temperature

Figure 51.9 The distribution of major terrestrial biomes.



Animation: Terrestrial Biomes

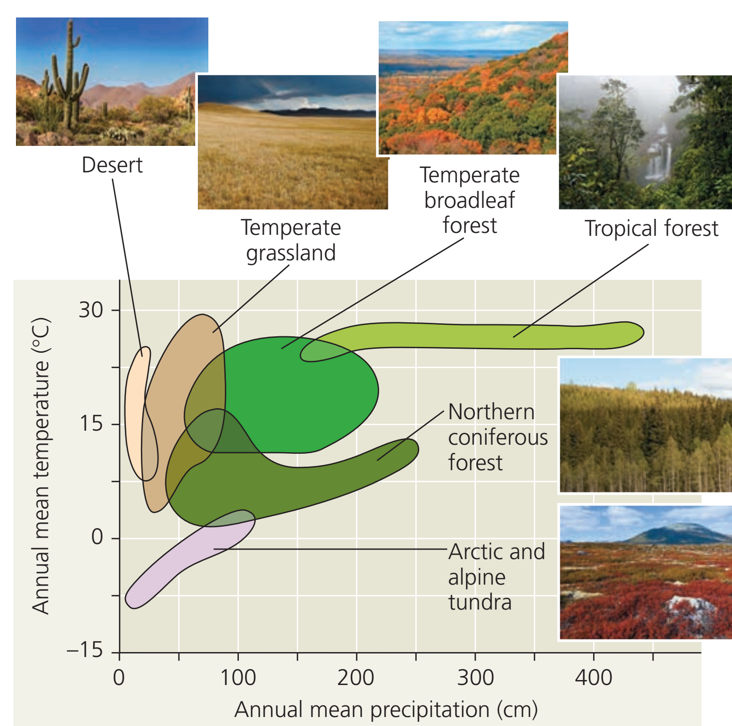
and precipitation in a particular region. **Figure 51.10** is a climograph for some of the biomes found in North America. Notice, for instance, that the range of precipitation in northern coniferous and temperate forests is similar but that temperate forests are generally warmer. Grasslands are typically drier than either kind of forest, and deserts are drier still.

Factors other than mean temperature and precipitation also play a role in determining where biomes exist. Some areas in North America with a particular combination of temperature and precipitation support a temperate broadleaf forest, but other areas with similar values for these variables support a coniferous forest (see the overlap in Figure 51.10). What could explain this variation? One thing to remember is that the climograph is based on annual *averages*. Often, however, the pattern of climatic variation is as important as the average climate. For example, some areas may receive regular precipitation throughout the year, whereas other areas may have distinct wet and dry seasons.

General Features of Terrestrial Biomes

Most terrestrial biomes are named for major physical or climatic features and for their predominant vegetation. Temperate grasslands, for instance, are generally found in middle latitudes, where the climate is more moderate than in the tropics or polar regions, and are dominated by various grass species. Each biome is also characterized by

Figure 51.10 A climograph for some major biomes in North America. The areas plotted here encompass the ranges of annual mean temperature and precipitation in the biomes.



INTERPRET THE DATA ➤ *Some arctic tundra ecosystems receive as little rainfall as deserts but have much more dense vegetation. What climatic factor could cause this difference? Explain.*

microorganisms, fungi, and animals adapted to that particular environment. Temperate grasslands are usually more likely than temperate forests to be populated by arbuscular mycorrhizal fungi (see Figure 37.15) and by large grazing mammals.

Although Figure 51.9 shows distinct boundaries between the biomes, terrestrial biomes usually grade into neighboring biomes, sometimes over large areas. The area of intergradation, called an **ecotone**, may be wide or narrow.

Vertical layering of vegetation is an important feature of terrestrial biomes. In many forests, the layers from top to bottom consist of the upper **canopy**, the low-tree layer, the shrub understory, the ground layer of herbaceous plants, the forest floor (litter layer), and the root layer. Nonforest biomes have similar, though usually less pronounced, layers. Layering of vegetation provides many different habitats for animals, which sometimes exist in well-defined feeding groups, from the insectivorous birds and bats that feed above canopies to the small mammals, numerous worms, and arthropods that search for food in the litter and root layers below.

The species composition of each kind of biome varies from one location to another. For instance, in the northern coniferous forest (taiga) of North America, red spruce is common in the east but does not occur in most other areas, where black spruce and white spruce are abundant. As **Figure 51.11** shows, cacti living in deserts of North and South America are similar morphologically to plants called euphorbs found in African deserts. But since cacti and euphorbs belong to different evolutionary lineages, their similarities are due to convergent evolution rather than shared ancestry.

Disturbance and Terrestrial Biomes

Biomes are dynamic, and disturbance rather than stability tends to be the rule. In ecological terms, **disturbance** is an event such as a storm, fire, or human activity that changes a community, removing organisms from it and altering resource availability. Frequent fires can kill woody plants and keep a savanna from becoming the woodland that climate alone would support. Hurricanes and other storms create openings for new species in many tropical and temperate forests and can alter forest composition. After Hurricane Katrina struck the Gulf coast of the United States in 2005, mixed swamp forests in the area shifted toward a dominance of baldcypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) because these species are less susceptible to wind damage than other tree species found there. As a result of disturbances, biomes are often patchy, containing several different communities in a single area.

In many biomes, even the dominant plants depend on periodic disturbance. Natural wildfires are an integral component of grasslands, savannas, chaparral, and many coniferous forests. Before agricultural and urban development, much of the southeastern United States was dominated by a single conifer species, the longleaf pine. Without periodic burning, broadleaf trees tended to replace the pines. Forest managers now use fire as a tool to help maintain many coniferous forests.

Figure 51.12 summarizes the major features of terrestrial biomes. As you read about the characteristics of each biome, remember that humans have altered much of Earth's surface, replacing natural communities with urban and agricultural ones. The central United States, for example, is classified as grassland and once contained extensive areas of tallgrass prairie. Very little of the original prairie remains today, however, having been converted to farmland.

CONCEPT CHECK 51.2

1. Based on the climograph in Figure 51.10, what mainly differentiates temperate grassland from temperate broadleaf forest?
2. Using Figure 51.12, identify the natural biome in which you live, and summarize its abiotic and biotic characteristics. Do these reflect your actual surroundings? Explain.
3. **WHAT IF?** ➤ If global warming increases average temperatures on Earth by 4°C in this century, predict which biome is most likely to replace tundra in some locations as a result. Explain your answer.

For suggested answers, see Appendix A.

Figure 51.11 Convergent evolution in a cactus and a euphorb. Cacti in the genus *Cereus* are found in the Americas; *Euphorbia canariensis*, a euphorb, is native to the Canary Islands, off the northwest coast of Africa.

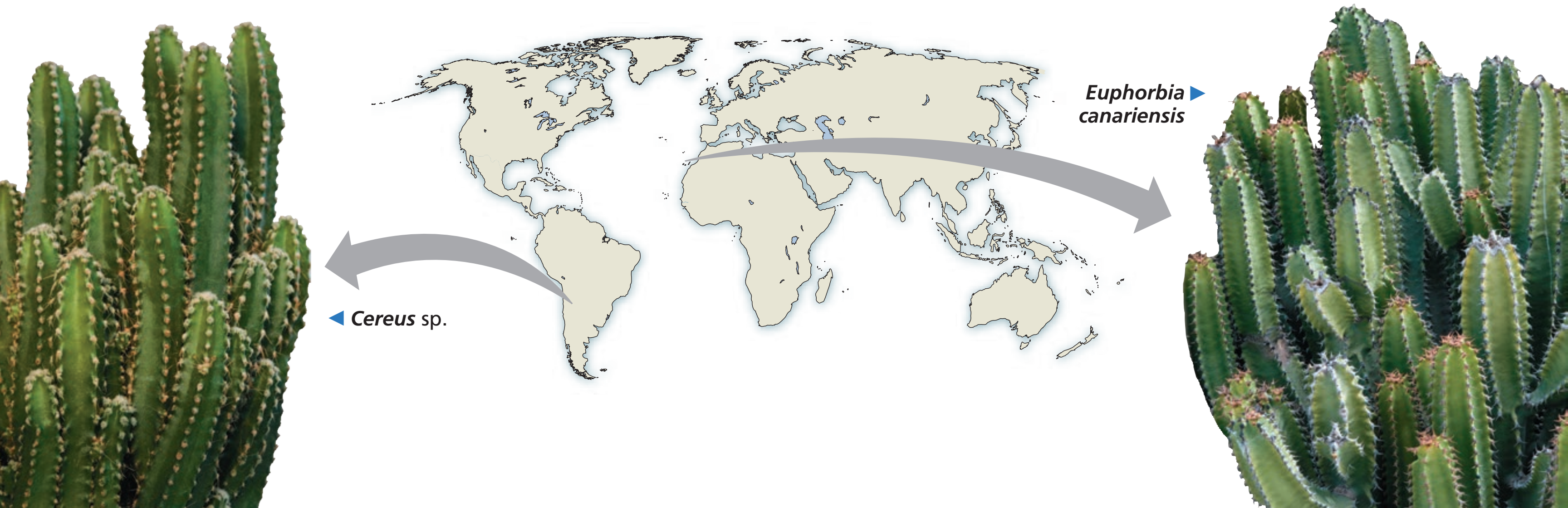


Figure 51.12 Exploring Terrestrial Biomes

Tropical Forest

Distribution Tropical forest occurs in equatorial and subequatorial regions.

Precipitation In **tropical rain forests**, rainfall is relatively constant, about 200–400 cm annually. In **tropical dry forests**, precipitation is highly seasonal, about 150–200 cm annually, with a six- to seven-month dry season.

Temperature High year-round, averaging 25–29°C with little seasonal variation.

Plants Tropical forests are vertically layered, and competition for light is intense. Layers in rain forests include trees that grow above a closed canopy, the canopy trees, one or two layers of subcanopy trees, and layers of shrubs and herbs (small, nonwoody plants). There are generally fewer layers in tropical dry forests. Broadleaf evergreen trees are dominant in tropical rain forests, whereas many tropical dry forest trees drop their leaves during the dry season. Epiphytes such as bromeliads and orchids generally cover tropical forest trees but are less abundant in dry forests. Thorny shrubs and succulent plants are common in some tropical dry forests.

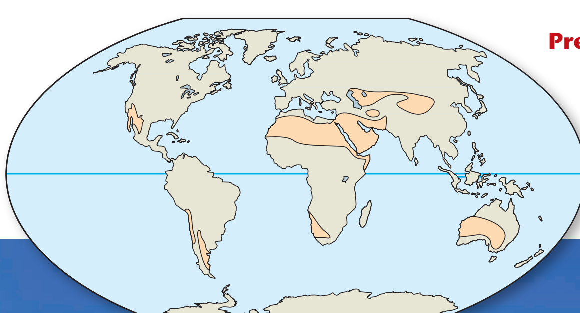
A tropical rain forest in Costa Rica

Animals Earth's tropical forests are home to millions of species, including an estimated 5–30 million still undescribed species of insects, spiders, and other arthropods. In fact, animal diversity is higher in tropical forests than in any other terrestrial biome. The animals, including amphibians, birds and other reptiles, mammals, and arthropods, are adapted to the vertically layered environment and are often inconspicuous.

Human Impact Humans have long had thriving communities in tropical forests. Many tropical forests are now being cut down and converted to farmland, urban areas, and other types of land use.

Desert

Distribution **Deserts** occur in bands near 30° north and south latitude or at other latitudes in the interior of continents (for instance, the Gobi Desert of north-central Asia).



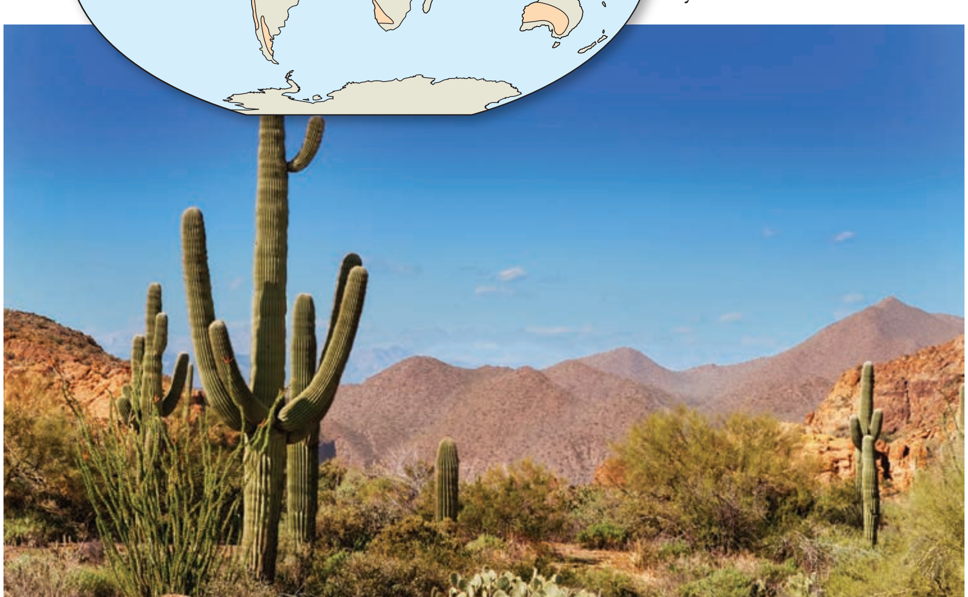
Precipitation Precipitation is low and highly variable, generally less than 30 cm per year.

Temperature Temperature is variable seasonally and daily. Maximum air temperature in hot deserts may exceed 50°C; in cold deserts air temperature may fall below –30°C.

Plants Deserts are dominated by low, widely scattered vegetation; the proportion of bare ground is high compared with other biomes. The plants include succulents such as cacti or euphorbs, deeply rooted shrubs, and herbs that grow during the infrequent moist periods. Desert plant adaptations include tolerance of heat and dessication, water storage, and reduced leaf surface area. Physical defenses, such as spines, and chemical defenses, such as toxins in the leaves of shrubs, are common. Many of the plants exhibit C_4 or CAM photosynthesis.

Animals Common desert animals include snakes and lizards, scorpions, ants, beetles, migratory and resident birds, and seed-eating rodents. Many species are nocturnal. Water conservation is a common adaptation, with some species surviving solely on water obtained from breaking down carbohydrates in seeds.

Human Impact Long-distance transport of water and deep groundwater wells have allowed humans to maintain substantial populations in deserts. Urbanization and conversion to irrigated agriculture have reduced the natural biodiversity of some deserts.



Saguaro and ocotillo, Arizona

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▼ Figure 51.12 Exploring Terrestrial Biomes (continued)

Savanna

Distribution Savanna occurs in equatorial and subequatorial regions.

Precipitation Seasonal rainfall averages 30–50 cm per year. The dry season can last up to eight or nine months.

Temperature The **savanna** is warm year-round, averaging 24–29°C, but with somewhat more seasonal variation than in tropical forests.

Plants The scattered trees found at different densities in the savanna often are thorny and have small leaves, an apparent adaptation to the relatively dry conditions. Fires are common in the dry season, and the dominant plant species are fire-adapted and tolerant of seasonal drought. Grasses and small nonwoody plants called forbs, which make up most of the ground cover, grow rapidly in response to seasonal rains and are tolerant of grazing by large mammals and other herbivores.

A savanna in Kenya

Animals Large plant-eating mammals, such as wildebeests and zebras, and predators, including lions and hyenas, are common inhabitants. However, the dominant herbivores are actually insects, especially termites. During seasonal droughts, grazing mammals often migrate to parts of the savanna with more forage and scattered watering holes.

Human Impact The earliest humans may have lived in savannas. Fires set by humans may help maintain this biome, though overly frequent fires reduce tree regeneration by killing the seedlings and saplings. Cattle ranching and overhunting have led to declines in large-mammal populations.

Chaparral

Distribution This biome occurs in midlatitude coastal regions on several continents, and its many names reflect its far-flung distribution: **chaparral** in North America, *matorral* in Spain and Chile, *garigue* and *maquis* in southern France, and *fynbos* in South Africa.

Precipitation Precipitation is highly seasonal, with rainy winters and dry summers. Annual precipitation generally falls within the range of 30–50 cm.

Temperature Fall, winter, and spring are cool, with average temperatures in the range of 10–12°C. Average summer temperature can reach 30°C, and daytime maximum temperature can exceed 40°C.

Plants Chaparral is dominated by shrubs and small trees, along with many kinds of grasses and herbs. Plant diversity is high, with many species confined to a specific, relatively small geographic area. Adaptations of the woody plants to drought include their tough evergreen leaves, which reduce water loss. Adaptations to fire are also prominent. Some of the shrubs produce seeds that will germinate only after a hot fire; food reserves stored in their fire-resistant roots enable them to resprout quickly and use nutrients released by the fire.

Animals Native mammals include browsers, such as deer and goats, that feed on twigs and buds of woody vegetation, and a high diversity of small mammals. Chaparral areas also support many species of amphibians, birds and other reptiles, and insects.

Human Impact Chaparral areas have been heavily settled and reduced through conversion to agriculture and urbanization. Humans contribute to the fires that sweep across the chaparral.

An area of chaparral in California

Temperate Grassland

Distribution The veldts of South Africa, the *puszta* of Hungary, the pampas of Argentina and Uruguay, the steppes of Russia, and the plains and prairies of central North America are examples of **temperate grasslands**.

Precipitation Precipitation is often highly seasonal, with relatively dry winters and wet summers. Annual precipitation generally averages between 30 and 100 cm. Periodic drought is common.

Temperature Winters are generally cold, with average temperatures falling below –10°C. Summers, with average temperatures often approaching 30°C, are hot.

Plants The dominant plants are grasses and forbs, which vary in height from a few centimeters to 2 m in tallgrass prairie. Many grassland plants have adaptations that help them survive periodic, protracted droughts and fire. For example, grasses can sprout quickly following fire. Grazing by large mammals helps prevent establishment of woody shrubs and trees.

Animals Native mammals include large grazers such as bison and wild horses. Temperate grasslands are also inhabited by a wide variety of burrowing mammals, such as prairie dogs in North America.

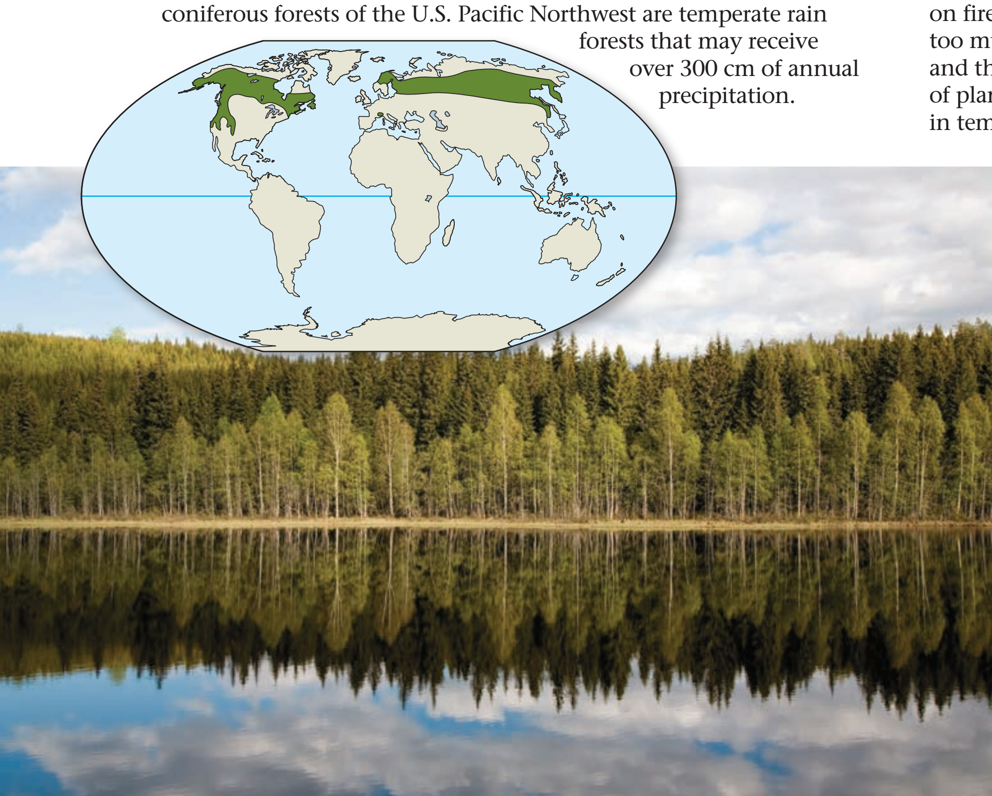
A grassland in Mongolia

Human Impact Deep, fertile soils make temperate grasslands ideal places for agriculture, especially for growing grains. As a consequence, most grassland in North America and much of Eurasia has been converted to farmland. In some drier grasslands, cattle and other grazers have turned parts of the biome into desert.

Northern Coniferous Forest

Distribution Extending in a broad band across northern North America and Eurasia to the edge of the arctic tundra, the **northern coniferous forest**, or *taiga*, is the largest terrestrial biome on Earth.

Precipitation Annual precipitation generally ranges from 30 to 70 cm, and periodic droughts are common. However, some coastal coniferous forests of the U.S. Pacific Northwest are temperate rain forests that may receive over 300 cm of annual precipitation.



Temperature Winters are usually cold; summers may be hot. Some areas of coniferous forest in Siberia typically range in temperature from –50°C in winter to over 20°C in summer.

Plants Northern coniferous forests are dominated by cone-bearing trees, such as pine, spruce, fir, and hemlock, some of which depend on fire to regenerate. The conical shape of many conifers prevents too much snow from accumulating and breaking their branches, and their needle- or scale-like leaves reduce water loss. The diversity of plants in the shrub and herb layers of these forests is lower than in temperate broadleaf forests.

Animals While many migratory birds nest in northern coniferous forests, other species reside there year-round. The mammals of this biome, which include moose, brown bears, and Siberian tigers, are diverse. Periodic outbreaks of insects that feed on the dominant trees can kill vast tracts of trees.

Human Impact Although they have not been heavily settled by human populations, northern coniferous forests are being logged at an alarming rate, and the old-growth stands of these trees may soon disappear.

A coniferous forest in Norway

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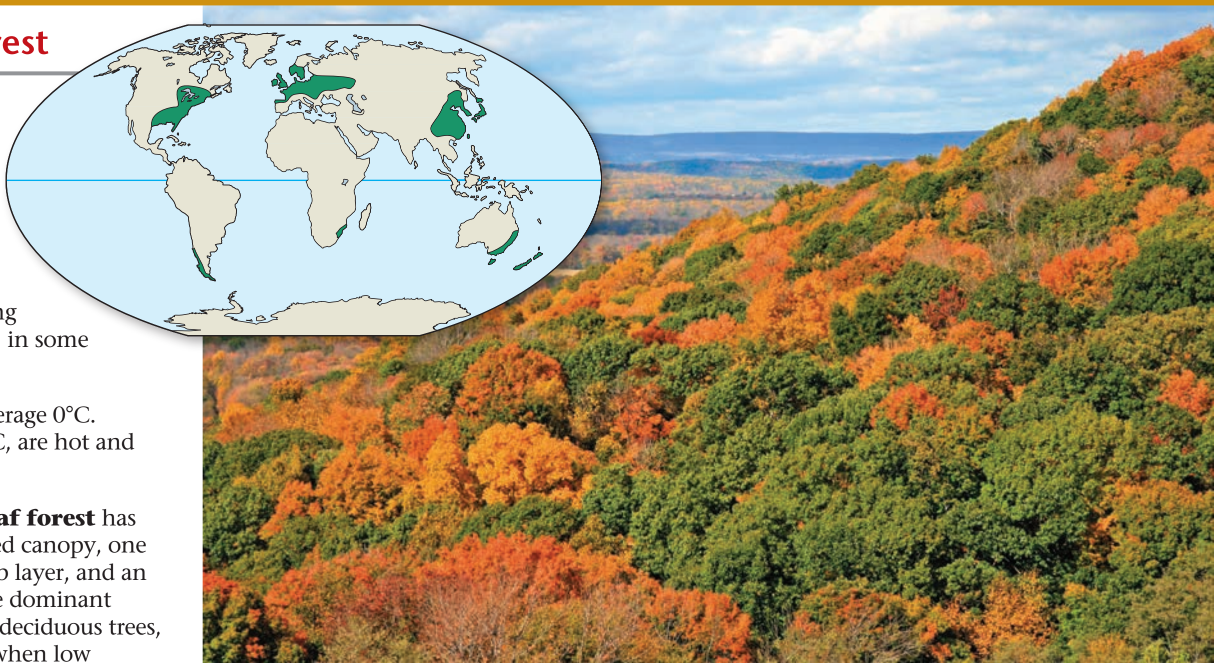
▼ Figure 51.12 Exploring Terrestrial Biomes (continued)

Temperate Broadleaf Forest



Distribution Temperate broadleaf forest is found mainly at midlatitudes in the Northern Hemisphere, with smaller areas in Chile, South Africa, Australia, and New Zealand.

Precipitation Precipitation can average from about 70 to over 200 cm annually. Significant amounts fall during all seasons, including summer rain and, in some forests, winter snow.

Temperature Winter temperatures average 0°C. Summers, with temperatures up to 35°C, are hot and humid.

Plants A mature **temperate broadleaf forest** has distinct vertical layers, including a closed canopy, one or two strata of understory trees, a shrub layer, and an herb layer. There are few epiphytes. The dominant plants in the Northern Hemisphere are deciduous trees, which drop their leaves before winter, when low temperatures would reduce photosynthesis and make water uptake from frozen soil difficult. In Australia, evergreen eucalyptus trees dominate these forests.

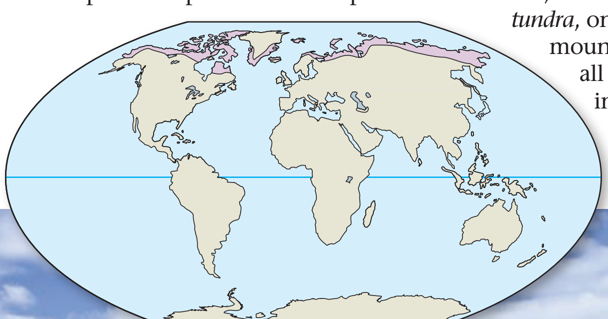
Animals In the Northern Hemisphere, many mammals hibernate in winter, while many bird species migrate to warmer climates. Mammals, birds, and insects make use of all the vertical layers of the forest.

A temperate broadleaf forest in New Jersey

Human Impact Temperate broadleaf forest has been heavily settled on all continents. Logging and land clearing for agriculture and urban development cleared virtually all the original deciduous forests in North America. However, owing to their capacity for recovery, these forests are returning over much of their former range.

Tundra

Distribution **Tundra** covers expansive areas of the Arctic, amounting to 20% of Earth's land surface. High winds and low temperatures produce similar plant communities, called *alpine tundra*, on very high mountaintops at all latitudes, including the tropics.



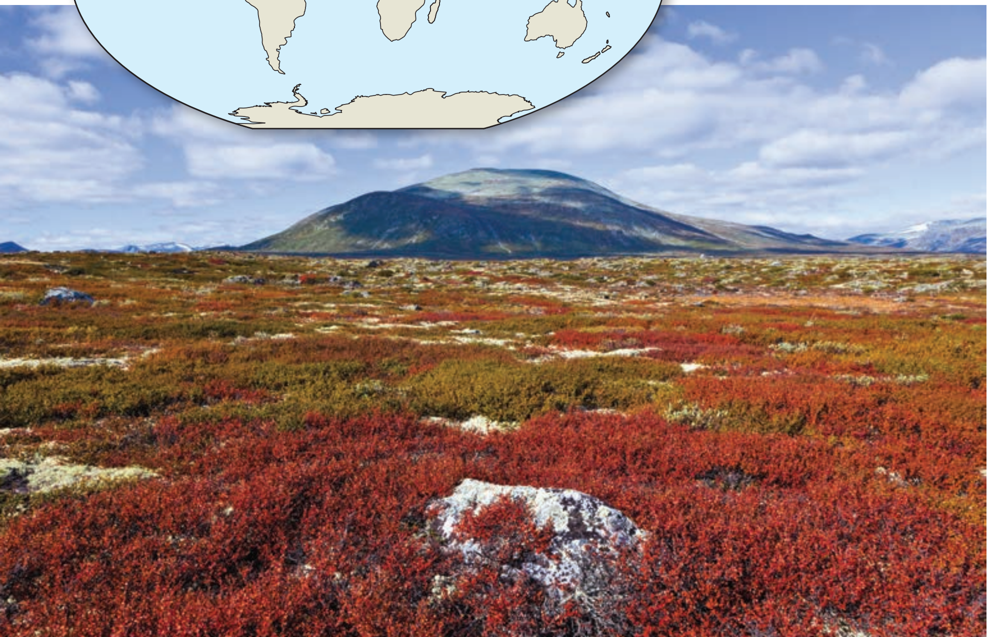
Precipitation Precipitation averages from 20 to 60 cm annually in arctic tundra but may exceed 100 cm in alpine tundra.

Temperature Winters are cold, with averages in some areas below –30°C. Summer temperatures generally average less than 10°C.

Plants The vegetation of tundra is mostly herbaceous, consisting of a mixture of mosses, grasses, and forbs, along with some dwarf shrubs and trees and lichens. A permanently frozen layer of soil called permafrost restricts the growth of plant roots.

Animals Large grazing musk oxen are resident, while caribou and reindeer are migratory. Predators include bears, wolves, and foxes. Many bird species migrate to the tundra for summer nesting.

Human Impact Tundra is sparsely settled but has become the focus of significant mineral and oil extraction in recent years.



Dovrefjell-Sunndalsfjella National Park, Norway, in autumn

CONCEPT 51.3

Aquatic biomes are diverse and dynamic systems that cover most of Earth

Unlike terrestrial biomes, aquatic biomes are characterized primarily by their physical and chemical environment. They also show far less latitudinal variation, with all types found across the globe. For example, marine biomes generally have salt concentrations that average 3%, whereas freshwater biomes are usually characterized by a salt concentration of less than 0.1%.

The oceans make up the largest marine biome, covering about 75% of Earth's surface. Because of their vast size, they greatly impact the biosphere. Water evaporated from the oceans provides most of the planet's rainfall. Marine algae and photosynthetic bacteria supply much of the world's oxygen and consume large amounts of atmospheric carbon dioxide. Ocean temperatures have a major effect on global climate and wind patterns (see Figure 51.3), and along with large lakes, oceans tend to moderate the climate of nearby land.

Freshwater biomes are closely linked to the soils and biotic components of the surrounding terrestrial biome. The particular characteristics of a freshwater biome are also influenced by the patterns and speed of water flow and the climate to which the biome is exposed.

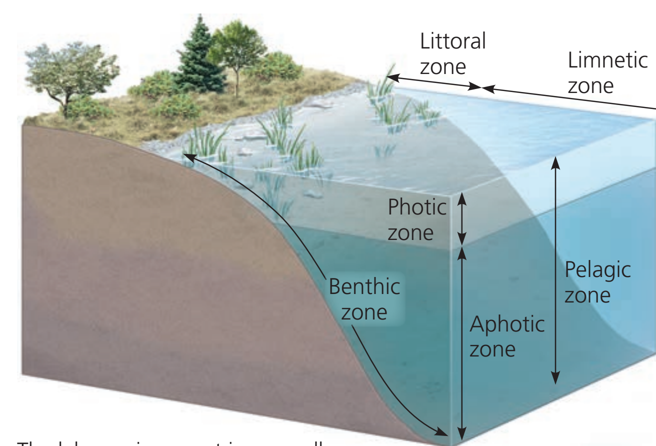
Zonation in Aquatic Biomes

Many aquatic biomes are physically and chemically stratified (layered), vertically and horizontally, as illustrated for both a lake and a marine environment in **Figure 51.13**. Light is absorbed by water and by photosynthetic organisms, so its intensity decreases rapidly with depth. The upper **photic zone** is the region where there is sufficient light for photosynthesis, while the lower **aphotic zone** is the region where little light penetrates. The photic and aphotic zones together make up the **pelagic zone**. Deep in the aphotic zone lies the **abyssal zone**, the part of the ocean 2,000–6,000 m below the surface. At the bottom of all of these aquatic zones, deep or shallow, is the **benthic zone**. Made up of sand and organic and inorganic sediments, the benthic zone is occupied by communities of organisms collectively called the **benthos**. A major source of food for many benthic species is dead organic matter called **detritus**, which "rains" down from the productive surface waters of the photic zone.

Thermal energy from sunlight warms surface waters to whatever depth the sunlight penetrates, but the deeper waters remain quite cold. In the ocean and in most lakes, a narrow layer of abrupt temperature change called a **thermocline** separates the more uniformly warm upper layer from more uniformly cold deeper waters. Lakes tend to be particularly layered with respect to temperature, especially during summer and winter, but many temperate lakes undergo a semiannual mixing of their waters as a result of changing

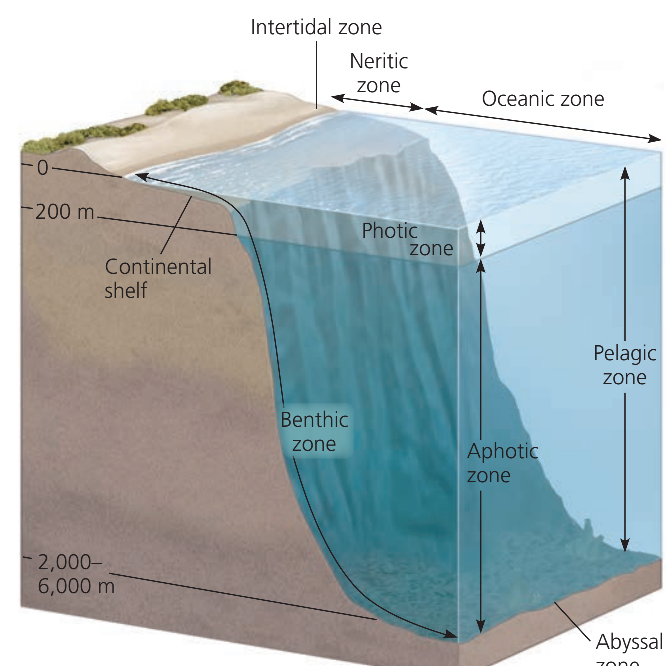
Figure 51.13 Zonation in aquatic environments.

(a) Zonation in a lake



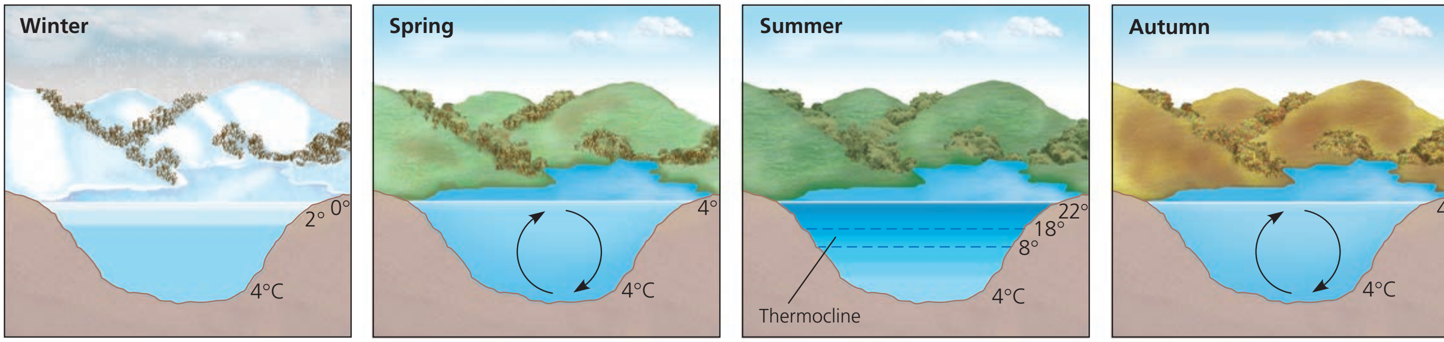
The lake environment is generally classified on the basis of three physical criteria: light penetration (photic and aphotic zones), distance from shore and water depth (littoral and limnetic zones), and whether the environment is open water (pelagic zone) or on the bottom (benthic zone).

(b) Marine zonation



Like lakes, the marine environment is generally classified on the basis of light penetration (photic and aphotic zones), distance from shore and water depth (intertidal, neritic, and oceanic zones), and whether the environment is open water (pelagic zone) or on the bottom (benthic and abyssal zones).

▼ Figure 51.14 Seasonal turnover in lakes with winter ice cover. Seasonal turnover causes the lake waters to be well oxygenated at all depths in spring and autumn; in winter and summer, when the lake is stratified by temperature, the oxygen concentration decreases with depth.



1 In winter, the coldest water in the lake (0°C) lies just below the surface ice; water becomes progressively warmer at deeper levels of the lake, typically 4°C at the bottom.

2 In spring, the surface water warms to 4°C and mixes with the layers below, eliminating thermal stratification. Spring winds help mix the water, bringing oxygen to the bottom and nutrients to the surface.

3 In summer, the lake regains a distinctive thermal profile, with warm surface water separated from cold bottom water by a narrow vertical zone of abrupt temperature change, called a thermocline.

4 In autumn, as surface water cools rapidly, it sinks beneath the underlying layers, remixing the water until the surface begins to freeze and the winter temperature profile is reestablished.

temperature profiles **(Figure 51.14)**. This **turnover**, as it is called, sends oxygenated water from a lake's surface to the bottom and brings nutrient-rich water from the bottom to the surface in both spring and autumn.

In both freshwater and marine environments, communities are distributed according to water depth, degree of light penetration, distance from shore, and whether they are found in open water or near the bottom. Marine communities, in particular, illustrate the limitations on species distribution that result from these abiotic factors. Plankton and many fish species live in the relatively shallow photic zone (see Figure 51.13b). Because water absorbs light so well and the ocean is so deep, most of the ocean volume is dark (the aphotic zone) and harbors relatively little life.

Figure 51.15 explores the main characteristics of Earth's major aquatic biomes.

CONCEPT CHECK 51.3

1. Why are coral reefs restricted to the photic zone? What impact would a rise in the sea level have on coral reefs?
2. **MAKE CONNECTIONS ➤** Many organisms living in estuaries experience freshwater and saltwater conditions each day with the rising and falling of tides. Explain how these changing conditions challenge the survival of these organisms (see Concept 44.1).
3. **MAKE CONNECTIONS ➤** As noted in Figure 51.15, the addition of nutrients to a lake can cause an algal bloom. When these algae die, complex molecules in their bodies are broken down by decomposers using aerobic respiration. Explain why this would reduce the lake's oxygen levels (see Concept 10.1).

For suggested answers, see Appendix A.

CONCEPT 51.4

Interactions between organisms and the environment limit the distribution of species

Species distributions are a consequence of both ecological factors and evolutionary history. Consider kangaroos, which are found in Australia and nowhere else in the world. Fossil evidence indicates that kangaroos and their close relatives originated in Australia, roughly 5 million years ago. By that time, Australia had moved close to its present location (by continental drift; see Concept 25.4), and it was not connected to other landmasses. Thus, kangaroos occur only in Australia in part because of an accident of history: The kangaroo lineage originated there at a point in time when the continent was geographically isolated.

But ecological factors are also important. To date, kangaroos have not dispersed (on their own) to other continents; hence, they are restricted to the continent on which they originated. And within Australia, kangaroos are found in some habitats but not in others. The red kangaroo, for example, occurs in the arid grasslands of central Australia, but not in the tall, open forests of eastern Australia. Moreover, kangaroos are not unusual in this respect—all species are found in some habitats but not others. Hence, ecologists ask not only *where* species occur, but also *why* species occur where they do: What ecological factors—biotic and abiotic—determine their distribution?

In many cases, both biotic and abiotic factors affect the distribution of a species, as is true of the saguaro cactus (*Carnegiea gigantea*). Saguaros are found almost exclusively

Figure 51.15 Exploring Aquatic Biomes

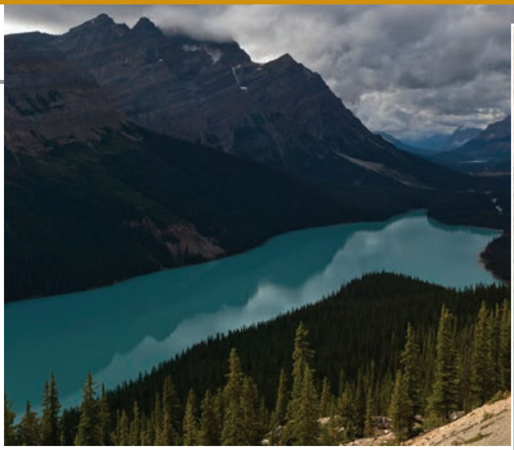
Lakes

Physical Environment Standing bodies of water range from ponds a few square meters in area to lakes covering thousands of square kilometers. Light decreases with depth, creating stratification. Temperate lakes may have a seasonal thermocline; tropical lowland lakes have a thermocline year-round.

Chemical Environment The salinity, oxygen concentration, and nutrient content differ greatly among lakes and can vary with season. **Oligotrophic lakes** tend to be nutrient-poor and generally oxygen-rich; **eutrophic lakes** are nutrient-rich and often depleted of oxygen in the deepest zone in summer and if covered with ice in winter. The amount of decomposable organic matter in bottom sediments is low in oligotrophic lakes and high in eutrophic lakes; high rates of decomposition in deeper layers of eutrophic lakes cause periodic oxygen depletion.

Geologic Features Oligotrophic lakes tend to have less surface area relative to their depth than eutrophic lakes. Oligotrophic lakes may become more eutrophic over time as runoff adds sediments and nutrients.

Photosynthetic Organisms Rooted and floating aquatic plants in lakes live in the **littoral zone**, the shallow, well-lit waters close to shore. Farther from shore, where water is too deep to support rooted aquatic plants, the **limnetic zone** is inhabited by a variety of phytoplankton, including cyanobacteria.



An oligotrophic lake in Canada

Heterotrophs In the limnetic zone, small drifting heterotrophs, or zooplankton, graze on the phytoplankton. The benthic zone is inhabited by assorted invertebrates whose species composition depends partly on oxygen levels. Fishes live in all zones with sufficient oxygen.

A eutrophic lake in the Okavango Delta, Botswana

Human Impact Runoff from fertilized land and dumping of wastes lead to nutrient enrichment, which can produce large numbers of algae (an algal "bloom") oxygen depletion, and fish kills.

Wetlands

Physical Environment A **wetland** is a habitat that is inundated by water at least some of the time and that supports plants adapted to water-saturated soil. Some wetlands are inundated at all times, whereas others flood infrequently.

Chemical Environment Because of high organic production by plants and decomposition by microbes and other organisms, both the water and the soils are periodically low in dissolved oxygen. Wetlands have a high capacity to filter dissolved nutrients and chemical pollutants.

Geologic Features *Basin wetlands* develop in shallow basins, ranging from upland depressions to filled-in lakes and ponds. *Riverine wetlands* develop along shallow and periodically flooded banks of rivers and streams. *Fringe wetlands* occur along the coasts of large lakes and seas, where water flows back and forth because of rising lake levels or tidal action. Thus, fringe wetlands include both freshwater and marine biomes.

Photosynthetic Organisms Wetlands are among the most productive biomes on Earth. Their water-saturated soils favor the growth of plants such as pond lilies and cattails, many sedges, bald cypress, and black spruce, which have adaptations enabling them to grow in water or in soil that is periodically anaerobic owing to the presence of unaerated water. Woody plants dominate the vegetation of swamps, while bogs are dominated by sphagnum mosses.

Heterotrophs Wetlands are home to a diverse community of invertebrates, birds, and many other organisms. Herbivores, from crustaceans and aquatic insect larvae to muskrats, consume algae, detritus, and plants. Carnivores are also varied and may include dragonflies, otters, frogs, alligators, and herons.

Human Impact Wetlands help purify water and reduce peak flooding. Draining and filling have destroyed up to 90% of wetlands in Europe.

A basin wetland in the United Kingdom

Continued on next page

Streams and Rivers

Physical Environment The most prominent physical characteristic of streams and rivers is the speed and volume of their flow. Headwater streams are generally cold, clear, swift, and turbulent. Farther downstream, where numerous tributaries may have joined, forming a river, the water is generally warmer and more turbid because of suspended sediment. Streams and rivers are stratified into vertical zones.

Chemical Environment The salt and nutrient content of streams and rivers increases from the headwaters to the mouth. Headwaters are generally rich in oxygen. Downstream water may also contain substantial oxygen, except where there has been organic enrichment. A large fraction of the organic matter in rivers consists of dissolved or highly fragmented material that is carried by the current from forested streams.

Geologic Features Headwater stream channels are often narrow, have a rocky bottom, and alternate between shallow sections and deeper pools. The downstream stretches of rivers are generally wide and meandering. River bottoms are often silty from sediments deposited over long periods of time.

A headwater stream in Washington

Photosynthetic Organisms Headwater streams that flow through grasslands or deserts may be rich in phytoplankton or rooted aquatic plants.

Heterotrophs A great diversity of fishes and invertebrates inhabit unpolluted rivers and streams, distributed according to, and throughout, the vertical zones. In streams flowing through temperate or tropical forests, organic matter from terrestrial vegetation is the primary source of food for aquatic consumers.

The Loire River in France, far from its headwaters

Human Impact Municipal, agricultural, and industrial pollution degrade water quality and kill aquatic organisms. Damming and flood control impair the natural functioning of stream and river ecosystems and threaten migratory species such as salmon.

Estuaries

Physical Environment An **estuary** is a transition area between river and sea. Seawater flows up the estuary channel during a rising tide and flows back down during the falling tide. Often, higher-density seawater occupies the bottom of the channel and mixes little with the lower-density river water at the surface.

Chemical Environment Salinity varies spatially within estuaries, from nearly that of fresh water to that of seawater. Salinity also varies with the rise and fall of the tides. Nutrients from the river make estuaries, like wetlands, among the most productive biomes.

Geologic Features Estuarine flow patterns combined with the sediments carried by river and tidal waters create a complex network of tidal channels, islands, natural levees, and mudflats.

Photosynthetic Organisms Saltmarsh grasses and algae, including phytoplankton, are the major producers in estuaries.

Heterotrophs Estuaries support an abundance of worms, oysters, crabs, and many fish species that humans consume. Many marine invertebrates and fishes use estuaries as a breeding ground or migrate through them to freshwater habitats upstream. Estuaries are also crucial feeding areas for waterfowl and some marine mammals.

Human Impact Filling, dredging, and pollution from upstream have disrupted estuaries worldwide.

An estuary in southern Spain

Intertidal Zones

Physical Environment An **intertidal zone** is periodically submerged and exposed by the tides, twice daily on most marine shores. Upper zones experience longer exposures to air and greater variations in temperature and salinity. Changes in physical conditions from the upper to the lower intertidal zones limit the distributions of many organisms to particular strata, as shown in the photograph.

Chemical Environment Oxygen and nutrient levels are generally high and are renewed with each turn of the tides.

Geologic Features The substrates of intertidal zones, which are generally either rocky or sandy, select for particular behavior and anatomy among intertidal organisms. The configuration of bays or coastlines influences the magnitude of tides and the relative exposure of intertidal organisms to wave action.

Photosynthetic Organisms A high diversity and biomass of attached marine algae inhabit rocky intertidal zones, especially in the lower zone. Sandy intertidal zones exposed to vigorous wave action generally lack attached plants or algae, while sandy intertidal zones in protected bays or lagoons often support rich beds of seagrass and algae.

Heterotrophs Many of the animals in rocky intertidal environments have structural adaptations that enable them to attach to the hard substrate. The composition, density, and diversity of animals change markedly from the upper to the lower intertidal zones. Many of the animals in sandy or muddy intertidal zones, such as worms, clams, and predatory crustaceans, bury themselves and feed as the tides bring sources of food. Other common animals are sponges, sea anemones, echinoderms, and small fishes.

Human Impact Oil pollution has disrupted many intertidal areas. The construction of rock walls and barriers to reduce erosion from waves and storm surges has disrupted this zone in some locations.

A rocky intertidal zone on the Oregon coast

Oceanic Pelagic Zone

Physical Environment The **oceanic pelagic zone** is a vast realm of open blue water, constantly mixed by wind driven oceanic currents. Because of higher water clarity, the photic zone extends to greater depths than in coastal marine waters.

Chemical Environment Oxygen levels are generally high. Nutrient concentrations are generally lower than in coastal waters. Because they are thermally stratified year-round, some tropical areas of the oceanic pelagic zone have lower nutrient concentrations than temperate oceans. Turnover between fall and spring renews nutrients in the photic zones of temperate and high-latitude ocean areas.

Geologic Features This biome covers approximately 70% of Earth's surface and has an average depth of nearly 4,000 m. The deepest point in the ocean is more than 10,000 m beneath the surface.

Photosynthetic Organisms The dominant photosynthetic organisms are phytoplankton, including photosynthetic bacteria, that drift with the oceanic currents. Spring turnover renews nutrients in temperate oceans, producing a surge of phytoplankton growth. Because of this biome's large size, photosynthetic plankton account for about half of the photosynthetic activity on Earth.

Heterotrophs The most abundant heterotrophs in this biome are zooplankton. These protists, worms, copepods, shrimp-like krill, jellies, and small larvae of invertebrates and fishes graze on photosynthetic plankton. The oceanic pelagic zone also includes numerous free-swimming animals, such as large squids, fishes, sea turtles, and marine mammals.

Human Impact Overfishing has depleted fish stocks in all Earth's oceans; marine life has also been harmed by pollution, ocean acidification, and global warming.

Continued on next page

Open ocean near Iceland

Coral Reefs

A coral reef in the Red Sea

Physical Environment **Coral reefs** are formed largely from the calcium carbonate skeletons of corals. Shallow reef-building corals live in the photic zone of relatively stable tropical marine environments with high water clarity, primarily near islands and along the edge of some continents. They are sensitive to temperatures below about 18–20°C and above 30°C. Deep-sea coral reefs, found between 200 and 1,500 m deep, are less known than their shallow counterparts but harbor as much diversity as many shallow reefs do.

Chemical Environment Corals require high oxygen levels and are excluded by high inputs of fresh water and nutrients.

Geologic Features Corals require a solid substrate for attachment. A typical coral reef begins as a *fringing reef* on a young, high island, forming an offshore *barrier reef* later in the history of the island and becoming a *coral atoll* as the older island submerges.

Photosynthetic Organisms Unicellular algae live within the tissues of the corals, forming a mutualistic relationship that provides the corals with organic molecules. Diverse multicellular red and green algae growing on the reef also contribute substantial amounts of photosynthesis.

Heterotrophs Corals, a diverse group of cnidarians, are themselves the predominant animals on coral reefs. However, fish and invertebrate diversity is exceptionally high. Overall animal diversity on coral reefs rivals that of tropical forests.

Human Impact Collecting of coral skeletons and overfishing have reduced populations of corals and reef fishes. Global warming and pollution may be contributing to large-scale coral death. Development of coastal mangroves for aquaculture has also reduced spawning grounds for many species of reef fishes.

Marine Benthic Zone

Physical Environment The **marine benthic zone** consists of the seafloor below the surface waters of the coastal, or **neritic**, zone and the offshore pelagic zone. Except for shallow, near-coastal areas, the marine benthic zone receives no sunlight. Water temperature declines with depth, while pressure increases. As a result, organisms in the very deep benthic, or abyssal, zone are adapted to continuous cold (about 3°C) and very high water pressure.

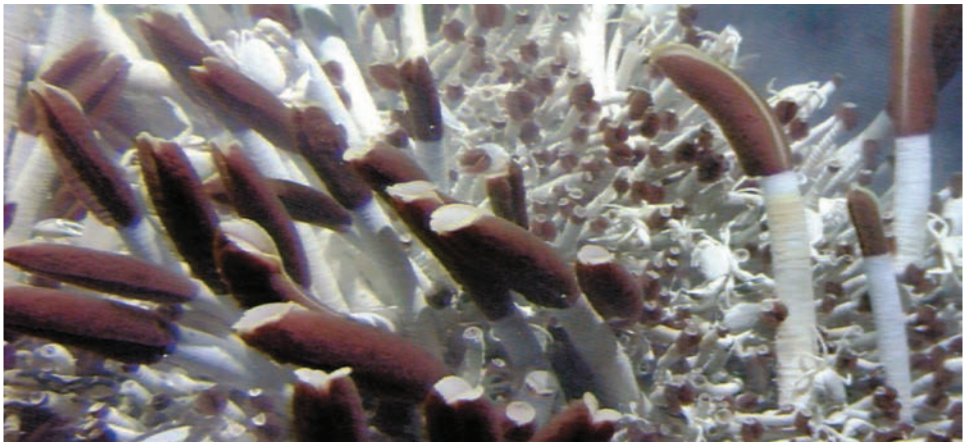
Chemical Environment Except in areas of organic enrichment, oxygen is usually present at sufficient concentrations to support diverse animal life.

Geologic Features Soft sediments cover most of the benthic zone. However, there are areas of rocky substrate on reefs, submarine mountains, and new oceanic crust.

Autotrophs Photosynthetic organisms, mainly seaweeds and filamentous algae, are limited to shallow benthic areas with sufficient light to support them. Unique assemblages of organisms live near deep-sea **hydrothermal vents** on mid-ocean ridges. In these dark, hot environments, the food producers are chemoautotrophic prokaryotes that obtain energy by oxidizing H_2S formed by a reaction of the hot water with dissolved sulfate (SO_4^{2-}).

Heterotrophs Neritic benthic communities include numerous invertebrates and fishes. Beyond the photic zone, most consumers depend entirely on organic matter raining down from above. Among the animals of the deep-sea hydrothermal vent communities are giant tube worms (pictured at left), some more than 1 m long. They are nourished by chemoautotrophic prokaryotes that live as symbionts within their bodies. Many other invertebrates, including arthropods and echinoderms, are also abundant around the hydrothermal vents.

Human Impact Overfishing has decimated important benthic fish populations, such as the cod of the Grand Banks off Newfoundland. Dumping of organic wastes has created oxygen-deprived benthic areas.



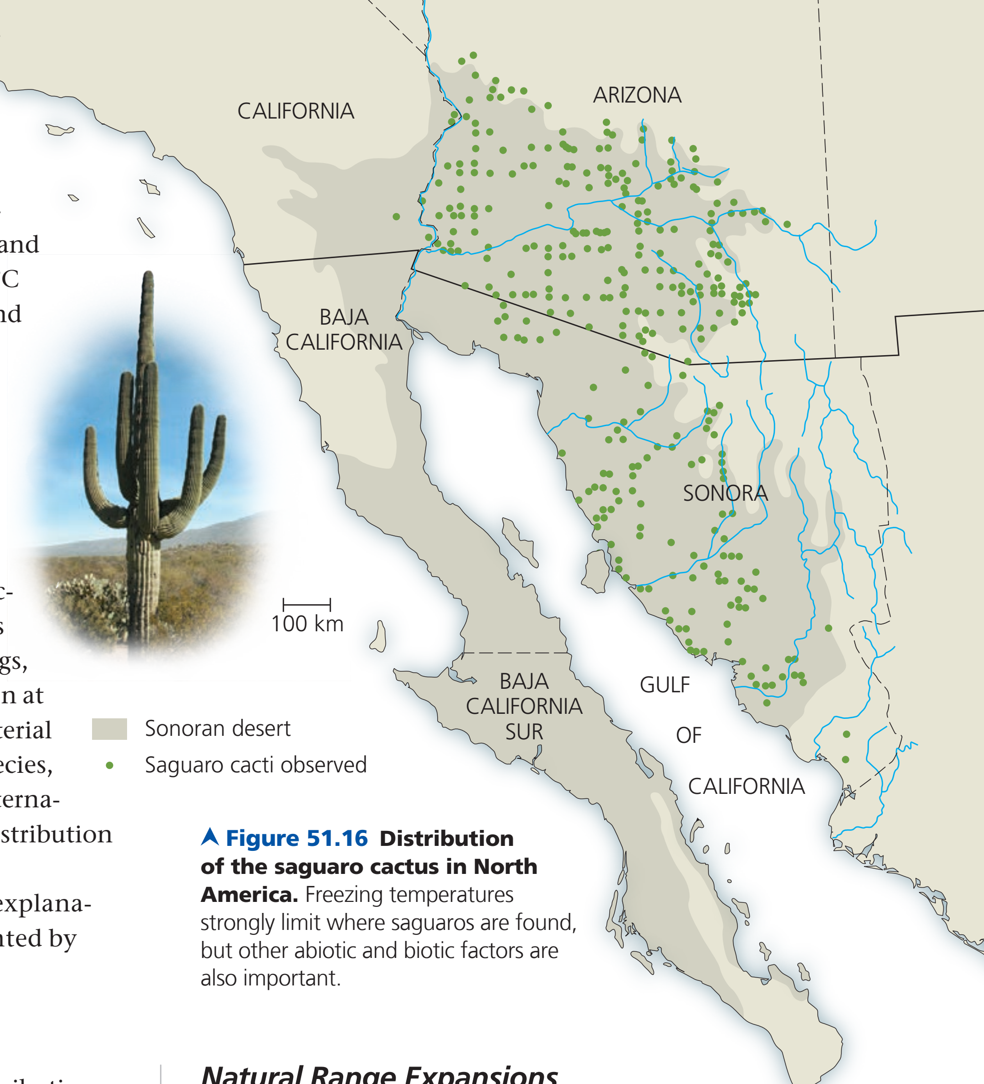
A deep-sea hydrothermal vent community

MB Video: Tubeworms

in the Sonoran Desert of the southwestern United States and northwestern Mexico **(Figure 51.16)**. To the north, their range is limited by an abiotic factor: temperature. Saguaros tolerate freezing temperatures only briefly, typically for less than a day, and generally cannot survive at temperatures below −4°C (25°F). For the same reason, saguaros are rarely found at elevations above 1,200 m (4,000 feet).

However, temperature alone does not fully explain the distribution of saguaros, including why they are missing from the western portion of the Sonoran Desert. Water availability is critical because seedling survival typically requires consecutive years of moist conditions, something that may occur only a few times each century. Biotic factors almost certainly influence their distribution as well. Mice and grazers such as goats eat the seedlings, and bats pollinate the large, white flowers that open at night. Saguaros are also vulnerable to a deadly bacterial disease. Thus, for the saguaro, as for most other species, ecologists need to consider multiple factors and alternative hypotheses when attempting to explain the distribution of a species.

To see how ecologists might arrive at such an explanation, let's examine the ecological factors highlighted by the questions in the flowchart in **Figure 51.17**.



▲ **Figure 51.16 Distribution of the saguaro cactus in North America.** Freezing temperatures strongly limit where saguaros are found, but other abiotic and biotic factors are also important.

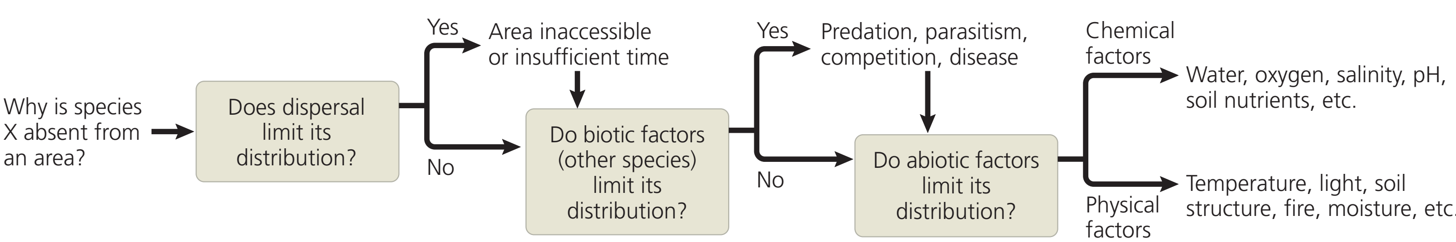
Dispersal and Distribution

One factor that contributes greatly to the global distribution of organisms is **dispersal**, the movement of individuals or gametes away from their area of origin or from centers of high population density. For example, while land-bound kangaroos have not reached Africa under their own power, other organisms that disperse more readily, such as some birds, have. The dispersal of organisms is critical to understanding the role of geographic isolation in evolution (see Concept 24.2) as well as the patterns of species distribution we see today, including that of the Pacific diatom discussed earlier in this chapter.

Natural Range Expansions and Adaptive Radiation

The importance of dispersal is most evident when organisms reach an area where they did not exist previously, called a *range expansion*. For instance, 200 years ago, the cattle egret (*Bubulcus ibis*) was found only in Africa and southwestern Europe. But in the late 1800s, some of these birds managed to cross the Atlantic Ocean and colonize northeastern South America. From there, cattle egrets gradually spread southward and also northward through Central America and into North America,

▼ **Figure 51.17 Flowchart of factors limiting geographic distribution.** An ecologist studying factors limiting a species' distribution might consider questions like these. As suggested by the arrows leading from the "yes" responses, the ecologist would answer all of these questions because more than one factor can limit a species' distribution.



? *How might the importance of various abiotic factors differ for aquatic and terrestrial ecosystems?*

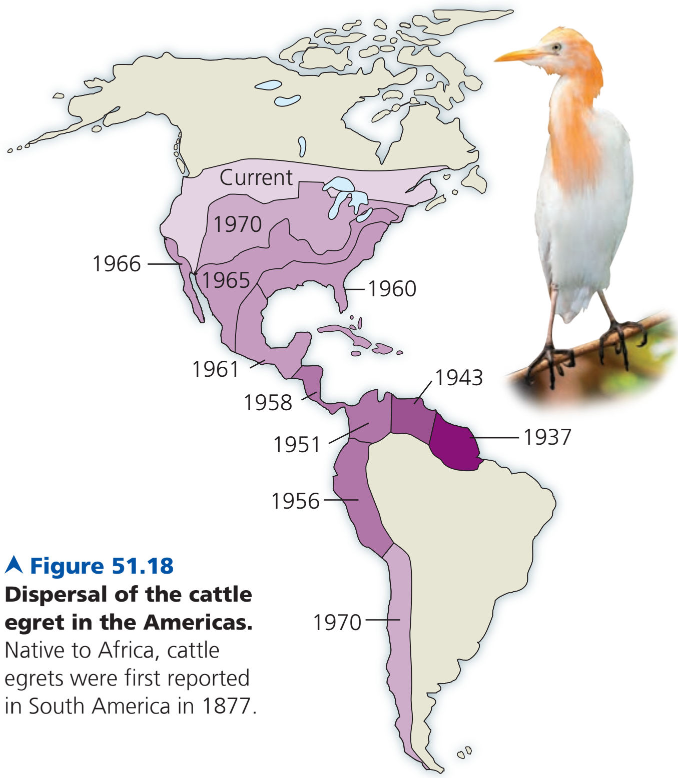


Figure 51.18 **Dispersal of the cattle egret in the Americas.** Native to Africa, cattle egrets were first reported in South America in 1877.

reaching Florida by 1960 **(Figure 51.18)**. Today they have breeding populations as far west as the Pacific coast of the United States and as far north as southern Canada.

In rare cases, such long-distance dispersal can lead to adaptive radiation, the rapid evolution of an ancestral species into new species that fill many ecological niches. The diversity of Hawaiian silverswords is one example of adaptive radiation that was possible only with the long-distance dispersal of an ancestral tarweed from North America (see Figure 25.22).

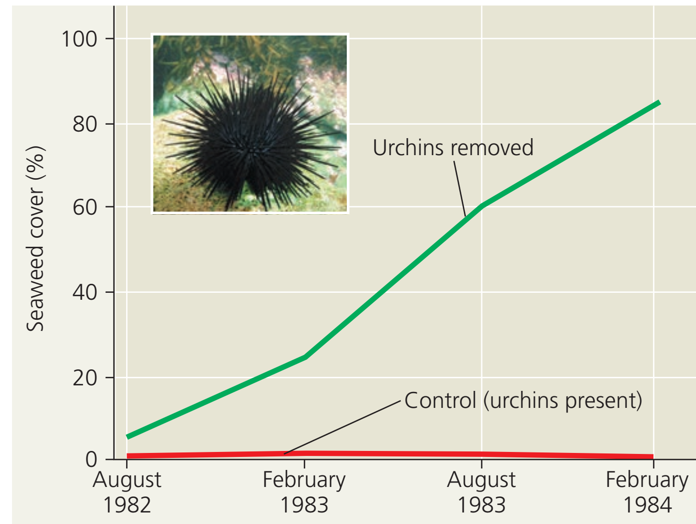
Natural range expansions clearly show the influence of dispersal on distribution. However, opportunities to observe such dispersal directly are rare, so ecologists often turn to experimental methods to better understand the role of dispersal in limiting the distribution of species.

Species Transplants

To determine if dispersal is a key factor limiting the distribution of a species, ecologists may observe the results of intentional or accidental transplants of the species to areas where it was previously absent. For a transplant to be successful, some of the organisms must not only survive in the new area but also reproduce there sustainably. If a transplant is successful, then we can conclude that the *potential* range of the species is larger than its *actual* range; in other words, the species *could* live in certain areas where it currently does not.

Species introduced to new geographic locations can disrupt the communities and ecosystems to which they have been introduced (see Concept 56.1). Consequently, ecologists rarely move species to new regions. Instead, they document the outcome when a species has been transplanted for other purposes, as when a predator is introduced to control a pest species, or when a species has been moved accidentally to a new region.

Figure 51.19 **Effects of feeding by sea urchins on seaweed distribution.** Seaweed abundance in areas from which the long-spined sea urchin (*Centrostephanus rodgersii*) had been removed was much higher than seaweed abundance in adjacent control sites from which the urchin was not removed.



Biotic Factors

Our next question is whether biotic factors—other species—limit the distribution of a species. Often, the ability of a species to survive and reproduce is reduced by its interactions with other species, such as predators (organisms that kill their prey) or herbivores (organisms that eat plants or algae). **Figure 51.19** describes a specific case in which an herbivore, the long-spined sea urchin (*Centrostephanus rodgersii*), has the potential to limit the distribution of a food species. In certain marine ecosystems, there is often an inverse relationship between the abundance of sea urchins and seaweeds (multicellular algae, such as kelp). Where urchins that graze on seaweeds and other algae are common, large stands of seaweeds do not become established. As shown in Figure 51.19, Australian researchers tested whether *C. rodgersii* is a biotic factor limiting seaweed distribution. When this urchin was removed from experimental plots, seaweed cover increased dramatically, showing that *C. rodgersii* limited the distribution of seaweeds.

In addition to predation and herbivory, the presence or absence of pollinators, food resources, parasites, pathogens, and competing organisms can act as a biotic limitation on species distribution. Such biotic limitations are common in nature.

Abiotic Factors

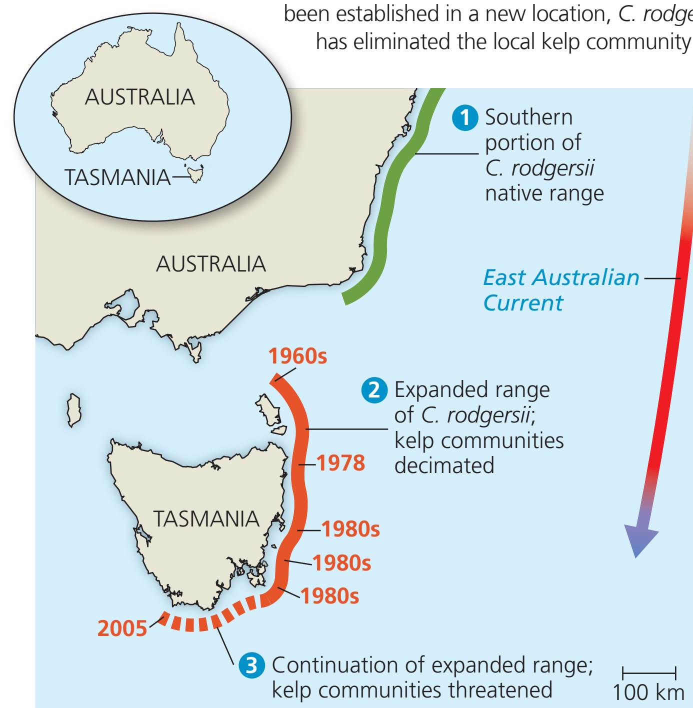
The last question in the flowchart in Figure 51.17 considers whether abiotic factors, such as temperature, water, oxygen, salinity, sunlight, or soil, might be limiting a species' distribution. If the physical conditions at a site do not allow a species to survive and reproduce, then the species will not be found there. Throughout this discussion, keep in mind that most abiotic factors vary substantially over space and time. Daily and annual fluctuations of abiotic factors may either blur or accentuate regional distinctions. Furthermore, organisms can avoid some stressful conditions temporarily through behaviors such as dormancy or hibernation (see Concept 40.4).

Temperature

Environmental temperature is an important factor in the distribution of organisms because of its effect on biological processes. Cells may rupture if the water they contain freezes (at temperatures below 0°C), and the proteins of most organisms denature at temperatures above 45°C. Organisms typically function best within a specific range of environmental temperature. Temperatures outside that range may force some animals to expend energy regulating their internal temperature, as mammals and birds do (see Figure 40.17). Extraordinary adaptations enable certain organisms, such as thermophilic prokaryotes, to live outside the temperature range habitable by other life.

As mentioned earlier, climate change has already caused hundreds of species to alter their geographic ranges. A shift in the range of one species can also have profound effects on the distribution of other species. Consider how rising sea temperatures have affected the geographic range of the sea urchin *C. rodgersii*. Since 1950, water temperatures along the coast of Tasmania, an island south of mainland Australia, have increased from 11.5°C to 12.5°C. This has enabled *C. rodgersii*—whose larvae fail to develop properly if temperatures drop below 12°C—to expand its range to the south **(Figure 51.20)**. The urchin is a voracious consumer of kelp and other algae. As a result, algal communities that once harbored a rich diversity of other species have been completely destroyed in regions where the urchin has become well established (denoted by a solid orange line in Figure 51.20).

Figure 51.20 A sea urchin's expanding range. Since the 1950s, water temperatures along the coast of Tasmania have increased, allowing the sea urchin *C. rodgersii* to expand its range to the south. The bold orange type indicates the years when *C. rodgersii* was first observed colonizing those locations. Once its population has been established in a new location, *C. rodgersii* has eliminated the local kelp community.



Water and Oxygen

The dramatic variation in water availability among habitats is another important factor in species distribution. Species living at the seashore or in tidal wetlands can desiccate (dry out) as the tide recedes. Terrestrial organisms face a nearly constant threat of desiccation, and the distribution of terrestrial species reflects their ability to obtain and conserve water. Many amphibians are particularly vulnerable to drying because they use their moist, delicate skin for gas exchange. Desert organisms exhibit a variety of adaptations for acquiring and conserving water in dry environments, as described in Concept 44.4.

Water affects oxygen availability in aquatic environments and in flooded soils, where the slow diffusion of oxygen in water can limit cellular respiration and other physiological processes. Oxygen concentrations can be particularly low in deep ocean and deep lake waters as well as in sediments where organic matter is abundant. Flooded wetland soils may also have low oxygen content. Mangroves and other trees have specialized roots that project above the water and help the root system obtain oxygen (see Figure 35.4). Unlike many flooded wetlands, the surface waters of streams and rivers tend to be well oxygenated because of rapid exchange of gases with the atmosphere.

Salinity

The salt concentration of water in the environment affects the water balance of organisms through osmosis. Most aquatic organisms are restricted to either freshwater or saltwater habitats by their limited ability to osmoregulate (see Concept 44.1). Although most terrestrial organisms can excrete excess salts from specialized glands or in feces or urine, high-salinity habitats typically have few species of plants or animals. In the **Scientific Skills Exercise**, you can interpret data from an experiment investigating the influence of salinity on plant distributions.

Salmon that migrate between freshwater streams and the ocean use both behavioral and physiological mechanisms to osmoregulate. They balance their salt content by adjusting the amount of water they drink and by switching their gills from taking up salt in fresh water to excreting salt in the ocean.

Sunlight

Sunlight provides the energy that drives most ecosystems, and too little sunlight can limit the distribution of photosynthetic species. In forests, shading by leaves makes competition for light especially intense, particularly for seedlings growing on the forest floor. In aquatic environments, every meter of water depth absorbs about 45% of the red light and about 2% of the

SCIENTIFIC SKILLS EXERCISE

Making a Bar Graph and a Line Graph to Interpret Data

How Do Salinity and Competition Affect the Distribution of Plants in an Estuary? Field observations show that *Spartina patens* (salt marsh hay) is a dominant plant in salt marshes and *Typha angustifolia* (cattail) is a dominant plant in freshwater marshes. In this exercise, you will graph and interpret data from an experiment that examined the influence of an abiotic factor, salinity, and a biotic factor, competition, on the growth of these two species.

How the Experiment Was Done Researchers planted *S. patens* and *T. angustifolia* in salt marshes and freshwater marshes with and without neighboring plants. After two growing seasons (1.5 years), they measured the biomass of each species in each treatment. The researchers also grew both species in a greenhouse at six salinity levels and measured the biomass at each level after eight weeks.

Data from the Field Experiment (averages of 16 replicate samples)

	Average Biomass ($g/100\ cm^2$)			
	Spartina patens		*Typha angustifolia*	
	Salt Marshes	Freshwater Marshes	Salt Marshes	Freshwater Marshes
With neighbors	8	3	0	18
Without neighbors	10	20	0	33

Data from the Greenhouse Experiment

Salinity (parts per thousand)	0	20	40	60	80	100
% maximum biomass (*S. patens*)	77	40	29	17	9	0
% maximum biomass (*T. angustifolia*)	80	20	10	0	0	0

Data from C. M. Crain et al., Physical and biotic drivers of plant distribution across estuarine salinity gradients, *Ecology* 85:2539–2549 (2004).

▲ *Spartina patens*

▲ *Typha angustifolia*

INTERPRET THE DATA

1. Make a bar graph of the data from the field experiment. (For additional information about graphs, see the Scientific Skills Review in Appendix F.) What do these data indicate about the salinity tolerances of *S. patens* and *T. angustifolia*?
2. What do the data from the field experiment indicate about the effect of competition on the growth of these two species? Which species was limited more by competition?
3. Make a line graph of the data from the greenhouse experiment. Decide which values constitute the dependent and independent variables, and use these values to set up the axes of your graph.
4. (a) In the field, *S. patens* is typically absent from freshwater marshes. Based on the data, does this appear to be due to salinity or competition? Explain your answer. (b) *T. angustifolia* does not grow in salt marshes. Does this appear to be due to salinity or competition? Explain your answer.

MB **Instructors**: A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

blue light passing through it. As a result, most photosynthesis occurs relatively near the water surface.

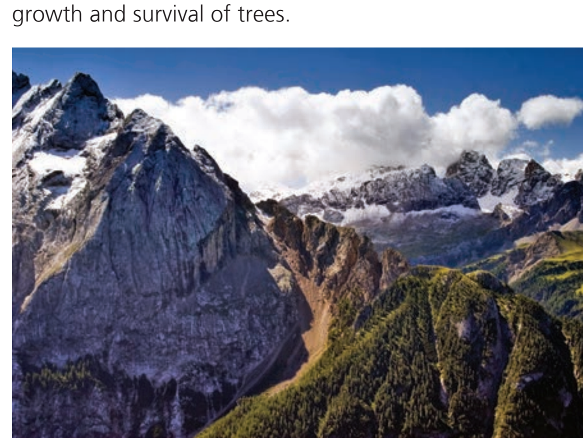
Too much light can also limit the survival of organisms. In some ecosystems, such as deserts, high light levels can increase temperature stress if animals and plants are unable to avoid the light or to cool themselves through evaporation (see Figure 40.12). At high elevations, the sun's rays are more likely to damage DNA and proteins because the atmosphere is thinner, absorbing less ultraviolet (UV) radiation. Damage from UV radiation, combined with other abiotic stresses, prevents trees from surviving above a certain elevation, resulting in the appearance of a tree line on mountain slopes **(Figure 51.21)**.

Rocks and Soil

In terrestrial environments, the pH, mineral composition, and physical structure of rocks and soil limit the distribution of plants and thus of the animals that feed on them, contributing to the patchiness of terrestrial ecosystems. The pH of soil can limit the distribution of organisms directly, through extreme acidic or basic conditions, or indirectly, by affecting the solubility of toxins and nutrients. Soil phosphorus, for instance, is relatively insoluble in basic soils and precipitates into forms unavailable to plants.

In a river, the composition of rocks and soil that make up the substrate (riverbed) can affect water chemistry, which in turn influences the resident organisms. In freshwater and

▼ **Figure 51.21 Alpine tree line on Marmolada, the highest mountain of the Dolomites, Italy.** Organisms living at high elevations are exposed not only to high levels of ultraviolet radiation but also to freezing temperatures, moisture deficits, and strong winds. Above the tree line, the combination of such factors restricts the growth and survival of trees.



marine environments, the structure of the substrate determines the organisms that can attach to it or burrow into it.

CONCEPT CHECK 51.4

1. Give examples of human actions that could expand a species' distribution by changing its (a) dispersal or (b) biotic interactions.
2. **WHAT IF?** ➤ You suspect that deer are restricting the distribution of a tree species by preferentially eating the seedlings of the tree. How might you test this hypothesis?
3. **MAKE CONNECTIONS** ➤ Hawaiian silverswords underwent a remarkable adaptive radiation after their ancestor reached Hawaii, while the islands were still young (see Figure 25.22). Would you expect the cattle egret to undergo a similar adaptive radiation in the Americas (see Figure 51.18)? Explain.

For suggested answers, see Appendix A.

CONCEPT 51.5

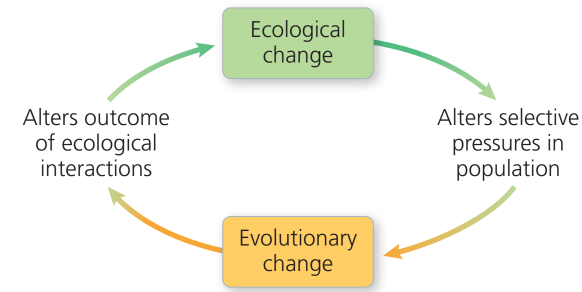
Ecological change and evolution affect one another over long and short periods of time

Biologists have long recognized that ecological interactions can cause evolutionary change, and vice versa **(Figure 51.22)**. The history of life includes many examples of these reciprocal effects occurring over long periods of time. Consider the origin and diversification of plants. As described in Concept 29.3, the evolutionary origin of plants altered the chemical cycling of carbon, leading to the removal of large quantities of carbon dioxide from the atmosphere. As the adaptive radiation of plants continued over time, the appearance of new plant species provided new habitats and new sources of food for insects and other animals. In turn, the availability of new habitats and new food sources stimulated bursts of speciation in animals, leading to further ecological changes. Here, as in many other such examples, ecological and evolutionary changes had ongoing and major effects upon one another.

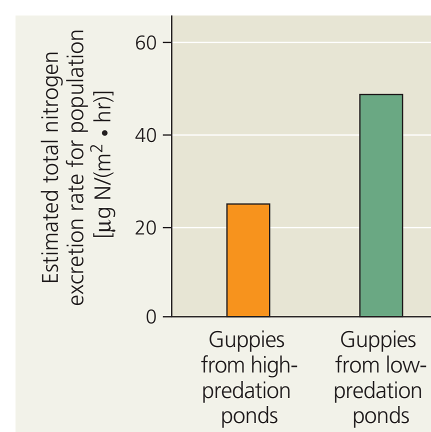
The interplay between ecological and evolutionary change illustrated by the origin of plants occurred over millions of years. Reciprocal "eco-evolutionary" effects occurring over centuries or thousands of years are also well documented, as in the examples of the mosquitofish and the apple maggot fly discussed in Concept 24.2. But are such joint effects common over much shorter periods of time? As we've seen in previous chapters, ecological change can cause evolutionary change over the course of a few years to decades; examples include beak length evolution in soapberry bugs (see Figure 21.13) and the formation of new sunflower species (see Figure 24.18).

Recent studies show that the causation can run both ways: Rapid evolution can also cause ecological change. For example, Trinidadian guppy (*Poecilia reticulata*) populations evolve rapidly when predators are removed: guppy color patterns change (see the Chapter 21 Scientific Skills Exercise) and guppies produce fewer but larger offspring. In turn, the evolution of larger body sizes altered the availability of nitrogen in these stream ecosystems **(Figure 51.23)**. Larger fish excrete more nitrogen than do smaller fish, and nitrogenous wastes contribute to the growth of primary producers such as algae. Overall, this and other studies show that ecological change and evolution have the potential to exert rapid feedback effects on each other. This additional layer of complexity must be considered when predicting how human actions or other events will affect the natural world.

▼ Figure 51.22 Reciprocal effects of ecological and evolutionary change. An ecological change, such as the expansion of a predator's range, can alter the selective pressures faced by prey populations. This could cause evolutionary change, such as an increase in the frequency of a new defensive mechanism in a prey population; that change, in turn, could alter the outcome of ecological interactions.



➤ Figure 51.23 An example of reciprocal eco-evolutionary effects. In low-predation ponds, evolution in the guppy (*Poecilia reticulata*) leads to larger body sizes. Populations of these larger fish excrete more nitrogen than do the smaller fish found in high-predation ponds.



CONCEPT CHECK 51.5

1. Describe a scenario showing how ecological change and evolution can affect one another.
2. **MAKE CONNECTIONS** ➤ Commercial fisheries target older, larger cod fish, causing cod that reproduce at a younger age and smaller size to be favored by natural selection. Younger, smaller cod have fewer offspring than do older, larger cod. Predict how evolution in response to fishing would affect the ability of a cod population to recover from overfishing. What other reciprocal eco-evolutionary effects might occur? (See Concept 23.3.)

For suggested answers, see Appendix A.

51 Chapter Review

Go to **MasteringBiology™** for Videos, Animations, Vocab Self-Quiz, Practice Tests, and more in the Study Area.

SUMMARY OF KEY CONCEPTS

VOCAB SELF-QUIZ goo.gl/Rn5Uax

CONCEPT 51.1

Earth's climate varies by latitude and season and is changing rapidly *(pp. 1199–1202)*

- Global **climate** patterns are largely determined by the input of solar energy and Earth's revolution around the sun.
- The changing angle of the sun over the year, bodies of water, and mountains exert seasonal, regional, and local effects on climate.
- Fine-scale differences in certain **abiotic** (nonliving) factors, such as sunlight and temperature, determine **microclimate**.
- Increasing greenhouse gas concentrations in the air are warming Earth and altering the distributions of many species. Some species will not be able to shift their ranges quickly enough to reach suitable habitat in the future.

? *Suppose global air circulation suddenly reversed, with moist air ascending at 30° north and south latitude and descending at the equator. At what latitude would you most likely find deserts in this scenario?*

CONCEPT 51.2

The distribution of terrestrial biomes is controlled by climate and disturbance *(pp. 1202–1208)*

- **Climographs** show that temperature and precipitation are correlated with **biomes**. Because other factors also play roles in biome location, biomes overlap.
- Terrestrial biomes are often named for major physical or climatic factors and for their predominant vegetation. Vertical layering is an important feature of terrestrial biomes.
- **Disturbance**, both natural and human-induced, influences the type of vegetation found in biomes. Humans have altered much of Earth's surface, replacing the natural terrestrial communities described and depicted in Figure 51.12 with urban and agricultural ones.
- The pattern of climatic variation is as important as the average climate in determining where biomes occur.

? *In what ways are disturbances important for savanna ecosystems and the plants in them?*

CONCEPT 51.3

Aquatic biomes are diverse and dynamic systems that cover most of Earth *(pp. 1209–1210)*

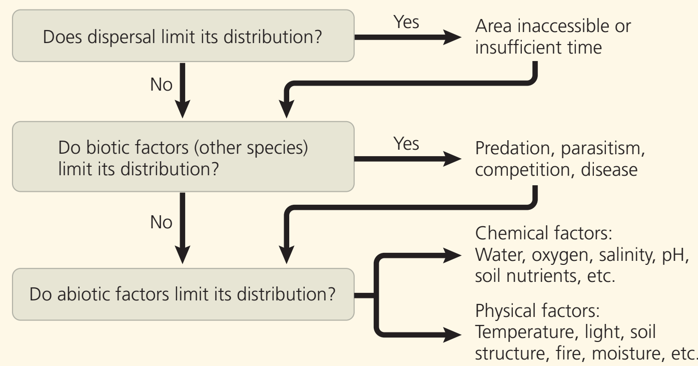
- Aquatic biomes are characterized primarily by their physical environment rather than by climate and are often layered with regard to light penetration, temperature, and community structure. Marine biomes have a higher salt concentration than freshwater biomes.
- In the ocean and in most lakes, an abrupt temperature change called a **thermocline** separates a more uniformly warm upper layer from more uniformly cold deeper waters.
- Many temperate lakes undergo a **turnover**, or mixing of water in spring and fall, that sends deep, nutrient-rich water to the surface and shallow, oxygen-rich water to deeper layers.

? *In which aquatic biomes might you find an aphotic zone?*

CONCEPT 51.4

Interactions between organisms and the environment limit the distribution of species *(pp. 1210–1219)*

- Ecologists want to know not only *where* species occur but also *why* those species occur where they do.



VISUAL SKILLS ➤ *If you were an ecologist studying the chemical and physical limits to the distributions of species, how might you rearrange the flowchart preceding this question?*

CONCEPT 51.5

Ecological change and evolution affect one another over long and short periods of time *(p. 1219)*

- Ecological interactions can cause evolutionary change, as when predators cause natural selection in a prey population.
- Likewise, an evolutionary change, such as an increase in the frequency of a new defensive mechanism in a prey population, can alter the outcome of ecological interactions.

? *Suppose humans introduced a species to a new continent where it had few predators or parasites. How might this lead to eco-evolutionary feedback effects?*

TEST YOUR UNDERSTANDING

Multiple-choice Self-Quiz questions 1–8 can be found in the Study Area in MasteringBiology.

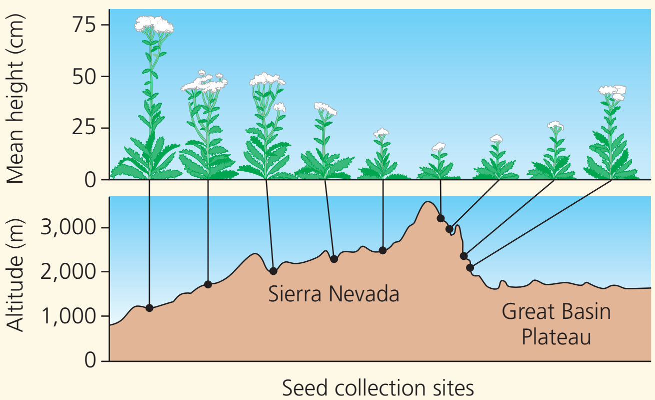
PRACTICE TEST goo.gl/iAsVgL

9. INTERPRET THE DATA After examining Figure 51.19, you decide to study feeding relationships among sea otters, sea urchins, and kelp. You know that sea otters prey on sea urchins and that urchins eat kelp. At four coastal sites, you measure kelp abundance. Then you spend one day at each site and mark whether otters are present or absent every 5 minutes during the day. Graph kelp abundance (on the y-axis) versus otter density (on the x-axis), using the data below. Then formulate a hypothesis to explain any pattern you observe.

Site	Otter Density (# sightings per day)	Kelp Abundance (% cover)
1	98	75
2	18	15
3	85	60
4	36	25

10. EVOLUTION CONNECTION Discuss how the distribution of a species can be affected both by its evolutionary history and by ecological factors. Could ongoing evolutionary change also affect its distribution? Explain.

11. SCIENTIFIC INQUIRY Jens Clausen and colleagues, at the Carnegie Institution of Washington, studied how the size of yarrow plants (*Achillea lanulosa*) growing on the slopes of the Sierra Nevada varied with elevation. They found that plants from low elevations were generally taller than plants from high elevations, as shown in the diagram.



Data from J. Clausen et al., Experimental studies on the nature of species. III. Environmental responses of climatic races of *Achillea*, Carnegie Institution of Washington Publication No. 581 (1948).

Clausen and colleagues proposed two hypotheses to explain this variation within a species: (1) There are genetic differences between populations of plants found at different elevations. (2) The species has developmental flexibility and can assume tall or short growth forms, depending on local abiotic factors. If you had seeds from yarrow plants found at low and high elevations, how would you test these hypotheses?

12. WRITE ABOUT A THEME: INTERACTIONS Global warming is occurring rapidly in arctic marine and terrestrial ecosystems. The reflective white snow and ice cover are melting quickly and extensively, uncovering darker-colored ocean water, plants, and rocks. In a short essay (100–150 words), explain how this process might exemplify positive feedback.

13. SYNTHESIZE YOUR KNOWLEDGE

If you were to hike up Mount Kilimanjaro in Tanzania, you would pass through several habitats, including savanna at the base, forest on the slopes, and alpine tundra near the top. Explain how such diverse habitats can be found at one location near the equator.

For selected answers, see Appendix A.

For additional practice questions, check out the **Dynamic Study Modules** in MasteringBiology. You can use them to study on your smartphone, tablet, or computer anytime, anywhere!

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52 Behavioral Ecology

Figure 52.1 What prompts a male fiddler crab to display his giant claw?

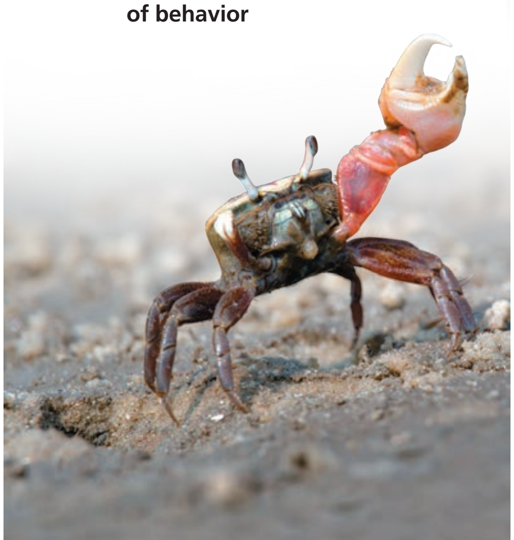
KEY CONCEPTS

52.1 Discrete sensory inputs can stimulate both simple and complex behaviors

52.2 Learning establishes specific links between experience and behavior

52.3 Selection for individual survival and reproductive success can explain diverse behaviors

52.4 Genetic analyses and the concept of inclusive fitness provide a basis for studying the evolution of behavior



The How and Why of Animal Activity

Unlike most animals, male fiddler crabs (genus *Uca*) are highly asymmetrical: One claw grows to giant proportions, up to half the mass of the entire body **(Figure 52.1)**. The name *fiddler* refers to the crab's behavior and appearance while feeding: As it grazes on algae, the crab moves the small claw to and from the mouth in front of the large claw, much like a musician playing a violin. However, at other times the male waves his large claw in the air. What triggers this behavior? What purpose does it serve?

Claw waving by a male fiddler crab has two functions. Waving the claw, which can be used as a weapon, helps the crab *repel* other males wandering too close to his burrow. Vigorous claw waving also helps him *attract* females, who wander through the crab colony in search of a mate. After the male fiddler crab lures a female to his burrow, he seals her in with mud or sand in preparation for mating.

Animal behavior, be it solitary or social, fixed or variable, is based on physiological systems and processes. An individual **behavior** is an action carried out by muscles under control of the nervous system. Examples include an animal using its throat muscles to produce a song, releasing a scent to mark its territory, or simply waving a claw. Behavior is an essential part of acquiring nutrients and finding a partner for sexual reproduction. Behavior also contributes to homeostasis, as when honeybees huddle to conserve heat. In short, all of animal physiology contributes to behavior, and behavior influences all of physiology.

When you see this blue icon, log in to **MasteringBiology** and go to the Study Area for digital resources.

MB Get Ready for This Chapter

Being essential for survival and reproduction, behavior is subject to substantial natural selection over time. This evolutionary process of selection also affects anatomy because the recognition and communication that underlie many behaviors depend on body form and appearance. Thus, the enlarged claw of the male fiddler crab is an adaptation that enables the display essential for recognition by other members of the species. Similarly, the positioning of the eyes on stalks held well above the crab's head enables him to see intruders from far off.

In this chapter, we'll examine how behavior is controlled, how it develops during an animal's life, and how it is influenced by genes and the environment. We'll also explore the ways in which behavior evolves over many generations.

CONCEPT 52.1

Discrete sensory inputs can stimulate both simple and complex behaviors

What approach do biologists use to determine how behaviors arise and what functions they serve? The Dutch scientist Niko Tinbergen, a pioneer in the study of animal behavior, suggested that understanding any behavior requires answering four questions, which can be summarized as follows:

1. What stimulus elicits the behavior, and what physiological mechanisms mediate the response?
2. How does the animal's experience during growth and development influence the response?
3. How does the behavior aid survival and reproduction?
4. What is the behavior's evolutionary history?

The first two questions ask about *proximate causation—how* a behavior occurs or is modified. The last two questions ask about *ultimate causation—why* a behavior occurs in the context of natural selection.

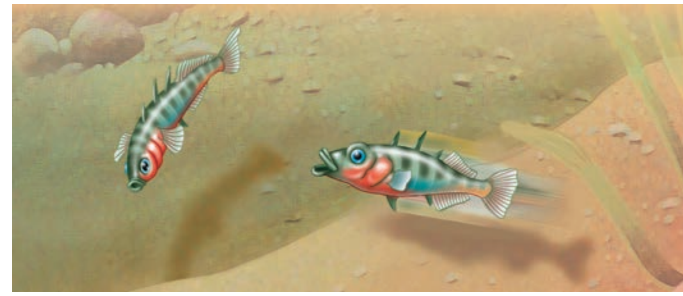
Studies on proximate causation by Tinbergen earned him a share of a Nobel Prize awarded in 1973. We'll consider those and related experiments in the early part of the chapter. The concept of ultimate causation is central to behavioral ecology, the main subject of this chapter. We'll explore this vibrant area of modern biological research in the rest of the chapter.

Fixed Action Patterns

In addressing Tinbergen's first question, the nature of the stimuli that trigger behavior, we'll begin with behavioral responses to well-defined stimuli, starting with an example from one of Tinbergen's own experiments.

As part of his research, Tinbergen kept fish tanks containing three-spined sticklebacks (*Gasterosteus aculeatus*), a species in which males, but not females, have red bellies. Male sticklebacks attack other males that invade their nesting territories **(Figure 52.2)**. Tinbergen noticed that his male sticklebacks also behaved aggressively when a red truck passed within view of their tank. Inspired by this chance observation, he carried out experiments showing that the red color of an intruder's underside is the proximate cause of the attack behavior. A male stickleback will not attack a fish lacking red coloration, but will attack even unrealistic models if they contain areas of red color.

▼ **Figure 52.2 Sign stimuli in a classic fixed action pattern.** A male stickleback fish attacks other male sticklebacks that invade its nesting territory. The red belly of the intruding male (left) acts as a sign stimulus that releases the aggressive behavior.



? *Suggest an explanation for why this behavior evolved (its ultimate causation).*

The territorial response of male sticklebacks is an example of a **fixed action pattern**, a sequence of unlearned acts directly linked to a simple stimulus. Fixed action patterns are essentially unchangeable and, once initiated, are usually carried to completion. The trigger for the behavior is an external cue called a **sign stimulus**, such as a red object that prompts the male stickleback's aggressive behavior.

Migration

Environmental stimuli not only trigger behaviors but also provide cues that animals use to carry out those behaviors. For example, a wide variety of birds, fishes, and other animals use environmental cues to guide **migration**—a regular, long-distance change in location **(Figure 52.3)**. In the course of migration, many animals pass through environments they have not previously encountered. How, then, do they find their way in these foreign settings?

Some migrating animals track their position relative to the sun, even though the sun's position relative to Earth changes throughout the day. Animals can adjust for these changes by means of a *circadian clock*, an internal mechanism that maintains a 24-hour activity rhythm or cycle (see Concept 49.2). For example, experiments have shown that migrating birds orient differently relative to the sun at distinct times of the day. Nocturnal animals can instead use the North Star, which has a constant position in the night sky.

Figure 52.3 Migration. Wildebeest herds migrate long distances twice each year, changing their feeding grounds in coordination with the dry and rainy seasons.

and darkness in the environment. For example, studies with several bird species have shown that an artificial environment with extended daylight can induce out-of-season migratory behavior.

Not all biological rhythms are linked to the light and dark cycles in the environment. Consider, for instance, the fiddler crab shown in Figure 52.1. The male's claw-waving courtship behavior is linked to the timing of the new and full moon. This timing helps the development of offspring. Fiddler crabs begin their lives as larvae settling in the mudflats. The tides disperse larvae to deeper waters, where they complete early development in relative safety before returning to the tidal flats. By courting at the time of the new or full moon, crabs link their reproduction to the times of greatest tidal movement.

Although the sun and stars can provide useful clues for navigation, clouds can obscure these landmarks. How do migrating animals overcome this problem? A simple experiment with homing pigeons provided one answer. On an overcast day, placing a small magnet on the head of a homing pigeon prevented it from returning efficiently to its roost. Researchers concluded that pigeons sense their position relative to Earth's magnetic field and can thereby navigate without solar or celestial cues.

Behavioral Rhythms

Although the circadian clock plays a small but significant role in navigation by some migrating species, it has a major role in the daily activity of all animals. As discussed in Concepts 40.2 and 49.2, the clock is responsible for a circadian rhythm, a daily cycle of rest and activity. The clock is normally synchronized with the light and dark cycles of the environment but can maintain rhythmic activity even under constant environmental conditions, such as during hibernation.

Some behaviors, such as migration and reproduction, reflect biological rhythms with a longer cycle, or period, than the circadian rhythm. Behavioral rhythms linked to the yearly cycle of seasons are called *circannual rhythms*. Although migration and reproduction typically correlate with food availability, these behaviors are not a direct response to changes in food intake. Instead, circannual rhythms, like circadian rhythms, are influenced by the periods of daylight

Animal Signals and Communication

Claw waving by fiddler crabs during courtship is an example of one animal (the male crab) generating the stimulus that guides the behavior of another animal (the female crab). A stimulus transmitted from one organism to another is called a **signal**. The transmission and reception of signals between animals constitute **communication**, which often has a role in the proximate causation of behavior.

MB **Video: Albatross Courtship Ritual**
Video: Giraffe Courtship Ritual

Forms of Animal Communication

Let's consider the courtship behavior of the fruit fly, *Drosophila melanogaster*, as an introduction to the four common modes of animal communication: visual, chemical, tactile, and auditory.

Fruit fly courtship constitutes a *stimulus-response chain*, in which the response to each stimulus is itself the stimulus for the next behavior. In the first step, a male detects a female in his field of vision and orients his body toward hers. To confirm she belongs to his species, he uses his olfactory system to detect chemicals she releases into the air. The male then approaches and touches the female with a foreleg **(Figure 52.4)**. This touching, or tactile communication, alerts the female to the male's presence.

Figure 52.4 Male fruit fly tapping female with foreleg.

In the third stage of courtship, the male extends and vibrates one wing, producing a courtship song. This auditory communication informs the female whether he is of the same species. Only if all of these forms of communication are successful will the female allow the male to attempt copulation.

In general, the form of communication that evolves is closely related to an animal's lifestyle and environment. For example, most terrestrial mammals are nocturnal, which makes visual displays relatively ineffective. Instead, these species use olfactory and auditory signals, which work as well in the dark as in the light. In contrast, most birds are diurnal (active mainly in daytime) and communicate primarily by visual and auditory signals. Humans are also diurnal and, like birds, use primarily visual and auditory communication. We can thus detect and appreciate the songs and bright colors used by birds to communicate but miss many chemical cues on which other mammals base their behavior.

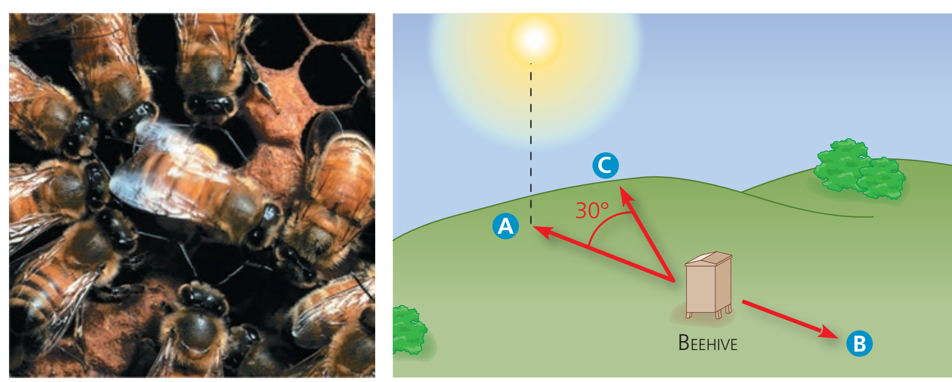
The information content of animal communication varies considerably. One of the most remarkable examples is the symbolic language of the European honeybee (*Apis mellifera*), discovered in the early 1900s by Austrian researcher Karl von Frisch. Using glass-walled observation hives, he and his students spent several decades observing honeybees. Methodical recordings of bee movements enabled von Frisch to decipher a "dance language" that returning foragers use to inform other bees about the distance and direction of travel to a source of nectar.

When a successful forager returns to the hive, its movements, as well as sounds and odors, quickly become the center of attention for other bees, called followers (**Figure 52.5**). Moving along the vertical wall of the honeycomb, the forager performs a "waggle dance" that communicates to the follower bees both the direction and distance of the food source in relation to the hive. In performing the dance, the bee follows a half-circle swing in one direction, a straight run during which it waggles its abdomen, and a half-circle swing in the other direction. What von Frisch and colleagues deduced was that the angle of the straight run relative to the hive's vertical surface indicates the horizontal angle of the food in relation to the sun. Thus, if the returning bee runs at a 30° angle to the right of vertical, the follower bees leaving the hive fly 30° to the right of the horizontal direction of the sun.

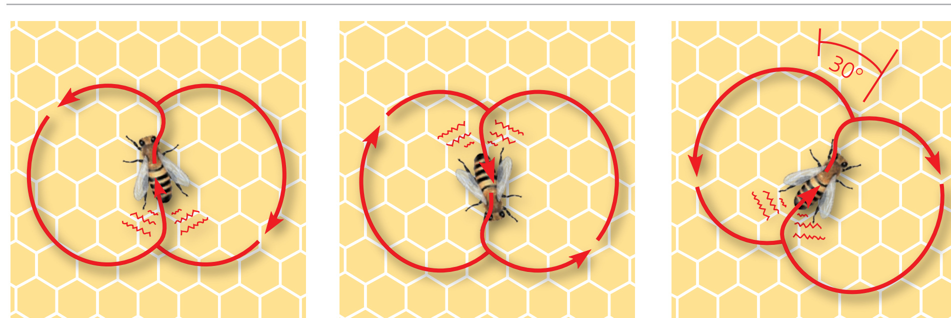
How does the waggle dance communicate distance to the nectar source? It turns out that a dance with a longer straight run, and therefore more abdominal waggles per run, indicates a greater distance to the food found by the forager. As follower bees exit the hive, they fly almost directly to the area indicated by the waggle dance. By using flower odor and other clues, they locate the source of nectar within this area.

If the food source is close to the hive (less than 50 m away), the waggle dance takes a slightly different form that primarily advertises the availability of nectar nearby. In this form of the waggle dance, which von Frisch called "round," the returning bee moves in tight circles while moving its abdomen from side to side. In response, the follower bees leave the hive and search in all directions for nearby flowers rich in nectar.

Figure 52.5 Honeybee dance language. Honeybees returning to the hive communicate the location of food sources through the symbolic language of a dance.



Worker bees cluster around a recently returned bee.



Location **A**: Food source is in same direction as sun.

Location **B**: Food source is in direction opposite sun.

Location **C**: Food source is 30° to right of sun.

The waggle dance performed when food is distant. The waggle dance resembles a figure eight. Distance is indicated by the number of abdominal waggles performed in the straight-run part of the dance. Direction is indicated by the angle (in relation to the vertical surface of the hive) of the straight run.

VISUAL SKILLS ➤ *What information, if any, might be conveyed by the portions of the waggle dance between the straight runs? Explain.*

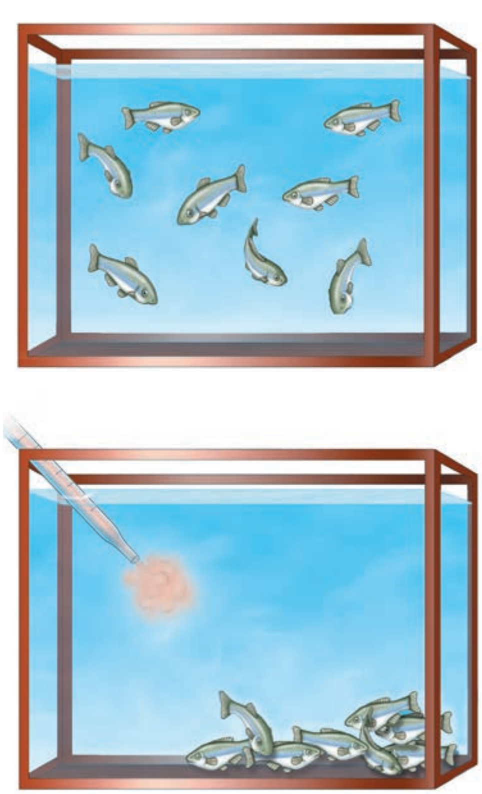
Pheromones

Animals that communicate through odors or tastes emit chemical substances called **pheromones**. Pheromones are especially common among mammals and insects and often relate to reproductive behavior. For example, pheromones are the basis for the chemical communication in fruit fly courtship (see Figure 52.4). Pheromones are not limited to short-distance signaling, however. Male silkworm moths have receptors that can detect the pheromone from a female moth from several kilometers away (see Figure 50.6).

In a honeybee colony, pheromones produced by the queen and her daughters, the workers, maintain the hive's complex social order. One pheromone (once called the queen substance) has a particularly wide range of effects. It attracts workers to the queen, inhibits development of ovaries in workers, and attracts males (drones) to the queen during her mating flights out of the hive.

Pheromones can also serve as alarm signals. For example, when a minnow or catfish is injured, a substance released from the fish's skin disperses in the water, inducing a fright response in other fish. These nearby fish become more vigilant and often form tightly packed schools near the river or lake bottom, where they are safer from attack **(Figure 52.6)**. Pheromones can be very effective at remarkably low concentrations. For instance, just 1 cm^2 of skin from a fathead minnow contains sufficient alarm substance to induce a reaction in 58,000 L of water.

Figure 52.6 Minnows responding to the presence of an alarm substance.



1 Minnows are widely dispersed in an aquarium before an alarm substance is introduced.

2 Within seconds of the alarm substance being introduced, minnows aggregate near the bottom of the aquarium and reduce their movement.

So far in this chapter, we have explored the types of stimuli that elicit behaviors—the first part of Tinbergen's first question. The second part of that question—the physiological mechanisms that mediate responses—involves the nervous, muscular, and skeletal systems: Stimuli activate sensory systems, are processed in the central nervous system, and result in motor outputs that constitute behavior. Thus, we are ready to focus on Tinbergen's second question—how experience influences behavior.

CONCEPT CHECK 52.1

1. If an egg rolls out of the nest, a mother greylag goose will retrieve it by nudging it with her beak and head. If researchers remove the egg or substitute a ball during this process, the goose continues to bob her beak and head while she moves back to the nest. Explain how and why this behavior occurs.
2. **WHAT IF?** ➤ Suppose you exposed various fish species from the minnows' environment to the alarm substance from minnows. Thinking about natural selection, suggest why some species might respond like minnows, some might increase their activity, and some might show no change.
3. **MAKE CONNECTIONS** ➤ How is the lunar-linked rhythm of fiddler crab courtship similar in mechanism and function to the seasonal timing of plant flowering? (See Concept 39.3.)

For suggested answers, see Appendix A.

CONCEPT 52.2

Learning establishes specific links between experience and behavior

For some behaviors—such as a fixed action pattern, a courtship stimulus-response chain, or pheromone signaling—nearly all individuals in a population behave alike. Behavior that is developmentally fixed in this way is known as **innate behavior**. Other behaviors, however, vary with experience and thus differ between individuals.

Experience and Behavior

Tinbergen's second question asks how an animal's experiences during growth and development influence the response to stimuli. One informative approach to this question is a **cross-fostering study**, in which the young of one species are placed in the care of adults from another species in the same or a similar environment. The extent to which the offspring's behavior changes in such a situation provides a measure of how the social and physical environment influences behavior.

Certain mouse species have behaviors well suited for cross-fostering studies. Male California mice (*Peromyscus*

Table 52.1 Influence of Cross-Fostering on Male Mice*

Species	Aggression Toward an Intruder	Aggression In Neutral Situation	Paternal Behavior
California mice fostered by white-footed mice	Reduced	No difference	Reduced
White-footed mice fostered by California mice	No difference	Increased	No difference

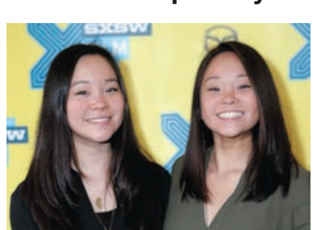
*Comparisons are with mice raised by parents of their own species.

californicus) are highly aggressive toward other mice and provide extensive parental care. In contrast, male white-footed mice (*Peromyscus leucopus*) are less aggressive and engage in little parental care. When the pups of each species were placed in the nests of the other species, the cross-fostering altered some behaviors of both species **(Table 52.1)**. For instance, male California mice raised by white-footed mice were less aggressive toward intruders. Thus, experience during development can strongly influence aggressive behavior in these rodents.

One of the most important findings of the cross-fostering experiments with mice was that the influence of experience on behavior can be passed on to progeny: When the cross-fostered California mice became parents, they spent less time retrieving offspring who wandered off than did California mice raised by their own species. Thus, experience during development can modify physiology in a way that alters parental behavior, extending the influence of environment to a subsequent generation.

For humans, the influence of genetics and environment on behavior can be explored by a **twin study**, in which researchers compare the behavior of identical twins raised apart with the behavior of those raised in the same household. Twin studies have been instrumental in studying disorders that alter human behavior, such as anxiety disorders, schizophrenia, and alcoholism.

▼ Identical twins who were raised separately.



Learning

One powerful way that an animal's environment can influence its behavior is through **learning**, the modification of behavior as a result of specific experiences. The capacity for learning depends on nervous system organization established during development following instructions encoded in the genome. Learning itself involves the formation of memories by specific changes in neuronal connectivity (see Concept 49.4). Therefore, the essential challenge for research into learning is not to decide between nature (genes) and nurture (environment), but rather to explore the contributions of *both* nature and nurture in shaping learning and, more generally, behavior.

Imprinting

In some species, the ability of offspring to recognize and be recognized by a parent is essential for survival. In the young, this learning often takes the form of **imprinting**, the establishment of a long-lasting behavioral response to a particular individual or object. Imprinting can take place only during a specific time period in development, called the **sensitive period**. Among gulls, for instance, the sensitive period for a parent to bond with its young lasts one to two days. During the sensitive period, the young imprint on their parent and learn basic behaviors, while the parent learns to recognize its offspring. If bonding does not occur, the parent will not care for the offspring, leading to the death of the offspring and a decrease in the reproductive success of the parent.

How do the young know on whom—or what—to imprint? Experiments with many species of waterfowl indicate that young birds have no innate recognition of "mother." Rather, they identify with the first object they encounter that has certain key characteristics. In the 1930s, experiments showed that the principal imprinting stimulus in greylag geese (*Anser anser*) is a nearby object that is moving away from the young. When incubator-hatched goslings spent their first few hours with a person rather than with a goose, they imprinted on the human and steadfastly followed that person from then on **(Figure 52.7)**. Furthermore, they showed no recognition of their biological mother.

Imprinting has become an important component of efforts to save endangered species, such as the whooping crane (*Grus americana*). Scientists tried raising whooping cranes in captivity by using sandhill cranes (*Grus canadensis*) as foster parents. However, because the whooping cranes imprinted on their foster parents, none formed a *pair-bond* (strong attachment) with a whooping crane mate. To avoid such problems, captive breeding programs now isolate young cranes, exposing them to the sights and sounds of members of their own species.

Until recently, scientists made further use of imprinting to teach cranes born in captivity to migrate along safe routes. Young whooping cranes were imprinted on humans in "crane suits" and then allowed to follow these "parents" as they flew ultralight aircraft along selected migration routes. Beginning in 2016, efforts shifted to a focus on minimizing human intervention as part of an overall strategy aimed at fostering self-sustaining crane populations.

Figure 52.7 Imprinting. Young graylag geese imprinted on a man.

WHAT IF? ➤ *Suppose the geese shown in (a) were bred to each other. How might their imprinting on a human affect their offspring? Explain.*

Video: Ducklings

Spatial Learning and Cognitive Maps

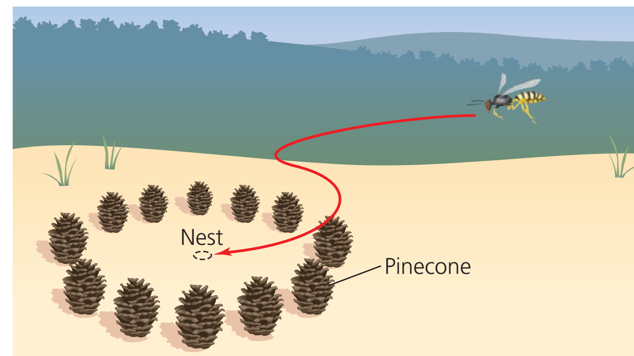
Every natural environment has spatial variation, as in locations of nest sites, hazards, food, and prospective mates. Therefore, an organism's fitness may be enhanced by the capacity for **spatial learning**, the establishment of a memory that reflects the environment's spatial structure.

The idea of spatial learning intrigued Tinbergen while he was a graduate student in the Netherlands. At that time, he was studying females of a digger wasp species (*Philanthus triangulum*) that nests in small burrows dug into sand dunes. When a wasp leaves her nest to go hunting, she hides the entrance from potential intruders by covering it with sand. When she returns, however, she flies directly to her hidden nest, despite the presence of hundreds of other burrows in the area. How does she accomplish this feat? Tinbergen hypothesized that a wasp locates her nest by learning its position relative to visible landmarks. To test his hypothesis, he carried out an experiment in the wasps' natural habitat **(Figure 52.8)**. By manipulating objects around nest entrances, he demonstrated that digger wasps engage in spatial learning. This experiment was so simple and

Figure 52.8

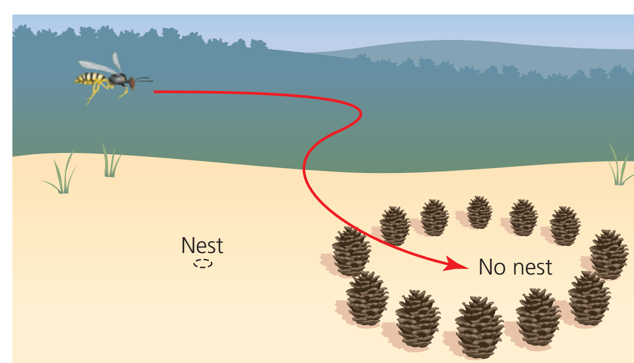
Inquiry Does a digger wasp use landmarks to find her nest?

Experiment A female digger wasp covers the entrance to her nest while foraging for food, but finds the correct wasp nest reliably upon her return 30 minutes or more later. Niko Tinbergen wanted to test the hypothesis that a wasp learns visual landmarks that mark her nest before she leaves on hunting trips. First, he marked one nest with a ring of pinecones while the wasp was in the burrow. After leaving the nest to forage, the wasp returned to the nest successfully.



Two days later, after the wasp had again left, Tinbergen shifted the ring of pinecones away from the nest. Then he waited to observe the wasp's behavior.

Results When the wasp returned, she flew to the center of the pinecone circle instead of to the nearby nest. Repeating the experiment with many wasps, Tinbergen obtained the same results.



Conclusion The experiment supported the hypothesis that digger wasps use visual landmarks to keep track of their nests.

Data from N. Tinbergen, *The Study of Instinct*, Clarendon Press, Oxford (1951).

WHAT IF? ➤ *Suppose the digger wasp had returned to her original nest site, despite the pinecones having been moved. What alternative hypotheses might you propose regarding how the wasp finds her nest and why the pinecones didn't misdirect the wasp?*

Animation: Digger Wasps and Landmarks

informative that it could be summarized very concisely. In fact, at 32 pages, Tinbergen's Ph.D. thesis from 1932 is still the shortest ever approved at Leiden University.

In some animals, spatial learning involves formulating a **cognitive map**, a representation in an animal's nervous system of the spatial relationships between objects in its surroundings. One striking example is found in the Clark's nutcracker (*Nucifraga columbiana*), a relative of ravens, crows, and jays. In the fall, nutcrackers hide pine seeds for retrieval during the winter. By experimentally varying the distance between landmarks in the birds' environment, researchers discovered that the birds kept track of the halfway point between landmarks, rather than a fixed distance, to find their hidden food stores.

Associative Learning

Learning often involves making associations between experiences. Consider, for example, a blue jay (*Cyanocitta cristata*) that ingests a brightly colored monarch butterfly (*Danaus plexippus*). Substances that the monarch accumulates from milkweed plants cause the blue jay to vomit almost immediately **(Figure 52.9)**. Following such experiences, blue jays avoid attacking monarchs and similar-looking butterflies. The ability to associate one environmental feature (such as a color) with another (such as a foul taste) is called **associative learning**.

Associative learning is well suited to study in the laboratory. Such studies typically involve either classical conditioning or operant conditioning. In *classical conditioning*, an arbitrary stimulus becomes associated with a particular outcome. Russian physiologist Ivan Pavlov carried out early experiments in classical conditioning, demonstrating that if he always rang a bell just before feeding a dog, the dog would eventually salivate when the bell sounded, anticipating food. In *operant conditioning*, also called trial-and-error learning, an animal first learns to associate one of its behaviors with a reward or punishment and then tends to repeat or avoid that behavior (see Figure 52.9). B. F. Skinner, an American pioneer in the study of operant conditioning, explored this process in the laboratory by, for example, having a rat learn through trial and error to obtain food by pressing a lever.

Figure 52.9 Associative learning. Having ingested and vomited a monarch butterfly, a blue jay has probably learned to avoid this species.

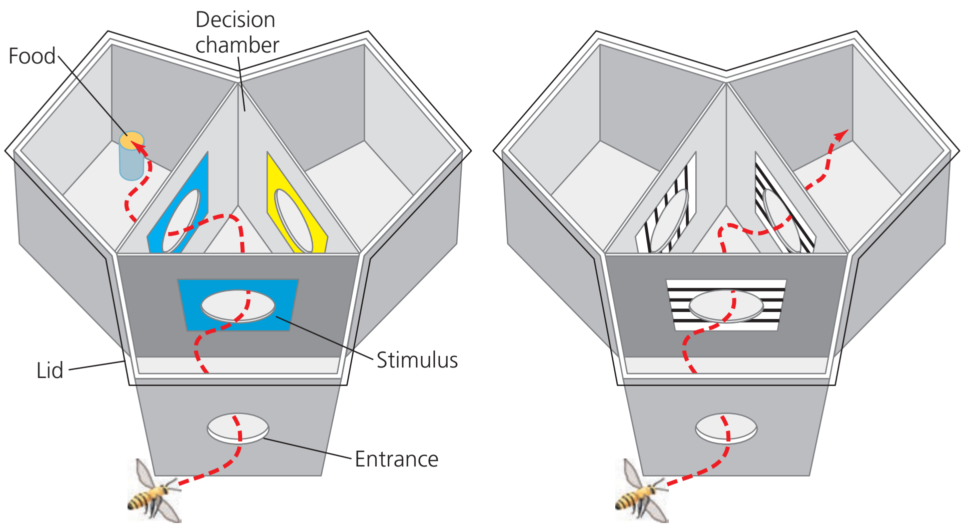
Studies reveal that animals can learn to link many pairs of features of their environment, but not all. For example, pigeons can learn to associate danger with a sound but not with a color. However, they can learn to associate a color with food. What does this mean? The development and organization of the pigeon's nervous system apparently restrict the associations that can be formed. Moreover, such restrictions are not limited to birds. Rats, for example, can learn to avoid illness-inducing foods on the basis of smells, but not on the basis of sights or sounds.

If we consider how behavior evolves, the fact that some animals can't learn to make particular associations appears logical. The associations an animal can readily form typically reflect relationships likely to occur in nature. Conversely, associations that can't be formed are those unlikely to be of selective advantage in a native environment. In the case of a rat's diet in the wild, for example, a harmful food is far more likely to have a certain odor than to be associated with a particular sound.

Cognition and Problem Solving

The most complex forms of learning involve **cognition**—the process of knowing that involves awareness, reasoning, recollection, and judgment. Although it was once argued that only primates and certain marine mammals have high-level thought processes, many other groups of animals, including insects, appear to exhibit cognition in controlled laboratory studies. For example, an experiment using Y-shaped mazes provided evidence for abstract thinking in honeybees. One maze had different colors, and one had different black-and-white striped patterns, either vertical or horizontal bars. Two groups of honeybees were trained in the color maze. Upon entering, a bee would see a sample color and could then choose between an arm of the maze with the same color or an arm with a different color. Only one arm contained a food reward. The first group of bees were rewarded for flying into the arm with the *same* color as the sample **(Figure 52.10, 1)**; the second group were rewarded for choosing the arm with the *different* color. Next, bees from each group were tested in the bar maze, which had no food reward. After encountering a sample black-and-white pattern of bars, a bee could choose an arm with the same pattern or an arm with a different pattern. The bees in the first group most often chose the arm with the same pattern **(Figure 52.10, 2)**, whereas those in the second group typically chose the arm with the different pattern.

Figure 52.10 A maze test of abstract thinking by honeybees. These mazes are designed to test whether honeybees can distinguish "same" from "different."



1 Bees were trained in a color maze. As shown here, one group were rewarded for choosing the same color as the stimulus.

2 Bees were tested in a pattern maze. If previously rewarded for choosing the same color, bees most often chose lines oriented the same way as the stimulus.

VISUAL SKILLS ➤ *Describe how you would set up the pattern maze to control for an inherent preference for or against a particular orientation of the black bars.*

The maze experiments provide strong experimental support for the hypothesis that honeybees can distinguish on the basis of "same" and "different." Remarkably, research published in 2010 indicates that honeybees can also learn to distinguish between human faces.

The information-processing ability of a nervous system can also be revealed in **problem solving**, the cognitive activity of devising a method to proceed from one state to another in the face of real or apparent obstacles. For example, if a chimpanzee is placed in a room with several boxes on the floor and a banana hung high out of reach, the chimpanzee can assess the situation and stack the boxes, enabling it to reach the food. Problem-solving behavior is highly developed in some mammals, especially primates and dolphins. Notable examples have also been observed in some bird species, especially corvids. In one study, ravens were confronted with food hanging from a branch by a string. After failing to grab the food in flight, one raven flew to the branch and alternately pulled up and stepped on the string until the food was within reach. A number of other ravens eventually arrived at similar solutions. Nevertheless, some ravens failed to solve the problem, indicating that problem-solving success in this species, as in others, varies with individual experience and abilities.

Development of Learned Behaviors

Most of the learned behaviors we have discussed develop over a relatively short time. Some behaviors develop more gradually. For example, some bird species learn songs in stages.

In the case of the white-crowned sparrow (*Zonotrichia leucophrys*), the first stage of song learning takes place early in life, when the fledgling sparrow first hears the song. If a fledgling is prevented from hearing real sparrows or recordings of sparrow songs during the first 50 days of its life, it fails to develop the adult song of its species. Although the young bird does not sing during the sensitive period, it memorizes the song of its species by listening to other white-crowned sparrows sing. During the sensitive period, fledglings chirp more in response to songs of their own species than to songs of other species. Thus, when young white-crowned sparrows learn the songs they will sing later on, that learning appears to be bounded by genetically controlled preferences.

The sensitive period when a white-crowned sparrow memorizes its species' song is followed by a second learning phase when the juvenile bird sings tentative notes called a subsong. The juvenile bird hears its own singing and compares it with the song memorized during the sensitive period. Once a sparrow's own song matches the one it memorized, the song "crystallizes" as the final song, and the bird sings only this adult song for the rest of its life.

The song-learning process can be quite different in other bird species. Canaries, for example, do not have a single sensitive period for song learning. A young canary begins with a subsong, but the full song does not crystallize in the same way as in white-crowned sparrows. Between breeding seasons, the song becomes flexible again, and an adult male may learn new song "syllables" each year, adding to the song it already sings.

Song learning is one of many examples of how animals learn from other members of their species. In finishing our exploration of learning, we'll look at several more examples that reflect the more general phenomenon of social learning.

Social Learning

Many animals learn to solve problems by observing the behavior of other individuals. This type of learning through observing others is called **social learning**. Young wild chimpanzees, for example, learn how to crack open oil

Figure 52.11 A young chimpanzee learning to crack oil palm nuts by observing an experienced elder.

Video: Chimp Cracking Nut

palm nuts with two stones by copying experienced chimpanzees **(Figure 52.11)**.

Another example of how social learning can modify behavior comes from studies of the vervet monkeys (*Chlorocebus pygerythrus*) in Amboseli National Park, Kenya. Vervet monkeys, which are about the size of a domestic cat, produce a complex set of alarm calls. Amboseli vervets give distinct alarm calls for leopards, eagles, and snakes. When a vervet sees a leopard, it gives a loud barking sound; when it sees an eagle, it gives a short double-syllable cough; and the snake alarm call is a "chutter." Upon hearing a particular alarm call, other vervets in the group behave in an appropriate way: They run up a tree on hearing the alarm for a leopard (vervets are nimbler than leopards in the trees); look up on hearing the alarm for an eagle; and look down on hearing the alarm for a snake **(Figure 52.12)**.

Infant vervet monkeys give alarm calls, but in a relatively undiscriminating way. For example, they give the "eagle" alarm on seeing any bird, including harmless birds such as bee-eaters. With age, the monkeys improve their accuracy. In fact, adult vervet monkeys give the eagle alarm only on seeing an eagle belonging to either of the two species that eat vervets. Infants probably learn how to give the right call by observing other members of the group and receiving social confirmation. For instance, if the infant gives the call on the right occasion—say, an eagle alarm when there is an eagle overhead—another member of the group will also give the eagle call. But if the infant gives the call when a bee-eater flies by, the adults in the group are silent. Thus, vervet monkeys have an initial, unlearned tendency to give calls upon seeing potentially threatening objects in the environment. Learning fine-tunes the call so that adult vervets give calls only in response to genuine danger and can fine-tune the alarm calls of the next generation.

Social learning forms the roots of **culture**, a system of information transfer through social learning or teaching

Figure 52.12 Vervet monkeys learning correct use of alarm calls. On seeing a python (foreground), vervet monkeys give a distinct "snake" alarm call (inset), and the members of the group stand upright and look down.

that influences the behavior of individuals in a population. Cultural transfer of information can alter behavioral phenotypes and thereby influence the fitness of individuals.

Changes in behavior that result from natural selection occur on a much longer time scale than does learning. In Concept 52.3, we'll examine the relationship between particular behaviors and the processes of selection related to survival and reproduction.

CONCEPT CHECK 52.2

1. How might associative learning explain why different species of distasteful or stinging insects have similar colors?
2. **WHAT IF?** ➤ How might you position and manipulate a few objects in a lab to test whether an animal can use a cognitive map to remember the location of a food source?
3. **MAKE CONNECTIONS** ➤ How might a learned behavior contribute to speciation? (See Concept 24.1.)

For suggested answers, see Appendix A.

CONCEPT 52.3

Selection for individual survival and reproductive success can explain diverse behaviors

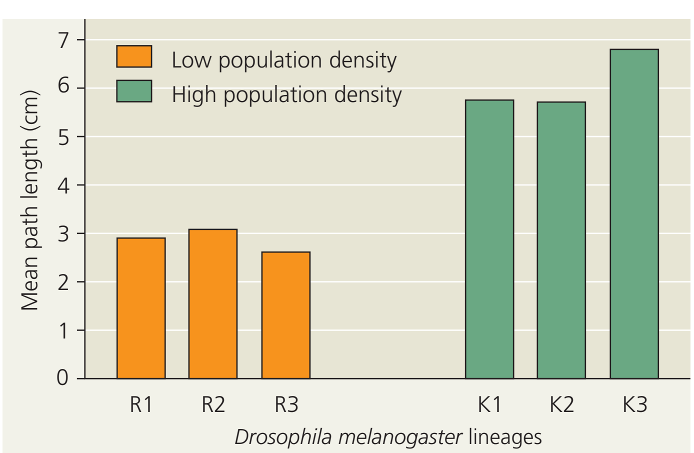
EVOLUTION We turn now to Tinbergen's third question—how behavior enhances survival and reproduction in a population. The focus thus shifts from proximate causation—the "how" questions—to ultimate causation—the "why" questions. We'll begin by considering the activity of gathering food. Food-obtaining behavior, or **foraging**, includes not only eating but also any activities an animal uses to search for, recognize, and capture food items.

Evolution of Foraging Behavior

The fruit fly allows us to examine one way that foraging behavior might have evolved. Variation in a gene called *forager* (*for*) dictates how far *Drosophila* larvae travel when foraging. On average, larvae carrying the for^R ("Rover") allele travel nearly twice as far while foraging as do larvae with the for^s ("sitter") allele.

Both the for^R and for^s alleles are present in natural populations. What circumstances might favor one or the other allele? The answer became apparent in experiments that maintained flies at either low or high population densities for many generations. Larvae in populations kept at a low density foraged over shorter distances than those in populations kept at high density **(Figure 52.13)**. Furthermore, the for^s allele increased in frequency in the low-density populations, whereas the for^R allele increased in frequency in the high-density group. These changes make sense. At a low population density, short-distance foraging yields sufficient food, while long-distance foraging would result in unnecessary energy expenditure. Under crowded conditions, long-distance foraging could enable larvae to move beyond areas depleted of food. Thus, an interpretable evolutionary change in behavior occurred in the course of the experiment.

Figure 52.13 Evolution of foraging behavior by laboratory populations of *Drosophila melanogaster*. After 74 generations of living at low population density, *Drososphila* larvae (populations R1–R3) followed foraging paths significantly shorter than those of *Drososphila* larvae that had lived at high density (populations K1–K3).



INTERPRET THE DATA ➤ *What alternative hypothesis is made far less likely by having three R and K lines, rather than one of each?*

Optimal Foraging Model

To study the ultimate causation of foraging strategies, biologists sometimes apply a type of cost-benefit analysis used in economics. This idea proposes that foraging behavior is a compromise between the benefits of nutrition and the costs of obtaining food. These costs might include the energy expenditure of foraging as well as the risk of being eaten while foraging. According to this **optimal foraging model**, natural selection should favor a foraging behavior that minimizes the costs of foraging and maximizes the benefits. The **Scientific Skills Exercise** provides an example of how this model can be applied to animals in the wild.

Balancing Risk and Reward

One of the most significant potential costs to a forager is risk of predation. Maximizing energy gain and minimizing energy costs are of little benefit if the behavior makes the forager a likely meal for a predator. It seems logical, therefore, that predation risk would influence foraging behavior. Such appears to be the case for the mule deer (*Odocoileus hemionus*), which lives in the mountains of western North America. Researchers found that the food available for mule deer was fairly uniform across the potential foraging areas, although somewhat lower in open, nonforested areas. In contrast, the risk of predation differed greatly; mountain lions (*Puma concolor*), the major predator, killed large numbers of mule deer at forest edges and only a small number in open areas and forest interiors.

How does mule deer foraging behavior reflect the differences in predation risk in particular areas? Mule deer feed predominantly in open areas. Thus, it appears that mule deer foraging behavior reflects the large variation in predation risk and not the smaller variation in food availability. This result underscores the point that behavior typically reflects a compromise between competing selective pressures.

Mating Behavior and Mate Choice

Just as foraging is crucial for individual survival, mating behavior and mate choice play a major role in determining reproductive success. These behaviors include seeking or attracting mates, choosing among potential mates, competing for mates, and caring for offspring.

Mating Systems and Sexual Dimorphism

Although we tend to think of mating simply as the union of a male and female, species vary greatly with regard to *mating systems*, the length and number of relationships between males and females. In some animal species, mating is *promiscuous*, with no strong pair-bonds. In others, mates form a relationship of some duration that is **monogamous** (one male mating

SCIENTIFIC SKILLS EXERCISE

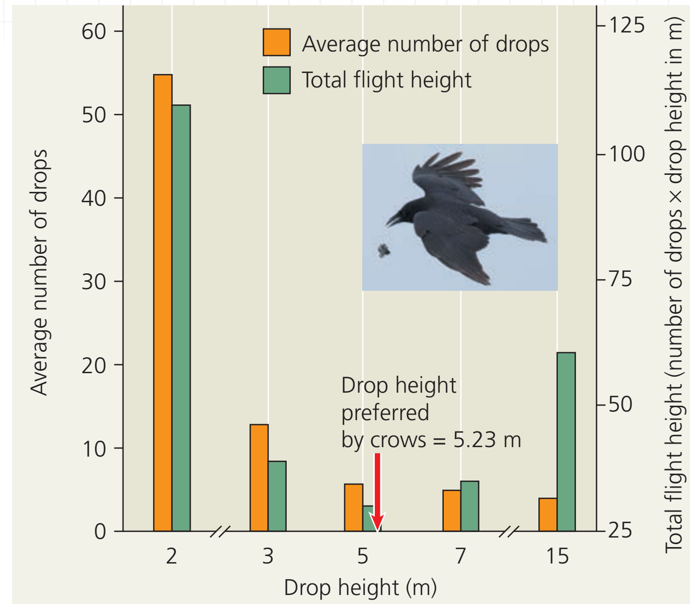
Testing a Hypothesis with a Quantitative Model

Do Crows Display Optimal Foraging Behavior? On islands off British Columbia, Canada, Northwestern crows (*Corvus caurinus*) search rocky tide pools for sea snails called whelks. After spotting a whelk, the crow picks it up in its beak, flies upward, and drops the whelk onto the rocks. If the drop is successful, the shell breaks and the crow can dine on the whelk's soft parts. If not, the crow flies up and drops the whelk again and again until the shell breaks. What determines how high the crow flies? If energetic considerations dominated selection for the crow's foraging behavior, the average drop height might reflect a trade-off between the cost of flying higher and the benefit of more frequent success. In this exercise you'll test how well this optimal foraging model predicts the average drop height observed in nature.

How the Experiments Were Done The height of drops made by crows in the wild was measured by referring to a marked pole erected nearby. In the test, the crow's behavior was simulated using a device that dropped a whelk onto the rocks from a fixed platform. The average number of drops required to break whelks from various platform heights was recorded and averaged over many trials with the device. Combining the data for each platform height, total "flight" height was calculated by multiplying the height times the average number of drops required.

Data from the Experiment

The graph summarizes the results of the experiment.



Data from R. Zach, Shell-dropping: Decision-making and optimal foraging in northwestern crows, *Behavior* 68:106–117 (1979).

INTERPRET THE DATA

1. How does the average number of drops required to break open a whelk depend on platform height for a drop of 5 meters or less? For drops of more than 5 meters?
2. Total flight height can be considered to be a measure of the total energy required to break open a whelk. Why is this value lower for a platform set at 5 meters than for one at 2 or 15 meters?
3. Compare the drop height preferred by crows with the graph of total flight height for the platform drops. Are the data consistent with the hypothesis of optimal foraging? Explain.
4. In testing the optimal foraging model, it was assumed that changing the height of the drop only changed the total energy required. Do you think this is a realistic limitation, or might other factors than total energy be affected by height?
5. Researchers observed that the crows only gather and drop the largest whelks. What are some reasons crows might favor larger whelks?
6. It turned out that the probability of a whelk breaking was the same for a whelk dropped for the first time as for an unbroken whelk dropped several times previously. If the probability of breaking instead increased, what change might you predict in the crow's behavior?

MB **Instructors**: A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

with one female) or **polygamous** (an individual of one sex mating with several of the other). Polygamous relationships involve either *polygyny*, a single male and many females, or *polyandry*, a single female and multiple males.

The extent to which males and females differ in appearance, a characteristic known as *sexual dimorphism*, typically varies with the type of mating system **(Figure 52.14)**. Among monogamous species, males and females often look very similar. In contrast, among polygamous species, the sex that attracts multiple mating partners is typically showier and larger than the opposite sex. We'll discuss the evolutionary basis of these differences shortly.

Mating Systems and Parental Care

The needs of the young are an important factor constraining the evolution of mating systems. Most newly hatched birds, for instance, cannot care for themselves. Rather, they require a large, continuous food supply, a need that is difficult for a single parent to meet. In such cases, a male that stays with and helps a single mate may ultimately have more viable offspring than it would by going off to seek additional mates. This may explain why many birds are monogamous. In contrast, for birds with young that can feed and care for themselves almost immediately after hatching, the males derive less benefit from staying

Figure 52.14 Relationship between mating system and male and female forms.

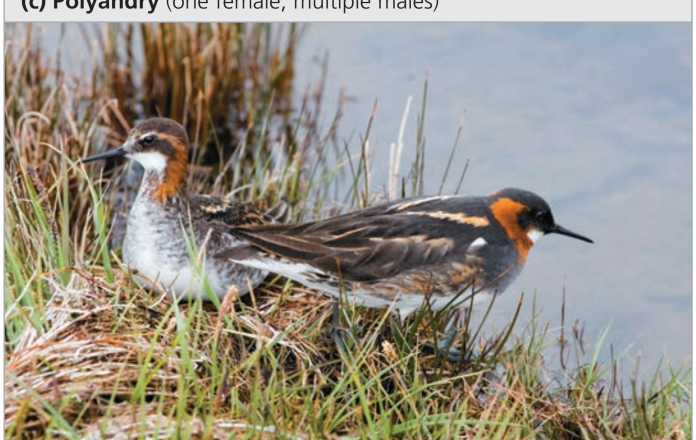
(a) Monogamy (one male, one female)

In monogamous species, such as these western gulls (*Larus occidentalis*), males and females are often difficult to distinguish using external characteristics only.

(b) Polygyny (one male, multiple females)

Among polygynous species, such as elk (*Cervus canadensis*), the male (right) is often highly ornamented.

(c) Polyandry (one female, multiple males)



In polyandrous species, such as these red-necked phalaropes (*Phalaropus lobatus*), females (right) are generally more ornamented than males.

with their partner. Males of these species, such as pheasants and quail, can maximize their reproductive success by seeking other mates, and polygyny is relatively common in such birds. In the case of mammals, the lactating female is often the only food source for the young, and males usually play no role in raising the young. In mammalian species where males protect the females and young, such as lions, a male or small group of males typically cares for a harem of many females.

Another factor influencing mating behavior and parental care is *certainty of paternity*. Young born to or eggs laid by a female definitely contain that female's genes. However, even within a normally monogamous relationship, a male other than the female's usual mate may have fathered that female's offspring. The certainty of paternity is relatively low in most species with internal fertilization because the acts of mating and birth (or mating and egg laying) are separated over time. This could explain why exclusively male parental care is rare in bird and mammal species. However, the males of many species with internal fertilization engage in behaviors that appear to increase their certainty of paternity. These behaviors include guarding females, removing any sperm from the female reproductive tract before copulation, and introducing large quantities of sperm that displace the sperm of other males.

Certainty of paternity is high when egg laying and mating occur together, as in external fertilization. This may explain why parental care in aquatic invertebrates, fishes, and amphibians, when it occurs at all, is at least as likely to be by males as by females (**Figure 52.15**; see also Figure 45.6). Among fishes and amphibians, parental care occurs in fewer than 10% of species with internal fertilization but in more than half of species with external fertilization.

It is important to point out that certainty of paternity does not mean that animals are aware of those factors when they behave a certain way. Parental behavior correlated with

Figure 52.15 Paternal care by a male jawfish. The male jawfish, which lives in tropical marine environments, holds the eggs it has fertilized in its mouth, keeping them aerated and protecting them from egg predators until the young hatch.

certainty of paternity exists because it has been reinforced over generations by natural selection. The intriguing relationship between certainty of paternity and male parental care remains an area of active research.

Sexual Selection and Mate Choice

Sexual dimorphism results from sexual selection, a form of natural selection in which differences in reproductive success among individuals are a consequence of differences in mating success (see Concept 23.4). Sexual selection can take the form of *intersexual selection*, in which members of one sex choose mates on the basis of characteristics of the other sex, such as courtship songs, or *intrasexual selection*, which involves competition between members of one sex for mates.

Mate Choice by Females Mate preferences of females may play a central role in the evolution of male behavior and anatomy through intersexual selection. Consider, for example, the courtship behavior of stalk-eyed flies. The eyes of these insects are at the tips of stalks, which are longer in males than in females. During courtship, a male approaches the female headfirst. Researchers have shown that females are more likely to mate with males that have relatively long eyestalks. Why would females favor this seemingly arbitrary trait? Ornaments such as long eyestalks in these flies and bright coloration in birds correlate in general with health and vitality. A female whose mate choice is a healthy male is likely to produce more offspring that survive to reproduce. As a result, males may compete with each other in ritualized contests to attract female attention **(Figure 52.16)**. In faceoffs between male stalkeyed flies, the male whose eyestalk length is smaller usually retreats peacefully.

Figure 52.16 A face-off between male stalk-eyed flies competing for female attention.

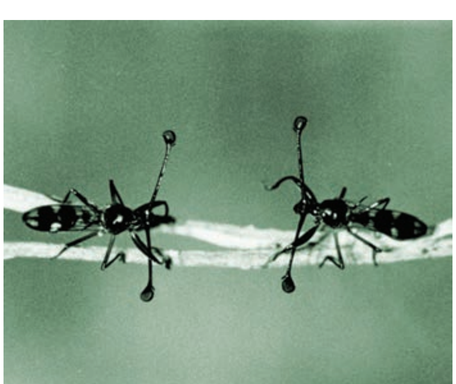
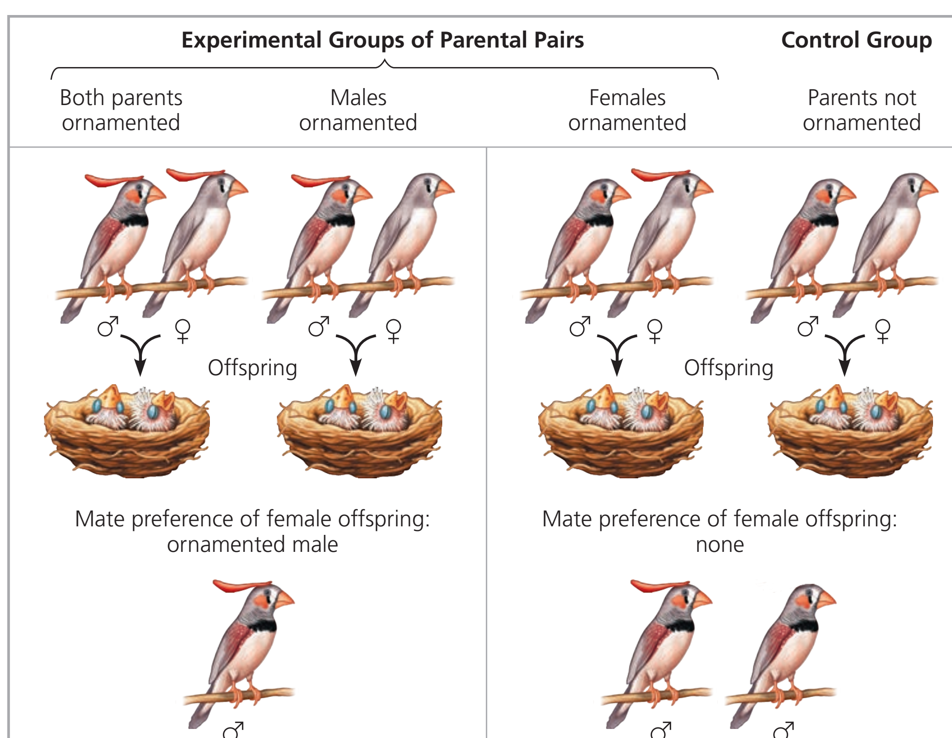


Figure 52.17 Appearance of zebra finches in nature. The male zebra finch (left) is more highly patterned and colorful than the female zebra finch.

Mate choice can also be influenced by imprinting, as revealed by experiments carried out with zebra finches (*Taeniopygia guttata*). Both male and female zebra finches normally lack any feather crest on their head **(Figure 52.17)**. To explore whether parental appearance affects mate preference in offspring independent of any genetic influence, researchers provided zebra finches with artificial ornamentation. A 2.5-cm-long red feather was taped to the forehead feathers of either or both zebra finch parents when their chicks were 8 days old, approximately 2 days before they opened their eyes. A control group of zebra finches was raised by unadorned parents. When the chicks matured, they were presented with prospective mates that were either artificially ornamented with a red feather or non-ornamented **(Figure 52.18)**. Males showed

Figure 52.18 Sexual selection influenced by imprinting. Experiments demonstrated that female zebra finch chicks that had imprinted on artificially ornamented fathers preferred ornamented males as adult mates. For all experimental groups, male offspring showed no preference for either ornamented or non-ornamented female mates.



no preference. Females raised by a male parent that was not ornamented also showed no preference. However, females raised by an ornamented male parent preferred ornamented males as their own mates. Thus, female finches apparently take cues from their fathers in choosing mates.

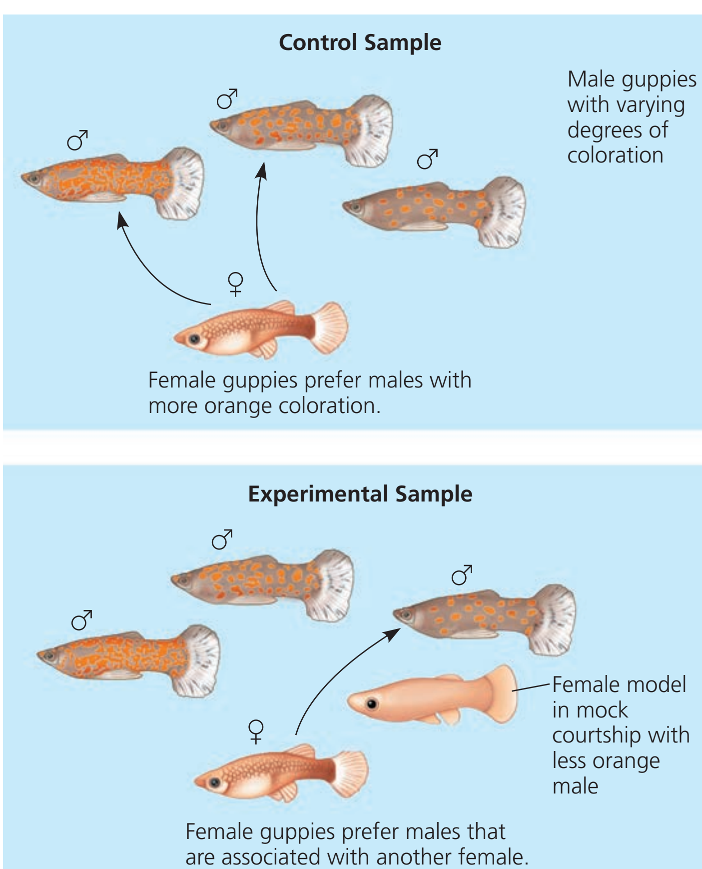
Mate-choice copying, a behavior in which individuals in a population copy the mate choice of others, has been studied in the guppy, *Poecilia reticulata*. When a female guppy chooses between males with no other females present, the female almost always chooses the male with more orange coloration. To explore if the behavior of other females could influence this preference, an experiment was set up using both living females and artificial model females **(Figure 52.19)**. If a female guppy observed the model "courting" a male with less extensive orange markings, she often copied the preference of the model female. That is, the female chose the male that had been presented in association with a model female rather than a more orange alternative. The exceptions were also informative. Mate-choice behavior typically did not change when the difference in coloration was particularly large. Mate-choice copying can thus mask genetically controlled female preference below a certain threshold of difference, in this case for male color.

Mate-choice copying, a form of social learning, has also been observed in several other fish and bird species. What is the selective pressure for such a mechanism? One possibility is that a female that mates with males that are attractive to other females increases the probability that her male offspring will also be attractive and have high reproductive success.

Male Competition for Mates The previous examples show how female choice can select for one best type of male in a given situation, resulting in low variation among males. Similarly, male competition for mates can reduce variation among males. Such competition may involve *agonistic behavior*, an often-ritualized contest that determines which competitor gains access to a resource, such as food or a mate **(Figure 52.20**; see also Figure 52.16).

Despite the potential for male competition to select for reduced variation, behavioral and morphological variation in males is extremely high in some vertebrate species,

▼ Figure 52.19 Mate choice copying by female guppies (*Poecilia reticulata*). In the absence of other females (control group), female guppies generally choose males with more orange coloration. However, when a female model is placed near one of the males (experimental group), female guppies often copy the apparent mate choice of the model, even if the male is less colorful than others. Guppy females ignored the mate choice of the model only if an alternative male had much more orange coloration.



▼ Figure 52.20 Agonistic interaction. Male eastern grey kangaroos (*Macropus giganteus*) often "box" in contests that determine which male is most likely to mate with an available female. Typically, one male snorts loudly and strikes the other with his forelimbs. If the male under attack does not retreat, the fight may escalate into grappling or the two males balancing on their tails while attempting to kick each other with the sharp toenails of their hind feet.

MB **Video: Agonistic Behavior in Wolves**
Video: Snake Ritual Wrestling

including species of fish and deer, as well as in a wide variety of invertebrates. In some species, sexual selection has led to the evolution of alternative male mating behavior and morphology. How do scientists analyze situations where more than one mating behavior can result in successful reproduction? One approach relies on the rules that govern games.

Applying Game Theory

Often, the fitness of a particular behavioral phenotype is influenced by other behavioral phenotypes in the population. In studying such situations, behavioral ecologists use a range of tools, including game theory. Developed by American mathematician John Nash and others to model human economic behavior, **game theory** evaluates alternative strategies in situations where the outcome depends on the strategies of all the individuals involved.

As an example of applying game theory to mating behavior, let's consider the side-blotched lizard (*Uta stansburiana*) of California. Genetic variations give rise to males with orange, blue, or yellow throats **(Figure 52.21)**. One would expect that natural selection would favor one of the three color types, yet all three persist. Why? The answer appears to lie in the fact that each throat color is associated with a different pattern of behavior: Orange-throat males are the most aggressive and defend large territories that contain many females. Blue-throat males are also territorial but defend smaller territories and fewer females. Yellow-throats are nonterritorial males that mimic females and use "sneaky" tactics to gain the chance to mate.

Evidence indicates that the mating success of each male lizard type is influenced by the relative abundance of the other types, an example of frequency-dependent selection. In one study population, the most frequent throat coloration changed over a period of several years from blue to orange to yellow and back to blue.

▼ Figure 52.21 Male polymorphism in the side-blotched lizard (*Uta stansburiana*). An orange-throat male, left; a blue-throat male, center; a yellow-throat male, right.

By comparing the competition between common side-blotched lizard males to the children's game of rock-paper-scissors, scientists devised an explanation for the cycles of variation in the lizard population. In the game, paper defeats rock, rock defeats scissors, and scissors defeats paper. Each hand symbol thus wins one matchup but loses the other. Similarly, each type of male lizard has an advantage over one of the other two types. When blue-throats are abundant, they can defend the few females in their territories from the advances of the sneaky yellow-throat males. However, blue-throats cannot defend their territories against the hyperaggressive orange-throats. Once the orange-throats become the most abundant, the larger number of females in each territory provides the opportunity for the yellow-throats to have greater mating success. The yellow-throats become more frequent, but then give way to the blue-throats, whose tactic of guarding small territories once again allows them the most success. Thus, following the population over time, one sees a persistence of all three color types and a periodic shift in which type is most prevalent.

Game theory provides a way to think about complex evolutionary problems in which relative performance (reproductive success relative to other phenotypes), not absolute performance, is the key to understanding the evolution of behavior. This makes game theory an important tool because the relative performance of one phenotype compared with others is a measure of Darwinian fitness.

CONCEPT CHECK 52.3

1. Why does the mode of fertilization correlate with the presence or absence of male parental care?
2. **MAKE CONNECTIONS ➤** Balancing selection can maintain variation at a locus (see Concept 23.4). Based on the foraging experiments described in this chapter, devise a simple hypothesis to explain the presence of both for^R and for^s alleles in natural fly populations.
3. **WHAT IF? ➤** Suppose an infection in a common side-blotched lizard population killed many more males than females. What would be the immediate effect on male competition for reproductive success?

For suggested answers, see Appendix A.

CONCEPT 52.4

Genetic analyses and the concept of inclusive fitness provide a basis for studying the evolution of behavior

EVOLUTION We'll now explore issues related to Tinbergen's fourth question—the evolutionary history of behaviors. We will first look at the genetic control of a behavior. Next, we will examine the genetic variation underlying the evolution of particular behaviors. Finally, we will see how expanding the definition of fitness beyond individual survival can help explain "selfless" behavior.

Genetic Basis of Behavior

In exploring the genetic basis of behavior, we'll begin with the courtship behavior of the male fruit fly (see Figure 52.4). During courtship, the male fly carries out a complex series of actions in response to multiple sensory stimuli. Genetic studies have revealed that a single gene called *fru* controls this entire courtship ritual. If the *fru* gene is mutated to an inactive form, males do not court or mate with females. (The name *fru* is short for *fruitless*, reflecting the absence of offspring from the mutant males.) Normal male and female flies express distinct forms of the *fru* gene. When females are genetically manipulated to express the male form of *fru*, they court other females, performing the role normally played by the male.

How does the *fru* gene control so many different actions? Experiments carried out cooperatively in several laboratories demonstrated that *fru* is a master regulatory gene that directs the expression and activity of many genes with narrower functions. Together, genes that are controlled by the *fru* gene bring about sex-specific development of the fly nervous system. In effect, *fru* programs the fly for male courtship behavior by overseeing a male-specific wiring of the central nervous system.

In many cases, differences in behavior arise not from gene inactivation, but from variation in the activity or amount of a gene product. One striking example comes from the study of two related species of voles, which are small, mouse-like rodents. Male meadow voles (*Microtus pennsylvanicus*) are solitary and do not form lasting relationships with mates. Following mating, they pay little attention to their pups. In contrast, male prairie voles (*Microtus ochrogaster*) form a pair-bond with a single female after they mate **(Figure 52.22)**. Male prairie voles provide care for their young pups, hovering over them, licking them, and carrying them, while acting aggressively toward intruders.

A peptide neurotransmitter is critical for the partnering and parental behavior of male voles. Known as **antidiuretic hormone (ADH)** or **vasopressin** (see Concept 44.5), this peptide is released during mating and binds to a specific receptor in the central nervous system. When male prairie voles are given a drug that inhibits the receptor in the brain that detects vasopressin, the male voles fail to form pair-bonds after mating.

The vasopressin receptor gene is much more highly expressed in the brain of prairie voles than in the brain of meadow voles. Testing the hypothesis that vasopressin receptor levels in the brain regulate postmating behavior, researchers inserted the vasopressin receptor gene from prairie voles into the genome of meadow voles. The male meadow voles carrying this gene not only developed brains with higher levels of the vasopressin receptor but also showed many of the same mating behaviors as male prairie voles, such as pair-bonding. Thus, although many genes influence pair-bonding and parenting in male voles, a change in the level of expression of the vasopressin receptor is sufficient to alter the development of these behaviors.

▼ Figure 52.22 A pair of prairie voles (*Microtus ochrogaster*) huddling. Male North American prairie voles associate closely with their mates, as shown here, and contribute substantially to the care of young.

Genetic Variation and the Evolution of Behavior

Behavioral differences between closely related species, such as meadow and prairie voles, are common. Significant differences in behavior can also be found *within* a species but are often less obvious. When behavioral variation between populations of a species correlates with variation in environmental conditions, it may reflect natural selection.

Case Study: *Variation in Prey Selection*

An example of genetically based behavioral variation within a species involves prey selection by the western garter snake (*Thamnophis elegans*). The natural diet of this species differs widely across its range in California. Coastal

Figure 52.23 Western garter snake from a coastal habitat eating a banana slug. Experiments indicate that the preference of these snakes for banana slugs may be influenced more by genetics than by environment.

populations feed predominantly on banana slugs (*Ariolimax californicus*) **(Figure 52.23)**. Inland populations feed on frogs, leeches, and fish, but not banana slugs. In fact, banana slugs are rare or absent in the inland habitats.

When researchers offered banana slugs to snakes collected from each wild population, most coastal snakes readily ate them, whereas inland snakes tended to refuse. To what extent does genetic variation among snake species contribute to a fondness for banana slugs? To answer this question, researchers collected pregnant snakes from the wild coastal and inland populations and then housed these females in separate cages in the laboratory. While the offspring were still very young, they were each offered a small piece of banana slug on ten successive days. More than 60% of the young snakes from coastal mothers ate banana slugs on eight or more of the ten days. In contrast, fewer than 20% of the young snakes from inland mothers ate a piece of banana slug even once. Perhaps not surprisingly, banana slugs thus appear to be a genetically acquired taste.

How did a genetically determined difference in feeding preference come to match the snakes' habitats so well? It turns out that the coastal and inland populations also vary with respect to their ability to recognize and respond to odor molecules produced by banana slugs. Researchers hypothesize that when inland snakes colonized coastal habitats more than 10,000 years ago, some of them could recognize banana slugs by scent. Because these snakes took advantage of this food source, they had higher fitness than snakes in the population that ignored the slugs. Over hundreds or thousands of generations, the capacity to recognize the slugs as prey increased in frequency in the coastal population. The marked variation in behavior observed today between the coastal and inland populations may be evidence of this past evolutionary change.

Case Study: *Variation in Migratory Patterns*

Another species suited to the study of behavioral variation is the blackcap (*Sylvia atricapilla*), a small migratory warbler. Blackcaps that breed in Germany generally migrate southwest to Spain and then south to Africa for the winter. In the 1950s, a few blackcaps began to spend their winters in Britain, and over time the population of blackcaps wintering in Britain grew to many thousands. Leg bands showed that some of these birds had migrated westward from central Germany. Was this change in the pattern of migration the outcome of natural selection? If so, the birds wintering in Britain must have a heritable difference in migratory behavior. To test this hypothesis, researchers at the Max Planck Institute for Ornithology in Radolfzell, Germany, devised a strategy to study migratory orientation in the laboratory **(Figure 52.24)**. The results demonstrated that the two patterns of migration—to the west and to the southwest—do in fact reflect genetic differences between the two populations.

The study of western European blackcaps indicated that the change in their migratory behavior occurred both recently and rapidly. Before the year 1950, there were no known westward-migrating blackcaps in Germany. By the 1990s, westward migrants made up 7–11% of the blackcap populations of Germany. Once westward migration began, it persisted and increased in frequency, perhaps due to the widespread use of winter bird feeders in Britain, as well as shorter migration distances.

Altruism

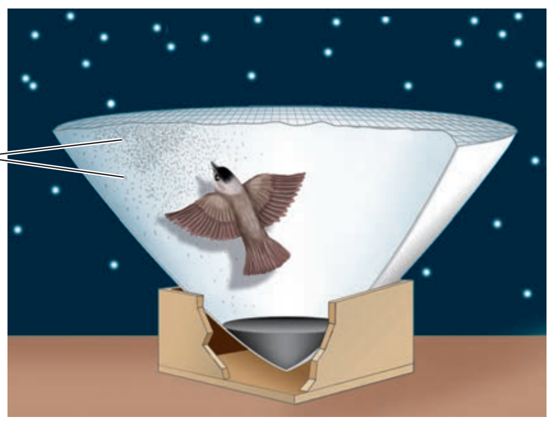
We typically assume that behaviors are selfish; that is, they benefit the individual at the expense of others, especially competitors. For example, superior foraging ability by one individual may leave less food for others. The problem comes with "unselfish" behaviors. How can such behaviors arise through natural selection? To answer this question, let's look more closely at some examples of unselfish behavior and consider how they might arise.

In discussing selflessness, we will use the term **altruism** to describe a behavior that reduces an animal's individual fitness but increases the fitness of other individuals in the population. Consider, for example, the Belding's ground squirrel, which lives in the western United States and is vulnerable to predators such as coyotes and hawks. A squirrel that sees a predator approach often gives a high-pitched alarm call that alerts unaware individuals to retreat to their burrows. Note that for the squirrel that warns others, the conspicuous alarm behavior increases the risk of being killed because it brings attention to the caller's location.

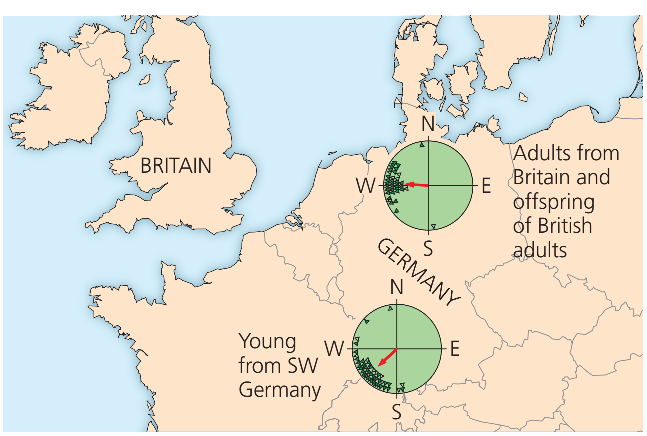
Figure 52.24

Inquiry **Are differences in migratory orientation within a species genetically determined?**

Experiment Birds known as blackcaps that live in Germany winter elsewhere. Most migrate to Spain and Africa, but a few fly to Britain, where they find food left out by city dwellers. German scientist Peter Berthold and colleagues wondered if this change had a genetic basis. To test this hypothesis, they captured blackcaps wintering in Britain and bred them in Germany in an outdoor cage. They also collected young blackcaps from nests in Germany and raised them in cages. In the autumn, the blackcaps captured in Britain and the birds raised in cages were placed in large, glass-covered funnel cages. When the funnels were lined with carbon-coated paper and placed outside at night, the birds moved around, making marks on the paper that indicated the direction in which they were trying to "migrate."



Results The wintering adult birds captured in Britain and their laboratory-raised offspring both attempted to migrate to the west. In contrast, the young birds collected from nests in southern Germany attempted to migrate to the southwest.



Conclusion The young of the British blackcaps and the young birds from Germany (the control group) were raised under similar conditions but showed very different migratory orientations, indicating that their migratory orientation has a genetic basis.

Data from P. Berthold et al., Rapid microevolution of migratory behavior in a wild bird species, *Nature* 360:668–690 (1992).

WHAT IF? ➤ *Suppose the birds had not shown a difference in orientation in these experiments. Could you conclude that the behavior was not genetically based? Explain.*

Another example of altruistic behavior occurs in honeybee societies, in which the workers are sterile. The workers themselves never reproduce, but they labor on behalf of a single fertile queen. Furthermore, the workers sting intruders, a behavior that helps defend the hive but results in the death of those workers.

Altruism is also observed in naked mole rats (*Heterocephalus glaber*), highly social rodents that live in underground chambers and tunnels in southern and northeastern Africa. The naked mole rat, which is almost hairless and nearly blind, lives in colonies of 20 to 300 individuals **(Figure 52.25)**. Each colony has only one reproducing female, the queen, who mates with one to three males, called kings. The rest of the colony consists of nonreproductive females and males who at times sacrifice themselves to protect the queen or kings from snakes or other predators that invade the colony.

Inclusive Fitness

With these examples from ground squirrels, honeybees, and mole rats in mind, let's return to the question of how altruistic behavior arises during evolution. The easiest case to consider is that of parents sacrificing for their offspring. When parents sacrifice their own well-being to produce and aid offspring, this act actually increases the fitness of the parents because it maximizes their genetic representation in the population. By this logic, altruistic behavior can be maintained by evolution even though it does not enhance the survival and reproductive success of the self-sacrificing individuals.

What about circumstances when individuals help others who are not their offspring? By considering a broader group of relatives than just parents and offspring, Biologist William Hamilton found an answer. He began by proposing that an animal could increase its genetic representation in the next generation by helping close relatives other than its

Figure 52.25 Naked mole rats, a species of colonial mammal that exhibits altruistic behavior. Pictured here is a queen nursing offspring while surrounded by other members of the colony.

own offspring. Like parents and offspring, full siblings have half their genes in common. Therefore, selection might also favor helping siblings or helping one's parents produce more siblings. This thinking led Hamilton to the idea of **inclusive fitness**, the total effect an individual has on proliferating its genes by producing its own offspring *and* by providing aid that enables other close relatives to produce offspring.

Hamilton's Rule and Kin Selection

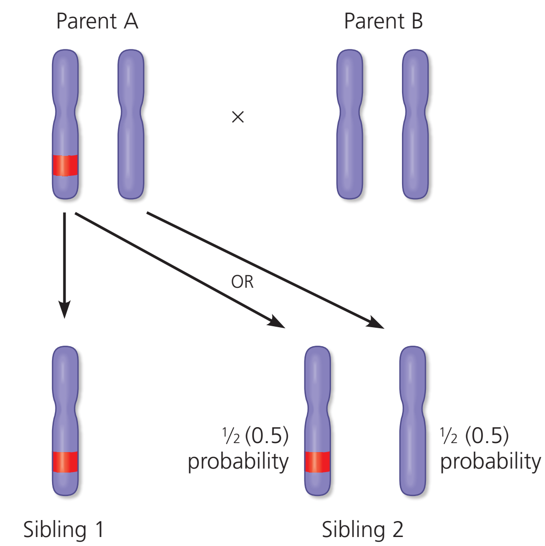
The power of Hamilton's hypothesis was that it provided a way to measure, or quantify, the effect of altruism on fitness. According to Hamilton, the three key variables in an act of altruism are the benefit to the recipient, the cost to the altruist, and the coefficient of relatedness. The benefit, B, is the average number of *extra* offspring that the recipient of an altruistic act produces. The cost, C, is how many *fewer* offspring the altruist produces. The **coefficient of relatedness**, r, equals the fraction of genes that, on average, are shared. Natural selection favors altruism when the benefit to the recipient multiplied by the coefficient of relatedness exceeds the cost to the altruist—in other words, when $rB > C$. This statement is called **Hamilton's rule**.

To better understand Hamilton's rule, let's apply it to a human population in which the average individual has two children. We'll imagine that a young man is close to drowning in heavy surf, and his sister risks her life to swim out and pull her sibling to safety. If the young man had drowned, his reproductive output would have been zero; but now, if we use the average, he can father two children. The benefit to the man is thus two offspring ($B = 2$). What cost does his sister incur? Let's say that she has a 25% chance of drowning in attempting the rescue. The cost of the altruistic act to the sister is then 0.25 times 2, the number of offspring she would be expected to have if she had stayed on shore ($C = 0.25 \times 2 = 0.5$). Finally, we note that a brother and sister share half their genes on average ($r = 0.5$). One way to see this is in terms of the separation of homologous chromosomes that occurs during meiosis of gametes (**Figure 52.26**; see also Figure 13.7).

We can use our values of B, C, and r to evaluate whether natural selection would favor the altruistic act in our imaginary scenario. For the surf rescue, $rB = 0.5 \times 2 = 1$, whereas $C = 0.5$. Because rB is greater than C, Hamilton's rule is satisfied; thus, natural selection would favor this altruistic act.

Averaging over many individuals and generations, any particular gene in a sister faced with the situation described will be passed on to more offspring if she risks the rescue than if she does not. Among the genes propagated in this way may be some that contribute to altruistic behavior. Natural selection that thus favors altruism by enhancing the reproductive success of relatives is called **kin selection**.

▼ Figure 52.26 The coefficient of relatedness between siblings. The red band indicates a particular allele (version of a gene) present on one chromosome, but not its homolog, in parent A. Sibling 1 has inherited the allele from parent A. There is a probability of ½ that sibling 2 will also inherit this allele from parent A. Any allele present on one chromosome of either parent will behave similarly. The coefficient of relatedness between the two siblings is thus ½, or 0.5.

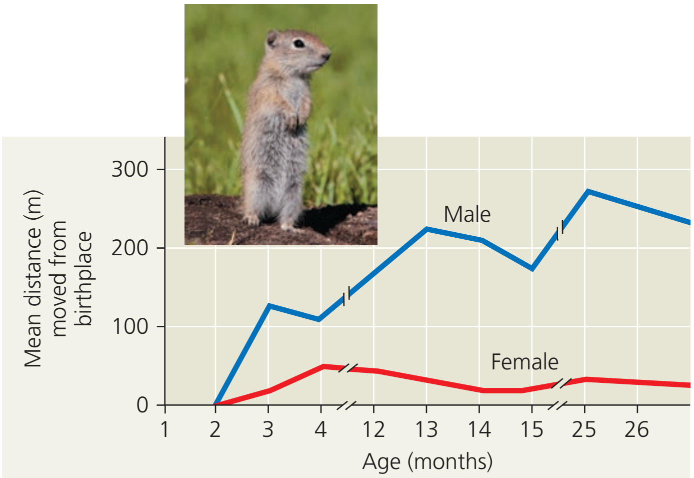


WHAT IF? ➤ *The coefficient of relatedness of an individual to a full (nontwin) sibling or to either parent is the same: 0.5. Does this value also hold true in cases of polyandry and polygyny?*

Kin selection weakens with hereditary distance. Siblings have an r of 0.5, but between an aunt and her niece, $r = 0.25$ (¼), and between first cousins, $r = 0.125$ (⅛). Notice that as the degree of relatedness decreases, the rB term in the Hamilton inequality also decreases. Would natural selection favor rescuing a cousin? Not unless the surf were less treacherous. For the original conditions, $rB = 0.125 \times 2 = 0.25$, which is only half the value of C (0.5). British geneticist J. B. S. Haldane appears to have anticipated these ideas when he jokingly stated that he would not lay down his life for one brother, but would do so for two brothers or eight cousins.

If kin selection explains altruism, then the examples of unselfish behavior we observe among diverse animal species should involve close relatives. This is apparently the case, but often in complex ways. Like most mammals, female Belding's ground squirrels settle close to their site of birth, whereas males settle at distant sites **(Figure 52.27)**. Since nearly all alarm calls are given by females, they are most likely aiding close relatives. In the case of worker bees, who are all sterile, anything they do to help the entire hive benefits the only permanent member who is reproductively active—the queen, who is their mother.

Figure 52.27 Kin selection and altruism in Belding's ground squirrels. This graph helps explain the male-female difference in altruistic behavior of ground squirrels. Once weaned (pups are nursed for about one month), females are more likely than males to live near close relatives. Alarm calls that warn these relatives increase the inclusive fitness of the female altruist.



In the case of naked mole rats, DNA analyses have shown that all the individuals in a colony are closely related. Genetically, the queen appears to be a sibling, daughter, or mother of the kings, and the nonreproductive mole rats are the queen's direct descendants or her siblings. Therefore, when a nonreproductive individual enhances a queen's or king's chances of reproducing, the altruist increases the chance that some genes identical to its own will be passed to the next generation.

Reciprocal Altruism

Some animals occasionally behave altruistically toward others who are not relatives. A baboon may help an unrelated companion in a fight, or a wolf may offer food to another wolf even though they share no kinship. Such behavior can be adaptive if the aided individual returns the favor in the future. This sort of exchange of aid, called **reciprocal altruism**, is commonly invoked to explain altruism that occurs between unrelated humans. Reciprocal altruism is rare in other animals; it is limited largely to species (such as chimpanzees) with social groups stable enough that individuals have many chances to exchange aid. It is generally thought to occur when individuals are likely to meet again and when there would be negative consequences associated with not returning favors to individuals who had been helpful in the past, a pattern of behavior that behavioral ecologists refer to as "cheating."

Since cheating may benefit the cheater substantially, how could reciprocal altruism evolve? Game theory provides a possible answer in the form of a behavioral strategy called *tit for tat*. In the tit-for-tat strategy, an individual treats another in the same way it was treated the last time they met. Individuals adopting this behavior are always altruistic, or cooperative, on the first encounter with another individual and will remain so as long as their altruism is reciprocated. When their cooperation is not reciprocated, however, individuals employing tit for tat will retaliate immediately but return to cooperative behavior as soon as the other individual becomes cooperative. The tit-for-tat strategy has been used to explain the few apparently reciprocal altruistic interactions observed in animals—ranging from blood sharing between nonrelated vampire bats to social grooming in primates.

Evolution and Human Culture

As animals, humans behave (and, sometimes, misbehave). Just as humans vary extensively in anatomical features, we display substantial variations in behavior. Environment intervenes in the path from genotype to phenotype for physical traits, but does so much more profoundly for behavioral traits. Furthermore, as a consequence of our marked capacity for learning, humans are probably more able than any other animal to acquire new behaviors and skills **(Figure 52.28)**.

Some human activities have a less easily defined function in survival and reproduction than do, for example, foraging or courtship. One of these activities is play, which is sometimes defined as behavior that appears purposeless. We recognize play in children and what we think is play in the young of other vertebrates. Behavioral biologists describe "object play," such as chimpanzees playing with leaves, "locomotor play," such as the acrobatics of an antelope, and "social play," such as the interactions and antics of lion cubs. These categories, however, do little to inform us about the function of play. One idea is that, rather than generating specific skills or experience, play serves as preparation for unexpected events and for circumstances that cannot be controlled.

Human behavior and culture are related to evolutionary theory in the discipline of **sociobiology**. The main premise of sociobiology is that certain behavioral characteristics exist because they are expressions of genes that have been perpetuated by

Figure 52.28 Learning a new behavior.

natural selection. In his seminal 1975 book *Sociobiology: The New Synthesis,* E. O. Wilson speculated about the evolutionary basis of certain kinds of social behavior. By including a few examples from human culture, he sparked a debate that continues today.

Over our recent evolutionary history, we have built up structured societies with governments, laws, cultural values, and religions that define what is acceptable behavior and what is not, even when unacceptable behavior might enhance an individual's Darwinian fitness. Perhaps it is our social and cultural institutions that make us distinct and that provide those qualities that at times make less apparent the continuum between humans and other animals. One such quality, our considerable capacity for reciprocal altruism, will be essential as we tackle current challenges, including global climate change, in which individual and collective interests often appear to be in conflict.

MB **Interview with E. O. Wilson: Pioneering the field of sociobiology**

CONCEPT CHECK 52.4

1. Explain why geographic variation in garter snake prey choice might indicate that the behavior evolved by natural selection.
2. Suppose an individual organism aids the survival and reproductive success of the offspring of its sibling. How might this behavior result in indirect selection for certain genes carried by that individual?
3. **WHAT IF? ➤** Suppose you applied Hamilton's logic to a situation in which one individual is past reproductive age. Could there still be selection for an altruistic act?

For suggested answers, see Appendix A.

52 Chapter Review

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SUMMARY OF KEY CONCEPTS

CONCEPT 52.1

Discrete sensory inputs can stimulate both simple and complex behaviors *(pp. 1224–1227)*

VOCAB SELF-QUIZ goo.gl/Rn5Uax

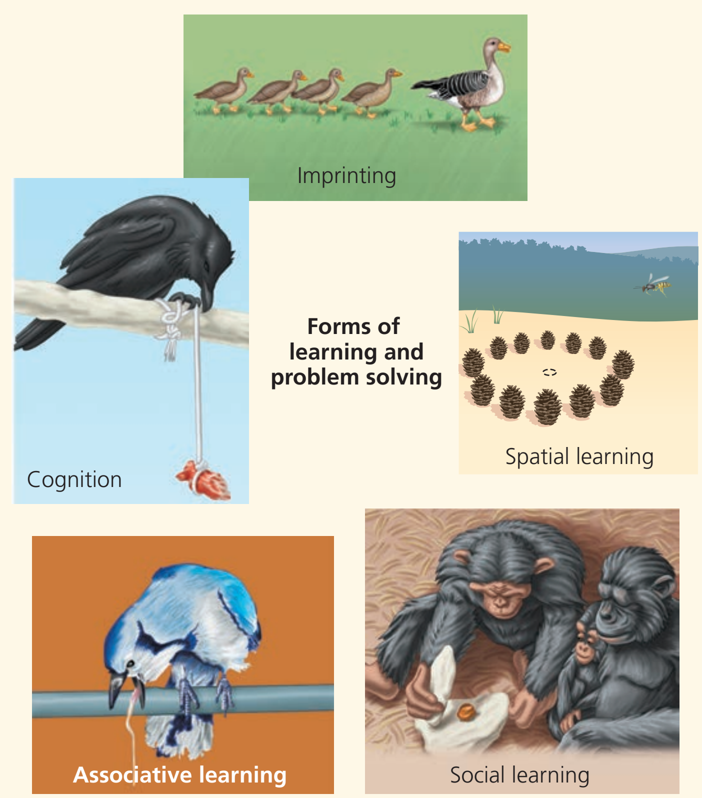
- **Behavior** is the sum of an animal's responses to external and internal stimuli. In behavior studies, proximate, or "how," questions focus on the stimuli that trigger a behavior and on genetic, physiological, and anatomical mechanisms underlying a behavioral act. Ultimate, or "why," questions address evolutionary significance.
- A **fixed action pattern** is a largely invariant behavior triggered by a simple cue known as a **sign stimulus**. **Migratory** movements involve navigation, which can be based on orientation relative to the sun, the stars, or Earth's magnetic field. Animal behavior is often synchronized to the circadian cycle of light and dark in the environment or to cues that cycle over the seasons.
- The transmission and reception of **signals** constitute animal **communication**. Animals use visual, auditory, chemical, and tactile signals. Chemical substances called **pheromones** transmit species-specific information between members of a species in behaviors ranging from foraging to courtship.

? *How is migration based on circannual rhythms poorly suited for adaptation to global climate change?*

CONCEPT 52.2

Learning establishes specific links between experience and behavior *(pp. 1227–1232)*

- **Cross-fostering studies** can be used to measure the influence of social environment and experience on behavior.
- **Learning**, the modification of behavior as a result of experience, can take many forms:



? *How do imprinting in geese and song development in sparrows differ with regard to the resulting behavior?*

CONCEPT 52.3

Selection for individual survival and reproductive success can explain diverse behaviors *(pp. 1232–1238)*

- Controlled experiments in the laboratory can give rise to interpretable evolutionary changes in behavior.
- An **optimal foraging model** is based on the idea that natural selection should favor **foraging** behavior that minimizes the costs of foraging and maximizes the benefits.
- Sexual dimorphism correlates with the types of mating relationship, which include **monogamous** and **polygamous** mating systems. Variations in mating system and mode of fertilization affect certainty of paternity, which in turn has a significant influence on mating behavior and parental care.
- **Game theory** provides a way of thinking about evolution in situations where the fitness of a particular behavioral phenotype is influenced by other behavioral phenotypes in the population.

? *In some spider species, the female eats the male immediately after copulation. How might you explain this behavior from an evolutionary perspective?*

CONCEPT 52.4

Genetic analyses and the concept of inclusive fitness provide a basis for studying the evolution of behavior *(pp. 1238–1244)*

- Genetic studies in insects have revealed the existence of master regulatory genes that control complex behaviors. Within the underlying hierarchy, multiple genes influence specific behaviors, such as a courtship song. Research on voles illustrates how variation in a single gene can determine differences in complex behaviors.
- Behavioral variation within a species that corresponds to environmental variation may be evidence of past evolution.
- **Altruism** can be explained by the concept of **inclusive fitness**, the effect an individual has on proliferating its genes by producing its own offspring *and* by providing aid that enables close relatives to reproduce. The **coefficient of relatedness** and **Hamilton's rule** provide a way of measuring the strength of the selective forces favoring altruism against the potential cost of the "selfless" behavior. **Kin selection** favors altruistic behavior by enhancing the reproductive success of relatives.

? *What insight about the genetic basis of behavior emerges from studying the effects of courtship mutations in fruit flies and of pair-bonding in voles?*

TEST YOUR UNDERSTANDING

Multiple-choice Self-Quiz questions 1–6 can be found in the Study Area in MasteringBiology.

7. DRAW IT You are considering two optimal foraging models for the behavior of a mussel-feeding shorebird, the oystercatcher. In model A, the energetic reward increases solely with mussel size. In model B, you take into consideration that larger mussels are more difficult to open. Draw a graph of reward (energy benefit on a scale of 0–10) versus mussel length (scale of 0–70 mm) for each model. Assume that mussels under 10 mm provide no benefit and are ignored by the birds. Also assume that mussels start becoming difficult to open when they reach 40 mm in length and impossible to open when 70 mm long. Considering the graphs you have drawn, indicate what observations and measurements you would want to make in this shorebird's habitat to help determine which model is more accurate.

PRACTICE TEST
goo.gl/iAsVgL

8. EVOLUTION CONNECTION We often explain our behavior in terms of subjective feelings, motives, or reasons, but evolutionary explanations are based on reproductive fitness. Discuss the relationship between the two kinds of explanation. For instance, is an explanation for behavior such as "falling in love" incompatible with an evolutionary explanation?

9. SCIENTIFIC INQUIRY Scientists studying scrub jays found that "helpers" often assist mated pairs of birds by gathering food for their offspring.

(A) Propose a hypothesis to explain what advantage there might be for the helpers to engage in this behavior instead of seeking their own territories and mates.

(B) Explain how you would test your hypothesis. If it is correct, what results would you expect your tests to yield?

10. SCIENCE, TECHNOLOGY, AND SOCIETY Researchers are very interested in studying identical twins separated at birth and raised apart. So far, the data reveal that such twins frequently have similar personalities, mannerisms, habits, and interests. What general question do you think researchers hope to answer by studying such twins? Why do identical twins make good subjects for this research? What are the potential pitfalls of this research? What abuses might occur if the studies are not evaluated critically? Explain your thinking.

11. WRITE ABOUT A THEME: INFORMATION Learning is defined as a change in behavior as a result of experience. In a short essay (100–150 words), describe how heritable information contributes to the acquisition of learning, using some examples from imprinting and associative learning.

12. SYNTHESIZE YOUR KNOWLEDGE

Acorn woodpeckers (*Melanerpes formicivorus*) stash acorns in storage holes they drill in trees. When these woodpeckers breed, the offspring from previous years often help with parental duties. Activities of these nonbreeding helpers include incubating eggs and defending stashed acorns. Propose some questions about the proximate and ultimate causation of these behaviors that a behavioral biologist could ask.

For selected answers, see Appendix A.

For additional practice questions, check out the **Dynamic Study Modules** in MasteringBiology. You can use them to study on your smartphone, tablet, or computer anytime, anywhere!

Populations and Life History Traits

53

Figure 53.1 What causes the survival of turtle hatchlings to vary from year to year?

KEY CONCEPTS

53.1 Biotic and abiotic factors affect population density, dispersion, and demographics

53.2 The exponential model describes population growth in an idealized, unlimited environment

53.3 The logistic model describes how a population grows more slowly as it nears its carrying capacity

53.4 Life history traits are products of natural selection

53.5 Density-dependent factors regulate population growth

53.6 The human population is no longer growing exponentially but is still increasing rapidly

Turtle Tracks

Each year along the Florida coast, thousands of loggerhead turtle (*Caretta curette*) hatchlings break out of their eggshells, dig up through the sand, and crawl down the beach for their first journey to the ocean **(Figure 53.1)**. How many turtles will successfully hatch, navigate the perils of the beach, and reach the water? This number can vary widely from year to year. The number of females returning to lay eggs fluctuates, as does the percentage of eggs eaten by raccoons and other predators. Of the hatchlings that do manage to dig to the surface, some become disoriented by lights and wander away from the ocean or are eaten by birds or crabs before they reach the water.

Investigating how factors such as predators and light affect the size of a loggerhead turtle population is an example of **population ecology**, the study of populations in relation to their environment. Population ecology explores how biotic and abiotic factors influence the abundance, dispersion, and age structure of populations.

Recall that populations evolve as natural selection acts on heritable variations among individuals, changing the frequencies of alleles and traits over time (see Concept 23.3). Evolution remains a central theme as we now view populations in the context of ecology.

When you see this blue icon, log in to **MasteringBiology** and go to the Study Area for digital resources.

MB **Get Ready for This Chapter**

In this chapter, we will first examine some of the basic characteristics of populations. We will then explore the tools and models ecologists use to analyze populations and the factors that can determine the abundance of organisms. Finally, we will apply these concepts as we examine recent trends in the size and makeup of the human population.

CONCEPT 53.1

Biotic and abiotic factors affect population density, dispersion, and demographics

A **population** is a group of individuals of a single species living in the same general area. Members of a population rely on the same resources, are influenced by similar environmental factors, and are likely to interact and breed with one another.

Populations are often described by their boundaries and size (the number of individuals living within those boundaries). Ecologists usually begin investigating a population by defining boundaries appropriate to the organism under study and to the questions being asked. A population's boundaries may be natural ones, as in the case of an island or a lake, or they may be arbitrarily defined by an investigator—for example, a specific county in Minnesota for a study of oak trees.

Density and Dispersion

The **density** of a population is the number of individuals per unit area or volume: the number of oak trees per square kilometer in the Minnesota county or the number of *Escherichia coli* bacteria per milliliter in a test tube. **Dispersion** is the pattern of spacing among individuals within the boundaries of the population.

Density: A Dynamic Perspective

In some cases, population size and density can be determined by counting all individuals within the boundaries of the population. We could count all the sea stars in a tide pool, for instance. Large mammals that live in herds, such as elephants, can sometimes be counted accurately from airplanes.

In most cases, however, it is impractical or impossible to count all individuals in a population. Instead, ecologists use various sampling techniques to estimate densities and total population sizes. They might count the number of oak trees in several randomly located 100 × 100 m plots, calculate the average density in the plots, and then extend the estimate to the population size in the entire area. Such estimates are most accurate when there are many sample plots and when the habitat is fairly homogeneous. In other cases, instead of counting single organisms, ecologists estimate density from an indicator of population size, such as the number of nests, burrows, tracks, or fecal droppings. Ecologists also use the **mark-recapture method** to estimate the size of wildlife populations **(Figure 53.2)**.

Figure 53.2

Research Method Determining Population Size Using the Mark-Recapture Method

Application Ecologists cannot count all the individuals in a population if the organisms move too quickly or are hidden from view. In such cases, researchers often use the mark-recapture method to estimate population size. Andrew Gormley and his colleagues at the University of Otago applied this method to a population of endangered Hector's dolphins (*Cephalorhynchus hectori*) near Banks Peninsula, in New Zealand.

▲ **Hector's dolphins**

Technique Scientists typically begin by capturing a random sample of individuals in a population. They tag, or "mark," each individual and then release it. With some species, researchers can identify individuals without physically capturing them. For example, Gormley and colleagues identified 180 Hector's dolphins by photographing their distinctive dorsal fins from boats.

After waiting for the marked or otherwise identified individuals to mix back into the population, usually a few days or weeks, scientists capture or sample a second set of individuals. At Banks Peninsula, Gormley's team encountered 44 dolphins in their second sampling, 7 of which they had photographed before. The number of marked animals captured in the second sampling (x) divided by the total number of animals captured in the second sampling (n) should equal the number of individuals marked and released in the first sampling (s) divided by the estimated population size (N):

$$\frac{x}{n} = \frac{s}{N} \quad \text{or, solving for population size,} \quad N = \frac{sn}{x}$$

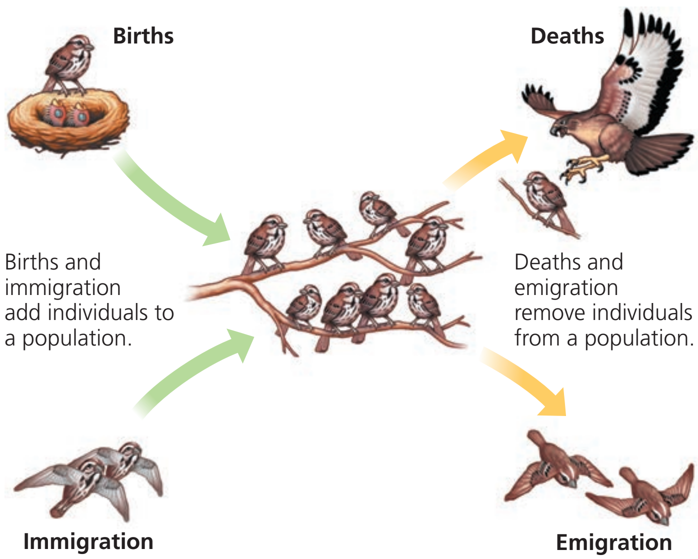
The method assumes that marked and unmarked individuals have the same probability of being captured or sampled, that the marked organisms have mixed completely back into the population, and that no individuals are born, die, immigrate, or emigrate during the resampling interval.

Results Based on these initial data, the estimated population size of Hector's dolphins at Banks Peninsula would be 180 × 44/7 = 1,131 individuals. Repeated sampling by Gormley and colleagues suggested a true population size closer to 1,100.

Data from A. M. Gormley et al., Capture-recapture estimates of Hector's dolphin abundance at Banks Peninsula, New Zealand, *Marine Mammal Science* 21:204–216 (2005).

INTERPRET THE DATA ➤ *Suppose that none of the 44 dolphins encountered in the second sampling had been photographed before. Would you be able to solve the equation for N? What might you conclude about population size in this case?*

Figure 53.3 Population dynamics.



Density is not a static property but changes as individuals are added to or removed from a population **(Figure 53.3)**. Additions occur through birth (which we define here to include all forms of reproduction) and **immigration**, the influx of new individuals from other areas. The factors that remove individuals from a population are death (mortality) and **emigration**, the movement of individuals out of a population and into other locations.

While birth and death rates influence the density of all populations, immigration and emigration also alter the density of many populations. Studies of a population of Hector's dolphins (see Figure 53.2) in New Zealand showed that immigration was approximately 15% of the total population size each year. Emigration of dolphins in the area tends to occur during the winter season when the animals move farther from shore. Both immigration and emigration represent important biological exchanges among populations through time.

Animation: Techniques for Estimating Population Density and Size

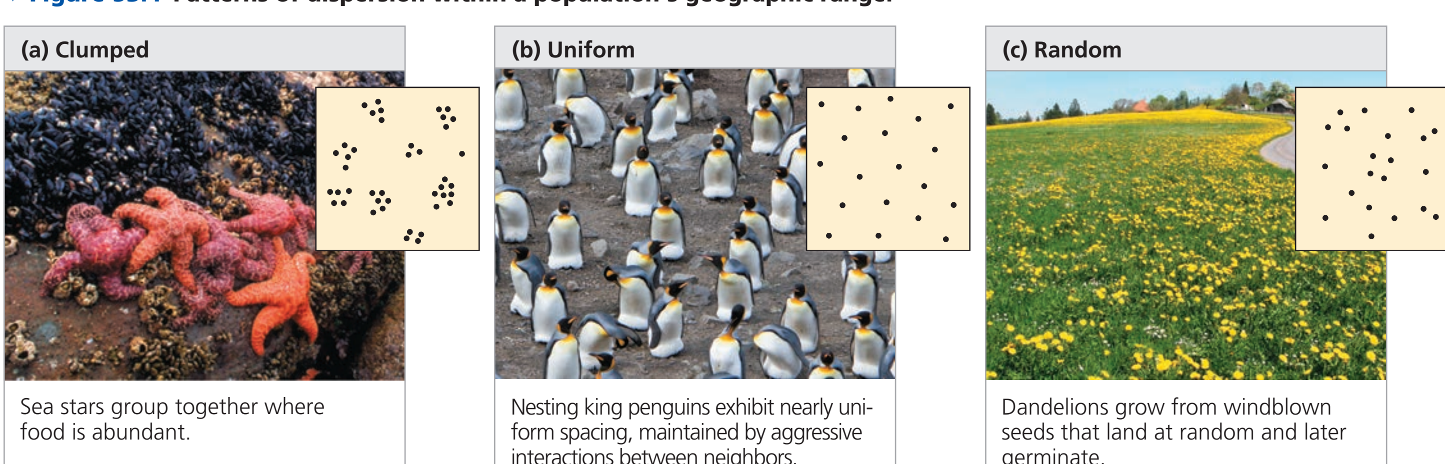
Patterns of Dispersion

Within a population's geographic range, local densities may differ substantially, creating contrasting patterns of dispersion. Differences in local density are among the most important characteristics for a population ecologist to study, since they provide insight into the biotic and abiotic factors that affect individuals in the population.

The most common pattern of dispersion is *clumped*, in which individuals are aggregated in patches. Plants and fungi are often clumped where soil conditions and other environmental factors favor germination and growth. Mushrooms, for instance, may be clumped within and on top of a rotting log. Insects and salamanders may be clumped under the same log because of the higher humidity there. Clumping of animals may also be associated with mating behavior. Sea stars group together in tide pools, where food is readily available and where they can breed successfully **(Figure 53.4a)**. The aggregation of individuals into groups may also increase the effectiveness of predation or defense; for example, a wolf pack is more likely than a single wolf to subdue a moose, and a flock of birds is more likely than a single bird to warn of a potential attack.

A *uniform*, or evenly spaced, pattern of dispersion may result from direct interactions between individuals in the population. Some plants secrete chemicals that inhibit the germination and growth of nearby individuals that could compete for resources. Animals often exhibit uniform dispersion as a result of antagonistic social interactions, such

Figure 53.4 Patterns of dispersion within a population's geographic range.



(a) Sea stars group together where food is abundant.

(b) Nesting king penguins exhibit nearly uniform spacing, maintained by aggressive interactions between neighbors.

(c) Dandelions grow from windblown seeds that land at random and later germinate.

? *Patterns of dispersion can depend on scale. How might the penguin dispersion look from an airplane flying over the ocean?*

as **territoriality**—the defense of a bounded physical space against encroachment by other individuals **(Figure 53.4b)**.

In *random* dispersion (unpredictable spacing), the position of each individual in a population is independent of other individuals. This pattern occurs in the absence of strong attractions or repulsions among individuals or where key physical or chemical factors are relatively constant across the study area. Plants established by windblown seeds, such as dandelions, may be randomly distributed in a fairly uniform habitat **(Figure 53.4c)**.

Demographics

The biotic and abiotic factors that influence population density and dispersion patterns also influence other characteristics of populations, including birth, death, and migration rates. **Demography** is the study of these vital statistics of populations and how they change over time. A useful way to summarize demographic information for a population is to make a life table.

Life Tables

A **life table** summarizes the survival and reproductive rates of individuals in specific age-groups within a population. To construct a life table, researchers often follow the fate of a **cohort**, a group of individuals of the same age, from birth until all of the individuals are dead. Building the life table requires determining the proportion of the cohort that survives from one age-group to the next. It is also necessary to keep track of the number of offspring produced by females in each age-group.

Demographers who study sexually reproducing species often ignore the males and concentrate on the females in a population because only females produce offspring. Using this approach, a population is viewed in terms of females giving rise to new females. **Table 53.1** is a life table built in this way for female Belding's ground squirrels (*Urocitellus beldingi*) from a population located in the Sierra Nevada mountains of California. Next, we'll take a closer look at some of the data presented in a life table.

Survivorship Curves

The survival rate data in a life table can be represented graphically as a **survivorship curve**, a plot of the proportion or numbers in a cohort still alive at each age. As an example, let's use the data for female Belding's ground squirrels in Table 53.1 to draw a survivorship curve. Often, a survivorship curve begins with a cohort of a convenient size—say, 1,000 individuals. To obtain the other points in the curve for the ground squirrel population, we multiply the proportion alive at the start of each year (the third column of Table 53.1) by 1,000 (the hypothetical beginning cohort).

Table 53.1 Life Table for Female Belding's Ground Squirrels (Tioga Pass, in the Sierra Nevada of California)

Age (years)	Number Alive at Start of Year	Proportion Alive at Start of Year*	Death Rate†	Average Number of Female Offspring per Female
0–1	653	1.000	0.614	0.00
1–2	252	0.386	0.496	1.07
2–3	127	0.197	0.472	1.87
3–4	67	0.106	0.478	2.21
4–5	35	0.054	0.457	2.59
5–6	19	0.029	0.526	2.08
6–7	9	0.014	0.444	1.70
7–8	5	0.008	0.200	1.93
8–9	4	0.006	0.750	1.93
9–10	1	0.002	1.00	1.58

▲ Researchers working with a Belding's ground squirrel

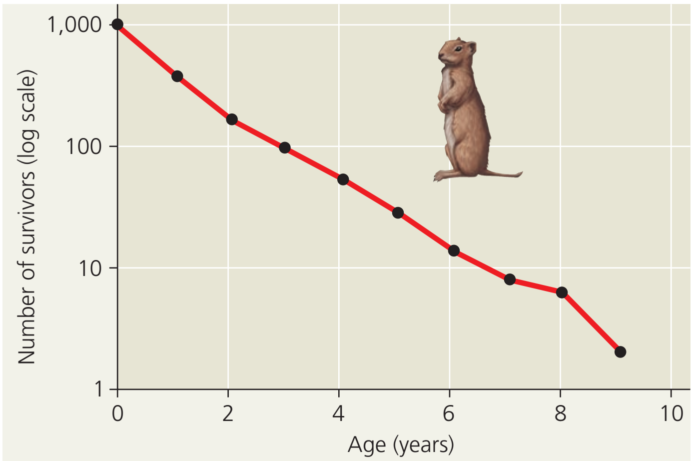
Data from P. W. Sherman and M. L. Morton, Demography of Belding's ground squirrel, *Ecology* 65: 1617–1628 (1984).

*Indicates the proportion of the original cohort of 653 individuals that are still alive at the start of a time interval.

†The death rate is the proportion of individuals alive at the start of a time interval that die during that time interval.

Table Walkthrough

Figure 53.5 Survivorship curve for female Belding's ground squirrels. The logarithmic scale on the *y*-axis allows the number of survivors to be visible across the entire range (2–1,000 individuals) on the graph.

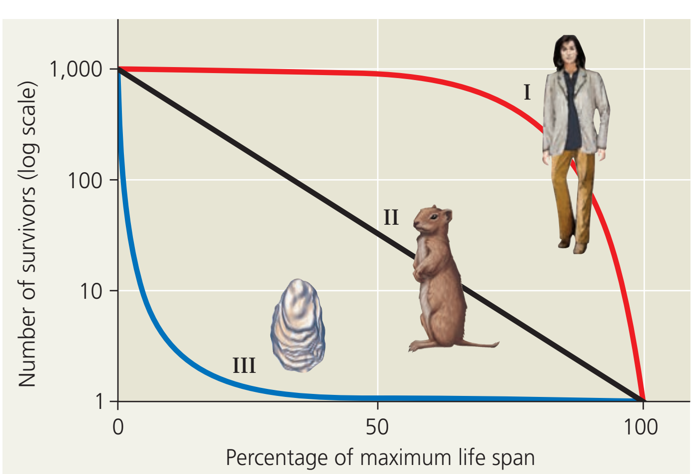


What percentage of females survive to be three years old?

The result is the number alive at the start of each year. Plotting these numbers versus age for female Belding's ground squirrels yields **Figure 53.5**. The approximately straight line of the plot indicates a relatively constant rate of death.

Figure 53.5 represents just one of many patterns of survivorship exhibited by natural populations. Though diverse, survivorship curves can be classified into three general types **(Figure 53.6)**. A Type I curve is flat at the start, reflecting low death rates during early and middle life, and then drops steeply as death rates increase among older age-groups. Many large mammals, including humans and elephants, that produce few offspring but provide them with good care exhibit this kind of curve.

Figure 53.6 Idealized survivorship curves: Types I, II, and III. The *y*-axis is logarithmic and the *x*-axis is on a relative scale so that species with widely varying life spans can be presented together on the same graph.



Animation: Investigating the Survivorship Curve of Oysters

In contrast, a Type III curve drops sharply at the start, reflecting very high death rates for the young, but flattens out as death rates decline for those few individuals that survive the early period of die-off. This type of curve is usually associated with organisms that produce very large numbers of offspring but provide little or no care, such as long-lived plants, many fishes, and most marine invertebrates. An oyster, for example, may release millions of eggs, but most larvae hatched from fertilized eggs die from predation or other causes. Those few offspring that survive long enough to attach to a suitable substrate and begin growing a hard shell tend to survive for a relatively long time. Type II curves are intermediate, with a constant death rate over the organism's life span. This kind of survivorship occurs in Belding's ground squirrels and some other rodents, many invertebrates, lizards, and annual plants.

Many species fall somewhere between these basic types of survivorship or show more complex patterns. In birds, mortality is often high among the youngest individuals (as in a Type III curve) but fairly constant among adults (as in a Type II curve). Some invertebrates, such as crabs, may show a "stair-stepped" curve, with brief periods of increased mortality during molts, followed by periods of lower mortality when their protective exoskeleton is hard.

In populations not experiencing large amounts of immigration or emigration, survivorship is one of the two key factors determining changes in population size. The other key factor that affects how population size changes over time is reproductive rate.

Reproductive Rates

As mentioned above, demographers often ignore the males and concentrate on the females in a population because only females produce offspring. Therefore, demographers view populations in terms of females giving rise to new females. The simplest way to describe the reproductive pattern of a population is to identify how reproductive output varies with the number of breeding females and their ages.

How do ecologists estimate the number of breeding females in a population? Possible approaches include direct counts and the mark-recapture method (see Figure 53.2). Increasingly, ecologists also use molecular tools. For example, scientists working in the state of Georgia collected skin samples from 198 female loggerhead turtles between 2005 and 2009. From these samples, they amplified nuclear short tandem repeats at 14 loci using the polymerase chain reaction (PCR) and produced a genetic profile for each female **(Figure 53.7)**. They then extracted DNA from an eggshell from each turtle nest on the beaches they studied and, using their database of genetic

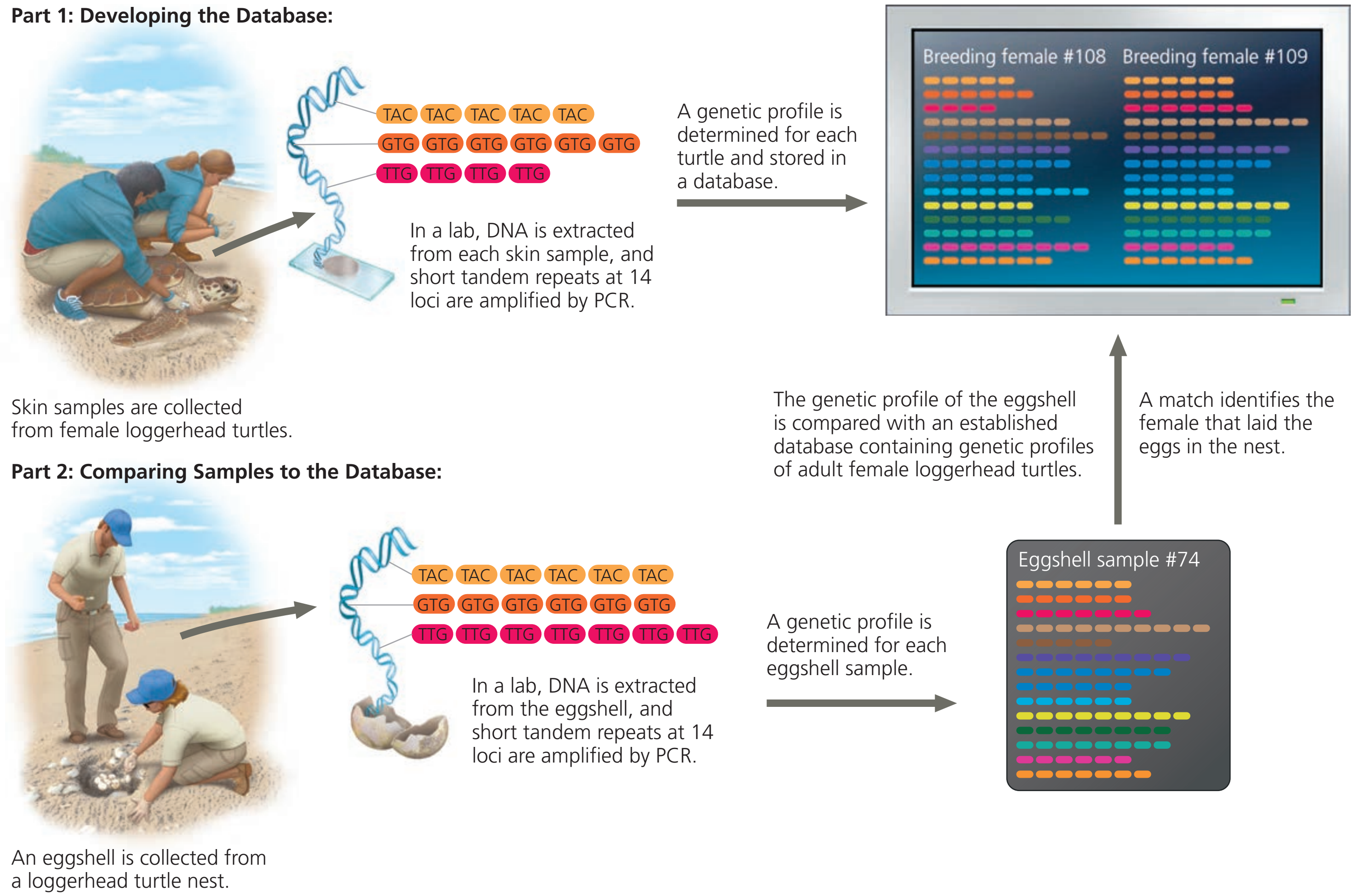


Figure 53.7 Using genetic profiles from loggerhead turtle eggshells to identify which female laid the eggs.

VISUAL SKILLS ➤ *Use the profiles displayed in the figure to determine which breeding female laid the eggs in the nest from which eggshell sample #74 was taken.*

profiles, matched the nest to a specific female. This approach allowed them to determine how many of the 198 females were breeding—and how many offspring each female produced—without having to disturb the females during egg laying.

Reproductive output for sexual organisms such as birds and mammals is typically measured as the average number of female offspring produced by the females in a given age-group. For some organisms, the number of offspring for each female can be counted directly; alternatively, molecular methods can be used (see Figure 53.7). Researchers directly counted the offspring of the Belding's ground squirrels, which begin to reproduce at age 1 year. The squirrels' reproductive output rises to a peak at 4–5 years of age and then gradually falls off in older females (see Table 53.1).

Age-specific reproductive rates vary considerably by species. Squirrels, for example, have a litter of two to six young once a year for less than a decade, whereas oak trees drop thousands of acorns each year for tens or hundreds of years. Mussels and other invertebrates may release millions of eggs and sperm in a spawning cycle. However, a high reproductive rate will not lead to rapid population growth unless conditions are near ideal for the growth and survival of offspring, as you'll learn in the next section.

CONCEPT CHECK 53.1

1. **DRAW IT** ➤ Each female of a particular fish species produces millions of eggs per year. Draw and label the most likely survivorship curve for this species, and explain your choice.
2. **WHAT IF?** ➤ Imagine that you are constructing a life table like Table 53.1 for a different population of Belding's ground squirrels. If 485 individuals are alive at the start of year 0–1 and 218 are still alive at the start of year 1–2, what is the proportion alive at the start of each of these years (see column 3 in Table 53.1)?
3. **MAKE CONNECTIONS** ➤ A male stickleback fish attacks other males that invade its nesting territory (see Figure 52.2). Predict the likely pattern of dispersion for male sticklebacks, and explain your reasoning.

For suggested answers, see Appendix A.

CONCEPT 53.2

The exponential model describes population growth in an idealized, unlimited environment

Populations of all species have the potential to expand greatly when resources are abundant. To appreciate the potential for population increase, consider a bacterium that can reproduce by fission every 20 minutes under ideal laboratory conditions. There would be two bacteria after 20 minutes, four after 40 minutes, and eight after 60 minutes. If reproduction continued at this rate for a day and a half without mortality, there would be enough bacteria to form a layer 30 cm deep over the entire globe! But unlimited growth does not occur for long in nature, where individuals typically have access to fewer resources as a population grows. Nonetheless, ecologists study population growth in ideal, unlimited environments to reveal how fast populations are capable of growing and the conditions under which rapid growth might actually occur.

Changes in Population Size

Imagine a population consisting of a few individuals living in an ideal, unlimited environment. Under these conditions, there are no external limits on the abilities of individuals to harvest energy, grow, and reproduce. The population will increase in size with every birth and with the immigration of individuals from other populations, and it will decrease in size with every death and with the emigration of individuals out of the population. We can thus define a change in population size during a fixed time interval with the following verbal equation:

$$\text{Change in population size} = \text{Births} + \text{Immigrants entering population} - \text{Deaths} - \text{Emigrants leaving population}$$

For now, we will simplify our discussion by ignoring the effects of immigration and emigration.

We can use mathematical notation to express this simplified relationship more concisely. If N represents population size and t represents time, then ΔN is the change in population size and Δt is the time interval (appropriate to the life span or generation time of the species) over which we are evaluating population growth. (The Greek letter delta, Δ, indicates change, such as change in time.) Using B for the number of births in the population during the time interval and D for the number of deaths, we can rewrite the verbal equation:

$$\frac{\Delta N}{\Delta t} = B - D$$

Typically, population ecologists are most interested in changes in population size—the number of individuals that are added to or subtracted from a population during a given time interval, symbolized by R. Here, R represents the *difference* between the number of births (B) and the number of deaths (D) that occur in the time interval. Thus, $R = B - D$, and we can simplify our equation by writing:

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

Next, we can convert our model to one in which changes in population size are expressed on a per individual (per capita) basis. The *per capita* change in population size ($r_{\Delta t}$) represents the contribution that an average member of the population makes to the number of individuals added to or subtracted from the population during the time interval Δt. If, for example, a population of 1,000 individuals increases by 16 individuals per year, then on a per capita basis, the annual change in population size is 16/1,000, or 0.016. If we know the annual per capita change in population size, we can use the formula $R = r_{\Delta t}N$ to calculate how many individuals will be added to (or subtracted from) a population each year. For example, if $r_{\Delta t} = 0.016$ and the population size is 500,

$$R = r_{\Delta t}N = 0.016 \times 500 = 8 \text{ per year}$$

Since the number of individuals added to or subtracted from the population (R) can be expressed on a per capita basis as $R = r_{\Delta t}N$, we can revise our population growth equation to take this into account:

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

Remember that our equation is for a specific time interval (often one year). However, many ecologists prefer to use differential calculus to express population growth as a rate of change *at each instant in time*:

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

In this case, r represents the per capita change in population size that occurs at each instant in time (whereas $r_{\Delta t}$ represented the per capita change that occurred during the time interval Δt). If you have not yet studied calculus, don't be intimidated by the last equation; it is similar to the previous one, except that the time intervals Δt are very short and are expressed in the equation as dt. In fact, as Δt becomes shorter, $r_{\Delta t}$ and r become increasingly close to one another in value.

Exponential Growth

Earlier we described a population whose members all have access to abundant food and are free to reproduce at their physiological capacity. In some cases, a population that experiences such ideal conditions increases in size by a constant proportion at each instant in time. When this occurs, the pattern of growth that results is called **exponential population growth**. The equation for exponential growth is the one presented at the end of the previous section, namely:

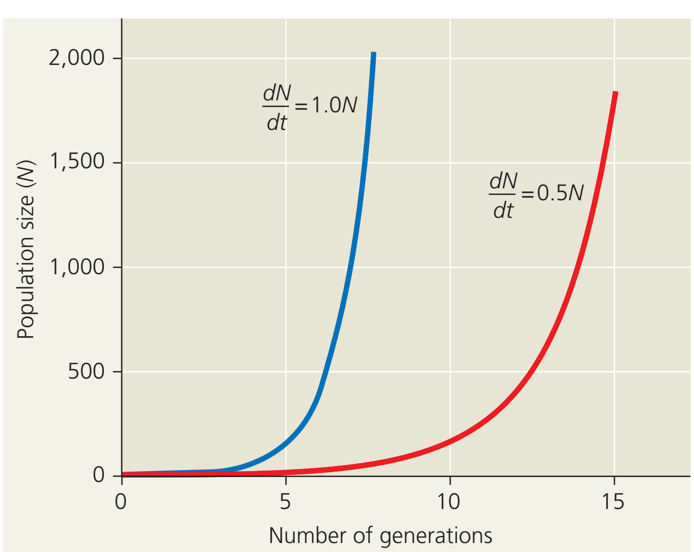
$$\frac{dN}{dt} = rN$$

In this equation, dN/dt represents the rate at which the population is increasing in size at each moment in time, akin to how a glance at the speedometer of a car reveals the speed at that instant in time. As seen in the equation, dN/dt equals the current population size, N, multiplied by a constant, r. Ecologists refer to r as the **intrinsic rate of increase**, the per capita rate at which an exponentially growing population increases in size at each instant in time.

The size of a population that is growing exponentially increases at a constant rate per individual, resulting eventually in a J-shaped growth curve when population size is plotted over time **(Figure 53.8)**. Although the per capita rate of population growth is constant (and equals r), more new individuals are added per unit of time when the population is large than when it is small; thus, the curves in Figure 53.8 get progressively steeper over time. This occurs because population growth depends on N as well as r, and hence more individuals are added to larger populations than to small ones growing at the same per capita rate. It is also clear from Figure 53.8 that a population with a higher intrinsic rate of increase ($dN/dt = 1.0N$) will grow faster than one with a lower intrinsic rate of increase ($dN/dt = 0.5N$).

The J-shaped curve of exponential growth is characteristic of some populations that are introduced into a new environment or whose numbers have been drastically reduced by a catastrophic event and are rebounding. For example, the population of elephants in Kruger National Park, South Africa, grew exponentially for approximately 60 years after they were first protected from hunting **(Figure 53.9)**. The increasingly

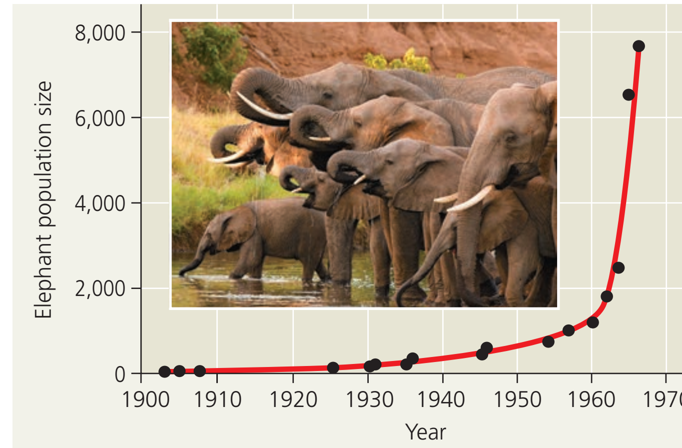
Figure 53.8 Population growth predicted by the exponential model. This graph compares growth in a population with $r = 1.0$ (blue curve) to growth in a population with $r = 0.5$ (red curve).



How many generations does it take these populations to reach a size of 1,500 individuals?

BioFlix® Animation: Exponential Growth

Figure 53.9 Exponential growth in the African elephant population of Kruger National Park, South Africa.



large number of elephants eventually caused enough damage to vegetation in the park that a collapse in their food supply was likely. To protect other species and the park ecosystem before that happened, park managers began limiting the elephant population by giving females birth control medication and by exporting elephants to other countries.

CONCEPT CHECK 53.2

1. Explain why a constant per capita rate of growth (r) for a population produces a curve that is J-shaped.
2. Unlimited population growth does not occur for long in nature. Why? Why do ecologists still study population growth in unlimited environments?
3. **WHAT IF?** In 2014, the United States had a population of 320 million people. If the (annual) per capita change in population size ($r_{\Delta t}$) was 0.005, how many people were added to the population that year (ignoring immigration and emigration)? What would you need to know to determine whether the United States is currently experiencing exponential growth?

For suggested answers, see Appendix A.

CONCEPT 53.3

The logistic model describes how a population grows more slowly as it nears its carrying capacity

The exponential growth model assumes that resources remain abundant, which is rarely the case in the real world. Instead, as the size of a population increases, each individual has access to fewer resources. Ultimately, there is a limit to the number of individuals that can occupy a habitat. Ecologists define the **carrying capacity**, symbolized by K, as the maximum population size that a particular environment can sustain. Carrying capacity varies over space and time with the abundance of limiting resources. Energy, shelter, refuge from predators, nutrient availability, water, and suitable nesting sites can all be limiting factors. For example, the carrying capacity for bats may be high in a habitat with abundant flying insects and roosting sites but lower where there is abundant food but fewer suitable shelters.

Crowding and resource limitation can have a profound effect on population growth rate. If individuals cannot obtain sufficient resources to reproduce, then the per capita birth rate will decline. Similarly, if starvation or disease increases with density, the per capita death rate may increase. Falling per capita birth rates or rising per capita death rates will cause the per capita rate of population growth to drop, a very different situation from the constant per capita growth rate (r) seen in a population that is growing exponentially.

The Logistic Growth Model

We can modify our mathematical model so that the per capita population growth rate decreases as N increases. In the **logistic population growth** model, the per capita rate of population growth approaches zero as the population size nears the carrying capacity (K).

To construct the logistic model, we start with the exponential population growth model and add an expression that reduces the per capita rate of population growth as N increases. If the carrying capacity is K, then $K - N$ is the number of additional individuals the environment can support, and $(K - N)/K$ is the fraction of K that is still available for population growth. By multiplying the exponential rate of population growth rN by $(K - N)/K$, we modify the change in population size as N increases:

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

When N is small compared to K, the term $(K - N)/K$ is close to 1. In this scenario, the per capita rate of population growth, $r(K - N)/K$, will be close to (but slightly less than) r, the intrinsic rate of increase seen in exponential population growth. But when N is large and resources are limiting, then $(K - N)/K$ is close to 0, and the per capita population growth rate is small. When N equals K, the population stops growing. **Table 53.2** shows calculations of population growth rate for a hypothetical population growing according to the logistic model, with $r = 1.0$ per individual per year. Notice that the overall population growth rate is highest, +375 individuals per year, when the population size is 750, or half the carrying capacity. At a population size of 750, the per capita population growth rate remains relatively high (one-half the value of r), but there are more reproducing individuals (N) in the population than at lower population sizes.

As shown in **Figure 53.10**, the logistic model of population growth produces a sigmoid (S-shaped) growth curve when N is plotted over time (the red line). New individuals are added to the population most rapidly at intermediate population sizes, when there is not only a breeding population of substantial size, but also lots of available space and other resources in the environment. The number of individuals added to the population decreases dramatically as N approaches K. As a result, the population growth rate (dN/dt) also decreases as N approaches K.

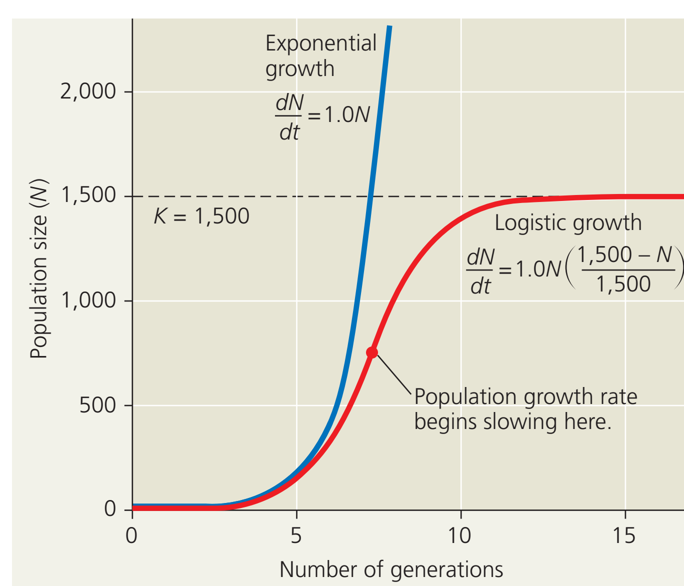
Note that we haven't said anything yet about *why* the population growth rate decreases as N approaches K. For

Table 53.2 Logistic Growth of a Hypothetical Population (K = 1,500)

Population Size (N)	Intrinsic Rate of Increase (r)	$\frac{K - N}{K}$	Per Capita Population Growth Rate $r\frac{(K - N)}{K}$	Population Growth Rate* $rN\frac{(K - N)}{K}$
25	1.0	0.983	0.983	+25
100	1.0	0.933	0.933	+93
250	1.0	0.833	0.833	+208
500	1.0	0.667	0.667	+333
750	1.0	0.500	0.500	+375
1,000	1.0	0.333	0.333	+333
1,500	1.0	0.000	0.000	0

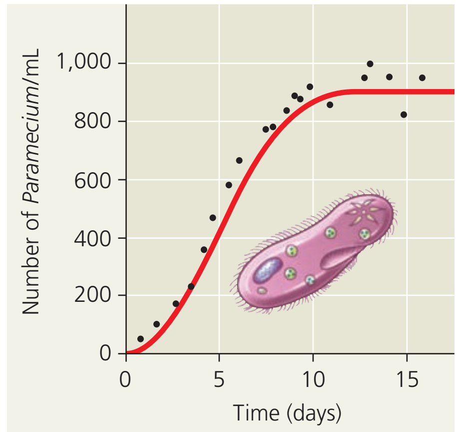
*Rounded to the nearest whole number.

▼ Figure 53.10 Population growth predicted by the logistic model. The rate of population growth decreases as population size (N) approaches the carrying capacity (K) of the environment. The red line shows logistic growth in a population where $r = 1.0$ and $K = 1,500$ individuals. For comparison, the blue line illustrates a population continuing to grow exponentially with the same r.

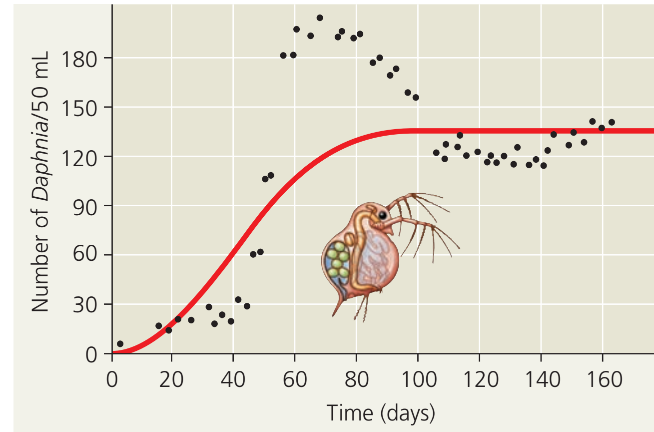


BioFlix® Animation: Logistic Growth

Figure 53.11 How well do these populations fit the logistic growth model? In each graph, the black dots plot the measured growth of the population, and the red curve is the growth predicted by the logistic model.



(a) A *Paramecium* population in the lab. The growth (black dots) of *Paramecium aurelia* in a small culture closely approximates logistic growth (red curve) if the researcher maintains a constant environment.



(b) A *Daphnia* population in the lab. The growth (black dots) of a population of water fleas (*Daphnia*) in a small laboratory culture does not correspond well to the logistic model (red curve). This population overshoots the carrying capacity of its artificial environment before it settles down to an approximately stable population size.

a population's growth rate to decrease, the birth rate must decrease, the death rate must increase, or both. Later in the chapter, we'll consider some of the factors affecting these rates, including the presence of disease, predation, and limited amounts of food and other resources.

The Logistic Model and Real Populations

The growth of laboratory populations of some small animals, such as beetles and crustaceans, and of some microorganisms, such as bacteria, *Paramecium*, and yeasts, fits an S-shaped curve fairly well under conditions of limited resources **(Figure 53.11a)**. These populations are grown in a constant environment lacking predators and competing species that may reduce growth of the populations, conditions that rarely occur in nature.

Some of the assumptions built into the logistic model clearly do not apply to all populations. The logistic model assumes that populations adjust instantaneously to growth and approach carrying capacity smoothly. In reality, there is often a delay before the negative effects of an increasing population are realized. If food becomes limiting for a population, for instance, reproduction will decline eventually, but females may use their energy reserves to continue reproducing for a short time. This may cause the population to overshoot its carrying capacity temporarily, as shown for the water fleas in **Figure 53.11b**. In the **Scientific Skills Exercise**, you can model what can happen to such a population when N becomes greater than K. Other populations fluctuate greatly, making it difficult even to define carrying capacity. We will examine some possible reasons for such fluctuations later in the chapter.

The logistic model provides a useful starting point for thinking about how populations grow and for constructing more complex models. As such, its role is similar to that played by the Hardy-Weinberg equation for thinking about the evolution of populations. The logistic model is also important in conservation biology for predicting how rapidly a particular population might increase in numbers after it has been reduced to a small size and for estimating sustainable harvest rates for wildlife populations. Conservation biologists can also use the model to estimate the critical size below which populations of certain organisms, such as the northern subspecies of the white rhinoceros (*Ceratotherium simum*), may become extinct **(Figure 53.12)**.

Figure 53.12 White rhinoceros mother and calf. The two animals pictured here are members of the southern subspecies, which has a population of more than 20,000 individuals. The northern subspecies is critically endangered, with just a few known individuals.

SCIENTIFIC SKILLS EXERCISE

Using the Logistic Equation to Model Population Growth

What Happens to the Size of a Population When It Overshoots Its Carrying Capacity? In the logistic population growth model, the per capita rate of population increase approaches zero as the population size (N) approaches the carrying capacity (K). Under some conditions, however, a population in the laboratory or the field can overshoot K, at least temporarily. If food becomes limiting to a population, for instance, there may be a delay before reproduction declines, and N may briefly exceed K. In this exercise, you will use the logistic equation to model the growth of the hypothetical population in Table 53.2 when $N > K$.

▶ *Daphnia*

INTERPRET THE DATA

1. Assuming that $r = 1.0$ and $K = 1{,}500$, calculate the population growth rate for four cases where population size (N) is greater than carrying capacity (K): $N = 1{,}510$, 1,600, 1,750, and 2,000 individuals. To do this, first write the equation for population growth rate given in Table 53.2. Plug in the values for each of the four cases, starting with $N = 1{,}510$, and solve the equation for each one. Which population size has the highest growth rate?
2. If r is doubled, predict how the population growth rates will change for the four population sizes given in question 1. Now calculate the population growth rate for the same four cases, this time assuming that $r = 2.0$ (and with K still $= 1{,}500$).
3. Now let's see how the growth of a real-world population of *Daphnia* corresponds to this model. At what times in Figure 53.11b is the *Daphnia* population changing in ways that correspond to the values you calculated? Hypothesize why the population drops below the carrying capacity briefly late in the experiment.

Instructors: A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

CONCEPT CHECK 53.3

1. Explain why a population that fits the logistic growth model increases more rapidly at intermediate size than at relatively small and large sizes.
2. **WHAT IF?** ➤ Given the latitudinal differences in sunlight intensity (see Figure 51.3), how might you expect the carrying capacity of plant species found at the equator to compare with that of plant species found at high latitudes?
3. **MAKE CONNECTIONS** ➤ Suppose that a sudden change in environmental conditions caused a substantial drop in a population's carrying capacity. Predict how natural selection and genetic drift might affect this population. (See Concept 21.2.)

For suggested answers, see Appendix A.

CONCEPT 53.4

Life history traits are products of natural selection

EVOLUTION Natural selection favors traits that improve an organism's chances of survival and reproductive success. In every species, there are trade-offs between survival and reproductive traits such as frequency of reproduction, number of offspring (number of seeds produced by plants; litter or clutch size for animals), or investment in parental care. The traits that affect an organism's schedule of reproduction and survival make up its **life history**. Life history traits of an organism are evolutionary outcomes reflected in its development, physiology, and behavior.

Diversity of Life Histories

We'll focus on three key components of an organism's life history: when reproduction begins (the age at first reproduction or age at maturity), how often the organism reproduces, and how many offspring are produced per reproductive episode. The fundamental idea that evolution accounts for the diversity of life is manifest in the broad range of these life history characteristics in nature. For example, the age at which reproduction begins varies considerably across species. A typical loggerhead turtle is about 30 years old when it first crawls onto a beach to lay eggs (see Figure 53.1). In contrast, the coho salmon (*Oncorhynchus kisutch*) is often only three or four years old when it spawns.

Organisms also vary in how often they reproduce. The coho salmon is an example of organisms that undergo a "one-shot" pattern of big-bang reproduction, or **semelparity** (from the Latin *semel*, once, and *parere*, to beget). It hatches in the headwaters of a freshwater stream and then migrates to the Pacific Ocean, where it typically requires a few years to mature. The salmon eventually returns to the same stream to spawn, producing thousands of eggs in a single reproductive opportunity before it dies. Semelparity also occurs in some plants, such as the agave, or "century plant" **(Figure 53.13a)**. Agaves generally grow in arid climates with

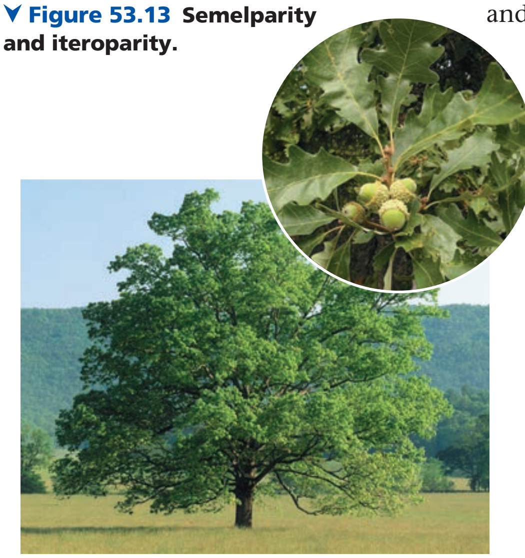


Figure 53.13 Semelparity and iteroparity.

(a) Semelparity, one-time reproducer. An agave (*Agave americana*) is an example of semelparity. The leaves of the plant are visible at the base of the giant flowering stalk, which is produced only at the end of the agave's life.

(b) Iteroparity, repeat reproducer. Organisms that reproduce repeatedly, such as the bur oak (*Quercus macrocarpa*), undergo iteroparity. One oak tree can produce thousands of acorns (inset) per year over the course of many decades.

unpredictable rainfall and poor soils. An agave grows for years, accumulating nutrients in its tissues, until there is an unusually wet year. It then sends up a large flowering stalk, produces seeds, and dies. This life history appears to be an adaptation to the agave's harsh desert environment.

In contrast to semelparity is **iteroparity** (from the Latin *iterare*, to repeat), or repeated reproduction. As an example, a female loggerhead turtle produces four clutches totaling approximately 300 eggs in a year. It then typically waits two to three years before laying more eggs; presumably, the turtles lack sufficient resources to produce that many eggs every year. A mature turtle may lay eggs for 30 years after the first clutch. Horses and other large mammals also reproduce repeatedly, as do many fish, sea urchins, and long-lived trees, such as maples and oaks **(Figure 53.13b)**.

Finally, organisms also vary in how many offspring they produce. Some species, such as the white rhinoceros (see Figure 53.12), produce a single calf when they reproduce, while most insects and many plants produce large numbers of offspring. Such variation in offspring number has other consequences as well; as you'll read, a species that produces one or a few offspring may provision them better than does a species that produces many offspring.

"Trade-offs" and Life Histories

No organism could produce thousands of offspring yet provision each of them as well as does a white rhinoceros caring for its single calf. There is a trade-off between offspring number and the amount of resources a parent can devote to each offspring. Such trade-offs occur because organisms do not have access to unlimited amounts of resources. As a result, the use of resources for one function (such as reproduction) can reduce the resources available for supporting another function (such as survival). In Eurasian kestrels, for example, caring for a larger number of young lowered the survival rates of the parents **(Figure 53.14)**. In another study, in Scotland, researchers found that female red deer that reproduced in a given summer were more likely to die the next winter than were females that did not reproduce.

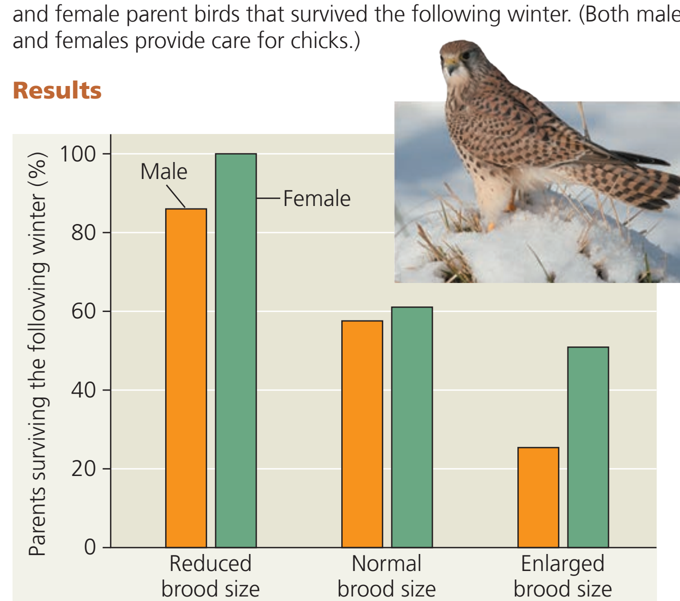
Selective pressures also influence trade-offs between the number and size of offspring. Plants and animals whose young have a low change of survival often produce many small offspring. Plants

Figure 53.14

Inquiry **How does caring for offspring affect parental survival in kestrels?**

Experiment Cor Dijkstra and colleagues in the Netherlands studied the effects of parental caregiving in Eurasian kestrels over five years. The researchers transferred chicks among nests to produce reduced broods (three or four chicks), normal broods (five or six), and enlarged broods (seven or eight). They then measured the percentage of male and female parent birds that survived the following winter. (Both males and females provide care for chicks.)

Results



Conclusion The lower survival rates of kestrels with larger broods indicate that caring for more offspring negatively affects survival of the parents.

Data from C. Dijkstra et al., Brood size manipulations in the kestrel (*Falco tinnunculus*): effects on offspring and parent survival, *Journal of Animal Ecology* 59:269–285 (1990).

INTERPRET THE DATA ➤ *The males of some bird species provide no parental care. If this were true for the Eurasian kestrel, predict how the experimental results would differ from those shown here.*

Figure 53.15 Variation in the number and size of seeds in plants.

(a) Dandelions grow quickly and release a large number of tiny fruits, each containing a single seed. Producing numerous seeds ensures that at least some will grow into plants that eventually produce seeds themselves.

(b) Some plants, such as the Brazil nut tree (right), produce a moderate number of large seeds in pods (above). Each seed's large endosperm provides nutrients for the embryo, an adaptation that helps a relatively large fraction of offspring survive.

that colonize disturbed environments, for example, usually produce many small seeds, only a few of which may reach a suitable habitat. Small size may also increase the chance of seedling establishment by enabling the seeds to be carried longer distances to a broader range of habitats **(Figure 53.15a)**. Animals that suffer high predation rates, such as quail, sardines, and mice, also tend to produce many offspring.

In other organisms, extra investment on the part of the parent greatly increases the offspring's chances of survival. Walnut and Brazil nut trees produce large seeds packed with nutrients that help the seedlings become established **(Figure 53.15b)**. Primates generally bear only one or two offspring at a time; parental care and an extended period of learning in the first several years of life are very important to offspring fitness. Such provisioning and extra care can be especially important in habitats with high population densities.

One way to categorize variation in life history traits is related to the logistic growth model discussed in Concept 53.3. Selection for traits that are advantageous at high densities is referred to as ***K*-selection**. In contrast, selection for traits that maximize reproductive success in uncrowded environments (low densities) is called ***r*-selection**. These names follow from the variables of the logistic equation. *K*-selection is said to operate in populations living at a density near the limit imposed by their resources (the carrying capacity, *K*), where competition among individuals is stronger. Mature trees growing in an old-growth forest are an example of *K*-selected organisms. In contrast, *r*-selection is said to maximize *r*, the intrinsic rate of increase, and occurs in environments in which population densities are well below carrying capacity or individuals face little competition. Such conditions are often found in disturbed habitats that are being recolonized. Weeds growing in an abandoned agricultural field are an example of *r*-selected organisms.

The concepts of *K*- and *r*-selection represent two extremes in a range of actual life histories. The framework of *K*- and *r*-selection, grounded in the idea of carrying capacity, also relates to the important question we alluded to earlier: *Why does population growth rate decrease as population size approaches carrying capacity?* Answering this question is the focus of the next section.

CONCEPT CHECK 53.4

1. Identify three key life history traits, and give examples of organisms that vary widely in each of these traits.
2. In the fish called the peacock wrasse (*Symphodus tinca*), females disperse some of their eggs widely and lay other eggs in a nest. Only the latter receive parental care. Explain the trade-offs in reproduction that this behavior illustrates.
3. **WHAT IF?** ➤ Mice that experience stress such as a food shortage will sometimes abandon their young. Explain how this behavior might have evolved in the context of reproductive trade-offs and life history.

For suggested answers, see Appendix A.

CONCEPT 53.5

Density-dependent factors regulate population growth

What environmental factors keep populations from growing indefinitely? Why are some populations fairly stable in size, while others are not?

Answers to such questions can be important in practical applications. Farmers may want to reduce the abundance of insect pests or stop the growth of an invasive weed that is spreading rapidly. Conservation ecologists need to know what environmental factors create favorable feeding or breeding habitats for endangered species, such as the white rhinoceros and the whooping crane. Overall, whether seeking to reduce the size of an unwanted population or increase the size of one that is endangered, it is helpful to understand factors that affect population abundance.

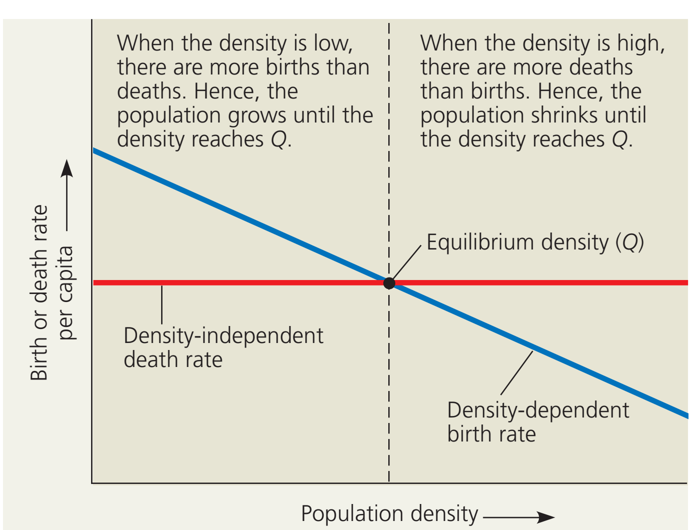
Population Change and Population Density

To understand why a population stops growing when it reaches a certain size, ecologists study how the rates of birth, death, immigration, and emigration change as population density rises. If immigration and emigration offset each other, then a population grows when the birth rate exceeds the death rate and declines when the death rate exceeds the birth rate.

A birth rate or death rate that does *not* change with population density is said to be **density independent**. For example, researchers found that the mortality of dune fescue grass (*Vulpia fasciculata*) is mainly due to physical factors that kill similar proportions of a local population, regardless of its density. Drought stress that arises when the roots of the grass are uncovered by shifting sands is a density-independent factor that can kill these plants. In contrast, a death rate that increases with population density or a birth rate that falls with rising density is said to be **density dependent**. Researchers found that reproduction by dune fescue declines as population density increases, in part because water or nutrients become more scarce. Thus, the key factors affecting birth rate in this population are density dependent, while death rate is largely determined by density-independent factors. **Figure 53.16** shows how the combination of density-dependent reproduction and density-independent mortality can stop population growth, leading to an equilibrium population density in species such as dune fescue.

Variation in density-independent factors such as temperature and precipitation can cause dramatic changes in population size. For example, a drought or heat wave can cause a sharp increase in mortality rates, causing the abundance of a population to plummet. Note, however, that a density-independent factor cannot consistently cause a population to decrease in size when it is large or increase in size when it is small—only a density-dependent factor can consistently cause such changes. With this in mind, a population is said to be *regulated* when one or more density-dependent factors cause its size to decrease when large (or increase when small).

Figure 53.16 Determining equilibrium for population density. This simple model considers only birth and death rates. (Immigration and emigration rates are assumed to be either zero or equal.) In this example, the birth rate changes with population density, while the death rate is constant. At the equilibrium density (*Q*), the birth and death rates are equal.



DRAW IT ➤ *Redraw this figure for the case where the birth and death rates are both density dependent, as occurs for many species.*

MB BioFlix® Animation: Density Dependence

Mechanisms of Density-Dependent Population Regulation

The principle of feedback regulation (see Concept 40.2) applies to population dynamics. Without some type of negative feedback between population density and the rates of birth and death, a population would never stop growing. But no population can increase in size indefinitely. Ultimately, at large population sizes, negative feedback is provided by density-dependent regulation, which halts population growth through mechanisms that reduce birth rates or increase death rates. For example, a study of kelp perch (*Brachyistius frenatus*) populations showed that the fish's mortality rose proportionally as its density increased **(Figure 53.17)**. Without sufficient kelp to hide in, the perch was vulnerable to predation by another fish species, the kelp bass (*Paralabrax clathratus*). Predation and other mechanisms of density-dependent regulation are explored further in **Figure 53.18**.

These various examples of population regulation by negative feedback show how increased densities cause population growth rates to decline by affecting reproduction,

Figure 53.17 Density-dependent regulation by predation. As the density of kelp perch increased, predation by kelp bass increased, resulting in a higher proportion of kelp perch deaths.

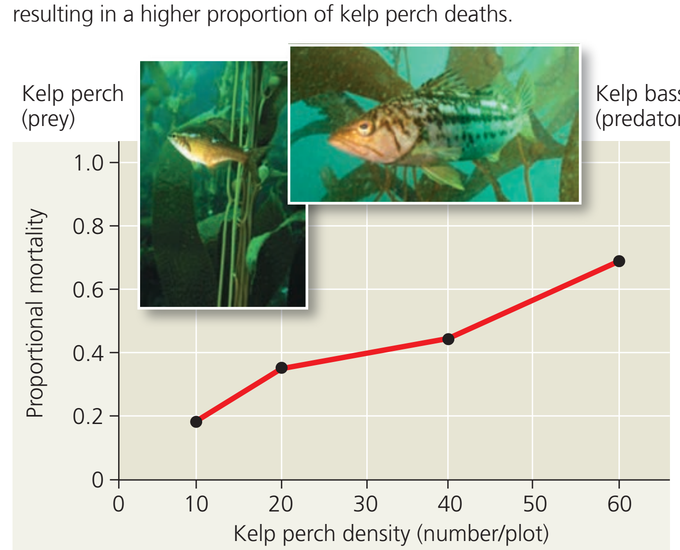


Figure 53.18 Exploring Mechanisms of Density-Dependent Regulation

As population density increases, many density-dependent mechanisms slow or stop population growth by decreasing birth rates or increasing death rates.

Competition for Resources

Increasing population density intensifies competition for nutrients and other resources, reducing reproductive rates. Farmers minimize the effect of resource competition on the growth of wheat (*Triticum aestivum*) and other crops by applying fertilizers to reduce nutrient limitations on crop yield.

Disease

If the transmission rate of a disease increases as a population becomes more crowded, then the disease's impact is density dependent. In humans, the respiratory diseases influenza (flu) and tuberculosis are spread through the air when an infected person sneezes or coughs. Both diseases strike a greater percentage of people in densely populated cities than in rural areas.

Predation

Predation can be an important cause of density-dependent mortality if a predator captures more food as the population density of the prey increases. As a prey population builds up, predators may also feed preferentially on that species. Population increases in the collared lemming (*Dicrostonyx groenlandicus*) lead to density-dependent predation by several predators, including the snowy owl (*Bubo scandiacus*).

growth, and survival. Although negative feedback helps explain why populations stop growing, it does not address why some populations fluctuate dramatically while others remain relatively stable.

Population Dynamics

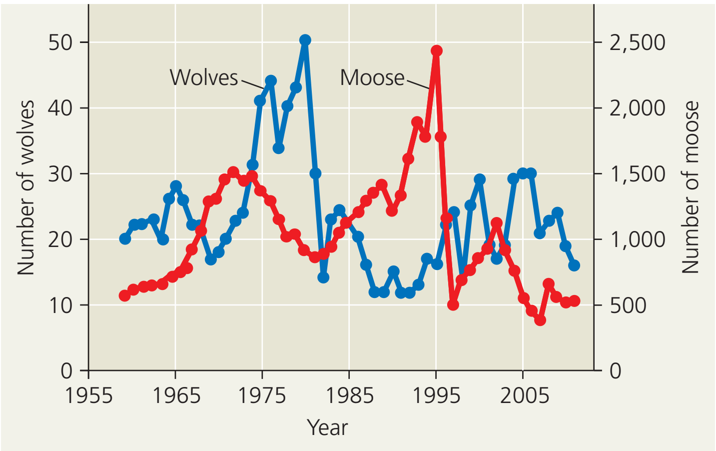
All populations show some fluctuation in size. Such population fluctuations from year to year or place to place, called **population dynamics**, are influenced by many factors and in turn affect other species. For example, fluctuations in fish populations affect populations of seabirds that eat fish. The study of population dynamics focuses on the complex interactions between biotic and abiotic factors that cause variation in population sizes.

Stability and Fluctuation

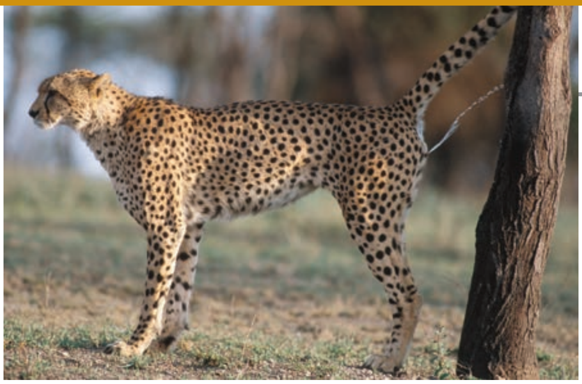
Populations of large mammals were once thought to remain relatively stable, but long-term studies have challenged that idea. For instance, the moose population on Isle Royale in Lake Superior has fluctuated substantially since around 1900. At that time, moose from the Ontario mainland (25 km away) colonized the island, perhaps by walking across the lake when it was frozen. Wolves, which rely on moose for most of their food, reached the island around 1950 by walking across the frozen lake. The lake has not frozen over in recent years, and both populations appear to have been isolated from immigration and emigration since then. Despite this isolation, the moose population experienced two major increases and collapses during the last 50 years **(Figure 53.19)**.

What factors cause the size of the moose population to change so dramatically? Harsh weather, particularly cold

Figure 53.19 Fluctuations in moose and wolf populations on Isle Royale, 1959–2011.



BioFlix® Animation: Predator-Prey



Territoriality

Territoriality can limit population density when space becomes the resource for which individuals compete. Cheetahs (*Acinonyx jubatus*) use a chemical marker in urine to warn other cheetahs of their territorial boundaries. The presence of surplus, or nonbreeding, individuals is a good indication that territoriality is restricting population growth.

Intrinsic Factors

Intrinsic physiological factors can regulate population size. Reproductive rates of white-footed mice (*Peromyscus leucopus*) in a field enclosure can drop even when food and shelter are abundant. This drop in reproduction at high population density is associated with aggressive interactions and hormonal changes that delay sexual maturation and depress the immune system.

Toxic Wastes

Yeasts, such as the brewer's yeast *Saccharomyces cerevisiae*, are used to convert carbohydrates to ethanol in winemaking. The ethanol that accumulates in the wine is toxic to yeasts and contributes to density-dependent regulation of yeast population size. The alcohol content of wine is usually less than 13% because that is the maximum concentration of ethanol that most wine-producing yeast cells can tolerate.

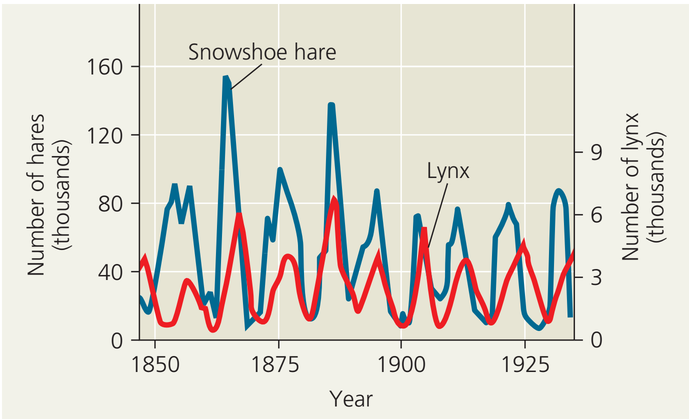
winters with heavy snowfall, can weaken moose and reduce food availability, decreasing the population size. When moose numbers are low and the weather is mild, food is readily available and the population grows quickly. Conversely, when moose numbers are high, factors such as predation and an increase in the density of ticks and other parasites cause the population to shrink. The effects of some of these factors can be seen in Figure 53.19. The first major collapse coincided with a peak in the numbers of wolves from 1975 to 1980. The second major collapse, around 1995, coincided with harsh winter weather, which increased the energy needs of the moose and made it harder for them to find food under the deep snow.

Population Cycles: *Scientific Inquiry*

While many populations fluctuate at unpredictable intervals, others undergo regular boom-and-bust cycles. Some small herbivorous mammals, such as voles and lemmings, tend to have 3- to 4-year cycles, while some birds, such as ruffed grouse and ptarmigans, have 9- to 11-year cycles.

One striking example of population cycles is the roughly 10-year cycling of snowshoe hares (*Lepus americanus*) and lynx (*Lynx canadensis*) in the far northern forests of Canada and Alaska. Lynx are predators that feed predominantly on snowshoe hares, so lynx numbers might be expected to rise and fall with the numbers of hares **(Figure 53.20)**.

Figure 53.20 Population cycles in the snowshoe hare and lynx. Population counts are based on the number of pelts sold by trappers to the Hudson Bay Company.



INTERPRET THE DATA ➤ *What do you observe about the relative timing of the peaks in lynx numbers and hare numbers? What might explain this observation?*

But why do hare numbers rise and fall in approximately 10-year cycles? Two main hypotheses have been proposed. First, the cycles may be caused by food shortage during winter. Hares eat the terminal twigs of small shrubs such as willow and birch in winter, although why this food supply might cycle in 10-year intervals is uncertain. Second, the cycles may be due to predator-prey interactions. Many predators other than lynx eat hares, and they may overexploit their prey.

Let's consider the evidence for the two hypotheses. If hare cycles are due to winter food shortage, then the cycles should stop if extra food is provided to a field population. Researchers conducted such experiments in the Yukon for 20 years—over two hare cycles. They found that hare populations in the areas with extra food increased about threefold in density but continued to cycle in the same way as the unfed control populations. Therefore, food supplies alone do not cause the hare cycles shown in Figure 53.20, so we can reject the first hypothesis.

To study the effects of predation, ecologists used radio collars to track individual hares to determine why they died. Predators, including lynx, coyotes, hawks, and owls, killed 95% of the hares in such studies. None of the hares appeared to have died of starvation. These data support the second hypothesis. When ecologists set up electric fences to exclude predators from certain areas, the collapse in survival that normally occurs in the decline phase of the cycle was nearly eliminated. Overexploitation by predators thus seems to be an essential part of snowshoe hare cycles; without predators, it is unlikely that hare populations would cycle in northern Canada.

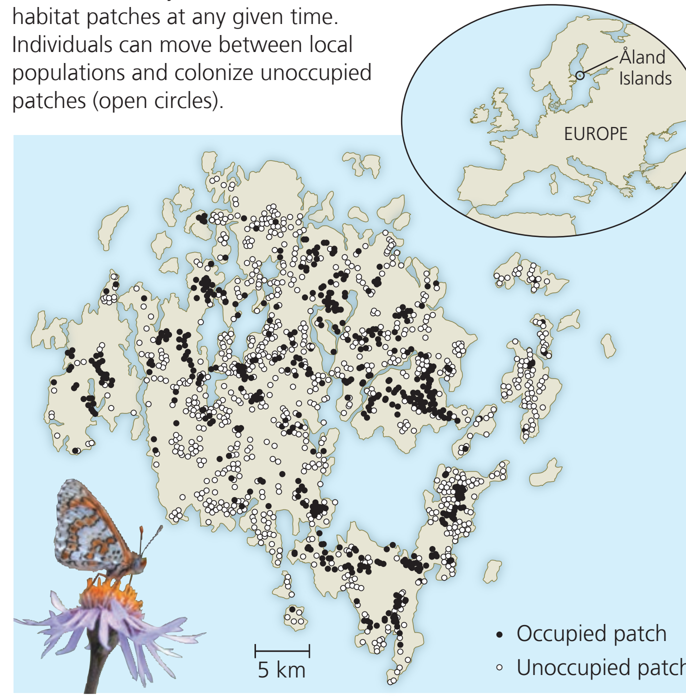
Immigration, Emigration, and Metapopulations

So far, our discussion of population dynamics has focused mainly on the contributions of births and deaths. However, immigration and emigration also influence populations. When a population becomes crowded and resource competition increases, emigration often increases.

Immigration and emigration are particularly important when a number of local populations are linked, forming a **metapopulation**. Local populations in a metapopulation can be thought of as occupying discrete patches of suitable habitat in a sea of otherwise unsuitable habitat. Such patches vary in size, quality, and isolation from other patches, factors that influence how many individuals move among the populations. If one population becomes extinct, the patch it occupied may be recolonized by immigrants from another population.

The Glanville fritillary (*Melitaea cinxia*) illustrates the movement of individuals between populations. This butterfly is found in about 500 meadows across the Åland Islands of Finland, but its potential habitat in the islands is much larger, approximately 4,000 suitable patches. New populations of the butterfly regularly appear and existing populations become extinct, constantly shifting the locations of the 500 colonized patches **(Figure 53.21)**. The species persists in a balance of local extinctions and recolonizations.

Figure 53.21 The Glanville fritillary: a metapopulation. On the Åland Islands, local populations of this butterfly (filled circles) are found in only a fraction of the suitable habitat patches at any given time. Individuals can move between local populations and colonize unoccupied patches (open circles).



An individual's ability to move between populations depends on a number of factors, including its genetic makeup. One gene that has a strong effect on the Glanville fritillary's ability to move is *Pgi*, which codes for the enzyme phosphoglucoisomerase. This enzyme catalyzes the second step of glycolysis (see Figure 10.9), and its activity correlates with the rate of CO_2 production from respiration by the butterflies. Ecologists studied butterflies known to be heterozygous or homozygous for a single nucleotide polymorphism in *Pgi*. They tracked the movements of individual butterflies using radar and transponders attached to the butterflies that emit an identifying signal. Butterfly movements ranged widely, from 10 m to 4 km, in two-hour periods. Heterozygous individuals flew more than twice as far in the morning and at lower ambient temperatures than did homozygous individuals. The results indicated a fitness advantage

A Glanville fritillary (*Melitaea cinxia*) wearing a tracking transponder.

to the heterozygous genotype in low temperatures and a greater likelihood of heterozygotes colonizing new locations in the metapopulation.

The metapopulation concept underscores the significance of immigration and emigration for the Glanville fritillary and many other species. It also helps ecologists understand population dynamics and gene flow in patchy habitats, providing a framework for the conservation of species living in a network of habitat fragments and reserves.

CONCEPT CHECK 53.5

1. Describe three attributes of habitat patches that could affect population density and rates of immigration and emigration.
2. **WHAT IF?** ➤ Suppose you were studying a species that has a population cycle of about ten years. How long would you need to study the species to determine if its population size were declining? Explain.
3. **MAKE CONNECTIONS** ➤ Negative feedback is a process that regulates biological systems (see Concept 40.2). Explain how the density-dependent birth rate of dune fescue grass exemplifies negative feedback.

For suggested answers, see Appendix A.

CONCEPT 53.6

The human population is no longer growing exponentially but is still increasing rapidly

In the last few centuries, the human population has grown at an unprecedented rate, more like the elephant population in Kruger National Park (see Figure 53.9) than the fluctuating populations we considered in Concept 53.5. No population can grow indefinitely, however. In this section of the chapter, we'll apply the concepts of population dynamics to the specific case of the human population.

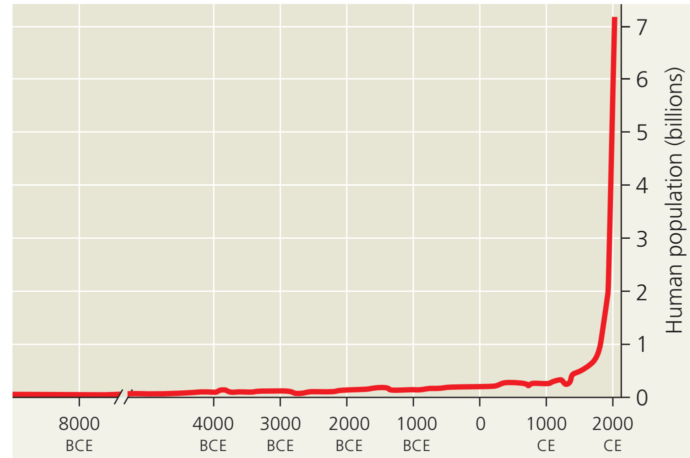
The Global Human Population

The human population has grown explosively over the last four centuries (**Figure 53.22**). In 1650, about 500 million people inhabited Earth. Our population doubled to 1 billion within the next two centuries, doubled again to 2 billion by 1930, and doubled still again to 4 billion by 1975. Notice that the time it took our population to double in size decreased from 200 years in 1650 to just 45 years in 1930. Thus, historically our population has grown even *faster* than exponential growth, which has a constant rate of increase and hence a constant doubling time.

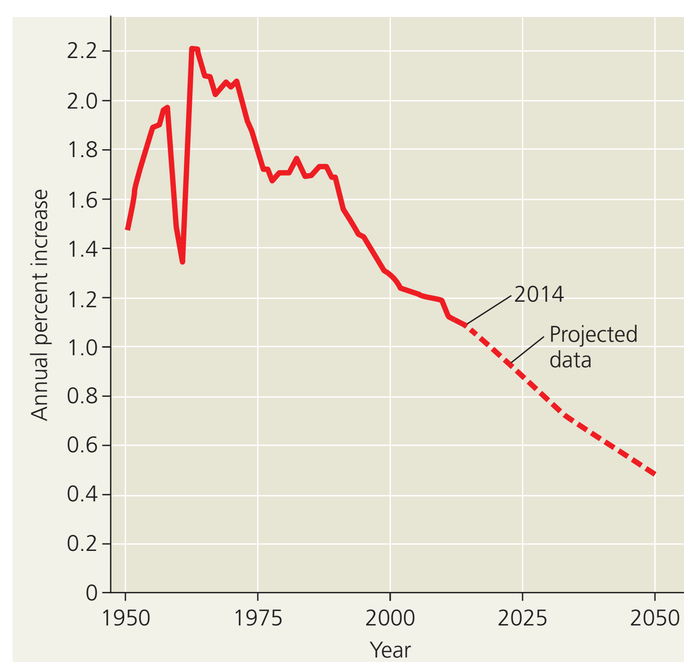
The global population is now more than 7.2 billion people and is increasing by about 78 million each year. This translates into more than 200,000 people each day, the equivalent of adding a city the size of Amarillo, Texas. At this rate, it takes only about four years to add the equivalent of another United States to the world population. Ecologists predict there will be 8.1–10.6 billion people on Earth by the year 2050.

Though the global population is still growing, the *rate* of growth began to slow during the 1960s (**Figure 53.23**). The annual rate of increase in the global population peaked at 2.2% in 1962 but was only 1.1% in 2014. Current models

▼ **Figure 53.22 Human population growth (data as of 2015).** The global human population has grown almost continuously throughout history, but it skyrocketed after the Industrial Revolution. Though it is not apparent at this scale, the rate of population growth has slowed in recent decades, mainly as a result of decreased birth rates throughout the world.



▼ **Figure 53.23 Annual percent increase in the global human population (data as of 2014).** The sharp dip in the 1960s is due mainly to a famine in China in which about 60 million people died.



project a growth rate of 0.5% by 2050, which would add 45 million more people per year if the population climbs to a projected 9 billion. The reduction in annual growth rate observed over the past four decades shows that the human population is now growing more slowly than expected in exponential growth. This change resulted from fundamental shifts in population dynamics due to diseases, including AIDS, and to voluntary population control.

Regional Patterns of Population Change

We have described changes in the global population, but population dynamics vary widely from region to region. In a stable regional population, birth rate equals death rate (disregarding the effects of immigration and emigration). Two possible configurations for a stable population are

$$\text{Zero population growth} = \text{High birth rate} - \text{High death rate}$$

or

$$\text{Zero population growth} = \text{Low birth rate} - \text{Low death rate}$$

The movement from high birth and death rates toward low birth and death rates, which tends to accompany industrialization and improved living conditions, is called the **demographic transition**. In Sweden, this transition took about 150 years, from 1810 to 1975, when birth rates finally approached death rates. In Mexico, where the human population is still growing rapidly, the transition is projected to take until at least 2050. Demographic transition is associated with an increase in the quality of health care and sanitation as well as improved access to education, especially for women.

After 1950, death rates declined rapidly in most developing countries, but birth rates have declined more variably. Birth rates have fallen most dramatically in China. In 1970, the Chinese birth rate predicted an average of 5.9 children per woman per lifetime (total fertility rate); by 2011, largely because of the government's strict one-child policy, the total fertility rate was 1.6 children. In some countries of Africa, the transition to lower birth rates has also been rapid, though birth rates remain high in most of sub-Saharan Africa.

How do such variable birth rates affect the growth of the world's population? In industrialized nations, populations are near equilibrium, with reproductive rates near the replacement level of 2.1 children per female (over their lifetime). In many industrialized countries, including Canada, Germany, Japan, and the United Kingdom, total reproductive rates are in fact *below* the replacement level. These populations will eventually decline if there is no immigration and if the birth rate does not change. In fact, the population is already declining in many eastern and central European countries. Most of the current global population growth occurs in less industrialized countries, where about 80% of the world's people now live.

A unique feature of human population growth is our ability to control family sizes through planning and voluntary contraception. Social change and the rising educational and career aspirations of women in many cultures encourage women to delay marriage and postpone reproduction. Delayed reproduction helps to decrease population growth rates and to move a society toward zero population growth under conditions of low birth rates and low death rates. However, there is a great deal of disagreement as to how much support should be provided for global family planning efforts.

Age Structure

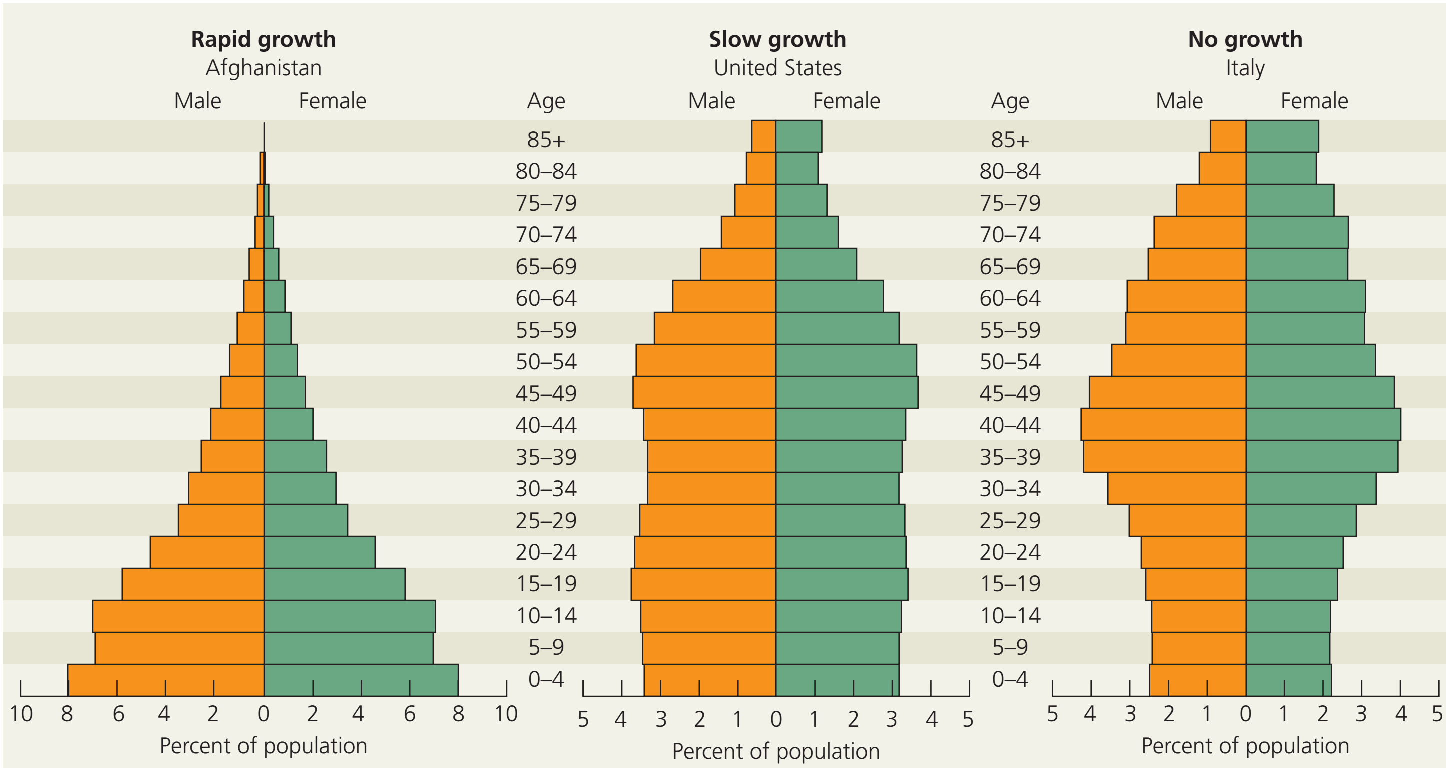
Another important factor that can affect population growth is a country's **age structure**, the relative number of individuals of each age in the population. Age structure is commonly graphed as "pyramids" like those in **Figure 53.24**. For Afghanistan, the pyramid is bottom heavy, skewed toward young individuals who will grow up and perhaps sustain the explosive growth with their own reproduction. The age structure for the United States is relatively even until the older, postreproductive ages. Although the current total reproductive rate in the United States is about 2.1 children per woman—near the replacement rate—the population is projected to grow slowly through 2050 as a result of immigration. For Italy, the pyramid has a small base, indicating that individuals younger than reproductive age are relatively underrepresented in the population. This situation contributes to the projection of a future population decrease in Italy.

Age-structure diagrams not only predict a population's growth trends but also can illuminate social conditions. Based on the diagrams in Figure 53.24, we can predict that employment and education opportunities will continue to be a problem for Afghanistan in the foreseeable future. In the United States and Italy, a decreasing proportion of younger working-age people will soon be supporting an increasing population of retired "boomers." This demographic feature has made the future of Social Security and Medicare a major political issue in the United States. Understanding age structures is necessary to plan for the future.

Infant Mortality and Life Expectancy

Infant mortality, the number of infant deaths per 1,000 live births, and *life expectancy at birth*, the predicted average length of life at birth, vary widely in different countries. In 2011, for example, the infant mortality rate was 149 (14.9%) in Afghanistan but only 2.8 (0.28%) in Japan. Life expectancy at birth was only 48 years in Afghanistan but 82 years in Japan. These differences reflect the quality of

Figure 53.24 Age-structure pyramids for the human population of three countries (data as of 2010). The annual growth rate was approximately 2.6% in Afghanistan, 1.0% in the United States, and 0.0% in Italy.



Animation: Analyzing Age-Structure Pyramids

life faced by children at birth and influence the reproductive choices parents make. If infant mortality is high, then parents are likely to have more children to ensure that some reach adulthood.

Although global life expectancy has been increasing since about 1950, it has recently dropped in a number of regions, including countries of the former Soviet Union and in sub-Saharan Africa. In these regions, social upheaval, decaying infrastructure, and infectious diseases such as AIDS and tuberculosis are reducing life expectancy. In the African country of Angola, life expectancy in 2011 was 43 years, about half of that in Japan, Sweden, Italy, and Spain.

Global Carrying Capacity

No ecological question is more important than the future size of the human population. As noted earlier, population ecologists project a global population of approximately 8.1–10.6 billion people in 2050. That means that an estimated 1–4 billion people will be added to the population in the next four decades because of the momentum of population growth. But just how many humans can the biosphere support? Will the world be overpopulated in 2050? Is it *already* overpopulated?

Estimates of Carrying Capacity

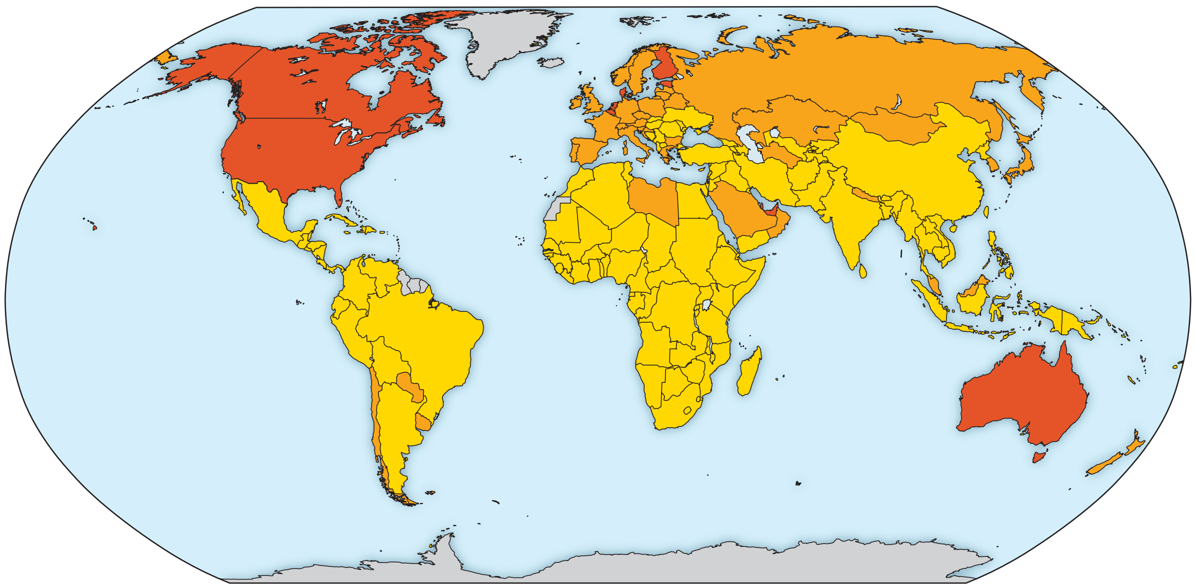
For over three centuries, scientists have attempted to estimate the human carrying capacity of Earth. The first known estimate, 13.4 billion people, was made in 1679 by Anton van Leeuwenhoek (a Dutch scientist who also discovered protists; see the introduction to Chapter 28). Since then, estimates have varied from less than 1 billion to more than 1,000 billion (1 trillion).

Carrying capacity is difficult to estimate, and scientists use different methods to produce their estimates. Some researchers use curves like that produced by the logistic equation (see Figure 53.10) to predict the future maximum of the human population. Others generalize from existing “maximum” population density and multiply this number by the area of habitable land. Still others base their estimates on a single limiting factor, such as food, and consider variables such as the amount of farmland, the average yield of crops, the prevalent diet—vegetarian or meat based—and the number of calories needed per person per day.

Limits on Human Population Size

A more comprehensive approach to estimating the carrying capacity of Earth is to recognize that humans have multiple

Figure 53.25 Per capita ecological footprint by country.



Earth has a total of 11.9 billion gha of productive land. How many people could Earth support sustainably if the average ecological footprint were 8 gha per person (as in the United States)?

constraints: We need food, water, fuel, building materials, and other resources, such as clothing and transportation. The **ecological footprint** concept summarizes the aggregate land and water area required by each person, city, or nation to produce all the resources it consumes and to absorb all the waste it generates.

What is a sustainable ecological footprint for the entire human population? One way to estimate this footprint is to add up all the ecologically productive land on the planet and divide by the size of the human population. Typically, this estimate is made using *global hectares*, where a global hectare (gha) represents a hectare of land or water with a productivity equal to the average of all biologically productive areas on Earth (1 hectare = 2.47 acres). This calculation yields an allotment of 1.7 gha per person—the benchmark for comparing actual ecological footprints. Anyone who consumes resources that require more than 1.7 gha to produce is using an unsustainable share of Earth's resources, as is the case for the citizens of many countries **(Figure 53.25)**. For example, a typical ecological footprint for a person in the United States is 8 gha.

Our impact on the planet can also be assessed using currencies other than area, such as energy use. Average energy use differs greatly across different regions of the world **(Figure 53.26)**. A typical person in the United States, Canada, or Norway consumes roughly 30 times the energy that a person in central Africa does. Moreover, fossil fuels, such as oil, coal, and natural gas, are the source of 80%

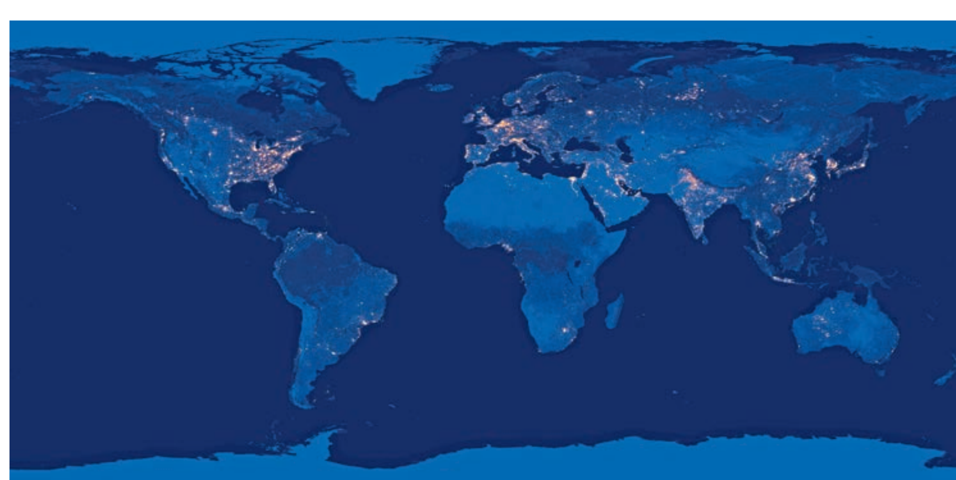


Figure 53.26 The uneven electrification of the planet. This composite image taken from space of Earth's surface at night illustrates the varied density of electric lights worldwide, one aspect of energy use by humans.

or more of the energy used in most developed nations. As Chapter 56 discusses in more detail, this unsustainable reliance on fossil fuels is changing Earth's climate and increasing the amount of waste that humans produce. Ultimately, the combination of resource use per person and population density determines our global ecological footprint.

What factors will eventually limit the growth of the human population? Perhaps food will be the main limiting factor. Malnutrition and famine are common in some regions, but they result mainly from the unequal distribution of food rather than from inadequate production. So far, technological improvements in agriculture have allowed food supplies to keep up with global population growth. In contrast, the demands of many populations have already far exceeded the local and even regional supplies of one renewable resource—fresh water. More than 1 billion people do not have access to sufficient water to meet their basic sanitation needs. The human population may also be limited by the capacity of the environment to absorb its wastes. If so, then Earth's current human occupants could lower the planet's long-term carrying capacity for future generations.

Technology has substantially increased Earth's carrying capacity, but no population can grow indefinitely. After reading this chapter, you should realize that there is no single carrying capacity. How many people our planet can sustain depends on the quality of life each of us has and the distribution of wealth across people and nations, topics of great concern and political debate. We can decide whether zero population growth will be attained through social changes based on human choices or, instead, through increased mortality due to resource limitation, plagues, war, and environmental degradation.

CONCEPT CHECK 53.6

1. How does a human population's age structure affect its growth rate?
2. How have the rate and number of people added to the human population each year changed in recent decades?
3. **WHAT IF?** ➤ Type "personal ecological footprint calculator" into a search engine and use one of the resulting calculators to estimate your footprint. Is your current lifestyle sustainable? If not, what choices can you make to influence your own ecological footprint?

For suggested answers, see Appendix A.

53 Chapter Review

Go to **MasteringBiology**™ for Videos, Animations, Vocab Self-Quiz, Practice Tests, and more in the Study Area.

SUMMARY OF KEY CONCEPTS

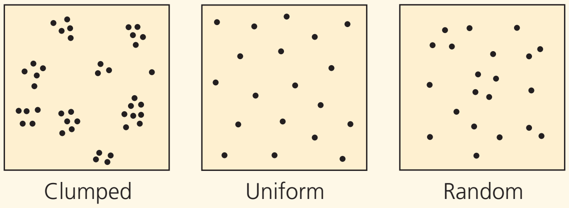
VOCAB SELF-QUIZ goo.gl/Rn5Uax

CONCEPT 53.1

Biotic and abiotic factors affect population density, dispersion, and demographics *(pp. 1247–1251)*

- Population **density**—the number of individuals per unit area or volume—reflects the interplay of births, deaths, immigration, and emigration. Environmental and social factors influence the **dispersion** of individuals.

Patterns of dispersion



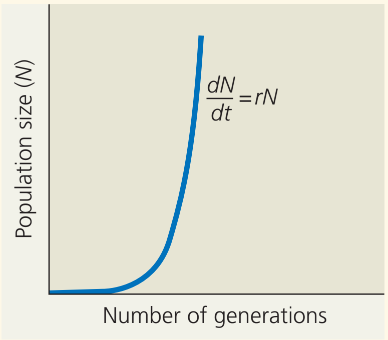
- Populations increase from births and **immigration** and decrease from deaths and **emigration**. **Life tables** and **survivorship curves** summarize specific trends in **demography**.

? *Gray whales (*Eschrichtius robustus*) gather each winter near Baja California to give birth. How might such behavior make it easier for ecologists to estimate birth and death rates for the species?*

CONCEPT 53.2

The exponential model describes population growth in an idealized, unlimited environment *(pp. 1252–1253)*

- If immigration and emigration are ignored, a population's per capita growth rate equals its birth rate minus its death rate.
- The **exponential growth** equation $dN/dt = rN$ represents a population's growth when resources are relatively abundant, where r is the **intrinsic rate of increase** and N is the number of individuals in the population.

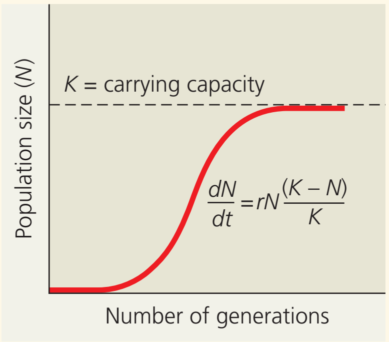


? *Suppose one population has an* r *that is twice as large as the* r *of another population. What is the maximum size that both populations will reach over time, based on the exponential model?*

CONCEPT 53.3

The logistic model describes how a population grows more slowly as it nears its carrying capacity *(pp. 1253–1256)*

- Exponential growth cannot be sustained in any population. A more realistic population model limits growth by incorporating **carrying capacity** (K), the maximum population size the environment can support.
- According to the **logistic growth** equation $dN/dt = rN(K - N)/K$, growth levels off as population size approaches the carrying capacity.



- The logistic model fits few real populations perfectly, but it is useful for estimating possible growth.

As an ecologist who manages a wildlife preserve, you want to increase the preserve's carrying capacity for a particular endangered species. How might you go about accomplishing this?

CONCEPT 53.4

Life history traits are products of natural selection *(pp. 1256–1258)*

- **Life history** traits are evolutionary outcomes reflected in the development, physiology, and behavior of organisms.
- Big-bang, or **semelparous**, organisms reproduce once and die. **Iteroparous** organisms produce offspring repeatedly.
- Life history traits such as brood size, age at maturity, and parental caregiving represent trade-offs between conflicting demands for time, energy, and nutrients. Two hypothetical life history patterns are ***K*-selection** and ***r*-selection**.

Explain why ecological trade-offs are common.

CONCEPT 53.5

Density-dependent factors regulate population growth *(pp. 1258–1263)*

- In **density-dependent** population regulation, death rates rise and birth rates fall with increasing density. A birth or death rate that does not vary with density is said to be **density independent**.
- Density-dependent changes in birth and death rates curb population increase through negative feedback and can eventually stabilize a population near its carrying capacity. Density-dependent limiting factors include intraspecific competition for limited food or space, increased predation, disease, intrinsic physiological factors, and buildup of toxic substances.
- Because changing environmental conditions periodically disrupt them, all populations exhibit some size fluctuations. Many populations undergo regular boom-and-bust cycles that are influenced by complex interactions between biotic and abiotic factors. A **metapopulation** is a group of populations linked by immigration and emigration.

Give an example of one biotic and one abiotic factor that contribute to yearly fluctuations in the size of the human population.

CONCEPT 53.6

The human population is no longer growing exponentially but is still increasing rapidly *(pp. 1263–1267)*

- Since about 1650, the global human population has grown exponentially, but within the last 50 years, the rate of growth has fallen by half. Differences in **age structure** show that while some nations' populations are growing rapidly, those of others are stable or declining in size. Infant mortality rates and life expectancy at birth vary widely in different countries.
- **Ecological footprint** is the aggregate land and water area needed to produce all the resources a person or group of people consume and to absorb all of their waste. It is one measure of how close we are to the carrying capacity of Earth, which is uncertain. With a world population of more than 7.2 billion people, we are already using many resources in an unsustainable manner.

How do humans differ from other species in the ability to "choose" a carrying capacity for their environment?

TEST YOUR UNDERSTANDING

Multiple-choice Self-Quiz questions 1–9 can be found in the Study Area in MasteringBiology.

10. INTERPRET THE DATA To estimate which age cohort in a population of females produces the most female offspring, you need information about the number of offspring produced per capita within that cohort and the number of individuals alive in the cohort. Make this estimate for Belding's ground squirrels by multiplying the number of females alive at the start of the year (column 2 in Table 53.1) by the average number of female offspring produced per female (column 5 in Table 53.1). Draw a bar graph with female age in years on the x-axis (0–1, 1–2, and so on) and total number of female offspring produced for each age cohort on the y-axis. Which cohort of female Belding's ground squirrels produces the most female young?

PRACTICE TEST
goo.gl/iAsVgL

11. EVOLUTION CONNECTION Contrast the selective pressures operating in high-density populations (those near the carrying capacity, K) versus low-density populations.

12. SCIENTIFIC INQUIRY You are testing the hypothesis that increased population density of a particular plant species increases the rate at which a pathogenic fungus infects the plant. Because the fungus causes visible scars on the leaves, you can easily determine whether a plant is infected. Design an experiment to test your hypothesis. Describe your experimental and control groups, how you would collect data, and what results you would see if your hypothesis is correct.

13. **SCIENCE, TECHNOLOGY, AND SOCIETY** Some people regard the rapid population growth of less industrialized countries as our most serious environmental problem. Others think that the population growth in industrialized countries, though smaller, is actually a greater environmental threat. What problems result from population growth in (a) less industrialized countries and (b) industrialized nations? Which do you think is a greater threat, and why?

14. **WRITE ABOUT A THEME: INTERACTIONS** In a short essay (100–150 words), identify the factor or factors in Figure 53.18 that you think may ultimately be most important for density-dependent population regulation in humans, and explain your reasoning.

15. **SYNTHESIZE YOUR KNOWLEDGE**

Locusts (grasshoppers in the family Acrididae) undergo cyclic population outbreaks, leading to massive swarms such as this one in the Canary Islands, off the west coast of Africa. Of the mechanisms of density-dependent regulation shown in Figure 53.18, choose the two that you think most apply to locust swarms, and explain why.

For selected answers, see Appendix A.

For additional practice questions, check out the **Dynamic Study Modules** in MasteringBiology. You can use them to study on your smartphone, tablet, or computer anytime, anywhere!

54 Biodiversity and Communities

▲ **Figure 54.1** **Which species benefits from this interaction?**

KEY CONCEPTS

54.1 Community interactions are classified by whether they help, harm, or have no effect on the species involved

54.2 Diversity and trophic structure characterize biological communities

54.3 Disturbance influences species diversity and composition

54.4 Biogeographic factors affect community diversity

54.5 Pathogens alter community structure locally and globally

Communities in Motion

At first glance, you might think the situation looks dire for this bluestreak cleaner wrasse, which has ventured into the mouth of the giant moray eel, a voracious predator in its coral reef habitat **(Figure 54.1)**. With one snap of its jaw, the eel could easily crush the fish and swallow it. However, the wrasse is not in danger of becoming this eel's dinner. The much larger animal remains still, with its mouth open, and allows the smaller fish free passage as it picks out and eats tiny parasites living inside the eel's mouth and on its skin.

In this interaction, both organisms benefit: The cleaner wrasse gains access to a supply of food, and its moray eel client is freed of parasites that might weaken it or spread disease. There are many other examples of such mutually beneficial "cleaner" and "client" relationships in marine habitats, such as the cleaner shrimp and eel interaction shown below. However, other interactions between species are less benign for one of the participants, and still other interactions can negatively affect the reproduction and survival of both species involved.

In Chapter 53, you learned how individuals within a population can affect other individuals of the same species. This chapter will examine ecological interactions between populations of different species. A group of populations of different species living in close enough proximity to interact is called a biological **community**.

When you see this blue icon, log in to **MasteringBiology** and go to the Study Area for digital resources.

MB **Get Ready for This Chapter**

Ecologists define the boundaries of a particular community to fit their research questions: They might study the community of decomposers and other organisms living on a rotting log, the benthic community in Lake Superior, or the community of trees and shrubs in Sequoia National Park in California.

We begin this chapter by exploring the kinds of interactions that occur between species in a community, such as the cleaner wrasse and eel in Figure 54.1. We'll then consider several of the factors that are most significant in structuring a community—in determining how many species there are, which particular species are present, and the relative abundance of these species. Finally, we'll apply some of the principles of community ecology to the study of human disease.

CONCEPT 54.1

Community interactions are classified by whether they help, harm, or have no effect on the species involved

Some key relationships in the life of an organism are its interactions with individuals of other species in the community. These **interspecific interactions** include competition, predation, herbivory, parasitism, mutualism, and commensalism. In this section, we'll define and describe each of these interactions, grouping them according to whether they have positive (+) or negative (−) effects on the survival and reproduction of each of the two species engaged in the interaction.

For example, predation is a +/− interaction, with a positive effect on the predator population and a negative effect on the prey population. Mutualism is a +/+ interaction because the survival and reproduction of both species are increased in the presence of the other. A 0 indicates that a species is not affected by the interaction in any known way. We'll consider three broad categories of ecological interactions: competition (−/−), exploitation (+/−), and positive interactions (+/+ or +/0).

Historically, most ecological research has focused on interactions that have a negative effect on at least one species, such as competition and predation. As we'll see, however, positive interactions are ubiquitous and have major effects on community structure.

Competition

Competition is a −/− interaction that occurs when individuals of different species compete for a resource that limits the survival and reproduction of each species. Weeds growing in a garden compete with garden plants for soil nutrients and water. Lynx and foxes in the northern forests of Alaska and Canada compete for prey such as snowshoe hares. In contrast, some resources, such as oxygen, are rarely in short supply on land; most terrestrial species use this resource but do not usually compete for it.

Competitive Exclusion

What happens in a community when two species compete for limited resources? In 1934, Russian ecologist G. F. Gause studied this question using laboratory experiments with two closely related ciliate species, *Paramecium aurelia* and *Paramecium caudatum* (see Figure 28.17a). He cultured the species under stable conditions, adding a constant amount of food each day. When Gause grew the two species separately, each population increased rapidly in number and then leveled off at the apparent carrying capacity of the culture (see Figure 53.11a for an illustration of the logistic growth of a *Paramecium* population). But when Gause grew the two species together, *P. caudatum* became extinct in the culture. Gause inferred that *P. aurelia* had a competitive edge in obtaining food. More generally, his results led him to conclude that two species competing for the same limiting resources cannot coexist permanently in the same place. In the absence of disturbance, one species will use the resources more efficiently and reproduce more rapidly than the other. Even a slight reproductive advantage will eventually lead to local elimination of the inferior competitor, an outcome called **competitive exclusion**.

Ecological Niches and Natural Selection

EVOLUTION Competition for limited resources can cause evolutionary change in populations. One way to examine how this occurs is to focus on an organism's **ecological niche**, the specific set of biotic and abiotic resources that an organism uses in its environment. The niche of a tropical tree lizard, for instance, includes the temperature range it tolerates, the size of branches on which it perches, the time of day when it is active, and the sizes and kinds of insects it eats. Such factors define the lizard's niche, or ecological role—how it fits into an ecosystem.

We can use the niche concept to restate the principle of competitive exclusion: Two species cannot coexist permanently in a community if their niches are identical. However, ecologically similar species *can* coexist in a community if one or more significant differences in their niches arise through time. Evolution by natural selection can result in one of the species using a different set of resources or similar resources at different times of the day or year. The differentiation of niches that enables similar species to coexist in a community is called **resource partitioning** **(Figure 54.2)**.

As a result of competition, a species' *fundamental niche*, which is the niche potentially occupied by that species, is often different from its *realized niche*, the portion of its fundamental niche that it actually occupies. Ecologists can identify the fundamental niche of a species by testing the range of conditions in which it grows and reproduces in the absence

Figure 54.2 Resource partitioning among Dominican Republic lizards. Seven species of *Anolis* lizards live in close proximity, and all feed on insects and other small arthropods. However, competition for food is reduced because each lizard species has a different preferred perch, thus occupying a distinct niche.

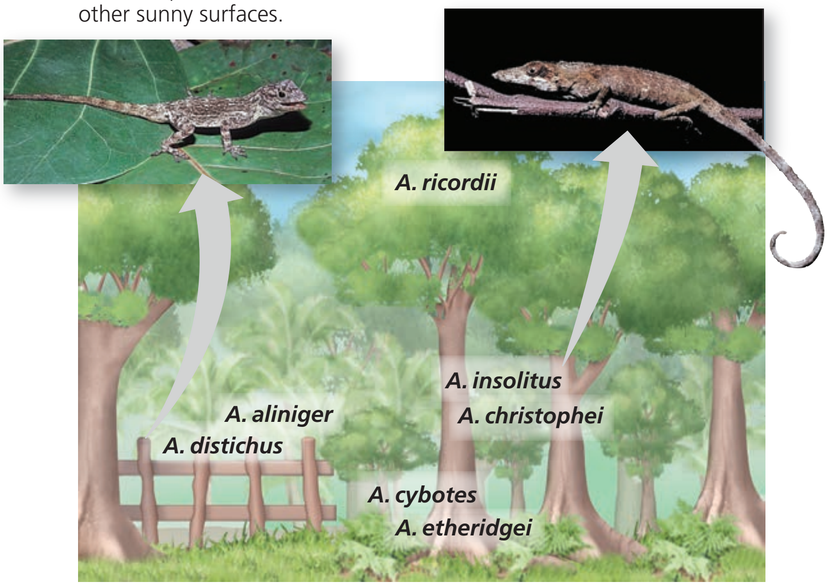
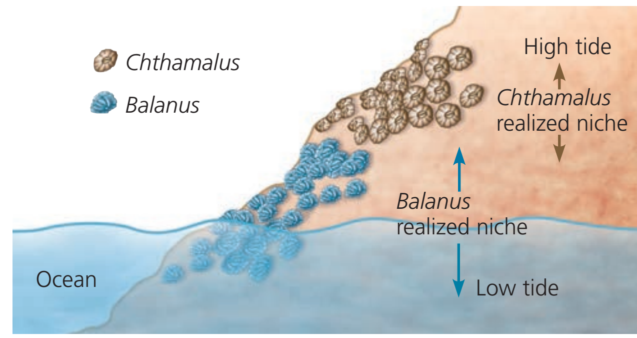


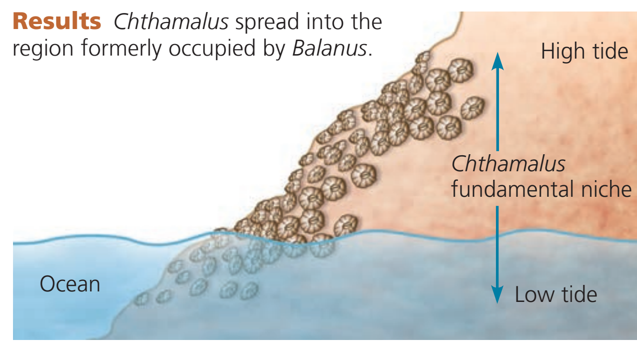
Figure 54.3

Inquiry **Can a species' niche be influenced by interspecific competition?**

Experiment Ecologist Joseph Connell studied two barnacle species—*Chthamalus stellatus* and *Balanus balanoides*—that have a stratified distribution on rocks along the coast of Scotland. *Chthamalus* is usually found higher on the rocks than *Balanus*. To determine whether the distribution of *Chthamalus* is the result of interspecific competition with *Balanus*, Connell removed *Balanus* from the rocks at several sites.



Results *Chthamalus* spread into the region formerly occupied by *Balanus*.



Conclusion Interspecific competition makes the realized niche of *Chthamalus* much smaller than its fundamental niche.

Data from J. H. Connell, The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus, Ecology* 42:710–723 (1961).

Instructors: A related Experimental Inquiry Tutorial can be assigned in MasteringBiology.

WHAT IF? *Other observations showed that* Balanus *cannot survive high on the rocks because it dries out during low tides. How would* Balanus's *realized niche compare with its fundamental niche?*

of competitors. They can also test whether a potential competitor limits a species' realized niche by removing the competitor and seeing if the first species expands into the newly available space. The classic experiment depicted in **Figure 54.3** clearly showed that competition between two barnacle species kept one species from occupying part of its fundamental niche.

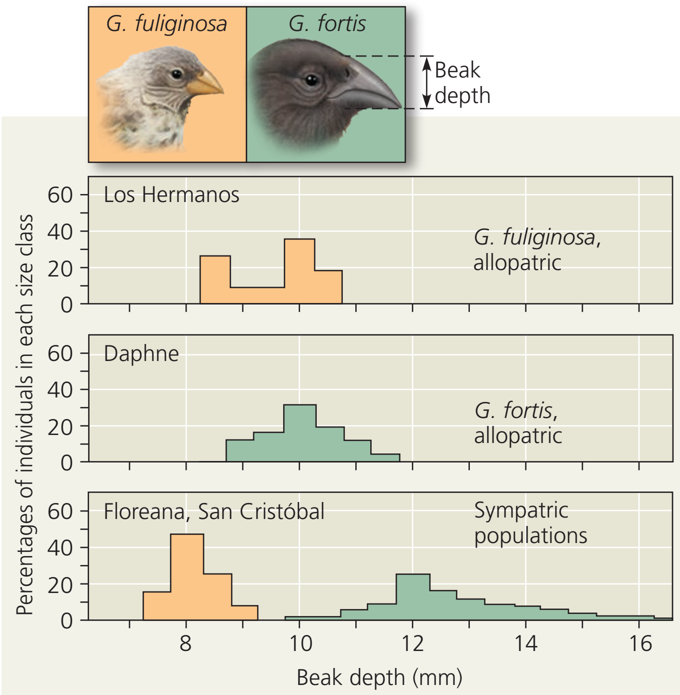
Species can partition their niches not just in space, as lizards and barnacles do, but in time as well. The common spiny mouse (*Acomys cahirinus*) and the golden spiny mouse (*A. russatus*) live in rocky habitats of the Middle East and Africa, sharing similar microhabitats and food sources. Where they coexist, *A. cahirinus* is nocturnal (active at night), while *A. russatus* is diurnal (active during the day). Surprisingly, laboratory research showed that *A. russatus* is naturally nocturnal. To be active during the day, it must override its biological clock in the presence of *A. cahirinus*. When researchers in Israel removed all *A. cahirinus* individuals from a site in the species' natural habitat, *A. russatus* individuals at that site became nocturnal, consistent with the laboratory results. This change in behavior suggests that competition exists between the species and that partitioning of their active time helps them coexist.

The golden spiny mouse (*Acomys russatus*)

Character Displacement

Closely related species whose populations are sometimes allopatric (geographically separate; see Concept 24.2) and sometimes sympatric (geographically overlapping) provide more evidence for the importance of competition in structuring communities. In some cases, the allopatric populations of such species are morphologically similar and use similar resources. By contrast, sympatric populations, which would potentially compete for resources, show differences in body structures and in the resources they use. This tendency for characteristics to diverge more in sympatric than in allopatric populations of two species is called **character displacement**. An example of character displacement can be seen in two species of Galápagos finches,

Figure 54.4 Character displacement: indirect evidence of past competition. Allopatric populations of *Geospiza fuliginosa* and *Geospiza fortis* on Los Hermanos and Daphne Islands have similar beak morphologies (top two graphs) and presumably eat similarly sized seeds. However, where the two species are sympatric on Floreana and San Cristóbal, *G. fuliginosa* has a shallower, smaller beak and *G. fortis* a deeper, larger one (bottom graph), adaptations that favor eating different-sized seeds.



INTERPRET THE DATA ➤ *If the beak length of* G. fortis *is typically 12% longer than the beak depth, what is the predicted beak length of* G. fortis *individuals with the smallest beak depths observed on Floreana and San Cristóbal Islands?*

Geospiza fuliginosa and *Geospiza fortis*: Beak depths in these species are similar in allopatric populations but have diverged considerably in sympatric populations **(Figure 54.4)**.

Exploitation

All nonphotosynthetic organisms must eat, and all organisms are at risk of being eaten. As a result, much of the drama in nature involves **exploitation**, a general term for any +/– interaction in which one species benefits by feeding on the other species, which is harmed by the interaction. Exploitative interactions include predation, herbivory, and parasitism.

Predation

Predation is a +/– interaction between species in which one species, the predator, kills and eats the other, the prey. Though the term *predation* generally elicits such images as a lion attacking and eating an antelope, it applies to a wide range of interactions. A rotifer (a tiny aquatic animal that is smaller than many unicellular protists) that kills a protist by eating it can also be considered a predator. Because eating and avoiding being eaten are prerequisites to reproductive success, the adaptations of both predators and prey tend to be refined through natural selection. In the **Scientific Skills Exercise**,

SCIENTIFIC SKILLS EXERCISE

Making a Bar Graph and a Scatter Plot

Can a Native Predator Species Adapt Rapidly to an Introduced Prey Species? Cane toads (*Bufo marinus*) were introduced to Australia in 1935 in a failed attempt to control an insect pest. Since then, the toads have spread across northeastern Australia, with a population of over 200 million today. Cane toads have glands that produce a toxin that is poisonous to snakes and other potential predators. In this exercise, you will graph and interpret data from a two-part experiment conducted to determine whether native Australian predators have developed resistance to the cane toad toxin.

How the Experiment Was Done In part 1, researchers collected 12 red-bellied black snakes (*Pseudechis porphyriacus*) from areas where cane toads had existed for 40–60 years and another 12 from areas free of cane toads. They recorded the percentage of snakes from each area that ate either a freshly killed native frog (*Limnodynastes peronii*, a species the snakes commonly eat) or a freshly killed cane toad from which the toxin gland had been removed (making the toad nonpoisonous). In part 2, researchers collected snakes from areas where cane toads had been present for 5–60 years. To assess how cane toad toxin affected the physiological activity of these snakes, they injected small amounts of the toxin into the snakes' stomachs and measured the snakes' swimming speed in a small pool.

Data from the Experiment, Part 1

Type of Prey Offered	% of Snakes From Each Area That Ate Each Type of Prey	
	Area with Cane Toads Present for 40–60 Years	Area with No Cane Toads
Native frog	100	100
Cane toad	0	50

Data from the Experiment, Part 2

Number of Years Cane Toads Had Been Present in the Area	5	10	10	20	50	60	60	60	60	60
% Reduction in Snake Swimming Speed	52	19	30	30	5	5	9	11	12	22

Data from B. L. Phillips and R. Shine, An invasive species induces rapid adaptive change in a native predator: cane toads and black snakes in Australia, *Proceedings of the Royal Society B* 273:1545–1550 (2006).

INTERPRET THE DATA

1. Make a bar graph of the data in part 1. (For additional information about graphs, see the Scientific Skills Review in Appendix F and in the Study Area in Mastering Biology.)
2. What do the data represented in the graph suggest about the effects of cane toads on the predatory behavior of red-bellied black snakes in areas where the toads are and are not currently found?
3. Suppose a novel enzyme that deactivates the cane toad toxin evolved in a snake population exposed to cane toads. If the researchers repeated part 1 of this study, predict how the results would change.
4. Identify the dependent and independent variables in part 2 and make a scatter plot. What conclusion would you draw about whether exposure to cane toads is having a selective effect on the snakes? Explain.
5. Explain why a bar graph is appropriate for presenting the data in part 1 and a scatter plot is appropriate for the data in part 2.

Instructors: A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

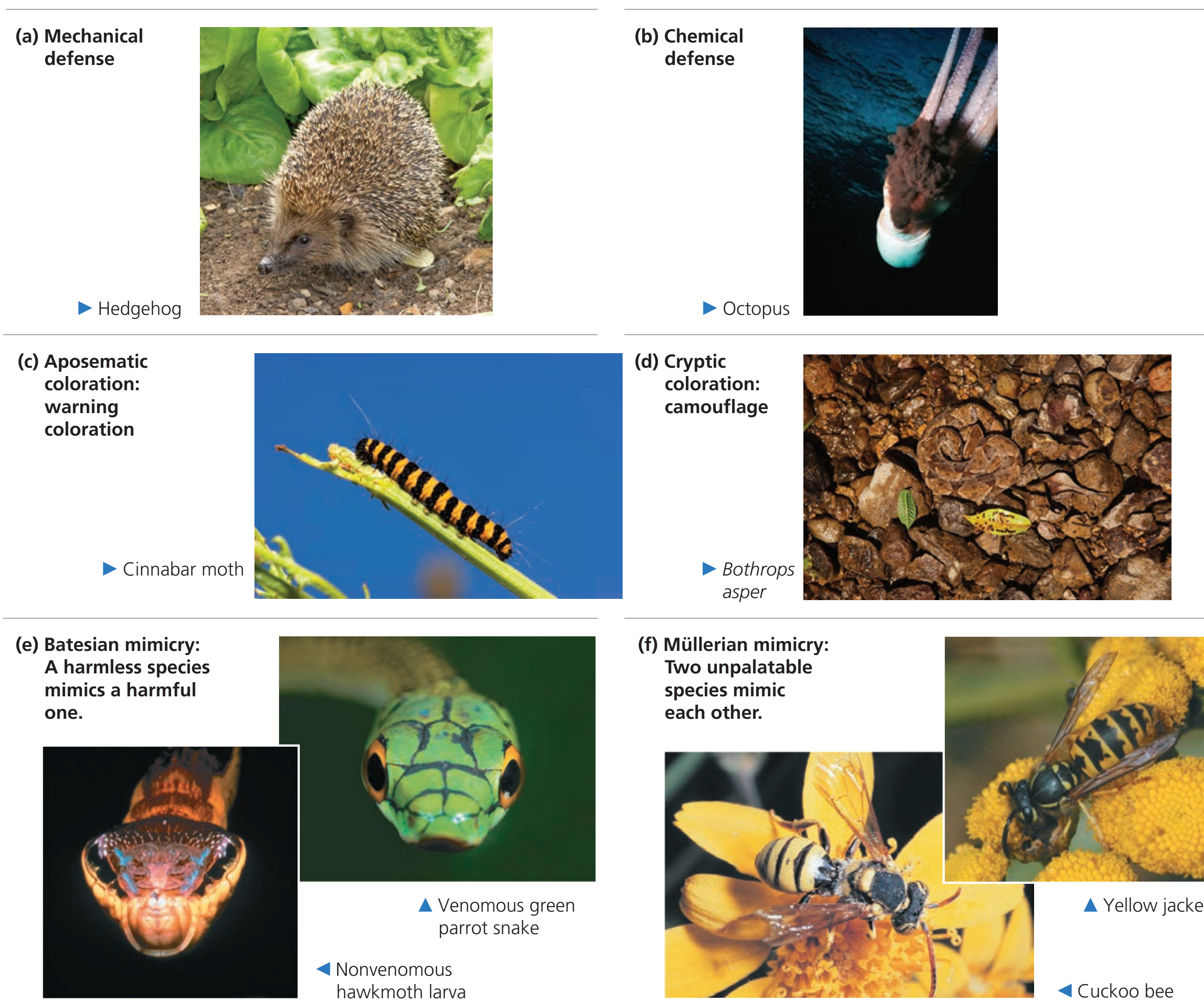
you can interpret data on the impact of natural selection for a specific predator-prey interaction.

Many important feeding adaptations of predators are obvious and familiar. Most predators have acute senses that enable them to find and identify potential prey. Rattlesnakes and other pit vipers, for example, find their prey with a pair of heat-sensing organs located between their eyes and nostrils (see Figure 50.7b). Owls have characteristically large eyes that help them see prey at night. Many predators also have adaptations such as claws, fangs, or poison that help them catch and subdue their food. Predators that pursue their prey are generally fast and agile, whereas those that lie in ambush are often disguised in their environments.

Just as predators possess adaptations for capturing prey, potential prey have adaptations that help them avoid being eaten. In animals, these adaptations include behavioral defenses such as hiding, fleeing, and forming herds or schools. Active self-defense is less common, though some large grazing mammals vigorously defend their young from predators.

Animals also display a variety of morphological and physiological defensive adaptations. Mechanical or chemical defenses protect species such as hedgehogs and octopi (**Figure 54.5a** and **b**). Some animals, such as the European fire salamander, can synthesize toxins; others accumulate toxins passively from the plants they eat. Animals with effective chemical defenses often exhibit bright

▼ Figure 54.5 Examples of defensive adaptations in animals.

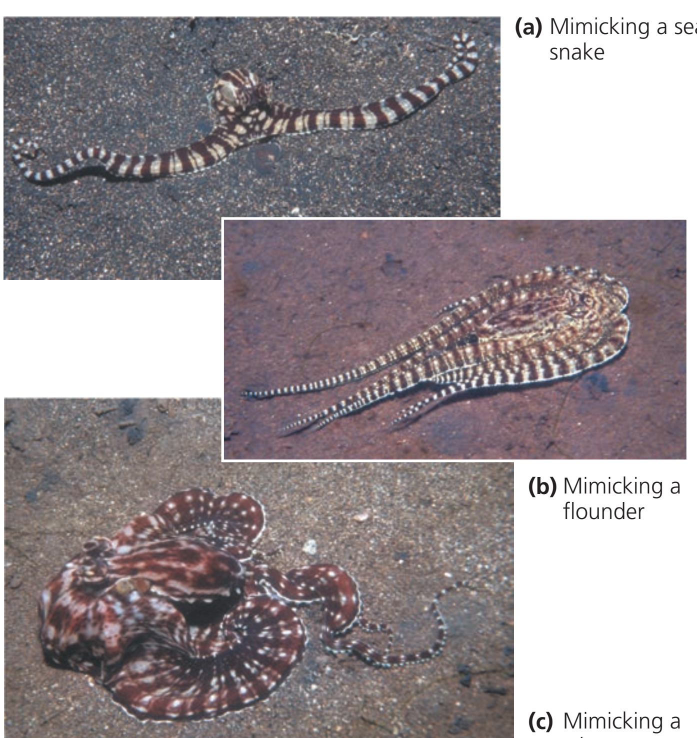


MAKE CONNECTIONS ➤ *Explain how natural selection could increase the resemblance of a harmless species to a distantly related harmful species. In addition to selection, what else could account for a harmless species resembling a closely related harmful species? (See Concept 21.2.)*

aposematic coloration, or warning coloration, such as that of cinnabar moths **(Figure 54.5c)**. Such coloration seems to be adaptive because predators often avoid brightly colored prey. **Cryptic coloration**, or camouflage, makes prey difficult to see **(Figure 54.5d)**.

Some prey species are protected by their resemblance to other species. For example, in **Batesian mimicry**, a palatable or harmless species mimics an unpalatable or harmful species to which it is not closely related. The larva of the hawkmoth *Hemeroplanes ornatus* puffs up its head and thorax when disturbed, looking like the head of a small venomous snake **(Figure 54.5e)**. In this case, the mimicry even involves behavior; the larva weaves its head back and forth and hisses like a snake. Such cases of Batesian mimicry are thought to result from natural selection, as individuals in the harmless species that happen to more closely resemble the harmful one are avoided by predators who have learned not to eat the harmful ones. Over time, closer and closer resemblance to the harmful species evolves. In **Müllerian mimicry**, two or more unpalatable species, such as the cuckoo bee and yellow jacket, resemble each other **(Figure 54.5f)**. Presumably, the more unpalatable prey there are, the faster predators learn to avoid prey with that particular appearance. Mimicry has also evolved in many predators. The mimic octopus *Thaumoctopus mimicus* **(Figure 54.6)** can take on the appearance and movement of more than a dozen marine animals, including crabs, sea stars, sea snakes, fish, and stingrays. This octopus's ability to mimic other animals enables it to approach prey—for example, imitating a crab to approach another crab and eat it. The octopus also can defend itself from predators through mimicry. When attacked by a damselfish, the octopus quickly mimics a banded sea snake, a known predator of the damselfish.

▼ Figure 54.6 The mimic octopus. (a) After hiding six of its tentacles in a hole in the seafloor, the octopus waves its other two tentacles to mimic a sea snake. **(b)** Flattening its body and arranging its arms to trail behind, the octopus mimics a flounder (a flat fish). **(c)** It can mimic a stingray by flattening most of its tentacles alongside its body while allowing one tentacle to extend behind it.



(a) Mimicking a sea snake

(b) Mimicking a flounder

(c) Mimicking a stingray

Interview with Tracy Langkilde: Studying the evolution of novel defensive adaptations in lizards

Herbivory

Ecologists use the term **herbivory** to refer to a exploitative (+/−) interaction in which an organism—an herbivore—eats parts of a plant or alga, thereby harming it. While large mammalian herbivores such as cattle, sheep, and water buffalo may be most familiar, most herbivores are actually invertebrates, such as grasshoppers, caterpillars, and beetles. In the ocean, herbivores include sea urchins, some tropical fishes, and certain mammals **(Figure 54.7)**.

Like predators, herbivores have many specialized adaptations. Many herbivorous insects have chemical sensors on their feet that enable them to distinguish between plants based on their toxicity or nutritional value. Some mammalian herbivores, such as goats, use their sense of smell to examine plants, rejecting some and eating others. They may also eat just a specific part of a plant, such as the flowers. Many herbivores also have specialized teeth or digestive systems adapted for processing vegetation (see Concept 42.4).

Unlike animals, plants cannot run away to avoid being eaten. Instead, a plant's arsenal against herbivores may feature chemical toxins or structures such as spines and

▼ Figure 54.7 An herbivorous marine mammal. This West Indian manatee (*Trichechus manatus*) in Florida is grazing on *Hydrilla*, an introduced plant species.

thorns. Among the plant compounds that serve as chemical defenses are the poison strychnine, produced by the tropical vine *Strychnos toxifera*; nicotine, from the tobacco plant; and tannins, from a variety of plant species. Compounds that are not toxic to humans but may be distasteful to many herbivores are responsible for the familiar flavors of cinnamon, cloves, and peppermint. Certain plants produce chemicals that cause abnormal development in some insects that eat them. For more examples of how plants defend themselves, see Make Connections Figure 39.27, "Levels of Plant Defenses Against Herbivores."

Parasitism

Parasitism is a +/− exploitative interaction in which one organism, the **parasite**, derives its nourishment from another organism, its **host**, which is harmed in the process. Parasites that live within the body of their host, such as tapeworms, are called **endoparasites**; parasites that feed on the external surface of a host, such as ticks and lice, are called **ectoparasites**. In one particular type of parasitism, parasitoid insects—usually small wasps—lay eggs on or in living hosts. The larvae then feed on the body of the host, eventually killing it. Some ecologists have estimated that at least one-third of all species on Earth are parasites.

Many parasites have complex life cycles involving multiple hosts. The blood fluke, which currently infects approximately 200 million people around the world, requires two hosts at different times in its development: humans and freshwater snails (see Figure 33.11). Some parasites change the behavior of their current host in ways that increase the likelihood that the parasite will reach its next host. For instance, crustaceans that are parasitized by acanthocephalan (spiny-headed) worms leave protective cover and move into the open, where they are more likely to be eaten by the birds that are the second host in the worm's life cycle.

Parasites can significantly affect the survival, reproduction, and density of their host population, either directly or indirectly. For example, ticks that feed as ectoparasites on moose can weaken their hosts by withdrawing blood and causing hair breakage and loss. In their weakened condition, the moose have a greater chance of dying from cold stress or predation by wolves.

Positive Interactions

While nature abounds with dramatic and gory examples of exploitative interactions, ecological communities are also heavily influenced by **positive interactions**, a term that refers to a +/+ or +/0 interaction in which at least one species benefits and neither is harmed. Positive interactions include mutualism and commensalism. As we'll see, positive interactions can affect the diversity of species found in an ecological community.

Mutualism

Mutualism is an interspecific interaction that benefits both species (+/+). Mutualisms are common in nature, as illustrated by examples seen in previous chapters, including cellulose digestion by microorganisms in the digestive systems of termites and ruminant mammals, animals that pollinate flowers or disperse seeds, nutrient exchange between fungi and plant roots in mycorrhizae, and photosynthesis by unicellular algae in corals. In some mutualisms, such as the acacia-ant example shown in **Figure 54.8**, each species depends on the other for their survival and reproduction. In other mutualisms, however, both species can survive on their own.

Typically, both partners in a mutualism incur costs as well as benefits. In mycorrhizae, for example, the plant

▼ Figure 54.8 Mutualism between acacia trees and ants.

(a) Certain species of acacia trees in Central and South America have hollow thorns (not shown) that house stinging ants of the genus *Pseudomyrmex*. The ants feed on nectar produced by the tree and on protein-rich swellings (yellow in the photograph) at the tips of leaflets.

(b) The acacia benefits because the pugnacious ants, which attack anything that touches the tree, remove fungal spores, small herbivores, and debris. They also clip vegetation that grows close to the acacia.

often transfers carbohydrates to the fungus, while the fungus transfers limiting nutrients, such as phosphorus, to the plant. Each partner benefits, but each partner also experiences a cost: It transfers materials that it could have used to support its own growth and metabolism. For an interaction to be considered a mutualism, the benefits to each partner must exceed the costs.

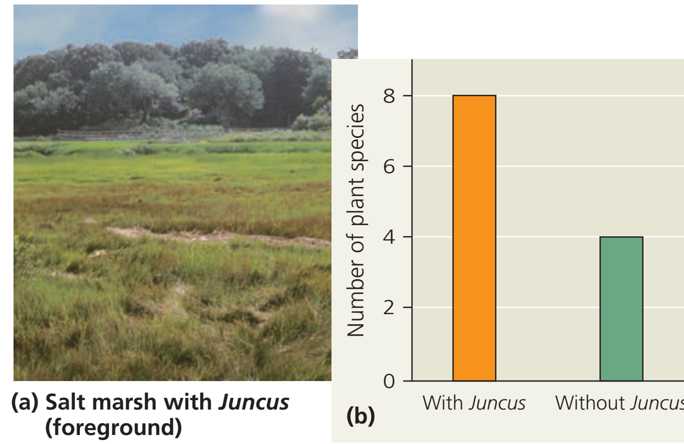
Commensalism

An interaction between species that benefits one of the species but neither harms nor helps the other (+/0) is called **commensalism**. Like mutualism, commensalisms are common in nature. For instance, many wildflower species that grow optimally in low light levels are only found in shaded, forest floor environments. Such shade-tolerant "specialists" depend entirely on the trees that tower above them—the trees provide their dim habitat. Yet the survival and reproduction of the trees are not affected by these wildflowers. Thus, these species are involved in a +/0 interaction in which the wildflowers benefit and the trees are not affected.

In another example of a commensalism, cattle egrets feed on insects flushed out of the grass by grazing bison, cattle, horses, and other herbivores **(Figure 54.9)**. Because the birds increase their feeding rates when following the herbivores, they clearly benefit from the association. Much of the time, the herbivores are not affected by the birds. At times, however, the herbivores too may derive some benefit; for example, the birds may remove and eat ticks and other ectoparasites from their skin, or they may warn the herbivores of a predator's approach. This example illustrates another key point about ecological interactions: Their effects can change over time. In this case, an interaction whose effects are typically +/0 (commensalism) may at times become +/+ (mutualism).

▼ Figure 54.9 Commensalism between cattle egrets and African buffalo.

▼ Figure 54.10 Facilitation by black rush (*Juncus gerardii*) in New England salt marshes. Black rush increases the number of plant species that can live in the upper middle zone of the marsh.



(a) Salt marsh with *Juncus* (foreground)

Positive interactions can have significant influence on the structure of ecological communities. For instance, the black rush *Juncus gerardii* makes the soil more hospitable for other plant species in some areas of New England salt marshes **(Figure 54.10a)**. *Juncus* helps prevent salt buildup in the soil by shading the soil surface, which reduces evaporation. *Juncus* also prevents the salt marsh soils from becoming oxygen depleted as it transports oxygen to its belowground tissues. In one study, when *Juncus* was removed from areas in the upper middle intertidal zone, those areas supported 50% fewer plant species **(Figure 54.10b)**.

Like positive interactions, competition and exploitation (predation, herbivory, and parasitism) also can strongly affect the structure of ecological communities, as examples throughout the rest of this chapter will show.

CONCEPT CHECK 54.1

1. What are the different types of symbioses? Is there really such a thing as a "neutral" interaction? Explain.
2. According to the principle of competitive exclusion, what outcome is expected when two species with identical niches compete for a resource? Why?
3. **MAKE CONNECTIONS ➤** Figure 24.14 illustrates how a hybrid zone can change over time. Imagine that two finch species colonize a new island and are capable of hybridizing (mating and producing viable offspring). The island contains two plant species, one with large seeds and one with small seeds, growing in isolated habitats. If the two finch species specialize in eating different plant species, would reproductive barriers be reinforced, weakened, or unchanged in this hybrid zone? Explain.

For suggested answers, see Appendix A.

CONCEPT 54.2

Diversity and trophic structure characterize biological communities

Ecological communities can be characterized by certain general attributes, including how diverse they are and the feeding relationships of their species. In some cases, as you'll read, a few species exert strong control on a community's structure, particularly on the composition, relative abundance, and diversity of its species.

Species Diversity

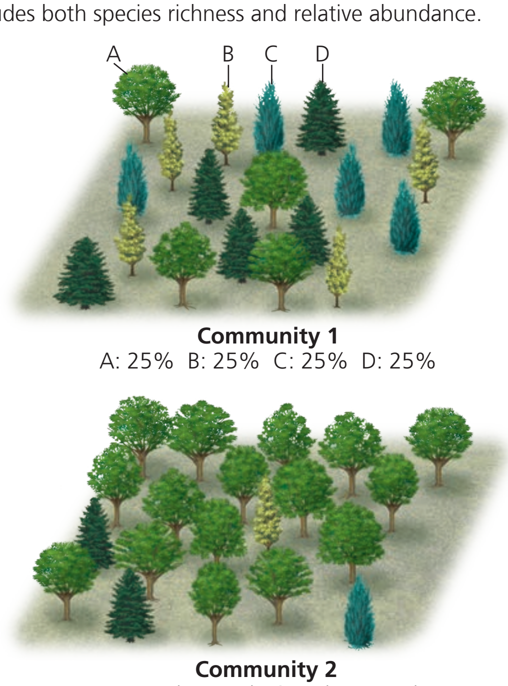
The **species diversity** of a community—the variety of different kinds of organisms that make up the community—has two components. One is **species richness**, the number of different species in the community. The other is the **relative abundance** of the different species, the proportion each species represents of all individuals in the community.

Imagine two small forest communities, each with 100 individuals distributed among four tree species (A, B, C, and D) as follows:

Community 1: 25A, 25B, 25C, 25D
Community 2: 80A, 5B, 5C, 10D

The species richness is the same for both communities because they both contain four species of trees, but the relative abundance is very different **(Figure 54.11)**. You would easily notice the four types of trees in community 1, but unless you looked carefully, you might see only the abundant species A in the second forest. Most observers would intuitively describe community 1 as the more diverse of the two communities.

Figure 54.11 Which forest is more diverse? Ecologists would say that community 1 has greater species diversity, a measure that includes both species richness and relative abundance.



Ecologists use many tools to compare the diversity of communities across time and space. They often calculate indexes of diversity based on species richness and relative abundance. One widely used index is **Shannon diversity** (H):

$$H = -(p_A \ln p_A + p_B \ln p_B + p_C \ln p_C + \ldots)$$

where A, B, C . . . are the species in the community, p is the relative abundance of each species, and ln is the natural logarithm; the ln of each value of p can be determined using the "ln" key on a scientific calculator. A higher value of H indicates a more diverse community. Let's use this equation to calculate the Shannon diversity index of the two communities in Figure 54.11. For community 1, $p = 0.25$ for each species, so

$$H = -4(0.25 \ln 0.25) = 1.39.$$

For community 2,

$$H = -[0.8 \ln 0.8 + 2(0.05 \ln 0.05) + 0.1 \ln 0.1] = 0.71.$$

These calculations confirm our intuitive description of community 1 as more diverse.

Determining the number and relative abundance of species in a community can be challenging. Because most species in a community are relatively rare, it may be hard to obtain a sample size large enough to be representative. It can also be difficult to identify some of the species in the community. If an unknown organism cannot be identified on the basis of morphology alone, it is useful to compare all or part of its genome to a reference database of DNA sequences from known organisms. For example, although the two samples of red algae shown here might appear to be two different species, comparing their sequences of a short standardized section of DNA—a *DNA "barcode"*—to a reference database shows that they belong to the same species. Researchers are increasingly using DNA sequencing for species identification as it becomes cheaper and as DNA sequences from more organisms are added to comparative databases.

Two samples, one species

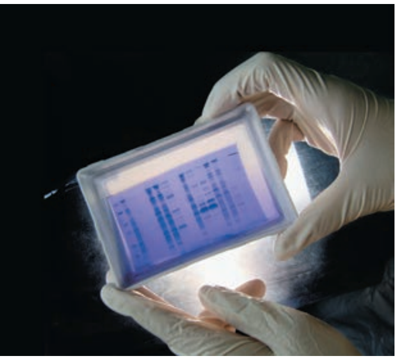
It can also be difficult to census the highly mobile or less visible members of communities, such as microorganisms, deep-sea creatures, and nocturnal species. The small size of microorganisms makes them particularly difficult to sample, so ecologists now commonly use molecular tools to help determine microbial diversity **(Figure 54.12)**.

⮟ Figure 54.12

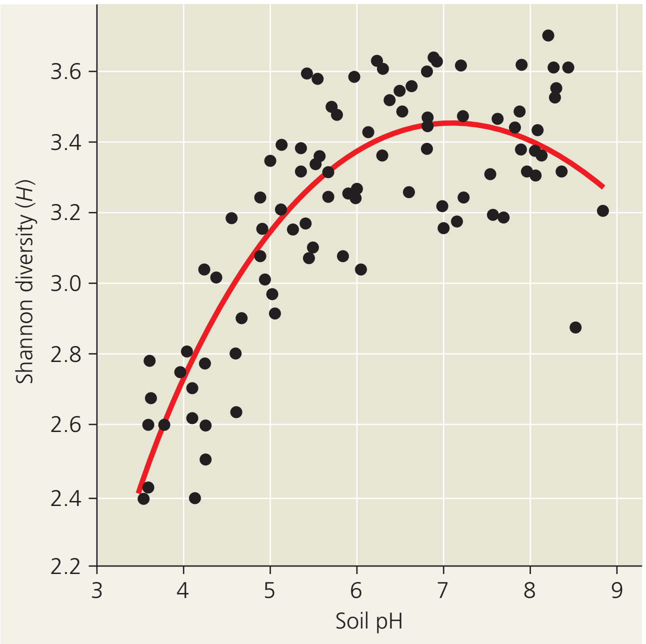
Research Method Determining Microbial Diversity Using Molecular Tools

Application Ecologists are increasingly using molecular techniques to determine microbial diversity and richness in environmental samples. One such technique produces a DNA profile for microbial taxa based on sequence variations in the DNA that encodes the small subunit of ribosomal RNA. Noah Fierer and Rob Jackson, then of Duke University, used this method to compare the diversity of soil bacteria in 98 habitats across North and South America to help identify environmental variables associated with high bacterial diversity.

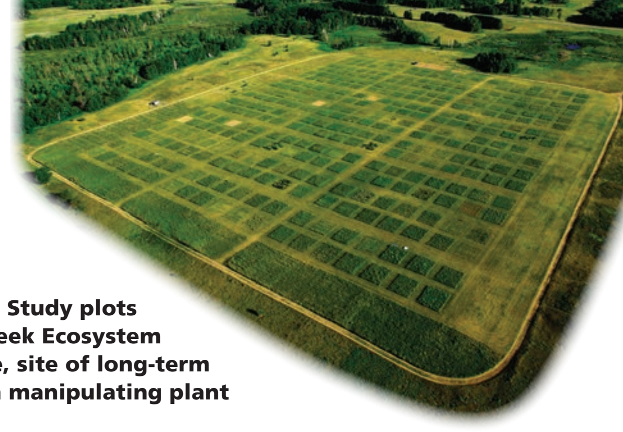
Technique Researchers first extract and purify DNA from the microbial community in each sample. They use the polymerase chain reaction (PCR; see Figure 19.8) to amplify the ribosomal DNA and label it with a fluorescent dye. Restriction enzymes then cut the amplified, labeled DNA into fragments of different lengths, which are separated by gel electrophoresis. (A gel is shown here; see also Figures 19.6 and 19.7.) The number and abundance of these fragments characterize the DNA profile of the sample. Based on their analysis, Fierer and Jackson calculated the Shannon diversity (*H*) of each sample. They then looked for a correlation between *H* and several environmental variables, including vegetation type, mean annual temperature and rainfall, and soil acidity.



Results The diversity of bacterial communities was related almost exclusively to soil pH, with the Shannon diversity being highest in neutral soils and lowest in acidic soils. Amazonian rain forests, which have extremely high plant and animal diversity, had the most acidic soils and the lowest bacterial diversity of the samples tested.



Data from N. Fierer and R. B. Jackson, The diversity and biogeography of soil bacterial communities, *Proceedings of the National Academy of Sciences USA* 103:626–631 (2006).



➤ Figure 54.13 Study plots at the Cedar Creek Ecosystem Science Reserve, site of long-term experiments on manipulating plant diversity.

Diversity and Community Stability

In addition to measuring species diversity, ecologists manipulate diversity in experimental communities in nature and in the laboratory. Many experiments examine the potential benefits of diversity, including increased productivity and stability of biological communities.

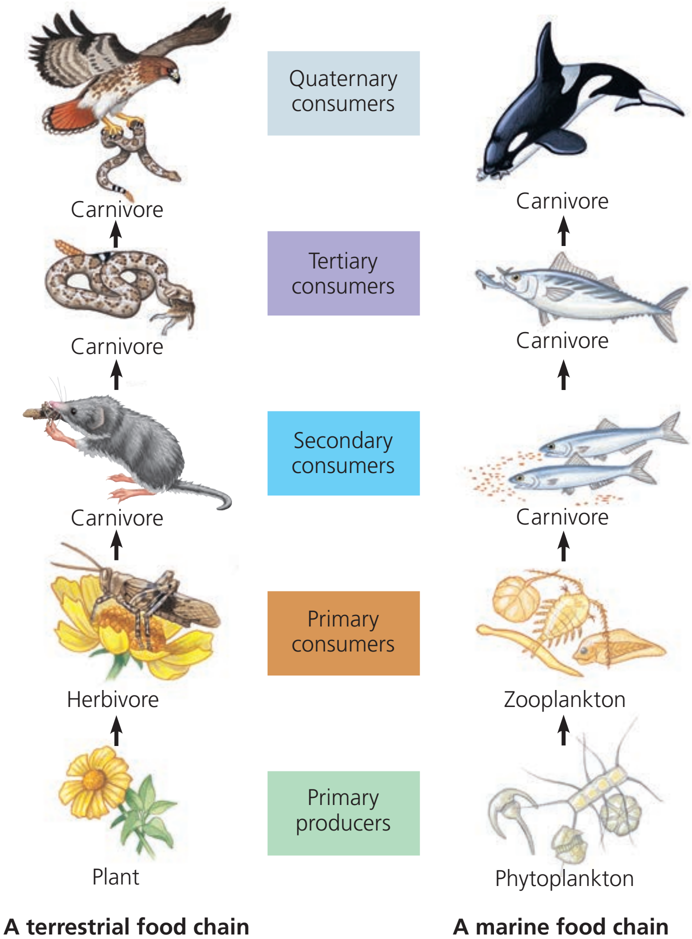
Researchers at the Cedar Creek Ecosystem Science Reserve, in Minnesota, have been manipulating plant diversity in experimental communities for more than two decades **(Figure 54.13)**. Higher-diversity communities generally are more productive and are better able to withstand and recover from environmental stresses, such as droughts. More diverse communities are also more stable year to year in their productivity. In one decade-long experiment, for instance, researchers at Cedar Creek created 168 plots, each containing 1, 2, 4, 8, or 16 perennial grassland species. The most diverse plots consistently produced more **biomass** (the total mass of all organisms in a habitat) than the single-species plots each year.

Higher-diversity communities are often more resistant to **invasive species**, which are organisms that become established outside their native range. Scientists working in Long Island Sound, off the coast of Connecticut, created communities of different levels of diversity consisting of sessile marine invertebrates, including tunicates (see Figure 34.5). They then examined how vulnerable these experimental communities were to invasion by an exotic tunicate. They found that the exotic tunicate was four times more likely to survive in lower-diversity communities than in higher-diversity ones. The researchers concluded that relatively diverse communities captured more of the resources available in the system, leaving fewer resources for the invader and decreasing its survival.

Trophic Structure

In addition to species diversity, the structure and dynamics of a community also depend on the feeding relationships between organisms—the **trophic structure** of the community. The transfer of food energy upward from its source in plants and other autotrophs (primary producers) through herbivores (primary consumers) to carnivores (secondary, tertiary, and

Figure 54.14 Examples of terrestrial and marine food chains. The arrows trace the transfer of food through the trophic levels of a community when organisms feed on one another. Decomposers, which "feed" on the remains of organisms from all trophic levels, are not shown here.



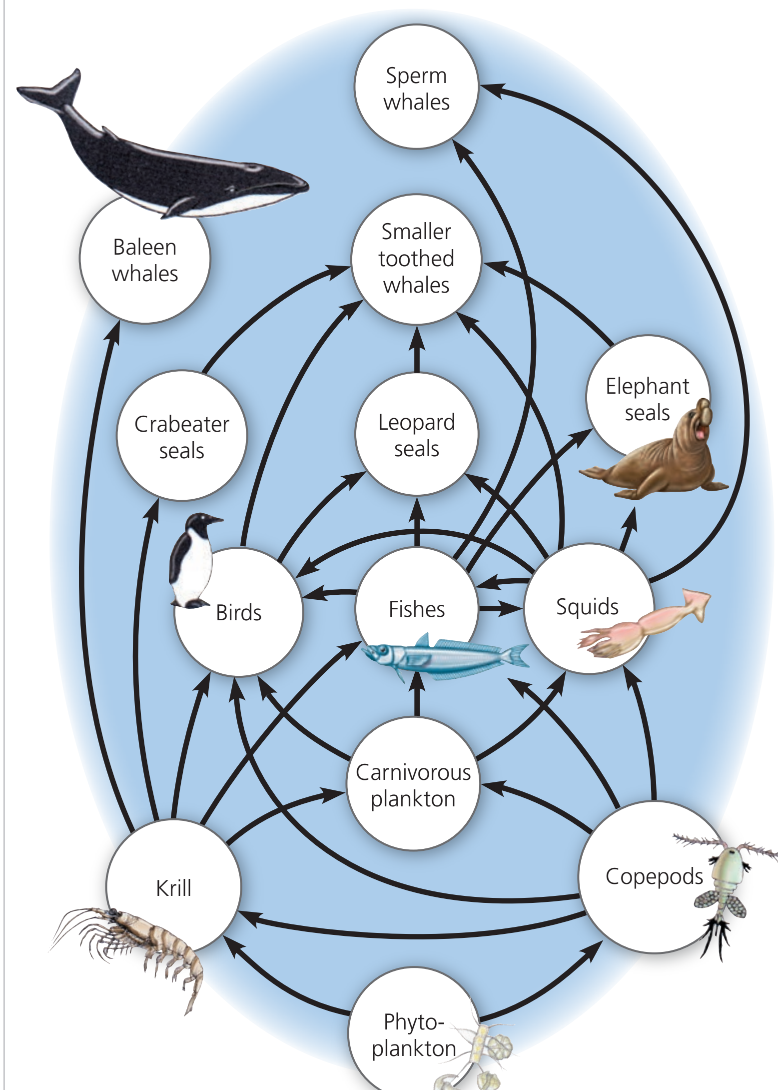
VISUAL SKILLS ➤ *Suppose the abundance of carnivores that eat zooplankton increased greatly. Use this diagram to infer how that might affect phytoplankton abundance.*

quaternary consumers) and eventually to decomposers is referred to as a **food chain** **(Figure 54.14)**. The position an organism occupies in a food chain is called its **trophic level**.

Food Webs

A food chain is not an isolated unit, separate from other feeding relationships in a community. Instead, a group of food chains are linked together to form a **food web**. Ecologists diagram the trophic relationships of a community using arrows that link species according to who eats whom. In an Antarctic pelagic community, for example, the primary producers are phytoplankton, which serve as food for the dominant grazing zooplankton, especially krill and copepods, both of which are crustaceans **(Figure 54.15)**. These zooplankton species are in turn eaten by various carnivores, including other plankton, penguins, seals, fishes, and baleen whales. Squids, which are carnivores that feed on fish and

Figure 54.15 An Antarctic marine food web. Arrows follow the transfer of food from the producers (phytoplankton) up through the trophic levels. For simplicity, this diagram omits decomposers. At various times over the last two centuries, humans have also played a role in the Antarctic food web as consumers of fish, krill, and whales.



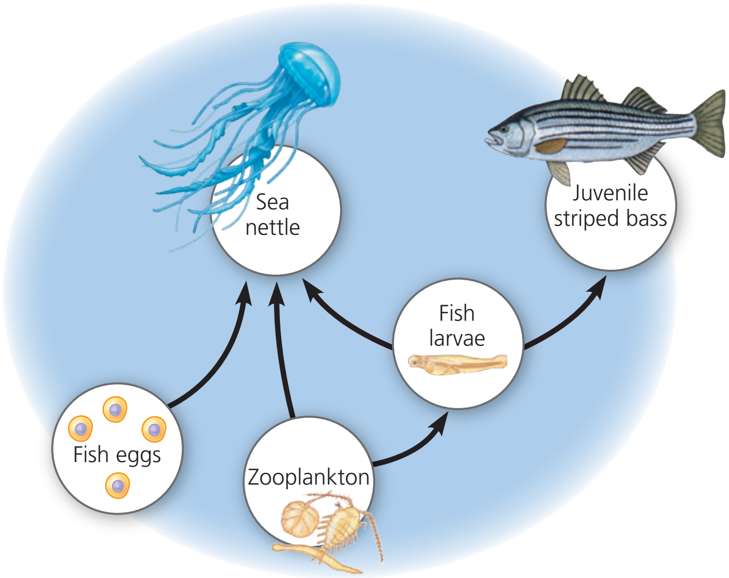
VISUAL SKILLS ➤ *For each organism in this food web, indicate the number of other kinds of organism that it eats. Which two organisms are both predator and prey for each other?*

MB Figure Walkthrough

zooplankton, are another important link in these food webs, as they are in turn eaten by seals and toothed whales.

How are food chains linked into food webs? A given species may weave into the web at more than one trophic level. In the food web shown in Figure 54.15, krill feed on phytoplankton as well as on other grazing zooplankton, such as copepods. Such "nonexclusive" consumers are also found in terrestrial communities. For instance, foxes are omnivores whose diet includes berries and other plant materials, herbivores such as mice, and other predators, such as weasels. Humans are among the most versatile of omnivores.

Figure 54.16 Partial food web for Chesapeake Bay estuary. The sea nettle (*Chrysaora quinquecirrha*) and the juvenile striped bass (*Morone saxatilis*) are the main predators of fish larvae (the bay anchovy (*Anchoa mitchilli*), along with several other species). Note that sea nettles are secondary consumers when they eat zooplankton, but tertiary consumers when they eat fish larvae, which are themselves secondary consumers of zooplankton.



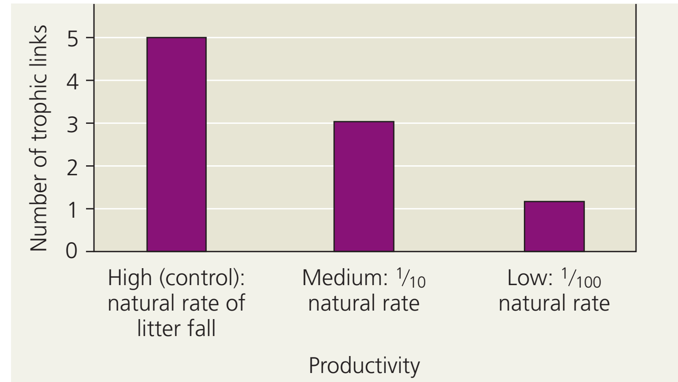
Complicated food webs can be simplified in two ways for easier study. First, species with similar trophic relationships in a given community can be grouped into broad functional groups. In Figure 54.15, more than 100 phytoplankton species are grouped as the primary producers in the food web. A second way to simplify a food web is to isolate a portion of the web that interacts very little with the rest of the community. **Figure 54.16** illustrates a partial food web for sea nettles (a type of cnidarian) and juvenile striped bass in the Chesapeake Bay estuary on the Atlantic coast of the United States.

Limits on Food Chain Length

Each food chain within a food web is usually only a few links long. In the Antarctic web of Figure 54.15, there are rarely more than seven links from the producers to any top-level predator, and most chains in this web have fewer links. In fact, most food webs studied to date have chains consisting of five or fewer links.

Why do food chains tend to be relatively short? The most common explanation, known as the **energetic hypothesis**, suggests that the length of a food chain is limited by the inefficiency of energy transfer along the chain. On average, only about 10% of the energy stored in the organic matter of each trophic level is converted to organic matter at the next trophic level (see Concept 55.3). Thus, a producer level consisting of 100 kg of plant material can support about 10 kg of herbivore biomass and 1 kg of carnivore biomass. The energetic hypothesis predicts that food chains should be relatively

Figure 54.17 Test of the energetic hypothesis for the restriction of food chain length. Researchers manipulated the productivity of experimental tree-hole communities in Queensland, Australia, by providing leaf litter input at three levels. Reducing energy input reduced food chain length, a result consistent with the energetic hypothesis.



longer in habitats characterized by higher photosynthetic production, since the amount of energy stored in primary producers is greater than in habitats with lower photosynthetic production.

Ecologists tested the energetic hypothesis in experiments that mimicked the "tree-hole" communities found in tropical forests. Many trees have small branch scars that rot, forming holes in the tree trunk. These tree holes hold water and provide a habitat for tiny communities consisting of microorganisms and insects that feed on leaf litter, as well as predatory insects. **Figure 54.17** shows the results of experiments in which researchers manipulated productivity by varying the amount of leaf litter in an experiment using artificial tree holes (water-filled pots placed around the trees); previous studies had shown that the communities that colonized these pots were similar to those in natural tree holes. As predicted by the energetic hypothesis, the pots with the most leaf litter, and hence the greatest total food supply at the producer level, supported the longest food chains.

Another factor that may limit food chain length is that carnivores in a food chain tend to be larger at higher trophic levels. The size of a carnivore puts an upper limit on the size of food it can take into its mouth. And except in a few cases, large carnivores cannot live on very small food items because they cannot obtain enough food in a given time to meet their metabolic needs. Among the exceptions are baleen whales, huge filter feeders with adaptations that enable them to consume enormous quantities of krill and other small organisms (see Figure 42.5).

Species with a Large Impact

Certain species have an especially large impact on the structure of entire communities because they are highly abundant or play a pivotal role in community dynamics. The impact of these species occurs through trophic interactions and their influence on the physical environment.

Dominant species in a community are the species that are the most abundant or that collectively have the highest biomass. There can be different explanations for why particular species become dominant. One hypothesis suggests that dominant species are competitively superior in exploiting limited resources such as space, water, or nutrients. Another hypothesis is that dominant species are most successful at avoiding herbivory or the impact of disease. The latter idea could explain the high biomass attained in some environments by invasive species such as kudzu (see Figure 56.8). Such species may not face the herbivores or parasites that would otherwise hold their populations in check.

The impact of a dominant species can be discovered when it is removed from the community. For example, the American chestnut was a dominant tree in deciduous forests of eastern North America before 1910, making up more than 40% of mature trees. Then humans accidentally introduced the fungal disease chestnut blight to New York City via nursery stock imported from Asia. Between 1910 and 1950, this fungus killed almost all of the chestnut trees in eastern North America. In this case, removing the dominant species had a relatively small impact on some species but large effects on others. Oaks, hickories, beeches, and red maples that were already present in the forest increased in abundance and replaced the chestnuts. No mammals or birds seemed to have been harmed by the loss of the chestnut, but seven species of moths and butterflies that fed on the tree became extinct.

In contrast to dominant species, **keystone species** are not usually abundant in a community. They exert strong control on community structure not by numerical might but by their pivotal ecological roles. **Figure 54.18** highlights the importance of a keystone species, a sea star, in maintaining the diversity of an intertidal community.

Still other organisms exert their influence on a community not through trophic interactions but by changing their physical environment. Species that dramatically alter their environment are called **ecosystem engineers** or, to avoid implying conscious intent, "foundation species." A familiar ecosystem engineer is the beaver **(Figure 54.19)**. The effects of ecosystem engineers on other species can be positive or negative, depending on the needs of the other species.

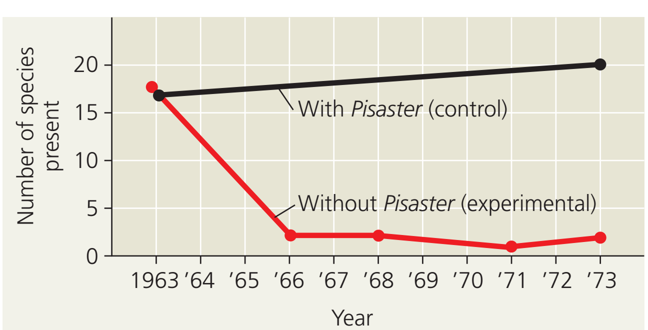
Figure 54.18

Inquiry Is *Pisaster ochraceus* a keystone species?

Experiment In rocky intertidal communities of western North America, the relatively uncommon sea star *Pisaster ochraceus* preys on mussels such as *Mytilus californianus*, a dominant species and strong competitor for space.

Robert Paine, of the University of Washington, removed *Pisaster* from an area in the intertidal zone and examined the effect on species richness.

Results In the absence of *Pisaster*, species richness declined as mussels monopolized the rock face and eliminated most other invertebrates and algae. In a control area where *Pisaster* was not removed, species richness changed very little.



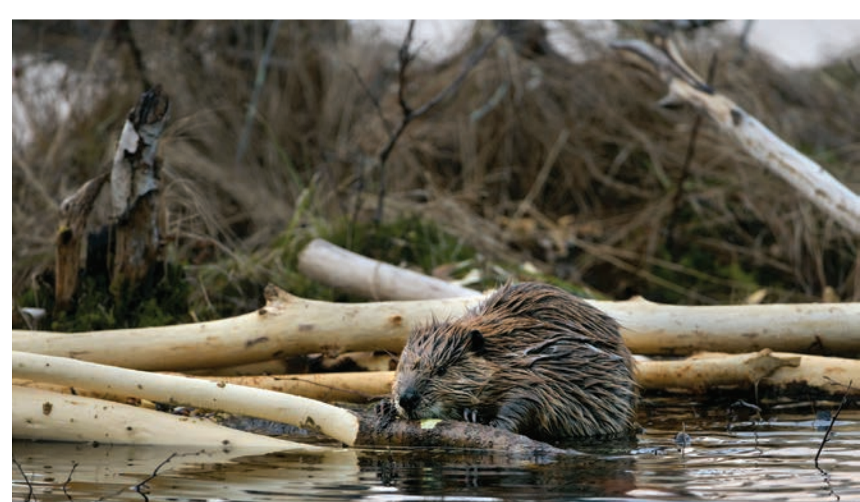
Conclusion *Pisaster* acts as a keystone species, exerting an influence on the community that is not reflected in its abundance.

Data from R. T. Paine, Food web complexity and species diversity, *American Naturalist* 100:65–75 (1966).

WHAT IF? ➤ *Suppose that an invasive fungus killed most individuals of* Mytilus *at these sites. Predict how species richness would be affected if* Pisaster *were then removed.*

HHMI Video: Some Animals Are More Equal than Others: Keystone Species and Trophic Cascades

Figure 54.19 Beavers as ecosystem engineers. By felling trees, building dams, and creating ponds, beavers can transform large areas of forest into flooded wetlands.



Bottom-Up and Top-Down Controls

The ways in which adjacent trophic levels affect one another can be useful for describing community organization. Let's consider the three possible relationships between plants (V for vegetation) and herbivores (H):

$$V \rightarrow H \qquad V \leftarrow H \qquad V \leftrightarrow H$$

The arrows indicate that a change in the biomass of one trophic level causes a change in the other trophic level. $V \rightarrow H$ means that an increase in vegetation will increase the numbers or biomass of herbivores, but not vice versa. In this situation, herbivores are limited by vegetation, but vegetation is not limited by herbivory. In contrast, $V \leftarrow H$ means that an increase in herbivore biomass will decrease the abundance of vegetation, but not vice versa. A double-headed arrow indicates that each trophic level is sensitive to changes in the biomass of the other.

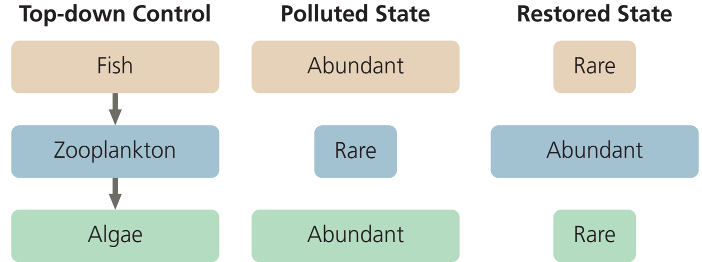
Two models of community organization are common: the bottom-up model and the top-down model. The $V \rightarrow H$ linkage suggests a **bottom-up model**, which postulates a unidirectional influence from lower to higher trophic levels. In this case, the presence or absence of mineral nutrients (N) controls plant (V) numbers, which control herbivore (H) numbers, which in turn control predator (P) numbers. The simplified bottom-up model is thus $N \rightarrow V \rightarrow H \rightarrow P$. To change the community structure of a bottom-up community, you need to alter biomass at the lower trophic levels, allowing those changes to propagate up through the food web. If you add mineral nutrients to stimulate plant growth, then the higher trophic levels should also increase in biomass. If you change predator abundance, however, the effect should not extend down to the lower trophic levels.

In contrast, the **top-down model** postulates the opposite: Predation mainly controls community organization because predators limit herbivores, herbivores limit plants, and plants limit nutrient levels through nutrient uptake. The simplified top-down model, $N \leftarrow V \leftarrow H \leftarrow P$, is also called the *trophic cascade model*. In a lake community with four trophic levels, the model predicts that removing the top carnivores will increase the abundance of primary carnivores, in turn decreasing the number of herbivores, increasing phytoplankton abundance, and decreasing concentrations of mineral nutrients. The effects thus move down the trophic structure as alternating +/− effects.

Ecologists have applied the top-down model to improve water quality in lakes with a high abundance of algae. This approach, called **biomanipulation**, attempts to prevent algal blooms by altering the density of higher-level consumers. In lakes with three trophic levels, removing fish should improve water quality by increasing zooplankton density, thereby decreasing algal populations **(Figure 54.20)**. In lakes with four trophic levels, adding top predators should have the same effect.

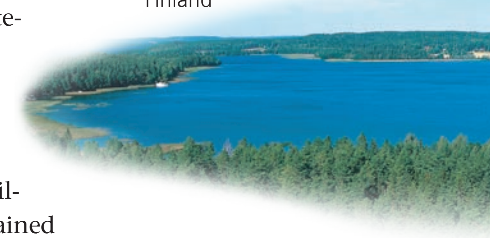
Ecologists in Finland used biomanipulation to help purify Lake Vesijärvi, a large lake that was polluted with city sewage

▼ Figure 54.20 Results of biomanipulation in a lake with top-down control of community organization. Decreasing the abundance of fish that ate zooplankton results in a decrease in the biomass of algae, improving water quality.



and industrial wastewater until 1976. After pollution controls reduced these inputs, the water quality of the lake began to improve. By 1986, however, massive blooms of cyanobacteria started to occur in the lake. These blooms coincided with an increase in the population of roach, a fish species that eats zooplankton, which otherwise keep the cyanobacteria and algae in check. To reverse these changes, ecologists removed nearly a million kilograms of fish from the lake between 1989 and 1993, reducing roach abundance by about 80%. At the same time, they added a fourth trophic level by stocking the lake with pike perch, a predatory fish that eats roach. The water became clear, and the last cyanobacterial bloom was in 1989. Ecologists continue to monitor the lake for evidence of cyanobacterial blooms and low oxygen availability, but the lake has remained clear, even though roach removal ended in 1993.

▼ Lake Vesijärvi, Finland



As these examples show, communities vary in their degree of bottom-up and top-down control. To manage agricultural landscapes, parks, reservoirs, and fisheries, we need to understand each particular community's dynamics.

CONCEPT CHECK 54.2

1. What two components contribute to species diversity? Explain how two communities with the same number of species can differ in species diversity.
2. How is a food chain different from a food web?
3. **WHAT IF?** ➤ Consider a grassland with five trophic levels: grasses, mice, snakes, raccoons, and bobcats. If you released additional bobcats into the grassland, how would grass biomass change if the bottom-up model applied? If the top-down model applied?
4. **MAKE CONNECTIONS** ➤ Rising atmospheric CO_2 levels lead to ocean acidification (see Figure 3.12) and higher ocean temperatures, both of which can reduce krill abundance. Predict how a drop in krill abundance might affect other organisms in the food web shown in Figure 54.15. Which organisms are particularly at risk? Explain.

For suggested answers, see Appendix A.

CONCEPT 54.3

Disturbance influences species diversity and composition

Decades ago, most ecologists favored the traditional view that biological communities are at equilibrium, a more or less stable balance, unless seriously disturbed by human activities. The "balance of nature" view focused on competition as a key factor determining community composition and maintaining stability in communities. *Stability* in this context refers to a community's tendency to reach and maintain a relatively constant composition of species.

One of the earliest proponents of this view, F. E. Clements, of the Carnegie Institution of Washington, argued in the early 1900s that the community of plants at a site had only one stable equilibrium, a *climax community* controlled solely by climate. According to Clements, biotic interactions caused the species in the community to function as an integrated unit—in effect, as a superorganism. His argument was based on the observation that certain species of plants are consistently found together, such as the oaks, maples, birches, and beeches in deciduous forests of the northeastern United States.

Other ecologists questioned whether most communities were at equilibrium or functioned as integrated units. A. G. Tansley, of Oxford University, challenged the concept of a climax community, arguing that differences in soils, topography, and other factors created many potential communities that were stable within a region. H. A. Gleason, of the University of Chicago, saw communities not as superorganisms but as chance assemblages of species found together because they happen to have similar abiotic requirements—for example, for temperature, rainfall, and soil type. Gleason and other ecologists also realized that disturbance keeps many communities from reaching a state of equilibrium in species diversity or composition. A **disturbance** is an event, such as a storm, fire, flood, drought, or human activity, that changes a community by removing organisms from it or altering resource availability.

This emphasis on change in communities has led to the formulation of the **nonequilibrium model**, which describes most communities as constantly changing after disturbance. Even relatively stable communities can be rapidly transformed into nonequilibrium communities. Let's examine some of the ways that disturbances influence community structure and composition.

Characterizing Disturbance

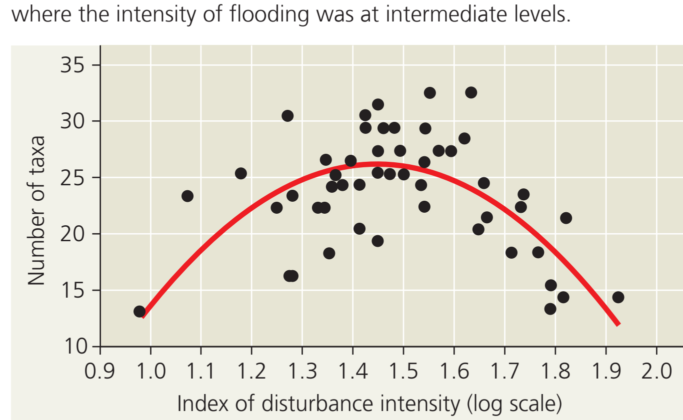
The types of disturbances and their frequency and severity vary among communities. Storms disturb almost all communities, even those in the oceans through the action of waves. Fire is a significant disturbance; in fact, chaparral and some grassland biomes require regular burning to maintain their structure and species composition. Many streams and ponds are disturbed by seasonal flooding and drying. A high level of disturbance is generally the result of frequent *and* intense disturbance, while low disturbance levels can result from either a low frequency or low intensity of disturbance.

The **intermediate disturbance hypothesis** states that moderate levels of disturbance foster greater species diversity than do high or low levels of disturbance. High levels of disturbance reduce diversity by creating environmental stresses that exceed the tolerances of many species or by disturbing the community so often that slow-growing or slow-colonizing species are excluded. At the other extreme, low levels of disturbance can reduce species diversity by allowing competitively dominant species to exclude less competitive ones. Meanwhile, intermediate levels of disturbance can foster greater species diversity by opening up habitats for occupation by less competitive species. Such intermediate disturbance levels rarely create conditions so severe that they exceed the environmental tolerances or recovery rates of potential community members.

The intermediate disturbance hypothesis is supported by many terrestrial and aquatic studies. In one study, ecologists in New Zealand compared the richness of invertebrates living in the beds of streams exposed to different frequencies and intensities of flooding **(Figure 54.21)**. When floods occurred either very frequently or rarely, invertebrate richness was low. Frequent floods made it difficult for some species to become established in the streambed, while rare floods resulted in species being displaced by superior competitors. Invertebrate richness peaked in streams that had an intermediate frequency or intensity of flooding, as predicted by the hypothesis.

Although moderate levels of disturbance appear to maximize species diversity in some cases, small and large

▼ Figure 54.21 Testing the intermediate disturbance hypothesis. Researchers identified the taxa (species or genera) of invertebrates at two locations in each of 27 New Zealand streams. They assessed the intensity of flooding at each location using an index of streambed disturbance. The number of invertebrate taxa peaked where the intensity of flooding was at intermediate levels.



disturbances also can have important effects on community structure. Small-scale disturbances can create patches of different habitats across a landscape, which help maintain diversity in a community. Large-scale disturbances are also a natural part of many communities. Much of Yellowstone National Park, for example, is dominated by lodgepole pine, a tree species that requires the rejuvenating influence of periodic fires. Lodgepole pine cones remain closed until exposed to intense heat. When a forest fire burns the trees, the cones open and the seeds are released. The new generation of lodgepole pines can then thrive on nutrients released from the burned trees and in the sunlight that is no longer blocked by taller trees.

In the summer of 1988, extensive areas of Yellowstone burned during a severe drought **(Figure 54.22a)**. By 1989, many burned areas in the park were largely covered with new vegetation, suggesting that the species in this community are adapted to rapid recovery after fire **(Figure 54.22b)**. In fact, large-scale fires have periodically swept through the lodgepole pine forests of Yellowstone and other northern areas for thousands of years. In contrast, more southerly pine forests were historically affected by frequent but low-intensity fires. In these forests, a century of human intervention to suppress small fires has allowed an unnatural buildup of fuels in some places and elevated the risk of large, severe fires to which the species are not adapted.

Studies of the Yellowstone forest community and many others indicate that they are nonequilibrium communities, changing continually because of natural disturbances and the internal processes of growth and reproduction. Mounting evidence suggests that nonequilibrium conditions are in fact the norm for most communities.

▼ **Figure 54.22 Recovery following a large-scale disturbance.** The 1988 Yellowstone National Park fires burned large areas of forests dominated by lodgepole pines.

(a) Soon after fire. While all trees in the foreground of this photograph were killed by the fire, unburned trees can be seen in other locations.

(b) One year after fire. The community has begun to recover. Herbaceous plants, different from those in the former forest, cover the ground.

Ecological Succession

Changes in the composition and structure of terrestrial communities are most apparent after a severe disturbance, such as a volcanic eruption or a glacier, strips away all the existing vegetation. The disturbed area may be colonized by a variety of species, which are gradually replaced by other species, which are in turn replaced by still other species—a process called **ecological succession**. When this process begins in a virtually lifeless area where soil has not yet formed, such as on a new volcanic island or on the rubble (moraine) left by a retreating glacier, it is called **primary succession**.

During primary succession, the only life-forms initially present are often prokaryotes and protists. Lichens and mosses, which grow from windblown spores, are commonly the first macroscopic photosynthesizers to colonize such areas. Soil develops gradually as rocks weather and organic matter accumulates from the decomposed remains of the early colonizers. Once soil is present, the lichens and mosses are usually overgrown by grasses, shrubs, and trees that sprout from seeds blown in from nearby areas or carried in by animals. Eventually, an area is colonized by plants that become the community's dominant form of vegetation. Producing such a community through primary succession may take hundreds or thousands of years.

Early-arriving species and later-arriving ones may be linked by one of three key processes. The early arrivals may *facilitate* the appearance of the later species by making the environment more favorable—for example, by increasing the fertility of the soil. Alternatively, the early species may *inhibit* establishment of the later species, so that successful colonization by later species occurs in spite of, rather than because of, the activities of the early species. Finally, the early species may be completely independent of the later species, which *tolerate*

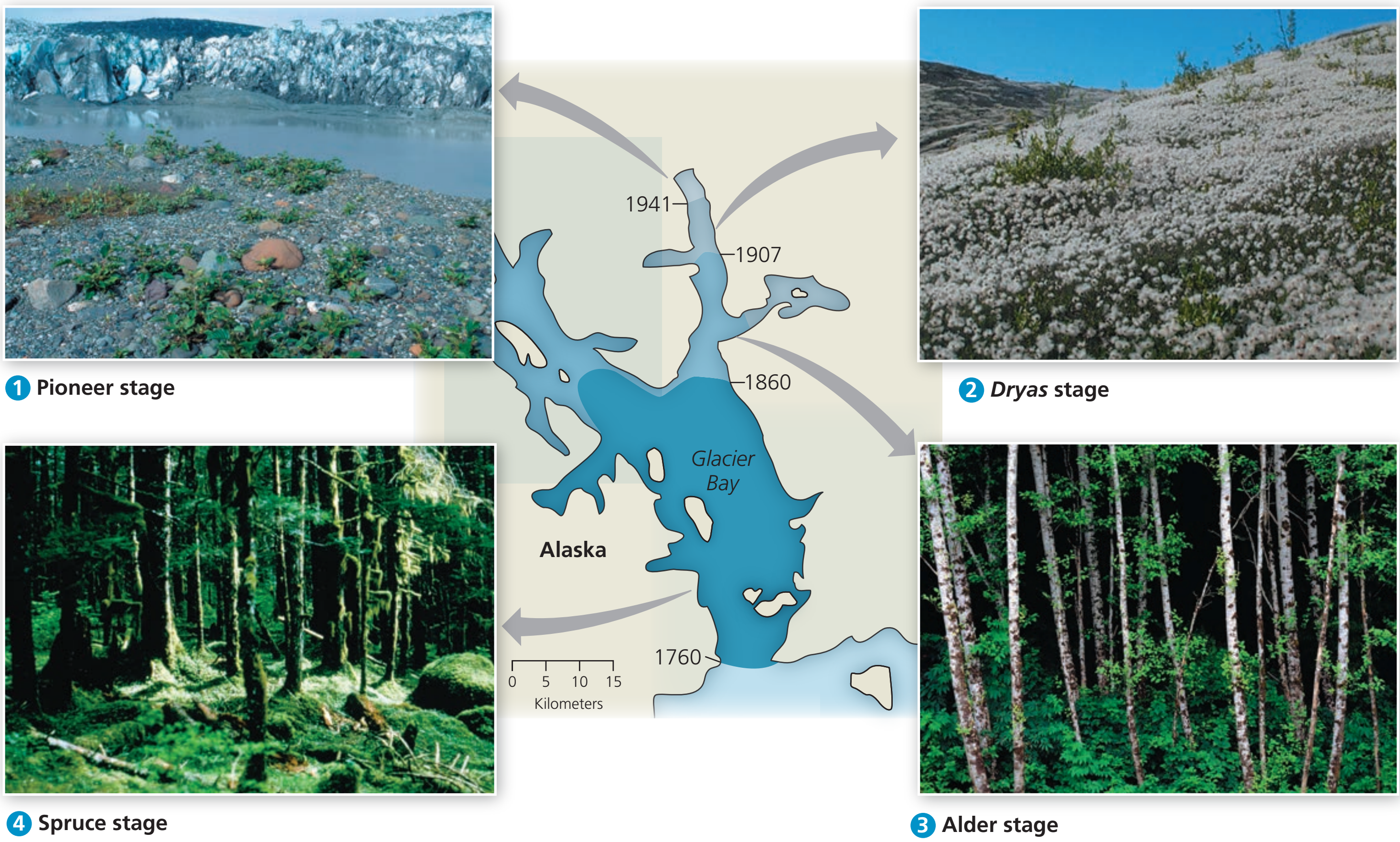


Figure 54.23 Glacial retreat and primary succession at Glacier Bay, Alaska. The different shades of blue on the map show retreat of the glacier since 1760, based on historical descriptions.

conditions created early in succession but are neither helped nor hindered by early species.

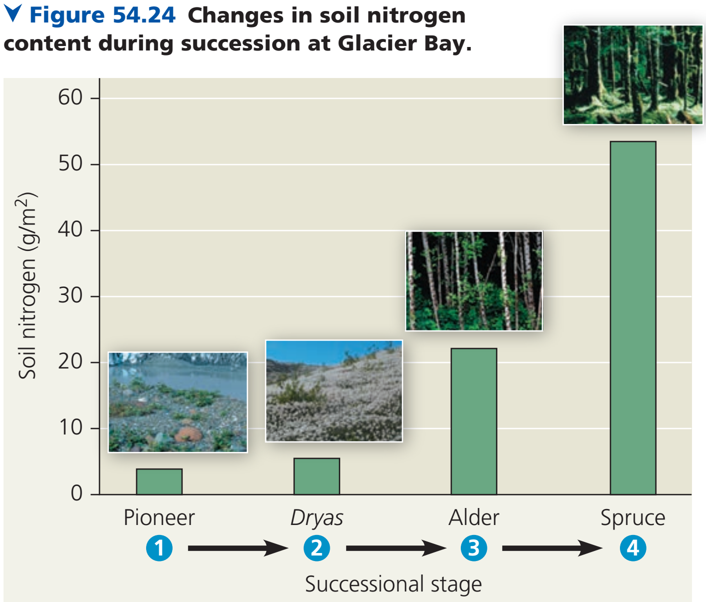
Ecologists have conducted some of the most extensive research on primary succession at Glacier Bay in southeastern Alaska, where glaciers have retreated more than 100 km since 1760 **(Figure 54.23)**. By studying the communities at different distances from the mouth of the bay, ecologists can examine different stages in succession. 1 The exposed glacial moraine is colonized first by pioneering species that include liverworts, mosses, fireweed, scattered *Dryas* (a mat-forming shrub), and willows. 2 After about three decades, *Dryas* dominates the plant community. 3 A few decades later, the area is invaded by alder, which forms dense thickets up to 9 m tall. 4 In the next two centuries, these alder stands are overgrown first by Sitka spruce and later by western hemlock and mountain hemlock. In areas of poor drainage, the forest floor of this spruce-hemlock forest is invaded by sphagnum moss, which holds water and acidifies the soil, eventually killing the trees. Thus, by about 300 years after glacial retreat, the vegetation consists of sphagnum bogs on the poorly drained flat areas and spruce-hemlock forest on the well-drained slopes.

Succession on glacial moraines is related to changes in soil nutrients and other environmental factors caused by transitions in the vegetation. Because the bare soil after glacial retreat is low in nitrogen content, almost all the pioneer plant species begin succession with poor growth and yellow leaves due to limited nitrogen supply. The exceptions are *Dryas* and alder, whose roots host symbiotic bacteria that fix atmospheric nitrogen (see photograph on this page and Figure 37.12). Soil nitrogen content increases quickly during the alder stage of succession and keeps increasing during the spruce stage **(Figure 54.24)**. By altering soil properties, pioneer plant species can facilitate colonization by new plant species during succession.

Alder root with a cluster of nodules containing nitrogen-fixing bacteria

In contrast to primary succession, **secondary succession** occurs when an existing community has been cleared by a disturbance that leaves the soil intact, as in Yellowstone following the 1988 fires (see Figure 54.22). Following the disturbance, the area may return to something like its original

Figure 54.24 Changes in soil nitrogen content during succession at Glacier Bay.



MAKE CONNECTIONS ➤ *Figure 37.12 illustrates two types of atmospheric nitrogen fixation by prokaryotes. At the earliest stages of primary succession, before any plants are present at a site, which type of nitrogen fixation would occur, and why?*

state. For instance, in a forested area that has been cleared for farming and later abandoned, the earliest plants to recolonize are often herbaceous species that grow from windblown or animal-borne seeds. If the area has not been burned or heavily grazed, woody shrubs may in time replace most of the herbaceous species, and forest trees may eventually replace most of the shrubs.

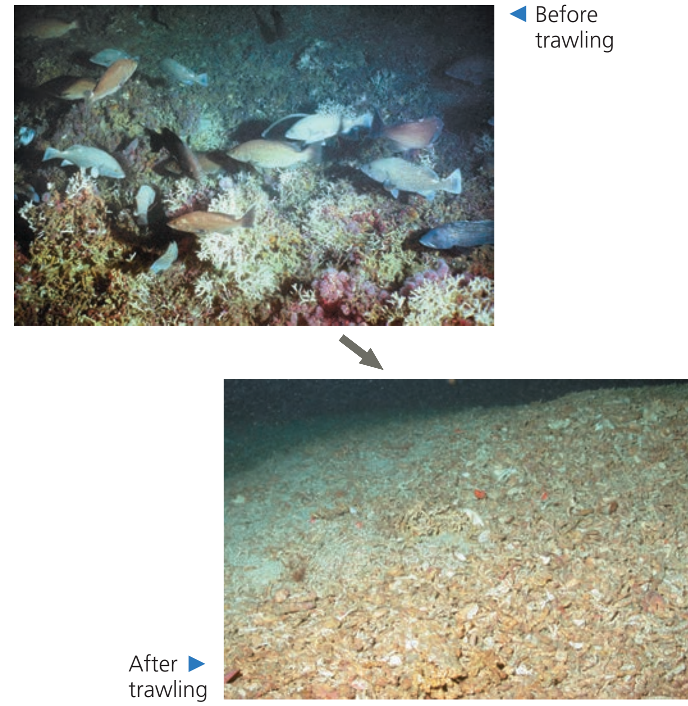
Human Disturbance

Ecological succession is a response to disturbance of the environment, and the strongest disturbances today are human activities. Agricultural development has disrupted what were once the vast grasslands of the North American prairie. Tropical rain forests are quickly disappearing as a result of clear-cutting for lumber, cattle grazing, and farmland. Centuries of overgrazing and agricultural disturbance have contributed to famine in parts of Africa by turning seasonal grasslands into vast barren areas.

Human actions have disturbed marine ecosystems as well as terrestrial ones. The effects of ocean trawling, in which boats drag weighted nets across the seafloor, are similar to those of clear-cutting a forest or plowing a field. The trawls scrape and scour corals and other life on the seafloor **(Figure 54.25)**. In a typical year, ships trawl an area about the size of South America, 150 times larger than the area of forests that are clear-cut annually.

Because disturbance by human activities is often severe, it reduces species diversity in many communities. In Chapter 56, we'll take a closer look at how human-caused disturbance is affecting the diversity of life.

Figure 54.25 Disturbance of the ocean floor by trawling. These photos show the seafloor off northwestern Australia before and after deep-sea trawlers have passed through.



CONCEPT CHECK 54.3

1. Why do high and low levels of disturbance usually reduce species diversity? Why does an intermediate level of disturbance promote species diversity?
2. During succession, how might the early species facilitate the arrival of other species?
3. **WHAT IF?** ➤ Most prairies experience regular fires, typically every few years. If these disturbances were relatively modest, how would the species diversity of a prairie likely be affected if no burning occurred for 100 years? Explain your answer.

For suggested answers, see Appendix A.

CONCEPT 54.4

Biogeographic factors affect community diversity

So far, we have examined relatively small-scale or local factors that influence the diversity of communities, including the effects of species interactions, dominant species, and many types of disturbances. Large-scale biogeographic factors also contribute to the tremendous range of diversity observed in biological communities. The contributions of two biogeographic factors in particular—the latitude of a community and the area it occupies—have been investigated for more than a century.

Latitudinal Gradients

In the 1850s, both Charles Darwin and Alfred Wallace pointed out that plant and animal life was generally more abundant and diverse in the tropics than in other parts of the globe. Since that time, many researchers have confirmed this observation. One study found that a 6.6-hectare (1 ha = 10,000 m^2) plot in tropical Malaysia contained 711 tree species, while a 2-ha plot of deciduous forest in Michigan typically contained just 10 to 15 tree species. Many groups of animals show similar latitudinal gradients. For instance, there are more than 200 species of ants in Brazil but only 7 in Alaska.

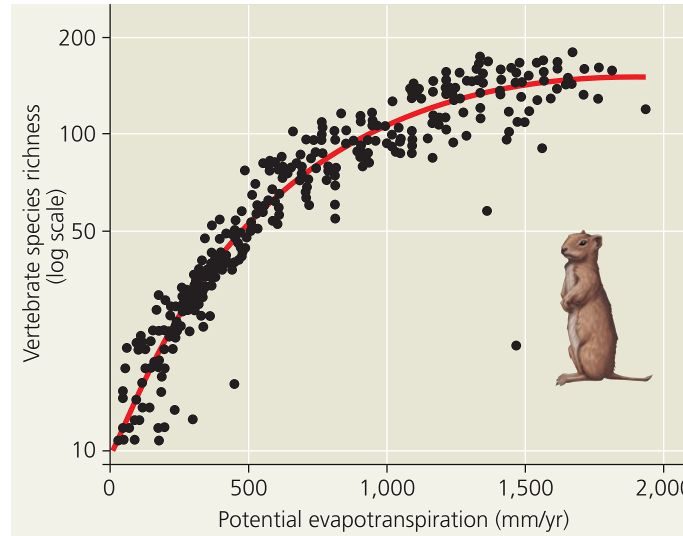
Two key factors that can affect latitudinal gradients of species richness are evolutionary history and climate. Over the course of evolution, a series of speciation events may lead to increased species richness in a community (see Concept 24.2). Tropical communities are generally older than temperate or polar communities, which have repeatedly "started over" after major disturbances such as glaciations. As a result, species diversity may be highest in the tropics simply because there has been more time for speciation to occur in tropical communities than in temperate or polar communities.

Climate is another key factor thought to affect latitudinal gradients of richness and diversity. In terrestrial communities, the two main climatic factors correlated with diversity are sunlight and precipitation, both of which occur at high levels in the tropics. These factors can be considered together by measuring a community's rate of **evapotranspiration**, the evaporation of water from soil and plants. Evapotranspiration, a function of solar radiation, temperature, and water availability, is much higher in hot areas with abundant rainfall than in areas with low temperatures or low precipitation. *Potential evapotranspiration*, a measure of potential water loss that assumes that water is readily available, is determined by the amount of solar radiation and temperature and is highest in regions where both are plentiful. The species richness of plants and animals correlates with both measures, as shown for vertebrates and potential evapotranspiration in **Figure 54.26**.

Area Effects

In 1807, naturalist and explorer Alexander von Humboldt described one of the first patterns of species richness to be recognized, the **species-area curve**: All other factors being equal, the larger the geographic area of a community, the more species it has. One explanation for this relationship is that larger areas offer a greater diversity of habitats and microhabitats. In conservation biology, developing species-area curves for key taxa in a community helps ecologists predict how the loss of a given area of habitat will affect the community's diversity.

Figure 54.26 Energy, water, and species richness. Vertebrate species richness in North America increases with potential evapotranspiration, expressed as rainfall equivalents (mm/yr).



The first, and still widely used, mathematical description of the species-area relationship was proposed a century ago:

$$S = cA^z$$

where S is the number of species found in a habitat, c is a constant, and A is the area of the habitat. The exponent z tells you how many more species should be found in a habitat as its area increases. In a log-log plot of S versus A, z is the slope of the line through the data points. A value of $z = 1$ would indicate a linear relationship between species number and area, meaning that ten times as many species would be found in a habitat that has ten times the area.

In the 1960s, Robert MacArthur and E. O. Wilson tested the predictions of the species-area relationship by examining the number of animals and plants on different island chains. As one example, in the Sunda Islands of Malaysia, they found that the number of bird species increased with island size, with a value of $z = 0.4$ **(Figure 54.27)**. These and other studies have shown that z is usually between 0.2 and 0.4.

Although the slopes of different species-area curves vary, the basic concept of diversity increasing with increasing area applies in many situations, from surveys of ant diversity in New Guinea to studies of plant species richness on islands of different sizes.

Island Equilibrium Model

Because of their isolation and limited size, islands provide excellent opportunities for studying the biogeographic factors that affect the species diversity of communities. By "islands," we mean not only oceanic islands, but also habitat islands on land, such as lakes, mountain peaks separated by lowlands, or habitat fragments—any patch surrounded by an

Figure 54.27 Species richness and island area. The number of bird species on the Sunda Islands of Malaysia increases with island size. The slope of the best-fit line through the data points (the parameter *z*) is about 0.4.

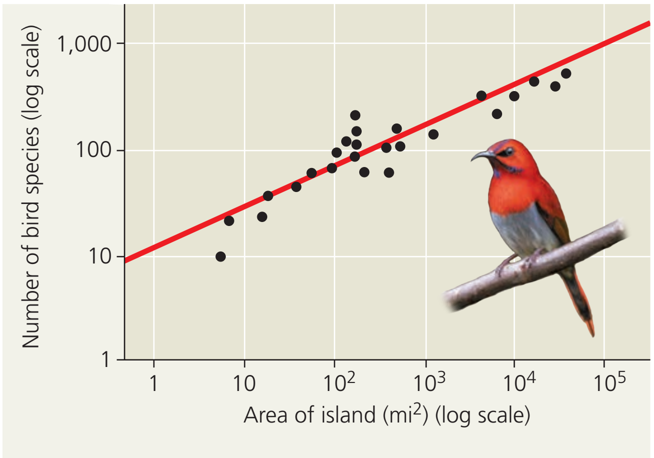
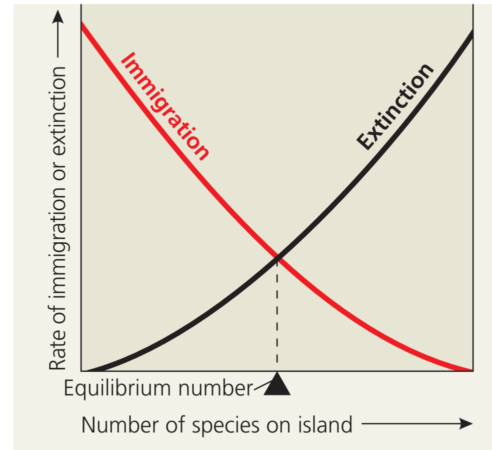


Figure 54.28 MacArthur and Wilson's island equilibrium model. The equilibrium number of species on an island represents a balance between the immigration of new species (red curve) and the extinction of species already there (black curve). The black triangle shows the predicted equilibrium number of species.



WHAT IF? ➤ *Suppose rising sea levels substantially decreased the size of the island. How would that affect (a) the population sizes of species already on the island, (b) the extinction curve shown above, and (c) the predicted equilibrium number of species?*

environment not suitable for the "island" species. While studying the species-area relationship, MacArthur and Wilson also developed a method for predicting the species diversity of islands **(Figure 54.28)**. In their approach, the number of species on an island represents a balance between the immigration of new species to the island and the extinction of species already there.

In Figure 54.28, note that the immigration rate *decreases* as the number of species on the island gets larger, while the extinction rate *increases*. To see why this is so, consider a newly formed oceanic island that receives colonizing species from a distant mainland. At any given time, an island's immigration and extinction rates are affected by the number of species already present. As the number of species already on the island increases, the immigration rate of new species decreases, because any individual reaching the island is less likely to represent a species that is not already present. At the same time, as more species inhabit an island, extinction rates on the island increase because of the greater likelihood of competitive exclusion.

Two physical features of the island further affect immigration and extinction rates: its size and its distance from the mainland. Small islands generally have lower immigration rates because potential colonizers are less likely to reach a small island than a large one. Small islands also have higher extinction rates because they generally contain fewer resources, have less diverse habitats, and have smaller population sizes. Distance from the mainland is also important; a closer island generally has a higher immigration rate and a lower extinction rate than one farther away. Arriving colonists help sustain the presence of a species on a near island and prevent its extinction.

MacArthur and Wilson's model is called the *island equilibrium model* because an equilibrium will eventually be reached where the rate of species immigration equals the rate of species extinction. The number of species at this equilibrium point is correlated with the island's size and distance from the mainland. Like any ecological equilibrium, this species equilibrium is dynamic: Although the number of species ultimately should stabilize at a constant level, immigration and extinction continue and hence the exact species composition on the island may change over time.

In 1967, Dan Simberloff, then a graduate student with E. O. Wilson at Harvard University, tested the island equilibrium model in an experiment on six small mangrove islands in the Florida Keys **(Figure 54.29)**. Simberloff and Wilson first painstakingly identified and counted all of the arthropod species on each island. As predicted by the model, they found more species on islands that were larger and closer to the mainland. They then fumigated four of the islands with methyl bromide to kill all of the arthropods. After about a year, the arthropod species richness on these islands increased to

Figure 54.29 Mangrove island. The islands that Simberloff and Wilson studied were small, each consisting of one or a few mangrove trees.

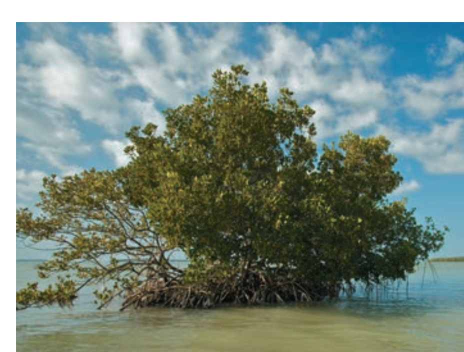
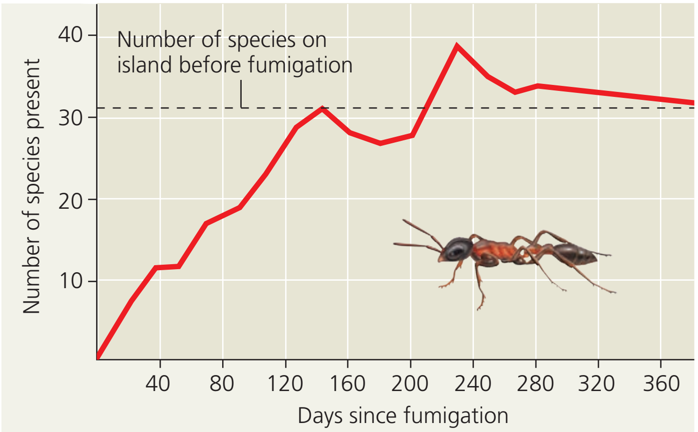


Figure 54.30 Testing the island equilibrium model. The graph shows results for one of the islands studied. The number of arthropod species increased over time; by 240 days, it had reached levels similar to those found on the island prior to the start of the experiment.



near their pre-fumigation values **(Figure 54.30)**. The island closest to the mainland recovered first, while the island farthest from the mainland was the slowest to recover. The number of arthropod species on the remaining two islands—which were not fumigated and hence served as controls—remained approximately constant during the study.

Over long periods, disturbances such as storms, adaptive evolutionary changes, and speciation generally alter the species composition and community structure on islands. Nonetheless, the island equilibrium model is widely applied in ecology. Conservation biologists in particular use it when designing habitat reserves or establishing a starting point for predicting the effects of habitat loss on species diversity.

MB **Animation: Exploring Island Biogeography**

CONCEPT CHECK 54.4

1. Describe two hypotheses that explain why species diversity is greater in tropical regions than in temperate and polar regions.
2. Describe how an island's size and distance from the mainland affect the island's species richness.
3. **WHAT IF?** ➤ Based on MacArthur and Wilson's island equilibrium model, how would you expect the richness of birds on islands to compare with the richness of snakes and lizards? Explain.

For suggested answers, see Appendix A.

CONCEPT 54.5

Pathogens alter community structure locally and globally

Now that we have examined several important factors that structure biological communities, we'll finish the chapter by examining community interactions involving **pathogens**, disease-causing microorganisms, viruses, viroids, or prions. (Viroids and prions are infectious RNA molecules and proteins, respectively; see Concept 26.3.) As scientists have recently come to appreciate, pathogens have universal effects in structuring ecological communities.

Pathogens produce especially clear effects when they are introduced into new habitats, as in the case of the fungus that causes chestnut blight (see Concept 54.2). A pathogen can be particularly virulent in a new habitat because new host populations have not had a chance to become resistant to the pathogen through natural selection. The invasive chestnut blight fungus had far stronger effects on the American chestnut, for instance, than it had on Asian chestnut species in the fungus's native habitat. Humans are similarly vulnerable to the effects of emerging diseases spread by our increasingly global economy.

Pathogens and Community Structure

The ecological importance of disease can be highlighted by how pathogens have affected coral reef communities. White-band disease, caused by an unknown pathogen, has resulted in dramatic changes in the structure and composition of Caribbean reefs. The disease kills corals by causing their tissue to slough off in a band from the base to the tip of the branches. Because of the disease, staghorn coral (*Acropora cervicornis*) has virtually disappeared from the Caribbean since the 1980s. Populations of elkhorn coral (*Acropora palmata*) have also been decimated. Such corals provide key habitat for lobsters as well as snappers and other fish species. When the corals die, they are quickly overgrown by algae. Surgeonfish and other herbivores that feed on algae come to dominate the fish community. Eventually, the corals topple because of damage from storms and other disturbances. The complex, three-dimensional structure of the reef disappears, and diversity plummets.

Pathogens also influence community structure in terrestrial ecosystems. Consider sudden oak death (SOD), a recently discovered disease that is caused by the protist *Phytophthora ramorum* (see Concept 28.6). SOD was first described in California in 1995, when hikers noticed trees dying around San Francisco Bay. By 2014, it had spread more than 1,000 km, from the central California coast to southern Oregon, and it had killed more than a million oaks and other trees. The loss of the oaks has led to the decreased abundance of at least five bird species, including the acorn woodpecker and the oak titmouse, that rely on oaks for food and habitat. Although there is currently no cure for SOD, scientists recently sequenced the genome of *P. ramorum* in hopes of finding a way to fight the pathogen.

Human activities are transporting pathogens around the world at unprecedented rates. Genetic analyses using DNA sequencing suggest that *P. ramorum* likely came to North America from Europe through the horticulture trade. Similarly, the pathogens that cause human diseases are spread by our global economy. H1N1, the virus that causes "swine flu" in humans, was first detected in Veracruz, Mexico, in early 2009. It quickly spread around the world when infected individuals flew on airplanes to other countries. By 2011, this flu outbreak had a confirmed death toll of more than 18,000 people. The actual number may have been significantly higher since many people with flu-like symptoms who died were not tested for H1N1.

Community Ecology and Zoonotic Diseases

Three-quarters of emerging human diseases and many of the most devastating established diseases are caused by **zoonotic pathogens**—those that are transferred to humans from other animals, either through direct contact with an infected animal or by means of an intermediate species, called a **vector**. The vectors that spread zoonotic diseases are often parasites, including ticks, lice, and mosquitoes.

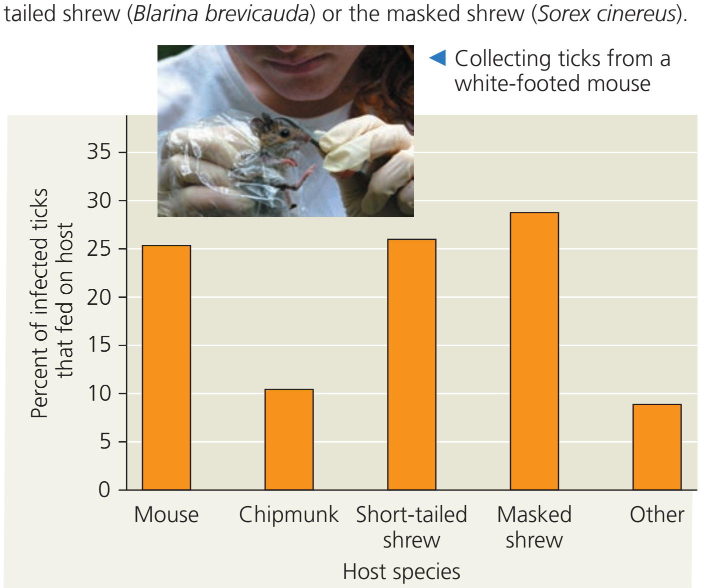
Identifying the community of hosts and vectors for a pathogen can help prevent illnesses such as Lyme disease, which is spread by ticks. For years, scientists thought that the primary host for the Lyme pathogen was the white-footed mouse because mice are heavily parasitized by young ticks. When researchers vaccinated mice against Lyme disease and released them into the wild, however, the number of infected ticks hardly changed. Further investigation in New York revealed that two inconspicuous shrew species were the source for more than half the infected ticks collected in the field **(Figure 54.31)**. Identifying the dominant hosts for a pathogen provides information that may be used to control the hosts most responsible for spreading diseases.

Ecologists also use their knowledge of community interactions to track the spread of zoonotic diseases. One example, avian flu, is caused by highly contagious viruses transmitted through the saliva and feces of birds (see Concept 26.3). Most of these viruses affect wild birds mildly, but they often cause stronger symptoms in domesticated birds, the most common source of human infections. Since 2003, one particular viral strain, called H5N1, has killed hundreds of millions of poultry and more than 300 people. In 2015, for example, H5N1 was one of three strains of avian flu that spread across poultry farms in the United States, killing more than 40 million birds. While this outbreak was devastating to the poultry industry, it did not result in any human cases.

Control programs that quarantine domestic birds or monitor their transport may be ineffective if avian flu spreads naturally through the movements of wild birds. From 2003 to 2006, the H5N1 strain spread rapidly from southeast Asia into Europe and Africa. The most likely place for infected wild birds to enter the Americas is Alaska, the entry point for ducks, geese, and shorebirds that migrate across the Bering Sea from Asia every year. Ecologists are studying the spread of the virus by trapping and testing migrating and resident birds in Alaska.

While our emphasis here has been on community ecology, pathogens are also greatly influenced by changes in the physical environment. To control pathogens and the diseases they cause, scientists need an ecosystem perspective—an intimate knowledge of how the pathogens interact with other species and with all aspects of their environment. Ecosystems are the subject of Chapter 55.

▼ **Figure 54.31 Unexpected hosts of the Lyme disease pathogen.** A combination of ecological data and genetic analyses enabled scientists to show that more than half of ticks carrying the Lyme pathogen became infected by feeding on the northern short-tailed shrew (*Blarina brevicauda*) or the masked shrew (*Sorex cinereus*).



MAKE CONNECTIONS ➤ *Concept 23.1 describes genetic variation between populations. How might genetic variation between shrew populations in different locations affect the number of infected ticks?*

➤ **Figure 54.32 Tracking avian flu.**

CONCEPT CHECK 54.5

1. What are pathogens?
2. **WHAT IF? ➤** Rabies, a viral disease in mammals, is not currently found in the British Isles. If you were in charge of disease control there, what practical approaches might you employ to keep the rabies virus from reaching these islands?

For suggested answers, see Appendix A.

54 Chapter Review

Go to **MasteringBiology**™ for Videos, Animations, Vocab Self-Quiz, Practice Tests, and more in the Study Area.

SUMMARY OF KEY CONCEPTS

VOCAB SELF-QUIZ goo.gl/Rn5Uax

CONCEPT 54.1

Community interactions are classified by whether they help, harm, or have no effect on the species involved *(pp. 1271–1277)*

- **Interspecific interactions** affect the survival and reproduction of the species that engage in them. As shown in the table, these interactions can be grouped into three broad categories: competition, exploitation, and positive interactions.

Interaction	Description
Competition (–/–)	Two or more species compete for a resource that is in short supply.
Exploitation (+/–)	One species benefits by feeding upon the other species, which is harmed. Exploitation includes the following:
Predation	One species, the predator, kills and eats the other, the prey.
Herbivory	An herbivore eats part of a plant or alga.
Parasitism	The parasite derives its nourishment from a second organism, its host, which is harmed.
Positive interactions (+/+ or 0/+)	One species benefits, while the other species benefits or is not harmed. Positive interactions include the following:
Mutualism (+/+)	Both species benefit from the interaction.
Commensalism (+/0)	One species benefits, while the other is not affected.

- **Competitive exclusion** states that two species competing for the same resource cannot coexist permanently in the same place. **Resource partitioning** is the differentiation of **ecological niches** that enables species to coexist in a community.

? *For each interaction listed in the table, give an example of a pair of species that exhibit the interaction.*

CONCEPT 54.2

Diversity and trophic structure characterize biological communities *(pp. 1278–1283)*

- **Species diversity** is affected by both the number of species in a community—its **species richness**—and their **relative abundance**.
- More diverse communities typically produce more **biomass** and show less year-to-year variation in growth than less diverse communities and are more resistant to invasion by exotic species.
- **Trophic structure** is a key factor in community dynamics. **Food chains** link the trophic levels from producers to top carnivores. Branching food chains and complex trophic interactions form **food webs**.
- **Dominant species** are the most abundant species in a community. **Keystone species** are usually less abundant species that exert a disproportionate influence on community structure. **Ecosystem engineers** influence community structure through their effects on the physical environment.
- The **bottom-up model** proposes a unidirectional influence from lower to higher trophic levels, in which nutrients and other abiotic factors primarily determine community structure. The **top-down model** proposes that control of each trophic level comes from the trophic level above, with the result that predators control herbivores, which in turn control primary producers.

? *Based on indexes such as Shannon diversity, is a community of higher species richness always more diverse than a community of lower species richness? Explain.*

CONCEPT 54.3

Disturbance influences species diversity and composition *(pp. 1284–1287)*

- Increasing evidence suggests that **disturbance** and lack of equilibrium, rather than stability and equilibrium, are the norm for most communities. According to the **intermediate disturbance hypothesis**, moderate levels of disturbance can foster higher species diversity than can low or high levels of disturbance.
- **Ecological succession** is the sequence of community and ecosystem changes after a disturbance. **Primary succession** occurs where no soil exists when succession begins; **secondary succession** begins in an area where soil remains after a disturbance.

? *Is the disturbance pictured in Figure 54.25 more likely to initiate primary or secondary succession? Explain.*

CONCEPT 54.4

Biogeographic factors affect community diversity *(pp. 1287–1290)*

- Species richness generally declines along a latitudinal gradient from the tropics to the poles. Climate influences the diversity gradient through energy (heat and light) and water. The greater age of tropical environments also may contribute to their greater species richness.
- Species richness is directly related to a community's geographic size, a principle formalized in the **species-area curve**.
- Species richness on islands depends on island size and distance from the mainland. The island equilibrium model maintains that species richness on an ecological island reaches an equilibrium where new immigrations are balanced by extinctions.

? *How have periods of glaciation influenced latitudinal patterns of diversity?*

CONCEPT 54.5

Pathogens alter community structure locally and globally *(pp. 1290–1291)*

- Recent work has highlighted the role that **pathogens** play in structuring terrestrial and marine communities.
- **Zoonotic pathogens** are transferred from other animals to humans and cause the largest class of emerging human diseases. Community ecology provides the framework for identifying key species interactions associated with such pathogens and for helping us track and control their spread.

? *Suppose a pathogen attacks a keystone species. Explain how this could alter the structure of a community.*

TEST YOUR UNDERSTANDING

Multiple-choice Self-Quiz questions 1–8 can be found in the Study Area in MasteringBiology.

9. Grassland 1 has 100 individuals distributed among four species: 20A, 25B, 25C, and 30D. Grassland 2 has 100 individuals distributed among three species: 80A, 15B, and 5C. Fertilizers were applied on grassland 2, but not on grassland 1. Calculate the Shannon diversity (H) for each grassland. Does the application of fertilizers increase biodiversity?

PRACTICE TEST
goo.gl/iAsVgL

10. DRAW IT In the Chesapeake Bay estuary, the blue crab is an omnivore that eats eelgrass and other primary producers as well as clams. It is also a cannibal. In turn, the crabs are eaten by humans and by the endangered Kemp's Ridley sea turtle. Based on this information, draw a food web that includes the blue crab. Assuming that the top-down model holds for this system, describe what would happen to the abundance of eelgrass if humans stopped eating blue crabs.

11. EVOLUTION CONNECTION Explain why adaptations of particular organisms to interspecific competition may not necessarily represent instances of character displacement. What would a researcher have to demonstrate about two competing species to make a convincing case for character displacement?

12. SCIENTIFIC INQUIRY A lichenologist performed the following experiment. She collected samples of lichens that have bipartite (fungi and cyanobacteria) and tripartite (fungi, cyanobacteria, and algae) partnerships. Fungi can gain carbon from algae and vegetative cells of cyanobacteria, and nitrogen from heterocysts of cyanobacteria. The lichenologist counted the number of heterocysts and vegetative cells in the cyanobacteria chains. She found that in the presence of algae, the proportion of the cyanobacteria chains dedicated to heterocysts was much higher. Using the principles of symbiosis, propose a hypothesis to explain her results. What additional evidence would support your hypothesis?

13. WRITE ABOUT A THEME: INTERACTIONS In Batesian mimicry, a palatable species gains protection by mimicking an unpalatable one. Imagine that individuals of a palatable, brightly colored fly species are blown to three remote islands. The first island has no predators of that species; the second has predators but no similarly colored, unpalatable species; and the third has both predators and a similarly colored, unpalatable species. In a short essay (100–150 words), predict what might happen to the coloration of the palatable species on each island through time if coloration is a genetically controlled trait. Explain your predictions.

14. SYNTHESIZE YOUR KNOWLEDGE

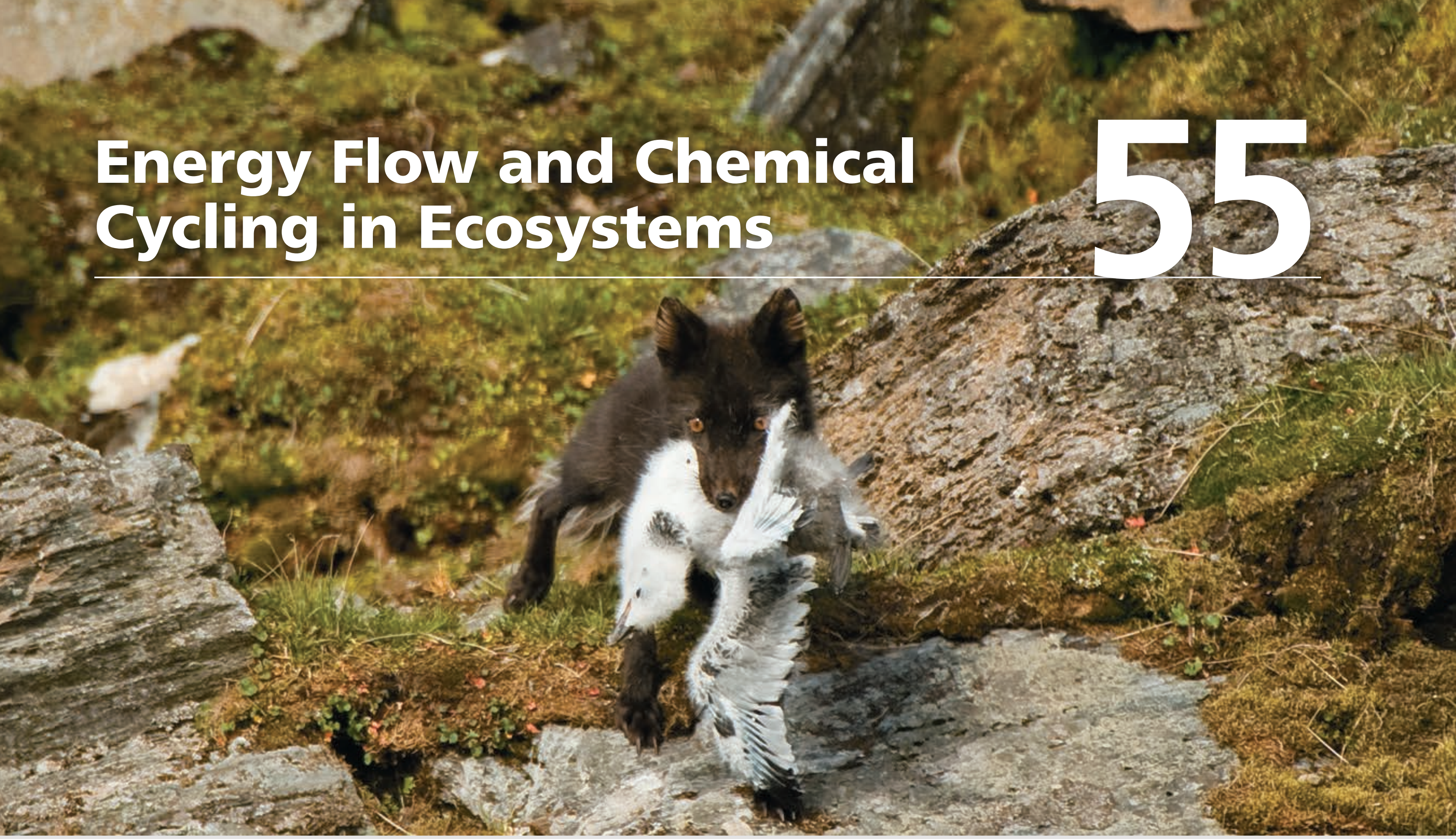
Describe two types of ecological interactions that appear to be occurring between the three species shown in this photo. What morphological adaptation can be seen in the species that is at the highest trophic level in this scene?

For selected answers, see Appendix A.

For additional practice questions, check out the **Dynamic Study Modules** in MasteringBiology. You can use them to study on your smartphone, tablet, or computer anytime, anywhere!

Energy Flow and Chemical Cycling in Ecosystems

55



▲ **Figure 55.1** **How can foxes transform a grassland into tundra?**

KEY CONCEPTS

55.1 Physical laws govern energy flow and chemical cycling in ecosystems

55.2 Energy and other limiting factors control primary production in ecosystems

55.3 Energy transfer between trophic levels is typically only 10% efficient

55.4 Biological and geochemical processes cycle nutrients and water in ecosystems

55.5 Restoration ecologists return degraded ecosystems to a more natural state

▼ Arctic terns, major guano generators

Transformed to Tundra

The arctic fox (*Vulpes lagopus*) is a predator native to arctic regions of North America, Europe, and Asia **(Figure 55.1)**. Valued for its fur, it was introduced onto hundreds of subarctic islands between Alaska and Russia around 1900 in an effort to establish populations that could be easily harvested. The fox's introduction had a surprising effect: It transformed many habitats on the islands from grassland to tundra.

How did the presence of foxes transform the islands' vegetation from one biome to another? The foxes fed voraciously on the islands' seabirds, decreasing their density almost 100-fold compared to that on fox-free islands. Fewer seabirds meant less bird guano (waste), a primary source of essential nutrients for plants on the islands. Researchers suspected that the scarcity of nutrients reduced the growth of nutrient-hungry grasses, favoring instead the slower-growing forbs (nonwoody plants other than grasses) and shrubs typical of tundra. To test this explanation, the scientists added fertilizer to plots of tundra on one of the fox-infested islands. Three years later, the fertilized plots had reverted back to grassland.

Each of these "fox islands" and the community of organisms on it is an example of an **ecosystem**, the sum of all the organisms living in a given area and the abiotic factors with which they interact. An ecosystem can encompass a large area, such as a lake, forest, or island, or a microcosm, such as the space under a fallen log or a small desert spring **(Figure 55.2)**. As with populations and communities, the boundaries of ecosystems are not always discrete. Many ecologists view the entire

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MB **Get Ready for This Chapter**

Figure 55.2 **A desert spring ecosystem.**

biosphere as a global ecosystem, a composite of all the local ecosystems on Earth.

An ecosystem, regardless of its size, has two key emergent properties: energy flow and chemical cycling. Energy enters most ecosystems as sunlight. This light energy is converted to chemical energy by autotrophs, passed to heterotrophs in the organic compounds of food, and dissipated as heat. As for chemical cycling, elements such as carbon and nitrogen are passed between the biotic and abiotic components of the ecosystem. Photosynthetic and chemosynthetic organisms take up these elements in inorganic form from the air, soil, and water and incorporate them into their biomass, some of which is consumed by animals. The elements are returned in inorganic form to the environment by the metabolism of organisms and by decomposers that break down organic wastes and dead organisms.

Both energy and chemicals are transformed in ecosystems through photosynthesis and feeding relationships. But unlike chemicals, energy cannot be recycled. An ecosystem must be powered by a continuous influx of energy from an external source—in most cases, the sun. As we'll see, energy flows through ecosystems, whereas chemicals cycle within them.

Ecosystem processes yield resources critical to human survival and welfare, ranging from the food we eat to the oxygen we breathe. In this chapter, we'll explore the dynamics of energy flow and chemical cycling, emphasizing the results of ecosystem experiments. We'll also consider how human activities have affected energy flow and chemical cycling. Finally, we'll examine the growing science of restoration ecology, which focuses on returning degraded ecosystems to a more natural state.

CONCEPT 55.1

Physical laws govern energy flow and chemical cycling in ecosystems

Cells transform energy and matter, subject to the laws of thermodynamics (see Concept 6.1). Cell biologists study these transformations within organelles and cells and measure the amounts of energy and chemical compounds that cross the cells' boundaries. Ecosystem ecologists do the same thing, except in their case the "cell" is an entire ecosystem. By determining trophic levels of feeding relationships (see Concept 54.2) and studying how organisms interact with their physical environment, ecologists can follow the transformations of energy in an ecosystem and map the movements of chemical elements.

Conservation of Energy

To study energy flow and chemical cycling, ecosystem ecologists use approaches based on laws of physics and chemistry. The first law of thermodynamics states that energy cannot be created or destroyed but only transferred or transformed (see Concept 6.1). Plants and other photosynthetic organisms convert solar energy to chemical energy, but the total amount of energy does not change: The amount of energy stored in organic molecules must equal the total solar energy intercepted by the plant minus the amounts reflected and dissipated as heat. Ecosystem ecologists often measure energy transfers within and across ecosystems, in part to understand how many organisms a habitat can support and the amount of food humans can harvest from a site.

The second law of thermodynamics states that every exchange of energy increases the entropy of the universe. One implication of this law is that energy conversions are inefficient. Some energy is always lost as heat. As a result, each unit of energy that enters an ecosystem eventually exits as heat. Thus, energy flows through ecosystems—it does not cycle within them for long periods of time. Because energy flowing through ecosystems is ultimately lost as heat, most ecosystems would vanish if the sun were not continuously providing energy to Earth.

Conservation of Mass

Matter, like energy, cannot be created or destroyed. This **law of conservation of mass** is as important for ecosystems as are the laws of thermodynamics. Because mass is conserved, we can determine how much of a chemical element cycles within an ecosystem or is gained or lost by that ecosystem over time.

Unlike energy, chemical elements are continually recycled within ecosystems. For example, a carbon atom in CO_2 might be released from the soil by a decomposer, taken up by a blade of grass through photosynthesis, consumed by a grazing animal, and returned to the soil in the animal's waste.

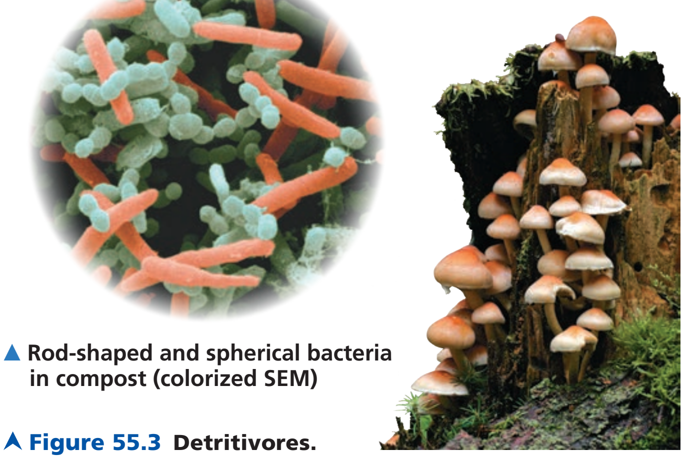
In addition to cycling within ecosystems, elements can also be gained or lost by an ecosystem. For example, a forest gains mineral nutrients—the essential elements that plants obtain from soil—that enter as dust or as solutes dissolved in rainwater or leached from rocks in the ground. Nitrogen is also supplied through the biological process of nitrogen fixation (see Figure 37.12). In terms of losses, some elements return to the atmosphere as gases, while others are carried out of the ecosystem by moving water or by wind. Like organisms, ecosystems are open systems, absorbing energy and mass and releasing heat and waste products.

Most gains and losses to ecosystems are small compared to the amounts that cycle within them. Even so, the balance between inputs and outputs is important because it determines whether an ecosystem stores or loses a given element. In particular, if a nutrient's outputs exceed its inputs, that nutrient will eventually limit production in that ecosystem. Human activities often change the balance of inputs and outputs considerably, as we'll see later in this chapter and in Concept 56.4.

Energy, Mass, and Trophic Levels

Ecologists group species in an ecosystem into trophic levels based on feeding relationships (see Concept 54.2). The trophic level that ultimately supports all others consists of autotrophs, also called the **primary producers** of the ecosystem. Most autotrophs are photosynthetic organisms that use light energy to synthesize sugars and other organic compounds, which they use as fuel for cellular respiration and as building material for growth. The most common autotrophs are plants, algae, and photosynthetic prokaryotes, although chemosynthetic prokaryotes are the primary producers in ecosystems such as deep-sea hydrothermal vents (see Figure 51.15) and places deep under the ground or ice.

Organisms in trophic levels above the primary producers are heterotrophs, which depend directly or indirectly on the outputs of primary producers for their source of energy. Herbivores, which eat plants and other primary producers, are **primary consumers**. Carnivores that eat herbivores are **secondary consumers**, and carnivores that eat other carnivores are **tertiary consumers**.



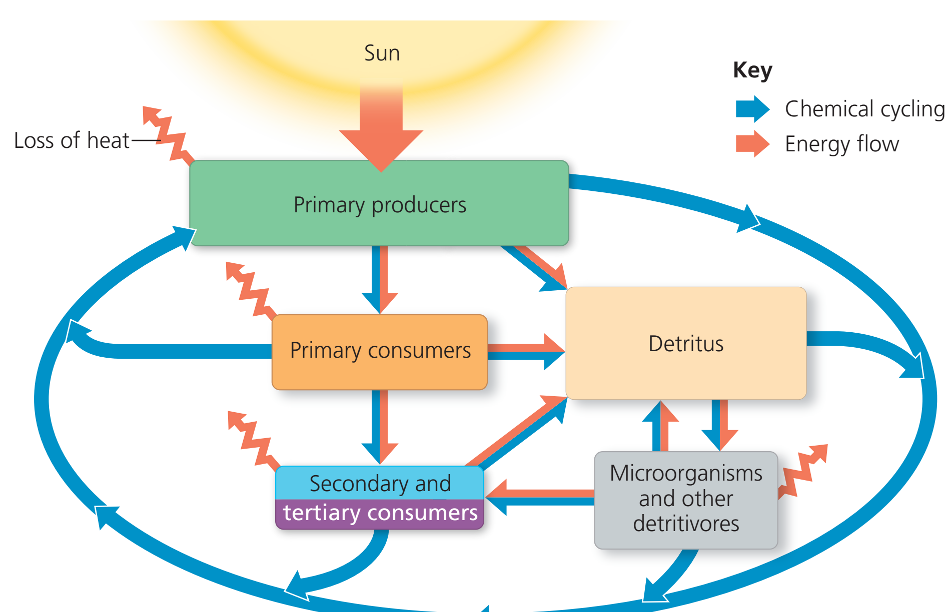
▼ **Fungi decomposing a dead tree**

▲ **Rod-shaped and spherical bacteria in compost (colorized SEM)**

▲ **Figure 55.3 Detritivores.**

Another group of heterotrophs is the **detritivores**, or **decomposers**, terms used synonymously in this text to refer to consumers that get their energy from detritus. **Detritus** is nonliving organic material, such as the remains of dead organisms, feces, fallen leaves, and wood. Although some animals (such as earthworms) feed on detritus, the main detritivores are prokaryotes and fungi **(Figure 55.3)**. These organisms secrete enzymes that digest organic material; they then absorb the breakdown products. Many detritivores are in turn eaten by secondary and tertiary consumers. In a forest, for instance, birds eat earthworms that have been feeding on leaf litter and its associated prokaryotes and fungi. As a result, chemicals originally synthesized by plants pass from the plants to leaf litter to detritivores to birds.

By recycling chemical elements to producers, detritivores also play a key role in the trophic relationships of an ecosystem **(Figure 55.4)**. Detritivores convert organic matter from all trophic levels to inorganic compounds usable by primary



➤ **Figure 55.4 An overview of energy and nutrient dynamics in an ecosystem.** Energy enters, flows through, and exits an ecosystem, whereas chemical nutrients cycle within it. Energy (dark orange arrows) entering from the sun as radiation is transferred as chemical energy through the food web; each of these units of energy ultimately exits as heat radiated into space. Most transfers of nutrients (blue arrows) through the food web lead eventually to detritus; the nutrients then cycle back to the primary producers.

VISUAL SKILLS ➤ *In this diagram, one blue arrow leads to the box labeled "Primary consumers," and three blue arrows come out of this box. For each of these four arrows, describe an example of nutrient transfer that the arrow could represent.*

producers. When the detritivores excrete waste products or die, those inorganic compounds are returned to the soil. Producers can then absorb these elements and use them to synthesize organic compounds. If decomposition stopped, life as we know it would cease as detritus piled up and the supply of ingredients needed to synthesize organic matter was exhausted.

MB Animation: Energy Flow and Chemical Cycling

CONCEPT CHECK 55.1

1. Why is the transfer of energy in an ecosystem referred to as energy flow, not energy cycling?
2. **WHAT IF?** ➤ You are studying nitrogen cycling on the Serengeti Plain in Africa. During your experiment, a herd of migrating wildebeests grazes through your study plot. What would you need to know to measure their effect on nitrogen balance in the plot?
3. **MAKE CONNECTIONS** ➤ Use the second law of thermodynamics to explain why an ecosystem's energy supply must be continually replenished (see Concept 6.1).

For suggested answers, see Appendix A.

CONCEPT 55.2

Energy and other limiting factors control primary production in ecosystems

The theme of energy transfer underlies all biological interactions (see Concept 1.1). In most ecosystems, the amount of light energy converted to chemical energy—in the form of organic compounds—by autotrophs during a given time period is the ecosystem's **primary production**. In ecosystems where the primary producers are chemoautotrophs, the initial energy input is chemical, and the initial products are the organic compounds synthesized by the microorganisms.

Ecosystem Energy Budgets

In most ecosystems, primary producers use light energy to synthesize energy-rich organic molecules, and consumers acquire their organic fuels secondhand (or even third- or fourth-hand) through food webs (see Figure 54.15). Therefore, the total amount of photosynthetic production sets the "spending limit" for the entire ecosystem's energy budget.

The Global Energy Budget

Each day, Earth's atmosphere is bombarded by approximately 10^{22} joules of solar radiation ($1\ J = 0.239$ cal). This is enough energy to supply the demands of the entire human population for 19 years at 2013 energy consumption levels. The intensity of the solar energy striking Earth varies with latitude, with the tropics receiving the greatest input (see Figure 51.3). About 50% of incoming solar radiation is absorbed, scattered, or reflected by clouds and dust in the atmosphere. The amount of solar radiation that ultimately reaches Earth's surface limits the possible photosynthetic output of ecosystems.

However, only a small fraction of the sunlight that reaches Earth's surface is actually used in photosynthesis. Much of the radiation strikes materials that don't photosynthesize, such as ice and soil. Of the radiation that does reach photosynthetic organisms, only certain wavelengths are absorbed by photosynthetic pigments (see Figure 11.9); the rest is transmitted, reflected, or lost as heat. As a result, only about 1% of the visible light that strikes photosynthetic organisms is converted to chemical energy. Nevertheless, Earth's primary producers create about 150 billion metric tons (1.50×10^{14} kg) of organic material each year.

Gross and Net Production

Total primary production in an ecosystem is known as that ecosystem's **gross primary production (GPP)**—the amount of energy from light (or chemicals, in chemoautotrophic systems) converted to the chemical energy of organic molecules per unit time. Not all of this production is stored as organic material in the primary producers because they use some of the molecules as fuel for their own cellular respiration. **Net primary production (NPP)** is equal to gross primary production minus the energy used by the primary producers (autotrophs) for their cellular respiration (R_a, where "a" stands for autotrophs):

$$\text{NPP} = \text{GPP} - R_a$$

On average, NPP is about one-half of GPP. To ecologists, NPP is the key measurement because it represents the storage of chemical energy that will be available to consumers in the ecosystem. Using the analogy of a paycheck, you can think of net primary production (NPP) as the take-home pay, which equals gross primary production (GPP), the gross pay, minus respiration (R_a), the taxes.

Net primary production can be expressed as energy per unit area per unit time [$J/(m^2 \cdot yr)$] or as biomass (mass of vegetation) added per unit area per unit time [$g/(m^2 \cdot yr)$]. (Note that biomass is usually expressed in terms of the dry mass of organic material.) An ecosystem's NPP should not be confused with the total biomass of photosynthetic autotrophs present. The net primary production is the amount of *new* biomass added in a given period of time. Although the total biomass of a forest is large, its NPP may actually be less than that of some grasslands; grasslands do not accumulate as much biomass as forests because animals consume the plants rapidly and because grasses and herbs decompose more quickly than trees do.

Satellites provide a powerful tool for studying global patterns of primary production. Images produced from satellite data show that different ecosystems vary considerably in

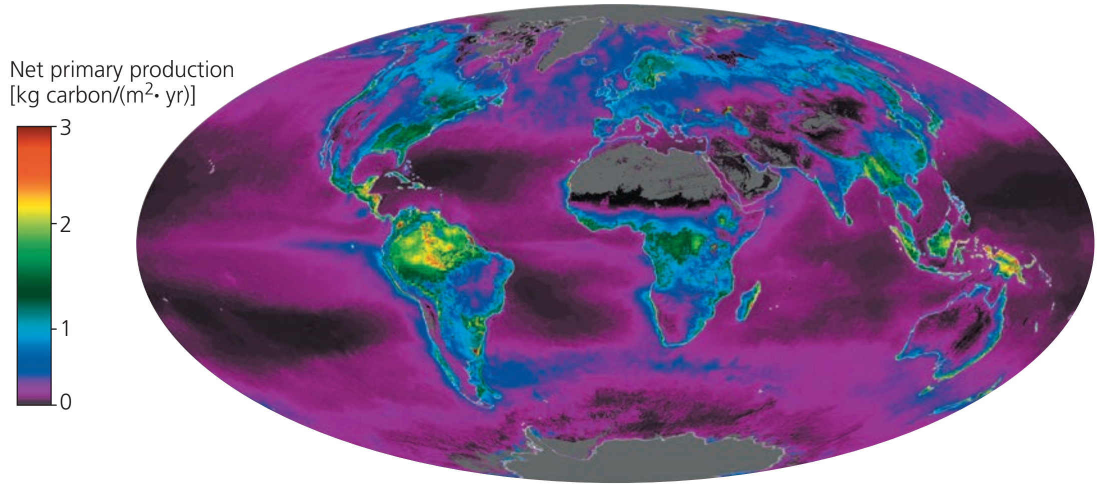


Figure 55.5 Global net primary production. The map is based on satellite-collected data, such as amount of sunlight absorbed by vegetation. Note that tropical land areas have the highest rates of production (yellow and red on the map).

VISUAL SKILLS *Does this map accurately reflect the significance of wetlands, coral reefs, and coastal zones, which are highly productive habitats? Explain.*

their NPP **(Figure 55.5)**. For example, tropical rain forests are among the most productive terrestrial ecosystems and contribute a large portion of the planet's NPP. Estuaries and coral reefs also have very high NPP, but their contribution to the global total is smaller because these ecosystems cover only about one-tenth the area covered by tropical rain forests. In contrast, while the open oceans are relatively unproductive, their vast size means that together they contribute as much global NPP as terrestrial systems do.

Whereas NPP can be expressed as the amount of new biomass added by producers in a given period of time, **net ecosystem production (NEP)** is a measure of the *total biomass accumulation* during that time. NEP is defined as gross primary production minus the total respiration of all organisms in the system (R_T)—not just primary producers, as for the calculation of NPP, but decomposers and other heterotrophs as well:

$$NEP = GPP - R_T$$

NEP is useful to ecologists because its value determines whether an ecosystem is gaining or losing carbon over time. A forest may have a positive NPP but still lose carbon if heterotrophs release it as CO_2 more quickly than primary producers incorporate it into organic compounds.

The most common way to estimate NEP is to measure the net flux (flow) of CO_2 or O_2 entering or leaving the ecosystem. If more CO_2 enters than leaves, the system is storing carbon. Because O_2 release is directly coupled to photosynthesis and respiration (see Figure 10.2), a system that is giving off O_2 is also storing carbon. On land, ecologists typically measure only the net flux of CO_2 from ecosystems because detecting small changes in O_2 flux in a large atmospheric O_2 pool is difficult.

Next, we'll examine factors that limit production in ecosystems, focusing first on aquatic ecosystems.

Primary Production in Aquatic Ecosystems

In aquatic (marine and freshwater) ecosystems, both light and nutrients are important in controlling primary production.

Light Limitation

Because solar radiation drives photosynthesis, you would expect light to be a key variable in controlling primary production in oceans. Indeed, the depth of light penetration affects primary production throughout the photic zone of an ocean or lake (see Figure 51.13). About half of the solar radiation is absorbed in the first 15 m of water. Even in "clear" water, only 5–10% of the radiation may reach a depth of 75 m.

If light were the main variable limiting primary production in the ocean, you would expect production to increase along a gradient from the poles toward the equator, which receives the greatest intensity of light. However, you can see in Figure 55.5 that there is no such gradient. What other factor strongly influences primary production in the ocean?

Nutrient Limitation

More than light, nutrients limit primary production in most oceans and lakes. A **limiting nutrient** is the element that must be added for production to increase. The nutrients that most often limit marine production are nitrogen and phosphorus. Concentrations of these nutrients are typically low in the photic zone because they are rapidly taken up by phytoplankton and because detritus tends to sink.

In one study, detailed in **Figure 55.6**, nutrient enrichment experiments found that nitrogen was limiting phytoplankton growth off the south shore of Long Island, New York. One practical application of this work is in preventing algal blooms caused by excess nitrogen runoff that fertilizes the phytoplankton. Preventing such blooms is critical because their occurrence can lead to the formation of large marine "dead zones," regions in which oxygen concentrations drop to levels that are fatal to many organisms (see Figure 56.24).

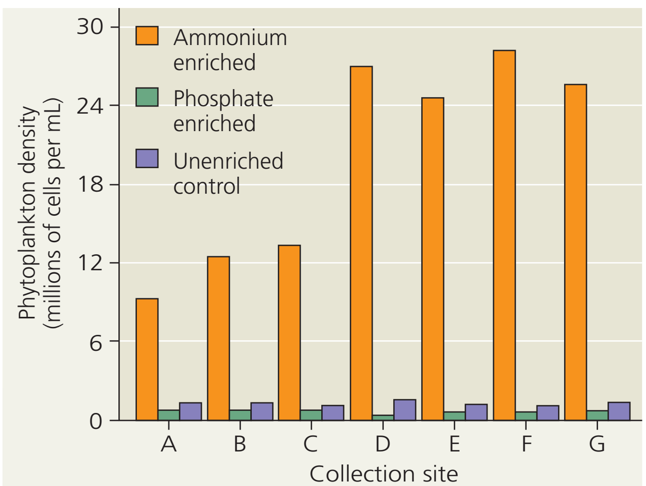
The macronutrients nitrogen and phosphorus are not the only nutrients that limit aquatic production. Several large areas of the ocean have low phytoplankton densities despite relatively high nitrogen concentrations. The Sargasso Sea, a subtropical region of the Atlantic Ocean, has some of the

Figure 55.6

Inquiry **Which nutrient limits phytoplankton production along the coast of Long Island?**

Experiment Pollution from duck farms concentrated near Moriches Bay adds both nitrogen and phosphorus to the coastal water off Long Island, New York. To determine which nutrient limits phytoplankton growth in this area, John Ryther and William Dunstan, of the Woods Hole Oceanographic Institution, cultured the phytoplankton *Nannochloris atomus* with water collected from several sites, identified as A through G. They added either ammonium (NH_4^+) or phosphate (PO_4^{3-}) to some of the cultures.

Results The addition of ammonium caused heavy phytoplankton growth in the cultures, but the addition of phosphate did not.



Conclusion The researchers concluded that nitrogen is the nutrient that limits phytoplankton growth in this ecosystem because adding phosphorus did not increase *Nannochloris* growth, whereas adding nitrogen increased phytoplankton density dramatically.

Data from J. H. Ryther and W. M. Dunstan, Nitrogen, phosphorus, and eutrophication in the coastal marine environment, *Science* 171:1008–1013 (1971).

WHAT IF? ➤ *Predict how the results would change if water samples were drawn from areas where new duck farms had greatly increased the amount of pollution in the water. Explain.*

clearest water in the world because of its low phytoplankton density. Nutrient enrichment experiments have revealed that the availability of the micronutrient iron limits primary production there **(Table 55.1)**. Windblown dust from land supplies most of the iron to the oceans but is relatively scarce in the Sargasso Sea and certain other regions compared to the oceans as a whole.

On the flip side, areas of *upwelling*, where deep, nutrient-rich waters circulate to the ocean surface, have exceptionally high primary production. This fact supports the hypothesis that nutrient availability determines marine primary production. Because upwelling stimulates growth of the phytoplankton that form the base of marine food webs, upwelling areas typically host highly productive, diverse ecosystems and are prime fishing locations. The largest areas of upwelling

Table 55.1 Nutrient Enrichment Experiment for Sargasso Sea Samples

Nutrients Added to Experimental Culture	Relative Uptake of ^{14}C by Cultures*
None (controls)	1.00
Nitrogen (N) + phosphorus (P) only	1.10
N + P + metals, excluding iron (Fe)	1.08
N + P + metals, including Fe	12.90
N + P + Fe	12.00

*^{14}C uptake by cultures measures primary production.

Data from D. W. Menzel and J. H. Ryther, Nutrients limiting the production of phytoplankton in the Sargasso Sea, with special reference to iron, *Deep Sea Research* 7:276–281 (1961).

INTERPRET THE DATA ➤ *The element molybdenum (Mo) is another micronutrient that can limit primary production in the oceans. If the researchers found the following results for additions of Mo, what would you conclude about its relative importance for growth?*

N + P + Mo	6.0
N + P + Fe + Mo	72.0

occur in the Southern Ocean (also called the Antarctic Ocean), along the equator, and in the coastal waters off Peru, California, and parts of western Africa.

Nutrient limitation is also common in freshwater lakes. During the 1970s, scientists showed that the sewage and fertilizer runoff from farms and lawns adds considerable nutrients to lakes, promoting the growth of primary producers. When the primary producers die, detritivores decompose them, depleting the water of much or all of its oxygen. The ecological impacts of this process, known as **eutrophication** (from the Greek *eutrophos*, well nourished), include the loss of many fish species from the lakes (see Figure 51.15).

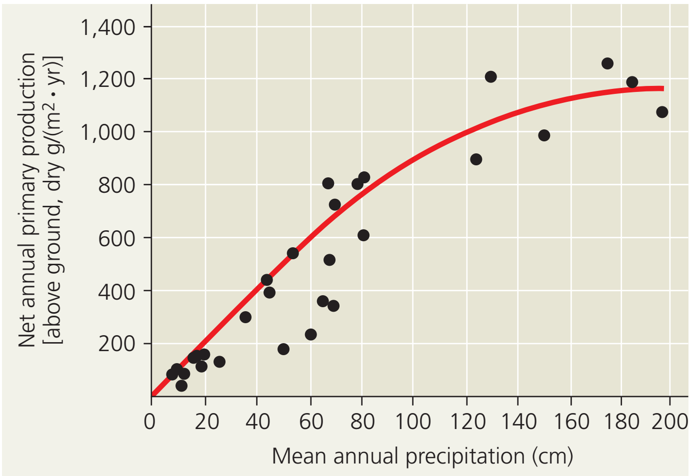
To control eutrophication, scientists need to know which nutrient is responsible. While nitrogen rarely limits primary production in lakes, many whole-lake experiments showed that phosphorus availability limited cyanobacterial growth. This and other ecological research led to the use of phosphate-free detergents and other water quality reforms.

Primary Production in Terrestrial Ecosystems

At regional and global scales, temperature and moisture are the main factors controlling primary production in terrestrial ecosystems. Tropical rain forests, with their warm, wet conditions that promote plant growth, are the most productive terrestrial ecosystems (see Figure 55.5). In contrast, low-productivity systems are generally hot and dry, like many deserts, or cold and dry, like arctic tundra. Between these extremes lie the temperate forest and grassland ecosystems, with moderate climates and intermediate productivity.

The climate variables of precipitation and temperature are very useful for predicting NPP in terrestrial ecosystems. For example, primary production is greater in wetter ecosystems, as shown for the plot of NPP and annual precipitation

Figure 55.7 A global relationship between net primary production and mean annual precipitation for terrestrial ecosystems.



in **Figure 55.7**. NPP also increases with temperature and the amount of solar energy available to drive evaporation and transpiration.

Nutrient Limitations and Adaptations That Reduce Them

EVOLUTION Soil nutrients can also limit primary production in terrestrial ecosystems. As in aquatic systems, nitrogen and phosphorus are the nutrients that most commonly limit terrestrial production. Globally, nitrogen limits plant growth most. Phosphorus limitations are common in older soils where phosphate molecules have been leached away by water, such as in many tropical ecosystems. Note that adding a nonlimiting nutrient, even one that is scarce, will not stimulate production. Conversely, adding more of the limiting nutrient will increase production until some other nutrient becomes limiting.

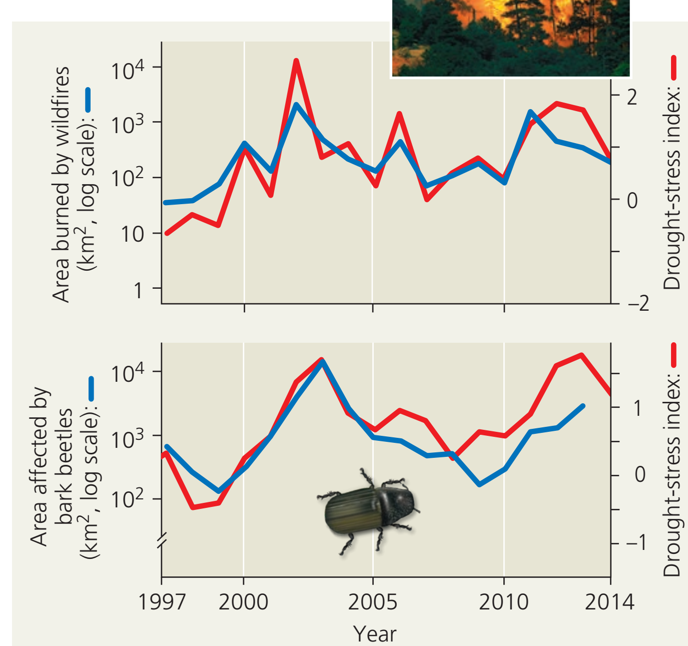
Various adaptations have evolved in plants that can increase their uptake of limiting nutrients. One important adaptation is the mutualism between plant roots and nitrogen-fixing bacteria. Another is the mycorrhizal association between plant roots and fungi that supply phosphorus and other limiting elements to plants (see Figure 37.15). Plant roots also have hairs and other anatomical features that increase the area of soil in contact with the roots (see Figures 33.9 and 35.3). Many plants release enzymes and other substances into the soil that increase the availability of limiting nutrients; such substances include phosphatases, which cleave a phosphate group from larger molecules, and certain molecules (called chelating agents) that make micronutrients such as iron more soluble in the soil.

Effects of Climate Change on Production

As we've seen, climatic factors such as temperature and precipitation affect terrestrial NPP. Thus, we might expect that climate change could affect production in terrestrial ecosystems—and it does. For example, satellite data showed that from 1982 to 1999, NPP increased by 6% in terrestrial ecosystems. Nearly half of this increase occurred in the tropical forests of the Amazon, where changing climate patterns had caused cloud cover to decrease, thereby increasing the amount of solar energy available to primary producers. Since 2000, however, these gains in NPP have been erased. This reversal was affected by another aspect of climate change: a series of major droughts in the southern hemisphere.

Another effect of climate change on NPP can be seen in the impact of "hotter droughts" on wildfires and insect outbreaks. Consider forests in the American southwest. In recent decades, the forests of this region have experienced droughts driven by climate warming and changing patterns of precipitation. These ongoing droughts, in turn, have led to increases in the area burned by wildfires and the area affected by outbreaks of bark beetles such as the mountain pine beetle *Dendroctonus ponderosae* **(Figure 55.8)**. As a result, tree mortality has increased and NPP has decreased in these forests.

Figure 55.8 Climate change, wildfires, and insect outbreaks. Forests in the American southwest are experiencing hotter droughts caused by rising temperatures in the summer and reduced snowfall in the winter. The drought-stress index indicates how greatly trees are stressed by these conditions; rising values of this index correspond to increasing drought. Higher drought stress correlates with increasing area burned by wildfires (top) and affected by bark beetles (bottom), which specifically target drought-stressed trees with weakened defenses.



PROBLEM-SOLVING EXERCISE

Can an insect outbreak threaten a forest's ability to absorb CO_2 from the atmosphere?

One way to combat climate change is to plant trees, since trees absorb large amounts of CO_2 from the atmosphere, converting it to biomass through photosynthesis. But what happens to the carbon stored as biomass in trees when an insect population explodes in number? Such insect outbreaks have become more frequent with climate change.

▲ A tree with dozens of "pitch tubes," indications of a damaging outbreak of mountain pine beetles (inset)

Instructors: A version of this Problem-Solving Exercise can be assigned in MasteringBiology.

In this exercise, you will test whether an outbreak of the mountain pine beetle (*Dendroctonus ponderosae*) alters the amount of CO_2 that a forest ecosystem absorbs from and releases to the atmosphere.

Your Approach The principle guiding your investigation is that every ecosystem both absorbs and releases CO_2. Net ecosystem production (NEP) indicates whether an ecosystem is a carbon sink (absorbing more CO_2 from the atmosphere than it releases; this occurs when NEP $>$ 0) or a carbon source (releasing more CO_2 than it absorbs; NEP $<$ 0). To find out if the mountain pine beetle affects NEP, you will determine a forest's NEP before and after a recent outbreak of this insect.

Your Data From 2000 to 2006, an outbreak of the mountain pine beetle killed millions of trees in British Columbia, Canada. The impact of such outbreaks on whether forests gain carbon (NEP $>$ 0) or lose carbon (NEP $<$ 0) was poorly understood. To find out, ecologists estimated net primary production (NPP) and cellular respiration by decomposers and other heterotrophs (R_h), before and after the outbreak. These data allow forest NEP to be calculated from the equation NEP $=$ NPP $-$ R_h.

	NPP $[g/(m^2 \cdot yr)]$	R_h $[g/(m^2 \cdot yr)]$
Before outbreak	440	408
After outbreak	400	424

Your Analysis

1. Before the outbreak, was the forest a carbon sink or a carbon source? After the outbreak?
2. NEP is often defined as NEP $=$ GPP $-$ R_T, where GPP is gross primary production and R_T equals cellular respiration by autotrophs (R_a) *plus* cellular respiration by heterotrophs (R_h). Use the relation NPP $=$ GPP $-$ R_a to show that the two equations for NEP introduced in this exercise are equivalent.
3. Based on your results in question 1, predict whether the mountain pine beetle outbreak could have feedback effects on the global climate. Explain.

Climate change can also affect whether an ecosystem stores or loses carbon over time. As discussed earlier, net ecosystem production, or NEP, reflects the total biomass accumulation that occurs during a given period of time. When NEP $>$ 0, the ecosystem gains more carbon than it loses; such ecosystems store carbon and are said to be a carbon *sink*. In contrast, when NEP $<$ 0, the ecosystem loses more carbon than it gains; such ecosystems are a carbon *source*.

Recent research shows that climate change can cause an ecosystem to switch from a carbon sink to a carbon source. For example, in some arctic ecosystems, climate warming has increased the metabolic activities of soil microorganisms, causing an uptick in the amount of CO_2 produced in cellular respiration. In these ecosystems, the total amount of CO_2 produced in cellular respiration now exceeds what is absorbed in photosynthesis. As a result, these ecosystems—which once were carbon sinks—are now carbon sources. When this happens, an ecosystem may contribute to climate change by releasing more CO_2 than it absorbs. In the **Problem-Solving Exercise**, you can examine how outbreaks of an insect population may affect the NEP of forest ecosystems.

CONCEPT CHECK 55.2

1. Why is only a small portion of the solar energy that strikes Earth's atmosphere stored by primary producers?
2. How can ecologists experimentally determine the factor that limits primary production in an ecosystem?
3. **WHAT IF? ➤** Suppose a forest was heavily burned by a wildfire. Predict how NEP of this forest would change over time.
4. **MAKE CONNECTIONS ➤** Explain how nitrogen and phosphorus, the nutrients that most often limit primary production, are necessary for the Calvin cycle to function in photosynthesis (see Concept 11.3).

For suggested answers, see Appendix A.

CONCEPT 55.3

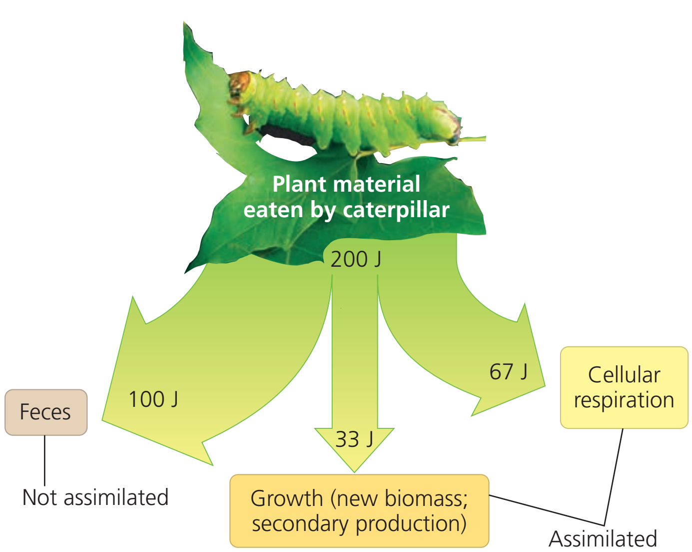
Energy transfer between trophic levels is typically only 10% efficient

The amount of chemical energy in consumers' food that is converted to their own new biomass during a given period is called the **secondary production** of the ecosystem. Consider the transfer of organic matter from primary producers to herbivores, the primary consumers. In most ecosystems, herbivores eat only a small fraction of plant material produced; globally, they consume only about one-sixth of total plant production. Moreover, they cannot digest all the plant material that they *do* eat, as anyone who has walked through a field where cattle have been grazing will attest. Most of an ecosystem's production is eventually consumed by detritivores. Let's analyze the process of energy transfer more closely.

Production Efficiency

We'll begin by examining secondary production in one organism—a caterpillar. When a caterpillar feeds on a leaf, only about 33 J out of 200 J, or one-sixth of the potential energy in the leaf, is used for secondary production, or growth **(Figure 55.9)**. The caterpillar stores some of the remaining energy in organic compounds that will be used for cellular respiration and passes the rest in its feces. The energy in the feces remains in the ecosystem temporarily, but most of it is lost as heat after the feces are consumed by detritivores. The energy used for the caterpillar's respiration is also eventually lost from the ecosystem as heat. Only the chemical energy stored by herbivores as biomass, through growth or the production of offspring, is available as food to secondary consumers.

▼ Figure 55.9 Energy partitioning within a link of the food chain.



INTERPRET THE DATA ➤ *What percentage of the energy in the caterpillar's food is actually used for secondary production (growth)?*

We can measure the efficiency of animals as energy transformers using the following equation:

$$\text{Production efficiency} = \frac{\text{Net secondary production} \times 100\%}{\text{Assimilation of primary production}}$$

Net secondary production is the energy stored in biomass represented by growth and reproduction. Assimilation consists of the total amount of energy an organism has consumed and used for growth, reproduction, and respiration. **Production efficiency**, therefore, is the percentage of energy stored in assimilated food that is used for growth and reproduction, *not* respiration. For the caterpillar in Figure 55.9, production efficiency is 33%; 67 J of the 100 J of assimilated energy is used for respiration. (The 100 J of energy lost as undigested material in feces does not count toward assimilation.) Birds and mammals typically have low production efficiencies, in the range of 1–3%, because they use so much energy in maintaining a constant, high body temperature. Fishes, which are mainly ectothermic (see Concept 40.3), have production efficiencies around 10%. Insects and microorganisms are even more efficient, with production efficiencies averaging 40% or more.

Trophic Efficiency and Ecological Pyramids

Let's scale up now from the production efficiencies of individual consumers to the flow of energy through trophic levels.

Trophic efficiency is the percentage of production transferred from one trophic level to the next. Trophic efficiencies must always be less than production efficiencies because they take into account not only the energy lost through respiration and contained in feces, but also the energy in organic material in a lower trophic level that is not consumed by the next trophic level. Trophic efficiencies range from roughly 5% to 20% in different ecosystems, but on average are only about 10%. In other words, 90% of the energy available at one trophic level typically is *not* transferred to the next. This loss is multiplied over the length of a food chain. If 10% of available energy is transferred from primary producers to primary consumers, such as caterpillars, and 10% of that energy is transferred to secondary consumers (carnivores), then only 1% of net primary production is available to secondary consumers (10% of 10%). In the **Scientific Skills Exercise**, you can calculate trophic efficiency and other measures of energy flow in a salt marsh ecosystem.

The progressive loss of energy along a food chain limits the abundance of top-level carnivores that an ecosystem can support. Only about 0.1% of the chemical energy fixed by photosynthesis can flow all the way through a food web to a tertiary consumer, such as a snake or a shark. This explains why most food webs include only about four or five trophic levels (see Figure 54.15).

The loss of energy with each transfer in a food chain can be represented by an *energy pyramid*, in which the net productions of different trophic levels are arranged in tiers **(Figure 55.10)**. The width of each tier is proportional to the

SCIENTIFIC SKILLS EXERCISE

Interpreting Quantitative Data

How Efficient Is Energy Transfer in a Salt Marsh Ecosystem?

In a classic experiment, John Teal studied the flow of energy through the producers, consumers, and detritivores in a salt marsh. In this exercise, you will use the data from this study to calculate some measures of energy transfer between trophic levels in this ecosystem.

How the Study Was Done Teal measured the amount of solar radiation entering a salt marsh in Georgia over a year. He also measured the aboveground biomass of the dominant primary producers, which were grasses, as well as the biomass of the dominant consumers, including insects, spiders, and crabs, and of the detritus that flowed out of the marsh to the surrounding coastal waters. To determine the amount of energy in each unit of biomass, he dried the biomass, burned it in a calorimeter, and measured the amount of heat produced.

Data from the Study

Form of Energy	kcal/($m^2 \cdot yr$)
Solar radiation	600,000
Gross grass production	34,580
Net grass production	6,585
Gross insect production	305
Net insect production	81
Detritus leaving marsh	3,671

Data from J. M. Teal, Energy flow in the salt marsh ecosystem of Georgia, *Ecology* 43:614–624 (1962).

INTERPRET THE DATA

1. What percentage of the solar energy that reaches the marsh is incorporated into gross primary production? Into net primary production?
2. How much energy is lost by primary producers as respiration in this ecosystem? How much is lost as respiration by the insect population?
3. If all of the detritus leaving the marsh is plant material, what percentage of all net primary production leaves the marsh as detritus each year?

Instructors: A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

net production, expressed in joules, of each trophic level. The highest level, which represents top-level predators, contains relatively few individuals. The small population size typical of top predators is one reason they tend to be vulnerable to extinction (and to the evolutionary consequences of small population size; see Concept 23.3).

One important ecological consequence of low trophic efficiencies is represented in a *biomass pyramid*, in which each tier represents the total dry mass of all organisms in one trophic level. Most biomass pyramids narrow sharply from primary producers at the base to top-level carnivores at the apex because energy transfers between trophic levels are so inefficient **(Figure 55.11a)**. Certain aquatic ecosystems, however, have inverted biomass pyramids: Primary consumers outweigh the producers in these ecosystems **(Figure 55.11b)**. Such inverted biomass pyramids occur because the producers—phytoplankton—grow, reproduce, and are consumed so quickly by the zooplankton that their total biomass remains at comparatively low levels. However, because the phytoplankton continually replace their biomass

Figure 55.10 An idealized pyramid of energy. This example assumes a trophic efficiency of 10% for each link in the food chain. Notice that primary producers convert only about 1% of the energy available to them to net primary production.

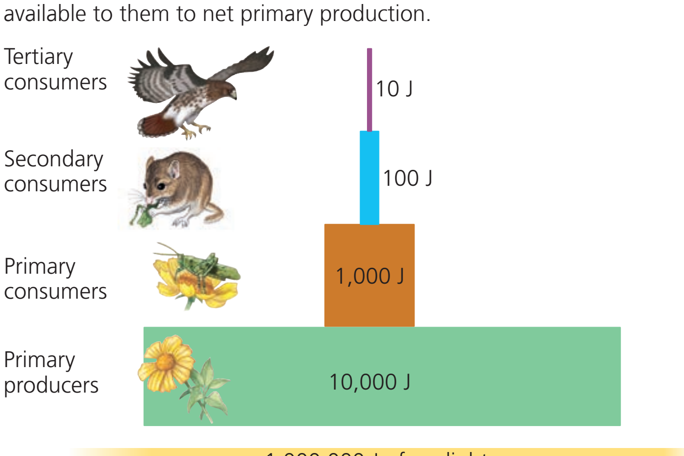
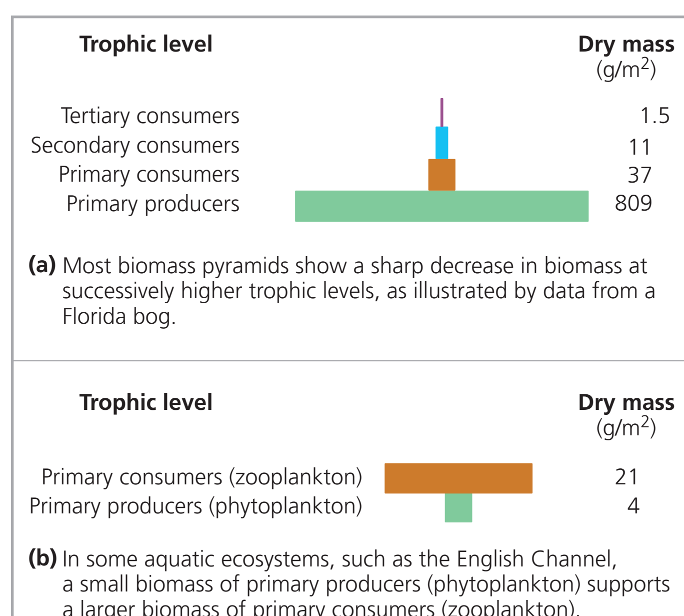


Figure 55.11 Pyramids of biomass. Numbers denote the dry mass of all organisms at each trophic level.



(a) Most biomass pyramids show a sharp decrease in biomass at successively higher trophic levels, as illustrated by data from a Florida bog.

(b) In some aquatic ecosystems, such as the English Channel, a small biomass of primary producers (phytoplankton) supports a larger biomass of primary consumers (zooplankton).

at such a rapid rate, they can support a biomass of zooplankton bigger than their own biomass. Likewise, because phytoplankton reproduce so quickly and have much higher production than zooplankton, the pyramid of *energy* for this ecosystem is still bottom-heavy, like the one in Figure 55.10.

The dynamics of energy flow through ecosystems have implications for human consumers. For example, eating meat is a relatively inefficient way of tapping photosynthetic production. The same pound of soybeans that a person could eat for protein produces only a fifth of a pound of beef or less when fed to a cow. Agriculture worldwide could, in fact, feed many more people and require less land if we all fed more efficiently—as primary consumers, eating plant material.

CONCEPT CHECK 55.3

1. If a cow that eats grass containing 200 J of energy uses 70 J of that energy for respiration and excretes 90 J in its feces, what is the cow's net secondary production? What is its production efficiency?
2. In aquatic ecosystems that have inverted biomass pyramids, how can a small biomass of primary producers support a larger biomass of primary consumers?
3. **WHAT IF?** ➤ Detritivores are consumers that obtain their energy from detritus. How many joules of energy are potentially available to detritivores in the ecosystem represented in Figure 55.10?

For suggested answers, see Appendix A.

CONCEPT 55.4

Biological and geochemical processes cycle nutrients and water in ecosystems

Although most ecosystems receive abundant solar energy, chemical elements are available only in limited amounts. Life therefore depends on the recycling of essential chemical elements. Much of an organism's chemical stock is replaced continuously as nutrients are assimilated and waste products are released. When the organism dies, the atoms in its body are returned to the atmosphere, water, or soil by decomposers. By liberating nutrients from organic matter, decomposition replenishes the pools of inorganic nutrients that plants and other autotrophs use to build new organic matter.

Decomposition and Nutrient Cycling Rates

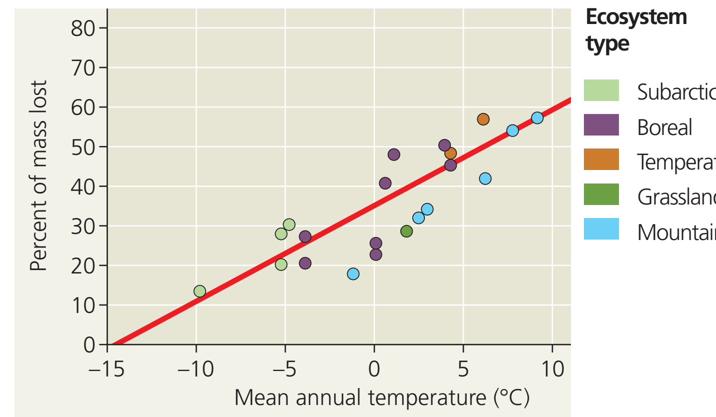
Decomposers are heterotrophs that get their energy from detritus. Their growth is controlled by the same factors that limit primary production in ecosystems, including temperature, moisture, and nutrient availability. Decomposers usually grow faster and decompose material more quickly in warmer ecosystems (**Figure 55.12**). In tropical rain forests, most organic material decomposes in a few months to a few years, whereas in temperate forests, decomposition takes four to six years, on average. The difference is largely the result of the higher temperatures and more abundant

Figure 55.12

Inquiry How does temperature affect litter decomposition in an ecosystem?

Experiment Researchers with the Canadian Forest Service placed identical samples of organic material—litter—on the ground in 21 sites across Canada. Three years later, they returned to see how much of each sample had decomposed.

Results The mass of litter in the warmest ecosystem decreased four times faster than in the coldest ecosystem.



Conclusion Decomposition rate increases with temperature across much of Canada.

Data from J. A. Trofymow and the CIDET Working Group, *The Canadian Intersite Decomposition Experiment: Project and Site Establishment Report* (Information Report BC-X-378), Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre (1998) and T. R. Moore et al., Litter decomposition rates in Canadian forests, *Global Change Biology* 5:75–82 (1999).

WHAT IF? ➤ *What factors other than temperature might also have varied across these 21 sites? How might this variation have affected the interpretation of the results?*

precipitation in tropical rain forests. Because decomposition in a tropical rain forest is rapid, relatively little organic material accumulates as leaf litter on the forest floor; about 75% of the ecosystem's nutrients is present in the woody trunks of trees, and only about 10% is contained in the soil. Thus, the relatively low concentrations of some nutrients in the soil of tropical rain forests result from a short cycling time, not from a lack of these elements in the ecosystem. In temperate forests, where decomposition is much slower, the soil may contain as much as 50% of all the organic material in the ecosystem. The nutrients that are present in temperate forest detritus and soil may remain there for years before plants assimilate them.

Decomposition on land is also slower when conditions are either too dry for decomposers to thrive or too wet to supply them with enough oxygen. Ecosystems that are cold and wet, such as peatlands, store large amounts of organic matter. Decomposers grow poorly there, and net primary production greatly exceeds the rate of decomposition.

In aquatic ecosystems, decomposition in anaerobic muds can take 50 years or longer. Bottom sediments are comparable to the detritus layer in terrestrial ecosystems, but algae and aquatic plants usually assimilate nutrients directly from the water. Thus, the sediments often constitute a nutrient sink, and aquatic ecosystems are very productive only when there is exchange between the bottom layers of water and surface waters (as occurs in the upwelling regions described earlier).

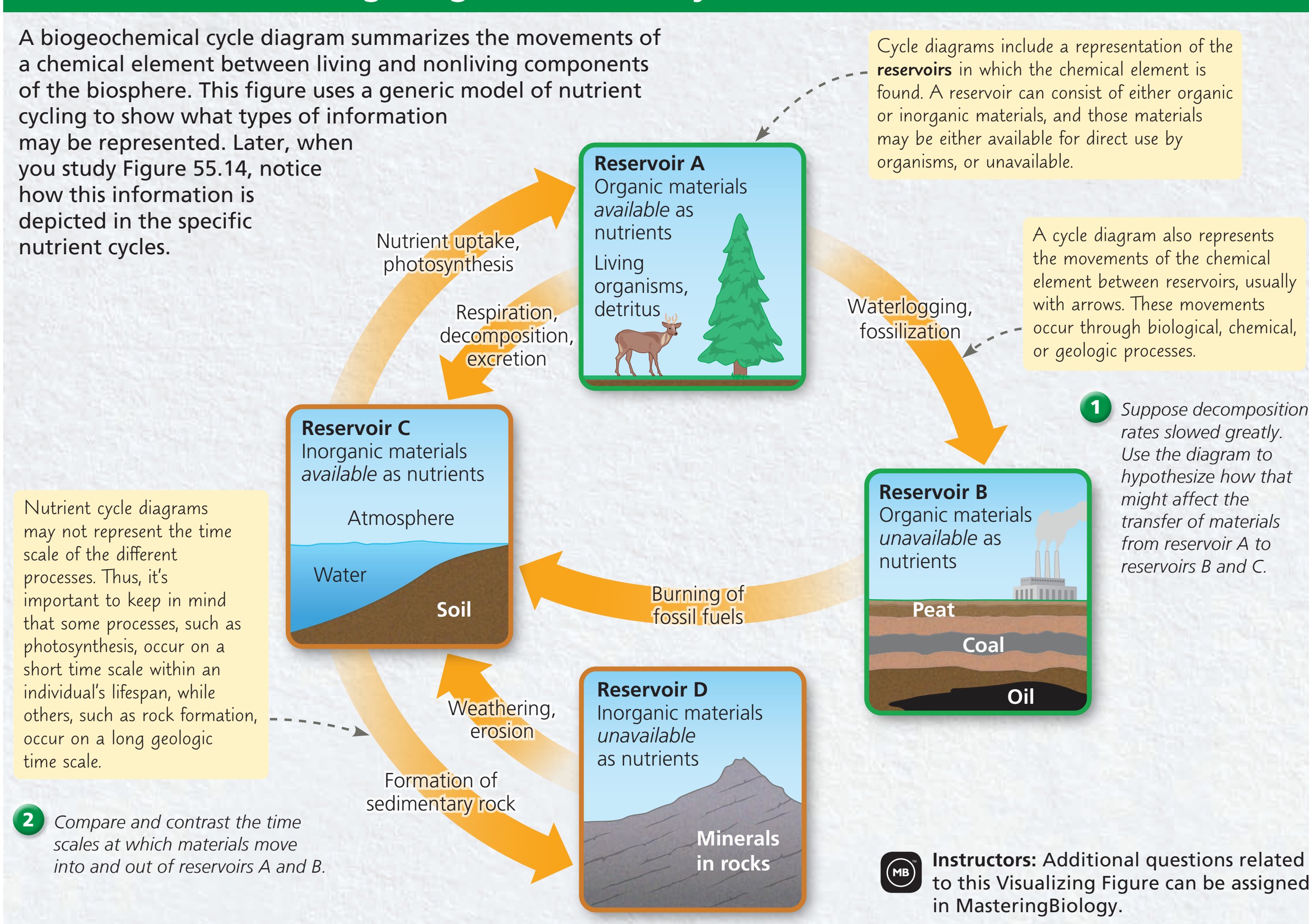
Biogeochemical Cycles

Because nutrient cycles involve both biotic and abiotic components, they are called **biogeochemical cycles**. We can recognize two general scales of biogeochemical cycles: global and local. Gaseous forms of carbon, oxygen, sulfur, and nitrogen occur in the atmosphere, and cycles of these elements are essentially global. For example, some of the carbon and oxygen atoms a plant acquires from the air as CO_2 may have been released into the atmosphere by the respiration of an organism in a distant locale. Other elements, including phosphorus, potassium, and calcium, are too heavy to occur as gases at Earth's surface, although they are transported in dust. In terrestrial ecosystems, these elements cycle more locally, absorbed from the soil by plant roots and eventually returned to the soil by decomposers. In aquatic systems, however, they cycle more broadly as dissolved forms carried in currents.

Let's first look at a general model of nutrient cycling that includes reservoirs where elements exist and processes that transfer elements between them **(Figure 55.13)**. The nutrients in living organisms and detritus (reservoir A) are available to other organisms when consumers feed and when detritivores consume nonliving organic matter. The low pH and low oxygen levels found in the waterlogged sediments of swamps can inhibit decomposition, leading to the formation of peat. When this occurs, organic materials from dead organisms can be transferred from reservoir A to reservoir B; eventually, peat may be converted to fossil fuels such as coal or oil. Inorganic materials that are dissolved in water or present in soil or air (reservoir C) are available for use. Although most organisms cannot directly tap into the inorganic elements tied up in rocks (reservoir D), these nutrients may slowly become available through weathering and erosion.

Figure 55.14 provides a detailed look at the cycling of water, carbon, nitrogen, and phosphorus. When you study each cycle, consider which steps are driven primarily by

▼ Figure 55.13 Visualizing Biogeochemical Cycles



▼ Figure 55.14 Exploring Water and Nutrient Cycling

Examine each cycle closely, considering the major reservoirs of water, carbon, nitrogen, and phosphorus and the processes that drive each cycle. The widths of the arrows in the diagrams approximately reflect the relative contribution of each process to the movement of water or a nutrient in the biosphere.

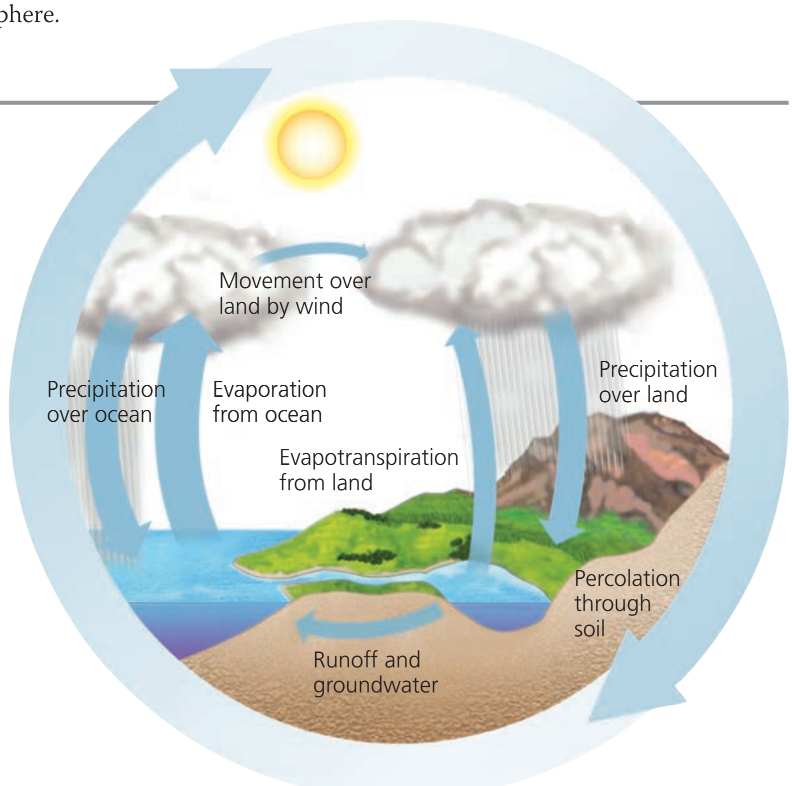
The Water Cycle

Biological importance Water is essential to all organisms, and its availability influences the rates of ecosystem processes, particularly primary production and decomposition in terrestrial ecosystems.

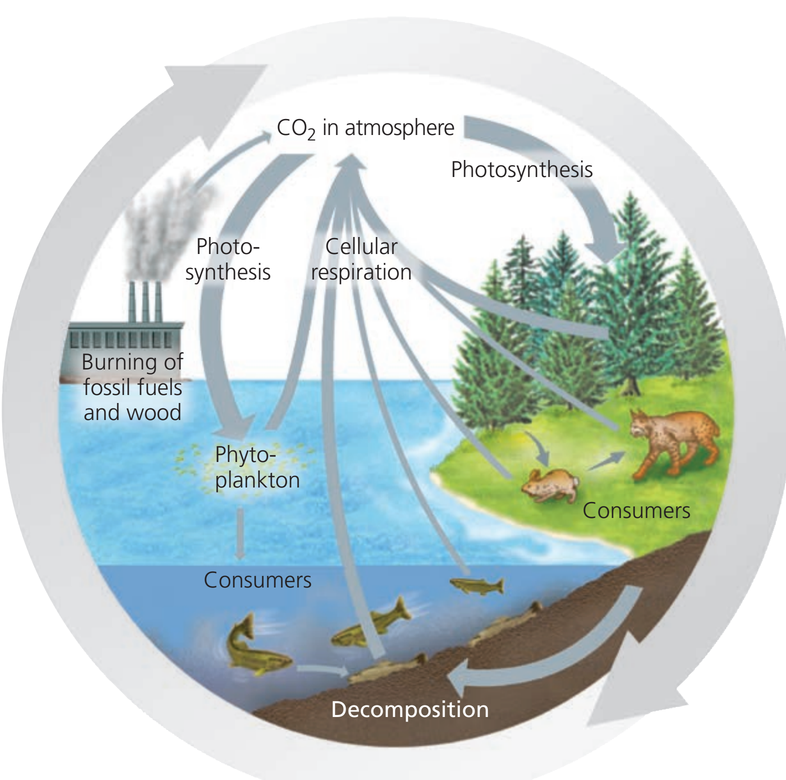
Forms available to life All organisms are capable of exchanging water directly with their environment. Liquid water is the primary physical phase in which water is used, though some organisms can harvest water vapor. Freezing of soil water can limit water availability to terrestrial plants.

Reservoirs The oceans contain 97% of the water in the biosphere. Approximately 2% is bound in glaciers and polar ice caps, and the remaining 1% is in lakes, rivers, and groundwater, with a negligible amount in the atmosphere.

Key processes The main processes driving the water cycle are evaporation of liquid water by solar energy, condensation of water vapor into clouds, and precipitation. Transpiration by terrestrial plants also moves large volumes of water into the atmosphere. Surface and groundwater flow can return water to the oceans, completing the water cycle.



The Carbon Cycle



Biological importance Carbon forms the framework of the organic molecules essential to all organisms.

Forms available to life Photosynthetic organisms utilize CO_2 during photosynthesis and convert the carbon to organic forms that are used by consumers, including animals, fungi, and heterotrophic protists and prokaryotes.

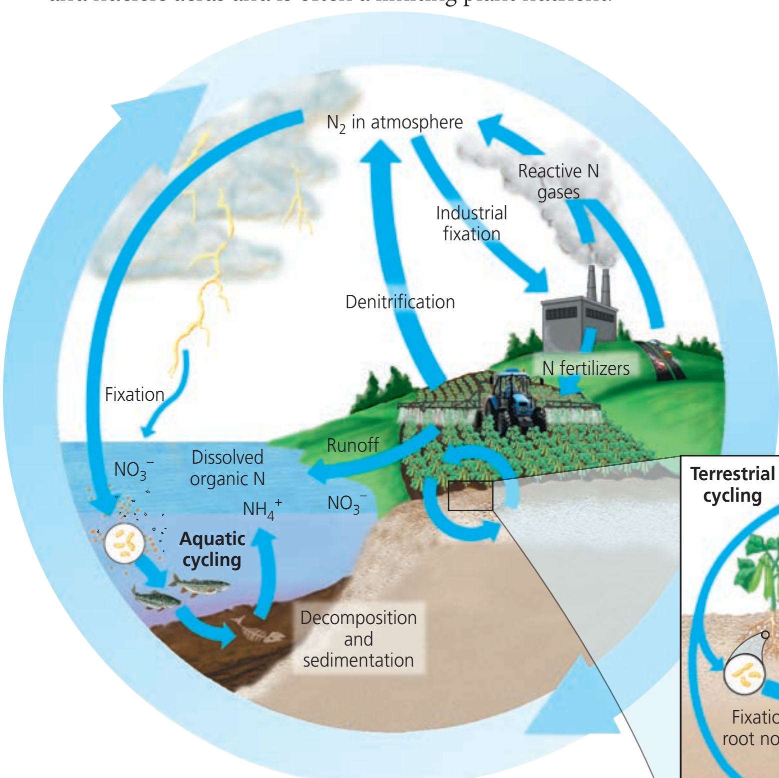
Reservoirs The major reservoirs of carbon include fossil fuels, soils, the sediments of aquatic ecosystems, the oceans (dissolved carbon compounds), plant and animal biomass, and the atmosphere (CO_2). The largest reservoir is sedimentary rocks such as limestone; however, carbon remains in this pool for long periods of time. All organisms are capable of returning carbon directly to their environment in its original form (CO_2) through respiration.

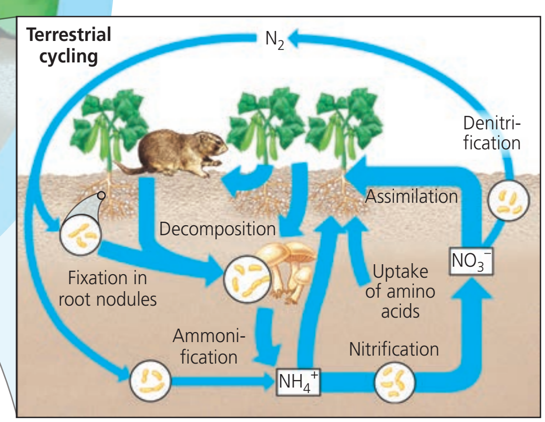
Key processes Photosynthesis by plants and phytoplankton removes substantial amounts of atmospheric CO_2 each year. This quantity is approximately equal to the CO_2 added to the atmosphere through cellular respiration by producers and consumers. The burning of fossil fuels and wood is adding significant amounts of additional CO_2 to the atmosphere. Over geologic time, volcanoes are also a substantial source of CO_2.

MB **BioFlix® Animation: The Carbon Cycle**

The Nitrogen Cycle

Biological importance Nitrogen is part of amino acids, proteins, and nucleic acids and is often a limiting plant nutrient.





Animation: The Nitrogen Cycle

Forms available to life Plants can assimilate (use) two inorganic forms of nitrogen—ammonium (NH_4^+) and nitrate (NO_3^-)—and some organic forms, such as amino acids. Various bacteria can use all of these forms as well as nitrite (NO_2^-). Animals can use only organic forms of nitrogen.

Reservoirs The main reservoir of nitrogen is the atmosphere, which is 80% free nitrogen gas (N_2). The other reservoirs of inorganic and organic nitrogen compounds are soils and the sediments of lakes, rivers, and oceans; surface water and groundwater; and the biomass of living organisms.

Key processes The major pathway for nitrogen to enter an ecosystem is via *nitrogen fixation*, the conversion of N_2 to forms that can be used to synthesize organic nitrogen compounds. Certain bacteria, as well as lightning and volcanic activity, fix nitrogen naturally. Nitrogen inputs from human activities now outpace natural inputs on land. Two major contributors are industrially produced fertilizers and legume crops that fix nitrogen via bacteria in their root nodules. Other bacteria in soil convert nitrogen to different forms. Examples include nitrifying bacteria, which convert ammonium to nitrate, and denitrifying bacteria, which convert nitrate to nitrogen gas. Human activities also release large quantities of reactive nitrogen gases, such as nitrogen oxides, to the atmosphere.

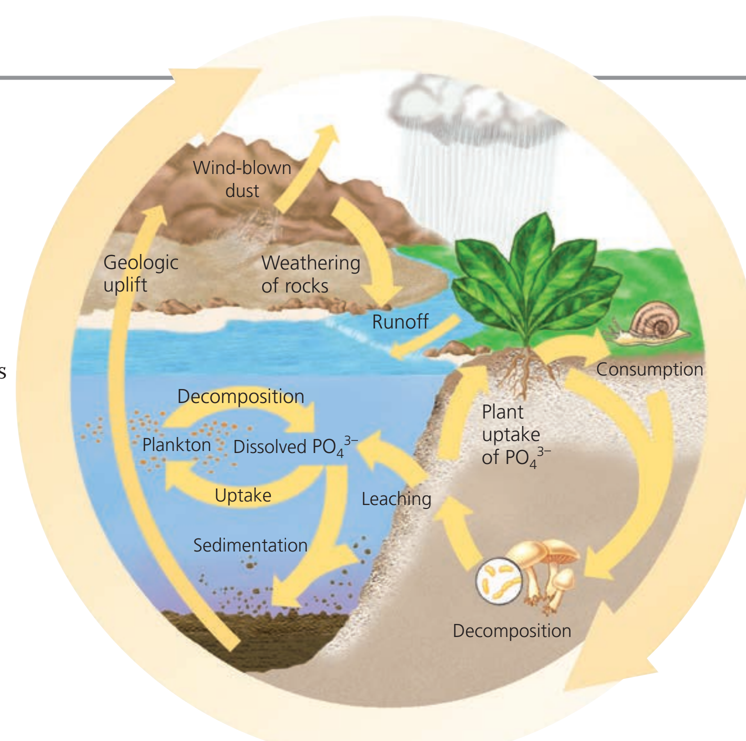
The Phosphorus Cycle

Biological importance Organisms require phosphorus as a major constituent of nucleic acids, phospholipids, and ATP and other energy-storing molecules and as a mineral constituent of bones and teeth.

Forms available to life The most biologically important inorganic form of phosphorus is phosphate (PO_4^{3-}), which plants absorb and use in the synthesis of organic compounds.

Reservoirs The largest accumulations of phosphorus are in sedimentary rocks of marine origin. There are also large quantities of phosphorus in soil, in the oceans (in dissolved form), and in organisms. Because soil particles bind PO_4^{3-}, the recycling of phosphorus tends to be quite localized in ecosystems.

Key processes Weathering of rocks gradually adds PO_4^{3-} to soil; some leaches into groundwater and surface water and may eventually reach the sea. Phosphate taken up by producers and incorporated into biological molecules may be eaten by consumers. Phosphate is returned to soil or water by either decomposition of biomass or excretion by consumers. Because there are no significant phosphorus-containing gases, only relatively small amounts of phosphorus move through the atmosphere, usually in the forms of dust and sea spray.



biological processes. For the carbon cycle, for instance, plants, animals, and other organisms control most of the key steps, including photosynthesis and decomposition. For the water cycle, however, purely physical processes control many key steps, such as evaporation from the oceans. Note also that human actions, such as the burning of fossil fuels and the production of fertilizers, have had major effects on the global cycling of carbon and nitrogen.

How have ecologists worked out the details of chemical cycling in various ecosystems? One common method is to follow the movement of naturally occurring, nonradioactive isotopes through the biotic (organic) and abiotic (inorganic) components of an ecosystem. Another method involves adding tiny amounts of radioactive isotopes of specific elements and tracing their progress. Scientists have also been able to make use of radioactive carbon (^{14}C) released into the atmosphere during atom bomb testing in the 1950s and early 1960s. This "spike" of ^{14}C can reveal where and how quickly carbon flows into ecosystem components, including plants, soils, and ocean water.

Case Study: Nutrient Cycling in the Hubbard Brook Experimental Forest

Since 1963, ecologist Gene Likens and colleagues have been studying nutrient cycling at the Hubbard Brook Experimental Forest in the White Mountains of New Hampshire. Their research site is a deciduous forest that grows in six small valleys, each drained by a single creek. Impermeable bedrock underlies the soil of the forest.

The research team first determined the mineral budget for each of six valleys by measuring the input and outflow of several key nutrients. They collected rainfall at several sites to measure the amount of water and dissolved minerals added to the ecosystem. To monitor the loss of water and minerals, they constructed a small concrete dam with a V-shaped spillway across the creek at the bottom of each valley **(Figure 55.15a)**. They found that about 60% of the water added to the ecosystem as rainfall and snow exits through the stream, and the remaining 40% is lost by evapotranspiration.

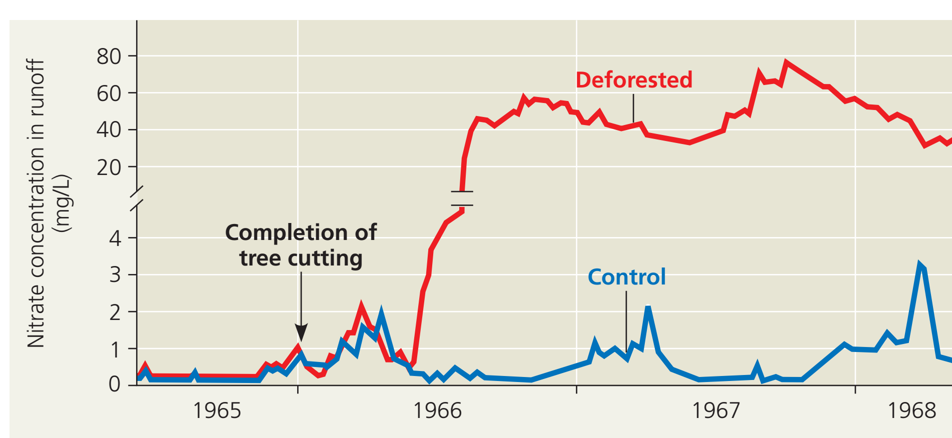
Preliminary studies confirmed that internal cycling conserved most of the mineral nutrients in the system. For example, only about 0.3% more calcium (Ca^{2+}) leaves a valley via its creek than is added by rainwater, and this small net loss is probably replaced by chemical decomposition of the bedrock. During most years, the forest even registers small net gains of a few mineral nutrients, including nitrogen.

Experimental deforestation of a watershed dramatically increased the flow of water and minerals leaving the watershed **(Figure 55.15b)**. Over three years, water runoff from the newly deforested watershed was 30–40% greater than in a control watershed, apparently because there were no plants to absorb and transpire water from the soil. Most remarkable was the loss of nitrate, whose concentration in the creek increased 60-fold, reaching levels considered unsafe for drinking water **(Figure 55.15c)**. The Hubbard Brook deforestation study showed that the amount of nutrients leaving an intact

▼ Figure 55.15 Nutrient cycling in the Hubbard Brook Experimental Forest: an example of long-term ecological research.

(a) Concrete dams and weirs built across streams at the bottom of watersheds enabled researchers to monitor the outflow of water and nutrients from the ecosystem.

(b) One watershed was clear-cut to study the effects of the loss of vegetation on drainage and nutrient cycling. All of the original plant material was left in place to decompose.



(c) The concentration of nitrate in runoff from the deforested watershed was 60 times greater than in a control (unlogged) watershed.

MB **Instructors**: A related Experimental Inquiry Tutorial can be assigned in MasteringBiology.

forest ecosystem is controlled mainly by the plants. Retaining nutrients in an ecosystem helps to maintain the productivity of the system, as well as to avoid algal blooms and other problems caused by excess nutrient runoff.

MB Interview with Eugene Likens: Co-founder of the Hubbard Brook Forest Study

CONCEPT CHECK 55.4

1. **DRAW IT** ➤ For each of the four biogeochemical cycles in Figure 55.14, draw a simple diagram that shows one possible path for an atom of that chemical from abiotic to biotic reservoirs and back.
2. Why does deforestation of a watershed increase the concentration of nitrates in streams draining the watershed?
3. **WHAT IF?** ➤ Why is nutrient availability in a tropical rain forest particularly vulnerable to logging?

For suggested answers, see Appendix A.

CONCEPT 55.5

Restoration ecologists return degraded ecosystems to a more natural state

Ecosystems can recover naturally from most disturbances (including the experimental deforestation at Hubbard Brook) through the stages of ecological succession (see Concept 54.3). Sometimes, however, that recovery takes centuries, particularly when humans have degraded the environment. Tropical areas that are cleared for farming may quickly become unproductive because of nutrient losses. Mining activities may last for several decades, and the lands are often abandoned in a degraded state. Ecosystems can also be damaged by salts that build up in soils from irrigation and by toxic chemicals or oil spills. Biologists increasingly are called on to help restore and repair damaged ecosystems.

Restoration ecologists seek to initiate or speed up the recovery of degraded ecosystems. One of the basic assumptions is that environmental damage is at least partly reversible. This optimistic view must be balanced by a second assumption—that ecosystems are not infinitely resilient. Restoration ecologists therefore work to identify and manipulate the processes that most limit recovery of ecosystems from disturbances. Where disturbance is so severe that restoring all of a habitat is impractical, ecologists try to reclaim as much of a habitat or ecological process as possible, within the limits of the time and money available to them.

In extreme cases, the physical structure of an ecosystem may need to be restored before biological restoration can occur. If a stream was straightened to channel water quickly through a suburb, ecologists may reconstruct a meandering channel to slow down the flow of water eroding the stream bank. To restore an open-pit mine, engineers may grade the site with heavy equipment to reestablish a gentle slope, spreading topsoil when the slope is in place (**Figure 55.16**).

After any physical reconstruction of the ecosystem is complete, the next step is biological restoration. The long-term objective of restoration is to return an ecosystem as closely as possible to its predisturbance state. **Figure 55.17** explores four ambitious and successful restoration projects. These and the many other such projects throughout the world often employ two key strategies: bioremediation and biological augmentation.

Bioremediation

Using organisms—usually prokaryotes, fungi, or plants—to detoxify polluted ecosystems is known as **bioremediation**. Some plants and lichens adapted to soils containing heavy metals can accumulate high concentrations of toxic metals such as lead and cadmium in their tissues. Restoration ecologists can introduce such species to sites polluted by mining and other human activities and then harvest these organisms to remove the metals from the ecosystem. For instance, researchers in the United Kingdom have discovered a lichen

▼ **Figure 55.16 A gravel and clay mine site in New Jersey before and after restoration.**

(a) In 1991, before restoration

(b) In 2000, near the completion of restoration

▼ Figure 55.17 Exploring Restoration Ecology Worldwide

The examples highlighted in this figure are just a few of the many restoration ecology projects taking place around the world.

Kissimmee River, Florida

In the 1960s, the Kissimmee River was converted from a meandering river to a 90-km canal to control flooding. This channelization diverted water from the floodplain, causing the wetlands to dry up, threatening many fish and wetland bird populations. Kissimmee River restoration has filled 12 km of drainage canal and reestablished 24 km of the original 167 km of natural river channel. Pictured here is a section of the Kissimmee canal that has been plugged (wide, light strip on the right side of the photo), diverting flow into remnant river channels (center of the photo). The project will also restore natural flow patterns, which will foster self-sustaining populations of wetland birds and fishes.

Succulent Karoo, South Africa

In the Succulent Karoo desert region of southern Africa, as in many arid regions, overgrazing by livestock has damaged vast areas. Private landowners and government agencies in South Africa are restoring large areas of this unique region, revegetating the land and employing more sustainable resource management. The photo shows a small sample of the exceptional plant diversity of the Succulent Karoo; its 5,000 plant species include the highest diversity of succulent plants in the world.

Maungatautari, New Zealand

Weasels, rats, pigs, and other introduced species pose a serious threat to New Zealand's native plants and animals, including kiwis, a group of flightless, ground-dwelling bird species. The goal of the Maungatautari restoration project is to exclude all exotic mammals from a 3,400-ha reserve located on a forested volcanic cone. A specialized fence around the reserve eliminates the need to continue setting traps and using poisons that can harm native wildlife. In 2006, a pair of critically endangered takahe (a species of flightless rail) were released into the reserve with the hope of reestablishing a breeding population of this colorful bird on New Zealand's North Island.

Coastal Japan

Seaweed and seagrass beds are important nursery grounds for a wide variety of fishes and shellfish. Once extensive but now reduced by development, these beds are being restored in the coastal areas of Japan. Techniques include constructing suitable seafloor habitat, transplanting seaweeds and seagrasses from natural beds using artificial substrates, and hand seeding (shown in this photograph).

species that grows on soil polluted with uranium dust left over from mining. The lichen concentrates uranium in a dark pigment, making it useful as a biological monitor and potentially as a remediator.

Ecologists already use the abilities of many prokaryotes to carry out bioremediation of soils and water (see Concept 27.6). Scientists have sequenced the genomes of at least ten prokaryotic species specifically for their bioremediation potential. One of the species, the bacterium *Shewanella oneidensis*, appears particularly promising. It can metabolize a dozen or more elements under aerobic and anaerobic conditions. In doing so, it converts soluble forms of uranium, chromium, and nitrogen to insoluble forms that are less likely to leach into streams or groundwater. Researchers at Oak Ridge National Laboratory, in Tennessee, stimulated the growth of *Shewanella* and other uranium-reducing bacteria by adding ethanol to groundwater contaminated with uranium; the bacteria can use ethanol as an energy source. In just five months, the concentration of soluble uranium in the ecosystem dropped by 80% **(Figure 55.18)**.

Biological Augmentation

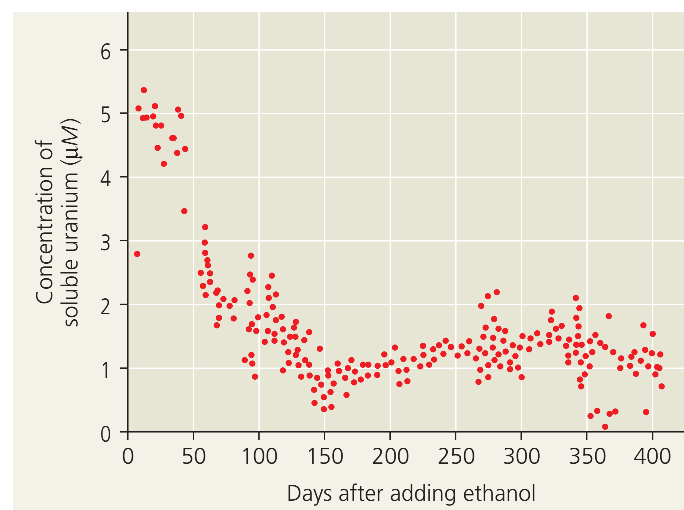
In contrast to bioremediation, which is a strategy for removing harmful substances from an ecosystem, **biological augmentation** uses organisms to *add* essential materials to a degraded ecosystem. To augment ecosystem processes, restoration ecologists need to determine which factors, such as chemical nutrients, have been lost from a system and are limiting its recovery.

Encouraging the growth of plants that thrive in nutrient-poor soils often speeds up succession and ecosystem recovery. In alpine ecosystems of the western United States, nitrogen-fixing plants such as lupines are often planted to raise nitrogen concentrations in soils disturbed by mining and other activities. Once these nitrogen-fixing plants become established, other native species are better able to obtain enough soil nitrogen to survive. In other systems where the soil has been severely disturbed or where topsoil is missing entirely, plant roots may lack the mycorrhizal symbionts that help them meet their nutritional needs (see Concept 31.1). Ecologists restoring a tallgrass prairie in Minnesota recognized this limitation and enhanced the recovery of native species by adding mycorrhizal symbionts to the soil they seeded.

Restoring the physical structure and plant community of an ecosystem does not always ensure that animal species will recolonize a site and persist there. Because animals provide critical ecosystem services, including pollination and seed dispersal, restoration ecologists sometimes help wildlife to reach and use restored ecosystems. They might release animals at a site or establish habitat corridors that connect a restored site to places where the animals are found. They sometimes establish artificial perches for birds to use. These and other efforts can increase the biodiversity of restored ecosystems and help the community persist.

▼ Figure 55.18 Bioremediation of groundwater contaminated with uranium at Oak Ridge National Laboratory, Tennessee.

(a) Wastes containing uranium were dumped in these four unlined pits for more than 30 years, contaminating soils and groundwater.



(b) After ethanol was added, microbial activity decreased the concentration of soluble uranium in groundwater near the pits.

Ecosystems: *A Review*

Figure 55.19 illustrates energy transfer, nutrient cycling, and other key processes for an arctic tundra ecosystem. Note the conceptual similarities between this figure and Make Connections Figure 11.23, "The Working Cell." The scale of the two figures is different, but the physical laws and biological rules that govern life apply equally to both systems.

CONCEPT CHECK 55.5

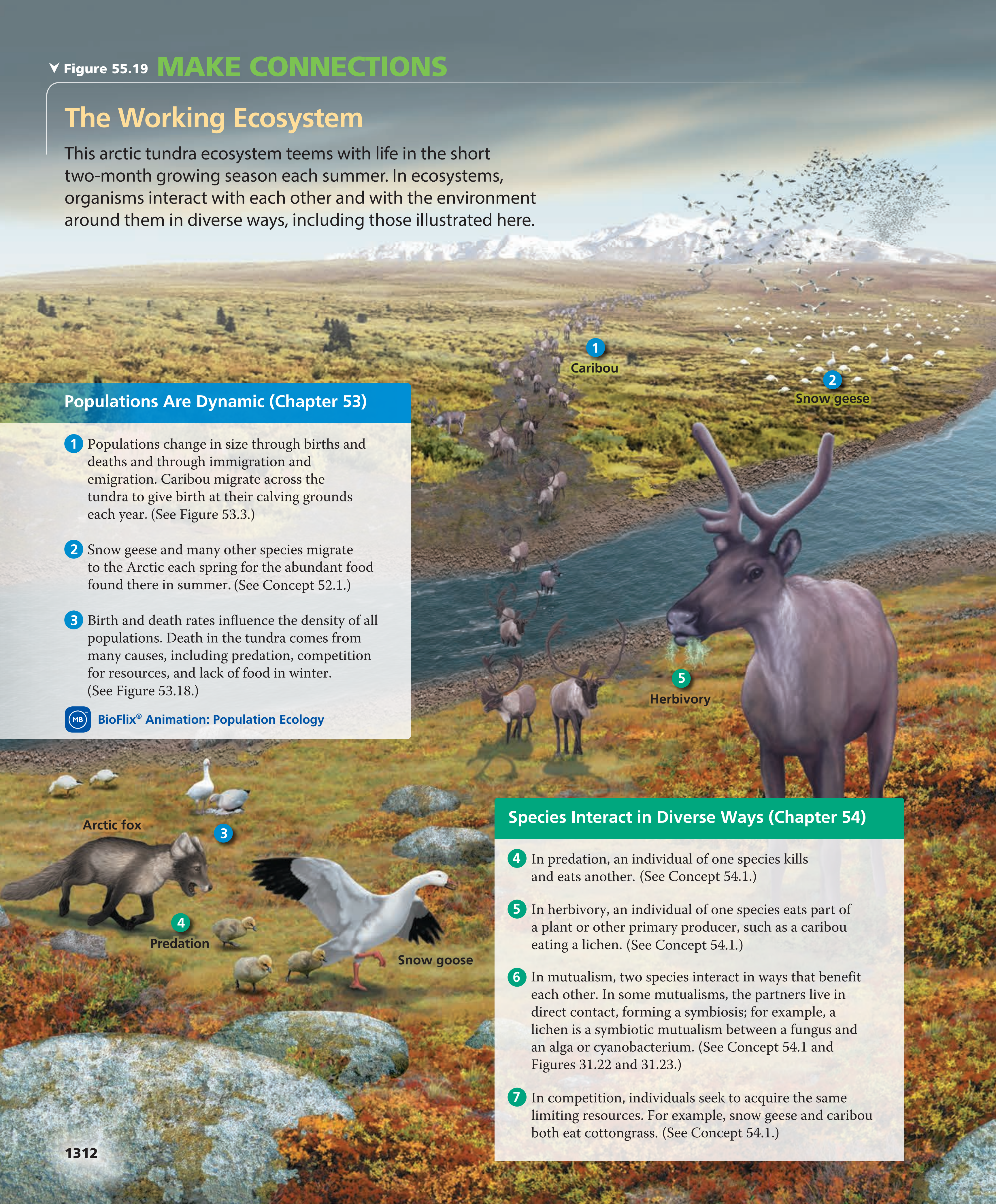
1. Identify the main goal of restoration ecology.
2. **WHAT IF?** ➤ In what way is the Kissimmee River project a more complete ecological restoration than the Maungatautari project (see Figure 55.17)?

For suggested answers, see Appendix A.

▼ **Figure 55.19** **MAKE CONNECTIONS**

The Working Ecosystem

This arctic tundra ecosystem teems with life in the short two-month growing season each summer. In ecosystems, organisms interact with each other and with the environment around them in diverse ways, including those illustrated here.



Populations Are Dynamic (Chapter 53)

1. Populations change in size through births and deaths and through immigration and emigration. Caribou migrate across the tundra to give birth at their calving grounds each year. (See Figure 53.3.)

2. Snow geese and many other species migrate to the Arctic each spring for the abundant food found there in summer. (See Concept 52.1.)

3. Birth and death rates influence the density of all populations. Death in the tundra comes from many causes, including predation, competition for resources, and lack of food in winter. (See Figure 53.18.)

MB **BioFlix® Animation: Population Ecology**

Species Interact in Diverse Ways (Chapter 54)

4. In predation, an individual of one species kills and eats another. (See Concept 54.1.)

5. In herbivory, an individual of one species eats part of a plant or other primary producer, such as a caribou eating a lichen. (See Concept 54.1.)

6. In mutualism, two species interact in ways that benefit each other. In some mutualisms, the partners live in direct contact, forming a symbiosis; for example, a lichen is a symbiotic mutualism between a fungus and an alga or cyanobacterium. (See Concept 54.1 and Figures 31.22 and 31.23.)

7. In competition, individuals seek to acquire the same limiting resources. For example, snow geese and caribou both eat cottongrass. (See Concept 54.1.)

Organisms Transfer Energy and Matter in Ecosystems (Chapter 55)

8 Primary producers convert the energy in sunlight to chemical energy through photosynthesis. Their growth is often limited by abiotic factors such as low temperatures, scarce soil nutrients, and lack of light in winter. (See Figures 11.6, 51.12, and 55.4.)

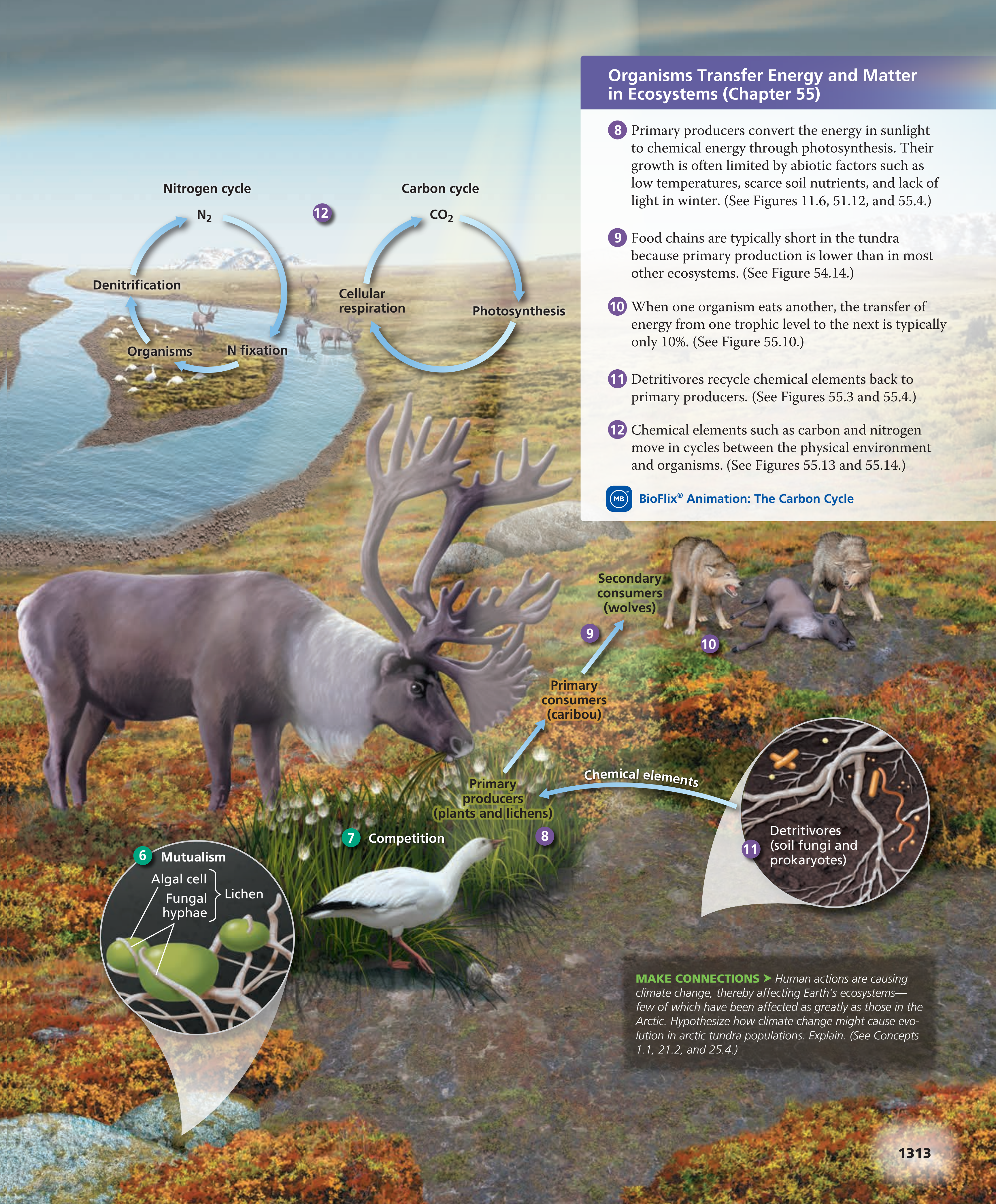
9 Food chains are typically short in the tundra because primary production is lower than in most other ecosystems. (See Figure 54.14.)

10 When one organism eats another, the transfer of energy from one trophic level to the next is typically only 10%. (See Figure 55.10.)

11 Detritivores recycle chemical elements back to primary producers. (See Figures 55.3 and 55.4.)

12 Chemical elements such as carbon and nitrogen move in cycles between the physical environment and organisms. (See Figures 55.13 and 55.14.)

BioFlix® Animation: The Carbon Cycle



MAKE CONNECTIONS ➤ *Human actions are causing climate change, thereby affecting Earth's ecosystems—few of which have been affected as greatly as those in the Arctic. Hypothesize how climate change might cause evolution in arctic tundra populations. Explain. (See Concepts 1.1, 21.2, and 25.4.)*

Case Study: *Restoration of Coastal Sand Dune Ecosystems in New Zealand*

Coastal sand dunes are important ecosystems that not only protect against storms and floods, but also provide harvestable natural resources and help sustain biodiversity. For example, in New Zealand, sand-binding grasses and sedges build sand dunes that provide habitats for many animals, such as spiders, moths, edible shellfish, and birds. But several factors are causing these ecosystems to decline. In New Zealand, the sand dunes now comprise less than 25% of their former area due to modification of the coastal area for the purposes of agriculture, urbanization, and tourism.

Several measures are being taken in New Zealand to restore the dune ecosystems. These include removal of exotic plant species through weeding and use of herbicides, and planting of native species. Native sand-binding plants are planted on fore dunes and other coastal plants, which require more stable and moist conditions, are planted on hind dunes and in dune slacks. These restoration activities are currently focused on reestablishing the native vegetation to create functioning dune ecosystems and on harvesting important coastal resources, such as *Paphies ventricosa* (an edible mollusc). The highly dynamic nature of the coastal environment and damages caused by humans, such as trampling, make the success rate of these restoration activities highly variable. Further research needs to be done to assess the recovery trajectory of the restored ecosystems and understand what other measures can be taken.

55 Chapter Review

Go to **MasteringBiology**™ for Videos, Animations, Vocab Self-Quiz, Practice Tests, and more in the Study Area.

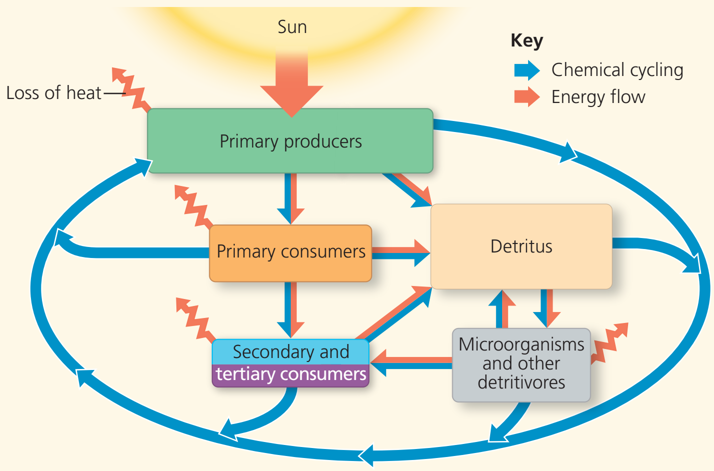
SUMMARY OF KEY CONCEPTS

CONCEPT 55.1

Physical laws govern energy flow and chemical cycling in ecosystems *(pp. 1295–1297)*

VOCAB SELF-QUIZ
goo.gl/Rn5Uax

- An **ecosystem** consists of all the organisms in a community and all the abiotic factors with which they interact. Energy is conserved but released as heat during ecosystem processes. As a result, energy flows through ecosystems (rather than being recycled).
- Chemical elements enter and leave an ecosystem and cycle within it, subject to the **law of conservation of mass**. Inputs and outputs are generally small compared to recycled amounts, but their balance determines whether the ecosystem gains or loses an element over time.



Considering the second law of thermodynamics, would you expect the typical biomass of primary producers in an ecosystem to be greater than or less than the biomass of secondary producers in the system? Explain your reasoning.

CONCEPT 55.2

Energy and other limiting factors control primary production in ecosystems *(pp. 1297–1301)*

- **Primary production** sets the spending limit for the global energy budget. **Gross primary production** is the total energy assimilated by an ecosystem in a given period. **Net primary production**, the energy accumulated in autotroph biomass, equals gross primary production minus the energy used by the primary producers for respiration. **Net ecosystem production** is the total biomass accumulation of an ecosystem, defined as the difference between gross primary production and total ecosystem respiration.
- In aquatic ecosystems, light and nutrients limit primary production. In terrestrial ecosystems, climatic factors such as temperature and moisture affect primary production at large scales, but a soil nutrient is often the limiting factor locally.

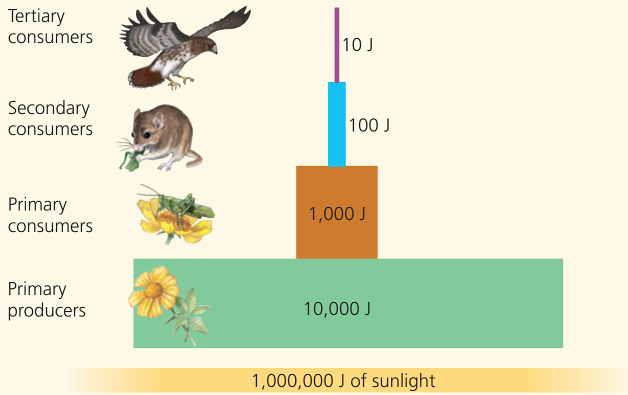
If you know NPP for an ecosystem, what additional variable do you need to know to estimate NEP? Why might measuring this variable be difficult, for instance, in a sample of ocean water?

CONCEPT 55.3

Energy transfer between trophic levels is typically only 10% efficient *(pp. 1302–1304)*

- The amount of energy available to each trophic level is determined by the net primary production and the **production efficiency**, the efficiency with which food energy is converted to biomass at each link in the food chain.

- The percentage of energy transferred from one trophic level to the next, called **trophic efficiency**, is typically 10%. Pyramids of energy and biomass reflect low trophic efficiency.



Why would runners have a lower production efficiency when running a long-distance race than when they are sedentary?

CONCEPT 55.4

Biological and geochemical processes cycle nutrients and water in ecosystems *(pp. 1304–1309)*

- Water moves in a global cycle driven by solar energy. The carbon cycle primarily reflects the reciprocal processes of photosynthesis and cellular respiration. Nitrogen enters ecosystems through atmospheric deposition and nitrogen fixation by prokaryotes.
- The proportion of a nutrient in a particular form varies among ecosystems, largely because of differences in the rate of decomposition.
- Nutrient cycling is strongly regulated by vegetation. The Hubbard Brook case study showed that logging increases water runoff and can cause large losses of minerals.

If decomposers usually grow faster and decompose material more quickly in warmer ecosystems, why is decomposition in hot deserts relatively slow?

CONCEPT 55.5

Restoration ecologists return degraded ecosystems to a more natural state *(pp. 1309–1311)*

- Restoration ecologists harness organisms to detoxify polluted ecosystems through the process of **bioremediation**.
- In **biological augmentation**, ecologists use organisms to add essential materials to ecosystems.

In preparing a site for surface mining and later restoration, why would engineers separate the topsoil from the deeper soil, rather than removing all soil at once and mixing it in a single pile?

TEST YOUR UNDERSTANDING

Multiple-choice Self-Quiz questions 1–8 can be found in the Study Area in MasteringBiology.

9. DRAW IT (a) Draw a simplified global water cycle showing ocean, land, atmosphere, and runoff from the land to the ocean. Label your drawing with these annual water fluxes:

- ocean evaporation, 425 km^3
- ocean evaporation that returns to the ocean as precipitation, 385 km^3
- ocean evaporation that falls as precipitation on land, 40 km^3
- evapotranspiration from plants and soil that falls as precipitation on land, 70 km^3
- runoff to the oceans, 40 km^3

(b) What is the ratio of ocean evaporation that falls as precipitation on land compared with runoff from land to the oceans? (c) How would this ratio change during an ice age, and why?

PRACTICE TEST
goo.gl/iAsVgL

10. EVOLUTION CONNECTION Some biologists have suggested that ecosystems are emergent, "living" systems capable of evolving. One manifestation of this idea is environmentalist James Lovelock's Gaia hypothesis, which views Earth itself as a living, homeostatic entity—a kind of superorganism. Are ecosystems capable of evolving? If so, would this be a form of Darwinian evolution? Why or why not? Explain.

11. SCIENTIFIC INQUIRY Using two neighboring ponds in a forest as your study site, design a controlled experiment to measure the effect of falling leaves on net primary production in a pond.

12. WRITE ABOUT A THEME: ENERGY AND MATTER Decomposition typically occurs quickly in moist tropical forests. However, waterlogging in the soil of some moist tropical forests results over time in a buildup of organic matter called "peat." In a short essay (100–150 words), discuss the relationship of net primary production, net ecosystem production, and decomposition for such an ecosystem. Are NPP and NEP likely to be positive? What do you think would happen to NEP if a landowner drained the water from a tropical peatland, exposing the organic matter to air?

13. SYNTHESIZE YOUR KNOWLEDGE

This dung beetle (genus *Scarabaeus*) is burying a ball of dung it has collected from a large mammalian herbivore in Kenya. Explain why this process is important for the cycling of nutrients and for primary production.

For selected answers, see Appendix A.

For additional practice questions, check out the **Dynamic Study Modules** in MasteringBiology. You can use them to study on your smartphone, tablet, or computer anytime, anywhere!

Conservation and Global Ecology

56

Figure 56.1 What will be the fate of this newly described lizard species?

KEY CONCEPTS

56.1 Human activities threaten Earth's biodiversity

56.2 Population conservation focuses on population size, genetic diversity, and critical habitat

56.3 Landscape and regional conservation help sustain biodiversity

56.4 Earth is changing rapidly as a result of human actions

56.5 Sustainable development can improve human lives while conserving biodiversity

Psychedelic Treasure

Scurrying across a rocky outcrop, a lizard stops abruptly in a patch of sunlight. It catches the eye of a conservation biologist, who is thrilled to observe the gecko splashed with rainbow colors, its bright orange legs and tail blending into a blue body, its head and neck splotched with yellow and green. This lizard, the psychedelic rock gecko (*Cnemaspis psychedelica*), was discovered in 2010 during an expedition to the Greater Mekong region of southeast Asia **(Figure 56.1)**. Its known habitat is restricted to an island of just 8 km^2 (3 mi^2) in southern Vietnam. Other new species found during the same series of expeditions include the striking Daklak orchid (*Dendrobium daklakense*), named for the Vietnamese province where it was observed. Between 2000 and 2010, biologists identified more than 1,000 new species in the Greater Mekong region alone.

To date, scientists have described and formally named about 1.8 million species of organisms. In addition to these named species, many others remain to be discovered: Estimates for the number of species that currently exist range from 5 million to 100 million. Some of the greatest concentrations of species are in the tropics. Unfortunately, tropical forests are being cleared at an alarming rate to make room for and support a burgeoning human population. Rates of deforestation in Vietnam are among the highest in the world **(Figure 56.2)**. What will become of the psychedelic rock gecko and other newly discovered species if such activities continue unchecked?

Daklak orchid

When you see this blue icon, log in to **MasteringBiology** and go to the Study Area for digital resources.

Get Ready for This Chapter

▲ **Figure 56.2 Tropical deforestation in Vietnam.** These hills were once covered with tropical forest, most of which has been cut down to make room for farmland such as the terraced rice fields on the lower slopes.

Throughout the biosphere, human activities are altering natural disturbances, trophic structures, energy flow, and chemical cycling—ecosystem processes on which we and all other species depend. We have physically altered nearly half of Earth's land surface, and we use over half of all accessible surface fresh water. In the oceans, stocks of most major fisheries are shrinking because of overharvesting. By some estimates, we may be pushing more species toward extinction than did the asteroid that triggered the Cretaceous mass extinction 66 million years ago (see Figure 25.18).

In this chapter, we'll examine changes happening across Earth, focusing on **conservation biology**, a discipline that integrates ecology, physiology, molecular biology, genetics, and evolutionary biology to conserve biological diversity at all levels. Efforts to sustain ecosystem processes and stem the loss of biodiversity also connect the life sciences with the social sciences, economics, and humanities.

We'll begin by taking a closer look at the biodiversity crisis and examining some of the conservation strategies being adopted to slow the rate of species loss. We'll also examine how human activities are altering the environment through climate change, ozone depletion, and other global processes. Finally, we'll consider how current decisions about long-term conservation priorities could affect life on Earth.

CONCEPT 56.1

Human activities threaten Earth's biodiversity

Extinction is a natural phenomenon that has been occurring since life first evolved; it is the high *rate* of extinction that is responsible for today's biodiversity crisis. More than 1,000 species have become extinct in the last 400 years, a rate that is 100 to 1,000 times the "background," or typical, extinction rate seen in the fossil record (see Concept 25.4). This comparison suggests that the extinction rate today is high and that human activities threaten Earth's biodiversity at all levels.

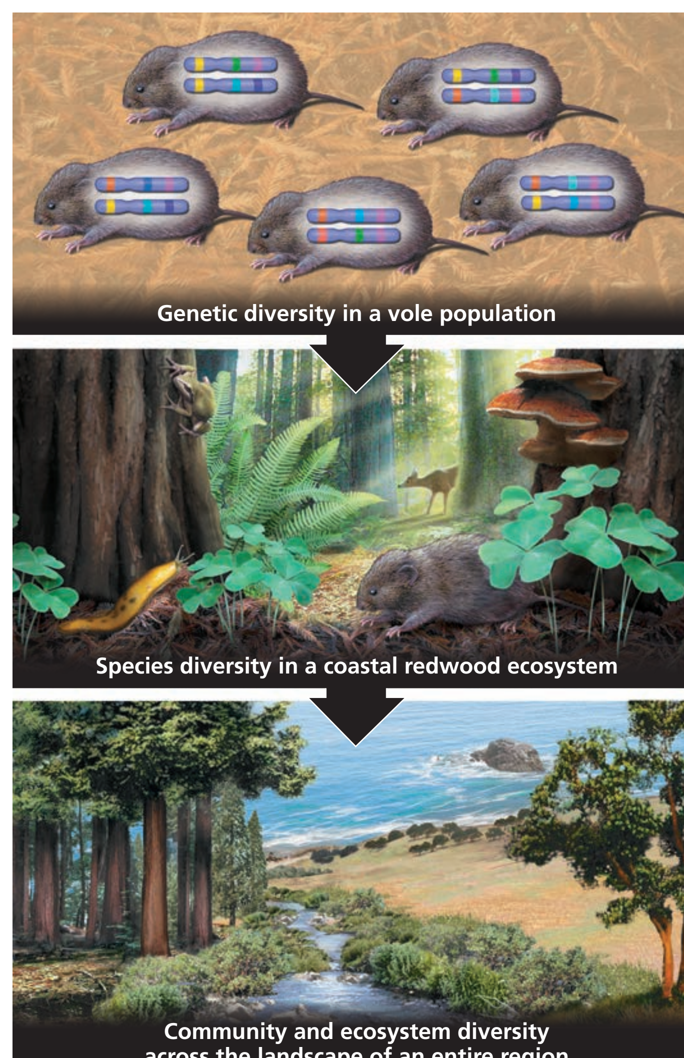
Three Levels of Biodiversity

Biodiversity—short for biological diversity—can be considered at three main levels: genetic diversity, species diversity, and ecosystem diversity **(Figure 56.3)**.

Genetic Diversity

Genetic diversity comprises not only the individual genetic variation *within* a population, but also the genetic variation *between* populations that is often associated with adaptations to local conditions. If one population becomes extinct, then a species may have lost some of the genetic diversity that makes microevolution possible. This erosion of genetic diversity in turn reduces the adaptive potential of the species.

▼ **Figure 56.3 Three levels of biodiversity.** The oversized chromosomes in the top diagram symbolize the genetic variation within the population.



Species Diversity

Public awareness of the biodiversity crisis centers on species diversity—the number of species in an ecosystem or across the biosphere. Of particular concern are species that are endangered or threatened. An **endangered species** is one that is in danger of extinction throughout all or much of its range **(Figure 56.4)**, while a **threatened species** is considered likely to become endangered in the near future. The following are just a few statistics that illustrate the problem of species loss:

- According to the International Union for Conservation of Nature and Natural Resources (IUCN), 12% of the 10,000 known species of birds and 21% of the 5,500 known species of mammals are threatened.
- A survey by the Center for Plant Conservation showed that of the nearly 20,000 known plant species in the United States, 200 have become extinct since such records have been kept, and 730 are endangered or threatened.
- In North America, at least 123 freshwater animal species have become extinct since 1900, and hundreds more species are threatened. The extinction rate for North American freshwater fauna is about five times as high as that for terrestrial animals.

The local populations of a species can also be driven to extinction; for example, populations of a species may be lost in one river system but survive in an adjacent one. Global extinction of a species means that it is lost from *all* the ecosystems in which it lived, leaving them permanently impoverished.

Figure 56.4 A hundred heartbeats from extinction. These are two members of what Harvard biologist E. O. Wilson calls the Hundred Heartbeat Club, species with fewer than 100 individuals remaining on Earth. The Yangtze River dolphin may be extinct, but a few individuals were reportedly sighted in 2007.

Philippine eagle

Yangtze River dolphin

To document that a species has actually become extinct, what factors would you need to consider?

MB HHMI Video: Surveying Gorongosa's Biodiversity

Ecosystem Diversity

The variety of ecosystems on Earth is a third level of biological diversity. Because of the many interactions between different species in an ecosystem, the extinction of populations of one species can have a negative impact on other species in the ecosystem (see Figure 54.18). For instance, bats called "flying foxes" are important pollinators and seed dispersers in the Pacific Islands, where they are increasingly hunted as a luxury food **(Figure 56.5)**. Conservation biologists fear that the extinction of flying foxes would also harm the native plants of the Samoan Islands, where four-fifths of the tree species depend on flying foxes for pollination or seed dispersal.

Some ecosystems have already been heavily affected by humans, and others are being altered at a rapid pace. Since European colonization, more than half of the wetlands in the contiguous United States have been drained and converted to agricultural and other uses. In California, Arizona, and New Mexico, roughly 90% of native riparian (streamside) communities have been affected by overgrazing, flood control, water diversions, lowering of water tables, and invasion by non-native plants.

Biodiversity and Human Welfare

Why should we care about the loss of biodiversity? One basic reason concerns our human sense of connection to nature and all forms of life, termed *biophilia*. Moreover, the belief that other species are entitled to life is a pervasive theme

Figure 56.5 The endangered Marianas "flying fox" bat (*Pteropus mariannus*), an important pollinator.

of many religions and the basis of a moral argument that we should protect biodiversity. There is also a concern for future human generations. Paraphrasing an old proverb, G. H. Brundtland, a former prime minister of Norway, said, “We must consider our planet to be on loan from our children, rather than being a gift from our ancestors.” In addition to such philosophical and moral justifications, species and genetic diversity bring us many practical benefits.

MB **Interview with E. O. Wilson: Advocate for protecting biodiversity**

Benefits of Species and Genetic Diversity

Many threatened species could potentially provide medicines, food, and fibers for human use, making biodiversity a crucial natural resource. Products from aspirin to antibiotics were derived originally from natural sources. If we lose wild populations of plants closely related to agricultural species, we lose genetic resources that could be used to improve crop qualities, such as disease resistance. For instance, in the 1970s, plant breeders responded to devastating outbreaks of the grassy stunt virus in rice (*Oryza sativa*) by screening 7,000 populations of this species and its close relatives for resistance to the virus. One population of a single relative, Indian rice (*Oryza nivara*), was found to be resistant to the virus, and scientists succeeded in breeding the resistance trait into commercial rice varieties. Today, the original disease-resistant population has apparently become extinct in the wild.

In the United States, about 25% of the prescriptions dispensed from pharmacies contain substances originally derived from plants. For example, researchers discovered that the rosy periwinkle, which grows in Madagascar, contains alkaloids that inhibit cancer cell growth **(Figure 56.6)**. This discovery led to treatments for two deadly forms of cancer, Hodgkin’s lymphoma and childhood leukemia, resulting in remission in most cases. Madagascar is also home to five other species of periwinkles, one of which is approaching extinction. Losing these species would mean the loss of any possible medicinal benefits they might offer.

➤ Figure 56.6 The rosy periwinkle (*Catharanthus roseus*), a plant that saves lives.

Each species lost means the loss of unique genes, some of which may code for enormously useful proteins. The enzyme Taq polymerase was first extracted from a bacterium, *Thermus aquaticus*, found in hot springs at Yellowstone National Park. This enzyme is essential for the polymerase chain reaction (PCR) because it is stable at the high temperatures required for automated PCR (see Figure 19.8). DNA from many other species of prokaryotes, living in a variety of environments, is used in the mass production of proteins for new medicines, foods, petroleum substitutes, industrial chemicals, and other products. However, because many species of prokaryotes and other organisms may become extinct before we discover them, we stand to lose the valuable genetic potential held in their unique libraries of genes.

Ecosystem Services

The benefits that individual species provide to humans are substantial, but saving individual species is only part of the reason for preserving ecosystems. Humans evolved in Earth’s ecosystems, and we rely on these systems and their inhabitants for our survival. **Ecosystem services** encompass all the processes through which natural ecosystems help sustain human life. Ecosystems purify our air and water. They detoxify and decompose our wastes and reduce the impacts of extreme weather and flooding. The organisms in ecosystems pollinate our crops, control pests, and create and preserve our soils. Moreover, these diverse services are provided for free.

If we had to pay for them, how much would the services of natural ecosystems be worth? In 1997, scientists estimated the value of Earth’s ecosystem services at $33 trillion per year, nearly twice the gross national product of all the countries on Earth at the time ($18 trillion). It may be more realistic to do the accounting on a smaller scale. In 1996, New York City invested more than $1 billion to buy land and restore habitat in the Catskill Mountains, the source of much of the city’s fresh water. This investment was spurred by increasing pollution of the water by sewage, pesticides, and fertilizers. By harnessing ecosystem services to purify its water naturally, the city saved $8 billion it would have otherwise spent to build a new water treatment plant and $300 million a year to run the plant.

There is growing evidence that the functioning of ecosystems, and hence their capacity to perform services, is linked to biodiversity. As human activities reduce biodiversity, we are reducing the capacity of the planet’s ecosystems to perform processes critical to our own survival.

Threats to Biodiversity

Many different human activities threaten biodiversity on local, regional, and global scales. The threats posed by these activities include four major types: habitat loss, introduced species, overharvesting, and global change.

Habitat Loss

Human alteration of habitat is the single greatest threat to biodiversity throughout the biosphere. Habitat loss has been brought about by factors such as agriculture, urban development, forestry, mining, and pollution. As discussed later in this chapter, global climate change is already altering habitats today and will have an even larger effect later this century. When no alternative habitat is available or a species is unable to move, habitat loss may mean extinction. The IUCN implicates destruction of habitat as a contributing cause for 73% of the species that have become extinct, endangered, vulnerable, or rare in the last few hundred years.

Habitat loss and fragmentation may occur over immense regions. Approximately 98% of the tropical dry forests of Central America and Mexico have been cut down. The clearing of tropical rain forest in the state of Veracruz, Mexico, mostly for cattle ranching, has resulted in the loss of more than 90% of the original forest, leaving relatively small, isolated patches of forest. Many other natural habitats have also been fragmented by human activities **(Figure 56.7)**.

Habitat fragmentation often leads to species loss because the smaller populations in habitat fragments have a higher probability of extinction. Prairie covered about 800,000 hectares of southern Wisconsin when Europeans first arrived in North America but occupies only 800 hectares today; most of the original prairie in this area is now used to grow crops. Plant diversity surveys of 54 Wisconsin prairie remnants conducted in 1948–1954 and 1987–1988 showed that the remnants lost 8–60% of their plant species in the time between the two surveys.

Habitat loss is also a major threat to aquatic biodiversity. About 70% of coral reefs, among Earth's most species-rich aquatic communities, have been damaged by human activities. At the current rate of destruction, 40–50% of the reefs, home to one-third of marine fish species, could disappear in the next 30 to 40 years. Freshwater habitats are also being lost, often as a result of the dams, reservoirs, channel modification, and flow regulation now affecting most of the world's rivers. For example, the more than 30 dams and locks built along the Mobile River basin in the southeastern United States changed river depth and flow. While providing the benefits of hydroelectric power and increased ship traffic, these dams and locks also helped drive more than 40 species of mussels and snails to extinction.

▼ Figure 56.7 Habitat fragmentation.

Introduced Species

Introduced species, also called non-native or exotic species, are those that humans move intentionally or accidentally from the species' native locations to new geographic regions. Human travel by ship and airplane has accelerated the transplant of species. Free from the predators, parasites, and pathogens that limit their populations in their native habitats, such transplanted species may spread rapidly through a new region.

Some introduced species disrupt their new community, often by preying on native organisms or outcompeting native organisms for resources. For example, the brown tree snake was accidentally introduced to the island of Guam from other parts of the South Pacific after World War II, as a "stowaway" in military cargo. Since then, 12 species of birds and 6 species of lizards that the snakes ate have become extinct on Guam. In 1988, the devastating zebra mussel, a suspension-feeding mollusc, was discovered in the Great Lakes of North America, most likely introduced in the ballast water of ships arriving from Europe. Zebra mussels form dense colonies and have disrupted freshwater ecosystems, threatening native aquatic species. They have also clogged water intake structures, causing billions of dollars in damage to domestic and industrial water supplies.

Humans have deliberately introduced many species with good intentions but disastrous effects. An Asian plant called kudzu, which the U.S. Department of Agriculture once introduced in the southern United States to help control erosion, has taken over large areas of the landscape there **(Figure 56.8)**.

▼ Figure 56.8 Kudzu, an introduced species, thriving in the southeastern United States.

The European starling was brought intentionally into New York's Central Park in 1890 by a citizens' group intent on introducing all the plants and animals mentioned in Shakespeare's plays. It quickly spread across North America, where its population now exceeds 100 million, displacing many native songbirds.

Introduced species are a worldwide problem, contributing to approximately 40% of the extinctions recorded since 1750 and costing billions of dollars each year in damage and control efforts. There are more than 50,000 introduced species in the United States alone.

Overharvesting

The term *overharvesting* refers generally to the harvesting of wild organisms at rates exceeding the ability of their populations to rebound. Species with restricted habitats, such as those that inhabit small islands, are particularly vulnerable to overharvesting. One such species was the great auk, a large, flightless seabird found on islands in the North Atlantic. By the 1840s, humans had hunted the great auk to extinction to satisfy demand for its feathers, eggs, and meat.

Also susceptible to overharvesting are large organisms with low reproductive rates, such as elephants, whales, and rhinoceroses. The decline of Earth's largest terrestrial animals, the African elephants, is a classic example of the impact of overhunting. Largely because of the trade in ivory, elephant populations have been declining in most of Africa for the last 50 years. An international ban on the sale of new ivory resulted in increased poaching (illegal hunting), so the ban had little effect in much of central and eastern Africa. Only in South Africa, where once-decimated herds have been well protected for nearly a century, have elephant populations been stable or increasing (see Figure 53.9).

Conservation biologists are increasingly using the tools of molecular genetics to track the origins of tissues harvested from endangered species. For example, researchers have used DNA isolated from samples of elephant dung to construct a DNA reference map for the African elephant (*Loxodonta africana*). By comparing this reference map with DNA isolated from ivory harvested legally or by poachers, they can determine to within a few hundred kilometers where the elephants were killed **(Figure 56.9)**. Such work in Zambia suggested that poaching rates were 30 times higher than previously estimated, a finding that has stimulated improved anti-poaching efforts by the Zambian government. Similarly, biologists using phylogenetic analyses of mitochondrial DNA (mtDNA) showed that some whale meat sold in Japanese fish markets came from illegally harvested species, including fin and humpback whales, which are endangered (see Figure 22.6).

Many commercially important fish populations, once thought to be inexhaustible, have been decimated by overfishing. Demands from an increasing human population for protein-rich food, coupled with new harvesting technologies, such as long-line fishing and modern trawlers, have reduced these fish populations to levels that cannot sustain further exploitation. Until the past few decades, the Atlantic bluefin tuna was considered a sport fish of little commercial value—just a few cents per pound for use in cat food. In the 1980s, however, wholesalers began airfreighting fresh, iced bluefin to Japan for sushi and sashimi. In that market, the fish now brings up to $100 per pound **(Figure 56.10)**. With increased harvesting spurred by such high prices, it took just ten years to reduce the western Atlantic bluefin population to less than 20% of its 1980 size.

▼ Figure 56.9 Ecological forensics and elephant poaching. These severed tusks were part of an illegal shipment of ivory intercepted on its way from Africa to Singapore in 2002. DNA-based evidence showed that the thousands of elephants killed for the tusks came from a relatively narrow east-west band centered in Zambia rather than from across Africa.

MAKE CONNECTIONS ➤ *Figure 22.6 describes a similar example in which conservation biologists used DNA analyses to compare harvested samples of whale meat with a reference DNA database. How are these examples similar, and how are they different? What limitations might there be to using such forensic methods in other suspected cases of poaching?*

▼ Figure 56.10 Overharvesting. Atlantic bluefin tuna are auctioned in a Japanese fish market.

Global Change

The fourth threat to biodiversity, global change, alters the fabric of Earth's ecosystems at regional to global scales. Global change includes alterations in climate, atmospheric chemistry, and broad ecological systems that reduce the capacity of Earth to sustain life.

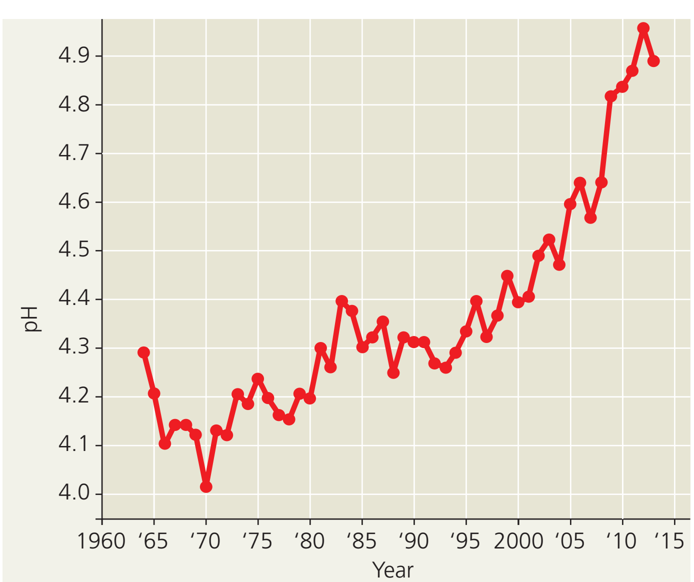
One of the first types of global change to cause concern was *acid precipitation*, which is rain, snow, sleet, or fog with a pH less than 5.2. The burning of wood and fossil fuels releases oxides of sulfur and nitrogen that react with water in air, forming sulfuric and nitric acids. The acids eventually fall to Earth's surface, where they cause chemical reactions that decrease nutrient supplies and increase concentrations of toxic metals. These changes to the soil and water harm some terrestrial and aquatic organisms.

In the 1960s, ecologists determined that lake-dwelling organisms in eastern Canada were dying because of air pollution from factories in the Midwestern United States. Newly hatched lake trout, for instance, die when the pH drops below 5.4. Lakes and streams in southern Norway and Sweden were losing fish because of pollution generated in Great Britain and central Europe. By 1980, the pH of precipitation in large areas of North America and Europe averaged 4.0–4.5 and sometimes dropped as low as 3.0. (To review pH, see Concept 3.3.)

Environmental regulations and new technologies have enabled many countries to reduce sulfur dioxide emissions in recent decades. In the United States, sulfur dioxide emissions decreased more than 75% between 1990 and 2013, gradually reducing the acidity of precipitation **(Figure 56.11)**. However, ecologists estimate that it will take decades for aquatic ecosystems to recover. Meanwhile, emissions of nitrogen oxides are increasing in the United States, and emissions of sulfur dioxide and acid precipitation continue to damage forests in central and eastern Europe.

We'll explore the importance of global change for Earth's biodiversity in more detail in Concept 56.4, where we examine such factors as climate change and ozone depletion. Next, we'll take a closer look at how scientists seek to protect populations and species under threat.

▼ Figure 56.11 Changes in the pH of precipitation at the Hubbard Brook Experimental Forest, New Hampshire.



MAKE CONNECTIONS ➤ *Describe the relationship between pH and acidity. (See Concept 3.3.) Overall, is the precipitation in this forest becoming more acidic or less acidic?*

CONCEPT CHECK 56.1

1. What are the different levels of biodiversity? Give one example of a benefit that humans derive from each level.
2. Identify the four main threats to biodiversity and explain how each damages diversity.
3. **WHAT IF? ➤** Imagine two populations of a fish species, one in the Mediterranean Sea and one in the Caribbean Sea. Now imagine two scenarios: (1) The populations breed separately, and (2) adults of both populations migrate yearly to the North Atlantic to interbreed. Which scenario would result in a greater loss of genetic diversity if the Mediterranean population were harvested to extinction? Explain your answer.

For suggested answers, see Appendix A.

CONCEPT 56.2

Population conservation focuses on population size, genetic diversity, and critical habitat

Biologists who work on conservation at the population and species levels use two main approaches. One approach focuses on populations that are small and hence often vulnerable. The other emphasizes populations that are declining rapidly, even if they are not yet small.

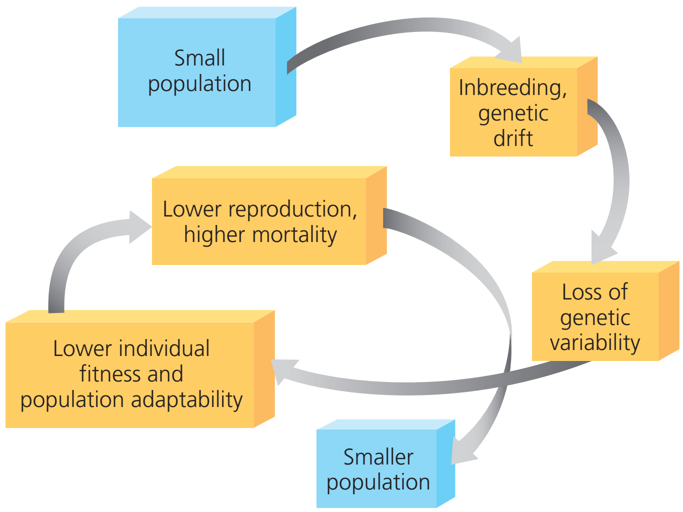
Small-Population Approach

Small populations are particularly vulnerable to overharvesting, habitat loss, and the other threats to biodiversity that you read about in Concept 56.1. After such factors have reduced a population's size to a small number of individuals, the small size itself can push the population to extinction. The small-population approach emphasizes the various processes that cause extinctions once population sizes have been greatly reduced.

The Extinction Vortex: Evolutionary Implications of Small Population Size

EVOLUTION A small population is vulnerable to inbreeding and genetic drift, which can draw the population down an **extinction vortex** toward smaller and smaller population

Figure 56.12 Processes driving an extinction vortex.



size until no individuals survive **(Figure 56.12)**. A key factor driving the extinction vortex is the loss of genetic variation that can enable evolutionary responses to environmental change, such as the appearance of new strains of pathogens. Both inbreeding and genetic drift can cause a loss of genetic variation (see Concept 23.3), and their effects become more harmful as a population shrinks. Inbreeding often reduces fitness because offspring are more likely to be homozygous for harmful recessive traits.

Not all small populations are doomed by low genetic diversity, and low genetic variability does not automatically lead to permanently small populations. For instance, overhunting of northern elephant seals in the 1890s reduced the species to only 20 individuals—clearly a bottleneck with reduced genetic variation. Since that time, however, the northern elephant seal populations have rebounded to about 150,000 individuals today, though their genetic variation remains relatively low.

Case Study: *The Greater Prairie Chicken and the Extinction Vortex*

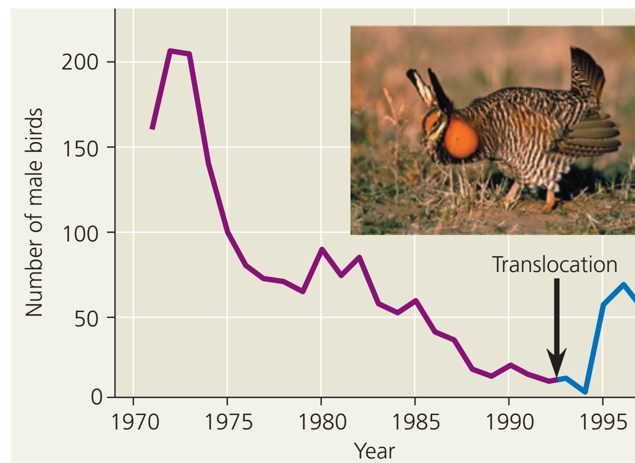
When Europeans arrived in North America, the greater prairie chicken (*Tympanuchus cupido*) was common from New England to Virginia and across the western prairies of the continent. Land cultivation for agriculture fragmented the populations of this species, and its abundance decreased rapidly (see Figure 23.11). Illinois had millions of greater prairie chickens in the 19th century but fewer than 50 by 1993. Researchers found that the decline in the Illinois population was associated with reduced genetic variation and a decrease in fertility. As a test of the extinction vortex hypothesis, scientists increased genetic variation by importing 271 birds from larger populations elsewhere **(Figure 56.13)**. The Illinois population rebounded, indicating that it had been on its way to extinction until rescued by the transfusion of genetic variation.

Figure 56.13

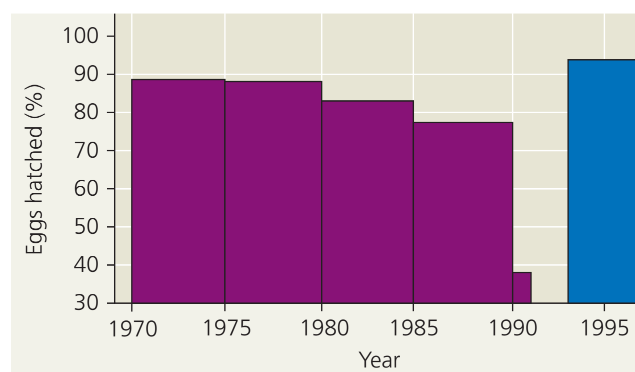
Inquiry What caused the drastic decline of the Illinois greater prairie chicken population?

Experiment Researchers had observed that the population collapse of the greater prairie chicken was mirrored in a reduction in fertility, as measured by the hatching rate of eggs. Comparison of DNA samples from the Jasper County, Illinois, population with DNA from feathers in museum specimens showed that genetic variation had declined in the study population (see Figure 23.11). In 1992, Ronald Westemeier and colleagues began translocating prairie chickens from neighboring states in an attempt to increase genetic variation.

Results After translocation (black arrow), the viability of eggs rapidly increased, and the population rebounded.



(a) Population dynamics



(b) Hatching rate. Bar height represents the average rate for the years spanned by the bar.

Conclusion Reduced genetic variation had started the Jasper County population of prairie chickens down the extinction vortex.

Data from R. L. Westemeier et al., Tracking the long-term decline and recovery of an isolated population, *Science* 282:1695–1698 (1998). © 1998 by AAAS. Reprinted with permission.

Inquiry in Action Read and analyze the original paper in *Inquiry in Action: Interpreting Scientific Papers.*

WHAT IF? ➤ *Given the success of using transplanted birds as a tool for increasing the percentage of hatched eggs in Illinois, would you support transplanting additional birds to Illinois? Why or why not?*

Minimum Viable Population Size

How small does a population have to be before it starts down an extinction vortex? The answer depends on the type of organism and other factors. Large predators that feed high on the food chain usually require extensive individual ranges, resulting in low population densities. Such species may be rare yet of little concern to conservation biologists. All populations, however, require some minimum size to remain viable.

The minimal population size at which a species is able to sustain its numbers is known as the **minimum viable population (MVP)**. MVP is usually estimated for a given species using computer models that integrate many factors. The calculation may include, for instance, an estimate of how many individuals in a small population are likely to be killed by a natural catastrophe such as a storm. Once in the extinction vortex, two or three consecutive years of bad weather could finish off a population that is already below its MVP.

Effective Population Size

Genetic variation is a key issue in the small-population approach. The *total* size of a population may be misleading because only certain members of the population breed successfully and pass their alleles on to offspring. Therefore, a meaningful estimate of MVP requires the researcher to determine the **effective population size**, which is based on the breeding potential of the population.

The following formula illustrates one way to estimate the effective population size, abbreviated N_e:

$$N_e = \frac{4N_f N_m}{N_f + N_m}$$

where N_f and N_m are, respectively, the number of females and the number of males that successfully breed. If we apply this formula to an idealized population whose total size is 1,000 individuals, N_e will also be 1,000 if every individual breeds and the sex ratio is 500 females to 500 males. In this case, $N_e = (4 \times 500 \times 500)/(500 + 500) = 1{,}000$. Any deviation from these conditions (not all individuals breed or there is not a 1:1 sex ratio) reduces N_e. For instance, if the total population size is 1,000 but only 400 females and 400 males breed, then $N_e = (4 \times 400 \times 400)/(400 + 400) = 800$, or 80% of the total population size. Numerous factors can influence N_e. Alternative formulas for estimating N_e take into account factors such as age at maturation, genetic relatedness among population members, the effects of gene flow, and population fluctuations.

In actual study populations, N_e is always some fraction of the total population. Thus, simply determining the total number of individuals in a small population does not necessarily provide a good measure of whether the population is large enough to avoid extinction. Whenever possible, conservation programs attempt to sustain total population sizes that include at least the minimum viable number of *reproductively active* individuals. The conservation goal of sustaining effective population size (N_e) above MVP stems from the concern that populations retain enough genetic diversity to adapt as their environment changes.

The MVP of a population is often used in population viability analysis. The objective of this analysis is to predict a population's chances for survival, usually expressed as a specific probability of survival, such as a 95% chance, over a particular time interval, perhaps 100 years. Such modeling approaches allow conservation biologists to explore the potential consequences of alternative management plans.

Case Study: *Analysis of Grizzly Bear Populations*

One of the first population viability analyses was conducted in 1978 by Mark Shaffer as part of a long-term study of grizzly bears in Yellowstone National Park and its surrounding areas **(Figure 56.14)**. A threatened species in the United States, the grizzly bear (*Ursus arctos horribilis*) is currently found in only 4 of the 48 contiguous states. Its populations in those states have been drastically reduced and fragmented. In 1800, an estimated 100,000 grizzlies ranged over about 500 million hectares of habitat, while today only 1,000 individuals in six relatively isolated populations range over less than 5 million hectares.

Shaffer attempted to determine viable sizes for the Yellowstone grizzly population. Using life history data obtained for individual Yellowstone bears over a 12-year period, he simulated the effects of environmental factors on survival and reproduction. His models predicted that, given a suitable habitat, a Yellowstone grizzly bear population of 70–90 individuals would have about a 95% chance of surviving for 100 years. A slightly larger population of only 100 bears would have a 95% chance of surviving for twice as long, about 200 years.

How does the actual size of the Yellowstone grizzly population compare with Shaffer's predicted MVP? A current estimate puts the total grizzly bear population in the greater Yellowstone

▼ Figure 56.14 Long-term monitoring of a grizzly bear population. The ecologist is fitting this tranquilized bear with a radio collar so that the bear's movements can be compared with those of other grizzlies in the Yellowstone National Park population.

ecosystem at about 400 individuals. The relationship of this estimate to the effective population size (N_e) depends on several factors. Usually, only a few dominant males breed, and it may be difficult for them to locate females, since individuals inhabit such large areas. Moreover, females may reproduce only when there is abundant food. As a result, N_e is only about 25% of the total population size, or about 100 bears.

Because small populations tend to lose genetic variation over time, researchers have used proteins, mitochondrial DNA, and short tandem repeats (see Concept 20.4) to assess genetic variability in the Yellowstone grizzly bear population. All results to date indicate that the Yellowstone population has less genetic variability than other grizzly bear populations in North America.

How might conservation biologists increase the effective size and genetic variation of the Yellowstone grizzly bear population? Migration between isolated populations of grizzlies could increase both effective and total population sizes. Computer models predict that introducing only two unrelated bears each decade into a population of 100 individuals would reduce the loss of genetic variation by about half. For the grizzly bear, and probably for many other species with small populations, finding ways to promote dispersal among populations may be one of the most urgent conservation needs.

This case study and that of the greater prairie chicken bridge small-population models and practical applications in conservation. Next, we look at an alternative approach to understanding the biology of extinction.

Declining-Population Approach

The declining-population approach focuses on threatened and endangered populations that show a downward trend, even if the population is far above its minimum viable population. The distinction between a declining population, which may not be small, and a small population, which may not be declining, is less important than the different priorities of the two approaches. While the small-population approach emphasizes smallness itself as an ultimate cause of a population's extinction, the declining-population approach emphasizes the environmental factors that caused a population decline in the first place. If, for instance, an area is deforested, then species that depend on trees will decline in abundance, whether or not they retain genetic variation.

The declining-population approach requires that researchers carefully evaluate the causes of a decline before taking steps to correct it. A key step in this process is to study the natural history of a declining species, including a review of the scientific literature, to determine the species' environmental needs. This information is then used to develop and test hypotheses of possible causes of the decline, including human activities and natural events. The following case study illustrates how the declining-population approach has been applied to the conservation of an endangered species.

Case Study: *Decline of the Bengal Florican*

The critically endangered Bengal florican (*Houbaropsis bengalensis*) is a large terrestrial bird belonging to the bustard family **(Figure 56.15a)**. It is found in two geographically isolated populations, one in India and Nepal, and the other in Cambodia. The Cambodian population was only rediscovered in 1999 but comprises two-thirds of the world's remaining Bengal florican; researchers estimated that it contained 416 males in 2005. In Cambodia, the species breeds during the dry season in open grasslands, which are then inundated by the rising waters of the Tonle Sap Lake in the wet season. These grasslands were once maintained by wild large herbivores (now extinct) whose grazing prevented the development of scrub that otherwise takes over the grasslands. This role has since been filled by herders who annually burn the grasslands to promote fresh growth for their domestic cattle, thus beneficially controlling scrub encroachment **(Figure 56.15b)**. In recent years, the floodplain has undergone rapid, large-scale conversion to irrigated commercial rice production **(Figure 56.15c)**.

Figure 56.15 Habitat disturbance and the Bengal florican.

(a) A Bengal florican

(b) Grazing and burning maintain grasslands.

(c) Grassland is being converted to irrigated commercial rice production

Research in collaboration with the Forestry Administration of Cambodia revealed that between January 2005 and March 2007, an additional 28% of the floodplain grasslands in Cambodia were inundated. The building of dams for irrigation also affects the quality of the remaining grassland habitat. The dams cause adjacent grasslands to become saturated with water and block access routes through the grasslands, so traditional cattle grazing is impeded. Both effects contribute to rapid scrub growth. The impact of these factors on the Bengal florican, coupled with previously high hunting pressure, has been catastrophic.

Although protected areas have been established for the Bengal florican in key sites, a limited understanding of this species' ecology initially hindered development of an effective conservation strategy. However, researchers used a combination of radiotelemetry and ecological studies of habitat to determine the florican's breeding season needs and management requirements. Lekking males need large expanses of short, open grasslands that are created by burning, grazing, and the fallowing of traditional, low-intensity rice fields. Females use these areas for nesting and feeding but also require areas of tall, unburnt grassland. Researchers are now tracking individuals by satellite to map their movements and identify their habitat requirements during the wet season, when they vacate the inundated grasslands. These studies indicate that the species is further threatened by the loss of wet-season habitat through clearance for extensive plantations. Satellite tracking will facilitate the creation of additional protected sites in wet-season areas and appropriate habitat management to meet the species' requirements.

Weighing Conflicting Demands

Determining population numbers and habitat needs is only part of a strategy to save species. Scientists also need to weigh a species' needs against other conflicting demands. Conservation biology often highlights the relationship between science, technology, and society. For example, an ongoing, sometimes bitter debate in the western United States pits habitat preservation for wolf, grizzly bear, and bull trout populations against job opportunities in the grazing and resource extraction industries. Programs that restocked wolves in Yellowstone National Park remain controversial for people concerned about human safety and for many ranchers concerned with potential loss of livestock outside the park.

Large, high-profile vertebrates are not always the focal point in such conflicts, but habitat use is almost always the issue. Should work proceed on a new highway bridge if it destroys the only remaining habitat of a species of freshwater mussel? If you were the owner of a coffee plantation growing varieties that thrive in bright sunlight, would you be willing to change to shade-tolerant varieties that produce less coffee per hectare but can grow beneath trees that support large numbers of songbirds?

Another important consideration is the ecological role of a species. Because we cannot save every endangered species, we must determine which species are most important for conserving biodiversity as a whole. Identifying keystone species and finding ways to sustain their populations can be central to maintaining communities and ecosystems.

Management aimed at conserving a single species carries with it the possibility of harming populations of other species. But in Cambodia, the protection of habitats for highprofile Bengal florican has also benefitted 11 other globally threatened bird species that depend on those habitats. In some cases, conservation measures may conflict with the interests of local communities. In the Cambodian grasslands, however, the creation of Integrated Farming and Biodiversity Areas (IFBAs) protects both the habitats required by the Bengal florican and the land-use entitlements and traditional farming practices of local communities, which are otherwise excluded by large-scale farming operations. Consequently, many local communities support habitat protection. The IFBAs should enable them to pursue their livelihoods while safeguarding the habitat of the Bengal florican and other grassland species.

CONCEPT CHECK 56.2

1. How does the reduced genetic diversity of small populations make them more vulnerable to extinction?
2. If there were 100 greater prairie chickens in a population, and 30 females and 10 males bred, what would be the effective population size (N_e)?
3. **WHAT IF?** ➤ In 2005, at least ten grizzly bears in the greater Yellowstone ecosystem were killed through contact with people. Most of these deaths resulted from three things: collisions with automobiles, hunters (of other animals) shooting when charged by a female grizzly bear with cubs nearby, and conservation managers killing bears that attacked livestock repeatedly. If you were a conservation manager, what steps might you take to minimize such encounters in Yellowstone?

For suggested answers, see Appendix A.

CONCEPT 56.3

Landscape and regional conservation help sustain biodiversity

Although conservation efforts have historically focused on saving individual species, efforts today often seek to sustain the biodiversity of entire communities, ecosystems, and landscapes. Such a broad view requires applying not just ecological principles, but aspects of human population dynamics and economics as well.

Landscape Structure and Biodiversity

The biodiversity of a given landscape is heavily influenced by its physical features, or *structure*. Understanding landscape structure is critically important in conservation because many species use more than one kind of ecosystem, and many live on the borders between ecosystems.

Figure 56.16 Natural edges between ecosystems in Siberia.

VISUAL SKILLS ➤ *What edges between ecosystems do you observe in this photo?*

Fragmentation and Edges

The boundaries, or *edges*, between ecosystems—such as between a lake and the surrounding forest or between cropland and suburban housing tracts—are defining features of landscapes **(Figure 56.16)**. An edge has its own set of physical conditions, which differ from those on either side of it. The soil surface of an edge between a forest patch and a burned area receives more sunlight and is usually hotter and drier than the forest interior, but it is cooler and wetter than the soil surface in the burned area.

Some organisms thrive in edge communities because they gain resources from both adjacent areas. The ruffed grouse (*Bonasa umbellus*) is a bird that needs forest habitat for nesting, winter food, and shelter, but it also needs forest openings with dense shrubs and herbs for summer food.

Ecosystems in which edges arise from human alterations often have reduced biodiversity and a preponderance of edge-adapted species. For example, white-tailed deer (*Odocoileus virginianus*) thrive in edge habitats, where they can browse on woody shrubs; deer populations often expand when forests are logged and more edges are generated. The brown-headed cowbird (*Molothrus ater*) is an edge-adapted species that lays its eggs in the nests of other birds, often migratory songbirds. Cowbirds need forests, where they can parasitize the nests of other birds, and open fields, where they forage on seeds and insects. Consequently, their populations are growing where forests are being cut and fragmented, creating more edge habitat and open land. Increasing cowbird parasitism and habitat loss are correlated with declining populations of several of the cowbird's host species.

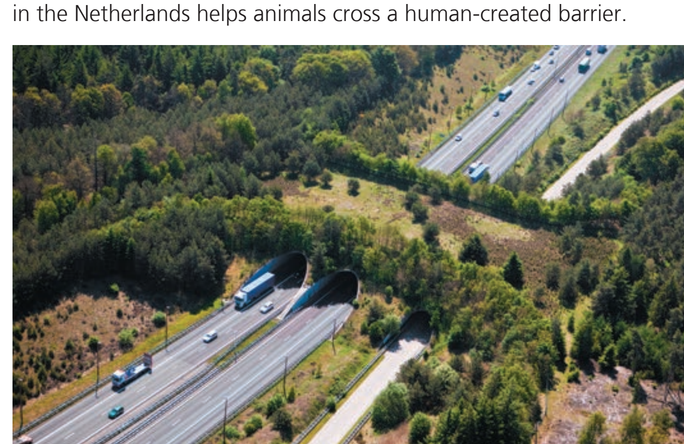
The influence of fragmentation on the structure of communities has been explored since 1979 in the long-term Biological Dynamics of Forest Fragments Project. Located in the heart of the Amazon River basin, the study area consists of isolated fragments of tropical rain forest separated from surrounding continuous forest by distances of 80–1,000 m **(Figure 56.17)**. Numerous researchers working on this project have clearly documented the effects of this fragmentation on organisms ranging from bryophytes to beetles to birds. They have consistently found that species adapted to forest interiors show the greatest declines when patches are the smallest, suggesting that landscapes dominated by small fragments will support fewer species.

Figure 56.17 Amazon rain forest fragments created as part of the Biological Dynamics of Forest Fragments Project.

Corridors That Connect Habitat Fragments

In fragmented habitats, the presence of a **movement corridor**, a narrow strip or series of small clumps of habitat connecting otherwise isolated patches, can be extremely important for conserving biodiversity. Riparian habitats often serve as corridors, and in some nations, government policy prohibits altering these habitats. In areas of heavy human use, artificial corridors are sometimes constructed. Bridges or tunnels, for instance, can reduce the number of animals killed trying to cross highways **(Figure 56.18)**.

Figure 56.18 An artificial corridor. This highway overpass in the Netherlands helps animals cross a human-created barrier.



Movement corridors can also promote dispersal and reduce inbreeding in declining populations. Corridors have been shown to increase the exchange of individuals among populations of many organisms, including butterflies, voles, and aquatic plants. Corridors are especially important to species that migrate between different habitats seasonally. However, a corridor can also be harmful—for example, by allowing the spread of disease. In a 2003 study, a scientist at the University of Zaragoza, Spain, showed that habitat corridors facilitate the movement of disease-carrying ticks among forest patches in northern Spain. All the effects of corridors are not yet understood, and their impact is an area of active research in conservation biology.

Establishing Protected Areas

Currently, governments have set aside about 7% of the world's land in various forms of reserves. Choosing where to place nature reserves and how to design them poses many challenges. Should the reserve be managed to minimize the risks of fire and predation to a threatened species? Or should the reserve be left as natural as possible, with such processes as fires ignited by lightning allowed to play out on their own? This is just one of the debates that arise among people who share an interest in the health of national parks and other protected areas.

Preserving Biodiversity Hot Spots

In deciding which areas are of highest conservation priority, biologists often focus on hot spots of biodiversity. A **biodiversity hot spot** is a relatively small area with numerous endemic species (species found nowhere else in the world) and a large number of endangered and threatened species **(Figure 56.19)**. Nearly 30% of all bird species can be found in hot spots that make up only about 2% of Earth's land area. Together, the "hottest" of the terrestrial biodiversity hot spots total less than 1.5% of Earth's land but are home to more than a third of all species of plants, amphibians, reptiles (including birds), and mammals. Aquatic ecosystems also have hot spots, such as coral reefs and certain river systems.

Biodiversity hot spots are good choices for nature reserves, but identifying them is not always simple. One problem is that a hot spot for one taxonomic group, such as butterflies, may not be a hot spot for some other taxonomic group, such as birds. Designating an area as a biodiversity hot spot is often biased toward saving vertebrates and plants, with less attention paid to invertebrates and microorganisms. Some biologists are also concerned that the hot-spot strategy places too much emphasis on such a small fraction of Earth's surface.

Global change makes the task of preserving hot spots even more challenging because the conditions that favor a particular community may not be found in the same location in the future. The biodiversity hot spot in the southwest corner of Australia (see Figure 56.19) holds thousands of species of endemic plants and numerous endemic vertebrates. Researchers recently concluded that between 5% and 25% of the plant species they examined may become extinct by 2080 because the plants will be unable to tolerate the increased dryness predicted for this region.

Philosophy of Nature Reserves

Nature reserves are protected "islands" of biodiversity in a sea of habitat altered or degraded by human activity. An earlier policy—that protected areas should be set aside to remain unchanged forever—was based on the concept that ecosystems are balanced, self-regulating units. However, disturbance is common in all ecosystems (see Concept 54.3). Management policies that ignore disturbances or attempt to prevent them have generally failed. For instance, setting aside an area of a fire-dependent community, such as a portion of a tallgrass prairie, chaparral, or dry pine forest, with the intention of saving it is unrealistic if periodic burning is excluded. Without the dominant disturbance, the fire-adapted species are usually outcompeted and biodiversity is reduced.

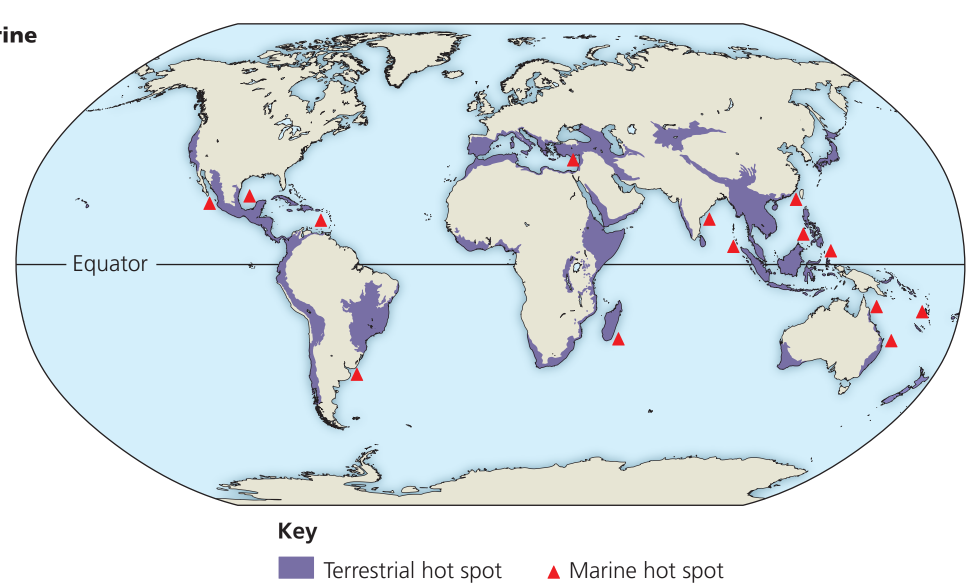


Figure 56.19 Earth's terrestrial and marine biodiversity hot spots.

An important conservation question is whether to create numerous small reserves or fewer large reserves. Small, unconnected reserves may slow the spread of disease between populations. One argument for large reserves is that large, far-ranging animals with low-density populations, such as the grizzly bear, require extensive habitats. Large reserves also have proportionately smaller perimeters than small reserves and are therefore less affected by edges.

As conservation biologists have learned more about the requirements for achieving minimum viable populations for endangered species, they have realized that most national parks and other reserves are far too small. The area needed for the long-term survival of the Yellowstone grizzly bear population, for instance, is more than 11 times the area of Yellowstone National Park. Areas of private and public land surrounding reserves will likely have to contribute to biodiversity conservation.

Zoned Reserves

Several nations have adopted a zoned reserve approach to landscape management. A **zoned reserve** is an extensive region that includes areas relatively undisturbed by humans surrounded by areas that have been changed by human activity and are used for economic gain. The key challenge of the zoned reserve approach is to develop a social and economic climate in the surrounding lands that is compatible with the long-term viability of the protected core. These surrounding areas continue to support human activities, but regulations prevent the types of extensive alterations likely to harm the protected area. As a result, the surrounding habitats serve as buffer zones against further intrusion into the undisturbed area.

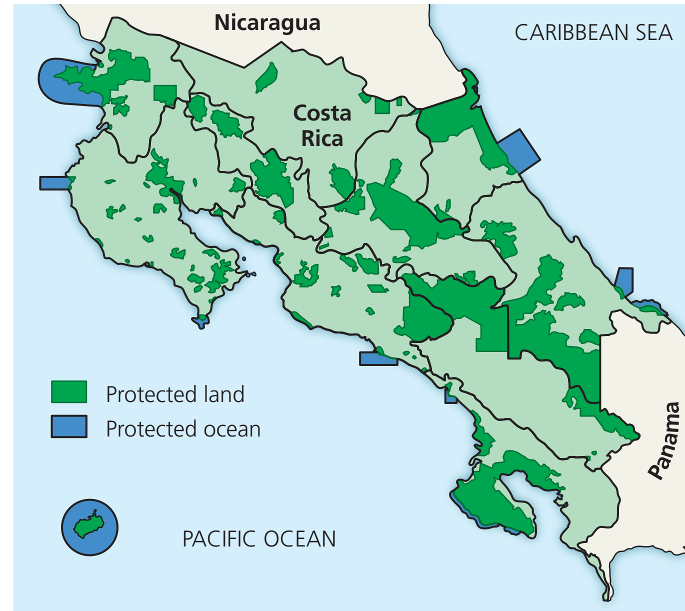
The Central American nation of Costa Rica has become a world leader in establishing zoned reserves. An agreement initiated in 1987 reduced Costa Rica's international debt in return for land preservation there. The country is now divided into 11 Conservation Areas, which include national parks and other protected areas, both on land and in the ocean **(Figure 56.20)**. Costa Rica is making progress toward managing its zoned reserves, and the buffer zones provide a steady, lasting supply of forest products, water, and hydroelectric power while also supporting sustainable agriculture and tourism, both of which employ local people.

Costa Rica relies on its zoned reserve system to maintain at least 80% of its native species, but the system is not without problems. A 2003 analysis of land cover change between 1960 and 1997 showed negligible deforestation within Costa Rica's national parks and a gain in forest cover in the 1-km buffer around the parks. However, significant losses in forest cover were discovered in the 10-km buffer zones around all national parks, threatening to turn the parks into isolated habitat islands.

Although marine ecosystems have also been heavily affected by human exploitation, reserves in the ocean are far less common than reserves on land. Many fish populations around the world have collapsed as increasingly sophisticated equipment puts nearly all potential fishing grounds within human reach. In response, scientists at the University of York, England, have proposed establishing marine reserves around the world that would be off-limits to fishing. They present strong evidence that a patchwork of marine reserves can serve as a means of both increasing fish populations within the reserves and improving fishing success in nearby areas. Their proposed system is a modern application of a centuries-old practice in the Fiji Islands in which some areas have historically remained closed to fishing—a traditional example of the zoned reserve concept.

The United States adopted such a system in creating a set of 13 national marine sanctuaries, including the Florida Keys National Marine Sanctuary, which was established in 1990

▼ Figure 56.20 Protected areas in Costa Rica.



(a) Boundaries of the Conservation Areas are indicated by black outlines.

(b) Tourists marvel at the diversity of life in one of Costa Rica's protected areas.

Figure 56.21 A diver measuring coral in the Florida Keys National Marine Sanctuary.

(Figure 56.21). Populations of marine organisms, including fishes and lobsters, recovered quickly after harvests were banned in the 9,500-km^2 reserve. Larger and more abundant fish now produce larvae that help repopulate reefs and improve fishing outside the sanctuary. The increased marine life within the sanctuary also makes it a favorite for recreational divers, increasing the economic value of this zoned reserve.

Urban Ecology

The zoned reserves that you just read about combine habitats that are relatively undisturbed by human activity with those that are used extensively by people for economic gain. Increasingly, ecologists are looking at species preservation even in the context of cities. The field of **urban ecology** examines organisms and their environment in urban settings.

For the first time in history, more than half of the people on Earth live in cities. By the year 2030, 5 billion people are expected to be living in urban environments. As cities expand in number and size, protected areas that were once outside city boundaries become incorporated into urban landscapes. Ecologists are now studying cities as ecological laboratories, seeking to balance species preservation and other ecological needs with the needs of people.

One critical area of research centers on urban streams, including the quality and flow of their water and the organisms living in them. Urban streams tend to rise and fall more quickly after rain than natural streams. This rapid change in water level occurs because of the concrete and other impervious surfaces in cities as well as the drainage systems that route water out of cities as quickly as possible to avoid flooding. Urban streams also tend to have higher concentrations of nutrients and contaminants and are often straightened or even channeled underground.

Near Vancouver, British Columbia, ecologists and volunteers have worked to restore a degraded urban stream, Guichon Creek. They stabilized its banks, removed invasive plants, and

Figure 56.22 Volunteers working to remove invasive species along the urban Guichon Creek.

planted native trees and shrubs along the creek **(Figure 56.22)**. Their efforts returned the water flow and the communities of invertebrates and fish in the stream much closer to what they had been 50 years before the stream became degraded. A few years ago, ecologists successfully reestablished cutthroat trout in the stream. The trout are now thriving.

As cities continue to expand into the landscapes around them, understanding the ecological effects of this expansion will only increase in importance. Research on and conservation of urban habitats will continue to grow.

CONCEPT CHECK 56.3

1. What is a biodiversity hot spot?
2. How do zoned reserves provide economic incentives for long-term conservation of protected areas?
3. **WHAT IF?** ➤ Suppose a developer proposes to clear-cut a forest that serves as a corridor between two parks. To compensate, the developer also proposes to add the same area of forest to one of the parks. As a professional ecologist, how might you argue for retaining the corridor?

For suggested answers, see Appendix A.

CONCEPT 56.4

Earth is changing rapidly as a result of human actions

As we've discussed, landscape and regional conservation help protect habitats and preserve species. However, environmental changes that result from human activities are creating new challenges. As a consequence of human-caused climate change, for example, the place where a vulnerable species is found today may not be the same place that is needed for preservation in the future. What would happen if *many* habitats on Earth changed so quickly that the locations of preserves today were unsuitable for their species in 10, 50, or 100 years? Such a scenario is increasingly possible.

The rest of this section describes four types of environmental change that humans are bringing about: nutrient enrichment, toxin accumulation, climate change, and ozone depletion. The impacts of these and other changes are evident not just in human-dominated ecosystems, such as cities and farms, but also in the most remote ecosystems on Earth.

Nutrient Enrichment

Human activity often removes nutrients from one part of the biosphere and adds them to another. Someone eating broccoli in Washington, DC, consumes nutrients that only days before were in the soil in California; a short time later, some of these nutrients will be in the Potomac River, having passed through the person's digestive system and a local sewage treatment facility. Likewise, nutrients in farm soil may run off into streams and lakes, depleting nutrients in one area, increasing them in another, and altering chemical cycles in both.

Farming illustrates how human activities can lead to nutrient enrichment. After vegetation is cleared from an area, the existing reserve of nutrients in the soil is depleted because many of these nutrients are exported from the area in crop biomass. The "free" period for crop production—when there is no need to replenish nutrients by adding fertilizer to the soil—varies greatly. When some of the early North American prairie lands were first tilled, good crops could be produced for decades because the large store of organic materials in the soil continued to decompose and provide nutrients. By contrast, some cleared land in the tropics can be farmed for only one or two years because so little of the ecosystems' nutrient load is contained in the soil. Despite such variations, in any area under intensive agriculture, the natural store of nutrients eventually becomes exhausted.

Consider nitrogen, the main nutrient lost through agriculture (see Figure 55.14). Plowing mixes the soil and speeds up decomposition of organic matter, releasing nitrogen that is then removed when crops are harvested. Fertilizers containing nitrates and other forms of nitrogen that plants can absorb are used to replace the nitrogen that is lost **(Figure 56.23)**. However, after crops are harvested, few plants remain to take up nitrates from the soil. As shown in Figure 55.15, without plants to absorb them, nitrates are often leached from the ecosystem.

Figure 56.23 Fertilization of a corn (maize) crop. To replace the nutrients removed in crops, farmers must apply fertilizers—either organic, such as manure or mulch, or synthetic, as shown here.

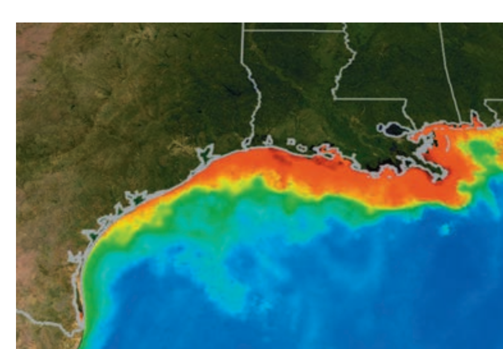
Recent studies indicate that human activities have more than doubled Earth's supply of fixed nitrogen available to primary producers. Industrial fertilizers provide the largest additional nitrogen source. Fossil fuel combustion also releases nitrogen oxides, which enter the atmosphere and dissolve in rainwater; the nitrogen ultimately enters ecosystems as nitrate. Increased cultivation of legumes, with their nitrogen-fixing symbionts, is a third way in which humans increase the amount of fixed nitrogen in the soil.

A problem arises when the nutrient level in an ecosystem exceeds the **critical load**, the amount of added nutrient, usually nitrogen or phosphorus, that can be absorbed by plants without damaging ecosystem integrity. For example, nitrogenous minerals in the soil that exceed the critical load eventually leach into groundwater or run off into freshwater and marine ecosystems, contaminating water supplies and killing fish. Nitrate concentrations in groundwater are increasing in most agricultural regions, sometimes reaching levels that are unsafe for drinking.

Many rivers contaminated with nitrates and ammonium from agricultural runoff and sewage drain into the Atlantic Ocean, with the highest inputs coming from northern Europe and the central United States. The Mississippi River carries nitrogen pollution to the Gulf of Mexico, fueling a phytoplankton bloom each summer. When the phytoplankton die, their decomposition by oxygen-using organisms creates an extensive "dead zone" of low oxygen levels along the coast **(Figure 56.24)**. When this occurs, fish and other marine animals disappear from some of the most economically important waters in the United States. To reduce the size of the dead zone, farmers have begun using fertilizers more efficiently, and managers are restoring wetlands in the Mississippi watershed.

Nutrient runoff can also lead to the eutrophication of lakes (see Concept 55.2). The bloom and subsequent die-off of algae and cyanobacteria and the ensuing depletion of oxygen are similar to what occurs in a marine dead zone. Such conditions threaten the survival of many organisms. For example, eutrophication of Lake Erie coupled with overfishing wiped out commercially important fishes such as blue pike, whitefish,

Figure 56.24 A phytoplankton bloom arising from nitrogen pollution in the Mississippi basin that leads to a dead zone. In this satellite image from 2004, red and orange represent high concentrations of phytoplankton in the Gulf of Mexico.



and lake trout by the 1960s. Since then, tighter regulations on the dumping of sewage into the lake have enabled some fish populations to rebound, but many native species of fish and invertebrates have not recovered.

Animation: Water Pollution from Nitrates

Toxins in the Environment

Humans release an immense variety of toxic chemicals, including thousands of synthetic compounds previously unknown in nature, with little regard for the ecological consequences. Organisms acquire toxic substances from the environment along with nutrients and water. Some of the poisons are metabolized or excreted, but others accumulate in specific tissues, often fat. One of the reasons accumulated toxins are particularly harmful is that they become more concentrated in successive trophic levels of a food web. This phenomenon, called **biological magnification**, occurs because the biomass at any given trophic level is produced from a much larger biomass ingested from the level below (see Concept 55.3). Thus, top-level carnivores tend to be most severely affected by toxic compounds in the environment.

Chlorinated hydrocarbons are a class of industrially synthesized compounds that have demonstrated biological magnification. Chlorinated hydrocarbons include the industrial chemicals called PCBs (polychlorinated biphenyls) and many pesticides, such as DDT. Current research implicates many of these compounds in endocrine system disruption in numerous animal species, including humans. Biological magnification of PCBs has been found in the food web of the Great Lakes, where the concentration of PCBs in herring gull eggs, at the top of the food web, is nearly 5,000 times that in phytoplankton, at the base **(Figure 56.25)**.

An infamous case of biological magnification that harmed top-level carnivores involved DDT, a chemical used to control insects such as mosquitoes and agricultural pests. In the decade after World War II, the use of DDT grew rapidly; its ecological consequences were not yet fully understood. By the 1950s, scientists were learning that DDT persists in the environment and is transported by water to areas far from where it is applied. One of the first signs that DDT was a serious environmental problem was a decline in the populations of pelicans, ospreys, and eagles, birds that feed at the top of food webs. The accumulation of DDT (and DDE, a product of its breakdown) in the tissues of these birds interfered with the deposition of calcium in their eggshells. When the birds tried to incubate their eggs, the weight of the parents broke the shells of affected eggs, resulting in catastrophic declines in the birds' reproduction rates. Rachel Carson's book *Silent Spring* helped bring the problem to public attention in the 1960s **(Figure 56.26)**, and DDT was banned in the United States in 1971. A dramatic recovery in populations of the affected bird species followed.

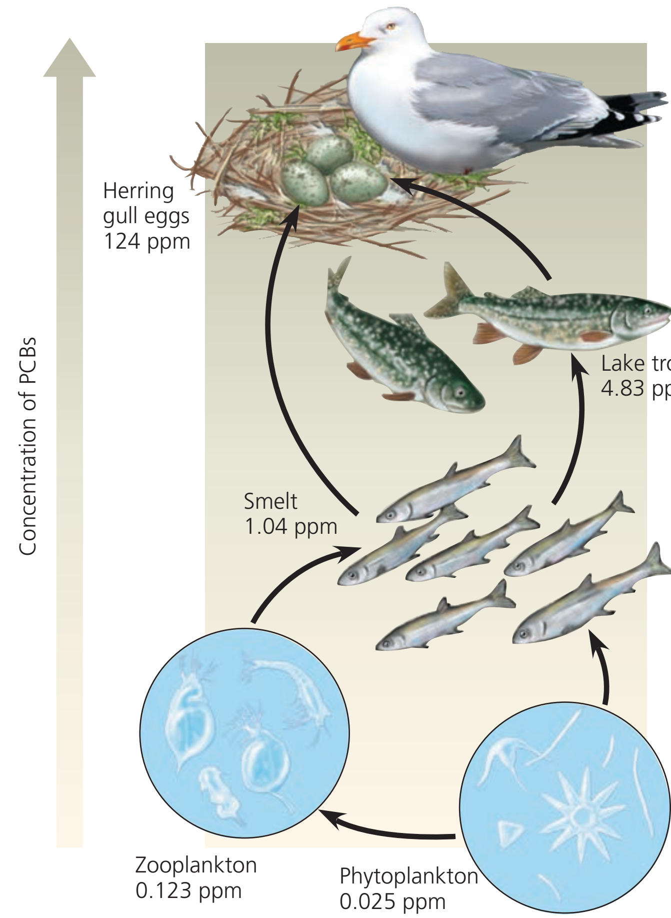


Figure 56.25 Biological magnification of PCBs in a Great Lakes food web. (ppm = parts per million)

Calculate how much the PCB concentration increased at each step in the food web.

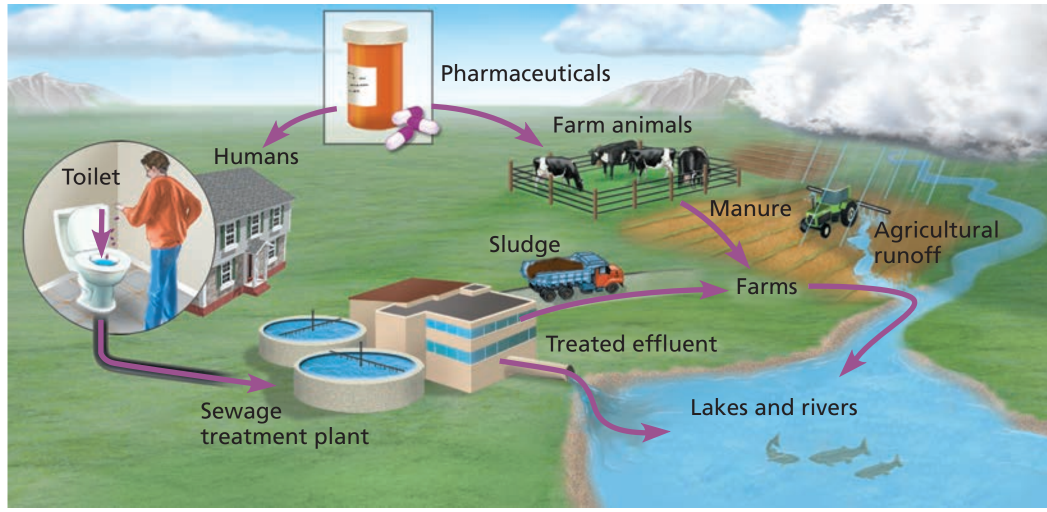
In much of the tropics, DDT is still used to control the mosquitoes that spread malaria and other diseases. Societies there face a trade-off between saving human lives and protecting other species. The best approach seems to be to apply DDT sparingly and to couple its use with mosquito netting and other low-technology solutions. The complicated history of DDT illustrates the importance of understanding the ecological connections between diseases and communities (see Concept 54.5).

Pharmaceuticals make up another group of toxins in the environment, one that is a growing concern among ecologists. The use of over-the-counter and prescription drugs has risen in recent years, particularly in industrialized nations. People who consume such products excrete residual chemicals in their waste and may also dispose of unused drugs

Figure 56.26 Rachel Carson. Through her writing and her testimony before the U.S. Congress, biologist and author Carson helped promote a new environmental ethic. Her efforts led to a ban on DDT use in the United States and stronger controls on the use of other chemicals.

improperly, such as in their toilets or sinks. Drugs that are not broken down in sewage treatment plants may then enter rivers and lakes with the material discharged from these plants. Growth-promoting drugs given to farm animals can also enter rivers and lakes with agricultural runoff. As a consequence, many pharmaceuticals are spreading in low concentrations across the world's freshwater ecosystems **(Figure 56.27)**.

Figure 56.27 Sources and movements of pharmaceuticals in the environment.



Among the pharmaceuticals that ecologists are studying are the sex steroids, including forms of estrogen used for birth control. Some fish species are so sensitive to certain estrogens that concentrations of a few parts per trillion in their water can alter sexual differentiation and shift the female-to-male sex ratio toward females. Researchers in Ontario, Canada, conducted a seven-year experiment in which they applied the synthetic estrogen used in contraceptives to a lake in very low concentrations (5–6 ng/L). They found that chronic exposure of the fathead minnow (*Pimephales promelas*) to the estrogen led to feminization of males and a near extinction of the population of this species from the lake.

Many toxins cannot be degraded by microorganisms and persist in the environment for years or even decades. In other cases, chemicals released into the environment may be relatively harmless but are converted to more toxic products by reaction with other substances, by exposure to light, or by the metabolism of microorganisms. Mercury, a by-product of plastic production and coal-fired power generation, has been routinely expelled into rivers and the sea in an insoluble form. Bacteria in the bottom mud convert the waste to methylmercury (CH_3Hg^+), an extremely toxic water-soluble compound that accumulates in the tissues of organisms, including humans who consume fish from the contaminated waters.

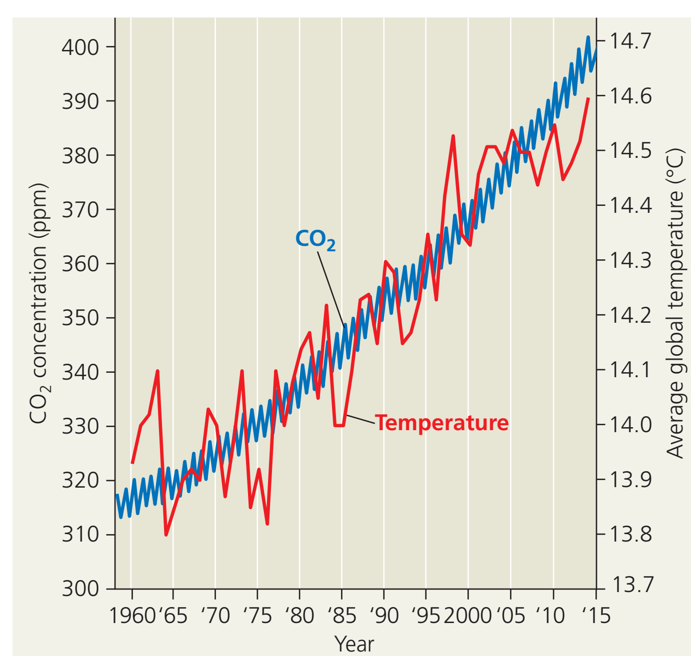
Greenhouse Gases and Climate Change

Human activities release a variety of gaseous waste products. People once thought that the vast atmosphere could absorb these materials indefinitely, but we now know that such additions can lead to **climate change**, a directional change to the global climate that lasts for three decades or more (as opposed to short-term changes in the weather).

Rising Atmospheric CO_2 Levels

To see how human actions can cause climate change, consider atmospheric CO_2 levels. Over the past 150 years, the concentration of CO_2 in the atmosphere has been increasing as a result of the burning of fossil fuels and deforestation. Scientists estimate that the average CO_2 concentration in the atmosphere before 1850 was about 274 ppm. In 1958, a monitoring station began taking very accurate measurements on Hawaii's Mauna Loa peak, a location far from cities and high enough for the atmosphere to be well mixed. As shown in **Figure 56.28**, at that time, the average CO_2

Figure 56.28 Increase in atmospheric carbon dioxide concentration at Mauna Loa, Hawaii, and average global temperatures. Aside from normal seasonal fluctuations, the CO_2 concentration (blue curve) increased steadily from 1958 to 2015. Though average global temperatures (red curve) fluctuated a great deal over the same period, there is a clear warming trend.



MB MP3 Tutor: Global Warming

SCIENTIFIC SKILLS EXERCISE

Graphing Cyclic Data

How Does the Atmospheric CO_2 Concentration Change During a Year and from Decade to Decade? The blue curve in Figure 56.28 shows how the concentration of CO_2 in Earth's atmosphere has changed over a span of more than 50 years. For each year in that span, two data points are plotted, one in May and one in November. A more detailed picture of the change in CO_2 concentration can be obtained by looking at measurements made at more frequent intervals. In this exercise, you'll graph monthly CO_2 concentrations for each of three one-year periods.

Data from the Study The data in the table below are average CO_2 concentrations (in parts per million) at the Mauna Loa monitoring station for each month in 1990, 2000, and 2010.

▶ A researcher samples the air at the Mauna Loa monitoring station, Hawaii.

Month	1990	2000	2010
January	353.79	369.25	388.45
February	354.88	369.50	389.82
March	355.65	370.56	391.08
April	356.27	371.82	392.46
May	359.29	371.51	392.95
June	356.32	371.71	392.06
July	354.88	369.85	390.13
August	352.89	368.20	388.15
September	351.28	366.91	386.80
October	351.59	366.91	387.18
November	353.05	366.99	388.59
December	354.27	369.67	389.68

Data from National Oceanic & Atmospheric Administration, Earth System Research Laboratory, Global Monitoring Division.

INTERPRET THE DATA

1. Plot the data for each of the three years on one graph (producing three curves). Select a type of graph that is appropriate for these data, and choose a vertical axis scale that allows you to clearly see the patterns of CO_2 concentration changes, both during each year and from decade to decade. (For additional information about graphs, see the Scientific Skills Review in Appendix F.)
2. Within each year, what is the pattern of change in CO_2 concentration? Why might this pattern occur?
3. The measurements taken at Mauna Loa represent average atmospheric CO_2 concentrations for the Northern Hemisphere. Suppose you could measure CO_2 concentrations under similar conditions in the Southern Hemisphere. What pattern would you expect to see in those measurements over the course of a year? Explain.
4. In addition to the changes within each year, what changes in CO_2 concentration occurred between 1990 and 2010? Calculate the average CO_2 concentration for the 12 months of each year. By what percentage did this average change from 1990 to 2000 and from 1990 to 2010?

MB **Instructors**: A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

concentration was 316 ppm. Today, it exceeds 400 ppm, an increase of more than 45% since the mid-19th century. In the **Scientific Skills Exercise**, you can graph and interpret changes in CO_2 concentration that occur during the course of a year and over longer periods.

The increase in the concentration of atmospheric CO_2 over the last 150 years concerns scientists because of its link to increased global temperature. Much of the solar radiation that strikes the planet is emitted toward space as infrared radiation (known informally as "heat radiation"). Although CO_2, methane, water vapor, and other greenhouse gases in the atmosphere are transparent to visible light, they intercept and absorb much of the infrared radiation that Earth emits, radiating most of it back toward Earth. This process, called the **greenhouse effect**, retains some of the solar heat **(Figure 56.29)**. If it were not for this greenhouse effect, the average air temperature at Earth's surface would be a frigid −18°C (−0.4°F), and most life as we know it could not exist.

As the concentrations of CO_2 and other greenhouse gases rise, more solar heat is retained, thereby increasing the temperature of our planet. So far, Earth has warmed by an average of 0.9°C (1.6°F) since 1900. At the current rates that CO_2 and other greenhouse gases are being added to the atmosphere, global models predict an additional rise of at least 3°C (5°F) by the end of the 21st century.

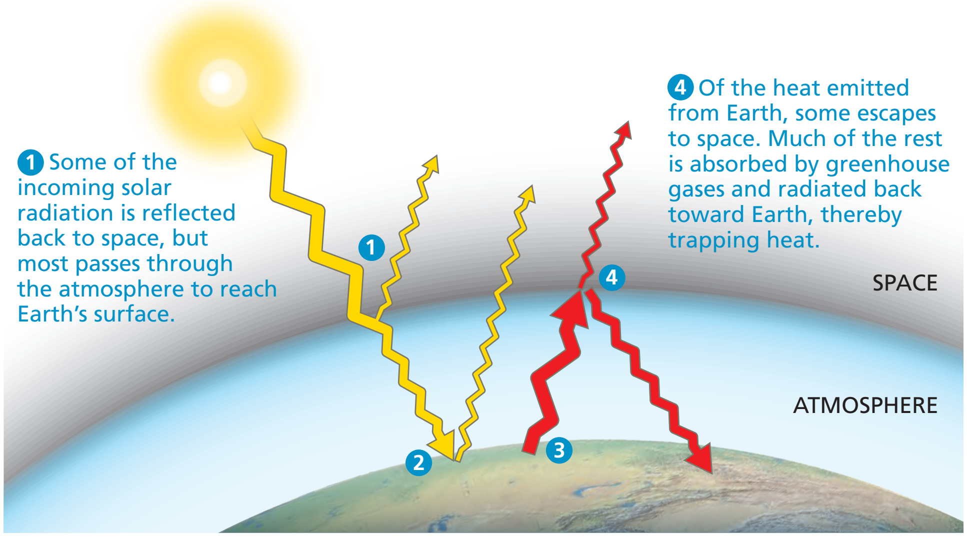
As our planet warms, the climate is changing in other ways as well: Wind and precipitation patterns are shifting, and extreme weather events (such as droughts and storms) are occurring more often. What are the consequences of such changes to Earth's climate?

MB **Animation: The Global Carbon Cycle and the Greenhouse Effect**

Biological Effects of Climate Change

Many organisms, especially plants that cannot disperse rapidly over long distances, may not be able to survive

Figure 56.29 The greenhouse effect. Carbon dioxide and other greenhouse gases in the atmosphere absorb heat emitted from Earth's surface and then radiate much of that heat back to Earth.



the rapid climate change projected to result from global warming. Furthermore, many habitats today are more fragmented than ever, further limiting the ability of many organisms to migrate now and in the future. Indeed, the climate change that has occurred to date has *already* altered the geographic ranges of hundreds of species, in some cases leading to declining population sizes and shrinking geographic ranges (see Concept 51.1). For example, a 2015 study of 67 species of bumblebees found that as the climate has warmed, the geographic distributions of these important pollinators have decreased in size.

The ecosystems where the climate has changed the most are those in the far north, particularly northern coniferous forests and tundra. As snow and ice melt and uncover darker, more absorptive surfaces, these systems reflect less radiation back to the atmosphere and warm further (see Figure 56.29). Arctic sea ice in the summer of 2012 covered the smallest area on record. Climate models suggest that there may be no summer ice there within a few decades, decreasing habitat for polar bears, seals, and seabirds. In addition, as discussed in Concept 55.2, rising temperatures have caused some Arctic regions to switch from being a CO_2 *sink* (absorbing more CO_2 from the atmosphere than they release to the atmosphere) to a CO_2 *source* (releasing more CO_2 than they absorb)—a worrisome change that could contribute to further climate warming.

Coniferous forests in western North America have also been hard hit, in this case by a combination of higher temperatures, decreased winter snowfall, and a lengthening of the summer dry period. As a result, since the latter half of the 20th century, otherwise healthy forests have experienced a steady increase in the percentage of trees that die each year. Higher temperatures and more frequent droughts also increase the likelihood of fires. In boreal forests of western North America and Russia, for example, fires have burned twice the usual area in recent decades, again leading to widespread tree mortality. As the climate continues to warm, this will likely bring other changes in the geographic distribution of precipitation, such as making agricultural areas of the central United States much drier.

Climate change has already affected many other ecosystems as well. In Europe and Asia, for example, plants are producing leaves earlier in the spring, while in tropical regions, the growth and survival of some species of coral have declined as water temperatures have warmed. Still other effects of climate change are discussed in **Figure 56.30**. A key take-home message from these examples is that a given effect of climate change may, in turn, cause a series of other biological changes. The exact nature of such cascading effects can be hard to predict, but it is clear that the more our planet warms, the more severely its ecosystems will be affected.

Finding Solutions to Address Climate Change

We will need many approaches to slow global warming and other aspects of climate change. Quick progress can be made by using energy more efficiently and by replacing fossil fuels with renewable solar and wind power and, more controversially, with nuclear power. Today, coal, gasoline, wood, and other organic fuels remain central to industrialized societies and cannot be burned without releasing CO_2. Stabilizing CO_2 emissions will require concerted international effort and changes in both personal lifestyles and industrial processes. International negotiations have yet to reach a global consensus on how to reduce greenhouse gas emissions.

Another important approach to slowing climate change is to reduce deforestation around the world, particularly in the tropics. Deforestation currently accounts for about 10% of greenhouse gas emissions. Recent research shows that paying countries *not* to cut forests could decrease the rate of deforestation by half within 10 to 20 years. Reduced deforestation would not only slow the buildup of greenhouse gases in our atmosphere, but also sustain native forests and preserve biodiversity, a positive outcome for all.

▼ **Figure 56.30** **MAKE CONNECTIONS**

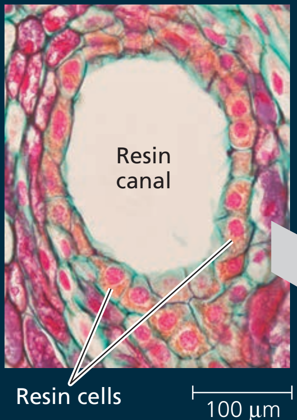
Climate Change Has Effects at All Levels of Biological Organization

The burning of fossil fuels by humans has caused atmospheric concentrations of carbon dioxide and other greenhouse gases to rise dramatically (see Figure 56.28). This, in turn, is changing Earth's climate: The planet's average temperature has increased by about 1°C since 1900, and extreme weather events are occurring more often in some regions of the globe. How are these changes affecting life on Earth today?

Effects on Cells

Temperature affects the rates of enzymatic reactions (see Figure 6.17), and as a result, the rates of DNA replication, cell division, and other key processes in cells are affected by rising temperatures.

Global warming and other aspects of climate change have also impaired some organisms' defense responses at the cellular level. For example, in the vast coniferous forests of western North America, climate change has reduced the ability of pine trees to defend themselves against attack by the mountain pine beetle (*Dendroctonus ponderosae*).



◀ Pine defenses include specialized resin cells that secrete a sticky substance (resin) that can entrap and kill mountain pine beetles. Resin cells produce less resin in trees that are stressed by rising temperatures and drought conditions.

▶ When beetles overwhelm a tree's cellular defenses, they produce large numbers of offspring that tunnel through the wood, causing extensive damage. Rising temperatures have shortened how long it takes beetles to mature and reproduce, resulting in even more beetles. The beetles can also infect the tree with a harmful fungus, which appears as blue stains on the wood.

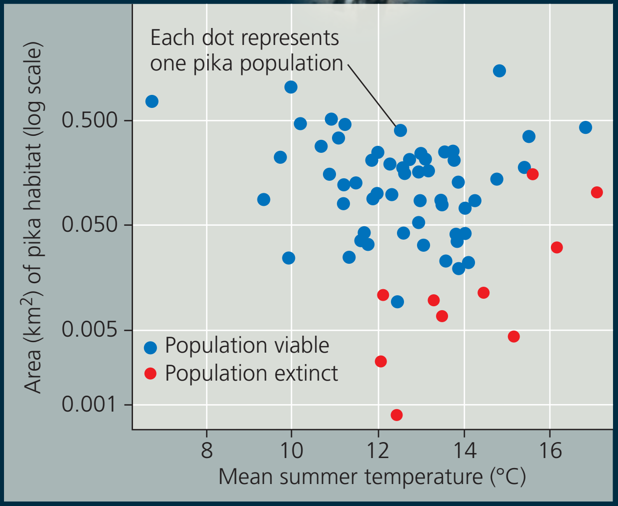
◀ This aerial view shows the scope of destruction in one North American forest due to mountain pine beetles; dead trees appear orange and red.

Effects on Individual Organisms

Organisms must maintain relatively constant internal conditions (see Concept 40.2); for example, an individual will die if its body temperature becomes too high. Global warming has increased the risk of overheating in some species, leading to reduced food intake and reproductive failure.

For instance, an American pika (*Ochotona princeps*) will die if its body temperature rises just 3°C above its resting temperature—and this can happen quickly in regions where climate change has already caused significant warming.

▶ As summer temperatures have risen, American pikas are spending more time in their burrows to escape the heat. Thus, they have less time to forage for food. Lack of food has caused mortality rates to increase and birth rates to drop. Pika populations have dwindled, some to the point of extinction. (See Figure 1.12 for another example.)



▲ This graph represents conditions in 2015 at 67 sites that previously supported a pika population; the populations at 10 of these sites had become extinct. Most extinctions occurred at sites with high summer temperatures and a small area of pika habitat. As temperatures continue to increase, more extinctions are expected.

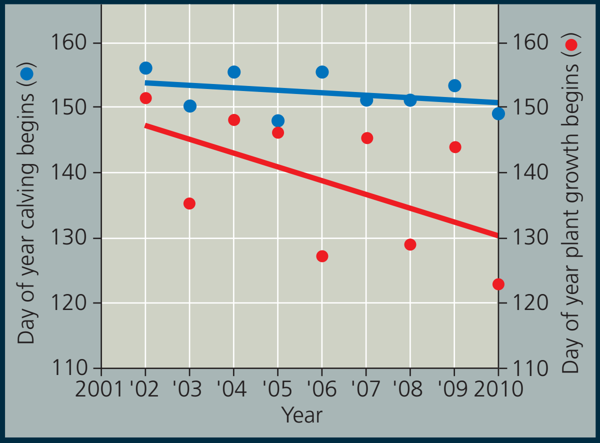
Effects on Populations

Climate change has caused some populations to increase in size, while others have declined (see Concepts 1.1 and 45.1). In particular, as the climate has changed, some species have adjusted when they grow, reproduce, or migrate—but others have not, causing their populations to face food shortages and reduced survival or reproductive success.

In one example, researchers have documented a link between rising temperatures and declining populations of caribou (*Rangifer tarandus*) in the Arctic.

▲ Caribou populations migrate north in the spring to give birth and to eat sprouting plants.

► Alpine chickweed is an early-flowering plant on which caribou depend.

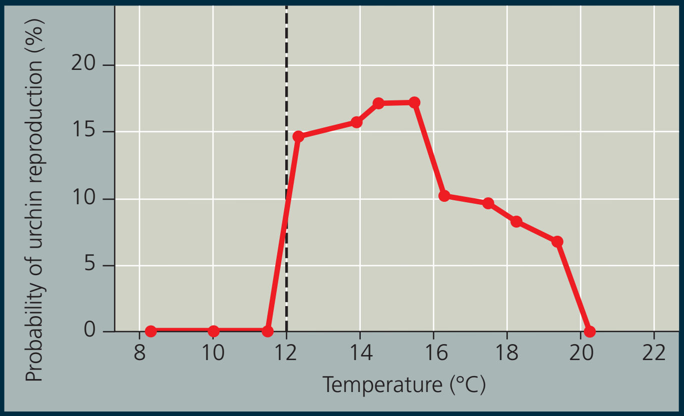


▲ As the climate has warmed, the plants on which caribou depend have emerged earlier in the spring. Caribou have not made similar changes in the timing of when they migrate and give birth. As a result, there is a shortage of food, and caribou offspring production has dropped fourfold.

Effects on Communities and Ecosystems

Climate affects where species live (see Figure 51.9). Climate change has caused hundreds of species to move to new locations, in some cases leading to dramatic changes in ecological communities. Climate change has also altered primary production (see Figure 28.30) and nutrient cycling in ecosystems.

In the example we discuss here, rising temperatures have enabled a sea urchin to invade southern regions along the coast of Australia, causing catastrophic changes to marine communities there.

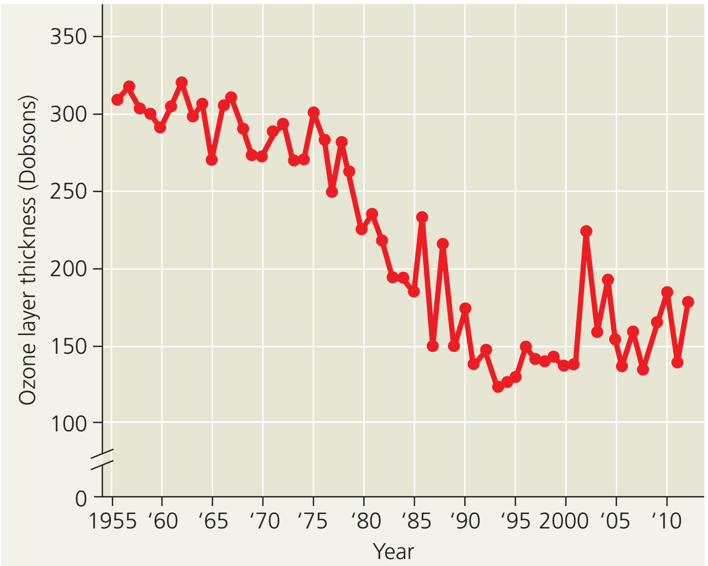


▲ The sea urchin *Centrostephanus rodgersii* requires water temperatures above 12°C to reproduce successfully, as shown in this graph. As ocean waters rise above this critical temperature, the urchin has been able to expand its range to the south, destroying kelp beds as it moves into new regions.

▲ As the urchin has expanded its range to the south, it has destroyed high-diversity kelp communities, leaving bare regions called "urchin barrens" in its wake.

MAKE CONNECTIONS ➤ *In addition to causing climate change, rising concentrations of CO_2 are contributing to ocean acidification (see Figure 3.12). Explain how ocean acidification can affect individual organisms, and how that, in turn, can cause dramatic changes in ecological communities.*

Figure 56.31 Thickness of the October ozone layer over Antarctica in units called Dobsons.



Depletion of Atmospheric Ozone

Like carbon dioxide and other greenhouse gases, atmospheric ozone (O_3) has also changed in concentration because of human activities. Life on Earth is protected from the damaging effects of ultraviolet (UV) radiation by a layer of ozone located in the stratosphere 17–25 km above Earth's surface. However, satellite studies of the atmosphere show that the springtime ozone layer over Antarctica has thinned substantially since the mid-1970s **(Figure 56.31)**. The destruction of atmospheric ozone results primarily from the accumulation of chlorofluorocarbons (CFCs), chemicals once widely used in refrigeration and manufacturing. In the stratosphere, chlorine atoms released from CFCs react with ozone, reducing it to molecular O_2 **(Figure 56.32)**. Subsequent chemical reactions liberate the chlorine, allowing it to react with other ozone molecules in a catalytic chain reaction.

The thinning of the ozone layer is most apparent over Antarctica in spring, where cold, stable air allows the chain reaction to continue **(Figure 56.33)**. The magnitude of ozone depletion and the size of the ozone hole have been slightly smaller in recent years than the average for the last 20 years, but the hole still sometimes extends as far as the southernmost portions of Australia, New Zealand, and South America. At the more heavily populated middle latitudes, ozone levels have decreased 2–10% during the past 20 years.

Decreased ozone levels in the stratosphere increase the intensity of UV rays reaching Earth's surface. The consequences of ozone depletion for life on Earth may be severe for plants, animals, and microorganisms. Some scientists expect increases in both lethal and nonlethal forms of skin cancer and in cataracts among humans, as well as unpredictable effects on crops and natural communities, especially the phytoplankton that are responsible for a large proportion of Earth's primary production.

Figure 56.32 How free chlorine in the atmosphere destroys ozone.

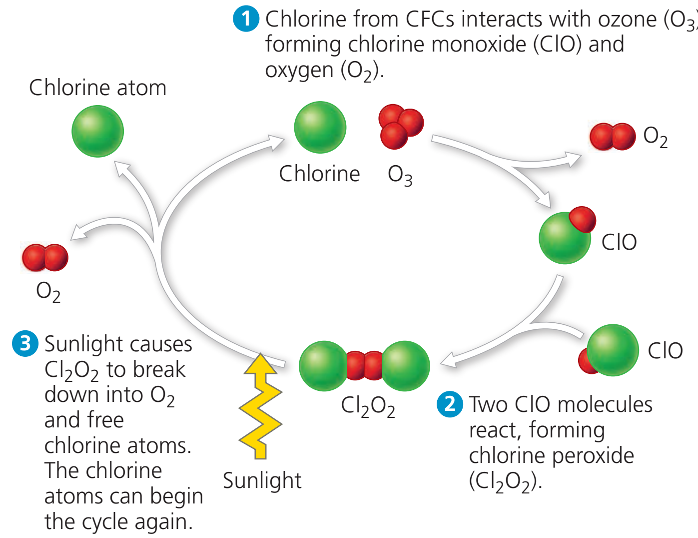
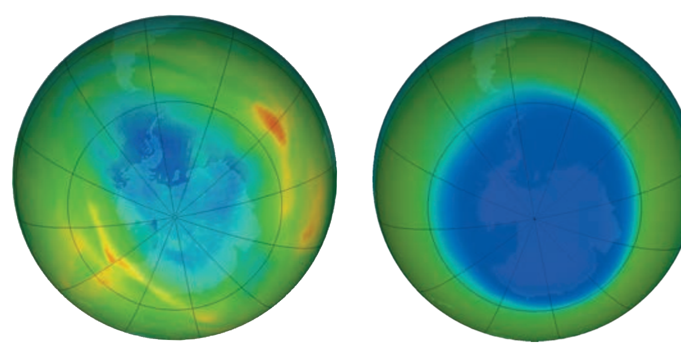


Figure 56.33 Erosion of Earth's ozone shield. The ozone hole over Antarctica is visible as the dark blue patch in these images based on atmospheric data.



To study the consequences of ozone depletion, ecologists have conducted field experiments in which they use filters to decrease or block the UV radiation in sunlight. One such experiment, performed on a scrub ecosystem near the tip of South America, showed that when the ozone hole passed over the area, the amount of UV radiation reaching the ground increased sharply, causing more DNA damage in plants that were not protected by filters. Scientists have shown similar DNA damage and a reduction in phytoplankton growth when the ozone hole opens over the Southern Ocean (Antarctic Ocean) each year.

The good news about the ozone hole is how quickly many countries have responded to it. Since 1987 , at least 197 nations, including the United States, have signed the Montreal Protocol, a treaty that regulates the use of ozone-depleting chemicals. Most nations, again including the United States, have ended the production of CFCs. As a consequence of these actions, chlorine concentrations in the stratosphere have stabilized and ozone depletion is slowing.

But even though CFC emissions today are close to zero, chlorine molecules already in the atmosphere will continue to influence stratospheric ozone levels for at least 50 years.

The partial destruction of Earth's ozone shield is one more example of how greatly humans can disrupt the dynamics of ecosystems and the biosphere. It also highlights our ability to solve environmental problems when we set our minds to it.

CONCEPT CHECK 56.4

1. How can the addition of excess mineral nutrients to a lake threaten its fish population?
2. **MAKE CONNECTIONS ➤** There are vast stores of organic matter in the soils of northern coniferous forests and tundra around the world. Suggest an explanation for why scientists who study global warming are closely monitoring these stores (see Figure 55.14).
3. **MAKE CONNECTIONS ➤** Mutagens are chemical and physical agents that induce mutations in DNA (see Concept 17.5). How does reduced ozone concentration in the atmosphere increase the likelihood of mutations in various organisms?

For suggested answers, see Appendix A.

CONCEPT 56.5

Sustainable development can improve human lives while conserving biodiversity

With the increasing loss and fragmentation of habitats, changes in Earth's physical environment and climate, and increasing human population (see Concept 53.6), we face difficult trade-offs in managing the world's resources. Preserving all habitat patches isn't feasible, so biologists must help societies set conservation priorities by identifying which habitat patches are most crucial. Ideally, implementing these priorities should also improve the quality of life for local people. Ecologists use the concept of *sustainability* as a tool to establish long-term conservation priorities.

Sustainable Development

We need to understand the interconnections of the biosphere if we are to protect species from extinction and improve the quality of human life. To this end, many nations, scientific societies, and other groups have embraced the concept of **sustainable development**, economic development that meets the needs of people today without limiting the ability of future generations to meet their needs. For example, the Ecological Society of America, the world's largest organization of professional ecologists, endorses a research agenda called the Sustainable Biosphere Initiative. The goal of this initiative is to define and acquire the basic ecological information needed to develop, manage, and conserve Earth's resources as responsibly as possible. The research agenda includes studies of global change, including interactions between climate and ecological processes, biological diversity and its role in maintaining ecological processes, and the ways in which the productivity of natural and artificial ecosystems can be sustained. This initiative requires a strong commitment of human and economic resources.

Achieving sustainable development is an ambitious goal. To sustain ecosystem processes and stem the loss of biodiversity, we must connect life science with the social sciences, economics, and the humanities. We must also reassess our personal values. Those of us living in wealthier nations have a larger ecological footprint than do people living in developing nations (see Concept 53.6). By including the long-term costs of consumption in our decision-making processes, we can learn to value the ecosystem services that sustain us.

Case Study: *Silverdale New Vision*

The deep coal mining industry of the UK, which once employed about 500,000 people at 483 facilities, ended in 2015 after experiencing a decline for about 50 years. Closures resulted in the deprivation of the mining communities, and gave rise to contaminated industrial sites. The mining families affected by the closure of Silverdale Colliery in 1998 traveled to Brussels to campaign for "Silverdale New Vision", which sought jobs, affordable homes, and green spaces for the local community. In 2008, a £13.6-million regeneration project put this vision into action. The Silverdale Enterprise Park opened in 2009, and is home to 18 companies. The Heritage Park was completed in 2015, and provided 350 energy-efficient houses. The 83-hectare Silverdale Country Park opened in 2011 to support wildlife conservation and provide recreational spaces. It protects some of the priority bird species listed in the UK Biodiversity

▼ Figure 56.34 Sustainable development of Silverdale Colliery: a. Silverdale Enterprise Park, b. Community building and sports field, c. Heritage Park housing estate on former pit head, d. edge of Silverdale Country Park

Action Plan, and is home to the largest colony of dingy skipper butterflies in the county. In 2015, the country park was designated as a Site of Biological Importance for its mosaic of early successional habitats and associated species. The Land Trust charity works with local schools, universities, and community groups on educational activities, and provides training in sustainable woodland practices, such as coppicing. Thus, "Silverdale New Vision" demonstrates that sustainable development benefits both nature and people.

The Future of the Biosphere

Our modern lives are very different from those of early humans, who hunted and gathered to survive. Their reverence for the natural world is evident in the early murals of wildlife they painted on cave walls **(Figure 56.35a)** and in the stylized visions of life they sculpted from bone and ivory **(Figure 56.35b)**.

Our lives reflect remnants of our ancestral attachment to nature and the diversity of life—the concept of *biophilia* that was introduced early in this chapter. We evolved in natural environments rich in biodiversity, and we still have an affinity for such settings **(Figure 56.35c** and **d)**. Indeed, our biophilia may be innate, an evolutionary product of natural selection acting on a brainy species whose survival depended on a close connection to the environment and a practical appreciation of plants and animals.

Our appreciation of life guides the field of biology today. We celebrate life by deciphering the genetic code that makes each species unique. We embrace life by using fossils and DNA to chronicle evolution through time. We preserve life through our efforts to classify and protect the millions of species on Earth. We respect life by using nature responsibly and reverently to improve human welfare.

Biology is the scientific expression of our desire to know nature. We are most likely to protect what we appreciate, and we are most likely to appreciate what we understand. By learning about the processes and diversity of life, we also become more aware of ourselves and our place in the biosphere. We hope this text has served you well in this lifelong adventure.

CONCEPT CHECK 56.5

1. What is meant by the term *sustainable development*?
2. How might biophilia influence us to conserve species and restore ecosystems?
3. **WHAT IF?** ➤ Suppose a new fishery is discovered, and you are put in charge of developing it sustainably. What ecological data might you want on the fish population? What criteria would you apply for the fishery's development?

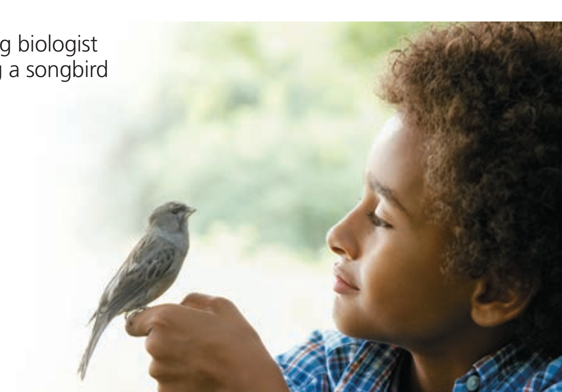
For suggested answers, see Appendix A.

▼ Figure 56.35 Biophilia, past and present.

(a) Detail of animals in a 17,000-year-old cave painting, Lascaux, France

(b) A 30,000-year-old ivory carving of a water bird, found in Germany

(c) Nature lovers on a wildlife-watching expedition



(d) A young biologist holding a songbird

56 Chapter Review

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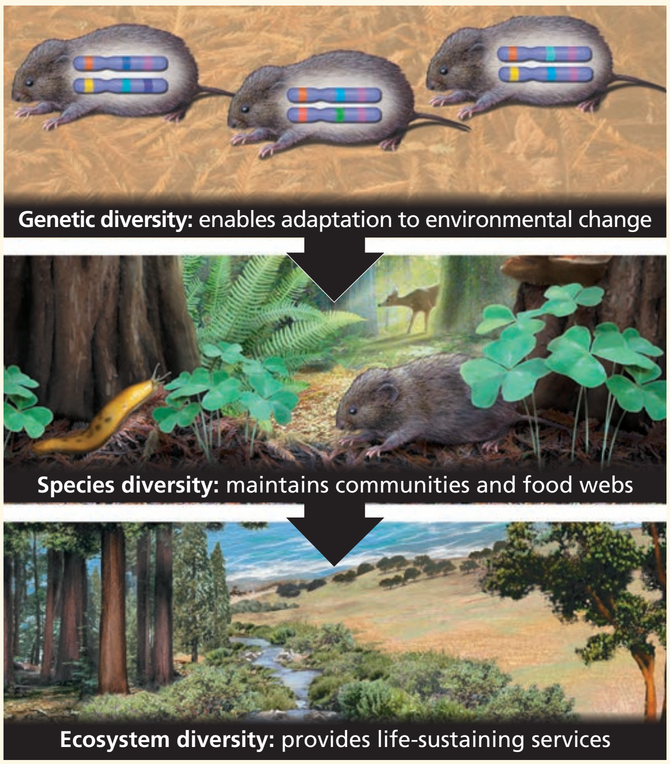
SUMMARY OF KEY CONCEPTS

VOCAB SELF-QUIZ
goo.gl/Rn5Uax

CONCEPT 56.1

Human activities threaten Earth's biodiversity *(pp. 1317–1322)*

- Biodiversity can be considered at three main levels:



- Our biophilia enables us to recognize the value of biodiversity for its own sake. Other species also provide humans with food, fiber, medicines, and **ecosystem services**.
- Four major threats to biodiversity are habitat loss, **introduced species**, overharvesting, and global change.

? *Give at least three examples of key ecosystem services that nature provides for people.*

CONCEPT 56.2

Population conservation focuses on population size, genetic diversity, and critical habitat *(pp. 1322–1326)*

- When a population drops below a **minimum viable population (MVP)** size, its loss of genetic variation due to nonrandom mating and genetic drift can trap it in an **extinction vortex**.
- The declining-population approach focuses on the environmental factors that cause decline, regardless of absolute population size. It follows a step-by-step conservation strategy.
- Conserving species often requires resolving conflicts between the habitat needs of **endangered species** and human demands.

? *Why is the minimum viable population size smaller for a genetically diverse population than for a less genetically diverse population?*

CONCEPT 56.3

Landscape and regional conservation help sustain biodiversity *(pp. 1326–1330)*

- The structure of a landscape can strongly influence biodiversity. As habitat fragmentation increases and edges become more extensive, biodiversity tends to decrease. **Movement corridors** can promote dispersal and help sustain populations.
- **Biodiversity hot spots** are also hot spots of extinction and thus prime candidates for protection. Sustaining biodiversity in parks and reserves requires management to ensure that human activities in the surrounding landscape do not harm the protected habitats. The **zoned reserve** model recognizes that conservation efforts often involve working in landscapes that are greatly affected by human activity.
- **Urban ecology** is the study of organisms and their environment in primarily urban settings.

? *Give two examples that show how habitat fragmentation can harm species in the long term.*

CONCEPT 56.4

Earth is changing rapidly as a result of human actions *(pp. 1330–1339)*

- Agriculture removes plant nutrients from ecosystems, so large supplements are usually required. The nutrients in fertilizer can pollute groundwater and surface-water aquatic ecosystems, where they can stimulate excess algal growth (eutrophication).
- The release of toxic wastes and pharmaceuticals has polluted the environment with harmful substances that often persist for long periods and become increasingly concentrated in successively higher trophic levels of food webs (**biological magnification**).
- Because of the burning of fossil fuels and other human activities, the atmospheric concentration of CO_2 and other greenhouse gases has been steadily increasing. These increases have caused **climate change**, including significant global warming and changing patterns of precipitation. Climate change has already affected many ecosystems.
- The ozone layer reduces the penetration of UV radiation through the atmosphere. Human activities, notably the release of chlorine-containing pollutants, have eroded the ozone layer, but government policies are helping to solve the problem.

? *Thinking about biological magnification of toxins, is it healthier to feed at a lower or higher trophic level? Explain.*

CONCEPT 56.5

Sustainable development can improve human lives while conserving biodiversity *(pp. 1339–1340)*

- The goal of the Sustainable Biosphere Initiative is to acquire the ecological information needed for the development, management, and conservation of Earth's resources.
- By learning about biological processes and the diversity of life, we become more aware of our close connection to the environment and the value of other organisms that share it.

? *Why is sustainability such an important goal for conservation biologists?*

TEST YOUR UNDERSTANDING

Multiple-choice Self-Quiz questions 1–6 can be found in the Study Area in MasteringBiology.

PRACTICE TEST
goo.gl/iAsVgL

7. **DRAW IT** Suppose that you are managing a forest reserve, and one of your goals is to protect local populations of woodland birds from parasitism by the brown-headed cowbird. You know that female cowbirds usually do not venture more than about 100 m into a forest and that nest parasitism is reduced when woodland birds nest away from forest edges. The reserve you manage extends about 6,000 m from east to west and 3,000 m from north to south. It is surrounded by a deforested pasture on the west, an agricultural field for 500 m in the southwest corner, and intact forest everywhere else. You must build a road, 10 m by 3,000 m, from the north to the south side of the reserve and construct a maintenance building that will take up 100 m^2 in the reserve. Draw a map of the reserve, showing where you would put the road and the building to minimize cowbird intrusion along edges. Explain your reasoning.

8. **EVOLUTION CONNECTION** The fossil record indicates that there have been five mass extinction events in the past 500 million years (see Concept 25.4). Many ecologists think we are on the verge of entering a sixth mass extinction event. Briefly discuss the history of mass extinctions and the length of time it typically takes for species diversity to recover through the process of evolution. Explain why this should motivate us to slow the loss of biodiversity today.

9. **SCIENTIFIC INQUIRY** (a) Estimate the average CO_2 concentration in 1975 and in 2012 using data provided in Figure 56.28. (b) On average, how rapidly did CO_2 concentration increase (ppm/yr) from 1975 to 2012? (c) Estimate the approximate CO_2 concentration in 2100, assuming that the CO_2 concentration continues to rise as fast as it did from 1975 to 2012. (d) Draw a graph of average CO_2 concentration from 1975 to 2012 and then use a dashed line to extend the graph to the year 2100. (e) Identify the ecological factors and human decisions that might influence the actual rise in CO_2 concentration. (f) Discuss how additional scientific data could help societies predict this value.

10. **WRITE ABOUT A THEME: INTERACTIONS** One factor favoring rapid population growth by an introduced species is the absence of the predators, parasites, and pathogens that controlled its population in the region where it evolved. In a short essay (100–150 words), explain how evolution by natural selection in a region of introduction would influence the rate at which native predators, parasites, and pathogens attack an introduced species.

11. **SYNTHESIZE YOUR KNOWLEDGE**

Big cats, such as the Siberian tiger (*Panthera tigris altaica*) shown here, are one of the most endangered groups of mammals in the world. Based on what you've learned in this chapter, discuss some of the approaches you would use to help preserve them.

For selected answers, see Appendix A.

For additional practice questions, check out the **Dynamic Study Modules** in MasteringBiology. You can use them to study on your smartphone, tablet, or computer anytime, anywhere!

APPENDIX A Answers

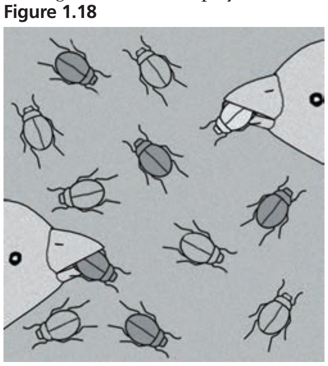
NOTE: Answers to Scientific Skills Exercises, Problem-Solving Exercises, Interpret the Data questions, and short-answer essay questions are available only for instructors in the Instructor Resources area of MasteringBiology. Scientific Skills Exercises, Problem-Solving Exercises, Interpret the Data questions, and additional questions for the Visualizing Figures can be assigned and automatically graded in MasteringBiology.

Chapter 1

Figure Questions

Figure 1.4 The scale bar is about 8.5 mm long, and it corresponds to 1 μm. The prokaryotic cell is about 2 cm = 20 mm long. Dividing by 8.5 mm/scale bar, the length of the prokaryotic cell is about 2.4 scale bars. Each scale bar represents 1 μm, so the prokaryotic cell is about 2.4 μm long. The eukaryotic cell is about 82 mm across (from lower left to upper right) divided by 8.5 mm/scale bar = 9.6 scale bars = 9.6 μm across. **Figure 1.10** The response to insulin is glucose uptake by cells and glucose storage in liver cells. The initial stimulus is high glucose levels, which are reduced when glucose is taken up by cells.

Figure 1.18



5 Environmental change resulting in survival of organisms with different traits

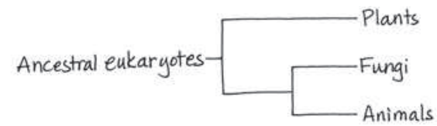
As the soil gradually becomes lighter brown, beetles that match the color of the soil will not be seen by birds and therefore will not be eaten. For example, when the soil is medium-colored, birds will be able to see and eat the darker beetles and any lighter beetles that arise. (Most or all of the lighter beetles will have been eaten earlier, but new light beetles will arise due to variation in the population.) Thus, over time, the population will become lighter as the soil becomes lighter.

Concept Check 1.1

1. Examples: A molecule consists of *atoms* bonded together. Each organelle has an orderly arrangement of *molecules*. Photosynthetic plant cells contain *organelles* called chloroplasts. A tissue consists of a group of similar *cells*. Organs such as the heart are constructed from several *tissues*. A complex multicellular organism, such as a plant, has several types of *organs*, such as leaves and roots. A population is a set of *organisms* of the same species. A community consists of *populations* of the various species inhabiting a specific area. An ecosystem consists of a biological *community* along with the nonliving factors important to life, such as air, soil, and water. The biosphere is made up of all of Earth's *ecosystems*. **2.** (a) New properties emerge at successive levels of biological organization: Structure and function are correlated. (b) Life's processes involve the expression and transmission of genetic information. (c) Life requires the transfer and transformation of energy and matter. **3.** Some possible answers: *Organization (Emergent properties)*: The ability of a human heart to pump blood requires an intact heart; it is not a capability of any of the heart's tissues or cells working alone. *Organization (Structure and function)*: The strong, sharp teeth of a wolf are well suited to grasping and dismembering its prey. *Information*: Human eye color is determined by the combination of genes inherited from the two parents. *Energy and Matter*: A plant, such as a grass, absorbs energy from the sun and transforms it into molecules that act as stored fuel. Animals can eat parts of the plant and use the food for energy to carry out their activities. *Interactions (Molecules)*: When your stomach is full, it signals your brain to decrease your appetite. *Interactions (Ecosystems)*: A mouse eats food, such as nuts or grasses, and deposits some of the food material as wastes (feces and urine). Construction of a nest rearranges the physical environment and may hasten degradation of some of its components. The mouse may also act as food for a predator.

Concept Check 1.2

1. The naturally occurring heritable variation in a population is "edited" by natural selection because individuals with heritable traits better suited to the environment survive and reproduce more successfully than others. Over time, better-suited individuals persist and their percentage in the population increases, while less well-suited individuals become less prevalent—a type of population editing. **2.** Here is one possible explanation: The ancestor species of the green warbler finch lived on an island where insects were a plentiful food source. Among individuals in the ancestor population, there was likely variation in beak shape and size. Individuals with slender, sharp beaks were likely more successful at picking up insects for food. Being well-nourished, they gave rise to more offspring than birds with thick, short beaks. Their many offspring inherited slender, sharp beaks (because of genetic information being passed from generation to generation, although Darwin didn't know this). In each generation, the offspring birds with the beaks of a shape best at picking up insects would eat more and have more offspring. Therefore, the green warbler finch of today has a slender beak that is very well matched (adapted) to its food source, insects.
3.



Concept Check 1.3

1. Mouse coat color matches the environment for both beach and inland populations. **2.** Inductive reasoning derives generalizations from specific cases; deductive reasoning predicts specific outcomes from general premises. **3.** Compared to a hypothesis, a scientific theory is usually more general and substantiated by a much greater amount of evidence. Natural selection is an explanatory idea that applies to all kinds of organisms and is supported by vast amounts of evidence of various kinds. **4.** Based on the mouse coloration in Figure 1.25, you might expect that the mice that live on the sandy soil would be lighter in color and those that live on the lava rock would be much darker. And in fact, that is what researchers have found. You would predict that each color of mouse would be less preyed upon in its native habitat than it would be in the other habitat. (Research results also support this prediction.) You could repeat the Hoekstra experiment with colored models, painted to resemble these two types of mouse. Or you could try transplanting some of each population to its non-native habitat and counting how many you can recapture over the next few days, then comparing the four samples as was done in Hoekstra's experiment. (The painted models are easier to recapture, of course!) In the live mouse transplantation experiment, you would have to do controls to eliminate the variable represented by the transplanted mice being in a new, unknown territory. You could control for the transplantation process by transplanting some dark mice from one area of lava rock to one far distant, and some light mice from one area of sandy soil to a distant area.

Concept Check 1.4

1. Science aims to understand natural phenomena and how they work, while technology involves application of scientific discoveries for a particular purpose or to solve a specific problem. **2.** Natural selection could be operating. Malaria is present in sub-Saharan Africa, so there might be an advantage to people with the sickle-cell disease form of the gene that makes them more able to survive and pass on their genes to offspring. Among those of African descent living in the United States, where malaria is absent, there would be no advantage, so they would be selected against more strongly, resulting in fewer individuals with the sickle-cell disease form of the gene.

Summary of Key Concepts Questions

1.1 Finger movements rely on the coordination of the many structural components of the hand (muscles, nerves, bones, etc.), each of which is composed of elements from lower levels of biological *organization* (cells, molecules). The development of the hand relies on the genetic *information* encoded in chromosomes found in cells throughout the body. To power the finger movements that result in a text message, muscle and nerve cells require chemical *energy* that they transform in powering muscle contraction or in propagating nerve impulses. Texting is in essence communication, an *interaction* that conveys information between organisms, in this case of the same species. **1.2** Ancestors of the beach mouse may have exhibited variations in their coat color. Because of the prevalence of visual predators, the better-camouflaged (lighter) mice in the beach habitat may have survived longer and been able to produce more offspring. Over time, a higher and higher proportion of individuals in the population would have had the adaptation of lighter fur that acted to camouflage the mouse in the beach habitat.
1.3 Gathering and interpreting data are core activities in the scientific process, and they are affected by, and affect in turn, three other arenas of the scientific process: exploration and discovery, community analysis and feedback, and societal benefits and outcomes. **1.4** Different approaches taken by scientists studying natural phenomena at different levels complement each other, so more is learned about each problem being studied. A diversity of backgrounds among scientists may lead to fruitful ideas in the same way that important innovations have often arisen where a mix of cultures coexist, due to multiple different viewpoints.

Test Your Understanding

8. Your figure should show the following: (1) for the biosphere, the Earth with an arrow coming out of a tropical ocean; (2) for the ecosystem, a distant view of a coral reef; (3) for the community, a collection of reef animals and algae, with corals, fishes, some seaweed, and any other organisms you can think of; (4) for the population, a group of fish of the same species; (5) for the organism, one fish from your population; (6) for the organ, the fish's stomach; (7) for a tissue, a group of similar cells from the stomach; (8) for a cell, one cell from the tissue, showing its nucleus and a few other organelles; (9) for an organelle, the nucleus, where most of the cell's DNA is located; and (10) for a molecule, a DNA double helix. Your sketches can be very rough!

Chapter 2

Figure Questions

Figure 2.7 Atomic number = 12; 12 protons, 12 electrons; 3 electron shells; 2 valence electrons

Figure 2.14 One possible answer:

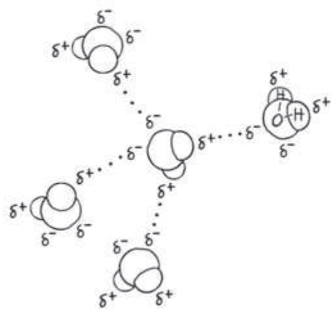
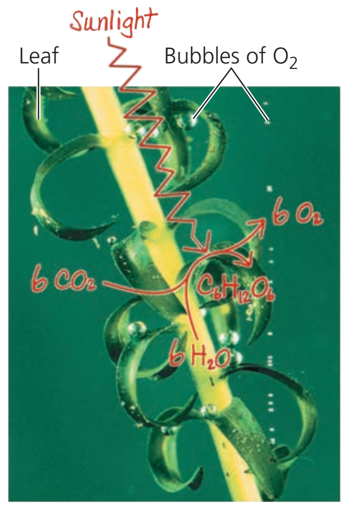


Figure 2.17



Concept Check 2.1

1. Table salt (sodium chloride) is made up of sodium and chlorine. We are able to eat the compound, showing that it has different properties from those of a metal (sodium) and a poisonous gas (chlorine). **2.** Yes, because an organism requires trace elements, even though only in small amounts **3.** A person with a potassium deficiency can have muscle cramps, diarrhea, frequent urination, low blood pressure, confusion, paralysis, and abnormal heart rhythms. **4.** Variant ancestral plants that could tolerate elevated levels of the elements in serpentine soils could grow and reproduce there. (Plants that were well adapted to nonserpentine soils would not be expected to survive in serpentine areas.) The offspring of the variants would also vary, with those most capable of thriving under serpentine conditions growing best and reproducing most. Over many generations, this probably led to the serpentine-adapted species we see today.

Concept Check 2.2

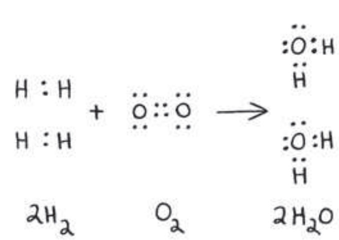
1. 7 **2.** $^{3}_{1}H$ **3.** 9 electrons; two electron shells; 1*s*, 2*s*, 2*p* (three orbitals); 1 electron is needed to fill the valence shell. **4.** The elements in a row all have the same number of electron shells. In a column, all the elements have the same number of electrons in their valence shells.

Concept Check 2.3

1. In this structure, each carbon atom has only three covalent bonds instead of the required four. **2.** The O—H bond, as oxygen is more electronegative than carbon. **3.** If you could synthesize molecules that mimic these shapes, you might be able to treat diseases or conditions caused by the inability of affected individuals to synthesize such molecules.

Concept Check 2.4

1.

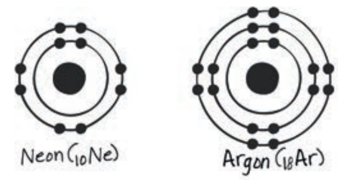


2. At equilibrium, the forward and reverse reactions occur at the same rate. **3.** $C_6H_{12}O_6 + 6\ O_2 \rightarrow 6\ CO_2 + 6\ H_2O$ + Energy. Glucose and oxygen react to form carbon dioxide and water, releasing energy. We breathe in oxygen because we need it for this reaction to occur, and we breathe out carbon dioxide because it is a by-product of this reaction. (This reaction is called cellular respiration, and you will learn more about it in Chapter 10.)

Summary of Key Concepts Questions

2.1 A compound is made up of two or more elements combined in a fixed ratio, while an element is a substance that cannot be broken down to other substances.

2.2

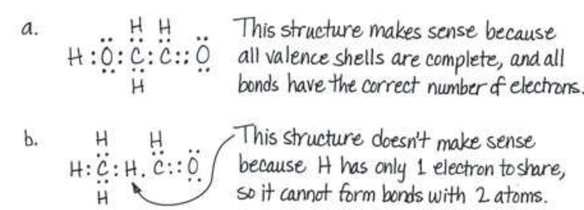


Both neon and argon have completed valence shells, containing 8 electrons. They do not have unpaired electrons that could participate in chemical bonds.

2.3 Electrons are shared equally between the two atoms in a nonpolar covalent bond. In a polar covalent bond, the electrons are drawn closer to the more electronegative atom. In the formation of ions, an electron is completely transferred from one atom to a much more electronegative atom. **2.4** The concentration of products would increase as the added reactants were converted to products. Eventually, an equilibrium would again be reached in which the forward and reverse reactions were proceeding at the same rate and the relative concentrations of reactants and products returned to where they were before the addition of more reactants.

Test Your Understanding

9.



Chapter 3

Figure Questions

Figure 3.2 One possible answer:

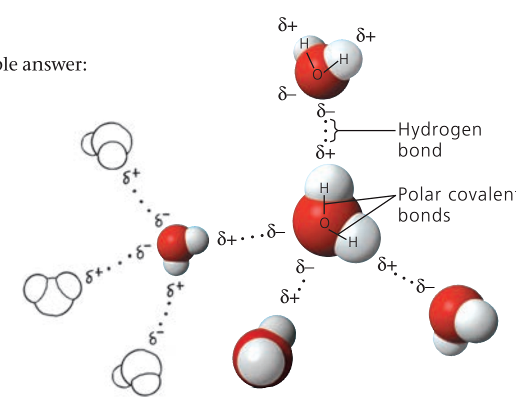


Figure 3.6 Without hydrogen bonds, water would behave like other small molecules, and the solid phase (ice) would be denser than liquid water. The ice would sink to the bottom and would no longer insulate the whole body of water, which would eventually freeze because of the freezing temperatures in the Southern Ocean near Antarctica. The krill would not survive. **Figure 3.8** Heating the solution would cause the water to evaporate faster than it is evaporating at room temperature. At a certain point, there wouldn't be enough water molecules to dissolve the salt ions. The salt would start coming out of solution and re-forming crystals. Eventually, all the water would evaporate, leaving behind a pile of salt like the original pile. **Figure 3.12** Adding excess CO_2 to the oceans ultimately reduces the rate at which calcification (by organisms) can occur.

Concept Check 3.1

1. Electronegativity is the attraction of an atom for the electrons of a covalent bond. Because oxygen is more electronegative than hydrogen, the oxygen atom in H_2O pulls electrons toward itself, resulting in a partial negative charge on the oxygen atom and partial positive charges on the hydrogen atoms. Atoms in neighboring water molecules with opposite partial charges are attracted to each other, forming a hydrogen bond. **2.** Due to its two polar covalent bonds, a water molecule has four regions of partial charge: two positive regions on the two hydrogens and two negative regions on the oxygen atom. Each of these can bind to a region of opposite partial charge on another water molecule. **3.** The hydrogen atoms of one molecule, with their partial positive charges, would repel the hydrogen atoms of the adjacent molecule. **4.** The covalent bonds of water molecules would not be polar, so no regions of the molecule would carry partial charges and water molecules would not form hydrogen bonds with each other.

Concept Check 3.2

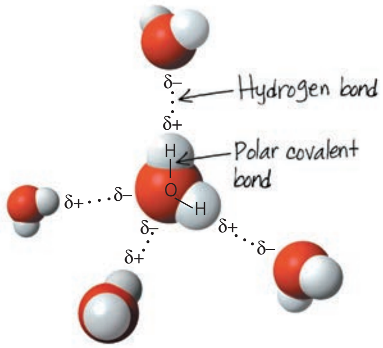
1. Hydrogen bonds hold neighboring water molecules together. This cohesion helps chains of water molecules move upward against gravity in water-conducting cells as water evaporates from the leaves. Adhesion between water molecules and the walls of the water-conducting cells also helps counter gravity. **2.** High humidity hampers cooling by suppressing the evaporation of sweat. **3.** As water freezes, it expands because water molecules move farther apart in forming ice crystals. When there is water in a crevice of a boulder, expansion due to freezing may crack the boulder. **4.** The hydrophilic ends of soap molecules attach to water molecules and point outward, while the hydrophobic ends attach to oil molecules and trap them in the center. This helps in the formation of small water-soluble micelles, which are washed away easily. If soaps lose their hydrophobic property, they would not be able to convert oil into water-soluble micelles.

Concept Check 3.3

1. 10^5, or 100,000 **2.** No. $[H^+] = 0.01\ M = 10^{-2}\ M$, so pH = 2. $[H^+] = 0.001\ M = 10^{-3}\ M$, so pH = 3. **3.** $CH_3COOH \rightarrow CH_3COO^- + H^+$. CH_3COOH is the acid (the H^+ donor), and CH_3COO^- is the base (the H^+ acceptor). **4.** Adding a strong base will result in the formation of OH^- ions in the solution. The OH^- ions will react with acetic acid to form acetate ions: $CH_3COOH + OH^- \rightleftharpoons CH_3COO^- + H_2O$. Thus, if a strong base is added, the reaction will shift to the right.

Summary of Key Concepts Questions

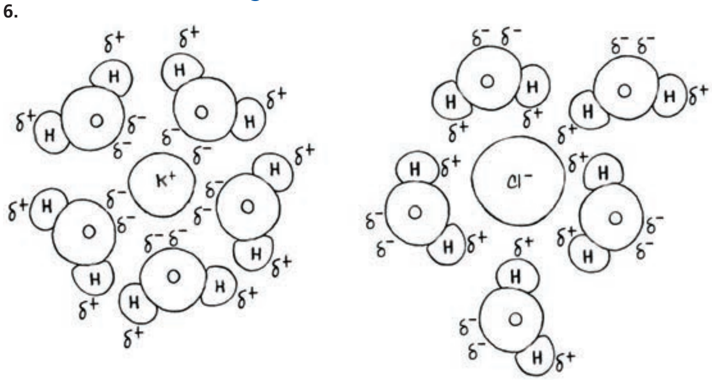
3.1



No. A covalent bond is a strong bond in which electrons are shared between two atoms. A hydrogen bond is a weak bond, which does not involve electron sharing, but is simply an attraction between two partial charges on neighboring atoms. **3.2** Ions dissolve in water when polar water molecules form a hydration shell around them, with partially charged regions of water molecules being attracted to ions of the opposite charge. Polar molecules dissolve as water molecules form hydrogen bonds with them and surround them. Solutions are homogeneous mixtures of solute and solvent. **3.3** The concentration of hydrogen ions (H^+) would be 10^{-11}, and the pH of the solution would be 11.

Test Your Understanding

6.



7. Due to intermolecular hydrogen bonds, water has a high specific heat (the amount of heat required to increase the temperature of water by 1°C). When water is heated, much of the heat is absorbed in breaking hydrogen bonds before the water molecules increase their motion and the temperature increases. Conversely, when water is cooled, many H bonds are formed, which releases a significant amount of heat. This release of heat can provide some protection against freezing of the plants' leaves, thus protecting the cells from damage. **8.** Both global warming and ocean acidification are caused by increasing levels of carbon dioxide in the atmosphere, the result of burning fossil fuels.

Chapter 4

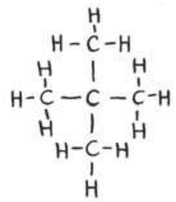
Figure Questions

Figure 4.2 Because the concentration of the reactants influences the equilibrium (as discussed in Concept 2.4), there might have been more HCN relative to CH_2O, since there would have been a higher concentration of the reactant gas containing nitrogen.

Figure 4.4

Figure 4.6 The tails of fats contain only carbon-hydrogen bonds, which are relatively nonpolar. Because the tails occupy the bulk of a fat molecule, they make the molecule as a whole nonpolar and therefore incapable of forming hydrogen bonds with water.

Figure 4.7

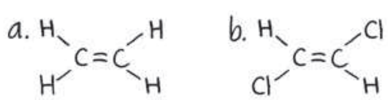


Concept Check 4.1

1. Prior to Wöhler's experiment, the prevailing view was that only living organisms could synthesize "organic" compounds. Wöhler made urea, an organic compound, without the involvement of living organisms. **2.** The sparks provided energy needed for the inorganic molecules in the atmosphere to react with each other. (You'll learn more about energy and chemical reactions in Chapter 6.)

Concept Check 4.2

1.

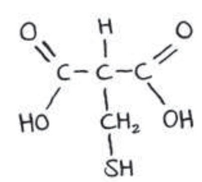


2. The forms of C_4H_{10} in (b) are structural isomers, as are the butenes (forms of C_4H_8) in (c). **3.** Both consist largely of hydrocarbon chains, which provide fuel—gasoline for engines and fats for plant embryos and animals. Reactions of both types of molecules release energy. **4.** No. There is not enough diversity in propane's atoms. It can't form structural isomers because there is only one way for three carbons to attach to each other (in a line). There are no double bonds, so *cis-trans* isomers are not possible. Each carbon has at least two hydrogens attached to it, so the molecule is symmetrical and cannot have enantiomers.

Concept Check 4.3

1. It has both an amino group (—NH_2), which makes it an amine, and a carboxyl group (—COOH), which makes it a carboxylic acid. **2.** The ATP molecule loses a phosphate, becoming ADP.

3.



A chemical group that can act as a base has been replaced with a group that can act as an acid, increasing the acidic properties of the molecule. The shape of the molecule would also change, likely changing the molecules with which it can interact. The original cysteine molecule has an asymmetric carbon in the center. After replacement of the amino group with a carboxyl group, this carbon is no longer asymmetric.

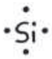
Summary of Key Concepts Questions

4.1 Miller showed that organic molecules could form under the physical and chemical conditions estimated to have been present on early Earth. This abiotic synthesis of organic molecules would have been a first step in the origin of life. **4.2** Acetone and propanal are structural isomers. Acetic acid and glycine have no asymmetric carbons, whereas glycerol phosphate has one. Therefore, glycerol phosphate can exist as forms that are enantiomers, but acetic acid and glycine cannot. **4.3** The methyl group is nonpolar and not reactive. The other six groups are called functional groups because they can participate in chemical reactions. Also, all except the sulfhydryl group are hydrophilic, increasing the solubility of organic compounds in water.

Test Your Understanding

8. The molecule on the right; the middle carbon is asymmetric.

9.

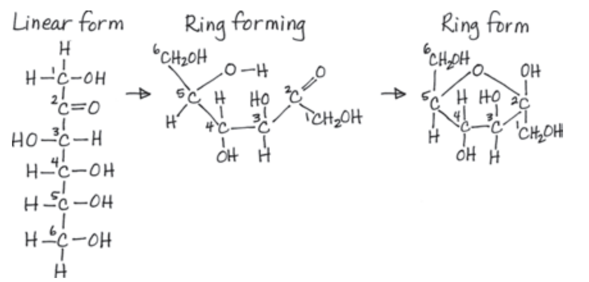


Silicon has 4 valence electrons, the same number as carbon. Therefore, silicon would be able to form long chains, including branches, that could act as skeletons for large molecules. It would clearly do this much better than neon (with no valence electrons) or aluminum (with 3 valence electrons).

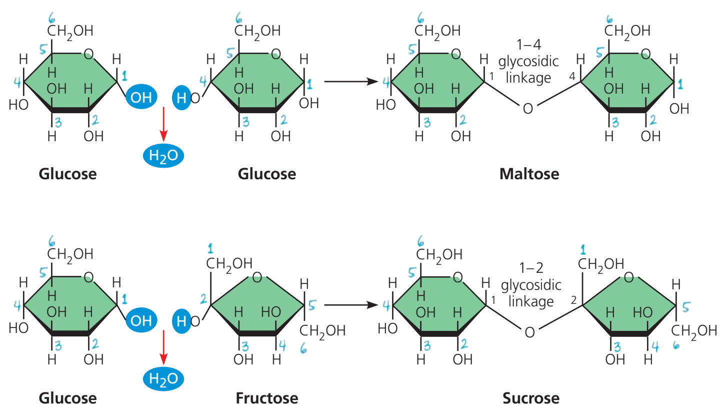
Chapter 5

Figure Questions

Figure 5.3 Glucose and fructose are structural isomers.
Figure 5.4



Note that the oxygen on carbon 5 lost its proton and that the oxygen on carbon 2, which used to be the carbonyl oxygen, gained a proton. Four carbons are in the fructose ring, and two are not. (The latter two carbons are attached to carbons 2 and 5, which are in the ring.) The fructose ring differs from the glucose ring, which has five carbons in the ring and one that is not. (Note that the orientation of this fructose molecule is flipped horizontally relative to that of the one in Figure 5.5b.)
Figure 5.5



(a) In maltose, the linkage is called a 1–4 glycosidic linkage because the number 1 carbon in the left monosaccharide (glucose) is linked to the number 4 carbon in the right monosaccharide (also glucose). (b) In sucrose, the linkage is called a 1–2 glycosidic linkage because the number 1 carbon in the left monosaccharide (glucose) is linked to the number 2 carbon in the right monosaccharide (fructose). (Note that the fructose molecule is oriented differently from glucose in Figure 5.5b and from the fructose shown in the answer for Figure 5.4, above. In Figure 5.5b and in this answer, carbon 2 of fructose is close to carbon 1 of glucose.)

Figure 5.11

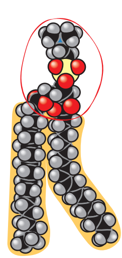


Figure 5.12

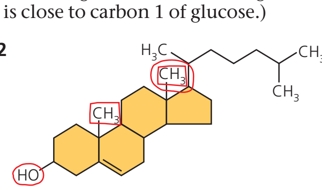


Figure 5.15

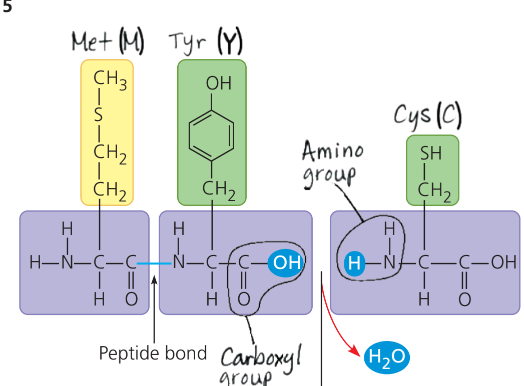
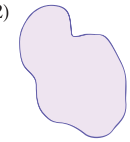


Figure 5.16 (1) The polypeptide backbone is most easily followed in the ribbon model.
(2)



(3) The point of this diagram is to show that a pancreas cell secretes insulin proteins, so the shape is not important to the process being illustrated. **Figure 5.17** We can see that their complementary shapes allow the two proteins to fit together quite precisely. **Figure 5.19** The R group on glutamic acid is acidic and hydrophilic, whereas that on valine is nonpolar and hydrophobic. Therefore, it is unlikely that valine and glutamic acid participate in the same intramolecular interactions. A change in these interactions could (and does) cause a disruption of molecular structure. **Figure 5.26** Using a genomics approach allows us to use gene sequences to identify species and to learn about evolutionary relationships among any two species. This is because all species are related by their evolutionary history, and the evidence is in the DNA sequences. Proteomics—looking at proteins that are expressed—allows us to learn about how organisms or cells are functioning at a given time or in an association with another species.

Concept Check 5.1

1. The four main classes are proteins, carbohydrates, lipids, and nucleic acids. Lipids are not polymers. **2.** Two. Two connections will be formed, and one water molecule will be released from each connection. **3.** The amino acids in the fish protein must be released in hydrolysis reactions and incorporated into other proteins in dehydration reactions.

Concept Check 5.2

1. $C_3H_6O_3$ **2.** $C_{12}H_{22}O_{11}$ **3.** The antibiotic treatment is likely to have killed the cellulose-digesting prokaryotes in the cow's gut. The absence of these prokaryotes would hamper the cow's ability to obtain energy from food and could lead to weight loss and possibly death. Thus, prokaryotic species are reintroduced, in appropriate combinations, in the gut culture given to treated cows.

Concept Check 5.3

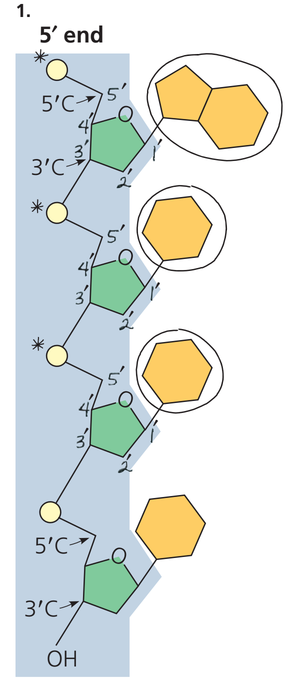
1. Both have a glycerol molecule attached to fatty acids. The glycerol of a fat has three fatty acids attached, whereas the glycerol of a phospholipid is attached to two fatty acids and one phosphate group. **2.** Human sex hormones are steroids, a type of compound that is hydrophobic and thus classified as a lipid. **3.** The mammal would alter the lipid composition of its cell membranes by incorporating more unsaturated fatty acids to maintain fluidity.

Concept Check 5.4

1. Secondary structure involves hydrogen bonds between atoms of the polypeptide backbone. Tertiary structure involves interactions between atoms of the side chains of the amino acid subunits. **2.** The two ring forms of glucose are called α and β, depending on how the glycosidic bond dictates the position of a hydroxyl group. Proteins have α helices and β pleated sheets, two types of repeating structures found in polypeptides due to interactions between the repeating constituents of the chain (not the side chains). The hemoglobin molecule is made up of two types of polypeptides: It contains two molecules each of α-globin and β-globin. **3.** These are all nonpolar, hydrophobic amino acids, so you would expect this region to be located in the interior of the folded polypeptide, where it would not contact the aqueous environment inside the cell.

Concept Check 5.5

1.



2.

5′–T A G G C C T–3′
3′–A T C C G G A–5′

Concept Check 5.6

1. The DNA of an organism encodes all of its proteins, and proteins are the molecules that carry out the work of cells, whether an organism is unicellular or multicellular. By knowing the DNA sequence of an organism, scientists would be able to catalog the protein sequences as well. **2.** Ultimately, the DNA sequence carries the information necessary to make the proteins that determine the traits of a particular species. Because the traits of the two species are similar, you would expect the proteins to be similar as well, and therefore the gene sequences should also have a high degree of similarity.

Summary of Key Concepts Questions

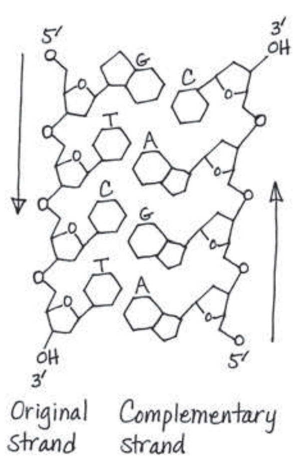
Concept 5.1 The polymers of large carbohydrates (polysaccharides), proteins, and nucleic acids are built from three different types of monomers (monosaccharides, amino acids, and nucleotides, respectively). **Concept 5.2** Both starch and cellulose are polymers of glucose, but the glucose monomers are in the α configuration in starch and the β configuration in cellulose. The glycosidic linkages thus have different geometries, giving the polymers different shapes and thus different properties. Starch is an energy-storage compound in plants; cellulose is a structural component of plant cell walls. Humans can hydrolyze starch to provide energy but cannot hydrolyze cellulose. Cellulose aids in the passage of food through the digestive tract. **Concept 5.3** Lipids are not polymers because they do not exist as a chain of linked monomers. They are not considered macromolecules because they do not reach the giant size of many polysaccharides, proteins, and nucleic acids. **Concept 5.4** A polypeptide, which may consist of hundreds of amino acids in a specific sequence (primary structure), has regions of coils and pleats (secondary structure), which are then folded into irregular contortions (tertiary structure) and may be noncovalently associated with other polypeptides (quaternary structure). The linear order of amino acids, with the varying properties of their side chains (R groups), determines what secondary and tertiary structures will form to produce a protein. The resulting unique three-dimensional shapes of proteins are key to their specific and diverse functions. **Concept 5.5** The complementary base pairing of the two strands of DNA makes possible the precise replication of DNA every time a cell divides, ensuring that genetic information is faithfully transmitted. In some types of RNA, complementary base pairing enables RNA molecules to assume specific three-dimensional shapes that facilitate diverse functions. **Concept 5.6** You would expect the human gene sequence to be most similar to that of the mouse (another mammal), then to that of the fish (another vertebrate), and least similar to that of the fruit fly (an invertebrate).

Test Your Understanding

8.

	Monomers or Components	Polymer or larger molecule	Type of linkage
Carbohydrates	Monosaccharides	Polysaccharides	Glycosidic linkages
Fats	Fatty acids	Triacylglycerols	Ester linkages
Proteins	Amino acids	Polypeptides	Peptide bonds
Nucleic acids	Nucleotides	Polynucleotides	Phosphodiester linkages

9.



Chapter 6

Figure Questions

Figure 6.5 With a proton pump (Figure 8.17), the energy stored in ATP is used to pump protons across the membrane and build up a higher (nonrandom) concentration outside of the cell, so this process results in higher free energy. When solute molecules (analogous to hydrogen ions) are uniformly distributed, similar to the random distribution in the bottom of (b), the system has less free energy than it does in the top of (b). The system in the bottom can do no work. Because the concentration gradient created by a proton pump (Figure 8.17) represents higher free energy, this system has the potential to do work once there is a higher concentration of protons on one side of the membrane (as you will see in Figure 10.15). **Figure 6.10** Glutamic acid has a carboxyl group at the end of its R group. Glutamine has exactly the same structure as glutamic acid, except that there is an amino group in place of the —O⁻ on the R group. (The O atom on the R group leaves during the synthesis reaction.) Thus, in this figure, Gln is drawn as a Glu with an attached NH_2.

Figure 6.13

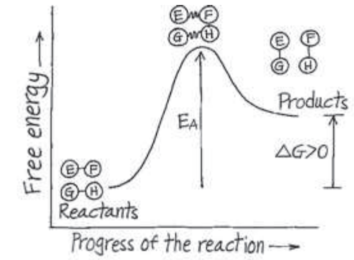
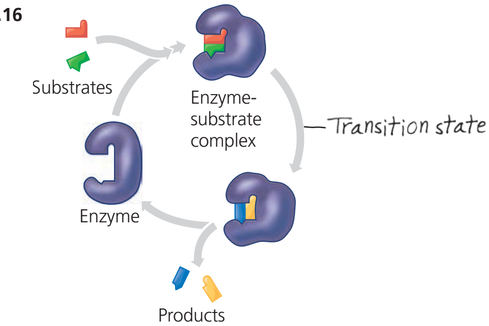


Figure 6.16



Concept Check 6.1

1. The second law is the trend toward randomization, or increasing entropy. When the concentrations of a substance on both sides of a membrane are equal, the distribution is more random than when they are unequal. Diffusion of a substance to a region where it is initially less concentrated increases entropy, making it an energetically favorable (spontaneous) process as described by the second law. This explains the process seen in Figure 8.10. **2.** The apple has potential energy in its position hanging on the tree, and the sugars and other nutrients it contains have chemical energy. The apple has kinetic energy as it falls from the tree to the ground. Finally, when the apple is digested and its molecules broken down, some of the chemical energy is used to do work, and the rest is lost as thermal energy. **3.** The sugar crystals become less ordered (entropy increases) as they dissolve and become randomly spread out in the water. Over time, the water evaporates, and the crystals form again because the water volume is insufficient to keep them in solution. While the reappearance of sugar crystals may represent a "spontaneous" increase in order (decrease in entropy), it is balanced by the decrease in order (increase in entropy) of the water molecules, which changed from a relatively compact arrangement as liquid water to a much more dispersed and disordered form as water vapor.

Concept Check 6.2

1. Cellular respiration is a spontaneous and exergonic process. The energy released from glucose is used to do work in the cell or is lost as heat.
2. Catabolism breaks down organic molecules, releasing their chemical energy and resulting in smaller products with more entropy, as when moving from the top to the bottom of Figure 6.5c. Anabolism consumes energy to synthesize larger molecules from simpler ones, as when moving from the bottom to the top of part (c). **3.** The reaction is exergonic because it releases energy—in this case, in the form of light. (This is a nonbiological version of the bioluminescence seen in Figure 6.1.)

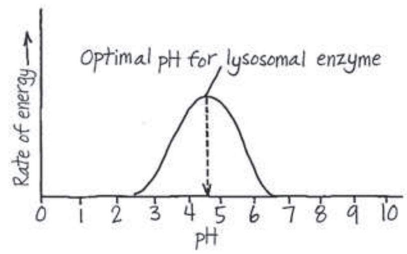
Concept Check 6.3

1. ATP usually transfers energy to an endergonic process by phosphorylating (adding a phosphate group to) another molecule. (Exergonic processes, in turn, phosphorylate ADP to regenerate ATP.) **2.** A set of coupled reactions can transform the first combination into the second. Since this is an exergonic process overall, ΔG is negative and the first combination must have more free energy (see Figure 6.10).

Concept Check 6.4

1. A spontaneous reaction is a reaction that is exergonic. However, if it has a high activation energy that is rarely attained, the rate of the reaction may be low. **2.** Only the specific substrate(s) will fit properly into the active site of an enzyme, the part of the enzyme that carries out catalysis. **3.** Maltose is formed from two units of glucose. If β-galactosidase breaks down maltose, it will lead to the formation of glucose, which can be detected by any reducing sugar estimation method. If β-galactosidase cannot break down maltose, no reducing sugars will be formed.

4.



Concept Check 6.5

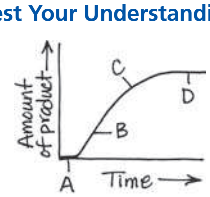
1. The activator binds in such a way that it stabilizes the active form of an enzyme, whereas the inhibitor stabilizes the inactive form. **2.** A catabolic pathway breaks down organic molecules, generating energy that is stored in ATP molecules. In feedback inhibition of such a pathway, ATP (one product) would act as an allosteric inhibitor of an enzyme catalyzing an early step in the catabolic process. When ATP is plentiful, the pathway would be turned off and no more would be made.

Summary of Key Concepts Questions

6.1 The process of "ordering" a cell's structure is accompanied by an increase in the entropy or disorder of the universe. For example, an animal cell takes in highly ordered organic molecules as the source of matter and energy used to build and maintain its structures. In the same process, however, the cell releases heat and the simple molecules of carbon dioxide and water to the surroundings. The increase in entropy of the latter process offsets the entropy decrease in the former. **6.2** A spontaneous reaction has a negative ΔG and is exergonic. For a chemical reaction to proceed with a net release of free energy ($-\Delta G$), the enthalpy or total energy of the system must decrease ($-\Delta H$), and/or the entropy or disorder must increase (yielding a more negative term, $-T\Delta S$). Spontaneous reactions supply the energy to perform cellular work. **6.3** The free energy released from the hydrolysis of ATP may drive endergonic reactions through the transfer of a phosphate group to a reactant molecule, forming a more reactive phosphorylated intermediate. ATP hydrolysis also powers the mechanical and transport work of a cell, often by powering shape changes in the relevant motor proteins. Cellular respiration, the catabolic breakdown of glucose, provides the energy for the endergonic regeneration of ATP from ADP and Ⓟ$_i$. **6.4** Activation energy barriers prevent the complex molecules of the cell, which are rich in free energy, from spontaneously breaking down to less ordered, more stable molecules. Enzymes permit a regulated metabolism by binding to specific substrates and forming enzyme-substrate complexes that selectively lower the E_A for the chemical reactions in a cell. **6.5** A cell tightly regulates its metabolic pathways in response to fluctuating needs for energy and materials. The binding of activators or inhibitors to regulatory sites on allosteric enzymes stabilizes either the active or inactive form of the subunits. For example, the binding of ATP to a catabolic enzyme in a cell with excess ATP would inhibit that pathway. Such types of feedback inhibition preserve chemical resources within a cell. If ATP supplies are depleted, binding of ADP to the regulatory site of catabolic enzymes would activate that pathway, generating more ATP.

Test Your Understanding

9.



A. The substrate molecules are entering the pancreatic cells, so no product is made yet.
B. There is sufficient substrate, so the reaction is proceeding at a maximum rate.
C. As the substrate is used up, the rate decreases (the slope is less steep).
D. The line is flat because no new substrate remains and thus no new product appears.

Chapter 7

Figure Questions

Figure 7.3 The cilia in the upper left were oriented lengthwise in the plane of the slice, while those on the right were oriented perpendicular to the plane of the slice. Therefore the former were cut in longitudinal section, and the latter in cross section. **Figure 7.4** You would use the pellet from the final fraction, which is rich in ribosomes. These are the sites of protein translation. **Figure 7.6** The dark bands in the TEM correspond to the hydrophilic heads of the phospholipids, while the light band corresponds to the hydrophobic fatty acid tails of the phospholipids. **Figure 7.9** The DNA in a chromosome dictates synthesis of a messenger RNA (mRNA) molecule, which then moves out to the cytoplasm. There, the information is used for the production, on ribosomes, of proteins that carry out cellular functions. **Figure 7.10** Any of the bound ribosomes (attached to the endoplasmic reticulum) could be circled, because any could be making a protein that will be secreted. **Figure 7.22** Each centriole has 9 sets of 3 microtubules, so the entire centrosome (two centrioles) has 54 microtubules. Each microtubule consists of a helical array of tubulin dimers (as shown in Table 7.1).

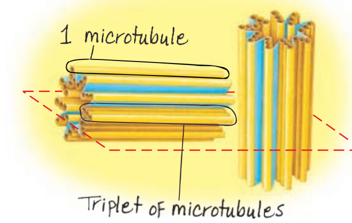


Figure 7.24 The two central microtubules terminate above the basal body, so they aren't present at the level of the cross section through the basal body, indicated by the lower red rectangle shown in the EM on the left.

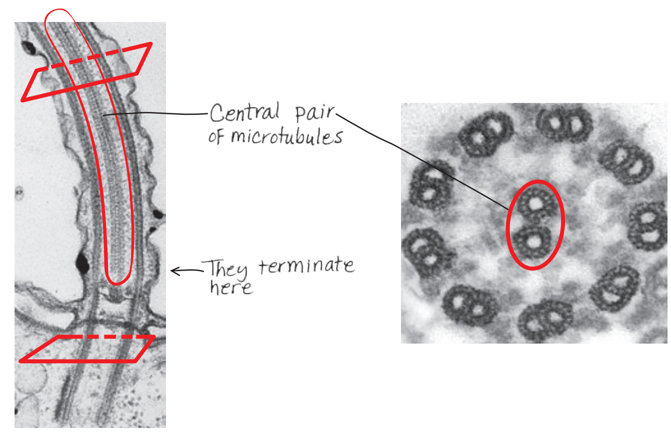


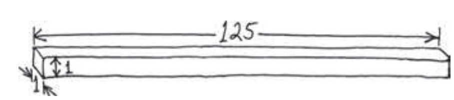
Figure 7.32 (1) nuclear pore, ribosome, proton pump, Cyt *c*. (2) As shown in the figure, the enzyme RNA polymerase moves along the DNA, transcribing the genetic information into an mRNA molecule. Given that RNA polymerase is somewhat larger than a nucleosome, the enzyme would not be able to fit between the histone proteins of the nucleosome and the DNA itself. Thus, the group of histone proteins must be separated from or moved along the DNA somehow in order for the RNA polymerase enzyme to access the DNA. (3) A mitochondrion.

Concept Check 7.1

1. Stains used for light microscopy are colored molecules that bind to cell components, affecting the light passing through, while stains used for electron microscopy involve heavy metals that affect the beams of electrons.
2. (a) Transmission electron microscope, (b) confocal microscope

Concept Check 7.2

1. See Figure 7.8.
2.



This cell would have the same volume as the cells in columns 2 and 3 in Figure 7.7 but proportionally more surface area than that in column 2 and less than that in column 3. Thus, the surface-to-volume ratio should be greater than 1.2 but less than 6. To obtain the surface area, you would add the area of the six sides (the top, bottom, sides, and ends): 125 + 125 + 125 + 125 + 1 + 1 = 502. The surface-to-volume ratio equals 502 divided by a volume of 125, or 4.0.

Concept Check 7.3

1. Ribosomes in the cytoplasm translate the genetic message, carried from the DNA in the nucleus by mRNA, into a polypeptide chain. **2.** Nucleoli consist of DNA and the ribosomal RNAs (rRNAs) made according to its instructions, as well as proteins imported from the cytoplasm. Together, the rRNAs and proteins are assembled into large and small ribosomal subunits. (These are exported through nuclear pores to the cytoplasm, where they will participate in polypeptide synthesis.) **3.** Each chromosome consists of one long DNA molecule attached to numerous protein molecules, a combination called chromatin. As a cell begins division, each chromosome becomes "condensed" as its diffuse mass of chromatin coils up.

Concept Check 7.4

1. The primary distinction between rough and smooth ER is the presence of bound ribosomes on the rough ER. Both types of ER make phospholipids, but membrane proteins and secretory proteins are all produced by the ribosomes on the rough ER. The smooth ER also functions in detoxification, carbohydrate metabolism, and storage of calcium ions. **2.** No. Lysosomal enzymes require an acidic pH to function effectively, but the cytosol has an almost neutral pH. However, excessive leakage can destroy a cell. **3.** The mRNA is synthesized in the nucleus and then passes out through a nuclear pore to the cytoplasm, where it is translated on a bound ribosome, attached to the rough ER. The protein is synthesized into the lumen of the ER and perhaps modified there. A transport vesicle carries the protein to the Golgi apparatus. After further modification in the Golgi, another transport vesicle carries it back to the ER, where it will perform its cellular function.

Concept Check 7.5

1. Both organelles are involved in energy transformation, mitochondria in cellular respiration and chloroplasts in photosynthesis. They both have multiple membranes that separate their interiors into compartments. In both organelles, the innermost membranes—cristae, or infoldings of the inner membrane, in mitochondria and the thylakoid membranes in chloroplasts—have large surface areas with embedded enzymes that carry out their main functions. **2.** Yes. Plant cells are able to make their own sugar by photosynthesis, but mitochondria in these eukaryotic cells are the organelles that are able to generate ATP molecules to be used for energy generation from sugars, a function required in all cells. **3.** Mitochondria and chloroplasts are not derived from the ER, nor are they connected physically or via transport vesicles to organelles of the endomembrane system. Mitochondria and chloroplasts are structurally quite different from vesicles derived from the ER, which are bounded by a single membrane.

Concept Check 7.6

1. Dynein arms, powered by ATP, move neighboring doublets of microtubules relative to each other. Because they are anchored within the flagellum or cilium and with respect to one another, the doublets bend instead of sliding past each other. Synchronized bending of the nine microtubule doublets brings about bending of both cilia and flagella. **2.** Such individuals have defects in the microtubule-based movement of cilia and flagella. Thus, the sperm can't move because of malfunctioning or nonexistent flagella, and the airways are compromised because cilia that line the trachea malfunction or don't exist, and so mucus cannot be cleared from the lungs.

Concept Check 7.7

1. The most obvious difference is the presence of direct cytoplasmic connections between cells of plants (plasmodesmata) and animals (gap junctions). These connections result in the cytoplasm being continuous between adjacent cells. **2.** Cell walls have small openings called plasmodesmata through which internal chemical environments of adjacent cells remain connected. Water, solutes, certain proteins, and RNA molecules can pass freely from one cell to another through these openings. Thus, plasmodesmata unify most of the plant into one living continuum. **3.** The parts of the protein that face aqueous regions would be expected to have polar or charged (hydrophilic) amino acids, while the parts that go through the membrane would be expected to have nonpolar (hydrophobic) amino acids. You would predict polar or charged amino acids at each end (tail), in the region of the cytoplasmic loop, and in the regions of the two extracellular loops. You would predict nonpolar amino acids in the four regions that go through the membrane between the tails and loops.

Concept Check 7.8

1. *Colpidium colpoda* moves around in freshwater using cilia, projections from the plasma membrane that enclose microtubules in a "9 + 2" arrangement. The interactions between motor proteins and microtubules cause the cilia to bend synchronously, propelling the cell through the water. This is powered by ATP, obtained via breaking down sugars from food in a process that occurs in mitochondria. *C. colpoda* obtains bacteria as their food source, maybe via the same process (involving filopodia) the macrophage uses in Figure 7.31. This process uses actin filaments and other elements of the cytoskeleton to ingest the bacteria. Once ingested, the bacteria are broken down by enzymes in lysosomes. The proteins involved in all of these processes are encoded by genes on DNA in the nucleus of the *C. colpoda*.

Summary of Key Concepts Questions

7.1 Both light and electron microscopy allow cells to be studied visually, thus helping us understand internal cellular structure and the arrangement of cell components. Cell fractionation techniques separate out different groups of cell components, which can then be analyzed biochemically to determine their function. Performing microscopy on the same cell fraction helps to correlate the biochemical function of the cell with the cell component responsible.
7.2 The separation of different functions in different organelles has several advantages. Reactants and enzymes can be concentrated in one area instead of spread throughout the cell. Reactions that require specific conditions, such as a lower pH, can be compartmentalized. And enzymes for specific reactions are often embedded in the membranes that enclose or partition an organelle.
7.3 The nucleus contains the genetic material of the cell in the form of DNA, which codes for messenger RNA, which in turn provides instructions for the synthesis of proteins (including the proteins that make up part of the ribosomes). DNA also codes for ribosomal RNAs, which are combined with proteins in the nucleolus into the subunits of ribosomes. Within the cytoplasm, ribosomes join with mRNA to build polypeptides, using the genetic information in the mRNA. **7.4** Transport vesicles move proteins and membranes synthesized by the rough ER to the Golgi for further processing and then to the plasma membrane, lysosomes, or other locations in the cell, including back to the ER.
7.5 According to the endosymbiont theory, mitochondria originated from an oxygen-using prokaryotic cell that was engulfed by an ancestral eukaryotic cell. Over time, the host and endosymbiont evolved into a single unicellular organism. Chloroplasts originated when at least one of these eukaryotic cells containing mitochondria engulfed and then retained a photosynthetic prokaryote.
7.6 Inside the cell, motor proteins interact with components of the cytoskeleton to move cellular parts. Motor proteins "walk" vesicles along microtubules. The movement of cytoplasm within a cell involves interactions of the motor protein myosin and microfilaments (actin filaments). Whole cells can be moved by the rapid bending of flagella or cilia, which is caused by the motor-protein-powered sliding of microtubules within these structures. Cell movement can also occur when pseudopodia form at one end of a cell (caused by actin polymerization into a filamentous network), followed by contraction of the cell toward that end; this amoeboid movement is powered by interactions of microfilaments with myosin. Interactions of motor proteins and microfilaments in muscle cells can cause muscle contraction that can propel whole organisms (for example, by walking or swimming). **7.7** A plant cell wall is primarily composed of microfibrils of cellulose embedded in other polysaccharides and proteins. The ECM of animal cells is primarily composed of collagen and other protein fibers, such as fibronectin and other glycoproteins. These fibers are embedded in a network of carbohydrate-rich proteoglycans. A plant cell wall provides structural support for the cell and, collectively, for the plant body. In addition to giving support, the ECM of an animal cell allows for communication of environmental changes into the cell. **7.8** The nucleus houses the chromosomes; each is made up of proteins and a single DNA molecule. The genes that exist along the DNA carry the genetic information necessary to make the proteins involved in ingesting a bacterial cell, such as the actin of microfilaments that form pseudopodia (filopodia), the proteins in the mitochondria responsible for providing the necessary ATP, and the enzymes present in the lysosomes that will digest the bacterial cell.

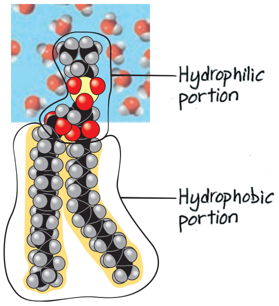
Test Your Understanding

6. See Figure 7.8.

Chapter 8

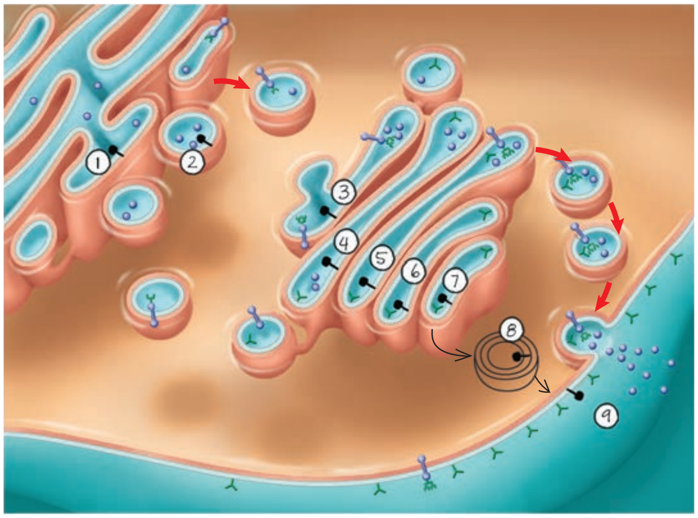
Figure Questions

Figure 8.2



The hydrophilic portion is in contact with an aqueous environment (cytosol or extracellular fluid), and the hydrophobic portion is in contact with the hydrophobic portions of other phospholipids in the interior of the bilayer. **Figure 8.4** You couldn't rule out movement of proteins within membranes of the same species. You might propose that the membrane lipids and proteins from one species weren't able to mingle with those from the other species because of some incompatibility. **Figure 8.7** A transmembrane protein like the dimer in (f) might change its shape upon binding to a particular extracellular matrix (ECM) molecule. The new shape might enable the interior portion of the protein to bind to a second, cytoplasmic protein that would relay the message to the inside of the cell, as shown in (c). **Figure 8.8** The shape of a protein on the HIV surface is likely to be complementary to the shape of the receptor (CD4) and also to that of the co-receptor (CCR5). A molecule with a shape similar to that of the HIV surface protein could bind CCR5, blocking HIV binding. (Another answer would be a molecule that bound to CCR5 and changed the shape of CCR5 so it could no longer bind HIV; in fact, this is how maraviroc works.)

Figure 8.9



The protein would contact the extracellular fluid. (Because one end of the protein is in the ER membrane, no part of the protein extends into the cytoplasm.) The part of the protein not in the membrane extends into the ER lumen. Once the vesicle fuses with the plasma membrane, the "inside" of the ER membrane, facing the lumen, will become the "outside" of the plasma membrane, facing the extracellular fluid. **Figure 8.11** The orange dye would be evenly distributed throughout the solution on both sides of the membrane. The solution levels would not be affected because the orange dye can diffuse through the membrane and equalize its concentration. Thus, no additional osmosis would take place in either direction.
Figure 8.16 The diamond solutes are moving into the cell (down), and the round solutes are moving out of the cell (up); each is moving against its concentration gradient. **Figure 8.19** (a) In the micrograph of the algal cell, the diameter of the algal cell is about 2.3 times longer than the scale bar, which represents 5 µm, so the diameter of the algal cell is about 11.5 µm. (b) In the micrograph of the coated vesicle, the diameter of the coated vesicle is about 1.2 times longer than the scale bar, which represents 0.25 µm, so the diameter of the coated vesicle is about 0.3 µm. (c) Therefore, the food vacuole around the algal cell will be about 40× larger than the coated vesicle.

Concept Check 8.1

1. They are on the inside of the transport vesicle membrane. **2.** The grasses living in the cooler region would be expected to have more unsaturated fatty acids in their membranes because those fatty acids remain fluid at lower temperatures. The grasses living immediately adjacent to the hot springs would be expected to have more saturated fatty acids, which would allow the fatty acids to "stack" more closely, making the membranes less fluid and therefore helping them to stay intact at higher temperatures. (In plants, cholesterol is generally not used to moderate the effects of temperature on membrane fluidity because it is found at vastly lower levels in membranes of plant cells than in those of animal cells.)

Concept Check 8.2

1. O_2 and CO_2 are both nonpolar molecules that can easily pass through the hydrophobic interior of a membrane. **2.** Water is a polar molecule, so it cannot pass very rapidly through the hydrophobic region in the middle of a phospholipid bilayer. **3.** The hydronium ion is charged, while glycerol is not. Charge is probably more significant than size as a basis for exclusion by the aquaporin channel.

Concept Check 8.3

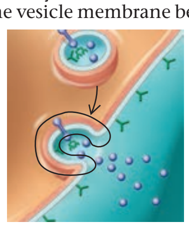
1. CO_2 is a nonpolar molecule that can diffuse through the plasma membrane. As long as it diffuses away so that the concentration remains low outside the cell, it will continue to exit the cell in this way. (This is the opposite of the case for O_2, described in this section of the text.) **2.** The activity of *Paramecium*'s contractile vacuole will decrease. The vacuole pumps out excess water that accumulates in the cell; this accumulation occurs only in a hypotonic environment.

Concept Check 8.4

1. These pumps use ATP. To establish a voltage, ions have to be pumped against their gradients, which requires energy. **2.** Each ion is being transported against its electrochemical gradient. If either ion were transported down its electrochemical gradient, this *would* be considered cotransport. **3.** The internal environment of a lysosome is acidic, so it has a higher concentration of H^+ than does the cytoplasm. Therefore, you might expect the membrane of the lysosome to have a proton pump such as that shown in Figure 8.17 to pump H^+ into the lysosome.

Concept Check 8.5

1. Exocytosis. When a transport vesicle fuses with the plasma membrane, the vesicle membrane becomes part of the plasma membrane.
2.



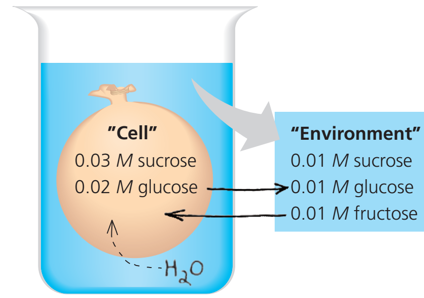
3. The glycoprotein would be synthesized in the ER lumen, move through the Golgi apparatus, and then travel in a vesicle to the plasma membrane, where it would undergo exocytosis and become part of the ECM.

Summary of Key Concepts Questions

8.1 Plasma membranes define the cell by separating the cellular components from the external environment. This allows conditions inside cells to be controlled by membrane proteins, which regulate entry and exit of molecules and even cell function (see Figure 8.7). The processes of life can be carried out inside the controlled environment of the cell, so membranes are crucial. In eukaryotes, membranes also function to subdivide the cytoplasm into different compartments where distinct processes can occur, even under differing conditions such as low or high pH. **8.2** Aquaporins are channel proteins that greatly increase the permeability of a membrane to water molecules, which are polar and therefore do not readily diffuse through the hydrophobic interior of the membrane. **8.3** There will be a net diffusion of water out of a cell into a hypertonic solution. The free water concentration is higher inside the cell than in the solution (where not as many water molecules are free, because many are clustered around the higher concentration of solute particles). **8.4** One of the solutes moved by the cotransporter is actively transported against its concentration gradient. The energy for this transport comes from the concentration gradient of the other solute, which was established by an electrogenic pump that used energy to transport the other solute across the membrane. Because energy is required overall to drive this process (because ATP is used to establish the concentration gradient), it is considered active transport. **8.5** In receptor-mediated endocytosis, specific molecules bind to receptors on the plasma membrane in a region where a coated pit develops. The cell can acquire bulk quantities of those specific molecules when the coated pit forms a vesicle and carries the bound molecules into the cell.

Test Your Understanding

6. (a)



(b) The solution outside is hypotonic. It has less sucrose, which is a nonpenetrating solute. (c) See answer for (a). (d) The artificial cell will become more turgid. (e) Eventually, the two solutions will have the same solute concentrations. Even though sucrose can't move through the membrane, water flow (osmosis) will lead to isotonic conditions.

Chapter 9

Figure Questions

Figure 9.6 Epinephrine is a signaling molecule; presumably, it binds to a cell-surface receptor protein. **Figure 9.8** This is an example of passive transport. The ion is moving down its concentration gradient, and no energy is required. **Figure 9.9** The aldosterone molecule, a steroid, is hydrophobic and can therefore pass directly through the hydrophobic lipid bilayer of the plasma membrane into the cell. (Hydrophilic molecules cannot do this.)
Figure 9.10 The entire phosphorylation cascade wouldn't operate. Regardless of whether or not the signaling molecule was bound, protein kinase 2 would always be inactive and would not be able to activate the purple-colored protein leading to the cellular response. **Figure 9.11** The signaling molecule (cAMP) would remain in its active form and would continue to signal.
Figure 9.12

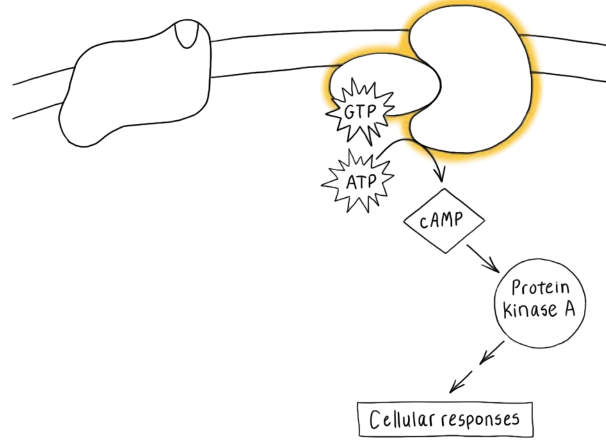


Figure 9.16 100,000,000 (one hundred million, or 10^8) glucose molecules are released. The first step results in 100× amplification (one epinephrine activates 100 G proteins); the next step does not amplify the response; the next step is a 100× amplification (10^2 active adenylyl cyclase molecules to 10^4 cyclic AMPs); the next step does not amplify; the next two steps are each 10× amplifications, and the final step is a 100× amplification. **Figure 9.17** The signaling pathway shown in **Figure 9.14** leads to the splitting of PIP_2 into the second messengers DAG and IP_3, which produce different responses. (The response elicited by DAG is mentioned but not shown.) The pathway shown for cell B is similar in that it branches and leads to two responses.

Concept Check 9.1

1. The two cells of opposite mating type (**a** and **α**) each secrete a certain signaling molecule, which can only be bound by receptors carried on cells of the opposite mating type. Thus, the **a** mating factor cannot bind to another **a** cell and cause it to grow toward the first **a** cell. Only an **α** cell can "receive" the signaling molecule and respond by directed growth. **2.** Distantly placed cells in a multicellular organism communicate by endocrine signaling. **3.** Glucose 1-phosphate would not be generated because the activation of the enzyme requires an intact cell, with an intact receptor in the membrane and an intact signal transduction pathway. The enzyme cannot be activated directly by interaction with the signaling molecule in the cell-free mixture.

Concept Check 9.2

1. NGF is water-soluble (hydrophilic), so it cannot pass through the lipid membrane to reach intracellular receptors, as steroid hormones can. Therefore, you'd expect the NGF receptor to be in the plasma membrane—which is, in fact, the case.

2. The cell with the faulty receptor would not be able to respond appropriately to the signaling molecule when it was present. This would most likely have dire consequences for the cell, since regulation of the cell's activities by this receptor would not occur appropriately. **3.** Binding of a ligand to a receptor changes the shape of the receptor, altering the ability of the receptor to transmit a signal. Binding of an allosteric regulator to an enzyme changes the shape of the enzyme, either promoting or inhibiting enzyme activity.

Concept Check 9.3

1. A protein kinase is an enzyme that transfers a phosphate group from ATP to a protein, usually activating that protein (often a second type of protein kinase). Many signal transduction pathways include a series of such interactions, in which each phosphorylated protein kinase in turn phosphorylates the next protein kinase in the series. Such phosphorylation cascades carry a signal from outside the cell to the cellular protein(s) that will carry out the response. **2.** Protein phosphatases reverse the effects of the kinases, and unless the signaling molecule is at a high enough concentration that it is continuously rebinding the receptor, the kinase molecules will all be returned to their inactive states by phosphatases. **3.** The signal that is being transduced is the *information* that a signaling molecule is bound to the cell-surface receptor. Information is transduced by way of sequential protein-protein interactions that change protein shapes, causing them to function in a way that passes the signal (the information) along. **4.** The IP_3-gated channel would open, allowing calcium ions to flow out of the ER and into the cytoplasm, which would raise the cytosolic Ca^{2+} concentration.

Concept Check 9.4

1. At each step in a cascade of sequential activations, one molecule or ion may activate numerous molecules functioning in the next step. This causes the response to be amplified at each such step and overall results in a large amplification of the original signal. **2.** Scaffolding proteins hold molecular components of signaling pathways in a complex with each other. Different scaffolding proteins would assemble different collections of proteins, facilitating different molecular interactions and leading to different cellular responses in the two cells. **3.** A malfunctioning protein phosphatase would not be able to dephosphorylate a particular receptor or relay protein. As a result, the signaling pathway, once activated, would not be able to be terminated. (In fact, one study found altered protein phosphatases in cells from 25% of colorectal tumors.)

Concept Check 9.5

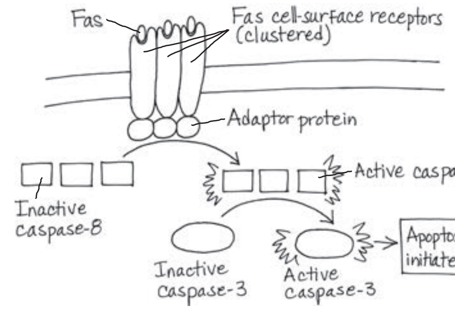
1. In formation of the hand or paw in mammals, cells in the regions between the digits are programmed to undergo apoptosis. This serves to shape the digits of the hand or paw so that they are not webbed. (A lack of apoptosis in these regions in water birds results in webbed feet.) **2.** If a receptor protein for a death-signaling molecule were defective such that it was activated even in the absence of the death signal, this would lead to apoptosis when it wouldn't normally occur. Similar defects in any of the proteins in the signaling pathway would have the same effect if the defective proteins activated relay or response proteins in the absence of interaction with the previous protein or second messenger in the pathway. Conversely, if any protein in the pathway were defective in its ability to respond to an interaction with an early protein or other molecule or ion, apoptosis would not occur when it normally should. For example, a receptor protein for a death-signaling ligand might not be able to be activated, even when ligand was bound. This would stop the signal from being transduced into the cell.

Summary of Key Concepts Questions

9.1 A cell is able to respond to a hormone only if it has a receptor protein on the cell surface or inside the cell that can bind to the hormone. The response to a hormone depends on the specific signal transduction pathway within the cell, which will lead to the specific cellular response. The response can vary for different types of cells. **9.2** Both GPCRs and RTKs have an extracellular binding site for a signaling molecule (ligand) and one or more α-helical regions of the polypeptide that spans the membrane. A GPCR functions singly, while RTKs tend to dimerize or form larger groups of RTKs. GPCRs usually trigger a single transduction pathway, whereas the multiple activated tyrosines on an RTK dimer may trigger several different transduction pathways at the same time. **9.3** A protein kinase is an enzyme that adds a phosphate group to another protein. Protein kinases are often part of a phosphorylation cascade that transduces a signal. A second messenger is a small, nonprotein molecule or ion that rapidly diffuses and relays a signal throughout a cell. Both protein kinases and second messengers can operate in the same pathway. For example, the second messenger cAMP often activates protein kinase A, which then phosphorylates other proteins. **9.4** In G protein-coupled pathways, the GTPase portion of a G protein converts GTP to GDP and inactivates the G protein. Protein phosphatases remove phosphate groups from activated proteins, thus stopping a phosphorylation cascade of protein kinases. Phosphodiesterase converts cAMP to AMP, thus reducing the effect of cAMP in a signal transduction pathway. **9.5** The basic mechanism of controlled cell suicide evolved early in eukaryotic evolution, and the genetic basis for these pathways has been conserved during animal evolution. Such a mechanism is essential to the development and maintenance of all animals.

Test Your Understanding

8. This is one possible drawing of the pathway. (Similar drawings would also be correct.)



Chapter 10

Figure Questions

Figure 10.4 The reduced form has an extra hydrogen, along with 2 electrons, bound to the carbon shown at the top of the nicotinamide (opposite the N). There are different numbers and positions of double bonds in the two forms: The oxidized form has three double bonds in the ring, while the reduced form has only two. (In organic chemistry you may have learned, or will learn, that three double bonds in a ring are able to "resonate," or act as a ring of electrons. Having three resonant double bonds is more "oxidized" than having only two double bonds in the ring.) In the oxidized form there is a + charge on the N (because it is sharing 4 electron pairs), whereas in the reduced form it is only sharing 3 electron pairs (having a pair of electrons to itself). **Figure 10.7** Because there is no external source of energy for the reaction, it must be exergonic, and the reactants must be at a higher energy level than the products. **Figure 10.9** The removal would probably stop glycolysis, or at least slow it down, since it would push the equilibrium for step 5 toward the bottom (toward DHAP). If less (or no) glyceraldehyde 3-phosphate were available, step 6 would slow down (or be unable to occur). **Figure 10.15** At first, some ATP could be made, since electron transport could proceed as far as complex III, and a small H^+ gradient could be built up. Soon, however, no more electrons could be passed to complex III because it could not be reoxidized by passing its electrons to complex IV. **Figure 10.16** First, there are 2 NADH from the oxidation of pyruvate plus 6 NADH from the citric acid cycle (CAC); 8 NADH $\times$ 2.5 ATP/NADH $=$ 20 ATP. Second, there are 2 $FADH_2$ from the CAC; 2 $FADH_2 \times$ 1.5 ATP/$FADH_2$ $=$ 3 ATP. Third, the 2 NADH from glycolysis enter the mitochondrion through one of two types of shuttle. They pass their electrons either to 2 FAD, which become $FADH_2$ and result in 3 ATP, or to 2 NAD^+, which become NADH and result in 5 ATP. Thus, $20 + 3 + 3 = 26$ ATP, or $20 + 3 + 5 = 28$ ATP from all NADH and $FADH_2$.

Concept Check 10.1

1. Both processes include glycolysis, the citric acid cycle, and oxidative phosphorylation. In aerobic respiration, the final electron acceptor is molecular oxygen (O_2); in anaerobic respiration, the final electron acceptor is a different substance. **2.** $C_4H_6O_4$ would be oxidized and FAD would be reduced.

Concept Check 10.2

1. NAD^+ acts as the oxidizing agent in step 6, accepting electrons from glyceraldehyde 3-phosphate (G3P), which thus acts as the reducing agent.

Concept Check 10.3

1. NADH and $FADH_2$; they will donate electrons to the electron transport chain. **2.** CO_2 is released from the pyruvate that is the end product of glycolysis, and CO_2 is also released during the citric acid cycle. **3.** In both cases, the precursor molecule loses a CO_2 molecule and then donates electrons to an electron carrier in an oxidation step. Also, the product has been activated due to the attachment of a CoA group.

Concept Check 10.4

1. Oxidative phosphorylation would eventually stop entirely, resulting in no ATP production by this process. Without oxygen to "pull" electrons down the electron transport chain, H^+ would not be pumped into the mitochondrion's intermembrane space and chemiosmosis would not occur. **2.** Decreasing the pH means addition of H^+. This would establish a proton gradient even without the function of the electron transport chain, and we would expect ATP synthase to function and synthesize ATP. (In fact, it was experiments like this that provided support for chemiosmosis as an energy-coupling mechanism.) **3.** One of the components of the electron transport chain, ubiquinone (Q), must be able to diffuse within the membrane. It could not do so if the membrane components were locked rigidly into place.

Concept Check 10.5

1. Ethanol is the end product of alcohol fermentation, and lactate is the end product of lactic acid fermentation. Two molecules of ATP are generated in each of these processes. **2.** The cell would need to consume glucose at a rate about 16 times the consumption rate in the aerobic environment (2 ATP are generated by fermentation versus up to 32 ATP by cellular respiration).

Concept Check 10.6

1. The fat is much more reduced; it has many —CH_2— units, and in all these bonds the electrons are equally shared. The electrons present in a carbohydrate molecule are already somewhat oxidized (shared unequally in bonds; there are more C—O and O—H bonds), as quite a few of them are bound to oxygen. Electrons that are equally shared, as in fat, have a higher energy level than electrons that are unequally shared, as in carbohydrates. Thus, fat is a much better fuel than carbohydrate.

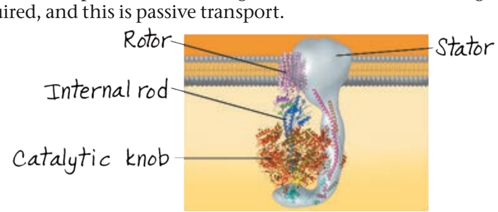
2. When we consume more food than necessary for metabolic processes, our body synthesizes fat as a way of storing energy for later use. **3.** AMP will accumulate, stimulating phosphofructokinase, and thus increasing the rate of glycolysis. Since oxygen is not present, the cell will convert pyruvate to lactate in lactic acid fermentation, providing a supply of ATP. **4.** When oxygen is present, the fatty acid chains containing most of the energy of a fat are oxidized and fed into the citric acid cycle and the electron transport chain. During intense exercise, however, oxygen is scarce in muscle cells, so ATP must be generated by glycolysis alone. A very small part of the fat molecule, the glycerol backbone, can be oxidized via glycolysis, but the amount of energy released by this portion is insignificant compared to that released by the fatty acid chains. (This is why moderate exercise, staying below 70% maximum heart rate, is better for burning fat—because enough oxygen remains available to the muscles.)

Summary of Key Concepts Questions

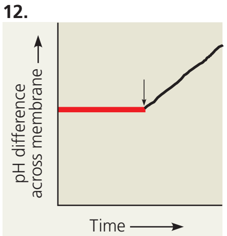
10.1 Most of the ATP produced in cellular respiration comes from oxidative phosphorylation, in which the energy released from redox reactions in an electron transport chain is used to produce ATP. In substrate-level phosphorylation, an enzyme directly transfers a phosphate group to ADP from an intermediate substrate. All ATP production in glycolysis occurs by substrate-level phosphorylation; this form of ATP production also occurs at one step in the citric acid cycle.
10.2 The oxidation of the three-carbon sugar, glyceraldehyde 3-phosphate, yields energy. In this oxidation, electrons and H^+ are transferred to NAD^+, forming NADH, and a phosphate group is attached to the oxidized substrate. ATP is then formed by substrate-level phosphorylation when this phosphate group is transferred to ADP. **10.3** The release of six molecules of CO_2 represents the complete oxidation of glucose. During the processing of two pyruvates to acetyl CoA, the fully oxidized carboxyl groups ($—COO^-$) are given off as 2 CO_2. The remaining four carbons are released as CO_2 in the citric acid cycle as citrate is oxidized back to oxaloacetate. **10.4** The flow of H^+ through the ATP synthase complex causes the rotor and attached rod to rotate, exposing catalytic sites in the knob portion that produce ATP from ADP and Ⓟ$_i$. ATP synthases are found in the inner mitochondrial membrane, the plasma membrane of prokaryotes, and membranes within chloroplasts. **10.5** Anaerobic respiration yields more ATP. The 2 ATP produced by substrate-level phosphorylation in glycolysis represent the total energy yield of fermentation. NADH passes its "high-energy" electrons to pyruvate or a derivative of pyruvate, recycling NAD^+ and allowing glycolysis to continue. In anaerobic respiration, the NADH produced during glycolysis, as well as additional molecules of NADH produced as pyruvate is oxidized, are used to generate ATP molecules. An electron transport chain captures the energy of the electrons in NADH via a series of redox reactions; ultimately, the electrons are transferred to an electronegative molecule other than oxygen. **10.6** The ATP produced by catabolic pathways is used to drive anabolic pathways. Also, many of the intermediates of glycolysis and the citric acid cycle are used in the biosynthesis of a cell's molecules.

Test Your Understanding

8. Since the overall process of glycolysis results in net production of ATP, it would make sense for the process to slow down when ATP levels have increased substantially. Thus, we would expect ATP to allosterically inhibit phosphofructokinase.
9. The proton pump in Figures 8.17 and 8.18 is carrying out active transport, using ATP hydrolysis to pump protons against their concentration gradient. Because ATP is required, this is active transport of protons. The ATP synthase in Figure 10.14 is using the flow of protons down their concentration gradient to power ATP synthesis. Because the protons are moving down their concentration gradient, no energy is required, and this is passive transport.
10.



12.



H^+ would continue to be pumped across the membrane into the intermembrane space, increasing the difference between the matrix pH and the intermembrane space pH. H^+ would not be able to flow back through ATP synthase, since the enzyme is inhibited by the poison, so rather than maintaining a constant difference across the membrane, the difference would continue to increase. (Ultimately, the H^+ concentration in the intermembrane space would be so high that no more H^+ would be able to be pumped against the gradient, but this isn't shown in the graph.)

Chapter 11

Figure Questions

Figure 11.3 Situating containers of algae near sources of CO_2 emissions makes sense because the algae need CO_2 to carry out photosynthesis. The higher their rate of photosynthesis, the more plant oil they will produce. At the same time, algae would be absorbing the CO_2 emitted from industrial plants or from car engines, reducing the amount of CO_2 entering the atmosphere—thus, lowering the contributions such CO_2 would make to global climate change. **Figure 11.12** In the leaf, most of the chlorophyll electrons excited by photon absorption are used to power the reactions of photosynthesis. **Figure 11.16** The person at the top of the photosystem I tower would not turn to his left and throw his electron into the NADPH bucket. Instead, he would throw it onto the top of the ramp at his right, next to the photosystem II tower. The electron would then roll down the ramp, get energized by a photon, and return to him. This cycle would continue as long as light was available. (This is why it's called cyclic electron flow.) **Figure 11.17** You would (a) decrease the pH outside the mitochondrion (thus increasing the H^+ concentration) and (b) increase the pH in the chloroplast stroma (thus decreasing the H^+ concentration). In both cases, this would generate an H^+ gradient across the membrane that would cause ATP synthase to synthesize ATP. **Figure 11.23** The gene encoding hexokinase is part of the DNA of a chromosome in the nucleus. There, the gene is transcribed into mRNA, which is transported to the cytoplasm where it is translated on a free ribosome into a polypeptide. The polypeptide folds into a functional protein with secondary and tertiary structure. Once functional, it carries out the first reaction of glycolysis in the cytoplasm.

Concept Check 11.1

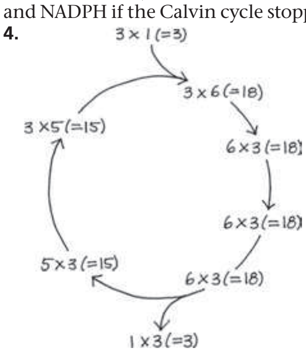
1. CO_2 enters the leaves via stomata, and being a nonpolar molecule, can cross the leaf cell membrane and the chloroplast membranes to reach the stroma of the chloroplast. **2.** Using ^{18}O, a heavy isotope of oxygen, as a label, researchers were able to confirm van Niel's hypothesis that the oxygen produced during photosynthesis comes from water, not from carbon dioxide. **3.** The light reactions could *not* keep producing NADPH and ATP without the $NADP^+$, ADP, and Ⓟ$_i$ that the Calvin cycle generates. The two cycles are interdependent.

Concept Check 11.2

1. Green, because green light is mostly transmitted and reflected—not absorbed—by photosynthetic pigments **2.** Water (H_2O) is the initial electron donor; $NADP^+$ accepts electrons at the end of the electron transport chain, becoming reduced to NADPH. **3.** In this experiment, the rate of ATP synthesis would slow and eventually stop. Because the added compound would not allow a proton gradient to build up across the membrane, ATP synthase could not catalyze ATP production.

Concept Check 11.3

1. 6, 18, 12 **2.** The more potential energy and reducing power a molecule stores, the more energy and reducing power are required for the formation of that molecule. Glucose is a valuable energy source because it is highly reduced (lots of C—H bonds), storing lots of potential energy in its electrons. To reduce CO_2 to glucose, much energy and reducing power are required in the form of large numbers of ATP and NADPH molecules, respectively. **3.** The light reactions require ADP and $NADP^+$, which would not be formed in sufficient quantities from ATP and NADPH if the Calvin cycle stopped.
4.



Three carbon atoms enter the cycle, one by one, as individual CO_2 molecules, and leave the cycle in one three-carbon molecule (G3P) per three turns of the cycle. **5.** In glycolysis, G3P acts as an intermediate. The 6-carbon sugar fructose 1,6-bisphosphate is cleaved into two 3-carbon sugars, one of which is G3P. The other is an isomer called dihydroxyacetone phosphate (DHAP), which can be converted to G3P by an isomerase. Because G3P is the substrate for the next enzyme, it is constantly removed, and the reaction equilibrium is pulled in the direction of conversion of DHAP to more G3P. In the Calvin cycle, G3P acts as both an intermediate and a product. For every three CO_2 molecules that enter the cycle, six G3P molecules are formed, five of which must remain in the cycle and become rearranged to regenerate three 5-carbon RuBP molecules. The one remaining G3P is a product, which can be thought of as the result of "reducing" the three CO_2 molecules that entered the cycle into a 3-carbon sugar that can later be used to generate energy.

Concept Check 11.4

1. Photorespiration decreases photosynthetic output by adding oxygen, instead of carbon dioxide, to the Calvin cycle. As a result, no sugar is generated (no carbon is fixed), and O_2 is used rather than generated. **2.** Without PS II, no O_2 is generated in bundle-sheath cells. This avoids the problem of O_2 competing with CO_2 for binding to rubisco in these cells. **3.** Both problems are caused by a drastic change in Earth's atmosphere due to burning of fossil fuels. The increase in CO_2 concentration affects ocean chemistry by decreasing pH, thus affecting calcification by marine organisms. On land, CO_2 concentration and air temperature are conditions that plants have become adapted to, and changes in these characteristics have a strong effect on photosynthesis by plants. Thus, alteration of these two fundamental factors could have critical effects on organisms all around the planet, in all different habitats.
4. The stomata of the plant would probably never open, and no carbon dioxide would be taken up.

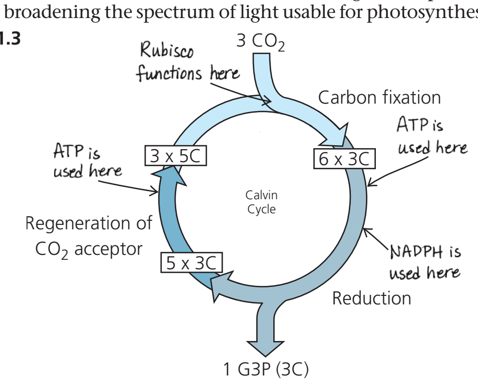
Concept Check 11.5

1. Yes, plants can break down the sugar (in the form of glucose) by cellular respiration, producing ATPs for various cellular processes such as endergonic chemical reactions, transport of substances across membranes, and movement of molecules in the cell. ATPs are also used for the movement of chloroplasts during cellular streaming in some plant cells (see Figure 7.26).

Summary of Key Concepts Questions

11.1 CO_2 and H_2O are the products of cellular respiration; they are the reactants in photosynthesis. In respiration, glucose is oxidized to CO_2 and electrons are passed through an electron transfer chain from glucose to O_2, producing H_2O. In photosynthesis, H_2O is the source of electrons, which are energized by light, temporarily stored in NADPH, and used to reduce CO_2 to carbohydrate. **11.2** The action spectrum of photosynthesis shows that some wavelengths of light that are not absorbed by chlorophyll *a* are still effective at promoting photosynthesis. The light-harvesting complexes of photosystems contain accessory pigments such as chlorophyll *b* and carotenoids, which absorb different wavelengths and pass the energy to chlorophyll *a*, broadening the spectrum of light usable for photosynthesis.

11.3

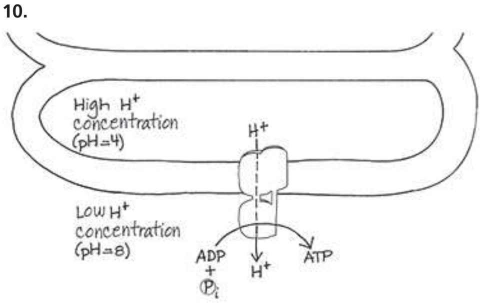


In the reduction phase of the Calvin cycle, ATP phosphorylates a three-carbon compound, and NADPH then reduces this compound to G3P. ATP is also used in the regeneration phase, when five molecules of G3P are converted to three molecules of the five-carbon compound RuBP. Rubisco catalyzes the first step of carbon fixation—the addition of CO_2 to RuBP.

11.4 Both C_4 photosynthesis and CAM photosynthesis involve initial fixation of CO_2 to produce a four-carbon compound (in mesophyll cells in C_4 plants and at night in CAM plants). These compounds are then broken down to release CO_2 (in the bundle-sheath cells in C_4 plants and during the day in CAM plants). ATP is required for recycling the molecule that is used initially to combine with CO_2. These pathways avoid the photorespiration that consumes ATP and reduces the photosynthetic output of C_3 plants when they close stomata on hot, dry, bright days. Thus, hot, arid climates would favor C_4 and CAM plants. **11.5** Photosynthetic organisms provide food (in the form of carbohydrates) to all other living organisms, either directly or indirectly. They do this by harnessing the energy of the sun to build carbohydrates, something that non-photosynthesizers cannot do. Photosynthetic organisms also produce oxygen (O_2), required by all aerobically respiring organisms.

Test Your Understanding

10.

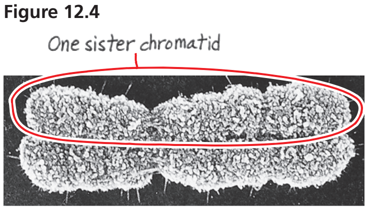


The ATP would end up outside the thylakoid. The thylakoids were able to make ATP in the dark because the researchers set up an artificial proton concentration gradient across the thylakoid membrane; thus, the light reactions were not necessary to establish the H^+ gradient required for ATP synthesis by ATP synthase.

Chapter 12

Figure Questions

Figure 12.4



Circling the other chromatid instead would also be correct. **Figure 12.5** The chromosome has four arms. The single (duplicated) chromosome in step 2 becomes two (unduplicated) chromosomes in step 3. The duplicated chromosome in step 2 is considered one single chromosome. **Figure 12.7** 12; 2; 2; 1

Figure 12.8

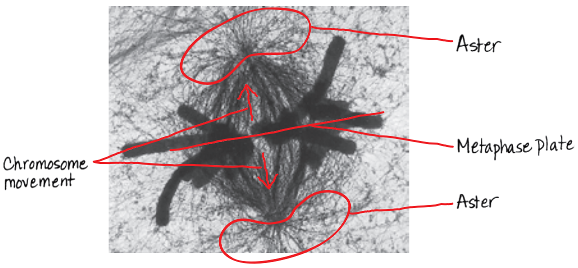


Figure 12.9 The mark would have moved toward the nearer pole. The lengths of fluorescent microtubules between that pole and the mark would have decreased, while the lengths between the chromosomes and the mark would have remained the same. **Figure 12.14** In both cases, the G_1 nucleus would have remained in G_1 until the time it normally would have entered the S phase. Chromosome condensation and spindle formation would not have occurred until the S and G_2 phases had been completed. **Figure 12.16** Passing the G_2 checkpoint in the diagram corresponds to the beginning of the "Time" axis of the graph, and entry into the mitotic phase (yellow background on the diagram) corresponds to the peaks of MPF activity and cyclin concentration on the graph (see the yellow M banner over the peaks). During G_1 and S phase in the diagram, Cdk is present without cyclin, so on the graph both cyclin concentration and MPF activity are low. The curved purple arrow in the diagram shows increasing cyclin concentration, seen on the graph during the end of S phase and throughout G_2 phase. Then the cell cycle begins again. **Figure 12.17** The cell would divide under conditions where it was inappropriate to do so. If the daughter cells and their descendants also ignored either of the checkpoints and divided, there would soon be an abnormal mass of cells. (This type of inappropriate cell division can contribute to the development of cancer.) **Figure 12.18** The cells in the vessel with PDGF would not be able to respond to the growth factor signal and thus would not divide. The culture would resemble that without the added PDGF.

Concept Check 12.1

1. 1; 1; 2 **2.** 16; 8; 8

Concept Check 12.2

1. 6 chromosomes; they are duplicated; 12 chromatids **2.** Following mitosis, cytokinesis results in two genetically identical daughter cells in both plant cells and animal cells. However, the mechanism of dividing the cytoplasm is different in animals and plants. In an animal cell, cytokinesis occurs by cleavage, which divides the parent cell in two with a contractile ring of actin filaments. In a plant cell, a cell plate forms in the middle of the cell and grows until its membrane fuses with the plasma membrane of the parent cell. A new cell wall grows inside the cell plate, thus eventually between the two new cells. **3.** During anaphase, when the cohesin proteins holding the sister chromatids together are cleaved. **4.** During eukaryotic cell division, tubulin is involved in spindle formation and chromosome movement, while actin functions during cytokinesis. In bacterial binary fission, it's the opposite: Actin-like molecules are thought to move the daughter bacterial chromosomes to opposite ends of the cell, and tubulin-like molecules are thought to act in daughter cell separation. **5.** A kinetochore connects the spindle (a motor; note that it has motor proteins) to a chromosome (the cargo it will move). **6.** Microtubules made up of tubulin in the cell provide "rails" along which vesicles and other organelles can travel, based on interactions of motor proteins with tubulin in the microtubules. In muscle cells, actin in microfilaments interacts with myosin filaments to cause muscle contraction.

Concept Check 12.3

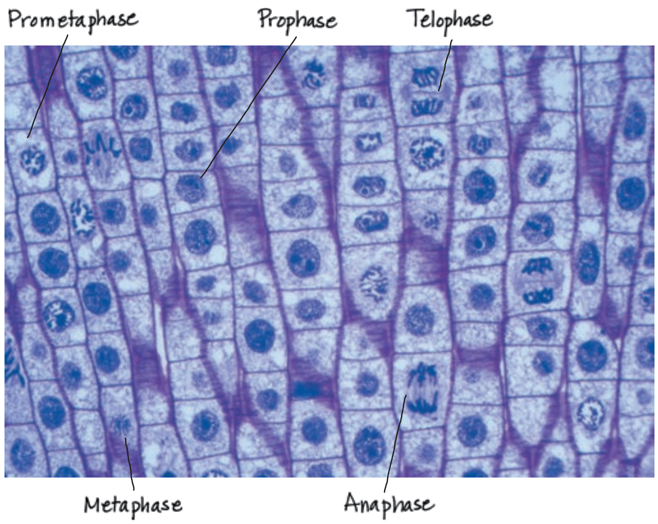
1. The nucleus on the right was originally in the G_1 phase; therefore, it had not yet duplicated its chromosomes. The nucleus on the left was in the M phase, so it had already duplicated its chromosomes. **2.** A sufficient amount of MPF has to exist for a cell to pass the G_2 checkpoint; this occurs through the accumulation of cyclin proteins, which combine with Cdk to form (active) MPF. MPF then phosphorylates other proteins, initiating mitosis. **3.** The intracellular receptor, once activated, would be able to act as a transcription factor in the nucleus, turning on genes that may cause the cell to pass a checkpoint and divide. The RTK receptor, when activated by a ligand, would form a dimer, and each subunit of the dimer would phosphorylate the other. This would lead to a series of signal transduction steps, ultimately turning on genes in the nucleus. As in the case of the estrogen receptor, the genes would code for proteins necessary to commit the cell to divide.

Summary of Key Concepts Questions

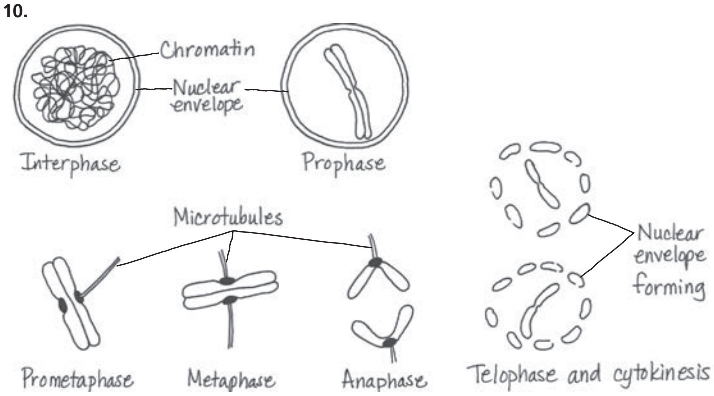
12.1 The DNA of a eukaryotic cell is packaged into structures called *chromosomes*. Each chromosome is a long molecule of DNA, which carries hundreds to thousands of genes, with associated proteins that maintain chromosome structure and help control gene activity. This DNA-protein complex is called *chromatin*. The chromatin of each chromosome is long and thin when the cell is not dividing. Prior to cell division, each chromosome is duplicated, and the resulting sister *chromatids* are attached to each other by proteins at the centromeres and, for many species, all along their lengths (a phenomenon called sister chromatid cohesion). **12.2** Chromosomes exist as single DNA molecules in G_1 of interphase and in anaphase and telophase of mitosis. During S phase, DNA replication produces sister chromatids, which persist during G_2 of interphase and through prophase, prometaphase, and metaphase of mitosis. **12.3** Checkpoints allow cellular surveillance mechanisms to determine whether the cell is prepared to go to the next stage. Internal and external signals move a cell past these checkpoints. The G_1 checkpoint determines whether a cell will proceed forward in the cell cycle or switch into the G_0 phase. The signals to pass this checkpoint often are external, such as growth factors. Passing the G_2 checkpoint requires sufficient numbers of active MPF complexes, which in turn orchestrate several mitotic events. MPF also initiates degradation of its cyclin component, terminating the M phase. The M phase will not begin again until sufficient cyclin is produced during the next S and G_2 phases. The signal to pass the M phase checkpoint is not activated until all chromosomes are attached to kinetochore fibers and are aligned at the metaphase plate. Only then will sister chromatid separation occur.

Test Your Understanding

9. See Figure 12.7 for a description of major events. Only one cell is indicated for each stage, but other correct answers are also present in this micrograph.



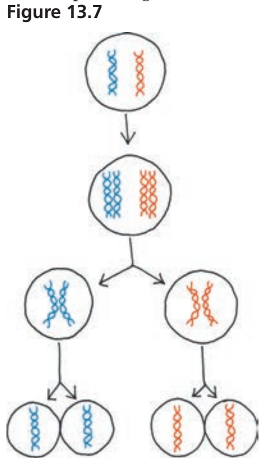
10.



Chapter 13

Figure Questions

Figure 13.4 Two sets of chromosomes are present. Three pairs of homologous chromosomes are present. **Figure 13.6** In (a), haploid cells do not undergo mitosis. In (b), haploid spores undergo mitosis to form the gametophyte, and haploid cells of the gametophyte undergo mitosis to form gametes. In (c), haploid cells undergo mitosis to form either a multicellular haploid organism or a new unicellular haploid organism, and these haploid cells undergo mitosis to form gametes. **Figure 13.7**



(A short strand of DNA is shown here for simplicity, but each chromosome or chromatid contains a very long coiled and folded DNA molecule.) **Figure 13.8** If a cell with six chromosomes undergoes two rounds of mitosis, each of the four resulting cells will have six chromosomes, while the four cells resulting from meiosis in Figure 13.8 each have three chromosomes. In mitosis, DNA replication (and thus chromosome duplication) precedes each prophase, ensuring that daughter cells have the same number of chromosomes as the parent cell. In meiosis, in contrast, DNA replication occurs only before prophase I (not prophase II). Thus, in two rounds of mitosis, the chromosomes duplicate twice and divide twice, while in meiosis, the chromosomes duplicate once and divide twice. **Figure 13.10** Yes. Each of the six chromosomes (three per cell) shown in telophase I has one nonrecombinant chromatid and one recombinant chromatid. Therefore, eight possible sets of chromosomes can be generated for the cell on the left and eight for the cell on the right.

Concept Check 13.1

1. Parents pass genes to their offspring; by dictating the production of messenger RNAs (mRNAs), the genes program cells to make specific enzymes and other proteins, whose cumulative action produces an individual's inherited traits. **2.** Such organisms reproduce by mitosis, which generates offspring whose genomes are exact copies of the parent's genome (in the absence of mutation). **3.** She should clone it. Crossbreeding it with another plant would generate offspring that have additional variation, which she no longer desires now that she has obtained her ideal orchid.

Concept Check 13.2

1. Each of the six chromosomes is duplicated, so each contains two DNA double helices. Therefore, there are 12 DNA molecules in the cell. The haploid number, *n*, is 3. One set is always haploid. **2.** There are 23 pairs of chromosomes and two sets. **3.** This organism has the life cycle shown in Figure 13.6c. Therefore, it must be a fungus or a protist, perhaps an alga.

Concept Check 13.3

1. The chromosomes are similar in that each is composed of two sister chromatids, and the individual chromosomes are positioned similarly at the metaphase plate. The chromosomes differ in that in a mitotically dividing cell, sister chromatids of each chromosome are genetically identical, but in a meiotically dividing cell, sister chromatids are genetically distinct because of crossing over in meiosis I. Moreover, the chromosomes in metaphase of mitosis can be a diploid set or a haploid set, but the chromosomes in metaphase of meiosis II always consist of a haploid set. **2.** If crossing over did not occur, the two homologs would not be associated in any way; each sister chromatid would be either all maternal or all paternal and would only be attached to its sister chromatid, not to a nonsister chromatid. This might result in incorrect arrangement of homologs during metaphase I and, ultimately, in formation of gametes with an abnormal number of chromosomes.

Concept Check 13.4

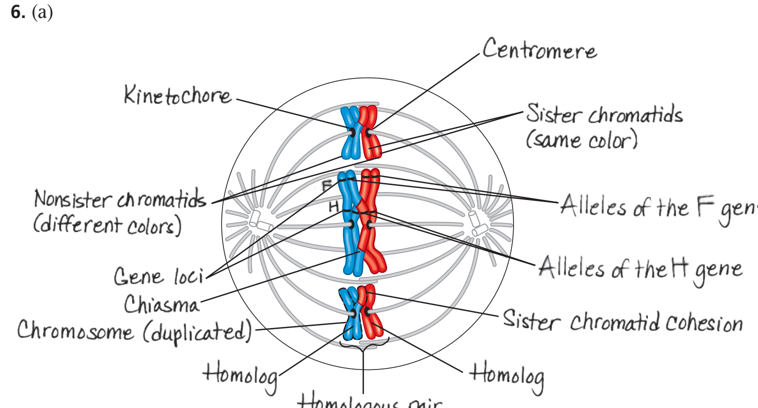
1. Mutations in a gene lead to the different versions (alleles) of that gene. **2.** Without crossing over, independent assortment of chromosomes during meiosis I theoretically can generate 2^n possible haploid gametes, and random fertilization can produce $2^n \times 2^n$ possible diploid zygotes. Because the haploid number (*n*) of grasshoppers is 23 and that of fruit flies is 4, two grasshoppers would be expected to produce a greater variety of zygotes than would two fruit flies. **3.** Chromosomes synapse at various points along their lengths for crossing over to occur. Shortening of chromosomes may decrease genetic diversity since the number of points along chromosomes where synapsis and crossing over can occur will be reduced.

Summary of Key Concepts Questions

13.1 Genes program specific traits, and offspring inherit their genes from each parent, accounting for similarities in their appearance to one or the other parent. Humans reproduce sexually, which ensures new combinations of genes (and thus traits) in the offspring. Consequently, the offspring are not clones of their parents (which would be the case if humans reproduced asexually). **13.2** Animals and plants both reproduce sexually, alternating meiosis with fertilization. Both have haploid gametes that unite to form a diploid zygote, which then goes on to divide mitotically, forming a diploid multicellular organism. In animals, haploid cells become gametes and don't undergo mitosis, while in plants, the haploid cells resulting from meiosis undergo mitosis to form a haploid multicellular organism, the gametophyte. This organism then goes on to generate haploid gametes. (In plants such as trees, the gametophyte is quite reduced in size and not obvious to the casual observer.) **13.3** At the end of meiosis I, the two members of a homologous pair end up in different cells, so they cannot pair up and undergo crossing over during prophase II. **13.4** First, during independent assortment in metaphase I, each pair of homologous chromosomes lines up independent of each other pair at the metaphase plate, so a daughter cell of meiosis I randomly inherits either a maternal or paternal chromosome of each pair. Second, due to crossing over, each chromosome is not exclusively maternal or paternal, but includes regions at the ends of the chromatid from a nonsister chromatid (a chromatid of the other homolog). (The nonsister segment can also be in an internal region of the chromatid if a second crossover occurs beyond the first one before the end of the chromatid.) This provides much additional diversity in the form of new combinations of alleles. Third, random fertilization ensures even more variation, since any sperm of a large number containing many possible genetic combinations can fertilize any egg of a similarly large number of possible combinations.

Test Your Understanding

6. (a)

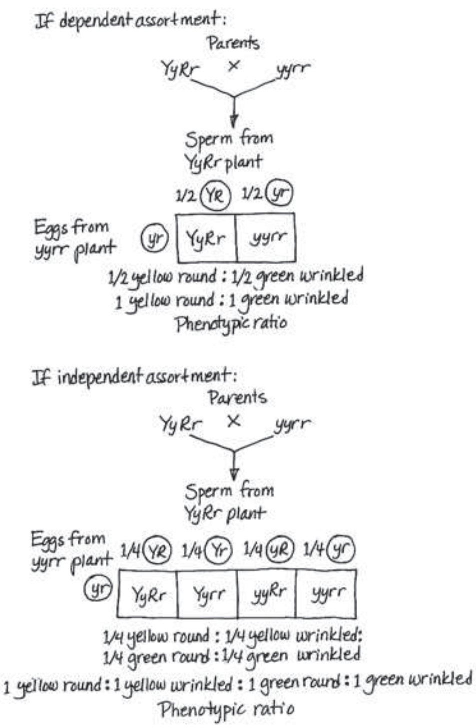


(b) A haploid set is made up of one long, one medium, and one short chromosome, no matter what combination of colors. For example, one red long, one blue medium, and one red short chromosome make up a haploid set. (In cases where crossovers have occurred, a haploid set of one color may include segments of chromatids of the other color.) All red and blue chromosomes together make up a diploid set. (c) Metaphase I **7.** A mutation in the enzyme in the first meiotic division will prevent the separation of homologous chromosomes; while in the second meiotic division, it will prevent the sister chromatids from separating.

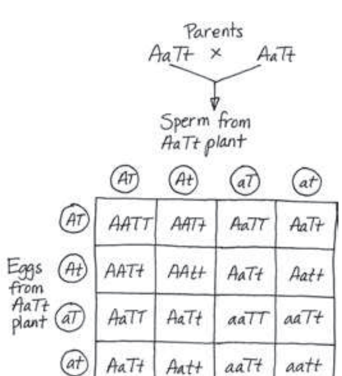
Chapter 14

Figure Questions

Figure 14.3 All offspring would have purple flowers. (The ratio would be 1 purple: 0 white.) The P generation plants are true-breeding, so mating two purple-flowered plants produces the same result as self-pollination: All the offspring have the same trait. If Mendel had stopped after the F_1 generation, he could have concluded that the white factor had disappeared entirely and would not ever reappear.
Figure 14.8



Yes, this cross would also have allowed Mendel to make different predictions for the two hypotheses, thereby allowing him to distinguish the correct one. **Figure 14.10** Your classmate would probably point out that the F_1 generation hybrids show an intermediate phenotype between those of the homozygous parents, which supports the blending hypothesis. You could respond that crossing the F_1 hybrids results in the reappearance of the white phenotype, rather than identical pink offspring, which fails to support the idea of traits blending during inheritance. **Figure 14.11** Both the I^A and I^B alleles are dominant to the *i* allele because the *i* allele results in no attached carbohydrate. The I^A and I^B alleles are codominant; both are expressed in the phenotype of I^AI^B heterozygotes, who have type AB blood. **Figure 14.12** In this cross, the final "3" and "1" of a standard cross are lumped together as a single phenotype. This occurs because in dogs that are *ee*, no pigment is deposited, thus the three dogs that have a *B* in their genotype (normally black) can no longer be distinguished from the dog that is *bb* (normally brown). **Figure 14.16** In the Punnett square, two of the three individuals with normal coloration are carriers, so the probability is ⅔. (Note that you must take into account everything you know when you calculate probability: You know she is not *aa*, so there are only three possible genotypes to consider.)



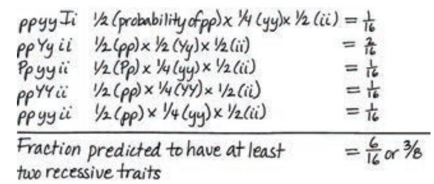
Concept Check 14.1

1. According to the law of independent assortment, 25 plants (1/16 of the offspring) are predicted to be *aatt*, or recessive for both characters. The actual result is likely to differ slightly from this value.

2. The plant could make eight different gametes (*YRI, YRi, YrI, Yri, yRI, yRi, yrI,* and *yri*). To fit all the possible gametes in a self-pollination, a Punnett square would need 8 rows and 8 columns. It would have spaces for the 64 possible unions of gametes in the offspring. **3.** Self-pollination is sexual reproduction because meiosis is involved in forming gametes, which unite during fertilization. As a result, the offspring in self-pollination are genetically different from the parent. (As mentioned in the footnote near the beginning of Concept 14.1, we have simplified the explanation in referring to the single pea plant as a parent. Technically, the gametophytes in the flower are the two "parents.")

Concept Check 14.2

1. 0 homozygous dominant (*FF*), ½ homozygous recessive (*ff*), and ½ heterozygous (*Ff*) **2.** 1/16 *AABB* and ¼ *AaBb* **3.** The genotypes that fulfill this condition are *ppyyIi, ppYyii, Ppyyii, ppYYii,* and *ppyyii*. Use the multiplication rule to find the probability of getting each genotype, and then use the addition rule to find the overall probability of meeting the conditions of this problem:



Concept Check 14.3

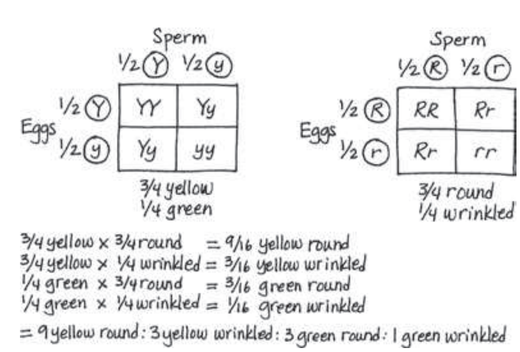
1. Incomplete dominance describes the relationship between two alleles of a single gene, whereas epistasis relates to the genetic relationship between two genes (and the respective alleles of each). **2.** Half of the children would be expected to have type A blood and half type B blood. **3.** The black and white alleles are incompletely dominant, with heterozygotes being gray in color. A cross between a gray rooster and a black hen should yield approximately equal numbers of gray and black offspring.

Concept Check 14.4

1. 1/9 (Since cystic fibrosis is caused by a recessive allele, Beth and Tom's siblings who have CF must be homozygous recessive. Therefore, each parent must be a carrier of the recessive allele. Since neither Beth nor Tom has CF, this means they each have a ⅔ chance of being a carrier. If they are both carriers, there is a ¼ chance that they will have a child with CF. ⅔ × ⅔ × ¼ = 1/9); virtually 0 (Both Beth and Tom would have to be carriers to produce a child with the disease, unless a very rare mutation (change) occurred in the DNA of cells making eggs or sperm in a non-carrier that resulted in the CF allele.) **2.** In normal hemoglobin, the sixth amino acid is glutamic acid (Glu), which is acidic (has a negative charge on its side chain). In sickle-cell hemoglobin, Glu is replaced by valine (Val), which is a nonpolar amino acid, very different from Glu. The primary structure of a protein (its amino acid sequence) ultimately determines the shape of the protein and thus its function. The substitution of Val for Glu enables the hemoglobin molecules to interact with each other and form long fibers, leading to the protein's deficient function and the deformation of the red blood cell. **3.** Joan's genotype is *Dd*. Because the allele for polydactyly (*D*) is dominant to the allele for five digits per appendage (*d*), the trait is expressed in people with either the *DD* or *Dd* genotype. But because Joan's father does not have polydactyly, his genotype must be *dd*, which means that Joan inherited a *d* allele from him. Therefore, Joan, who does have the trait, must be heterozygous. **4.** In the monohybrid cross involving flower color, the ratio is 3.15 purple: 1 white, while in the human family in the pedigree, the ratio in the third generation is 1 can taste PTC: 1 cannot taste PTC. The difference is due to the small sample size (two offspring) in the human family. If the second-generation couple in this pedigree were able to have 929 offspring as in the pea plant cross, the ratio would likely be closer to 3:1. (Note that none of the pea plant crosses in Table 14.1 yielded *exactly* a 3:1 ratio.)

Summary of Key Concepts Questions

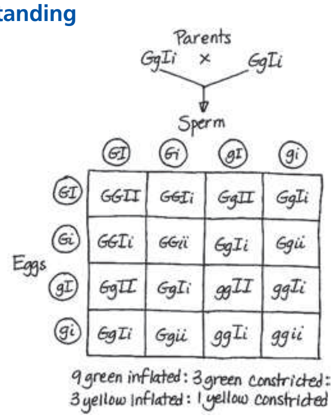
14.1 Alternative versions of genes, called alleles, are passed from parent to offspring during sexual reproduction. In a cross between purple- and white-flowered homozygous parents, the F_1 offspring are all heterozygous, each inheriting a purple allele from one parent and a white allele from the other. Because the purple allele is dominant, it determines the phenotype of the F_1 offspring to be purple, and the expression of the white allele is masked. Only in the F_2 generation is it possible for a white allele to exist in a homozygous state, which causes the white trait to be expressed.
14.2



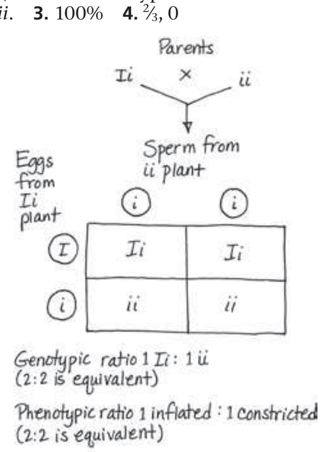
14.3 The ABO blood group is an example of multiple alleles because this single gene has more than two alleles (I^A, I^B, and i). Two of the alleles, I^A and I^B, exhibit codominance, since both carbohydrates (A and B) are present when these two alleles exist together in a genotype. I^A and I^B each exhibit complete dominance over the i allele. This situation is not an example of incomplete dominance because each allele affects the phenotype in a distinguishable way, so the result is not intermediate between the two phenotypes. Because this situation involves a single gene, it is not an example of epistasis or polygenic inheritance. **14.4** The chance of the fourth child having cystic fibrosis is $\frac{1}{4}$, as it was for each of the other children, because each birth is an independent event. We already know both parents are carriers, so whether their first three children are carriers or not has no bearing on the probability that their next child will have the disease. The parents' genotypes provide the only relevant information.

Test Your Understanding

1.



2. Man I^Ai; woman I^Bi; child ii. Genotypes for future children are predicted to be $\frac{1}{4}$ I^AI^B, $\frac{1}{4}$ I^Ai, $\frac{1}{4}$ I^Bi, $\frac{1}{4}$ ii. **3.** 100% **4.** $\frac{2}{3}$, 0

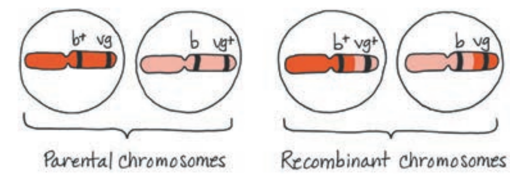


5. (a) $\frac{1}{64}$; (b) $\frac{1}{64}$; (c) $\frac{1}{8}$; (d) $\frac{1}{32}$ **6.** (a) $\frac{3}{4} \times \frac{3}{4} \times \frac{3}{4} = \frac{27}{64}$; (b) $1 - \frac{27}{64} = \frac{37}{64}$; (c) $\frac{1}{4} \times \frac{1}{4} \times \frac{1}{4} = \frac{1}{64}$; (d) $1 - \frac{1}{64} = \frac{63}{64}$ **7.** (a) $\frac{1}{256}$; (b) $\frac{1}{16}$; (c) $\frac{1}{256}$; (d) $\frac{1}{64}$; (e) $\frac{1}{128}$ **8.** (a) 1; (b) $\frac{1}{32}$; (c) $\frac{1}{8}$; (d) $\frac{1}{2}$ **9.** $\frac{1}{9}$ **10.** Matings of the original mutant cat with true-breeding noncurl cats will produce both curl and noncurl F_1 offspring if the curl allele is dominant, but only noncurl offspring if the curl allele is recessive. You would obtain some true-breeding offspring homozygous for the curl allele from matings between the F_1 cats resulting from the original curl × noncurl crosses whether the curl trait is dominant or recessive. You know that cats are true-breeding when curl × curl matings produce only curl offspring. As it turns out, the allele that causes curled ears is dominant. **11.** 25%, or $\frac{1}{4}$, will be cross-eyed; all (100%) of the cross-eyed offspring will also be white. **12.** The dominant allele I is epistatic to the P/p locus, and thus the genotypic ratio for the F_1 generation will be 9 I–P– (colorless) : 3 I–pp (colorless) : 3 iiP– (purple) : 1 $iipp$ (red). Overall, the phenotypic ratio is 12 colorless : 3 purple : 1 red. **13.** Recessive. All affected individuals (Arlene, Tom, Wilma, and Carla) are homozygous recessive aa. George is Aa, since some of his children with Arlene are affected. Sam, Ann, Daniel, and Alan are each Aa, since they are all unaffected children with one affected parent. Michael also is Aa, since he has an affected child (Carla) with his heterozygous wife Ann. Sandra, Tina, and Christopher can each have either the AA or Aa genotype. **14.** $\frac{2}{3}$, 0

Chapter 15

Figure Questions

Figure 15.2 The ratio would be 1 yellow round : 1 green round : 1 yellow wrinkled : 1 green wrinkled. **Figure 15.4** About $\frac{3}{4}$ of the F_2 offspring would have red eyes and about $\frac{1}{4}$ would have white eyes. About half of the white-eyed flies would be female and half would be male; similarly, about half of the red-eyed flies would be female and half would be male. (Note that the homologs with the eye color alleles would be the same shape in the Punnett square, and each offspring would inherit two alleles. The sex of the flies would be determined separately by inheritance of the sex chromosomes. Thus your Punnett square would have four possible combinations in sperm and four in eggs; it would have 16 squares altogether.) **Figure 15.7** All the males would be color-blind, and all the females would be carriers. (Another way to say this is that ½ the offspring would be color-blind males, and ½ the offspring would be carrier females.) **Figure 15.9** The two largest classes would still be the offspring with the phenotypes of the true-breeding P generation flies, but now would be gray vestigial and black normal, which is now the "parental type" because those were the specific allele combinations in the P generation. **Figure 15.10** The two chromosomes below, left, are like the two chromosomes inherited by the F_1 female, one from each P generation fly. They are passed by the F_1 female intact to the offspring and thus could be called "parental" chromosomes. The other two chromosomes result from crossing over during meiosis in the F_1 female. Because they have combinations of alleles not seen in either of the F_1 female's chromosomes, they can be called "recombinant" chromosomes. (Note that in this example, the alleles on the recombinant chromosomes, $b^+ vg^+$ and $b\ vg$, are the allele combinations that were on the parental chromosomes in the cross shown in Figures 15.9 and 15.10. The basis for calling them parental chromosomes is that they have the combination of alleles that was present on the P generation chromosomes.)



Concept Check 15.1

1. The law of segregation relates to the inheritance of alleles for a single character. The law of independent assortment of alleles relates to the inheritance of alleles for two characters. **2.** The physical basis for the law of segregation is the separation of homologs in anaphase I. The physical basis for the law of independent assortment is the alternative arrangements of all the different homologous chromosome pairs in metaphase I. **3.** To show the mutant phenotype, a male needs to possess only one mutant allele. If this gene had been on a pair of autosomes, the two alleles would both have had to be mutant in order for an individual to show the recessive mutant phenotype, a much less probable situation.

Concept Check 15.2

1. Because the gene for this eye color character is located on the X chromosome, all female offspring will be red-eyed and heterozygous ($X^{w^+}X^w$); all male offspring will inherit a Y chromosome from the father and be white-eyed (X^wY). (Another way to say this is that ½ the offspring will be red-eyed heterozygous [carrier] females, and ½ will be white-eyed males.) **2.** $\frac{1}{4}$ (½ chance that the child will inherit a Y chromosome from the father and be male × ½ chance that he will inherit the X carrying the disease allele from his mother). If the child is a boy, there is a ½ chance he will have the disease; a female would have zero chance (but ½ chance of being a carrier). **3.** In a disorder caused by a dominant allele, there is no such thing as a "carrier," since those with the allele have the disorder. Because the allele is dominant, the females lose any "advantage" in having two X chromosomes, since one disorder-associated allele is sufficient to result in the disorder. All fathers who have the dominant allele will pass it along to *all* their daughters, who will also have the disorder. A mother who has the allele (and thus the disorder) will pass it to half of her sons and half of her daughters.

Concept Check 15.3

1. Crossing over during meiosis I in the heterozygous parent produces some gametes with recombinant genotypes for the two genes. Offspring with a recombinant phenotype arise from fertilization of the recombinant gametes by homozygous recessive gametes from the double-mutant parent. **2.** In each case, the alleles contributed by the female parent (in the egg) determine the phenotype of the offspring because the male in this cross contributes only recessive alleles. Thus, identifying the phenotype of the offspring tells you what alleles were in the egg. **3.** No. The order could be *A-C-B* or *C-A-B*. To determine which possibility is correct, you need to know the recombination frequency between *B* and *C*.

Concept Check 15.4

1. In meiosis, a combined 14-21 chromosome will behave as one chromosome. If a gamete receives the combined 14-21 chromosome and a normal copy of chromosome 21, trisomy 21 will result when this gamete combines with a normal gamete (with its own chromosome 21) during fertilization. **2.** No. The child can be either I^AI^Ai or I^Aii. A sperm of genotype I^AI^A could result from nondisjunction in the father during meiosis II, while an egg with the genotype ii could result from nondisjunction in the mother during either meiosis I or meiosis II. **3.** Activation of this gene could lead to the production of too much of this kinase. If the kinase is involved in a signaling pathway that triggers cell division, too much of it could trigger unrestricted cell division, which in turn could contribute to the development of a cancer (in this case, a cancer of one type of white blood cell).

Concept Check 15.5

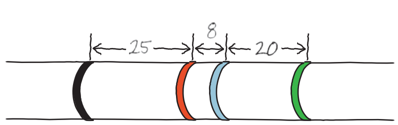
1. Inactivation of an X chromosome in females and genomic imprinting. Because of X inactivation, the effective dose of genes on the X chromosome is the same in males and females. As a result of genomic imprinting, only one allele of certain genes is phenotypically expressed. **2.** The genes for leaf coloration are located in plastids within the cytoplasm. Normally, only the maternal parent transmits plastid genes to offspring. Since variegated offspring are produced only when the female parent is of the B variety, we can conclude that variety B contains both the wild-type and mutant alleles of pigment genes, producing variegated leaves. (Variety A must contain only the wild-type allele of pigment genes.) **3.** Each cell contains numerous mitochondria, and in affected individuals, most cells contain a variable mixture of normal and mutant mitochondria. The normal mitochondria carry out enough cellular respiration for survival. (The situation is similar for chloroplasts.)

Summary of Key Concepts Questions

15.1 Because the sex chromosomes are different from each other and because they determine the sex of the offspring, Morgan could use the sex of the offspring as a phenotypic character to follow the parental chromosomes. (He could also have followed them under a microscope, as the X and Y chromosomes look different.) At the same time, he could record eye color to follow the eye color alleles. **15.2** Males have only one X chromosome, along with a Y chromosome, while females have two X chromosomes. The Y chromosome has very few genes on it, while the X has about 1,000. When a recessive X-linked allele that causes a disorder is inherited by a male on the X from his mother, there isn't a second allele present on the Y (males are hemizygous), so the male has the disorder. Because females have two X chromosomes, they must inherit two recessive alleles in order to have the disorder, a rarer occurrence. **15.3** Crossing over results in new combinations of alleles. Crossing over is a random occurrence, and the more distance there is between two genes, the more chances there are for crossing over to occur, leading to new allele combinations. **15.4** In inversions and reciprocal translocations, the same genetic material is present in the same relative amount but just organized differently. In aneuploidy, duplications, deletions, and nonreciprocal translocations, the balance of genetic material is upset, as large segments are either missing or present in more than one copy. Apparently, this type of imbalance is very damaging to the organism. (Although it isn't lethal in the developing embryo, the reciprocal translocation that produces the Philadelphia chromosome can lead to a serious condition, cancer, by altering the expression of important genes.) **15.5** In these cases, the sex of the parent contributing an allele affects the inheritance pattern. For imprinted genes, either the paternal or the maternal allele is expressed, depending on the imprint. For mitochondrial and chloroplast genes, only the maternal contribution will affect offspring phenotype because the offspring inherit these organelles from the mother, via the egg cytoplasm.

Test Your Understanding

1. $0; \frac{1}{2}; \frac{1}{16}$ **2.** In Peter's case, genomic imprinting may have led to incomplete penetrance, that is, he has inherited the genotype, but does not have the phenotype. The imprinted gene may have silenced the mutant allele, resulting in the normal number of digits. **3.** 17%; yes, it is consistent. In Figure 15.9, the recombination frequency was also 17%. (You'd expect this to be the case since these are the very same two genes, and their distance from each other wouldn't change from one experiment to another.) **4.** Between *T* and *A*, 12%; between *A* and *S*, 5% **5.** Between *T* and *S*, 18%; sequence of genes is *T–A–S* **6.** 6%; wild-type heterozygous for normal wings and red eyes × recessive homozygous for vestigial wings and purple eyes **7.** Fifty percent of the offspring will show phenotypes resulting from crossovers. These results would be the same as those from a cross where *A* and *B* were ***not*** on the same chromosome, and you would interpret the results to mean that the genes are unlinked. (Further crosses involving other genes on the same chromosome would reveal the genetic linkage and map distances.) **8.** 450 each of blue oval and white round (parentals) and 50 each of blue round and white oval (recombinants) **9.** It is unlikely that the two genes are linked. They are either located far from each other on the same chromosome or on different chromosomes. **10.** Because bananas are triploid, homologous pairs cannot line up during meiosis. Therefore, it is not possible to generate gametes that can fuse to produce a zygote with the triploid number of chromosomes. **12.** (a) For each pair of genes, you had to generate an F_1 dihybrid fly; let's use the *A* and *B* genes as an example. You obtained homozygous parental flies, either the first with dominant alleles of the two genes (*AABB*) and the second with recessive alleles (*aabb*), or the first with dominant alleles of gene *A* and recessive alleles of gene *B* (*AAbb*) and the second with recessive alleles of gene *A* and dominant alleles of gene *B* (*aaBB*). Breeding either of these pairs of P generation flies gave you an F_1 dihybrid, which you then testcrossed with a doubly homozygous recessive fly (*aabb*). You classed the offspring as parental or recombinant, based on the genotypes of the P generation parents (either of the two pairs described above). You added up the number of recombinant types and then divided by the total number of offspring. This gave you the recombination percentage (in this case, 8%), which you can translate into map units (8 map units) to construct your map.
(b)



Chapter 16

Figure Questions

Figure 16.2 The living S cells found in the blood sample were able to reproduce to yield more S cells, indicating that the S trait is a permanent, heritable change, rather than just a one-time use of the dead S cells' capsules. **Figure 16.4** The radioactivity would have been found in the pellet when proteins were labeled (batch 1) because proteins would have had to enter the bacterial cells to program them with genetic instructions. It's hard for us to imagine now, but the DNA might have played a structural role that allowed some of the proteins to be injected while it remained outside the bacterial cell (thus no radioactivity in the pellet in batch 2). **Figure 16.7** (1) The nucleotides in a single DNA strand are held together by covalent bonds between an oxygen on the 3′ carbon of one nucleotide and the phosphate group on the 5′ carbon of the next nucleotide in the chain. Instead of covalent bonds, the bonds that hold the two strands together are hydrogen bonds between a nitrogenous base on one strand and the complementary nitrogenous base on the other strand. (Hydrogen bonds are weaker than covalent bonds, but there are so many hydrogen bonds in a DNA double helix that, together, they are enough to hold the two strands together.) (2) The left diagram shows the most detail. It shows that each sugar-phosphate backbone is made up of sugars (blue pentagons) and phosphates (yellow circles) joined by covalent bonds (black lines). The middle diagram doesn't show any detail in the backbone. Both the left and middle diagrams label the bases and represent their complementarity by the complementary shapes at the ends of the bases (curves/indents for G/C or V's/notches for T/A). The diagram on the right is the least detailed, implying that the base pairs pair up, but showing all bases as the same shape so not including the information about specificity and complementarity visible in the other two diagrams. The left and right diagrams show that the strand on the left was synthesized most recently, as indicated by the light blue color. All three diagrams show the 5′ and 3′ ends of the strands. **Figure 16.11** The tube from the first replication would look the same, with a middle band of hybrid ^{15}N–^{14}N DNA, but the second tube would not have the upper band of two light blue strands. Instead, it would have a bottom band of two dark blue strands, like the bottom band in the result predicted after one replication in the conservative model. **Figure 16.12** In the bubble at the top of the micrograph in (b), arrows should be drawn pointing left and right to indicate the two replication forks. **Figure 16.14** Looking at any of the DNA strands, we see that one end is called the 5′ end and the other the 3′ end. If we proceed from the 5′ end to the 3′ end on the left-most strand, for example, we list the components in this order: phosphate group → 5′ C of the sugar → 3′ C → phosphate → 5′ C → 3′ C. Going in the opposite direction on the same strand, the components proceed in the reverse order: 3′ C → 5′ C → phosphate. Thus, the two directions are distinguishable, which is what we mean when we say that the strands have directionality. (Review Figure 16.5 if necessary.)
Figure 16.17

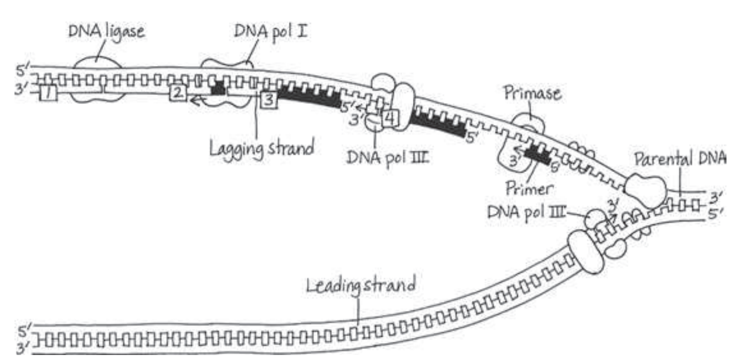


Figure 16.18

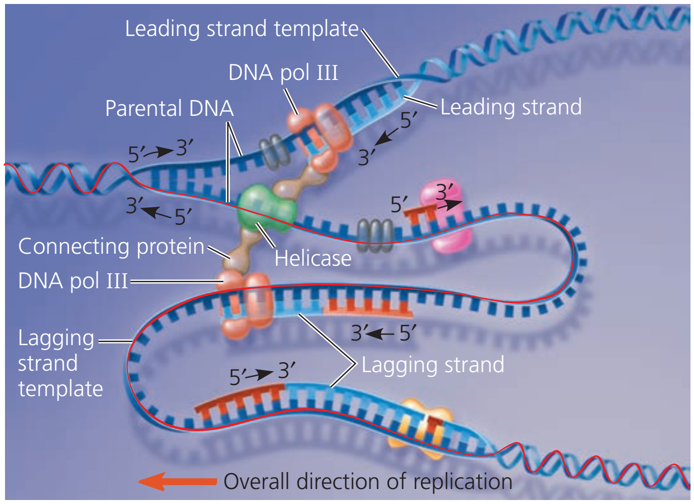


Figure 16.23 The two members of a homologous pair (which would be the same color) would be associated tightly together at the metaphase plate during metaphase I of meiosis I. In metaphase of mitosis, however, each chromosome would be lined up individually, so the two chromosomes of the same color would be in different places at the metaphase plate.

Concept Check 16.1

1. You can't tell which end is the 5′ end. You need to know which end has a phosphate group on the 5′ carbon (the 5′ end) or which end has an —OH group on the 3′ carbon (the 3′ end). **2.** He expected that the mouse injected with the mixture of heat-killed S cells and living R cells would survive, since neither type of cell alone would kill the mouse.

Concept Check 16.2

1. Complementary base pairing ensures that the two daughter molecules are exact copies of the parental molecule. When the two strands of the parental molecule separate, each serves as a template on which nucleotides are arranged, by the base-pairing rules, into new complementary strands. **2.** These cells express the enzyme telomerase, which catalyzes the lengthening of telomeres. **3.** In the cell cycle, DNA synthesis occurs during the S phase, between the G_1 and G_2 phases of interphase. DNA replication is therefore complete before the mitotic phase begins. **4.** Synthesis of the leading strand is initiated by an RNA primer, which must be removed and replaced with DNA, a task that could not be performed if the cell's DNA pol I were nonfunctional. In the overview box in Figure 16.17, just to the left of the top origin of replication, a functional DNA pol I would replace the RNA primer of the leading strand (shown in red) with DNA nucleotides (blue). The nucleotides would be added onto the 3′ end of the first Okazaki fragment of the upper lagging strand (the right half of the replication bubble).

Concept Check 16.3

1. A nucleosome is made up of eight histone proteins, two each of four different types, around which DNA is wound. Linker DNA runs from one nucleosome to the next. **2.** Euchromatin is chromatin that becomes less compacted during interphase and is accessible to the cellular machinery responsible for gene activity. Heterochromatin, on the other hand, remains quite condensed during interphase and contains genes that are largely inaccessible to this machinery. **3.** The nuclear lamina is a netlike array of protein filaments that provides mechanical support just inside the nuclear envelope and thus maintains the shape of the nucleus. Considerable evidence also supports the existence of a nuclear matrix, a framework of protein fibers extending throughout the nuclear interior.

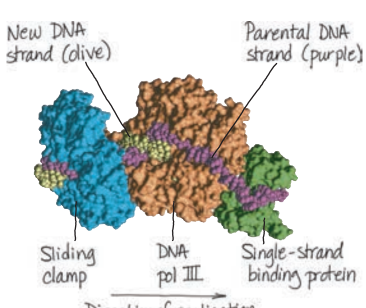
Summary of Key Concepts Questions

16.1 Each strand in the double helix has polarity; the end with a phosphate group on the 5′ carbon of the sugar is called the 5′ end, and the end with an —OH group on the 3′ carbon of the sugar is called the 3′ end. The two strands run in opposite directions, one running 5′ → 3′ and the other alongside it running 3′ → 5′. Thus, each end of the molecule has both a 5′ and a 3′ end. This arrangement is called "antiparallel." If the strands were parallel, they would both run 5′ → 3′ in the same direction, so an end of the molecule would have either two 5′ ends or two 3′ ends. **16.2** On both the leading and lagging strands, DNA polymerase adds onto the 3′ end of an RNA primer synthesized by primase, synthesizing DNA in the 5′ → 3′ direction. Because the parental strands are antiparallel, however, only on the leading strand does synthesis proceed continuously into the replication fork. The lagging strand is synthesized bit by bit in the direction away from the fork as a series of shorter Okazaki fragments, which are later joined together by DNA ligase. Each fragment is initiated by synthesis of an RNA primer by primase as soon as a given stretch of single-stranded template strand is opened up. Although both strands are synthesized at the same rate, synthesis of the lagging strand is delayed because initiation of each fragment begins only when sufficient template strand is available. **16.3** Much of the chromatin in an interphase nucleus is present as the 30-nm fiber, with some in the form of the 10-nm fiber and some as looped domains of the 30-nm fiber. (These different levels of chromatin packing may reflect differences in gene expression occurring in these regions.) Also, a small percentage of the chromatin, such as that at the centromeres and telomeres, is highly condensed heterochromatin.

Test Your Understanding

9. Like histones, the *E. coli* proteins would be expected to contain many basic (positively charged) amino acids, such as lysine and arginine, which can form weak bonds with the negatively charged phosphate groups on the sugar-phosphate backbone of the DNA molecule.

11.



Chapter 17

Figure Questions

Figure 17.3 The previously presumed pathway would have been wrong. The new results would support this pathway: precursor → citrulline → ornithine → arginine. They would also indicate that class I mutants have a defect in the second step and class II mutants have a defect in the first step. **Figure 17.5** The mRNA sequence (5′-UGGUUUGGCUCA-3′) is the same as the nontemplate DNA strand sequence (5′-TGGTTTGGCTCA-3′), except there is a U in the mRNA wherever there is a T in the DNA. The nontemplate strand is probably used to represent a DNA sequence because it represents the mRNA sequence, containing codons. (This is why it's called the coding strand.) **Figure 17.6** Arg (or R)–Glu (or E)–Pro (or P)–Arg (or R) **Figure 17.8** The processes are similar in that polymerases form polynucleotides complementary to an antiparallel DNA template strand. In replication, however, both strands act as templates, whereas in transcription, only one DNA strand acts as a template. **Figure 17.9** The RNA polymerase would bind directly to the promoter, rather than being dependent on the previous binding of transcription factors.

Figure 17.12

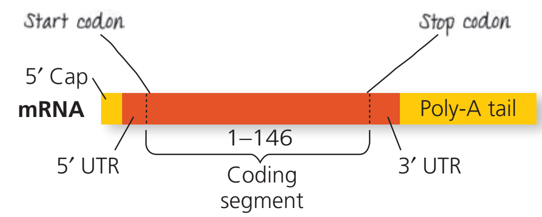


Figure 17.16 The anticodon on the tRNA is 3′-AAG-5′, so it would bind to the mRNA codon 5′-UUC-3′. This codon codes for phenylalanine, which is the amino acid this tRNA would carry. **Figure 17.22** It would be packaged in a vesicle, transported to the Golgi apparatus for further processing, and then transported via a vesicle to the plasma membrane. The vesicle would fuse with the membrane, releasing the protein outside the cell. **Figure 17.24** The mRNA farthest to the right (the longest one) started transcription first. The ribosome at the top, closest to the DNA, started translating first and thus has the longest polypeptide.

Concept Check 17.1

1. Recessive **2.** No. An enzyme can cleave this amino acid from the polypeptide after synthesis.

3.

"Template sequence" (from nontemplate sequence in problem, written 3′ → 5′): 3′-ACGACTGAA-5′

mRNA sequence: 5′-UGCUGACUU-3′

Translated: Cys-STOP

If the nontemplate sequence could have been used as a template for transcribing the mRNA, the protein translated from the mRNA would have a completely different amino acid sequence and would most likely be nonfunctional. (It would also be shorter because of the UGA stop signal shown in the mRNA sequence above—and possibly others earlier in the mRNA sequence.)

Concept Check 17.2

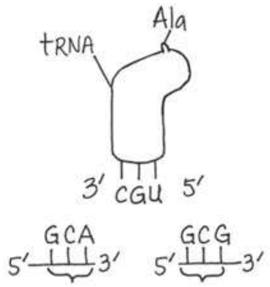
1. A promoter is the region of DNA to which RNA polymerase binds to begin transcription. It is at the upstream end of the gene (transcription unit). **2.** In a bacterial cell, part of the RNA polymerase recognizes the gene's promoter and binds to it. In a eukaryotic cell, transcription factors must bind to the promoter first, then the RNA polymerase binds to them. In both cases, sequences in the promoter determine the precise binding of RNA polymerase so the enzyme is in the right location and orientation. **3.** The transcription factor that recognizes the TATA sequence would be unable to bind, so RNA polymerase could not bind and transcription of that gene probably would not occur.

Concept Check 17.3

1. Due to alternative splicing of exons, each gene can result in multiple different mRNAs and can thus direct synthesis of multiple different proteins. **2.** In watching a show recorded with a DVR, you watch segments of the show itself (exons) and fast-forward through the commercials, which are thus like introns. However, unlike introns, commercials remain in the recording, while the introns are cut out of the RNA transcript during RNA processing. **3.** Once the mRNA has exited the nucleus, the cap prevents it from being degraded by hydrolytic enzymes and facilitates its attachment to ribosomes. If the cap were removed from all mRNAs, the cell would no longer be able to synthesize any proteins and would probably die.

Concept Check 17.4

1. First, each aminoacyl-tRNA synthetase specifically recognizes a single amino acid and attaches it only to an appropriate tRNA. Second, a tRNA charged with its specific amino acids binds only to an mRNA codon for that amino acid. **2.** Certain amino acids may be chemically modified by the addition of lipids, sugars, or phosphate groups. Enzymes may cleave a protein into several fragments. Two or more different proteins may combine to form a quaternary structure that is functional. **3.** Because of wobble, the tRNA could bind to either 5′-GCA-3′ or 5′-GCG-3′, both of which code for alanine (Ala). Alanine would be attached to the tRNA (see diagram, upper right). **4.** When one ribosome terminates translation and dissociates, the two subunits would be very close to the cap. This could facilitate their rebinding and initiating synthesis of a new polypeptide, thus increasing the efficiency of translation.



Concept Check 17.5

1. In the mRNA, the reading frame downstream from the deletion is shifted, leading to a long string of incorrect amino acids in the polypeptide, and in most cases, a stop codon will occur, leading to premature termination. The polypeptide will most likely be nonfunctional. **2.** Heterozygous individuals, said to have sickle-cell trait, have a copy each of the wild-type allele and the sickle-cell allele. Both alleles will be expressed, so these individuals will have both normal and sickle-cell hemoglobin molecules. Apparently, having a mix of the two forms of β-globin has no effect under most conditions, but during prolonged periods of low blood oxygen (such as at higher altitudes), these individuals can show some signs of sickle-cell disease.
3.

Normal DNA sequence (template strand is on top):	3′-TACTTGTCCGATATC-5′ 5′-ATGAACAGGCTATAG-3′
mRNA sequence:	5′-AUGAACAGGCUAUAG-3′
Amino acid sequence:	Met-Asn-Arg-Leu-STOP
Mutated DNA sequence (template strand is on top):	3′-TACTTGTCCAATATC-5′ 5′-ATGAACAGGTTATAG-3′
mRNA sequence:	5′-AUGAACAGGUUAUAG-3′
Amino acid sequence:	Met-Asn-Arg-Leu-STOP

No effect: The amino acid sequence is Met-Asn-Arg-Leu both before and after the mutation because the mRNA codons 5′-CUA-3′ and 5′-UUA-3′ both code for Leu. (The fifth codon is a stop codon.)

Summary of Key Concepts Questions

17.1 A gene contains genetic information in the form of a nucleotide sequence. The gene is first transcribed into an RNA molecule, and a messenger RNA molecule is ultimately translated into a polypeptide. The polypeptide makes up part or all of a protein, which performs a function in the cell and contributes to the phenotype of the organism. **17.2** Both bacterial and eukaryotic genes have promoters, regions where RNA polymerase ultimately binds and begins transcription. In bacteria, RNA polymerase binds directly to the promoter; in eukaryotes, transcription factors bind first to the promoter, and then RNA polymerase binds to the transcription factors and promoter together. **17.3** Both the 5′ cap and the 3′ poly-A tail help the mRNA exit from the nucleus and then, in the cytoplasm, help ensure mRNA stability and allow it to bind to ribosomes. **17.4** In the context of the ribosome, tRNAs function as translators between the nucleotide-based language of mRNA and the amino-acid-based language of polypeptides. A tRNA carries a specific amino acid, and the anticodon on the tRNA is complementary to the codon on the mRNA that codes for that amino acid. In the ribosome, the tRNA binds to the A site. Then the polypeptide being synthesized (currently on the tRNA in the P site) is joined to the new amino acid, which becomes the new (C-terminal) end of the polypeptide. Next, the tRNA in the A site moves to the P site. After the polypeptide is transferred to the new tRNA, thus adding the new amino acid, the now empty tRNA moves from the P site to the E site, where it exits the ribosome. **17.5** When a nucleotide base is altered chemically, its base-pairing characteristics may be changed. When that happens, an incorrect nucleotide is likely to be incorporated into the complementary strand during the next replication of the DNA, and successive rounds of replication will perpetuate the mutation. Once the gene is transcribed, the mutated codon may code for a different amino acid that inhibits or changes the function of a protein. If the chemical change in the base is detected and repaired by the DNA repair system before the next replication, no mutation will result.

Test Your Understanding

8. No. Transcription and translation are separated in space and time in a eukaryotic cell, as a result of the eukaryotic cell's nuclear membrane.

9.

Type of RNA	Functions
Messenger RNA (mRNA)	Carries information specifying amino acid sequences of polypeptides from DNA to ribosomes
Transfer RNA (tRNA)	Serves as translator molecule in protein synthesis; translates mRNA codons into amino acids
Ribosomal RNA (rRNA)	In a ribosome, plays a structural role; as a ribozyme, plays a catalytic role (catalyzes peptide bond formation)
Primary transcript	Is a precursor to mRNA, rRNA, or tRNA, before being processed; some intron RNA acts as a ribozyme, catalyzing its own splicing
Small RNAs in spliceosome	Play structural and catalytic roles in spliceosomes, the complexes of protein and RNA that splice pre-mRNA

Chapter 18

Figure Questions

Figure 18.3 As the concentration of tryptophan in the cell falls, eventually there will be none bound to *trp* repressor molecules. These will then change into their inactive shapes and dissociate from the operator, allowing transcription of the operon to resume. The enzymes for tryptophan synthesis will be made, and they will again synthesize tryptophan in the cell. **Figure 18.9** Each of the two polypeptides has two regions—one that makes up part of MyoD's DNA-binding domain and one that makes up part of MyoD's activation domain. Each functional domain in the complete MyoD protein is made up of parts of both polypeptides. **Figure 18.11** In both types of cell, the albumin gene enhancer has the three control elements colored yellow, gray, and red. The sequences in the liver and lens cells would be identical, since the cells are in the same organism. **Figure 18.18** Even if the mutant MyoD protein couldn't activate the *myoD* gene, it could still turn on genes for the other proteins in the pathway (other transcription factors, which would turn on the genes for muscle-specific proteins, for example). Therefore, some differentiation would occur. But unless there were other activators that could compensate for the loss of the MyoD protein's activation of the *myoD* gene, the cell would not be able to maintain its differentiated state. **Figure 18.22** Normal Bicoid protein would be made in the anterior end and compensate for the presence of mutant *bicoid* mRNA put into the egg by the mother. Development should be normal, with a head present. (This is what was observed.) **Figure 18.25** The mutation is likely to be recessive because it is more likely to have an effect if both copies of the gene are mutated and code for nonfunctional proteins. If one normal copy of the gene is present, its product could inhibit the cell cycle. (However, there are also known cases of dominant *p53* mutations.) **Figure 18.27** Cancer is a disease in which cell division occurs without its usual regulation. Cell division can be stimulated by growth factors (see Figure 12.18), which bind to cell-surface receptors (see Figure 9.8). Cancer cells evade these normal controls and can often divide in the absence of growth factors (see Figure 12.19). This suggests that the receptor proteins or some other components in a signaling pathway are abnormal in some way (see, for example, the mutant Ras protein in Figure 18.24) or are expressed at abnormal levels, as seen for the receptors in this figure. Under some circumstances in the mammalian body, steroid hormones such as estrogen and progesterone can also promote cell division. These molecules also use cell-signaling pathways, as described in Concept 9.2 (see Figure 9.9). Because signaling receptors are involved in triggering cells to undergo cell division, it is not surprising that altered genes encoding these proteins might play a significant role in the development of cancer. Genes might be altered through either a mutation that changes the function of the protein product or a mutation that causes the gene to be expressed at abnormal levels that disrupt the overall regulation of the signaling pathway.

Concept Check 18.1

1. Binding by the *trp* corepressor (tryptophan) activates the *trp* repressor, which binds to the *trp* operator, shutting off transcription of the *trp* operon. Binding by the *lac* inducer (allolactose) inactivates the *lac* repressor, so that it can no longer bind to the *lac* operator, leading to transcription of the *lac* operon. **2.** When glucose is scarce, cAMP is bound to CRP and CRP is bound to the *lac* promoter, favoring the binding of RNA polymerase. However, in the absence of lactose, the *lac* repressor is bound to the *lac* operator, blocking RNA polymerase binding to the *lac* promoter. Therefore, the *lac* operon genes are not transcribed. **3.** The cell would continuously produce β-galactosidase and the two other enzymes for using lactose, even in the absence of lactose, thus wasting cell resources.

Concept Check 18.2

1. Histone acetylation is generally associated with gene expression, while DNA methylation is generally associated with lack of expression. **2.** The same enzyme could not methylate both a histone and a DNA base. Enzymes are very specific in structure, and an enzyme that could methylate an amino acid of a protein would not be able to fit the base of a DNA nucleotide into the same active site. **3.** General transcription factors function in assembling the transcription initiation complex at the promoters for all genes. Specific transcription factors bind to control elements associated with a particular gene and, once bound, either increase (activators) or decrease (repressors) transcription of that gene. **4.** Regulation of translation initiation, degradation of the mRNA, activation of the protein (by chemical modification, for example), and protein degradation **5.** The three genes should have some similar or identical sequences in the control elements of their enhancers. Because of this similarity, the same specific transcription factors in muscle cells could bind to the enhancers of all three genes and stimulate their expression coordinately.

Concept Check 18.3

1. Both miRNAs and siRNAs are small, single-stranded RNAs that associate with a complex of proteins and then can base-pair with mRNAs that have a complementary sequence. This base pairing leads to either degradation of the mRNA or blockage of its translation. In some yeasts, siRNAs associated with proteins in a different complex can bind back to centromeric chromatin, recruiting enzymes that cause condensation of that chromatin into heterochromatin. Both miRNAs and siRNAs are processed from double-stranded RNA precursors but have subtle variations in the structure of those precursors. **2.** The mRNA would persist and be translated into the cell division–promoting protein, and the cell would probably divide. If the intact miRNA is necessary for inhibition of cell division, then division of this cell might be inappropriate. Uncontrolled cell division could lead to formation of a mass of cells (tumor) that prevents proper functioning of the organism and could contribute to the development of cancer. **3.** The *XIST* RNA is transcribed from the *XIST* gene on the X chromosome that will be inactivated. It then binds to that chromosome and induces heterochromatin formation. A likely model is that *XIST* RNA somehow recruits chromatin modification enzymes that lead to formation of heterochromatin.

Concept Check 18.4

1. Cells undergo differentiation during embryonic development, becoming different from each other. Therefore, the adult organism is made up of many highly specialized cell types. **2.** By binding to a receptor on the receiving cell's surface and triggering a signal transduction pathway, involving intracellular molecules such as second messengers and transcription factors that affect gene expression **3.** The products of maternal effect genes, made and deposited into the egg by the mother, determine the head and tail ends, as well as the back and belly, of the egg and embryo (and eventually the adult fly). **4.** The lower cell is synthesizing signaling molecules because the gene encoding them is activated, meaning that the appropriate specific transcription factors are binding to the gene's enhancer. The genes encoding these specific transcription factors are also being expressed in this cell because the transcriptional activators that can turn them on were expressed in the precursor to this cell. A similar explanation also applies to the cells expressing the receptor proteins. This scenario began with specific cytoplasmic determinants localized in specific regions of the egg. These cytoplasmic determinants were distributed unevenly to daughter cells, resulting in cells going down different developmental pathways.

Concept Check 18.5

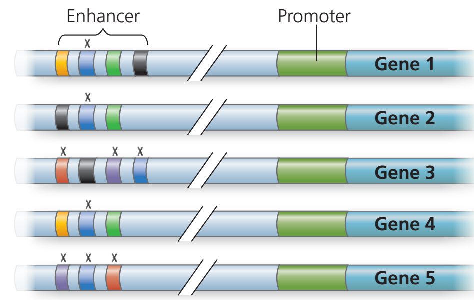
1. A cancer-causing mutation in a proto-oncogene usually makes the gene product overactive, whereas a cancer-causing mutation in a tumor-suppressor gene usually makes the gene product nonfunctional. **2.** When an individual has inherited an oncogene or a mutant allele of a tumor-suppressor gene **3.** Apoptosis is signaled by p53 protein when a cell has extensive DNA damage, so apoptosis plays a protective role in eliminating a cell that might contribute to cancer. If mutations in the genes in the apoptotic pathway blocked apoptosis, a cell with such damage could continue to divide and might lead to tumor formation.

Summary of Key Concepts Questions

18.1 A corepressor and an inducer are both small molecules that bind to the repressor protein in an operon, causing the repressor to change shape. In the case of a corepressor (like tryptophan), this shape change allows the repressor to bind to the operator, blocking transcription. In contrast, an inducer causes the repressor to dissociate from the operator, allowing transcription to begin. **18.2** The chromatin must not be tightly condensed because it must be accessible to transcription factors. The appropriate specific transcription factors (activators) must bind to the control elements in the enhancer of the gene, while repressors must not be bound. The DNA must be bent by a bending protein so the activators can contact the mediator proteins and form a complex with general transcription factors at the promoter. Then RNA polymerase must bind and begin transcription. **18.3** miRNAs do not "code" for the amino acids of a protein—they are never translated. Each miRNA associates with a group of proteins to form a complex. Binding of the complex to an mRNA with a complementary sequence causes that mRNA to be degraded or blocks its translation. This is considered gene regulation because it controls the amount of a particular mRNA that can be translated into a functional protein. **18.4** The first process involves cytoplasmic determinants, including mRNAs and proteins, placed into specific locations in the egg by maternal cells. The embryonic cells that are formed from different regions in the egg during early cell divisions will have different proteins in them, which will direct different programs of gene expression. The second process involves the cell in question responding to signaling molecules secreted by neighboring cells (induction). The signaling pathway in the responding cell also leads to a different pattern of gene expression. The coordination of these two processes results in each cell following a unique pathway in the developing embryo. **18.5** The protein product of a proto-oncogene is usually involved in a pathway that stimulates cell division. The protein product of a tumor-suppressor gene is usually involved in a pathway that inhibits cell division.

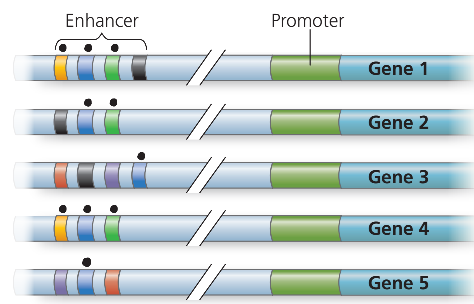
Test Your Understanding

11. (a)



The purple, blue, and red activator proteins would be present.

(b)



Only gene 4 would be transcribed.
(c) In nerve cells, the yellow, blue, green, and black activators would have to be present, thus activating transcription of genes 1, 2, and 4. In skin cells, the red, black, purple, and blue activators would have to be present, thus activating genes 3 and 5.

Chapter 19

Figure Questions

Figure 19.5

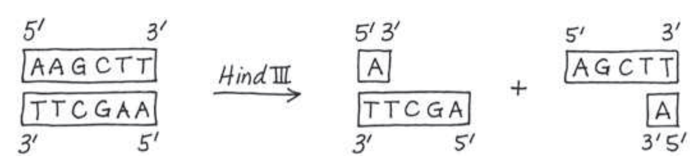
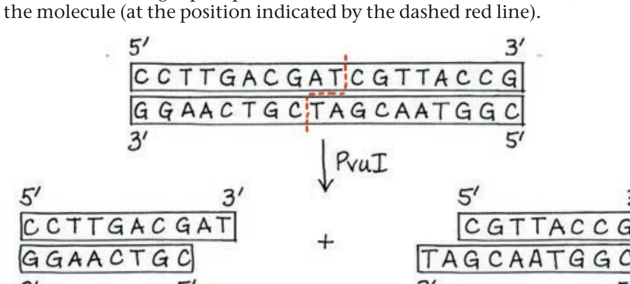


Figure 19.16 None of the eggs with the transplanted nuclei from the four-cell embryo at the upper left would have developed into a tadpole. Also, the result might include only some of the tissues of a tadpole, which might differ, depending on which nucleus was transplanted. (This assumes that there was some way to tell the four cells apart, as one can in some frog species.) **Figure 19.21** Using converted iPS cells would not carry the same risk, which is its major advantage. Because the donor cells would come from the patient, they would be perfectly matched. The patient's immune system would recognize them as "self" cells and would not mount an attack (which is what leads to rejection). On the other hand, cells that are rapidly dividing might carry a risk of inducing some type of tumor or contributing to development of cancer.

Concept Check 19.1

1. The covalent sugar-phosphate bonds of the DNA strands **2.** Yes, *Pvu*I will cut the molecule (at the position indicated by the dashed red line).



3. Some eukaryotic genes are too large to be incorporated into bacterial plasmids. Bacterial cells lack the means to process RNA transcripts into mRNA, and even if the need for RNA processing is avoided by using cDNA, bacteria lack enzymes to catalyze the post-translational processing that many eukaryotic proteins require to function properly. (This is often the case for human proteins, which are a focus of biotechnology.) **4.** During the replication of the ends of linear DNA molecules (see Figure 16.20), an RNA primer is used at the 5′ end of each new strand. The RNA must be replaced by DNA nucleotides, but DNA polymerase is incapable of starting from scratch at the 5′ end of a new DNA strand. During PCR, the primers are made of DNA nucleotides already, so they don't need to be replaced—they just remain as part of each new strand. Therefore, there is no problem with end replication during PCR, and the fragments don't shorten with each replication.

Concept Check 19.2

1. Complementary base pairing is involved in cDNA synthesis, which is required for the first three techniques: RT-PCR, DNA microarray analysis, and RNA sequencing. Reverse transcriptase uses mRNA as a template to synthesize the first strand of cDNA, adding nucleotides complementary to those on the mRNA. Complementary base pairing is also involved when DNA polymerase synthesizes the second strand of the cDNA. Furthermore, in RT-PCR, the primers must base-pair with their target sequences in the DNA mixture, locating one specific region among many. In DNA microarray analysis, the labeled cDNA probe binds only to the specific target sequence due to complementary nucleic acid hybridization (DNA-DNA hybridization). In RNA-seq, when sequencing the cDNAs, base complementarity plays a role in the sequencing process. During CRISPR-Cas9 editing, a guide RNA in the CRISPR-Cas9 complex must base-pair with its complementary sequence in the genome (in the target gene) before editing can occur. The repair system also uses complementarity of bases when using a template strand to repair breaks. **2.** As a researcher interested in cancer development, you would want to study genes represented by spots that are green or red because these are genes for which the expression level differs between the two types of tissues. Some of these genes may be expressed differently as a result of cancer, while others might play a role in causing cancer, so both would be of interest.

Concept Check 19.3

1. The state of chromatin modification in the nucleus from the intestinal cell was undoubtedly less similar to that of a nucleus from a fertilized egg, explaining why many fewer of these nuclei were able to be reprogrammed. In contrast, the chromatin in a nucleus from a cell at the four-cell stage would have been much more like that of a nucleus in a fertilized egg and therefore much more easily programmed to direct development. **2.** No, primarily because of subtle (and perhaps not so subtle) differences in the environment in which the clone develops and lives from that in which the original pet lived (see the differences noted in Figure 19.18). This does provoke ethical questions. To produce Dolly, also a mammal, several hundred embryos were cloned, but only one survived to adulthood. If any of the "reject" dog embryos survived to birth as defective dogs, would they be killed? Is it ethical to produce living animals that may be defective? You can probably think of other ethical issues as well. **3.** Given that muscle cell differentiation involves a master regulatory gene (*MyoD*), you might start by introducing either the MyoD protein or an expression vector carrying the *MyoD* gene into stem cells. (This is not likely to work, because the embryonic precursor cell in Figure 18.18 is more differentiated than the stem cells you are working with, and some other changes would have to be introduced as well. But it's a good way to start! And you may be able to think of others.)

Concept Check 19.4

1. Stem cells continue to reproduce themselves, ensuring that the corrective gene product will continue to be made. **2.** Herbicide resistance, pest resistance, disease resistance, salinity resistance, drought resistance, and delayed ripening **3.** Analysis of DNA fingerprints and short tandem repeats (STRs) can help identify the guilty. Every individual has a unique set of genetic markers. They produce a pattern on a gel, which is visually recognizable and is called DNA fingerprint. This method involves nucleic acid hybridization to detect similarities and differences in DNA samples. STRs take advantage of variations in lengths of genetic markers. STRs are tandemly repeated units of a few nucleotide sequences in specific regions. Their numbers in these regions vary highly from one person to another.

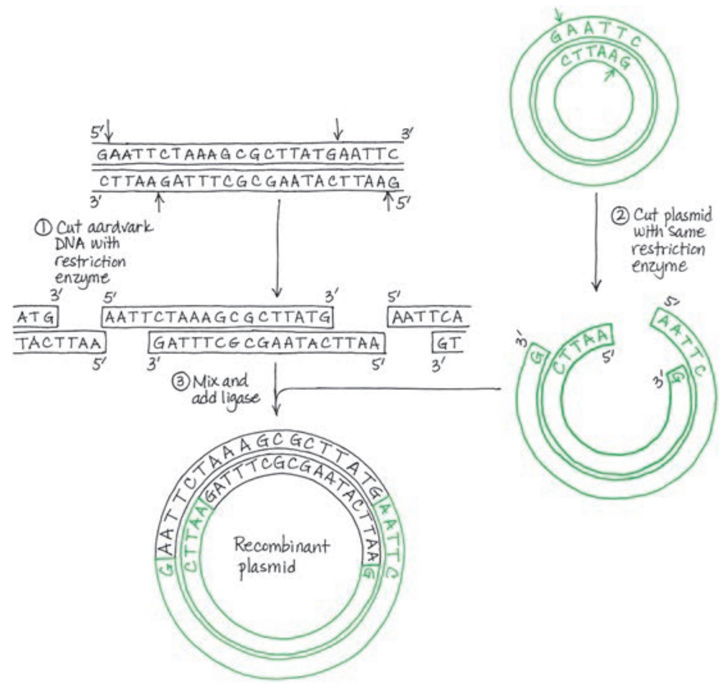
Summary of Key Concepts Questions

19.1 A plasmid vector and a source of foreign DNA to be cloned are both cut with the same restriction enzyme, generating restriction fragments with sticky ends. These fragments are mixed together, ligated, and reintroduced into bacterial cells. The plasmid has a gene for resistance to an antibiotic. That antibiotic is added to the host cells, and only cells that have taken up a plasmid will grow. (Another technique allows researchers to select only the cells that have a recombinant plasmid, rather than the original plasmid without an inserted gene.) **19.2** The genes that are expressed in a given tissue or cell type determine the proteins (and noncoding RNAs) that are the basis of the structure and functions of that tissue or cell type. Understanding which groups of interacting genes establish particular structures and carry out certain functions will help us learn how the parts of an organism work together. We will also be better able to treat diseases that occur when faulty gene expression leads to malfunctioning tissues. **19.3** (1) Cloning a mouse involves transplanting a nucleus from a differentiated mouse cell into a mouse egg cell that has had its own nucleus removed. Activating the egg cell and promoting its development into an embryo in a surrogate mother results in a mouse that is genetically identical to the mouse that donated the nucleus. In this case, the differentiated nucleus has been reprogrammed by factors in the egg cytoplasm. (2) Mouse ES cells are generated from inner cells in mouse blastocysts, so in this case the cells are "naturally" reprogrammed by the process of reproduction and development. (Cloned mouse embryos can also be used as a source of ES cells.) (3) iPS cells can be generated without the use of embryos from a differentiated adult mouse cell by adding certain transcription factors into the cell. In this case, the transcription factors are reprogramming the cells to become pluripotent. **19.4** First, the disease must be caused by a single gene, and the molecular basis of the problem must be understood. Second, the cells that are going to be introduced into the patient must be cells that will integrate into body tissues and continue to multiply (and provide the needed gene product). Third, the gene must be able to be introduced into the cells in question in a safe way, as there have been instances of cancer resulting from some gene therapy trials. (Note that this will require testing the procedure in mice; moreover, the factors that determine a safe vector are not yet well understood. Maybe one of you will go on to solve this problem!)

Test Your Understanding

9. You would use PCR to amplify the gene. This could be done from genomic DNA. Alternatively, mRNA could be isolated from lens cells and reverse-transcribed by reverse transcriptase to make cDNA. This cDNA could then be used for PCR. In either case, the gene would then be inserted into an expression vector so you could produce the protein and study it. **10.** Crossing over, which causes recombination, is a random event. The chance of crossing over occurring between two loci increases as the distance between them increases. If a SNP is located very close to a disease-associated allele, it is said to be genetically linked. Crossing over will rarely occur between the SNP and the allele, so the SNP can be used as a genetic marker indicating the presence of the particular allele.

11.



Chapter 20

Figure Questions

Figure 20.2 In step 2 of this figure, the order of the fragments relative to each other is not known and will be determined later by computer. The unordered nature of the fragments is reflected by their scattered arrangement in the diagram.
Figure 20.8 The transposon would be cut out of the DNA at the original site rather than copied, so the figure would show the original stretch of DNA without the transposon after the mobile transposon had been cut out. **Figure 20.10** The RNA transcripts extending from the DNA in each transcription unit are shorter on the left and longer on the right. This means that RNA polymerase must be starting on the left end of the unit and moving toward the right.

Figure 20.13

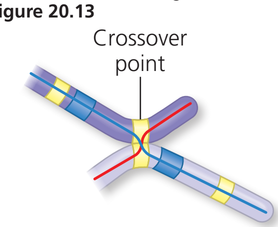


Figure 20.14 Pseudogenes are nonfunctional. They could have arisen by any mutations in the second copy that made the gene product unable to function. Examples are base changes that introduce stop codons in the sequence, alter amino acids, or change a region of the gene promoter so that the gene can no longer be expressed. **Figure 20.15** At position 5, there is an R (arginine) in lysozyme and a K (lysine) in α-lactalbumin; both of these are basic amino acids.

Figure 20.16 Let's say a transposable element (TE) existed in the intron to the left of the indicated EGF exon in the EGF gene, and the same TE was present in the intron to the right of the indicated F exon in the fibronectin gene. During meiotic recombination, these TEs could cause nonsister chromatids on homologous chromosomes to pair up incorrectly, as seen in Figure 20.13. One gene might end up with an F exon next to an EGF exon. Further mistakes in pairing over many generations might result in these two exons being separated from the rest of the gene and placed next to a single or duplicated K exon. In general, the presence of repeated sequences in introns and between genes facilitates these processes because it allows incorrect pairing of nonsister chromatids, leading to novel exon combinations. **Figure 20.18** Since you know that chimpanzees do not speak but humans do, you'd probably want to know how many amino acid differences there are between the human wild-type FOXP2 protein and that of the chimpanzee and whether these changes affect the function of the protein. (As we explain later in the text, there are two amino acid differences.) You know that humans with mutations in this gene have severe language impairment. You would want to learn more about the human mutations by checking whether they affect the same amino acids in the gene product that the chimpanzee sequence differences affect. If so, those amino acids might play an important role in the function of the protein in language. Going further, you could analyze the differences between the chimpanzee and mouse FOXP2 proteins. You might ask: Are they more similar than the chimpanzee and human proteins? (It turns out that the chimpanzee and mouse proteins have only one amino acid difference and thus are more similar than the chimpanzee and human proteins, which have two differences, and also are more similar than the human and mouse proteins, which have three differences.)

Concept Check 20.1

1. In the whole-genome shotgun approach, short fragments are generated by cutting the genome with multiple restriction enzymes. These fragments are cloned, sequenced, and then ordered by computer programs that identify overlapping regions.

Concept Check 20.2

1. Once the location of the gene has been identified, its sequence can be compared with that of genes from other closely related organisms. This will give a clue about its function. Since DNA sequences may vary widely among species, a scientist may compare the predicted protein sequence of the newly sequenced gene with available protein sequences, identify the protein domain, and thereby assign a function. Knock-out studies can also help in determining the function of a protein. **2.** Cancer is a disease caused by multiple factors. Focusing on a single gene or a single defect would mean ignoring other factors that may influence the cancer and even the behavior of the single gene being studied. The systems approach, because it takes into account many factors at the same time, is more likely to lead to an understanding of the causes and most useful treatments for cancer. **3.** Some of the transcribed region is accounted for by introns. The rest is transcribed into noncoding RNAs, including small RNAs, such as microRNAs (miRNAs), siRNAs, or piRNAs. These RNAs help regulate gene expression by blocking translation, causing degradation of mRNA, binding to the promoter and repressing transcription, or causing remodeling of chromatin structure. The longer noncoding RNAs (lncRNAs) may also contribute to gene regulation or to chromatin remodeling. **4.** Genome-wide association studies use the systems biology approach in that they consider the correlation of many single nucleotide polymorphisms (SNPs) with particular diseases, such as heart disease and diabetes, in an attempt to find patterns of SNPs that correlate with each disease.

Concept Check 20.3

1. Eukaryotes have far greater noncoding regions than prokaryotes in the form of introns and sequences between genes. **2.** At the top of the web page, you can see the number of genomes completed and those considered permanent drafts in a bar graph by year. Scrolling down, you can see the number of complete and incomplete sequencing projects by year, the number of projects by domain by year (the genomes of viruses and metagenomes are counted too, even though these are not "domains"), the phylogenetic distribution of bacterial genome projects, and projects by sequencing center. Finally, near the bottom, you can see a pie chart of the "Project Relevance of Bacterial Genome Projects," which shows that about 47% have medical relevance. The web page ends with another pie chart showing the sequencing centers for archaeal and bacterial projects. **3.** Prokaryotes are generally smaller cells than eukaryotic cells, and they reproduce by binary fission. The evolutionary process involved is natural selection for more quickly reproducing cells: The faster they can replicate their DNA and divide, the more likely they will be able to dominate a population of prokaryotes. The less DNA they have to replicate, then, the faster they will reproduce.

Concept Check 20.4

1. Simple sequence DNA refers to stretches of DNA that contain many copies of tandemly repeated short sequences. It is primarily located in telomeres and centromeres. **2.** The copy-and-paste transposon mechanism and retrotransposition **3.** In the rRNA gene family, identical transcription units for all three different RNA products are present in long arrays, repeated one after the other. The large number of copies of the rRNA genes enable organisms to produce the rRNA for enough ribosomes to carry out active protein synthesis, and the single transcription unit for the three rRNAs ensures that the relative amounts of the different rRNA molecules produced are correct—every time one rRNA is made, a copy of each of the other two is made as well. Rather than numerous identical units, each globin gene family consists of a relatively small number of nonidentical genes. The differences in the globin proteins encoded by these genes result in production of hemoglobin molecules adapted to particular developmental stages of the organism. **4.** The exons would be classified as exons (1.5%); the enhancer region containing the distal control elements, the region closer to the promoter containing the proximal control elements, and the promoter itself would be classified as regulatory sequences (5%); and the introns would be classified as introns (20%).

Concept Check 20.5

1. If meiosis is faulty, two copies of the entire genome can end up in a single cell. Errors in crossing over during meiosis can lead to one segment being duplicated while another is deleted. During DNA replication, slippage backward along the template strand can result in segment duplication. **2.** For either gene, a mistake in crossing over during meiosis could have occurred between the two copies of that gene, such that one ended up with a duplicated exon. (The other copy would have ended up with a deleted exon.) This could have happened several times, resulting in the multiple copies of a particular exon in each gene. **3.** Homologous transposable elements scattered throughout the genome provide sites where recombination can occur between different chromosomes. Movement of these elements into coding or regulatory sequences may change expression of genes, which can affect the phenotype in a way that is subject to natural selection. Transposable elements also can carry genes with them, leading to dispersion of genes and in some cases different patterns of expression. Transport of an exon during transposition and its insertion into a gene may add a new functional domain to the originally encoded protein, a type of exon shuffling. (For any of these changes to be heritable, they must happen in germ cells, cells that will give rise to gametes.) **4.** Because more offspring are born to women who have this inversion, it must provide some advantage during the process of reproduction and development. Because proportionally more offspring have this inversion, we would expect it to persist and spread in the population. (In fact, evidence in the study allowed the researchers to conclude that it has been increasing in proportion in the population.)

Concept Check 20.6

1. Because both humans and macaques are primates, their genomes are expected to be more similar than the macaque and mouse genomes are. The mouse lineage diverged from the primate lineage before the human and macaque lineages diverged. **2.** Homeotic genes differ in their *non*homeobox sequences, which determine the interactions of homeotic gene products with other transcription factors and hence which genes are regulated by the homeotic genes. These nonhomeobox sequences differ in the two organisms, as do the expression patterns of the homeobox genes. **3.** *Alu* elements must have undergone transposition more actively in the human genome for some reason. Their increased numbers may have then allowed more recombination errors in the human genome, resulting in more or different duplications. The divergence of the organization and content of the two genomes presumably made the chromosomes of each genome less similar to those of the other, thus accelerating divergence of the two species by making matings less and less likely to result in fertile offspring due to the mismatch of genetic information.

Summary of Key Concepts Questions

20.1 One focus of the Human Genome Project was to improve sequencing technology in order to speed up the process. During the project, many advances in sequencing technology allowed faster reactions and detection of products, which were therefore less expensive. **20.2** The most significant finding is that more than 75% of the human genome appears to be transcribed at some point in at least one of the cell types studied. Also, at least 80% of the genome contains an element that is functional, participating in gene regulation or maintaining chromatin structure in some way. The project was expanded to include other species to further investigate the functions of these transcribed DNA elements. It is necessary to carry out this type of analysis on the genomes of species that can be used in laboratory experiments. **20.3** (a) In general, bacteria and archaea have smaller genomes, lower numbers of genes, and higher gene density than eukaryotes. (b) Among eukaryotes, there is no apparent systematic relationship between genome size and phenotype. The number of genes is often lower than would be expected from the size of the genome—in other words, the gene density is often lower in larger genomes. (Humans are an example.) **20.4** Transposable element–related sequences can move from place to place in the genome, and a subset of these sequences make a new copy of themselves when they do so. Thus, it is not surprising that they make up a significant percentage of the genome, and this percentage might be expected to increase over evolutionary time. **20.5** Chromosomal rearrangements within a species lead to some individuals having different chromosomal arrangements. Each of these individuals could still undergo meiosis and produce gametes, and fertilization involving gametes with different chromosomal arrangements could result in viable offspring. However, during meiosis in the offspring, the maternal and paternal chromosomes might not be able to pair up, causing gametes with incomplete sets of chromosomes to form. Most often, when zygotes are produced from such gametes, they do not survive. Ultimately, a new species could form if two different chromosomal arrangements became prevalent within a population and individuals could mate successfully only with other individuals having the same arrangement. **20.6** Comparing the genomes of two closely related species can reveal information about more recent evolutionary events, perhaps events that resulted in the distinguishing characteristics of the two species. Comparing the genomes of very distantly related species can tell us about evolutionary events that occurred a very long time ago. For example, genes that are shared between two distantly related species must have arisen before the two species diverged.

Test Your Understanding

4.
1. ATETI...PKSSD...TSSTT...NARRD
2. ATETI...PKSSE...TSSTT...NARRD
3. ATETI...PKSSD...TSSTT...NARRD
4. ATETI...PKSSD...TSSNT...SARRD
5. ATETI...PKSSD...TSSTT...NARRD
6. VTETI...PKSSD...TSSTT...NARRD

(a) Lines 1, 3, and 5 are the C, G, R species. (b) Line 4 is the human sequence. See the above figure for the differences between the human and C, G, R sequences—the underlined amino acids at which the human sequence has an N where the C, G, R sequences have a T, and an S where C, G, R have an N. (c) Line 6 is the

O sequence. (d) See the above figure. There is one amino acid difference between the mouse (the circled E on line 2) and the C, G, R species (which have a D in that position). There are three amino acid differences between the mouse and the human. (The boxed E, T, and N in the mouse sequence are instead D, N, and S, respectively, in the human sequence.) (e) Because only one amino acid difference arose during the 60–100 million years since the mouse and C, G, R species diverged, it is somewhat surprising that two additional amino acid differences resulted during the 6 million years since chimpanzees and humans diverged. This indicates that the *FOXP2* gene has been evolving faster in the human lineage than in the lineages of other primates.

Chapter 21

Figure Questions

Figure 21.6 You should have circled the branch located at the far left of Figure 1.20. Although three of the descendants (*Certhidea olivacea, Camarhynchus pallidus*, and *Camarhynchus parvulus*) of this common ancestor ate insects, the other three species that descended from this ancestor did not eat insects. **Figure 21.8** The common ancestor lived about 5.5 million years ago. **Figure 21.12** The colors and body forms of these mantises allow them to blend into their surroundings, providing an example of how organisms are well suited for life in their environments. The mantises also share features with one another (and with other mantises), such as six legs, grasping forelimbs, and large eyes. These shared features illustrate another key observation about life: the unity that results from descent from a common ancestor. Over time, as these mantises diverged from a common ancestor, they accumulated different adaptations that made them well suited for life in their different environments. Eventually, as enough differences accumulated between mantis populations, new species were formed, thus contributing to the great diversity of life. **Figure 21.13** These results show that being reared from the egg stage on one plant species or the other did not result in the adult having a beak length appropriate for that host; instead, adult beak lengths were determined primarily by the population from which the eggs were obtained. Because an egg from a balloon vine population likely had long-beaked parents, while an egg from a goldenrain tree population likely had short-beaked parents, these results indicate that beak length is an inherited trait. **Figure 21.14** Both strategies should increase the time that it takes *S. aureus* to become resistant to a new drug. If a drug that harms *S. aureus* does not harm other bacteria, natural selection will not favor resistance to that drug in the other species. This would decrease the chance that *S. aureus* would acquire resistance genes from other bacteria—thus slowing the evolution of resistance. Similarly, selection for resistance to a drug that slows the growth but does not kill *S. aureus* is much weaker than selection for resistance to a drug that kills *S. aureus*—again slowing the evolution of resistance. **Figure 21.17** Based on this evolutionary tree, crocodiles are more closely related to birds than to lizards because they share a more recent common ancestor with birds (ancestor 5) than with lizards (ancestor 4). **Figure 21.20** Hind limb structure changed first. *Rodhocetus* lacked flukes, but its pelvic bones and hind limbs had changed substantially from how those bones were shaped and arranged in *Pakicetus*. For example, in *Rodhocetus*, the pelvis and hind limbs appear to be oriented for paddling, whereas they were oriented for walking in *Pakicetus*.

Concept Check 21.1

1. Hutton and Lyell proposed that geologic events in the past were caused by the same processes operating today, at the same gradual rate. This principle suggested that Earth must be much older than a few thousand years, the age that was widely accepted in the early 19th century. Hutton's and Lyell's ideas also stimulated Darwin to reason that the slow accumulation of small changes could ultimately produce the profound changes documented in the fossil record. In this context, the age of Earth was important to Darwin, because unless Earth was very old, he could not envision how there would have been enough time for evolution to occur. **2.** By this criterion, Cuvier's explanation of the fossil record and Lamarck's hypothesis of evolution are both scientific. Cuvier thought that species did not evolve over time. He also suggested that sudden, catastrophic events caused extinctions in particular areas and that such regions were later repopulated by a different set of species that immigrated from other areas. These assertions can be tested against the fossil record. Lamarck's principle of use and disuse can be used to make testable predictions for fossils of groups such as whale ancestors as they adapted to a new habitat. Lamarck's principle of use and disuse and his associated principle of the inheritance of acquired characteristics can also be tested directly in living organisms.

Concept Check 21.2

1. Organisms share characteristics (the unity of life) because they share common ancestors; the great diversity of life occurs because new species have repeatedly formed when descendant organisms gradually adapted to different environments, thereby becoming different from their ancestors. **2.** The fossil mammal species (or its ancestors) would most likely have colonized the Andes from within South America, whereas ancestors of mammals currently found in Asian mountains would most likely have colonized those mountains from other parts of Asia. As a result, the Andes fossil species would share a more recent common ancestor with South American mammals than with mammals in Asia. Thus, for many of its traits, the fossil mammal species would probably more closely resemble mammals that live in South American jungles than mammals that live on Asian mountains. It is also possible, however, that the Andean fossil mammal could resemble a mammal from the mountains of Asia because similar environments had selected for similar adaptations (even though the fossil and Asian species were only distantly related to one another). **3.** As long as the white phenotype (encoded by the genotype *pp*) continues to be favored by natural selection, the frequency of the *p* allele will likely increase over time in the population. If the proportion of white individuals increases relative to purple individuals, the frequency of the recessive *p* allele will also increase relative to that of the *p* allele, which only appears in purple individuals (some of which also carry a *p* allele).

Concept Check 21.3

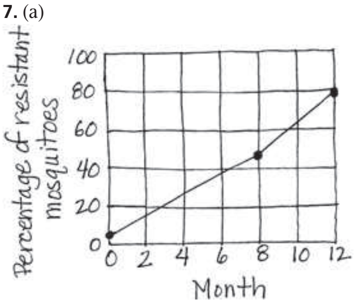
1. An environmental factor such as a drug does not create new traits, such as drug resistance, but rather selects for traits among those that are already present in the population. **2.** (a) Despite their different functions, the forelimbs of different mammals are structurally similar because they all represent modifications of a structure found in the common ancestor; thus, they are homologous structures. (b) In this case, the similar features of these mammals represent analogous features that arose by convergent evolution. The similarities between the sugar glider and flying squirrel indicate that similar environments selected for similar adaptations despite different ancestry. **3.** At the time that dinosaurs originated, Earth's landmasses formed a single large continent, Pangaea. Because many dinosaurs were large and mobile, it is likely that early members of these groups lived on many different parts of Pangaea. When Pangaea broke apart, fossils of these organisms would have moved with the rocks in which they were deposited. As a result, we would predict that fossils of early dinosaurs would have a broad geographic distribution (this prediction has been upheld).

Summary of Key Concepts Questions

Concept 21.1 Darwin thought that descent with modification occurred as a gradual, steplike process. The age of Earth was important to him because if Earth were only a few thousand years old (as conventional wisdom suggested), there wouldn't have been sufficient time for major evolutionary change. **Concept 21.2** All species have the potential to overreproduce—that is, to produce more offspring than can be supported by the environment. This ensures that there will be what Darwin called a "struggle for existence" in which many of the offspring are eaten, starved, diseased, or unable to reproduce for a variety of other reasons. Members of a population exhibit a range of heritable variations, some of which make it likely that their bearers will leave more offspring than other individuals (for example, the bearer may escape predators more effectively or be more tolerant of the physical conditions of the environment). Over time, natural selection resulting from factors such as predators, lack of food, or the physical conditions of the environment can increase the proportion of individuals with favorable traits in a population (evolutionary adaptation). **Concept 21.3** The hypothesis that cetaceans originated from a terrestrial mammal and are closely related to even-toed ungulates is supported by several lines of evidence. For example, fossils document that early cetaceans had hind limbs, as expected for organisms that descended from a land mammal; these fossils also show that cetacean hind limbs became reduced over time. Other fossils show that early cetaceans had a type of ankle bone that is otherwise found only in even-toed ungulates, providing strong evidence that even-toed ungulates are the land mammals to which cetaceans are most closely related. DNA sequence data also indicate that even-toed ungulates are the land mammals to which cetaceans are, most closely related.

Test Your Understanding

7. (a)



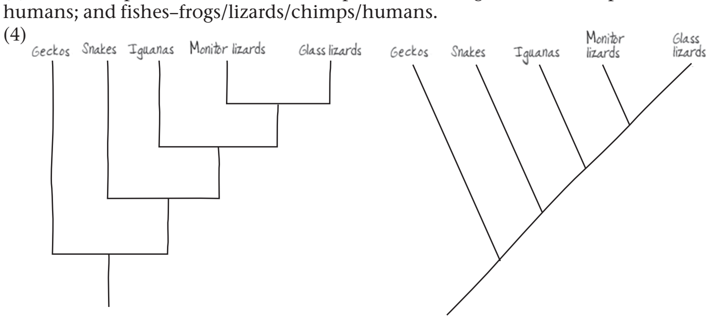
(b) The rapid rise in the percentage of mosquitoes resistant to DDT was most likely caused by natural selection in which mosquitoes resistant to DDT could survive and reproduce while other mosquitoes could not. (c) In India—where DDT resistance first appeared—natural selection would have caused the frequency of resistant mosquitoes to increase over time. If resistant mosquitoes then migrated from India (for example, transported by wind or in planes, trains, or ships) to other parts of the world, the frequency of DDT resistance would increase there as well. In addition, if resistance to DDT were to arise independently in mosquito populations outside of India, those populations would also experience an increase in the frequency of DDT resistance.

Chapter 22

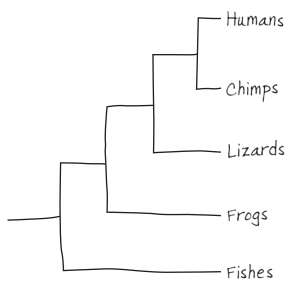
Figure Questions

Figure 22.5 (1) Frogs are most closely related to a group consisting of lizards, chimps, and humans in this tree. (2) You should have circled the branch point splitting the frog lineage from the lineage leading to lizards, chimps, and humans. (3) Four: chimps–humans, lizards–chimps/humans; frogs–lizards/chimps/humans; and fishes–frogs/lizards/chimps/humans.

(4)



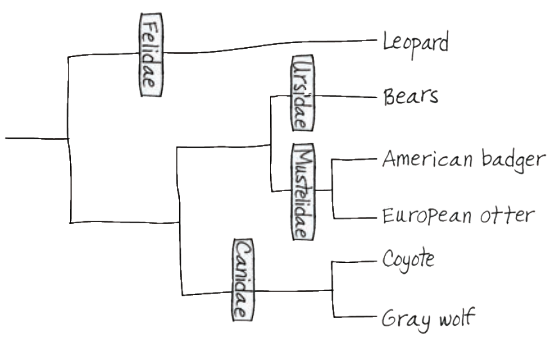
(5)



Each of the three trees identifies chimps and lizards as the two closest relatives of humans in these trees as they are the groups shown with whom we share the most recent common ancestors. **Figure 22.6** Unknown 1b (a portion of sample 1) and unknowns 9–13 all would have to be located on the branch of the tree that currently leads to Minke (Southern Hemisphere) and unknowns 1a and 2–8. **Figure 22.11** You should have circled the branch point that is drawn farthest to the left (the common ancestor of all taxa shown). Both cetaceans and seals descended from terrestrial lineages of mammals, indicating that the cetacean–seal common ancestor lacked a streamlined body form and hence would not be part of the cetacean–seal group. **Figure 22.12** Hinged jaws are a shared ancestral character for the group that includes frogs, turtles, and leopards. Thus, you should have circled the frog, turtle, and leopard lineages, along with their most recent common ancestor. **Figure 22.16** Crocodilians are the sister taxon to the dinosaur clade (which includes birds) because crocodilians and the dinosaur clade share an immediate common ancestor that is not shared by any other group. **Figure 22.21** This tree indicates that the sequences of rRNA and other genes in mitochondria are most closely related to those of proteobacteria, while the sequences of chloroplast genes are most closely related to those of cyanobacteria. These gene sequence relationships are what would be predicted from endosymbiont theory, which posits that both mitochondria and chloroplasts originated as engulfed prokaryotic cells.

Concept Check 22.1

1. We are classified the same from the domain level to the class level; both the leopard and human are mammals. Leopards belong to order Carnivora, whereas humans do not. **2.** The tree in (c) shows a different pattern of evolutionary relationships. In (c), C and B are sister taxa, whereas C and D are sister taxa in (a) and (b). **3.** The redrawn version of Figure 22.4 is shown below.



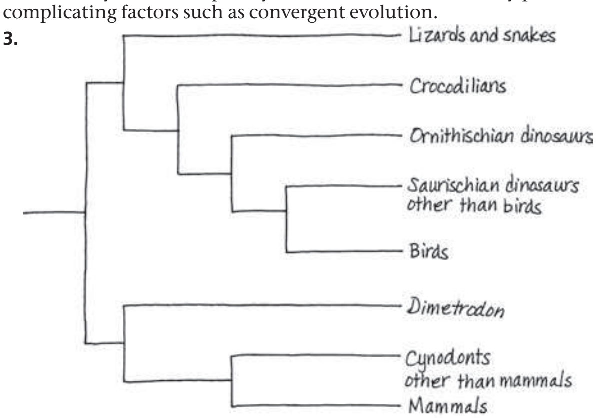
Concept Check 22.2

1. (a) Analogy, since porcupines and cacti are not closely related and since most other animals and plants do not have similar structures; (b) homology, since cats and humans are both mammals and have homologous forelimbs, of which the hand and paw are the lower part; (c) analogy, since owls and hornets are not closely related and since the structure of their wings is very different. **2.** Species B and C are more likely to be closely related. Small genetic changes (as between species B and C) can produce divergent physical appearances, but if many genes have diverged greatly (as in species A and B), then the lineages have probably been separate for a long time.

Concept Check 22.3

1. No; hair is a shared ancestral character common to all mammals and thus is not helpful in distinguishing different mammalian subgroups. **2.** The principle of maximum parsimony states that the hypothesis about nature we investigate first should be the simplest explanation found to be consistent with the facts. Actual evolutionary relationships may differ from those inferred by parsimony owing to complicating factors such as convergent evolution.

3.



The traditional classification provides a poor match to evolutionary history, thus violating the basic principle of cladistics—that classification should be based on common descent. Both birds and mammals originated from groups traditionally designated as reptiles, making reptiles (as traditionally delineated) a paraphyletic group. These problems can be addressed by removing *Dimetrodon* and cynodonts from the reptiles and by regarding birds as a group of reptiles (specifically, as a group of dinosaurs).

Concept Check 22.4

1. Proteins are gene products. Their amino acid sequences are determined by the nucleotide sequences of the DNA that codes for them. Thus, differences between comparable proteins in two species reflect underlying genetic differences that have accumulated as the species diverged from one another. As a result, differences between the proteins can reflect the evolutionary history of the species. **2.** These observations suggest that the evolutionary lineages leading to species 1 and species 2 diverged from one another before a gene duplication event in species 1 produced gene B from gene A. **3.** In RNA processing, the exons or coding regions of a gene can be spliced together in different ways, yielding different mRNAs and hence different protein products. As a result, different proteins could potentially be produced from the same gene in different tissues, thereby enabling the gene to perform different functions in these different tissues.

Concept Check 22.5

1. A molecular clock is a method of estimating the actual time of evolutionary events based on numbers of base changes in orthologous genes. It is based on the assumption that the regions of genomes being compared evolve at constant rates. **2.** There are many portions of the genome that do not code for genes; mutations that alter the sequence of bases in such regions could accumulate through drift without affecting an organism's fitness. Even in coding regions of the genome, some mutations may not have a critical effect on genes or proteins. **3.** The gene (or genes) used for the molecular clock may have evolved more slowly in these two taxa than in the species used to calibrate the clock; as a result, the clock would underestimate the time at which the taxa diverged from each other.

Concept Check 22.6

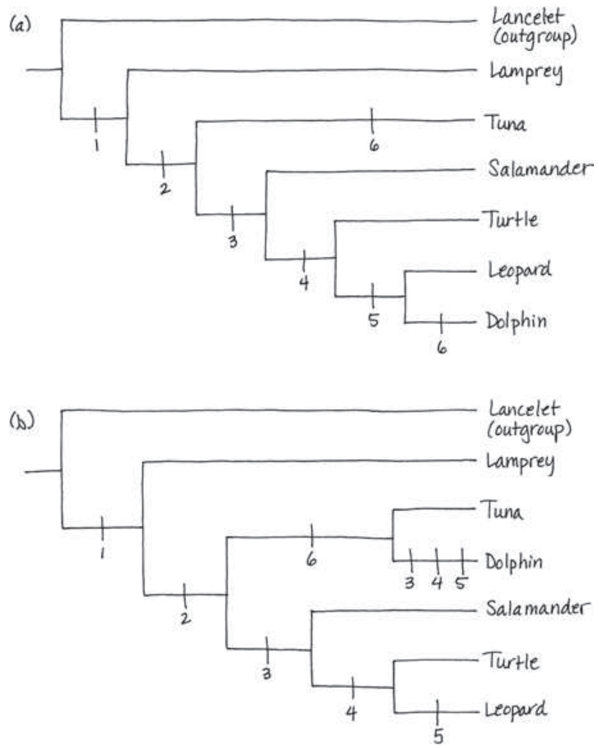
1. The kingdom Monera included bacteria and archaea, but we now know that these organisms are in separate domains. Kingdoms are subsets of domains, so a single kingdom (like Monera) that includes taxa from different domains is not valid. **2.** Because of horizontal gene transfer, some genes in eukaryotes are more closely related to bacteria, while others are more closely related to archaea; thus, depending on which genes are used, phylogenetic trees constructed from DNA data can yield conflicting results. **3.** Eukaryotes are hypothesized to have originated when a heterotrophic prokaryote (an archaeal host cell) engulfed a bacterium that would later become an organelle found in all eukaryotes—the mitochondrion. Over time, a fusion of organisms occurred as the archaeal host cell and its bacterial endosymbiont evolved to become a single organism. As a result, we would expect the cell of a eukaryote to include both archaeal DNA and bacterial DNA, making the origin of eukaryotes an example of horizontal gene transfer.

Summary of Key Concepts Questions

22.1 The fact that humans and chimpanzees are sister species indicates that we share a more recent common ancestor with chimpanzees than we do with any other living primate species. But that does not mean that humans evolved from chimpanzees, or vice versa; instead, it indicates that both humans and chimpanzees are descendants of that common ancestor. **22.2** Homologous characters result from shared ancestry. As organisms diverge over time, some of their homologous characters will also diverge. The homologous characters of organisms that diverged long ago typically differ more than do the homologous characters of organisms that diverged more recently. As a result, differences in homologous characters can be used to infer phylogeny. In contrast, analogous characters result from convergent evolution, not shared ancestry, and hence can give misleading estimates of phylogeny. **22.3** All features of organisms arose at some point in the history of life. In the group in which a new feature first arose, that feature is a shared derived character that is unique to that clade. The group in which each shared derived character first appeared can be determined, and the resulting nested pattern can be used to infer evolutionary history. **22.4** Orthologous genes should be used; for such genes, the homology results from speciation and hence reflects evolutionary history. **22.5** A key assumption of molecular clocks is that nucleotide substitutions occur at fixed rates, and hence the number of nucleotide differences between two DNA sequences is proportional to the time since the sequences diverged from each other. Some limitations of molecular clocks: No gene marks time with complete precision; natural selection can favor certain DNA changes over others; nucleotide substitution rates can change over long periods of time (causing molecular clock estimates of when events in the distant past occurred to be highly uncertain); and the same gene can evolve at different rates in different organisms. **22.6** Genetic data indicated that many prokaryotes differed as much from each other as they did from eukaryotes. This indicated that organisms should be grouped into three "super-kingdoms," or domains (Archaea, Bacteria, Eukarya). These data also indicated that the previous kingdom Monera (which had contained all the prokaryotes) did not make biological sense and should be abandoned. Later genetic and morphological data also indicated that the former kingdom Protista (which had primarily contained single-celled organisms) should be abandoned because some protists are more closely related to plants, fungi, or animals than they are to other protists.

Test Your Understanding

9.



(c) The tree in (a) requires seven evolutionary changes, while the tree in (b) requires nine evolutionary changes. Thus, the tree in (a) is more parsimonious, since it requires fewer evolutionary changes.

Chapter 23

Figure Questions

Figure 23.4 The genetic code is redundant, meaning that more than one codon can specify the same amino acid. As a result, a substitution at a particular site in a coding region of the *Adh* gene might change the codon but not the translated amino acid, and thus not the resulting protein encoded by the gene. One way an insertion in an exon would not affect the gene produced is if it occurs in an untranslated region of the exon. (This is the case for the insertion at location 1,703.) **Figure 23.7** There should be 24 red balls. **Figure 23.8** The predicted frequencies are 36% C^RC^R, 48% C^RC^W, and 16% C^WC^W. **Figure 23.9** Overall, by chance the frequency of the C^W allele first increases in generation 2 and then falls to zero in generation 3—causing the C^R allele to become fixed (reach a frequency of 100%). **Figure 23.12** The frequency of banded color patterns in island populations would probably increase. Since mainland populations did not decline in size, the number of individuals migrating from the mainland to the islands would probably not decline either. As a result, after island populations had decreased in size, alleles encoding banded coloration that were transferred from the mainland would comprise a larger proportion of the gene pool in island populations. This would cause the frequency of banded color patterns in island populations to increase. **Figure 23.13** Directional selection. Goldenrain tree has smaller fruit than does the native host, balloon vine. Thus, in soapberry bug populations feeding on goldenrain tree, bugs with shorter beaks had an advantage, resulting in directional selection for shorter beak length. **Figure 23.16** Crossing a single female's eggs with both an SC and an LC male's sperm allowed the researchers to directly compare the effects of the males' contribution to the next generation, since both batches of offspring had the same maternal contribution. This isolation of the male's impact enabled researchers to draw conclusions about differences in genetic "quality" between the SC and LC males. **Figure 23.18** Under prolonged low-oxygen conditions, some of the red blood cells of a heterozygote may sickle, leading to harmful effects. This does not occur in individuals with two wild-type hemoglobin alleles, suggesting that there may be selection against heterozygotes in malaria-free regions (where heterozygote advantage does not occur). However, since heterozygotes are healthy under most conditions, selection against them is unlikely to be strong.

Concept Check 23.1

1. Within a population, genetic differences among individuals provide the raw material on which natural selection and other mechanisms can act. Without such differences, allele frequencies could not change over time—and hence the population could not evolve. **2.** Many mutations occur in somatic cells, which do not produce gametes and so are lost when the organism dies. Of mutations that do occur in cell lines that produce gametes, many do not have a phenotypic effect on which natural selection can act. Others have a harmful effect and are thus unlikely to increase in frequency because they decrease the reproductive success of their bearers. **3.** Its genetic variation (whether measured at the level of the gene or at the level of nucleotide sequences) would probably drop over time. During meiosis, crossing over and the independent assortment of chromosomes produce many new combinations of alleles. In addition, a population contains a vast number of possible mating combinations, and fertilization brings together the gametes of individuals with different genetic backgrounds. Thus, via crossing over, independent assortment of chromosomes, and fertilization, sexual reproduction reshuffles alleles into fresh combinations each generation. Without sexual reproduction, the rate of forming new combinations of alleles would be vastly reduced, causing the overall amount of genetic variation to drop.

Concept Check 23.2

1. Each individual has two alleles, so the total number of alleles is 1,400. To calculate the frequency of allele A, note that each of the 85 individuals of genotype AA has two A alleles, each of the 320 individuals of genotype Aa has one A allele, and each of the 295 individuals of genotype aa has zero A alleles. Thus, the frequency (p) of allele A is

$$p = \frac{(2 \times 85) + (1 \times 320) + (0 \times 295)}{1{,}400} = 0.35$$

There are only two alleles (A and a) in our population, so the frequency of allele a must be $q = 1 - p = 0.65$. **2.** Because the frequency of allele a is 0.45, the frequency of allele A must be 0.55. Thus, the expected genotype frequencies are $p^2 = 0.3025$ for genotype AA, $2pq = 0.495$ for genotype Aa, and $q^2 = 0.2025$ for genotype aa. **3.** There are 120 individuals in the population, so there are 240 alleles. Of these, there are 124 V alleles—32 from the 16 VV individuals and 92 from the 92 Vv individuals. Thus, the frequency of the V allele is $p = 124/240 = 0.52$; hence, the frequency of the v allele is $q = 0.48$. Based on the Hardy-Weinberg equation, if the population were not evolving, the frequency of genotype VV should be $p^2 = 0.52 \times 0.52 = 0.27$; the frequency of genotype Vv should be $2pq = 2 \times 0.52 \times 0.48 = 0.5$; and the frequency of genotype vv should be $q^2 = 0.48 \times 0.48 = 0.23$. In a population of 120 individuals, these expected genotype frequencies lead us to predict that there would be 32 VV individuals (0.27×120), 60 Vv individuals (0.5×120), and 28 vv individuals (0.23×120). The actual numbers for the population (16 VV, 92 Vv, 12 vv) deviate from these expectations (fewer homozygotes and more heterozygotes than expected). This indicates that the population is not in Hardy-Weinberg equilibrium and hence may be evolving at this locus.

Concept Check 23.3

1. Natural selection is more "predictable" in that it alters allele frequencies in a nonrandom way: It tends to increase the frequency of alleles that increase the organism's reproductive success in its environment and decrease the frequency of alleles that decrease the organism's reproductive success. Alleles subject to genetic drift increase or decrease in frequency by chance alone, whether or not they are advantageous. **2.** Genetic drift results from chance events that cause allele frequencies to fluctuate at random from generation to generation; within a population, this process tends to decrease genetic variation over time. Gene flow is the transfer of alleles between populations, a process that can introduce new alleles to a population and hence may increase its genetic variation (albeit slightly, since rates of gene flow are often low). **3.** Selection is not important at this locus; furthermore, the populations are not small, and hence the effects of genetic drift should not be pronounced. Gene flow is occurring via the movement of pollen and seeds. Thus, allele and genotype frequencies in these populations should become more similar over time as a result of gene flow.

Concept Check 23.4

1. The relative fitness of a mule is zero, because fitness includes reproductive contribution to the next generation, and a sterile mule cannot produce offspring. **2.** Although both gene flow and genetic drift can increase the frequency of advantageous alleles in a population, they can also decrease the frequency of advantageous alleles or increase the frequency of harmful alleles. Only natural selection *consistently* results in an increase in the frequency of alleles that enhance survival or reproduction. Thus, natural selection is the only mechanism that consistently leads to adaptive evolution. **3.** The three modes of natural selection (directional, stabilizing, and disruptive) are defined in terms of the selective advantage of different *phenotypes*, not different genotypes. Thus, the type of selection represented by heterozygote advantage depends on the phenotype of the heterozygotes. In this question, because heterozygous individuals have a more extreme phenotype than either homozygote, heterozygote advantage represents directional selection.

Summary of Key Concepts Questions

23.1 Much of the nucleotide variability at a genetic locus occurs within introns. Nucleotide variation at these sites typically does not affect the phenotype because introns do not code for the protein product of the gene. (Note: In certain circumstances, it is possible that a change in an intron could affect RNA splicing and ultimately have some phenotypic effect on the organism, but such mechanisms are not covered in this introductory text.) There are also many variable nucleotide sites within exons. However, most of the variable sites within exons reflect changes to the DNA sequence that do not change the sequence of amino acids encoded by the gene (and hence may not affect the phenotype). **23.2** No, this is not an example of circular reasoning. Calculating p and q from observed genotype frequencies does not imply that those genotype frequencies must be in Hardy-Weinberg equilibrium. For example, consider a population that has 195 individuals of genotype *AA*, 10 of genotype *Aa*, and 195 of genotype *aa*. Calculating *p* and *q* from these values yields $p = q = 0.5$. Using the Hardy-Weinberg equation, the predicted equilibrium frequencies are $p^2 = 0.25$ for genotype *AA*, $2pq = 0.5$ for genotype *Aa*, and $q^2 = 0.25$ for genotype *aa*. Since there are 400 individuals in the population, these predicted genotype frequencies indicate that there should be 100 *AA* individuals, 200 *Aa* individuals, and 100 *aa* individuals—numbers that differ greatly from the values that we used to calculate *p* and *q*. **23.3** It is unlikely that two such populations would evolve in similar ways. Since their environments are very different, the alleles favored by natural selection would probably differ between the two populations. Although genetic drift may have important effects in each of these small populations, drift causes unpredictable changes in allele frequencies, so it is unlikely that drift would cause the populations to evolve in similar ways. Both populations are geographically isolated, suggesting that little gene flow would occur between them (again making it less likely that they would evolve in similar ways). **23.4** Compared to males, it is likely that the females of such species would be larger, more colorful, endowed with more elaborate ornamentation (for example, a large morphological feature such as the peacock's tail), and more apt to engage in behaviors intended to attract mates or prevent other members of their sex from obtaining mates.

Chapter 24

Figure Questions

Figure 24.7 If this had not been done, the strong preference of "starch flies" and "maltose flies" to mate with like-adapted flies could have occurred simply because the flies could detect (for example, by sense of smell) what their potential mates had eaten as larvae—and preferred to mate with flies that had a similar smell to their own. **Figure 24.12** In murky waters where females distinguish colors poorly, females of each species might mate often with males of the other species. Hence, since hybrids between these species are viable and fertile, the gene pools of the two species might become more similar over time. **Figure 24.13** The graph indicates that there has been gene flow of some fire-bellied toad alleles into the range of the yellow-bellied toad. Otherwise, all individuals located to the left of the hybrid zone portion of the graph would have allele frequencies equal to 1. **Figure 24.14** Because the populations had only just begun to diverge from one another at this point in the process, it is likely that any existing barriers to reproduction would weaken over time. **Figure 24.18** Over time, the chromosomes of the experimental hybrids came to resemble those of *H. anomalus*. This occurred even though conditions in the laboratory differed greatly from conditions in the field, where *H. anomalus* is found, suggesting that selection for laboratory conditions was not strong. Thus, it is unlikely that the observed rise in the fertility of the experimental hybrids was due to selection for life under laboratory conditions. **Figure 24.19** The presence of *M. cardinalis* plants that carry the *M. lewisii yup* allele would make it more likely that bumblebees would transfer pollen between the two monkey flower species. As a result, we would expect the number of hybrid offspring to increase.

Concept Check 24.1

1. (a) All except the biological species concept can be applied to both asexual and sexual species because they define species on the basis of characteristics other than the ability to reproduce. In contrast, the biological species concept can be applied only to sexual species. (b) The easiest species concept to apply in the field would be the morphological species concept because it is based only on the appearance of the organism. Additional information about its ecological habits or reproduction is not required. **2.** Because these birds live in fairly similar environments and can breed successfully in captivity, the reproductive barrier in nature is probably prezygotic; given the species' differences in habitat preference, this barrier could result from habitat isolation.

Concept Check 24.2

1. In allopatric speciation, a new species forms while in geographic isolation from its parent species; in sympatric speciation, a new species forms in the absence of geographic isolation. Geographic isolation greatly reduces gene flow between populations, whereas ongoing gene flow is more likely in sympatric populations. As a result, allopatric speciation is more common than sympatric speciation. **2.** Gene flow between subsets of a population that live in the same area can be reduced in a variety of ways. In some species—especially plants—changes in chromosome number can block gene flow and establish reproductive isolation in a single generation. Gene flow can also be reduced in sympatric populations by habitat differentiation (as seen in the apple maggot fly, *Rhagoletis*) and sexual selection (as seen in Lake Victoria cichlids). **3.** Allopatric speciation would be less likely to occur on an island near a mainland than on a more isolated island of the same size. We expect this result because continued gene flow between mainland populations and those on a nearby island reduces the chance that enough genetic divergence will take place for allopatric speciation to occur. **4.** If all of the homologs failed to separate during anaphase I of meiosis, some gametes would end up with an extra set of chromosomes (and others would end up with no chromosomes). If a gamete with an extra set of chromosomes fused with a normal gamete, a triploid would result; if two gametes with an extra set of chromosomes fused with each other, a tetraploid would result.

Concept Check 24.3

1. Hybrid zones are regions in which members of different species meet and mate, producing some offspring of mixed ancestry. Such regions can be viewed as "natural laboratories" in which to study speciation because scientists can directly observe factors that cause (or fail to cause) reproductive isolation. **2.** (a) If hybrids consistently survived and reproduced poorly compared with the offspring of intraspecific matings, reinforcement could occur. If it did, natural selection would cause prezygotic barriers to reproduction between the parent species to strengthen over time, decreasing the production of unfit hybrids and leading to a completion of the speciation process. (b) If hybrid offspring survived and reproduced as well as the offspring of intraspecific matings, indiscriminate mating between the parent species would lead to the production of large numbers of hybrid offspring. As these hybrids mated with each other and with members of both parent species, the gene pools of the parent species could fuse over time, reversing the speciation process.

Concept Check 24.4

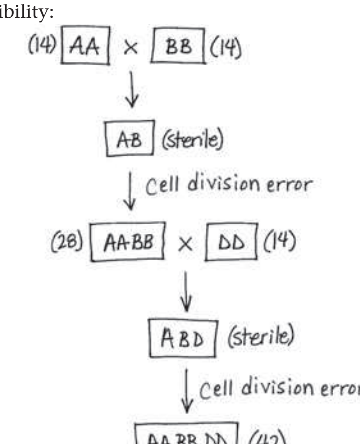
1. The time between speciation events includes (1) the length of time that it takes for populations of a newly formed species to begin diverging reproductively from one another and (2) the time it takes for speciation to be complete once this divergence begins. Although speciation can occur rapidly once populations have begun to diverge from one another, it may take millions of years for that divergence to begin. **2.** Investigators transferred alleles at the *yup* locus (which influences flower color) from each parent species to the other. *M. lewisii* plants with an *M. cardinalis yup* allele received many more visits from hummingbirds than usual; hummingbirds usually pollinate *M. cardinalis* but avoid *M. lewisii*. Similarly, *M. cardinalis* plants with an *M. lewisii yup* allele received many more visits from bumblebees than usual; bumblebees usually pollinate *M. lewisii* and avoid *M. cardinalis*. Thus, alleles at the *yup* locus can influence pollinator choice, which in these species provides the primary barrier to interspecific mating. Nevertheless, the experiment does not prove that the *yup* locus alone controls barriers to reproduction between *M. lewisii* and *M. cardinalis*; other genes might enhance the effect of the *yup* locus (by modifying flower color) or cause entirely different barriers to reproduction (for example, gametic isolation or a postzygotic barrier). **3.** Crossing over. If crossing over did not occur, each chromosome in an experimental hybrid would remain as in the F_1 generation: composed entirely of DNA from one parent species or the other.

Summary of Key Concepts Questions

24.1 According to the biological species concept, a species is a group of populations whose members interbreed and produce viable, fertile offspring; thus, gene flow occurs between populations of a species. In contrast, members of different species do not interbreed and hence no gene flow occurs between their populations. Overall, then, in the biological species concept, species can be viewed as designated by the *absence* of gene flow—making gene flow of central importance to the biological species concept. **24.2** Yes. Sympatric speciation can be promoted by factors such as polyploidy, sexual selection, and habitat shifts, all of which can reduce gene flow between the subpopulations of a larger population. But such factors can also occur in allopatric populations and hence can also promote allopatric speciation. **24.3** If the hybrids are selected against, the hybrid zone could persist if individuals from the parent species regularly travel into the zone, where they mate to produce hybrid offspring. If hybrids are not selected against, there is no cost to the continued production of hybrids, and large numbers of hybrid offspring may be produced. However, natural selection for life in different environments may keep the gene pools of the two parent species distinct, thus preventing the loss (by fusion) of the parent species and once again causing the hybrid zone to be stable over time. **24.4** As the goatsbeard plant, Bahamas mosquitofish, and apple maggot fly illustrate, speciation continues to happen today. A new species can begin to form whenever gene flow is reduced between populations of the parent species. Such reductions in gene flow can occur in many ways: A new, geographically isolated population may be founded by a few colonists; some members of the parent species may begin to utilize a new habitat; or sexual selection may isolate formerly connected populations or subpopulations. These and many other such events are happening today.

Test Your Understanding

7. Here is one possibility:



Chapter 25

Figure Questions

Figure 25.2 Proteins are almost always composed of the same 20 amino acids shown in Figure 5.14. However, many other amino acids could potentially form in this or any other experiment. For example, any molecule that had an R group that differed from those listed in Figure 5.14 would still be an amino acid as long as it also contained an α carbon, an amino group, and a carboxyl group—but that molecule would not be one of the 20 amino acids commonly found in nature. **Figure 25.4** The hydrophobic regions of such molecules are attracted to one another and excluded from water, whereas the hydrophilic regions have an affinity for water. As a result, the molecules can form a bilayer in which the hydrophilic regions are on the outside of the bilayer (facing water on each side of the bilayer) and the hydrophobic regions point toward each other (that is, toward the inside of the bilayer). **Figure 25.6** Because uranium-238 has a half-life of 4.5 billion years, the *x*-axis would be relabeled (in billions of years) as 4.5, 9, 13.5, and 18. **Figure 25.8** (1) The countdown timer and horizontal time scale indicate that prokaryotes originated 3.5 billion years ago and that the colonization of land took place 500 million years ago. On a 1-hour time scale, this indicates that prokaryotes appeared about 46 minutes ago, while the colonization of land took place less than 7 minutes ago. (2) From 3.5 billion years ago to 1.5 billion years ago, life on Earth consisted entirely of unicellular organisms. In fact, from 3.5 billion years ago to 1.8 billion years ago, all of Earth's organisms were prokaryotes; from 1.8 billion years ago until 1.5 billion years ago, these unicellular prokaryotes were joined by unicellular eukaryotes. The colonization of land did not occur until 500 million years ago. Hence, we can also infer that all or most of these unicellular organisms lived in the oceans or in freshwater environments for the first two billion years of life on Earth. **Figure 25.11** You should have circled the node, shown in the tree diagram at approximately 635 million years ago (mya), that leads to the echinoderm/chordate lineage and to the lineage that gave rise to brachiopods, annelids, molluscs, and arthropods. To determine a minimum estimate of the age of the ancestor represented by this node, note that the most recent common ancestor of chordates and annelids must be at least as old as any of its descendants. Since fossil molluscs date to about 560 mya, the common ancestor represented by the circled branch point must be at least 560 million years old. **Figure 25.16** The Australian plate's current direction of movement is roughly similar to the northeasterly direction the continent traveled over the past 66 million years. **Figure 25.26** The coding sequence of the *Pitx1* gene would differ between the marine and lake populations, but patterns of gene expression would not.

Concept Check 25.1

1. The several hypotheses related to the origin of organic molecules suggest that the synthesis could have been possible because of early Earth's reducing (electron-adding) atmosphere or due to the presence of deep-sea hydrothermal vents or alkaline vents. **2.** In contrast to random mingling of molecules in an open solution, segregation of molecular systems by membranes could concentrate organic molecules, assisting biochemical reactions. **3.** Today, genetic information usually flows from DNA to RNA, as when the DNA sequence of a gene is used as a template to synthesize the mRNA encoding a particular protein. However, the life cycle of retroviruses such as HIV shows that genetic information can flow in the reverse direction (from RNA to DNA). In these viruses, the enzyme reverse transcriptase uses RNA as a template for DNA synthesis, suggesting that a similar enzyme could have played a key role in the transition from an RNA world to a DNA world.

Concept Check 25.2

1. The fossil record shows that different groups of organisms dominated life on Earth at different points in time and that many organisms once alive are now extinct; specific examples of these points can be found in Figure 25.5. The fossil record also indicates that new groups of organisms can arise via the gradual modification of previously existing organisms, as illustrated by fossils that document the origin of mammals from their cynodont ancestors (see Figure 25.7). **2.** 22,920 years (four half-lives: $5{,}730 \times 4$)

Concept Check 25.3

1. Free oxygen attacks chemical bonds and can inhibit enzymes and damage cells. As a result, the appearance of oxygen in the atmosphere probably caused many prokaryotes that had thrived in anaerobic environments to survive and reproduce poorly, ultimately driving many of these species to extinction. **2.** All eukaryotes have mitochondria or remnants of these organelles, but not all eukaryotes have plastids. **3.** A fossil record of life today would include many organisms with hard body parts (such as vertebrates and many marine invertebrates), but might not include some species we are very familiar with, such as those that have small geographic ranges and/or small population sizes (for example, endangered species such as the giant panda, tiger, and several rhinoceros species).

Concept Check 25.4

1. The theory of plate tectonics describes the movement of Earth's continental plates, which alters the physical geography and climate of Earth, as well as the extent to which organisms are geographically isolated. Because these factors affect extinction and speciation rates, plate tectonics has a major impact on life on Earth. **2.** Mass extinctions; major evolutionary innovations; the diversification of another group of organisms (which can provide new sources of food); migration to new locations where few competitor species exist **3.** In theory, fossils of both common and rare species would be present right up to the time of the catastrophic event, then disappear. Reality is more complicated because the fossil record is not perfect. So the most recent fossil for a species might be a million years before the mass extinction—even though the species did not become extinct *until* the mass extinction. This complication is especially likely for rare species because few of their fossils will form and be discovered. Hence, for many rare species, the fossil record would not document that the species was alive immediately before the extinction (even if it was).

Concept Check 25.5

1. Heterochrony can cause a variety of morphological changes. For example, if the onset of sexual maturity changes, a retention of juvenile characteristics (paedomorphosis) may result. Paedomorphosis can be caused by small genetic changes that result in large changes in morphology, as seen in the axolotl salamander. **2.** In animal embryos, *Hox* genes influence the development of structures such as limbs and feeding appendages. As a result, changes in these genes—or in the regulation of these genes—are likely to have major effects on morphology. **3.** From genetics, we know that gene regulation is altered by how well transcription factors bind to noncoding DNA sequences called control elements. Thus, if changes in morphology are often caused by changes in gene regulation, portions of noncoding DNA that contain control elements are likely to be strongly affected by natural selection.

Concept Check 25.6

1. Complex structures do not evolve all at once, but in increments, with natural selection selecting for adaptive variants of the earlier versions. **2.** Although the myxoma virus is highly lethal, initially some of the rabbits are resistant (0.2% of infected rabbits are not killed). Thus, assuming resistance is an inherited trait, we would expect the rabbit population to show a trend for increased resistance to the virus. We would also expect the virus to show an evolutionary trend toward reduced lethality. We would expect this trend because a rabbit infected with a less lethal virus would be more likely to live long enough for a mosquito to bite it and hence potentially transmit the virus to another rabbit. (A virus that kills its rabbit host before a mosquito transmits the virus to another rabbit dies with its host.)

Summary of Key Concepts Questions

Concept 25.1 Particles of montmorillonite clay may have provided surfaces on which organic molecules became concentrated and hence were more likely to react with one another. Montmorillonite clay particles may also have facilitated the transport of key molecules, such as short strands of RNA, into vesicles. These vesicles can form spontaneously from simple precursor molecules, "reproduce" and "grow" on their own, and maintain internal concentrations of molecules that differ from those in the surrounding environment. These features of vesicles represent key steps in the emergence of protocells and (ultimately) the first living cells. **Concept 25.2** One challenge is that radioisotopes with very long half-lives are not used by organisms to build their bones or shells. As a result, fossils older than 75,000 years cannot be dated directly. Fossils are often found in sedimentary rock, but those rocks typically contain sediments of different ages, again posing a challenge when trying to date old fossils. To circumvent these challenges, geologists use radioisotopes with long half-lives to date layers of volcanic rock that surround old fossils. This approach provides minimum and maximum estimates for the ages of fossils sandwiched between two layers of volcanic rock. **Concept 25.3** The "Cambrian explosion" refers to a relatively short interval of time (535–525 million years ago) during which large forms of many present-day animal phyla first appear in the fossil record. The evolutionary changes that occurred during this time, such as the appearance of large predators and well-defended prey, were important because they set the stage for many of the key events in the history of life over the last 500 million years. **Concept 25.4** The broad evolutionary changes documented by the fossil record reflect the rise and fall of major groups of organisms. In turn, the rise or fall of any particular group results from a balance between speciation and extinction rates: A group increases in size when the rate at which its members produce new species is greater than the rate at which its member species are lost to extinction, while a group shrinks in size if extinction rates are greater than speciation rates. **Concept 25.5** A change in the sequence or regulation of a developmental gene can produce major morphological changes. In some cases, such morphological changes may enable organisms to perform new functions or live in new environments—thus potentially leading to an adaptive radiation and the formation of a new group of organisms. **Concept 25.6** Evolutionary change results from interactions between organisms and their current environments. No goal is involved in this process. As environments change over time, the features of organisms favored by natural selection may also change. When this happens, what once may have seemed like a "goal" of evolution (for example, improvements in the function of a feature previously favored by natural selection) may cease to be beneficial or may even be harmful.

Chapter 26

Figure Questions

Figure 26.2 Beijerinck might have concluded that the agent was a toxin produced by the plant that was able to pass through a filter but that became more and more dilute. In this case, he would have concluded that the infectious agent could not replicate.

Figure 26.4

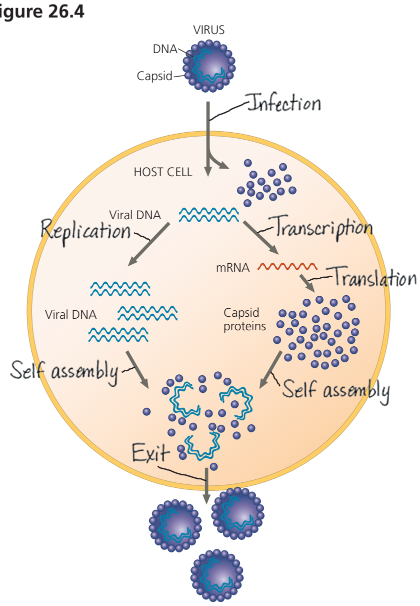


Figure 26.9 The main protein on the cell surface that HIV binds to is called CD4. However, HIV also requires a "co-receptor," which in many cases is a protein called CCR5. HIV binds to both of these proteins together and then is taken into the cell. Researchers discovered this requirement by studying individuals who seemed to be resistant to HIV infection despite multiple exposures. These individuals turned out to have mutations in the gene that encodes CCR5 such that the protein apparently cannot act as a co-receptor, and so HIV can't enter and infect cells.

Concept Check 26.1

1. TMV consists of one molecule of RNA surrounded by a helical array of proteins. The influenza virus has eight molecules of RNA, each associated with proteins and wound into a double helix. Another difference between the viruses is that the influenza virus has an outer envelope and TMV does not. **2.** The T2 phages were an excellent choice for use in the Hershey-Chase experiment because they consist of only DNA surrounded by a protein coat, and DNA and protein were the two candidates for macromolecules that carried genetic information. Hershey and Chase were able to radioactively label each type of molecule alone and follow it during separate infections of *E. coli* cells with T2. Only the DNA entered the bacterial cell during infection, and only labeled DNA showed up in some of the progeny phage. Hershey and Chase concluded that the DNA must carry the genetic information necessary for the phage to reprogram the cell and produce progeny phages.

Concept Check 26.2

1. Lytic phages can only carry out lysis of the host cell, whereas lysogenic phages may either lyse the host cell or integrate into the host chromosome. In the latter case, the viral DNA (prophage) is simply replicated along with the host chromosome. Under certain conditions, a prophage may exit the host chromosome and initiate a lytic cycle. **2.** Both the CRISPR-Cas system and miRNAs involve RNA molecules bound in a protein complex and acting as "homing devices" that enable the complex to bind a complementary sequence, but miRNAs are involved in regulating gene expression (by affecting mRNAs) and the CRISPR-Cas system protects bacterial cells from foreign invaders (infecting phages). Thus the CRISPR-Cas system is more like an immune system than are miRNAs. **3.** Both the viral RNA polymerase and the RNA polymerase in Figure 17.10 synthesize an RNA molecule complementary to a template strand. However, the RNA polymerase in Figure 17.10 uses one of the strands of the DNA double helix as a template, whereas the viral RNA polymerase uses the RNA of the viral genome as a template. **4.** HIV is called a retrovirus because it synthesizes DNA using its RNA genome as a template. This is the reverse ("retro") of the usual DNA → RNA information flow. **5.** There are many steps that could be interfered with: binding of the virus to the cell, reverse transcriptase function, integration into the host cell chromosome, genome synthesis (in this case, transcription of RNA from the integrated provirus), assembly of the virus inside the cell, and budding of the virus. (Many of these, if not all, are targets of actual medical strategies to block progress of the infection in HIV-infected people.)

Concept Check 26.3

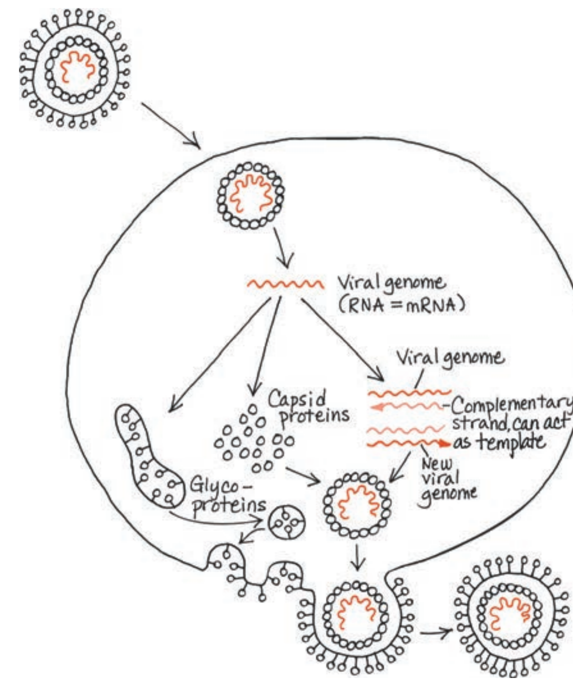
1. Mutations can lead to a new strain of a virus that can no longer be effectively fought by the immune system, even if an animal had been exposed to the original strain; a virus can jump from one species to a new host; and a rare virus can spread if a host population becomes less isolated. **2.** Prions are misfolded forms of proteins, and when they enter a cell, they tend to transform the normal proteins into misfolded forms. Several prions then aggregate into a complex that can transform other normal proteins into prions. An aggregation of this kind interferes with normal cellular functions and causes disease symptoms. **3.** Humans are not within the host range of TMV, so they can't be infected by the virus. (TMV can't bind to receptors on human cells and infect them.)

Summary of Key Concepts Questions

26.1 Viruses are generally considered nonliving, because they are not capable of replicating outside of a host cell and are unable to carry out the energy-transforming reactions of metabolism. To replicate and carry out metabolism, they depend completely on host enzymes and resources. **26.2** Single-stranded RNA viruses require an RNA polymerase that can make RNA using an RNA template. (Cellular RNA polymerases make RNA using a DNA template.) Retroviruses require reverse transcriptases to make DNA using an RNA template. (Once the first DNA strand has been made, the same enzyme can promote synthesis of the second DNA strand.) **26.3** The mutation rate of RNA viruses is higher than that of DNA viruses because RNA polymerase has no proofreading function, so errors in replication are not corrected. Their higher mutation rate means that RNA viruses change faster than DNA viruses, leading to their being able to have an altered host range and to evade immune defenses in possible hosts.

Test Your Understanding

6. As shown below, the viral genome would be translated into capsid proteins and envelope glycoproteins directly, rather than after a complementary RNA copy was made. A complementary RNA strand would still be made, however, that could be used as a template for many new copies of the viral genome.



Chapter 27

Figure Questions

Figure 27.7 The top ring, to which the hook is attached, is embedded within the interior, hydrophobic portion of the lipid bilayer of the outer membrane, suggesting that the top ring is hydrophobic. Likewise, the third ring down is embedded within the hydrophobic portion of the plasma membrane's lipid bilayer, suggesting that this ring also is hydrophobic. **Figure 27.10** It is likely that the expression or sequence of genes that affect glucose metabolism may have changed; genes for metabolic processes no longer needed by the cell also may have changed. **Figure 27.11** Transduction results in horizontal gene transfer when the host and recipient cells are members of different species. **Figure 27.15** Eukarya **Figure 27.17** Thermophiles live in very hot environments, so it is likely that their enzymes can continue to function normally at much higher temperatures than can the enzymes of other organisms. At low temperatures, however, the enzymes of thermophiles may not function as well as the enzymes of other organisms. **Figure 27.18** From the graph, plant uptake can be estimated as 0.72, 0.62, and 0.96 mg K^+ for strains 1, 2, and 3, respectively. These values average to 0.77 mg K^+. If bacteria had no effect, the average plant uptake of K^+ for strains 1, 2, and 3 should be close to 0.51 mg K^+, the value observed for plants grown in bacteria-free soil.

Concept Check 27.1

1. Adaptations include the capsule (shields prokaryotes from the host's immune system) and endospores (enable cells to survive harsh conditions and to revive when the environment becomes favorable). **2.** Gram-positive bacteria have relatively simple walls composed of a thick layer of peptidoglycan. The walls of gram-negative bacteria have less peptidoglycan and are structurally more complex, with an outer membrane that contains lipopolysaccharides. The lipopolysaccharides in the walls of many gram-negative bacteria are toxic, causing fever or shock. Their outer membranes shield them from the defenses of the human body and impede entry of antibiotics. **3.** Plastids such as chloroplasts are thought to have evolved from an endosymbiotic photosynthetic prokaryote. More specifically, the phylogenetic tree shown in Figure 22.21 indicates that plastids are closely related to cyanobacteria. Hence, we can hypothesize that the thylakoid membranes of chloroplasts resemble those of cyanobacteria because chloroplasts evolved from an endosymbiotic cyanobacterium.

Concept Check 27.2

1. Prokaryotes can have extremely large population sizes, in part because they often have short generation times. The large number of individuals in prokaryotic populations makes it likely that in each generation there will be many individuals that have new mutations at any particular gene, thereby adding considerable genetic diversity to the population. **2.** In transformation, naked, foreign DNA from the environment is taken up by a bacterial cell. In transduction, phages carry bacterial genes from one bacterial cell to another. In conjugation, a bacterial cell directly transfers plasmid or chromosomal DNA to another cell via a mating bridge that temporarily connects the two cells. **3.** Cells need the F factor (fertility factor) to be able to form pili and donate DNA during conjugation. Since F^- cells lack the F factor, they can only serve as recipients. **4.** Yes. Genes for antibiotic resistance could be transferred (by transformation, transduction, or conjugation) from the nonpathogenic bacterium to a pathogenic bacterium; this could make the pathogen an even greater threat to human health. In general, transformation, transduction, and conjugation tend to increase the spread of resistance genes.

Concept Check 27.3

1. A phototroph derives its energy from light, while a chemotroph gets its energy from chemical sources. An autotroph derives its carbon from CO_2, HCO_3^-, or related compounds, while a heterotroph gets its carbon from organic nutrients such as glucose. Thus, there are four nutritional modes: photoautotrophic, photoheterotrophic (unique to prokaryotes), chemoautotrophic (unique to prokaryotes), and chemoheterotrophic. **2.** Chemoheterotrophy; the bacterium must rely on chemical sources of energy, since it is not exposed to light, and it must be a heterotroph if it requires a source of carbon other than CO_2 (or a related compound, such as HCO_3^-). **3.** If humans could fix nitrogen, we could build proteins using atmospheric N_2 and hence would not need to eat high-protein foods such as meat, fish, or soy. Our diet would, however, need to include a source of carbon, along with minerals and water. Thus, a typical meal might consist of carbohydrates as a carbon source, along with fruits and vegetables to provide essential minerals (and additional carbon).

Concept Check 27.4

1. Molecular systematic studies indicate that some organisms once classified as bacteria are more closely related to eukaryotes and belong in a domain of their own: Archaea. Such studies have also shown that horizontal gene transfer is common and plays an important role in the evolution of prokaryotes. By not requiring that organisms be cultured in the laboratory, metagenomic studies have revealed an immense diversity of previously unknown prokaryotic species. Over time, the ongoing discovery of new species by metagenomic analyses may alter our understanding of prokaryotic phylogeny greatly. **2.** At present, all known methanogens are archaea in the clade Euryarchaeota; this suggests that this unique metabolic pathway probably arose in ancestral species within Euryarchaeota. Since Bacteria and Archaea have been separate evolutionary lineages for billions of years, the discovery of a methanogen from the domain Bacteria would suggest that adaptations that enabled the use of CO_2 to oxidize H_2 may have evolved twice—once in Archaea (within Euryarchaeota) and once in Bacteria. (It is also possible that a newly discovered bacterial methanogen could have acquired the genes for this metabolic pathway by horizontal gene transfer from a methanogen in domain Archaea. However, horizontal gene transfer is not a likely explanation because of the large number of genes involved and because gene transfers between species in different domains are relatively rare.)

Concept Check 27.5

1. Although prokaryotes are small, their large numbers and metabolic abilities enable them to play key roles in ecosystems by decomposing wastes, recycling chemicals, and affecting the concentrations of nutrients available to other organisms. **2.** Cyanobacteria produce oxygen when water is split in the light reactions of photosynthesis. The Calvin cycle incorporates CO_2 from the air into organic molecules, which are then converted to sugars.

Concept Check 27.6

1. Sample answers: eating fermented foods such as yogurt, sourdough bread, or cheese; receiving clean water from sewage treatment; taking medicines produced by bacteria **2.** No. If the poison is secreted as an exotoxin, live bacteria could be transmitted to another person. But the same is true if the poison is an endotoxin—only in this case, the live bacteria that are transmitted may be descendants of the (now-dead) bacteria that produced the poison. **3.** Some of the many different species of prokaryotes that live in the human gut compete with one another for resources (from the food that you eat). Because different prokaryotic species have different adaptations, a change in diet may alter which species can grow most rapidly, thus altering species abundance.

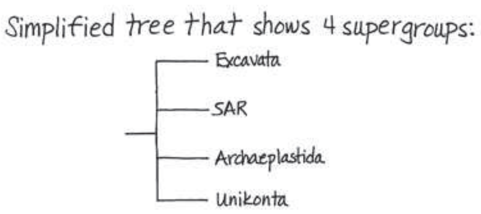
Summary of Key Concepts Questions

27.1 Specific structural features that enable prokaryotes to thrive in diverse environments include their cell walls (which provide shape and protection), flagella (which function in directed movement), and ability to form capsules or endospores (both of which can protect against harsh conditions). Prokaryotes also possess biochemical adaptations for growth in varied conditions, such as those that enable them to tolerate extremely hot or salty environments. **27.2** Many prokaryotic species can reproduce extremely rapidly, and their populations can number in the trillions. As a result, even though mutations are rare, every day many offspring are produced that have new mutations at particular gene loci. In addition, even though prokaryotes reproduce asexually and hence the vast majority of offspring are genetically identical to their parent, the genetic variation of their populations can be increased by transduction, transformation, and conjugation. Each of these (nonreproductive) processes can increase genetic variation by transferring DNA from one cell to another—even among cells that are of different species. **27.3** Prokaryotes have an exceptionally broad range of metabolic adaptations. As a group, prokaryotes perform all four modes of nutrition (photoautotrophy, chemoautotrophy, photoheterotrophy, and chemoheterotrophy), whereas eukaryotes perform only two of these (photoautotrophy and chemoheterotrophy). Prokaryotes are also able to metabolize nitrogen in a wide variety of forms (again unlike eukaryotes), and they frequently cooperate with other prokaryotic cells of the same or different species. **27.4** Phenotypic criteria such as shape, motility, and nutritional mode do not provide a clear picture of the evolutionary history of the prokaryotes. In contrast, molecular data have elucidated relationships among major groups of prokaryotes. Molecular data have also allowed researchers to sample genes directly from the environment; using such genes to construct phylogenies has led to the discovery of major new groups of prokaryotes. **27.5** Prokaryotes play key roles in the chemical cycles on which life depends. For example, prokaryotes are important decomposers, breaking down corpses and waste materials, thereby releasing nutrients to the environment where they can be used by other organisms. Prokaryotes also convert inorganic compounds to forms that other organisms can use. With respect to their ecological interactions, many prokaryotes form life-sustaining mutualisms with other species. In some cases, such as hydrothermal vent communities, the metabolic activities of prokaryotes provide an energy source on which hundreds of other species depend; in the absence of the prokaryotes, the community collapses. **27.6** Human well-being depends on our associations with mutualistic prokaryotes, such as the many species that live in our intestines and digest food that we cannot. Humans also can harness the remarkable metabolic capabilities of prokaryotes to produce a wide range of useful products and to perform key services such as bioremediation. Negative effects of prokaryotes result primarily from bacterial pathogens that cause disease.

Chapter 28

Figure Questions

Figure 28.2 The simplified version of the tree in Figure 28.2 and the modified tree showing unikonts as the sister group to all other eukaryotes would look as follows:



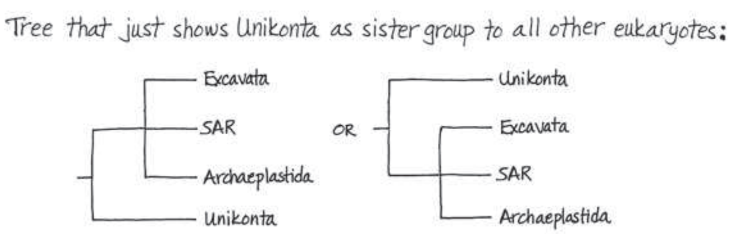


Figure 28.3 The diagram shows that a single secondary endosymbiosis event gave rise to the stramenopiles and alveolates—thus, these groups can trace their ancestry back to a single heterotrophic protist (shown in yellow) that ingested a red alga. In contrast, euglenids and chlorarachniophytes each descended from a different heterotrophic protist (one of which is shown in gray, the other in brown). Hence, it is likely that stramenopiles and alveolates are more closely related than are euglenids and chlorarachniophytes. **Figure 28.13** The sperm cells in the diagram are produced by the asexual (mitotic) division of cells in a single male gametophyte, which was itself produced by the asexual (mitotic) division of a single zoospore. Thus, the sperm cells are all derived from a single zoospore and so are genetically identical to one another. **Figure 28.16** Merozoites are produced by the asexual (mitotic) cell division of haploid sporozoites; similarly, gametocytes are produced by the asexual cell division of merozoites. Hence, it is likely that individuals in these three stages have the same complement of genes and that morphological differences between them result from changes in gene expression. **Figure 28.17** These events have a similar overall effect to fertilization. In both cases, haploid nuclei that were originally from two genetically different cells fuse to form a diploid nucleus. **Figure 28.23** The following stage should be circled: step 6, where a mature cell undergoes mitosis and forms four or more daughter cells. In step 7, the zoospores eventually grow into mature haploid cells, but they do not produce new daughter cells. Likewise, in step 2, a mature cell develops

into a gamete, but it does not produce new daughter cells. **Figure 28.24** If the assumption is correct, then their results indicate that the fusion of the genes for DHFR and TS may be a derived trait shared by members of three supergroups of eukaryotes (Excavata, SAR, and Archaeplastida). However, if the assumption is not correct, the presence or absence of the gene fusion may tell little about phylogenetic history. For example, if the genes fused multiple times, groups could share the trait because of convergent evolution rather than common descent. If instead the genes were secondarily split, a group with such a split could be placed (incorrectly) in Unikonta rather than its correct placement in one of the other three supergroups. **Figure 28.26** They would be haploid because originally each of these cells was a haploid, solitary amoeba.

Concept Check 28.1

1. Sample response: Protists include unicellular, colonial, and multicellular organisms; photoautotrophs, heterotrophs, and mixotrophs; species that reproduce asexually, sexually, or both ways; and organisms with diverse physical forms and adaptations. **2.** Strong evidence shows that eukaryotes acquired mitochondria after a host cell (either an archaean or a close relative of the archaeans) first engulfed and then formed an endosymbiotic association with an alpha proteobacterium. Similarly, chloroplasts in red and green algae appear to have descended from a photosynthetic cyanobacterium that was engulfed by an ancient heterotrophic eukaryote. Secondary endosymbiosis also played an important role: Various protist lineages acquired plastids by engulfing unicellular red or green algae. **3.** Four. The first (and primary) genome is the DNA located in the chlorarachniophyte nucleus. A chlorarachniophyte also contain remnants of a green alga's nuclear DNA, located in the nucleomorph. Finally, mitochondria and chloroplasts contain DNA from the (different) bacteria from which they evolved. These two prokaryotic genomes comprise the third and fourth genomes contained within a chlorarachniophyte.

Concept Check 28.2

1. Trypanosomes change the molecular structures of their surface proteins very frequently, making it difficult for the host's immune system to recognize and attack them. **2.** Since the unknown protist is more closely related to diplomonads than to euglenids, it must have originated after the lineage leading to the diplomonads and parabasalids diverged from the euglenozoans. In addition, since the unknown species has fully functional mitochondria—yet both diplomonads and parabasalids do not—it is likely that the unknown species originated *before* the last common ancestor of the diplomonads and parabasalids.

Concept Check 28.3

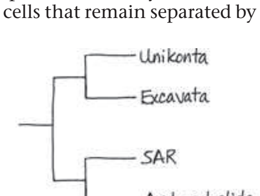
1. It is difficult to develop a vaccine against malaria because *Plasmodium*, the malaria-causing parasite, lives inside cells and frequently changes its surface proteins. **2.** The plastid DNA would likely be more similar to the chromosomal DNA of cyanobacteria based on the well-supported hypothesis that eukaryotic plastids (such as those found in the eukaryotic groups listed) originated by an endosymbiosis event in which a eukaryote engulfed a cyanobacterium. If the plastid is derived from the cyanobacterium, its DNA would be derived from the bacterial DNA. **3.** Figure 13.6b. Algae and plants with alternation of generations have a multicellular haploid stage *and* a multicellular diploid stage. In the other two life cycles, either the haploid stage or the diploid stage is unicellular. **4.** During photosynthesis, aerobic algae produce O_2 and use CO_2. O_2 is produced as a by-product of the light reactions, while CO_2 is used as an input to the Calvin cycle (the end products of which are sugars). Aerobic algae also perform cellular respiration, which uses O_2 as an input and produces CO_2 as a waste product.

Concept Check 28.4

1. Many red algae contain a photosynthetic pigment called phycoerythrin, which gives them a reddish color and allows them to carry out photosynthesis in relatively deep coastal water. Also unlike brown algae, red algae have no flagellated stages in their life cycle and must depend on water currents to bring gametes together for fertilization. **2.** *Ulva* contains many cells and its body is differentiated into leaflike blades and a rootlike holdfast. *Caulerpa*'s body is composed of multinucleate filaments without cross-walls, so it is essentially one large cell. **3.** Red algae have no flagellated stages in their life cycle and hence must depend on water currents to bring their gametes together. This feature of their biology might increase the difficulty of reproducing on land. In contrast, the gametes of green algae are flagellated, making it possible for them to swim in thin films of water. In addition, a variety of green algae contain compounds in their cytoplasm, cell wall, or zygote coat that protect against intense sunlight and other terrestrial conditions. Such compounds may have increased the chance that descendants of green algae could survive on land.

Concept Check 28.5

1. Amoebozoans have lobe- or tube-shaped pseudopodia, whereas forams have threadlike pseudopodia. **2.** During the feeding stage, a plasmodial slime mold forms a single mass of cytoplasm with many nuclei, whereas a cellular slime mold consists of multiple cells that remain separated by their individual plasma membranes.
3.



Concept Check 28.6

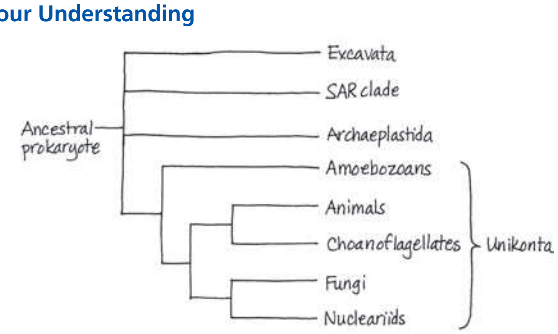
1. Because photosynthetic protists constitute the base of aquatic food webs, many aquatic organisms depend on them for food, either directly or indirectly. (In addition, a substantial percentage of the oxygen produced by photosynthesis is made by photosynthetic protists.) **2.** Protists form mutualistic and parasitic associations with other organisms. Examples include photosynthetic dinoflagellates that form a mutualistic symbiosis with coral polyps, parabasalids that form a mutualistic symbiosis with termites, and the stramenopile *Phytophthora ramorum*, a parasite of oak trees. **3.** Corals depend on their dinoflagellate symbionts for nourishment, so coral bleaching could cause the corals to die. As the corals died, less food would be available for fishes and other species that eat coral. As a result, populations of these species might decline, and that, in turn, might cause populations of their predators to decline. **4.** The two approaches differ in the evolutionary changes they may bring about. A strain of *Wolbachia* that confers resistance to infection by *Plasmodium* and does not harm mosquitoes would spread rapidly through the mosquito population. In this case, natural selection would favor any *Plasmodium* individuals that could overcome the resistance to infection conferred by *Wolbachia*. If insecticides are used, mosquitoes that are resistant to the insecticide would be favored by natural selection. Hence, use of *Wolbachia* could cause evolution in *Plasmodium* populations, while using insecticides could cause evolution in mosquito populations.

Summary of Key Concepts Questions

28.1 Sample response: Protists, plants, animals, and fungi are similar in that their cells have a nucleus and other membrane-enclosed organelles, unlike the cells of prokaryotes. These membrane-enclosed organelles make the cells of eukaryotes more complex than the cells of prokaryotes. Protists and other eukaryotes also differ from prokaryotes in having a well-developed cytoskeleton that enables them to have asymmetric forms and to change in shape as they feed, move, or grow. With respect to differences between protists and other eukaryotes, most protists are unicellular, unlike animals, plants, and most fungi. Protists also have greater nutritional diversity than other eukaryotes. **28.2** Unique cytoskeletal features are shared by many excavates. In addition, some members of Excavata have an "excavated" feeding groove for which the group was named. Moreover, recent genomic studies support the monophyly of the excavate supergroup. **28.3** Stramenopiles and alveolates are hypothesized to have originated by secondary endosymbiosis. Under this hypothesis, we can infer that the common ancestor of these two groups had a plastid, in this case of red algal origin. Thus, we would expect that apicomplexans (and alveolate or stramenopile protists) either would have plastids or would have lost their plastids over the course of evolution. **28.4** Red algae, green algae, and plants are placed in the same supergroup because considerable evidence indicates that these organisms all descended from the same ancestor, an ancient heterotrophic protist that acquired a cyanobacterial endosymbiont. **28.5** The unikonts are a diverse group of eukaryotes that includes many protists, along with animals and fungi. Most of the protists in Unikonta are amoebozoans, a clade of amoebas that have lobe- or tube-shaped pseudopodia (as opposed to the threadlike pseudopodia of rhizarians). Other protists in Unikonta include several groups that are closely related to fungi and several other groups that are closely related to animals. **28.6** Sample response: Ecologically important protists include photosynthetic dinoflagellates that provide essential sources of energy to their symbiotic partners, the corals that build coral reefs. Other important protistan symbionts include those that enable termites to digest wood and *Plasmodium*, the pathogen that causes malaria. Photosynthetic protists such as diatoms are among the most important producers in aquatic communities; as such, many other species in aquatic environments depend on them for food.

Test Your Understanding

7.



Pathogens that share a relatively recent common ancestor with humans will likely also share metabolic and structural characteristics with humans. Because drugs target the pathogen's metabolism or structure, developing drugs that harm the pathogen but not the patient should be most difficult for pathogens with whom we share the most recent evolutionary history. Working backward in time, we can use the phylogenetic tree to determine the order in which humans shared a common ancestor with pathogens in different taxa. This process leads to the prediction that it should be hardest to develop drugs to combat animal pathogens, followed by choanoflagellate pathogens, fungal and nucleariid pathogens, amoebozoans, other protists, and finally prokaryotes.

Chapter 29

Figure Questions

Figure 29.3 The life cycles of plants and some algae, shown in Figure 13.6b, have alternation of generations; other life cycles do not. Unlike in the animal life cycle (Figure 13.6a), in the plant/algal life cycle, meiosis produces spores, not gametes. These haploid spores then divide repeatedly by mitosis, ultimately forming a multicellular haploid individual that produces gametes. There is no multicellular haploid stage in the animal life cycle. An alternation of generations life cycle also has a multicellular diploid stage, whereas the life cycle of most fungi and some protists shown in Figure 13.6c does not. **Figure 29.6** Plants, vascular plants, and seed plants are monophyletic because each of these groups includes the common ancestor of the group and all of the descendants of that common ancestor. The other two categories of plants, the nonvascular plants and the seedless vascular plants, are paraphyletic: These groups do not include all of the descendants of the group's most recent common ancestor. **Figure 29.7** Yes. As shown in the diagram, the sperm cell and the egg cell that fuse each resulted from the mitotic division of spores produced by the same sporophyte. However, these spores would differ genetically from one another because they were produced by meiosis, a cell division process that generates genetic variation among the offspring cells. **Figure 29.9** Soil erosion and nutrient leaching would greatly increase. Natural regulation of the flow of water would be negatively affected, which would mean more frequent and stronger floods and landslides on the one hand, and longer and more pronounced dry spells on the other. **Figure 29.12** A fern that had wind-dispersed sperm would not require water for fertilization, thus removing a difficulty that ferns face when they live in arid environments. The fern would also be under strong selection to produce sperm above ground (as opposed to the current situation, where some fern gametophytes are located below ground).

Concept Check 29.1

1. Plants share some key traits only with charophytes: rings of cellulose-synthesizing complexes, similarity in sperm structure, and the formation of a phragmoplast in cell division. Comparisons of nuclear, chloroplast, and mitochondrial DNA sequences also indicate that certain groups of charophytes (such as *Zygnema* and *Coleochaete*) are the closest living relatives of plants. **2.** Spore walls toughened by sporopollenin (protects against harsh environmental conditions); multicellular, dependent embryos (provide nutrients and protection to the developing embryo); cuticle (reduces water loss); stomata (control gas exchange and reduce water loss) **3.** The multicellular diploid stage of the life cycle would not produce gametes. Instead, both males and females would produce haploid spores by meiosis. These spores would give rise to multicellular male and female haploid stages—a major change from the single-celled haploid stages (sperm and eggs) that we actually have. The multicellular haploid stages would produce gametes and reproduce sexually. An individual at the multicellular haploid stage of the human life cycle might look like us, or it might look completely different.

Concept Check 29.2

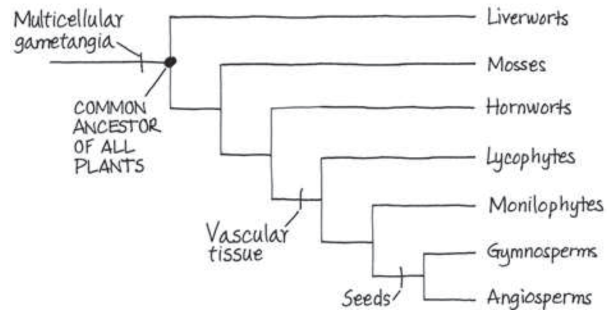
1. Most bryophytes do not have a vascular transport system, and their life cycle is dominated by gametophytes rather than sporophytes. **2.** Bryophytes do not have a vascular structure. Therefore, a moist environment helps them absorb water through the whole of their thin bodies. Also, most bryophyte species have separate male and female gametophytes, and the bryophyte sperm usually need a film of water to reach the eggs. **3.** Effects of global warming on peatlands could result in positive feedback, which occurs when an end product of a process increases its own production. In this case, global warming is expected to lower the water levels of some peatlands. This would expose peat to air and cause it to decompose, thereby releasing stored CO_2 to the atmosphere. The release of more stored CO_2 to the atmosphere could cause additional global warming, which in turn could cause further drops in water levels, the release of still more CO_2 to the atmosphere, additional warming, and so on: an example of positive feedback.

Concept Check 29.3

1. Lycophytes have microphylls, whereas seed plants and monilophytes (ferns and their relatives) have megaphylls. Monilophytes and seed plants also share other traits not found in lycophytes, such as the initiation of new root branches at various points along the length of an existing root. **2.** Both seedless vascular plants and bryophytes have flagellated sperm that require moisture for fertilization; this shared similarity poses challenges for these species in arid regions. With respect to key differences, seedless vascular plants have lignified, well-developed vascular tissue, a trait that enables the sporophyte to grow tall and that has transformed life on Earth (via the formation of forests). Seedless vascular plants also have true leaves and roots, which, when compared with bryophytes, provide increased surface area for photosynthesis and improve their ability to extract nutrients from soil. **3.** Three mechanisms contribute to the production of genetic variation in sexual reproduction: independent assortment of chromosomes, crossing over, and random fertilization. If fertilization were to occur between gametes from the same gametophyte, all of the offspring would be genetically identical. This would be the case because all of the cells produced by a gametophyte—including its sperm and egg cells—are the descendants of a single spore and hence are genetically identical. Although crossing over and the independent assortment of chromosomes would continue to generate genetic variation during the production of spores (which ultimately develop into gametophytes), overall the amount of genetic variation produced by sexual reproduction would drop.

Summary of Key Concepts Questions

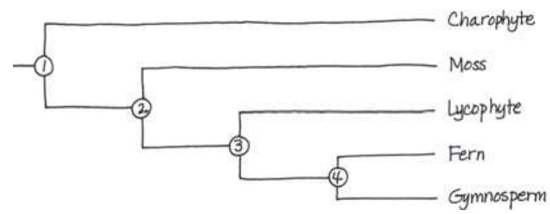
29.1



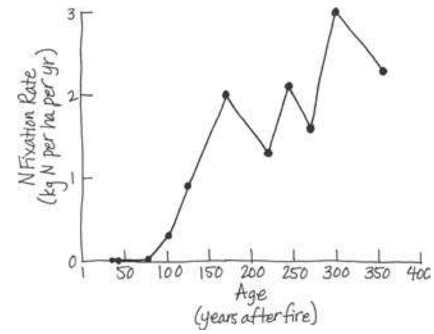
29.2 Some mosses colonize bare, sandy soils, leading to the increased retention of nitrogen in these otherwise low-nitrogen environments. Other mosses harbor nitrogen-fixing cyanobacteria that increase the availability of nitrogen in the ecosystem. The moss *Sphagnum* is often a major component of deposits of peat (partially decayed organic material). Boggy regions with thick layers of peat, known as peatlands, cover broad geographic regions and contain large reservoirs of carbon. By storing large amounts of carbon—in effect, removing CO_2 from the atmosphere—peatlands affect the global climate, making them of considerable ecological importance. **29.3** Lignified vascular tissue provided the strength needed to support a tall plant against gravity, as well as a means to transport water and nutrients to plant parts located high above ground. Roots were another key trait, anchoring the plant to the ground and providing additional structural support for plants that grew tall. Tall plants could shade shorter plants, thereby outcompeting them for light. Because the spores of a tall plant disperse farther than the spores of a short plant, it is also likely that tall plants could colonize new habitats more rapidly than short plants.

Test Your Understanding

6. (A) diploid; (B) haploid; (C) haploid; (D) diploid
7. Based on our current understanding of the evolution of major plant groups, the phylogeny has the four branch points shown here:



Derived characters unique to the charophyte and plant clade (indicated by branch point 1) include rings of cellulose-synthesizing complexes, flagellated sperm structure, and a phragmoplast. Derived characters unique to the plant clade (branch point 2) include alternation of generations; multicellular, dependent embryos; walled spores produced in sporangia; multicellular gametangia; and apical meristems. Derived characters unique to the vascular plant clade (branch point 3) include life cycles with dominant sporophytes, complex vascular systems (xylem and phloem), and well-developed roots and leaves. Derived characters unique to the monilophyte and seed plant clade (branch point 4) include megaphylls and roots that can branch at various points along the length of an existing root.
8. (a)



(b) In the first 40 years after a fire, nitrogen fixation rates were below 0.01 kg/(ha · yr), which was less than 1% of the amount of nitrogen deposited from the atmosphere. Thus, in the initial decades after a fire, the moss *Pleurozium* and the nitrogen-fixing bacteria it harbors had relatively little effect on the amount of nitrogen added to the forest. With time, however, *Pleurozium* and its symbiotic, nitrogen-fixing bacteria became increasingly important. By 170 years after a fire, the percentage of the ground surface covered by the moss had increased to about 70%, leading to a corresponding increase in populations of the symbiotic bacteria. As would be predicted from this result, in older forests considerably more nitrogen (130–300%) was added by nitrogen fixation than was deposited from the atmosphere.

Chapter 30

Figure Questions

Figure 30.2 Retaining the gametophyte within the sporophyte shields the egg-containing gametophyte from UV radiation. UV radiation is a mutagen. Hence, we would expect fewer mutations to occur in the egg cells produced by a gametophyte retained within the body of a sporophyte. Most mutations are harmful. Thus, the fitness of embryos should increase because fewer embryos would carry harmful mutations. **Figure 30.3** The seed contains cells from three generations: (1) the current sporophyte (cells of ploidy $2n$, found in the seed coat and in the megasporangium remnant that surrounds the spore wall), (2) the female gametophyte (cells of ploidy n, found in the food supply), and (3) the sporophyte of the next generation (cells of ploidy $2n$, found in the embryo). **Figure 30.4** Mitosis. A single haploid megaspore divides by mitosis to produce a multicellular, haploid female gametophyte. (Likewise, a single haploid microspore divides by mitosis to produce a multicellular male gametophyte.)

Figure 30.9

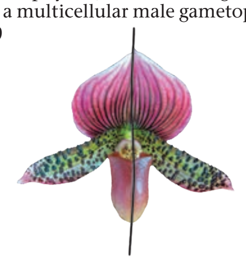


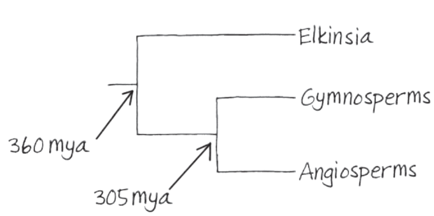
Figure 30.14 No. The branching order shown could still be correct if species on the lineages leading to basal angiosperms and magnolids had originated prior to 150 million years ago, but fossils of that age from those lineages had not yet been discovered. In such a situation, the 140-million-year-old date for the origin of the angiosperms shown on the phylogeny would be incorrect.

Concept Check 30.1

1. To reach the eggs, the flagellated sperm of seedless plants must swim through a film of water, usually over a distance of no more than a few centimeters. In contrast, the sperm of seed plants do not require water because they are produced within pollen grains that can be transported long distances by wind or by animal pollinators. Although flagellated in some species, the sperm of seed plants do not require mobility because pollen tubes convey them from the point at which the pollen grain is deposited (near the ovules) directly to the eggs. **2.** The reduced gametophytes of seed plants are nurtured by sporophytes and protected from stress, such as drought conditions and UV radiation. Pollen grains, with walls containing sporopollenin, provide protection during transport by wind or animals. Seeds have one or two layers of protective tissue, the seed coat, that improve survival by providing more protection from environmental stresses than do the walls of spores. Seeds also contain a stored supply of food, which provides nourishment for growth after dormancy is broken and the embryo emerges as a seedling. **3.** If a seed could not enter dormancy, the embryo would continue to grow after it was fertilized. As a result, the embryo might rapidly become too large to be dispersed, thus limiting its transport. The embryo's chance of survival might also be reduced because it could not delay growth until conditions become favorable.

Concept Check 30.2

1. Although gymnosperms are similar in not having their seeds enclosed in ovaries and fruits, their seed-bearing structures vary greatly. For instance, cycads have large cones, whereas some gymnosperms, such as *Ginkgo* and *Gnetum*, have small cones that look somewhat like berries, even though they are not fruits. Leaf shape also varies greatly, from the needles of many conifers to the palmlike leaves of cycads to *Gnetum* leaves that look like those of flowering plants. **2.** The scales of pollen cones are modified leaves, while the scales of ovulate cones are compound structures composed of both modified leaves and stem tissue. Pollen cones contain microsporangia, and produce haploid microspores. Ovulate cones contain megasporangia, and produce haploid megaspores. The microspores develop into male gametophytes. The megaspores develop into female gametophytes.
3.



Concept Check 30.3

1. In the oak's life cycle, the tree (the sporophyte) produces flowers, which contain gametophytes in pollen grains and ovules; the eggs in ovules are fertilized; the mature ovaries develop into dry fruits called acorns. We can view the oak's life cycle as starting when the acorn seeds germinate, resulting in embryos giving rise to seedlings and finally to mature trees, which produce flowers—and then more acorns. **2.** During double fertilization in angiosperms, one fertilization event produces a zygote and the other produces a triploid cell. Eventually, the zygote matures into a sporophyte embryo, and the triploid cell develops into endosperm. Double fertilization is rare among gymnosperms. It occurs in some of them, and it gives rise to two embryos. **3.** The fact that the clade with bilaterally symmetrical flowers had more species establishes a correlation between flower shape and the rate of plant speciation. Flower shape is not necessarily responsible for the result because the shape (that is, bilateral or radial symmetry) may have been correlated with another factor that was the actual cause of the observed result. Note, however, that flower shape was associated with increased speciation rates when averaged across 19 different pairs of plant lineages. Since these 19 lineage pairs were independent of one another, this association suggests—but does not establish—that differences in flower shape cause differences in speciation rates. In general, strong evidence for causation can come from controlled, manipulative experiments, but such experiments are usually not possible for studies of past evolutionary events.

Concept Check 30.4

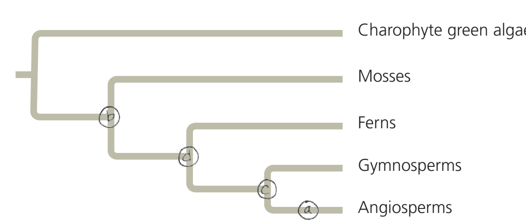
1. Plant diversity can be considered a resource because plants provide many important benefits to humans; as a resource, plant diversity is nonrenewable because if a species is lost to extinction, that loss is permanent. **2.** A detailed phylogeny of the seed plants would identify many different monophyletic groups of seed plants. Using this phylogeny, researchers could look for clades that contained species in which medicinally useful compounds had already been discovered. Identification of such clades would allow researchers to concentrate their search for new medicinal compounds among clade members—as opposed to searching for new compounds in species that were selected at random from the more than 250,000 existing species of seed plants.

Summary of Key Concepts Questions

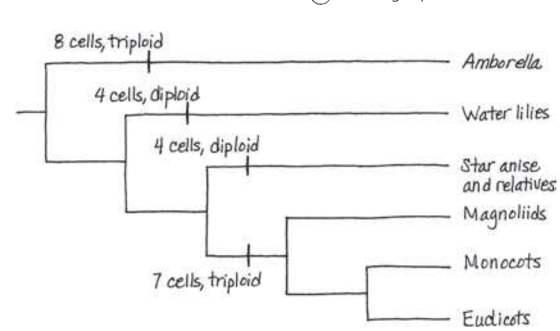
30.1 The integument of an ovule develops into the protective coat of a seed. The ovule's megaspore develops into a haploid female gametophyte, and two parts of the seed are related to that gametophyte: The food supply of the seed is derived from haploid gametophyte cells, and the embryo of the seed develops after the female gametophyte's egg cell is fertilized by a sperm cell. A remnant of the ovule's megasporangium surrounds the spore wall that encloses the seed's food supply and embryo. **30.2** Gymnosperms arose about 305 million years ago, making them a successful group in terms of their evolutionary longevity. Gymnosperms have the five derived traits common to all seed plants (reduced gametophytes, heterospory, ovules, pollen, and seeds), making them well adapted for life on land. Finally, because gymnosperms dominate immense geographic regions today, the group is also highly successful in geographic distribution. **30.3** Based on fossils known during his lifetime, Darwin was troubled by the relatively sudden and geographically widespread appearance of angiosperms in the fossil record. Recent fossil evidence shows that angiosperms arose and began to diversify over a period of 20–30 million years, a less rapid event than was suggested by the fossils known during Darwin's lifetime. Fossil discoveries have also uncovered extinct lineages of woody seed plants thought to have been more closely related to angiosperms than to gymnosperms; one such group, the Bennettitales, had flowerlike structures that may have been pollinated by insects. In addition, phylogenetic analyses have identified a woody species, *Amborella*, as the most basal lineage of extant angiosperms. The fact that both the extinct seed plant ancestors of angiosperms and the most basal taxon of extant angiosperms were woody suggests that the common ancestor of angiosperms also was woody. **30.4** The loss of tropical forests could contribute to global warming (which would have negative effects on many human societies). People also depend on Earth's biodiversity for many products and services and hence would be harmed by the loss of species that would occur if the world's remaining tropical forests were cut down. With respect to a possible mass extinction, tropical forests harbor at least 50% of the species on Earth. If the remaining tropical forests were destroyed, large numbers of these species could be driven to extinction, thus rivaling the losses that occurred in the five mass extinction events documented in the fossil record.

Test Your Understanding

6.



8. (a)



(b) The phylogeny indicates that basal angiosperms differed from other angiosperms in terms of the number of cells in female gametophytes and the ploidy of the endosperm. The ancestral state of the angiosperms cannot be determined from these data alone. It is possible that the common ancestor of angiosperms had seven-celled female gametophytes and triploid endosperm and hence that the eight-celled and four-celled conditions found in basal angiosperms represent derived traits for those lineages. Alternatively, either the eight-celled or four-celled condition may represent the ancestral state.

Chapter 31

Figure Questions

Figure 31.2 DNA from each of these mushrooms would be identical if each mushroom is part of a single hyphal network, as is likely. **Figure 31.5** The haploid spores produced in the sexual portion of the life cycle develop from haploid nuclei that were produced by meiosis; because genetic recombination occurs during meiosis, these spores will differ genetically from one another. In contrast, the haploid spores produced in the asexual portion of the life cycle develop from nuclei that were produced by mitosis; as a result, these spores are genetically identical to one another. **Figure 31.15** One or both of the following would apply to each species: DNA analyses would reveal that it is a member of the ascomycete clade, or aspects of its sexual life cycle would indicate that it is an ascomycete (for example, it would produce asci and ascospores). **Figure 31.16** The hypha is composed of cells that are haploid (n), as indicated by the teal-colored arrow behind it. **Figure 31.18** The mushroom is a basidiocarp, or fruiting body, of the dikaryotic mycelium, and so a cell from its stalk would be dikaryotic ($n + n$). **Figure 31.20** Two possible controls would be E–P– and E+P–. Results from an E–P– control could be compared with results from the E–P+ experiment, and results from an E+P– control could be compared with results from the E+P+ experiment. Together, these two comparisons would indicate whether the addition of the pathogen causes an increase in leaf mortality. Results from an E–P– experiment could also be compared with results from the second control (E+P–) to determine whether adding the fungal endophytes has a negative effect on the plant.

Concept Check 31.1

1. Mycorrhizal fungi grow in the roots of host plants, and use arbuscules to exchange nutrients with the plants. Arbuscules are more efficient than the plants' roots at acquiring phosphate ions and other minerals from the soil and, therefore, improve delivery of these minerals to the plants. In exchange, the plants supply the fungi with organic nutrients such as carbohydrates. **2.** The ancestors of such a mutualist most likely secreted powerful enzymes to digest the body of their insect host. Since such enzymes would harm a living host, it is likely that the mutualist would not produce such enzymes or would restrict their secretion and use.
3. Carbon that enters the plant through stomata is fixed into sugar through photosynthesis. Some of these sugars are absorbed by the fungus that partners with the plant to form mycorrhizae; others are transported within the plant body and used in the plant. Thus, the carbon may be deposited in either the body of the plant or the body of the fungus.

Concept Check 31.2

1. The majority of the fungal life cycle is spent in the haploid stage, whereas the majority of the human life cycle is spent in the diploid stage. **2.** The two mushrooms might be reproductive structures of the same mycelium (the same organism). Or they might be parts of two separate organisms that have arisen from a single parent organism through asexual reproduction (for example, from two genetically identical asexual spores) and thus carry the same genetic information.

Concept Check 31.3

1. DNA evidence indicates that fungi, animals, and their protistan relatives form a clade, the opisthokonts. Furthermore, some chytrids and other fungi thought to be members of basal lineages have posterior flagella, as do most other opisthokonts. This suggests that other fungal lineages lost their flagella after diverging from ancestors that had flagella. **2.** Mycorrhizae form extensive networks of hyphae through the soil, enabling nutrients to be absorbed more efficiently than a plant can do on its own; this is true today, and similar associations were probably very important for the earliest plants (which lacked roots). Evidence for the antiquity of mycorrhizal associations includes fossils showing arbuscular mycorrhizae in the early plant *Aglaophyton* and molecular results showing that genes required for the formation of mycorrhizae are present in liverworts and other basal plant lineages. **3.** Fungi are heterotrophs. Prior to the colonization of land by plants, terrestrial fungi would have lived where other organisms (or their remains) were present and provided a source of food. Thus, if fungi colonized land before plants, they could have fed on prokaryotes or protists that lived on land or by the water's edge—but not on the plants or animals on which many fungi feed today.

Concept Check 31.4

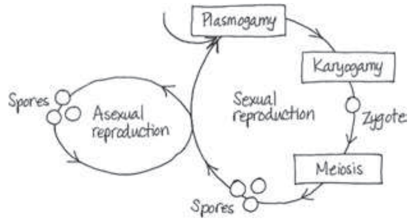
1. Flagellated spores; molecular evidence also suggests that chytrids include species that belong to lineages that diverged from other fungi early in the history of the group. **2.** Possible answers include the following: In zygomycetes, the sturdy, thick-walled zygosporangium can withstand harsh conditions and then undergo karyogamy and meiosis when the environment is favorable for reproduction. In glomeromycetes, the hyphae have a specialized morphology that enables the fungi to form arbuscular mycorrhizae with plant roots. In ascomycetes, the asexual spores (conidia) are often produced in chains or clusters at the tips of conidiophores, where they are easily dispersed by wind. The often cup-shaped ascocarps house the sexual spore-forming asci. In basidiomycetes, the basidiocarp supports and protects a large surface area of basidia, from which spores are dispersed. **3.** Such a change to the life cycle of an ascomycete would reduce the number and genetic diversity of ascospores that result from a mating event. Ascospore number would drop because a mating event would lead to the formation of only one ascus. Ascospore genetic diversity would also drop because in ascomycetes, one mating event leads to the formation of asci by many different dikaryotic cells. As a result, genetic recombination and meiosis occur independently many different times—which could not happen if only a single ascus was formed. It is also likely that if such an ascomycete formed an ascocarp, the shape of the ascocarp would differ considerably from that found in its close relatives.

Concept Check 31.5

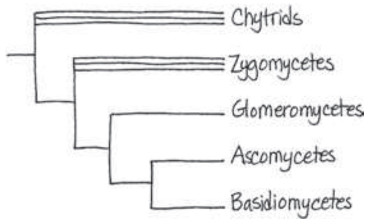
1. The leaf-cutter ants cannot digest leaves on their own. They feed the leaves to the fungi. This helps the fungi grow and their hyphae to develop nutrient-rich tips that the ants eat. **2.** A change in the body's normal microbiota, chemical environment, or immune system can turn a benign fungus into a pathogenic one. **3.** Many different outcomes might have occurred. Organisms that currently form mutualisms with fungi might have gained the ability to perform the tasks currently done by their fungal partners, or they might have formed similar mutualisms with other organisms (such as bacteria). Alternatively, organisms that currently form mutualisms with fungi might be less effective at living in their present environments. For example, the colonization of land by plants might have been more difficult. And if plants did eventually colonize land without fungal mutualists, natural selection might have favored plants that formed more highly divided and extensive root systems (in part replacing mycorrhizae).

Summary of Key Concepts Questions

31.1 The body of a multicellular fungus typically consists of thin filaments called hyphae. These filaments form an interwoven mass (mycelium) that penetrates the substrate on which the fungus grows and feeds. Because the individual filaments are thin, the surface-to-volume ratio of the mycelium is maximized, making nutrient absorption highly efficient.
31.2



31.3 Phylogenetic analyses show that fungi and animals are more closely related to each other than either is to other multicellular eukaryotes (such as plants or multicellular algae). These analyses also show that fungi are more closely related to single-celled protists called nucleariids than they are to animals, whereas animals are more closely related to a different group of single-celled protists, the choanoflagellates, than they are to fungi. In combination, these results indicate that multicellularity evolved in fungi and animals independently, from different single-celled ancestors.
31.4



31.5 As decomposers, fungi break down the bodies of dead organisms, thereby recycling elements between the living and nonliving environments. Without the activities of fungi and bacterial decomposers, essential nutrients would remain tied up in organic matter, and life would cease. As an example of their key role as mutualists, fungi form mycorrhizal associations with plants. These associations improve the growth and survival of plants, thereby indirectly affecting the many other species (humans included) that depend on plants. As pathogens, fungi harm other species. In some cases, fungal pathogens have caused their host populations to decline across broad geographic regions, as seen for the American chestnut.

Chapter 32

Figure Questions

Figure 32.3 As described in 1 and 2, choanoflagellates and a broad range of animals have collar cells. Since collar cells have never been observed in plants, fungi, or non-choanoflagellate protists, this suggests that choanoflagellates may be more closely related to animals than to other eukaryotes. If choanoflagellates are more closely related to animals than to any other group of eukaryotes, choanoflagellates and animals should share other traits that are not found in other eukaryotes. The data described in 3 are consistent with this prediction. **Figure 32.10** The cells of an early embryo with deuterostome development typically are not committed to a particular developmental fate, whereas the cells of an early embryo with protostome development typically are committed to a particular developmental fate. As a result, an embryo with deuterostome development would be more likely to contain stem cells that could give rise to cells of any type. **Figure 32.11** Cnidaria is the sister phylum in this tree.

Concept Check 32.1

1. In most animals, the zygote undergoes cleavage, which leads to the formation of a blastula. Next, in gastrulation, one end of the embryo folds inward, producing layers of embryonic tissue. As the cells of these layers differentiate, a wide variety of animal forms are produced. Despite the diversity of animal forms, animal development is controlled by a similar set of *Hox* genes across a broad range of taxa. **2.** The imaginary plant would require tissues composed of cells that were analogous to the muscle and nerve cells found in animals: "Muscle" tissue would be necessary for the plant to chase prey, and "nerve" tissue would be required for the plant to coordinate its movements when chasing prey. To digest captured prey, the plant would need to either secrete enzymes into one or more digestive cavities (which could be modified leaves, as in a Venus flytrap) or secrete enzymes outside of its body and feed by absorption. To extract nutrients from the soil—yet be able to chase prey—the plant would need something other than fixed roots, perhaps retractable "roots" or a way to ingest soil. To conduct photosynthesis, the plant would require chloroplasts. Overall, such an imaginary plant would be very similar to an animal that had chloroplasts and retractable roots.

Concept Check 32.2

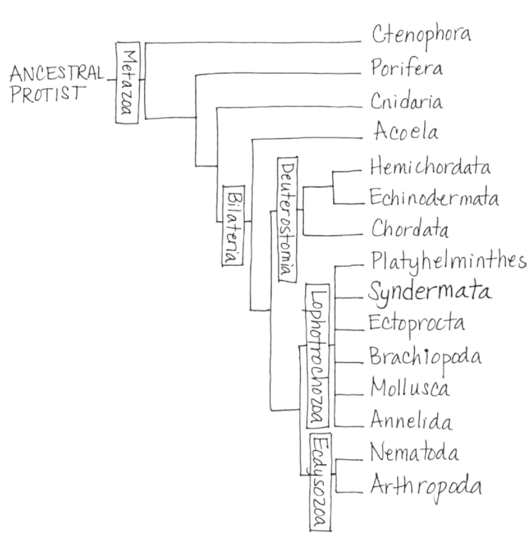
1. c, b, a, d **2.** The red-colored portion of the tree represents ancestors of animals that lived between 1 billion years ago and 770 million years ago. Although these ancestors are more closely related to animals than to fungi, they would not be classified as animals. One example of an ancestor represented by the red-colored portion of this tree is the most recent common ancestor shared by choanoflagellates and animals. **3.** In descent with modification, an organism shares characteristics with its ancestors (due to their shared ancestry), yet it also differs from its ancestors (because organisms accumulate differences over time as they adapt to their surroundings). As an example, consider the evolution of animal cadherin proteins, a key step in the origin of multicellular animals. These proteins illustrate both of these aspects of descent with modification: Animal cadherin proteins share many protein domains with a cadherin-like protein found in their choanoflagellate ancestors, yet they also have a unique "CCD" domain that is not found in choanoflagellates.

Concept Check 32.3

1. Grade-level characteristics are those that multiple lineages share regardless of evolutionary history. Some grade-level characteristics may have evolved multiple times independently. Features that unite clades are derived characteristics that originated in a common ancestor and were passed on to the various descendants. **2.** The ectoderm gives rise to the central nervous system, the mesoderm forms the muscles, and the endoderm gives rise to the lungs. **3.** Most coelomate triploblasts have two openings to their digestive tract, a mouth and an anus. As such, their bodies have a structure that is analogous to that of a doughnut: The digestive tract (the hole of the doughnut) runs from the mouth to the anus and is surrounded by various tissues (the solid part of the doughnut). The doughnut analogy is most obvious at early stages of development (see Figure 32.10c).

Concept Check 32.4

1. Cnidarians possess tissues, while sponges do not. Also unlike sponges, cnidarians exhibit body symmetry, though it is radial and not bilateral as in most other animal phyla.
2.



Under the hypothesis that ctenophores are basal metazoans, sponges (which lack tissues) would be nested within a clade whose other members all have tissues. As a result, a group composed of animals with tissues would not form a clade. **3.** The phylogeny in Figure 32.11 indicates that molluscs are members of Lophotrochozoa, one of the three main groups of bilaterians (the others being Deuterostomia and Ecdysozoa). As seen in Figure 25.11, the fossil record shows that molluscs were present tens of millions of years before the Cambrian explosion. Thus, long before the Cambrian explosion, the lophotrochoan clade had formed and was evolving independently of the evolutionary lineages leading to Deuterostomia and Ecdysozoa. Based on the phylogeny in Figure 32.11, we can also conclude that the lineages leading to Deuterostomia and Ecdysozoa were independent of one another before the Cambrian explosion. Since the lineages leading to the three main clades of bilaterians were evolving independently of one another prior to the Cambrian explosion, that explosion could be viewed as consisting of three "explosions," not one.

Summary of Key Concepts Questions

Concept 32.1 Unlike animals, which are heterotrophs that ingest their food, plants are autotrophs, and fungi are heterotrophs that grow on their food and feed by absorption. Animals lack cell walls, which are found in both plants and fungi. Animals also have muscle tissue and nerve tissue, which are not found in either plants or fungi. In addition, the sperm and egg cells of animals are produced by meiotic division, unlike what occurs in plants and fungi (where reproductive cells such as sperm and eggs are produced by mitotic division). Finally, animals regulate the development of body form with *Hox* genes, a unique group of genes that is not found in either plants or fungi. **Concept 32.2** Current hypotheses about the cause of the Cambrian explosion include new predator-prey relationships, an increase in atmospheric oxygen, and an increase in developmental flexibility provided by the origin of *Hox* genes and other genetic changes. **Concept 32.3** Body plans provide a helpful way to compare and contrast key features of organisms. However, phylogenetic analyses show that similar body plans have arisen independently in different groups of organisms. As such, similar body plans may have arisen by convergent evolution and hence may not be informative about evolutionary relationships. **Concept 32.4** Listed in order from the most to the least inclusive clade, humans belong to Metazoa, Eumetazoa, Bilateria, Deuterostomia, and Chordata.

Chapter 33

Figure Questions

Figure 33.8 The *Obelia* life cycle is most similar to the life cycle shown in Figure 13.6a. In *Obelia*, both the polyp and the medusa are diploid organisms. Typical of animals, only the single-celled gametes are haploid. By contrast, plants and some algae (Figure 13.6b) have a multicellular haploid generation and a multicellular diploid generation. *Obelia* also differs from fungi and some protists (Figure 13.6c) in that the diploid stage of those organisms is unicellular.
Figure 33.8 Both a feeding polyp and a medusa are diploid, as indicated by the pink arrow in the diagram. The medusa stage produces haploid gametes.
Figure 33.9 Possible examples might include the endoplasmic reticulum (flattening; increases area for biosynthesis), the cristae of mitochondria (folding; increases the surface area available for cellular respiration), root hairs (projections; increase area for absorption), or cardiovascular systems (branching; increase area for materials exchange in tissues). **Figure 33.11** Adding fertilizer to the water supply would probably increase the abundance of algae, and that, in turn, would likely increase the abundance of snails (which eat algae). If the water was also contaminated with infected human feces, an increase in the number of snails would likely lead to an increase in the abundance of blood flukes (which require snails as an intermediate host). As a result, the occurrence of schistosomiasis might increase. **Figure 33.22** The extinction of freshwater bivalves might lead to an increase in the abundance of photosynthetic protists and bacteria. Because these organisms are at the base of aquatic food webs, increases in their abundance could have major effects on aquatic communities (including both increases and decreases in the abundance of other species). **Figure 33.30** Such a result would be consistent with the origin of the *Ubx* and *abd-A Hox* genes having played a major role in the evolution of increased body segment diversity in arthropods. However, note that such a result would simply show that the presence of the *Ubx* and *abd-A Hox* genes was *correlated with* an increase in body segment diversity in arthropods; it would not provide direct experimental evidence that the origin of the *Ubx* and *abd-A* genes *caused* an increase in arthropod body segment diversity. **Figure 33.36** You should have circled the clade that includes the insects, remipedians, and other crustaceans, along with the branch point that represents their most recent common ancestor.

Concept Check 33.1

1. The flagella of choanocytes draw water through their collars, which trap food particles. The particles are engulfed by phagocytosis and digested, either by choanocytes or by amoebocytes. **2.** The collar cells of sponges bear a striking resemblance to a choanoflagellate cell. This suggests that the last common ancestor of animals and their protist sister group may have resembled a choanoflagellate. Nevertheless, mesomycetozoans could still be the sister group of animals. If this is the case, the lack of collar cells in mesomycetozoans would indicate that over time their structure evolved in ways that caused it to no longer resemble a choanoflagellate cell. It is also possible that choanoflagellates and sponges share similar-looking collar cells as a result of convergent evolution.

Concept Check 33.2

1. Both the polyp and the medusa are composed of an outer epidermis and an inner gastrodermis separated by a gelatinous layer, the mesoglea. The polyp is a cylindrical form that adheres to the substrate by its aboral end; the medusa is a flattened, mouth-down form that moves freely in the water. **2.** Cnidarian stinging cells (cnidocytes) function in defense and prey capture. They contain capsule-like organelles (cnidae), which in turn contain coiled threads. The threads either inject poison or stick to and entangle small prey. **3.** Evolution is not goal oriented; hence, it would not be correct to argue that cnidarians were not "highly evolved" simply because their form had changed relatively little over the past 560 million years. Instead, the fact that cnidarians have persisted for hundreds of millions of years indicates that the cnidarian body plan is a highly successful one.

Concept Check 33.3

1. Tapeworms can absorb food from their environment and release ammonia into their environment through their body surface because their body is very flat, due in part to the lack of a coelom. **2.** The inner tube is the alimentary canal, which runs the length of the body. The outer tube is the body wall. The two tubes are separated by the coelom. **3.** All molluscs have inherited a foot from their common ancestor. However, in different groups of molluscs, the structure of the foot has been modified over time by natural selection. In gastropods, the foot is used as a holdfast or to move slowly on the substrate. In cephalopods, the foot has been modified into part of the tentacles and into an excurrent siphon, through which water is propelled (resulting in movement in the opposite direction).

Concept Check 33.4

1. Nematodes lack body segments and a true coelom; annelids have both. **2.** The diversification of feeding appendages has enabled arthropods to feed on almost every kind of food. Their appendages have been specialized for biting, piercing, and chewing solids and also for taking in liquids by sucking, lapping, and sponging. **3.** Yes. Under the traditional hypothesis, we would expect body segmentation to be controlled by similar *Hox* genes in annelids and arthropods. However, if annelids are in Lophotrochozoa and arthropods are in Ecdysozoa (as current evidence suggests), body segmentation may have evolved independently in these two groups. In such a case, we might expect that different *Hox* genes would control the development of body segmentation in the two clades.

Concept Check 33.5

1. A sea star grasps large prey using its tube feet, and everts its stomach through its mouth and into the opening between the halves of the prey's shell. It secretes juices that begin digesting the prey within its shell. The sea star then brings its stomach back inside its body, where the digestion of the prey is completed. **2.** Both insects and nematodes are members of Ecdysozoa, one of the three major clades of bilaterians. Therefore, a characteristic shared by *Drosophila* and *Caenorhabditis* may be informative for other members of their clade—but not necessarily for members of Deuterostomia. Instead, Figure 33.2 suggests that a species within Echinodermata or Chordata might be a more appropriate invertebrate model organism from which to draw inferences about humans and other vertebrates. **3.** Echinoderms include species with a wide range of body forms. However, even echinoderms that look very different from one another, such as sea stars and sea cucumbers, share characteristics unique to their phylum, including a water vascular system and tube feet. The differences between echinoderm species illustrate the diversity of life, while the characteristics they share illustrate the unity of life. The match between organisms and their environments can be seen in such echinoderm features as the eversible stomachs of sea stars (enabling them to digest prey that are larger than their mouth) and the complex, jaw-like structure that sea urchins use to eat seaweed.

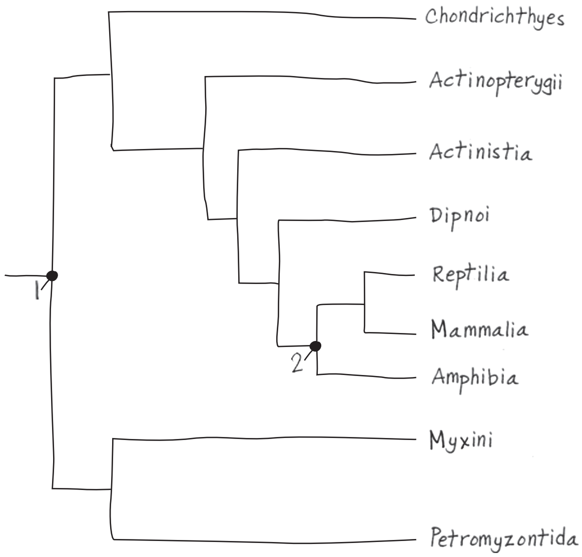
Summary of Key Concepts Questions

33.1 The sponge body consists of two layers of cells, both of which are in contact with water. As a result, gas exchange and waste removal occur as substances diffuse into and out of the cells of the body. Choanocytes and amoebocytes ingest food particles from the surrounding water. Choanocytes also release food particles to amoebocytes, which then digest the food particles and deliver nutrients to other cells. **33.2** The cnidarian body plan consists of a sac with a central digestive compartment, the gastrovascular cavity. The single opening to this compartment serves as both a mouth and an anus. The two main variations on this body plan are sessile polyps (which adhere to the substrate at the end of the body opposite to the mouth/anus) and motile medusae (which move freely through the water and resemble flattened, mouth-down versions of polyps). **33.3** No. Some lophotrochozoans have a crown of ciliated tentacles that function in feeding (called a lophophore), while others go through a distinctive developmental stage known as trochophore larvae. Many other lophotrochozoans do not have either of these features. As a result, the clade is defined primarily by DNA similarities, not morphological similarities. **33.4** Many nematode species live in soil and in sediments on the bottom of bodies of water. These free-living species play important roles in decomposition and nutrient cycling. Other nematodes are parasites, including many species that attack the roots of plants and some that attack animals (including humans). Arthropods have profound effects on all aspects of ecology. In aquatic environments, crustaceans play key roles as grazers (of algae), scavengers, and predators, and some species, such as krill, are important sources of food for whales and other vertebrates. On land, it is difficult to think of features of the natural world that are not affected in some way by insects and other arthropods, such as spiders and ticks. There are more than 1 million species of insects, many of which have enormous ecological effects as herbivores, predators, parasites, decomposers, and vectors of disease. Insects are also key sources of food for many organisms, including humans in some regions of the world. **33.5** Echinoderms and chordates are both members of Deuterostomia, one of the three main clades of bilaterian animals. As such, chordates (including humans) are more closely related to echinoderms than we are to animals in any of the other phyla covered in this chapter. Nevertheless, echinoderms and chordates have evolved independently for over 500 million years. This statement does not contradict the close relationship of echinoderms and chordates, but it does make clear that "close" is a relative term indicating that these two phyla are more closely related to each other than either is to animal phyla not in Deuterostomia.

Chapter 34

Figure Questions

Figure 34.2



The redrawn tree shows mammals (including humans) as nested near the middle of the evolutionary tree of vertebrates. Showing the vertebrate tree in this way provides a visual illustration of the fact that the evolutionary history of vertebrates did not consist of a series of steps "leading to" humans. **Figure 34.6** The patterns in these figures suggest that specific *Hox* genes, as well as the order in which they are expressed, have been highly conserved over the course of evolution. **Figure 34.20** *Tiktaalik* was a lobe-fin fish that had both fish and tetrapod characters. Like a fish, *Tiktaalik* had fins, scales, and gills. As described by Darwin's concept of descent with modification, such shared characters can be attributed to descent from ancestral species—in this case, *Tiktaalik*'s descent from fish ancestors. *Tiktaalik* also had traits that were unlike a fish but like a tetrapod, including a flat skull, a neck, a full set of ribs, and the skeletal structure of its fin. These characters illustrate the second part of descent with modification, showing how ancestral features had become modified over time. **Figure 34.21** Sometime between 370 mya and 340 mya. We can infer this because amphibians must have originated after the most recent common ancestor of *Tulerpeton* and living tetrapods (and that ancestor is said to have originated 370 mya), but no later than the date of the earliest known fossils of amphibians (shown in the figure as 340 mya). **Figure 34.25** Pterosaurs did not descend from the common ancestor of all dinosaurs; hence, pterosaurs are not dinosaurs. However, birds are descendants of the common ancestor of the dinosaurs. As a result, a monophyletic clade of dinosaurs must include birds. In that sense, birds are dinosaurs. **Figure 34.37** In a catabolic pathway, like the aerobic processes of cellular respiration, water is released as a by-product when an organic compound such as glucose is mixed with oxygen. The kangaroo rat can retain and use that water, decreasing its need to drink water. **Figure 34.38** In general, the process of exaptation occurs as a structure that had one function acquires a different function via a series of intermediate stages. Each of these intermediate stages typically has some function in the organism in which it is found. The incorporation of articular and quadrate bones into the mammalian ear illustrates exaptation because these bones originally evolved as part of the jaw, where they functioned as the jaw hinge, but over time they became co-opted for another function, namely, the transmission of sound. **Figure 34.44** As shown in this phylogeny, chimpanzees and humans represent the tips of separate branches of evolution. As such, the human and chimpanzee lineages have evolved independently after they diverged from their common ancestor—an event that took place between 6 million and 7 million years ago. Hence, it is incorrect to say that humans evolved from chimpanzees (or vice versa). If humans had descended from chimpanzees, for example, the human lineage would be nested within the chimpanzee lineage, much as birds are nested within the reptile clade (see Figure 34.25). **Figure 34.51** Fossil evidence indicates that Neanderthals did not live in Africa; hence there would have been little opportunity for mating (gene flow) between Neanderthals and humans in Africa. However, as humans migrated from Africa, mating may have occurred between Neanderthals and humans in the first region where the two species encountered one another: the Middle East. Humans carrying Neanderthal genes may then have migrated to other locations, explaining why Neanderthals are equally related to humans from France, China, and Papua New Guinea.

Concept Check 34.1

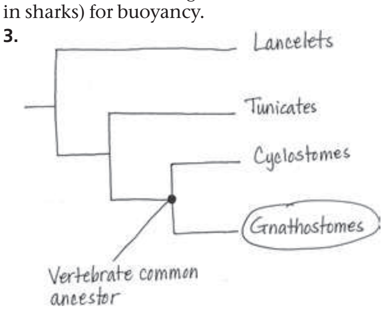
1. The four characters are a notochord; a dorsal, hollow nerve chord; pharyngeal slits or clefts; and a muscular, post-anal tail. **2.** In humans, these characters are present only in the embryo. The notochord becomes disks between the vertebrae; the dorsal, hollow nerve cord develops into the brain and spinal cord; the pharyngeal clefts develop into various adult structures, and the tail is almost completely lost. **3.** You would expect the vertebrate groups Actinopterygii, Actinistia, Dipnoi, Amphibia, Reptilia, and Mammalia to have lungs or lung derivatives. All of these groups originate to the right of (evolved after) the hatch mark indicating the appearance of this derived character in their lineage.

Concept Check 34.2

1. Parasitic lampreys have a round, rasping mouth, which they use to attach to fish. Non-parasitic lampreys feed only as larvae; these larvae resemble lancelets and like them, are suspension feeders. Conodonts had two sets of mineralized dental elements, which may have been used to impale prey and cut it into smaller pieces.
2. Such a finding suggests that early organisms with a head were favored by natural selection in several different evolutionary lineages. However, while a logical argument can be made that having a head was advantageous, fossils alone do not constitute proof. **3.** In armored jawless vertebrates, bone served as external armor that may have provided protection from predators. Some species also had mineralized mouthparts, which could be used for either predation or scavenging.

Concept Check 34.3

1. Both are gnathostomes and have jaws, four clusters of *Hox* genes, enlarged forebrains, and lateral line systems. Shark skeletons consist mainly of cartilage, whereas tuna have bony skeletons. Sharks also have a spiral valve. Tuna have an operculum and a swim bladder, as well as flexible rays supporting their fins. **2.** Aquatic gnathostomes have jaws (an adaptation for feeding) and paired fins and a tail (adaptations for swimming). Aquatic gnathostomes also typically have streamlined bodies for efficient swimming and swim bladders or other mechanisms (such as oil storage in sharks) for buoyancy.
3.



4. Yes, that could have happened. The paired appendages of aquatic gnathostomes other than the lobe-fins could have served as a starting point for the evolution of limbs. The colonization of land by aquatic gnathostomes other than the lobe-fins might have been facilitated in lineages that possessed lungs, as that would have enabled those organisms to breathe air.

Concept Check 34.4

1. Tetrapods are thought to have originated about 365 million years ago when the fins of some lobe-fins evolved into the limbs of tetrapods. In addition to their four limbs with digits—a key derived trait for which the group is named—other derived traits of tetrapods include a neck (consisting of vertebrae that separate the head from the rest of the body), and a pelvic girdle that is fused to the backbone. **2.** Some fully aquatic species are paedomorphic, retaining larval features for life in water as adults. Species that live in dry environments may avoid dehydration by burrowing or living under moist leaves, and they protect their eggs with foam nests, viviparity, and other adaptations. **3.** Many amphibians spend part of their life cycle in aquatic environments and part on land. Thus, they may be exposed to a wide range of environmental problems, including water and air pollution and the loss or degradation of aquatic and/or terrestrial habitats. In addition, amphibians have highly permeable skin, providing relatively little protection from external conditions, and their eggs do not have a protective shell.

Concept Check 34.5

1. The amniotic egg provides protection to the embryo and allows the embryo to develop on land, eliminating the necessity of a watery environment for reproduction. Another key adaptation is rib cage ventilation, which improves the efficiency of air intake and may have allowed early amniotes to dispense with breathing through their skin. Finally, not breathing through their skin allowed amniotes to develop relatively impermeable skin, thereby conserving water.
2. Yes. Although snakes lack limbs, they descended from lizards with legs. Some snakes retain vestigial pelvic and leg bones, providing evidence of their descent from an ancestor with legs. **3.** Birds have weight-saving modifications, including the absence of teeth, a urinary bladder, and a second ovary in females. The wings and feathers are adaptations that facilitate flight, as do efficient respiratory and circulatory systems that support a high metabolic rate.
4. (a) synapsids; (b) tuataras; (c) turtles

Concept Check 34.6

1. Monotremes lay eggs. Marsupials give birth to very small live young that attach to a nipple in the mother's pouch, where they complete development. Eutherians give birth to more developed live young. **2.** Hands and feet adapted for grasping, flat nails, large brain, forward-looking eyes on a flat face, parental care, and movable big toe and thumb **3.** Mammals are endothermic, enabling them to live in a wide range of habitats. Milk provides young with a balanced set of nutrients, and hair and a layer of fat under the skin help mammals retain heat. Mammals have differentiated teeth, enabling them to eat many different kinds of food. Mammals also have relatively large brains, and many species are capable learners. Following the mass extinction at the end of the Cretaceous period, the absence of large terrestrial dinosaurs may have opened many new ecological niches to mammals, promoting an adaptive radiation. Continental drift also isolated many groups of mammals from one another, promoting the formation of many new species.

Concept Check 34.7

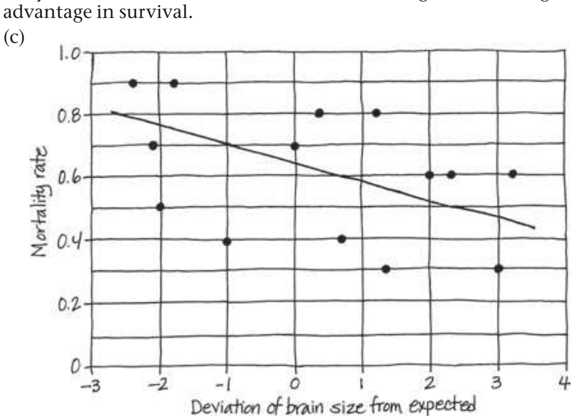
1. Hominins are a clade within the ape clade that includes humans and all species more closely related to humans than to other apes. The derived characters of hominins include bipedal locomotion and relatively larger brains. **2.** In hominins, bipedal locomotion evolved long before large brain size. *Homo ergaster*, for example, was fully upright, bipedal, and as tall as modern humans, but its brain was significantly smaller than that of modern humans. **3.** Yes, both can be correct. *Homo sapiens* may have established populations outside of Africa as early as 115,000 years ago, as indicated by the fossil record. However, those populations may have left few or no descendants today. Instead, all living humans may have descended from Africans that spread from Africa roughly 50,000 years ago, as indicated by genetic data.

Summary of Key Concepts Questions

34.1 Lancelets are the most basal group of living chordates, and as adults they have key derived characters of chordates. This suggests that the chordate common ancestor may have resembled a lancelet in having an anterior end with a mouth along with the following four derived characters: a notochord; a dorsal, hollow nerve cord; pharyngeal slits or clefts; and a muscular, post-anal tail.
34.2 Conodonts, among the earliest vertebrates in the fossil record, were very abundant for 300 million years. While jawless, their well-developed teeth provide early signs of bone formation. Other species of jawless vertebrates developed armor on the outside of their bodies, which probably helped protect them from predators. Like lampreys, these species had paired fins for locomotion and an inner ear with semicircular canals that provided a sense of balance. There were many species of these armored jawless vertebrates, but they all became extinct by the close of the Devonian period, 359 million years ago. **34.3** The origin of jaws altered how fossil gnathostomes obtained food, which in turn had large effects on ecological interactions. Predators could use their jaws to grab prey or remove chunks of flesh, stimulating the evolution of increasingly sophisticated means of defense in prey species. Evidence for these changes can be found in the fossil record, which includes fossils of 10-m-long predators with remarkably powerful jaws, as well as lineages of well-defended prey species whose bodies were covered by armored plates. **34.4** Amphibians require water for reproduction; their bodies can lose water rapidly through their moist, highly permeable skin; and amphibian eggs do not have a shell and hence are vulnerable to desiccation. **34.5** Birds are descended from theropod dinosaurs, and dinosaurs are nested within the archosaur lineage, one of the two main reptile lineages. Thus, the other living archosaur reptiles, the crocodilians, are more closely related to birds than they are to non-archosaur reptiles such as lizards. As a result, birds are considered reptiles. (Note that if reptiles were defined as excluding birds, the reptiles would not form a clade; instead, the reptiles would be a paraphyletic group.) **34.6** Mammals are members of a group of amniotes called synapsids. Early (nonmammalian) synapsids laid eggs and had a sprawling gait. Fossil evidence shows that mammalian features arose gradually over a period of more than 100 million years. For example, the jaw was modified over time in nonmammalian synapsids, eventually coming to resemble that of a mammal. By 180 million years ago, the first mammals had appeared. There were many species of early mammals, but most of them were small, and they were not abundant or dominant members of their community. Mammals did not rise to ecological dominance until after the extinction of the dinosaurs. **34.7** The fossil record shows that from 4.5 to 2.5 million years ago, a wide range of hominin species walked upright but had relatively small brain sizes. About 2.5 million years ago, the first members of genus *Homo* emerged. These species used tools and had larger brains than those of earlier hominins. Fossil evidence indicates that multiple members of our genus were alive at any given point in time. Furthermore, until about 1.3 million years ago, these various *Homo* species also coexisted with members of earlier hominin lineages, such as *Paranthropus*. The different hominins alive at the same periods of time varied in body size, body shape, brain size, dental morphology, and the capacity for tool use. Ultimately, except for *Homo sapiens*, all of these species became extinct. Overall, human evolution can be viewed as an evolutionary tree with many branches—the only surviving lineage of which is our own.

Test Your Understanding

8. (a) Because brain size tends to increase consistently in such lineages, we can conclude that natural selection favored the evolution of larger brains and hence that the benefits outweighed the costs. (b) As long as the benefits of brains that are large relative to body size are greater than the costs, large brains can evolve. Natural selection might favor the evolution of brains that are large relative to body size because such brains confer an advantage in obtaining mates and/or an advantage in survival.
(c)



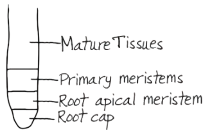
Adult mortality tends to be lower in birds with larger brains.

Chapter 35

Figure Questions

Figure 35.11

(1)



(2)

As a result of the addition of secondary xylem cells, the vascular cambium is pushed farther to the outside.

Figure 35.15

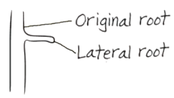
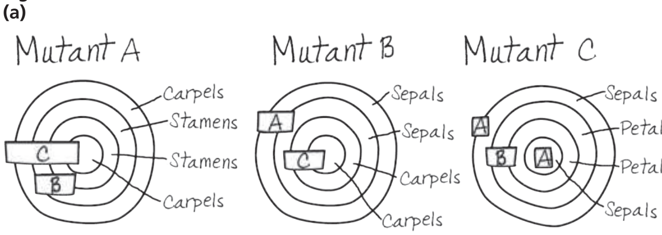


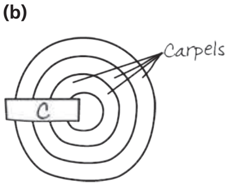
Figure 35.17 Pith and cortex are defined, respectively, as ground tissue that is internal and ground tissue that is external to vascular tissue. Since vascular bundles of monocot stems are scattered throughout the ground tissue, there is no clear distinction between internal and external relative to the vascular tissue. **Figure 35.19** The vascular cambium produces growth that increases the diameter of a stem or root. The tissues that are exterior to the vascular cambium cannot keep pace with the growth because their cells no longer divide. As a result, these tissues rupture. **Figure 35.23** Periderm (mainly cork and cork cambium), primary phloem, secondary phloem, vascular cambium, secondary xylem (sapwood and heartwood), primary xylem, and pith. At the base of ancient redwood that is many centuries old, the remnants of primary growth (primary phloem, primary xylem and pith would be quite insignificant. **Figure 35.33** Every root epidermal cell would develop a root hair. **Figure 35.35** Another example of homeotic gene mutation is the mutation in a *Hox* gene that causes legs to form in place of antennae in *Drosophila* (see Figure 18.20).

Figure 35.36

(a)



(b)



Concept Check 35.1

1. The vascular tissue system connects leaves and roots, allowing sugars to move from leaves to roots in the phloem and allowing water and minerals to move to the leaves in the xylem. **2.** To get sufficient energy from photosynthesis, we would need lots of surface area exposed to the sun. This large surface-to-volume ratio, however, would create a new problem—evaporative water loss. We would have to be permanently connected to a water source—the soil, also our source of minerals. In short, we would probably look and behave very much like plants. **3.** As plant cells enlarge, they typically form a huge central vacuole that contains a dilute, watery sap. Central vacuoles enable plant cells to become large with only a minimal investment of new cytoplasm. The orientation of the cellulose microfibrils in plant cell walls affects the growth pattern of cells.

Concept Check 35.2

1. Yes. In a woody plant, secondary growth is occurring in the older parts of the stem and root, while primary growth is occurring at the root and shoot tips. **2.** The largest, oldest leaves would be lowest on the shoot. Since they would probably be heavily shaded, they would not photosynthesize much regardless of their size. Determinate growth benefits the plant by keeping it from investing an ever-increasing amount of resources into organs that provide little photosynthetic product. **3.** No. The carrot roots will probably be smaller at the end of the second year because the food stored in the roots will be used to produce flowers, fruits, and seeds.

Concept Check 35.3

1. In roots, primary growth occurs in three successive stages, moving away from the tip of the root: the zones of cell division, elongation, and differentiation. In shoots, it occurs at the tip of apical buds, with leaf primordia arising along the sides of an apical meristem. Most growth in length occurs in older internodes below the shoot tip. **2.** No. Because vertically oriented leaves, such as those of maize, can capture light equally well on both sides of the leaf, you would expect them to have mesophyll cells that are not differentiated into palisade and spongy layers. This is typically the case. Also, vertically oriented leaves usually have stomata on both leaf surfaces. **3.** Root hairs are cellular extensions that increase the surface area of the root epidermis, thereby enhancing the absorption of minerals and water. Microvilli are extensions that increase the absorption of nutrients by increasing the surface area of the gut.

Concept Check 35.4

1. The sign will still be 2 m above the ground because this part of the tree is no longer growing in length (primary growth); it is now growing only in thickness (secondary growth). **2.** Stomata must be able to close because evaporation is much more intensive from leaves than from the trunks of woody trees as a result of the higher surface-to-volume ratio in leaves. **3.** Since there is little seasonal temperature variation in the tropics, the growth rings of a tree from the tropics would be difficult to discern unless the tree came from an area that had pronounced wet and dry seasons. **4.** The tree would die slowly. Girdling removes an entire ring of secondary phloem (part of the bark), completely preventing transport of sugars and starches from the shoots to the roots. After several weeks, the roots would have used all of their stored carbohydrate reserves and would die.

Concept Check 35.5

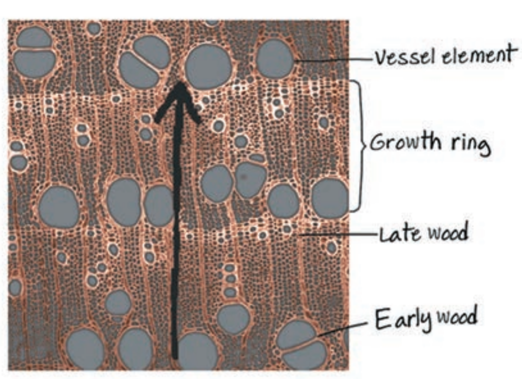
1. Although all the living vegetative cells of a plant have the same genome, they develop different forms and functions because of differential gene expression. **2.** Plants show indeterminate growth; juvenile and mature phases are found on the same individual plant; and cell differentiation in plants is more dependent on final position than on lineage. **3.** One hypothesis is that tepals arise if *B* gene activity is present in all three of the outer whorls of the flower.

Summary of Key Concepts Questions

35.1 Here are a few examples: The cuticle of leaves and stems protects these structures from desiccation. Collenchyma and sclerenchyma cells have thick walls that provide support for plants. Strong, branching root systems help anchor plants in the soil. **35.2** Primary growth arises from apical meristems and involves production and elongation of organs. Secondary growth arises from lateral meristems and adds to the diameter of roots and stems. **35.3** Lateral roots emerge from the pericycle and destroy plant cells as they emerge. In stems, branches arise from axillary buds and do not destroy any cells. **35.4** With the evolution of secondary growth, plants were able to grow taller and shade competitors. **35.5** The orientation of cellulose microfibrils in the innermost layers of the cell wall causes growth along one axis. Microtubules in the cell's outermost cytoplasm play a key role in regulating the axis of cell expansion because it is their orientation that determines the orientation of cellulose microfibrils.

Test Your Understanding

8.



Chapter 36

Figure Questions

Figure 36.2 Cellular respiration is occurring in all parts of a growing plant at all times, with mitochondria continuously releasing CO_2 and consuming O_2. In photosynthetic cells, the CO_2 produced by mitochondria during the day is consumed by chloroplasts, which also consume CO_2 from the air. Meanwhile, the mitochondria obtain O_2 from the chloroplasts, which also release O_2 into the air. At night, when photosynthesis does not occur, the mitochondria must exchange gases with the air rather than with the chloroplasts. As a result, at night photosynthetic cells are *releasing* CO_2 into the air and *consuming* O_2 from the air, the opposite of what happens during the day. **Figure 36.3** The leaves are being produced in a counterclockwise spiral. The next leaf primordium will emerge approximately between and to the inside of leaves 8 and 13. **Figure 36.4** A higher leaf area index will not necessarily increase photosynthesis because of upper leaves shading lower leaves. **Figure 36.6** A proton pump inhibitor would depolarize (increase) the membrane potential because fewer hydrogen ions would be pumped out across the plasma membrane. The immediate effect of an inhibitor of the H^+/sucrose transporter would be to hyperpolarize (decrease) the membrane potential because fewer hydrogen ions would be leaking back into the cell through these cotransporters. An inhibitor of the H^+/NO_3^- cotransporter would have no effect on the membrane potential because the simultaneous cotransport of a positively charged ion and a negatively charged ion has no net effect on charge difference across the membrane. An inhibitor of the potassium ion channels would decrease the membrane potential because additional positively charged ions would not be accumulating outside the cell. **Figure 36.8** Few, if any, mesophyll cells are more than three cells from a vein. **Figure 36.9** The Casparian strip blocks water and minerals from moving between endodermal cells or moving around an endodermal cell via the cell's wall. Therefore, water and minerals must pass through an endodermal cell's plasma membrane. **Figure 36.18** Because the xylem is under negative pressure (tension), excising a stylet that had been inserted into a tracheid or vessel element would probably introduce air into the cell. No xylem sap would exude unless positive root pressure was predominant.

Concept Check 36.1

1. Vascular plants must transport minerals and water absorbed by the roots to all the other parts of the plant. They must also transport sugars from sites of production to sites of use. **2.** Increased stem elongation would raise the plant's upper leaves. Erect leaves and reduced lateral branching would make the plant less subject to shading by the encroaching neighbors. **3.** Pruning shoot tips removes apical dominance, resulting in lateral shoots (branches) growing from axillary buds (see Concept 35.3). This branching produces a bushier plant with a higher leaf area index.

Concept Check 36.2

1. The cell's Ψ_P is 0.7 MPa. In a solution with a Ψ of $^-0.4$ MPa, the cell's Ψ_P at equilibrium would be 0.3 MPa. **2.** The cell would still adjust to changes in its osmotic environment, but its responses would be slower. Although aquaporins do not affect the water potential gradient across membranes, they allow for more rapid osmotic adjustments. **3.** If tracheids and vessel elements were alive at maturity, their cytoplasm would impede water movement, preventing rapid long-distance transport. **4.** The protoplasts would burst. Because the cytoplasm has many dissolved solutes, water would enter the protoplast continuously without reaching equilibrium. (When present, the cell wall prevents rupturing by limiting expansion of the protoplast.)

Concept Check 36.3

1. At dawn, a drop is exuded from the rooted stump because the xylem is under positive pressure due to root pressure. At noon, the xylem is under negative pressure (tension) when it is cut, and the xylem sap is pulled back into the rooted stump. Root pressure cannot keep pace with the increased rate of transpiration at noon. **2.** Perhaps greater root mass helps compensate for the lower water permeability of the plasma membranes. **3.** The Casparian strip and tight junctions both prevent movement of fluid between cells.

Concept Check 36.4

1. Stomatal opening at dawn is controlled mainly by light, CO_2 concentration, and a circadian rhythm. Environmental stresses such as drought, high temperature, and wind can stimulate stomata to close during the day. Water deficiency during the peak of the day can trigger release of the plant hormone abscisic acid, which signals guard cells to close stomata. **2.** The activation of the proton pumps of stomatal cells would cause the guard cells to take up K^+. The increased turgor of the guard cells would lock the stomata open and lead to extreme evaporation from the leaf. **3.** After the flowers are cut, transpiration from any leaves and from the petals (which are modified leaves) will continue to draw water up the xylem. If cut flowers are transferred directly to a vase, air pockets in xylem vessels prevent delivery of water from the vase to the flowers. Cutting stems again underwater, a few centimeters from the original cut, will sever the xylem above the air pocket. The water droplets prevent another air pocket from forming while the flowers are transferred to a vase. **4.** Water molecules are in constant motion, traveling at different speeds. If water molecules gain enough energy, the most energetic molecules near the liquid's surface will have sufficient speed, and therefore sufficient kinetic energy, to leave the liquid in the form of gaseous molecules (water vapor). As the molecules with the highest kinetic energy leave the liquid, the average kinetic energy of the remaining liquid decreases. Because a liquid's temperature is directly related to the average kinetic energy of its molecules, the temperature drops as evaporation proceeds.

Concept Check 36.5

1. In both cases, the long-distance transport is a bulk flow driven by a pressure difference at opposite ends of tubes. Pressure is generated at the source end of a sieve tube by the loading of sugar and resulting osmotic flow of water into the phloem, and this pressure *pushes* sap from the source end to the sink end of the tube. In contrast, transpiration generates a negative pressure potential (tension) that *pulls* the ascent of xylem sap. **2.** The main sources are fully grown leaves (producing sugar by photosynthesis) and fully developed storage organs (producing sugar by breakdown of starch). Roots, buds, stems, expanding leaves, and fruits are powerful sinks because they are actively growing. A storage organ may be a sink in the summer when accumulating carbohydrates but a source in the spring when breaking down starch into sugar for growing shoot tips. **3.** Positive pressure, whether it be in the xylem when root pressure predominates or in the sieve-tube elements of the phloem, requires active transport. Most long-distance transport in the xylem depends on bulk flow driven by the negative pressure potential generated ultimately by the evaporation of water from the leaf and does not require living cells. **4.** The spiral slash prevents optimal bulk flow of the phloem sap to the root sinks. Therefore, more phloem sap can move from the source leaves to the fruit sinks, making them sweeter.

Concept Check 36.6

1. Plasmodesmata, unlike gap junctions, have the ability to pass RNA, proteins, and viruses from cell to cell. **2.** Long-distance signaling is critical for the integrated functioning of all large organisms, but the speed of such signaling is much less critical to plants because their responses to the environment, unlike those of animals, do not typically involve rapid movements. **3.** Although this strategy would eliminate the systemic spread of viral infections, it would also severely impact the development of the plants.

Summary of Key Concepts Questions

36.1 Plants with tall shoots and elevated leaf canopies generally had an advantage over shorter competitors. A consequence of the selective pressure for tall shoots was the further separation of leaves from roots. This separation created problems for the transport of materials between root and shoot systems. Plants with xylem cells were more successful at supplying their shoot systems with soil resources (water and minerals). Similarly, those with phloem cells were more successful at supplying sugar sinks with carbohydrates. **36.2** Xylem sap is pulled up the plant by transpiration much more often than it is pushed up the plant by root pressure. **36.3** Hydrogen bonds are necessary for the cohesion of water molecules to each other and for the adhesion of water to other materials, such as cell walls. Both adhesion and cohesion of water molecules are involved in the ascent of xylem sap under conditions of negative pressure. **36.4** Although stomata account for most of the water lost from plants, they are necessary for exchange of gases—for example, for the uptake of carbon dioxide needed for photosynthesis. The loss of water through stomata also drives the long-distance transport of water that brings soil nutrients from roots to the rest of the plant. **36.5** Although the movement of phloem sap depends on bulk flow, the pressure gradient that drives phloem transport depends on the osmotic uptake of water in response to the loading of sugars into sieve-tube elements at sugar sources. Phloem loading depends on H^+ cotransport processes that ultimately depend on H^+ gradients established by active H^+ pumping. **36.6** Electrical signaling, cytoplasmic pH, cytoplasmic Ca^{2+} concentration, and viral movement proteins all affect symplastic communication, as do developmental changes in the number of plasmodesmata.

Chapter 37

Figure Questions

Figure 37.3 Cations. At low pH, there would be more protons (H^+) to displace mineral cations from negatively charged soil particles into the soil solution. **Figure 37.4** The A horizon, which consists of the topsoil. **Table 37.1** During photosynthesis, CO_2 is fixed into carbohydrates, which contribute to the dry mass. In cellular respiration, O_2 is reduced to H_2O and does not contribute to the dry mass. **Figure 37.10** Some other examples of mutualism are the following relationships. *Flashlight fish and bioluminescent bacteria:* The bacteria gain nutrients and protection from the fish, while the bioluminescence attracts prey and mates for the fish. *Flowering plants and pollinators:* Animals distribute the pollen and are rewarded by a meal of nectar or pollen. *Vertebrate herbivores and some bacteria in the digestive system:* Microorganisms in the alimentary canal break down cellulose to glucose and, in some cases, provide the animal with vitamins or amino acids. Meanwhile, the microorganisms have a steady supply of food and a warm environment. *Humans and some bacteria in the digestive system:* Some bacteria provide humans with vitamins, while the bacteria get nutrients from the digested food. **Figure 37.12** Both ammonium and nitrate. A decomposing animal would release amino acids into the soil that would be converted into ammonium by ammonifying bacteria. Some of this ammonium could be used directly by the plant. A large part of the ammonium, however, would be converted by nitrifying bacteria to form nitrate ions that could also be absorbed by the plant root system. **Figure 37.13** The legume plants benefit because the bacteria fix nitrogen that is absorbed by their roots. The bacteria benefit because they acquire photosynthetic products from the plants. **Figure 37.14** All three plant tissue systems are affected. Root hairs (dermal tissue) are modified to allow *Rhizobium* penetration. The cortex (ground tissue) and pericycle (vascular tissue) proliferate during nodule formation. The vascular tissue of the nodule connects to the vascular cylinder of the root to allow for efficient nutrient exchange.

Concept Check 37.1

1. Overwatering deprives roots of oxygen. Overfertilizing is wasteful and can lead to soil salinization and water pollution. **2.** As lawn clippings decompose, they restore mineral nutrients to the soil. If they are removed, the minerals lost from the soil must be replaced by fertilization. **3.** Because of their small size and negative charge, clay particles would increase the number of binding sites for cations and water molecules and would therefore increase cation exchange and water retention in the soil. **4.** Due to hydrogen bonding between water molecules, water expands when it freezes, and this causes mechanical fracturing of rocks. Water also coheres to many objects, and this cohesion combined with other forces, such as gravity, can help tug particles from rock. Finally, water, because it is polar, is an excellent solvent that allows many substances, including ions, to become dissolved in solution.

Concept Check 37.2

1. No. Even though macronutrients are required in greater amounts, all essential elements are necessary for the plant to complete its life cycle. **2.** No. The fact that the addition of an element results in an increase in the growth rate of a crop does not mean that the element is strictly required for the plant to complete its life cycle. **3.** Inadequate aeration of the roots of hydroponically grown plants would promote alcohol fermentation, which uses more energy and may lead to the accumulation of ethanol, a toxic by-product of fermentation.

Concept Check 37.3

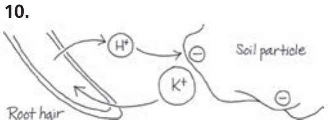
1. The rhizosphere is the zone in the soil immediately adjacent to living roots. It harbors many rhizobacteria with which the root systems form beneficial mutualisms. Some rhizobacteria produce antibiotics that protect roots from disease. Others absorb toxic metals or make nutrients more available to roots. Still others convert gaseous nitrogen into forms usable by the plant or produce chemicals that stimulate plant growth. **2.** Soil bacteria and mycorrhizae enhance plant nutrition by making certain minerals more available to plants. For example, many types of soil bacteria are involved in the nitrogen cycle, and the hyphae of mycorrhizae provide a large surface area for the absorption of nutrients, particularly phosphate ions. **3.** Mixotrophy refers to the strategy of using photosynthesis and heterotrophy for nutrition. Euglenids are well-known mixotrophic protists. **4.** Saturating rainfall may deplete the soil of oxygen. A lack of soil oxygen would inhibit nitrogen fixation by the peanut root nodules and decrease the nitrogen available to the plants. Alternatively, heavy rain may leach nitrate from the soil. A symptom of nitrogen deficiency is yellowing of older leaves.

Summary of Key Concepts Questions

37.1 The term *ecosystem* refers to the communities of organisms within a given area and their interactions with the physical environment around them. Soil is teeming with many communities of organisms, including bacteria, fungi, animals, and the root systems of plants. The vigor of these individual communities depends on nonliving factors in the soil environment, such as minerals, oxygen, and water, as well as on interactions, both positive and negative, between different communities of organisms. **37.2** No. Plants can complete their life cycle when grown hydroponically, that is, in aerated salt solutions containing the proper ratios of all the minerals needed by plants. **37.3** No. Some parasitic plants obtain their energy by siphoning off carbon nutrients from other organisms.

Test Your Understanding

10.



Chapter 38

Figure Questions

Figure 38.4 Having a specific pollinator is more efficient because less pollen gets delivered to flowers of the wrong species. However, it is also a risky strategy: If the pollinator population suffers to an unusual degree from predation, disease, or climate change, then the plant may not be able to produce seeds. **Figure 38.6** The part of the angiosperm life cycle characterized by the most mitotic divisions is the step between seed germination and the mature sporophyte. **Figure 38.8 Make Connections** In addition to having a single cotyledon, monocots have leaves with parallel leaf venation, scattered vascular bundles in their stems, a fibrous root system, floral parts in threes or multiples of threes, and pollen grains with only one opening. In contrast, dicots have two cotyledons, netlike leaf venation, vascular bundles in a ring, taproots, floral parts in fours or fives or multiples thereof, and pollen grains with three openings. **Figure 38.8 Visual Skills** The mature garden bean seed lacks an endosperm at maturity. Its endosperm was consumed during seed development, and its nutrients were stored anew in the cotyledons. **Figure 38.9** Beans use a hypocotyl hook to push through the soil. The delicate leaves and shoot apical meristem are also protected by being sandwiched between two large cotyledons. The coleoptile of maize seedlings helps protect the emerging leaves.

Concept Check 38.1

1. In angiosperms, pollination is the transfer of pollen from an anther to a stigma. Fertilization is the fusion of the egg and sperm to form the zygote; it cannot occur until after the growth of the pollen tube from the pollen grain. **2.** Long styles help to weed out pollen grains that are genetically inferior and not capable of successfully growing long pollen tubes. **3.** No. The haploid (gametophyte) generation of plants is multicellular and arises from spores. The haploid phase of the animal life cycles is a single-celled gamete (egg or sperm) that arises directly from meiosis: There are no spores.

Concept Check 38.2

1. Flowering plants can avoid self-fertilization by self-incompatibility, having male and female flowers on separate plants (dioecious species), or having stamens and styles of different heights on separate plants ("pin" and "thrum" flowers). **2.** Pear trees. Pollination is an integral part of sexual reproduction in angiosperms. Hence, the decline in the number of pollinators will affect the angiosperms that reproduce sexually. Aspen trees and dandelion plants reproduce asexually, whereas pear trees reproduce sexually. **3.** In the short term, selfing may be advantageous in a population that is so dispersed and sparse that pollen delivery is unreliable. In the long term, however, selfing is an evolutionary dead end because it leads to a loss of genetic diversity that may preclude adaptive evolution.

Concept Check 38.3

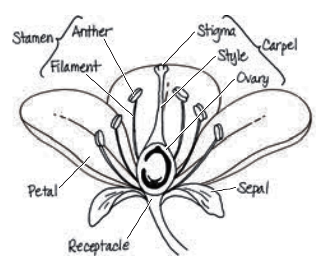
1. Traditional breeding and genetic engineering both involve artificial selection for desired traits. However, genetic engineering techniques facilitate faster gene transfer and are not limited to transferring genes between closely related varieties or species. **2.** *Bt* maize suffers less insect damage; therefore, *Bt* maize plants are less likely to be infected by fumonisin-producing fungi that infect plants through wounds. **3.** In such species, engineering the transgene into the chloroplast DNA would not prevent its escape in pollen; such a method requires that the chloroplast DNA be found only in the egg. An entirely different method of preventing transgene escape would therefore be needed, such as male sterility, apomixis, or self-pollinating closed flowers.

Summary of Key Concepts Questions

38.1 After pollination and fertilization, a flower changes into a fruit. The petals, sepals, and stamens typically fall off the flower. The stigma of the pistil withers, and the ovary begins to swell. The ovules (embryonic seeds) inside the ovary begin to mature. **38.2** Asexual reproduction can be advantageous in a stable environment because individual plants that are well suited to that environment pass on all their genes to offspring. Also, asexual reproduction generally results in offspring that are less fragile than the seedlings produced by sexual reproduction. However, sexual reproduction offers the advantage of dispersal of tough seeds. Moreover, sexual reproduction produces genetic variety, which may be advantageous in an unstable environment. The likelihood is better that at least one offspring of sexual reproduction will survive in a changed environment. **38.3** "Golden Rice," although not yet in commercial production, has been engineered to produce more vitamin A, thereby raising the nutritional value of rice. A protoxin gene from a soil bacterium has been engineered into *Bt* maize. This protoxin is lethal to invertebrates but harmless to vertebrates. *Bt* crops require less pesticide spraying and have lower levels of fungal infection and fungal toxins. The nutritional value of cassava is being increased in many ways by genetic engineering. Enriched levels of iron and beta-carotene (a vitamin A precursor) have been achieved, and cyanide-producing chemicals have been almost eliminated from the roots.

Test Your Understanding

8.



Chapter 39

Figure Questions

Figure 39.4 Panel B in Figure 9.17 shows a branching signal transduction pathway that resembles the branching phytochrome-dependent pathway involved in de-etiolation. **Figure 39.5** To determine which wavelengths of light are most effective in phototropism, you could use a glass prism to split white light into its component colors and see which colors cause the quickest bending (the answer is blue; see Figure 39.15). **Figure 39.6** No. Polar auxin transport depends on the distribution of auxin transport proteins at the basal ends of cells. **Figure 39.12** No. Since the *ein* mutation renders the seedling "blind" to ethylene, enhancing ethylene production by adding an *eto* mutation would have no effect on phenotype compared with the *ein* mutation alone. **Figure 39.16** Yes. The white light, which contains red light, would stimulate seed germination in all treatments. **Figure 39.20** Since far-red light, like darkness, causes an accumulation of the red-absorbing form (P_r) of phytochrome, single flashes of far-red light at night would have no effect on flowering beyond what the dark periods alone would have. **Figure 39.21** If this were true, florigen would be an inhibitor of flowering, not an inducer. **Figure 39.27** Photosynthetic adaptations can occur at the molecular level, as is apparent in the fact that C_3 plants use rubisco to fix carbon dioxide initially, whereas C_4 and CAM plants use PEP carboxylase. An adaptation at the tissue level is that plants have different stomatal densities based on their genotype and environmental conditions. At the organismal level, plants alter their shoot architectures to make photosynthesis more efficient. For example, self-pruning removes branches and leaves that respire more than they photosynthesize.

Concept Check 39.1

1. Dark-grown seedlings are etiolated: They have long stems, underdeveloped root systems, and unexpanded leaves, and their shoots lack chlorophyll. Etiolated growth is beneficial to seeds sprouting under the dark conditions they would encounter underground. By devoting more energy to stem elongation and less to leaf expansion and root growth, a plant increases the likelihood that the shoot will reach the sunlight before its stored foods run out. **2.** By inhibiting the activity of brassinosteroids, which enhance stem elongation, brassinazole would cause dwarfism of the plant. **3.** No. Applying Viagra, like injecting cyclic GMP as described in the text, should cause only a partial de-etiolation response. Full de-etiolation would require activation of the calcium branch of the signal transduction pathway.

Concept Check 39.2

1. Tumor-like growths are caused by uncontrolled cell division and differentiation. The pathogen interferes with the functions of cytokinin and auxin. **2.** The plant will exhibit a constitutive triple response. Because the kinase that normally prevents the triple response is dysfunctional, the plant will undergo the triple response regardless of whether ethylene is present or the ethylene receptor is functional. **3.** Since ethylene often stimulates its own synthesis, it is under positive-feedback regulation.

Concept Check 39.3

1. The enzyme may not be under circadian regulation. Light may act as an environmental cue for enhanced expression of the enzyme. To understand whether the enzyme is under circadian regulation, its expression should be measured under constant environmental conditions. **2.** It is impossible to say. To establish that this species is a short-day plant, it would be necessary to establish the critical night length for flowering and that this species only flowers when the night is longer than the critical night length. **3.** According to the action spectrum of photosynthesis, red and blue light are the most effective in photosynthesis. Thus, it is not surprising that plants assess their light environment using blue- and red-light-absorbing photoreceptors.

Concept Check 39.4

1. A plant that overproduces ABA would undergo less evaporative cooling because its stomata would not open as widely. **2.** The soil absorbed water from the tub and became waterlogged. This caused the air pores in the soil to be filled with water, preventing cellular respiration in the roots. The plants, therefore, died due to suffocation. **3.** No. Because root caps are involved in sensing gravity, roots that have their root caps removed are almost completely insensitive to gravity.

Concept Check 39.5

1. Some insects increase plants' productivity by eating harmful insects or aiding in pollination. **2.** Mechanical damage breaches a plant's first line of defense against infection, its protective dermal tissue. **3.** No. Pathogens that kill their hosts would soon run out of victims and might themselves go extinct. **4.** Perhaps the breeze dilutes the local concentration of a volatile defense compound that the plants produce.

Summary of Key Concepts Questions

39.1 Signal transduction pathways often activate protein kinases, enzymes that phosphorylate other proteins. Protein kinases can directly activate certain preexisting enzymes by phosphorylating them, or they can regulate gene transcription (and enzyme production) by phosphorylating specific transcription factors. **39.2** Yes, there is truth to the old adage that one bad apple spoils the whole bunch. Ethylene, a gaseous hormone that stimulates ripening, is produced by damaged, infected, or overripe fruits. Ethylene can diffuse to healthy fruit in the "bunch" and stimulate their rapid ripening. **39.3** Plant physiologists proposed the existence of a floral-promoting factor (florigen) based on the fact that a plant induced to flower could induce flowering in a second plant to which it was grafted, even though the second plant was not in an environment that would normally induce flowering in that species. **39.4** Plants subjected to drought stress are often more resistant to freezing stress because the two types of stress are quite similar. Freezing of water in the extracellular spaces causes free water concentrations outside the cell to decrease. This, in turn, causes free water to leave the cell by osmosis, leading to the dehydration of cytoplasm, much like what is seen in drought stress. **39.5** Chewing insects make plants more susceptible to pathogen invasion by disrupting the waxy cuticle of shoots, thereby creating an opening for infection. Moreover, substances released from damaged cells can serve as nutrients for the invading pathogens.

Test Your Understanding

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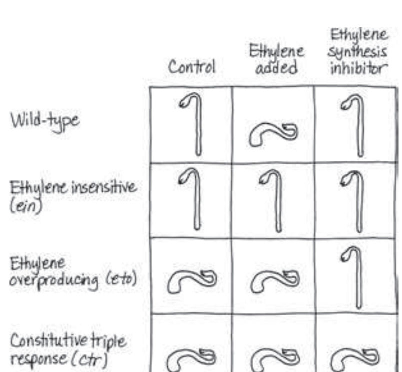


Chapter 40

Figure Questions

Figure 40.4 Such exchange surfaces are internal in the sense that they are inside the body. However, they are also continuous with openings on the external body surface that contact the environment. **Figure 40.6** Signals in the nervous system always travel on a direct route between the sending and receiving cell. In contrast, hormones that reach target cells can have an effect regardless of the path by which they arrive or how many times they travel through the circulatory system. **Figure 40.8** The stimuli (gray boxes) are the room temperature increasing in the top loop or decreasing in the bottom loop. The responses could include the heater turning off and the temperature decreasing in the top loop and the heater turning on and the temperature increasing in the bottom loop. The sensor/control center is the thermostat. The air conditioner would form a second control circuit, cooling the house when air temperature exceeded the set point. Such opposing, or antagonistic, pairs of control circuits increase the effectiveness of a homeostatic mechanism. **Figure 40.12** The conduction arrows would be in the opposite direction, transferring heat from the walrus to the ice because the walrus is warmer than the ice. **Figure 40.17** If a female Burmese python were not incubating eggs, her oxygen consumption would decrease with decreasing temperature, as for any other ectotherm. **Figure 40.18** The ice water would cool tissues in your head, including blood that would then circulate throughout your body. This effect would accelerate the return to a normal body temperature. If, however, the ice water reached the eardrum and cooled the blood vessel that supplies the hypothalamus, the hypothalamic thermostat would respond by inhibiting sweating and constricting blood vessels in the skin, slowing cooling elsewhere in the body. **Figure 40.19** The transport of nutrients across membranes and the synthesis of RNA and protein are coupled to ATP hydrolysis. These processes proceed spontaneously because there is an overall drop in free energy, with the excess energy given off as heat. Similarly, less than half of the free energy in glucose is captured in the coupled reactions of cellular respiration. The remainder of the energy is released as heat. **Figure 40.22** Nothing. Although genes that show a circadian variation in expression during euthermia exhibit constant RNA levels during hibernation, a gene that shows constant expression during hibernation might also show constant expression during euthermia. **Figure 40.23** In hot environments, both plants and animals experience evaporative cooling as a result of transpiration (in plants) or bathing, sweating, and panting (in animals); both plants and animals synthesize heat-shock proteins, which protect other proteins from heat stress; and animals also use various behavioral responses to minimize heat absorption. In cold environments, both plants and animals increase the proportion of unsaturated fatty acids in their membrane lipids and use antifreeze proteins that prevent or limit the formation of intracellular ice crystals; plants increase cytoplasmic levels of specific solutes that help reduce the loss of intracellular water during extracellular freezing; and animals increase metabolic heat production and use insulation, circulatory adaptations such as countercurrent exchange, and behavioral responses to minimize heat loss.

Concept Check 40.1

1. All types of epithelia consist of cells that line a surface, are tightly packed, are situated on top of a basal lamina, and form an active and protective interface with the external environment. **2.** An oxygen molecule must cross a plasma membrane when entering the body at an exchange surface in the respiratory system, in both entering and exiting the circulatory system, and in moving from the interstitial fluid to the cytoplasm of the body cell. **3.** You need the nervous system to perceive the danger and provoke a split-second muscular response to keep from falling. The nervous system, however, does not make a direct connection with blood vessels or glucose-storing cells in the liver. Instead, the nervous system triggers the release of a hormone (called epinephrine, or adrenaline) by the endocrine system, bringing about a change in these tissues in just a few seconds.

Concept Check 40.2

1. In thermoregulation, the product of the pathway (a change in temperature) decreases pathway activity by reducing the stimulus. In an enzyme-catalyzed biosynthetic process, the product of the pathway (in this case, isoleucine) inhibits the pathway that generated it. **2.** You would want to put the thermostat close to where you would be spending time, where it would be protected from environmental perturbations, such as direct sunshine, and not right in the path of the output of the heating system. Similarly, the sensors for homeostasis located in the human brain are separated from environmental influences and can monitor conditions in a vital and sensitive tissue. **3.** In convergent evolution, the same biological trait arises independently in two or more species. Gene analysis can provide evidence for an independent origin. In particular, if the genes responsible for the trait in one species lack significant sequence similarity to the corresponding genes in another species, scientists conclude that there is a separate genetic basis for the trait in the two species and thus an independent origin. In the case of circadian rhythms, the clock genes in cyanobacteria appear unrelated to those in humans.

Concept Check 40.3

1. "Wind chill" involves heat loss through convection, as the moving air contributes to heat loss from the skin surface. **2.** The hummingbird, being a very small endotherm, has a very high metabolic rate. If by absorbing sunlight certain flowers warm their nectar, a hummingbird feeding on these flowers is saved the metabolic expense of warming the nectar to its body temperature. **3.** To raise body temperature to the higher range of fever, the hypothalamus triggers heat generation by muscular contractions, or shivering. The person with a fever may in fact say that they feel cold, even though their body temperature is above normal.

Concept Check 40.4

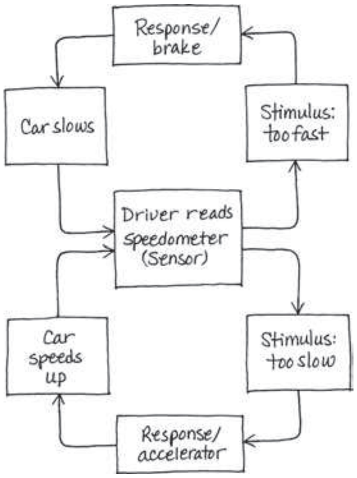
1. The mouse would consume oxygen at a higher rate because it is an endotherm, so its basal metabolic rate is higher than the ectothermic lizard's standard metabolic rate. **2.** The house cat; smaller animals have a higher metabolic rate per unit body mass and a greater demand for food per unit body mass. **3.** The alligator's body temperature would decrease along with the air temperature. Its metabolic rate would therefore also decrease as chemical reactions slowed. In contrast, the lion's body temperature would not change. Its metabolic rate would increase as it shivered and produced heat to keep its body temperature constant.

Summary of Key Concepts Questions

40.1 Animals exchange materials with their environment across their body surface, and a spherical shape has the minimum surface area per unit volume. As body size increases, the ratio of surface area to body volume decreases. **40.2** No; an animal's internal environment fluctuates slightly around set points or within normal ranges. Homeostasis is a dynamic state. Furthermore, there are sometimes programmed changes in set points, such as those resulting in radical increases in hormone levels at particular times in development. **40.3** Heat exchange across the skin is a primary mechanism for the regulation of body core temperature, with the result that the skin is cooler than the body core. **40.4** Small animals have a higher BMR per unit mass and therefore consume more oxygen per unit mass than large animals. A higher breathing rate is required to support this increased oxygen consumption.

Test Your Understanding

8.



Chapter 41

Figure Questions

Figure 41.4

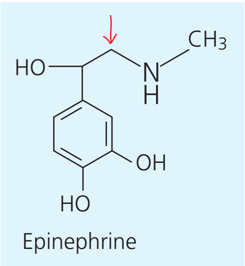


Figure 41.5 The hormone is water-soluble and has a cell-surface receptor. Such receptors, unlike those for lipid-soluble hormones, can cause observable changes in cells without hormone-dependent gene transcription. **Figure 41.6** ATP is enzymatically converted to cAMP. The other steps represent binding reactions. **Figure 41.21** The embryonic gonad can become either a testis or an ovary. In contrast, the ducts either form a particular structure or degenerate, and the bladder forms in both males and females.

Concept Check 41.1

1. Water-soluble hormones, which cannot penetrate the plasma membrane, bind to cell-surface receptors. This interaction triggers an intracellular signal transduction pathway that ultimately alters the activity of a preexisting protein in the cytoplasm and/or changes transcription of specific genes in the nucleus. Steroid hormones are lipid-soluble and can cross the plasma membrane into the cell interior, where they bind to receptors located in the cytosol or nucleus. The hormone-receptor complex then functions directly as a transcription factor that changes transcription of specific genes. **2.** An exocrine gland, because pheromones are not secreted into interstitial fluid, but instead are typically released onto a body surface or into the environment **3.** Because receptors for water-soluble hormones are located on the cell surface, facing the extracellular space, injecting the hormone into the cytosol would not trigger a response.

Concept Check 41.2

1. Prolactin regulates milk production, and oxytocin regulates milk release. **2.** The posterior pituitary, an extension of the hypothalamus that contains the axons of neurosecretory cells, is the storage and release site for two neurohormones, oxytocin and antidiuretic hormone (ADH). The anterior pituitary contains endocrine cells that make at least six different hormones. Secretion of anterior pituitary hormones is controlled by hypothalamic hormones that travel via blood vessels to the anterior pituitary. **3.** The hypothalamus and pituitary glands function in many different endocrine pathways. Many defects in these glands, such as those affecting growth or organization, would therefore disrupt many hormone pathways. Only a very specific defect, such as a mutation affecting a particular hormone receptor, would alter just one endocrine pathway. The situation is quite different for the final gland in a pathway, such as the thyroid gland. In this case, a wide range of defects that disrupt gland function would disrupt only the one pathway or small set of pathways in which that gland functions. **4.** Both diagnoses could be correct. In one case, the thyroid gland may produce excess thyroid hormone despite normal hormonal input from the hypothalamus and anterior pituitary. In the other, abnormally elevated hormonal input (elevated TSH levels) may be the cause of the overactive thyroid gland.

Concept Check 41.3

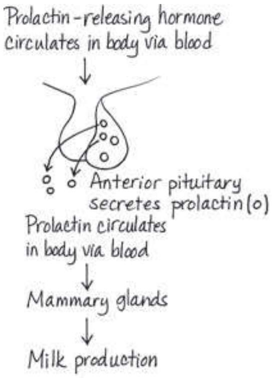
1. If the function of the pathway is to provide a transient response, a short-lived stimulus would be less dependent on negative feedback. **2.** You would be exploiting the anti-inflammatory activity of glucocorticoids. Local injection avoids the effects on glucose metabolism that would occur if glucocorticoids were taken orally and transported throughout the body in the bloodstream. **3.** Both hormones produce opposite effects in different target tissues. In the fight-or-flight response, epinephrine increases blood flow to skeletal muscles and reduces blood flow to smooth muscles in the digestive system. In establishing apical dominance, auxin promotes the growth of apical buds and inhibits the growth of lateral buds.

Summary of Key Concepts Questions

41.1 As shown in Figure 47.16, helper T cell activation by cytokines acting as local regulators involves both autocrine and paracrine signaling. **41.2** The pancreas, parathyroid glands, and pineal gland **41.3** Both the pituitary and the adrenal glands are formed by fusion of neural and nonneural tissue. ADH is secreted by the neurosecretory portion of the pituitary gland, and epinephrine is secreted by the neurosecretory portion of the adrenal gland.

Test Your Understanding

8.



Chapter 42

Figure Questions

Figure 42.6 Your diagram should show food entering through the hydra's mouth and being digested into nutrients in the large portion of the gastrovascular cavity. The nutrients then diffuse into the extensions of that cavity that reach into the tentacles. There, nutrients would be absorbed by cells of the gastrodermis and transported to cells of the epidermis of a tentacle. **Figure 42.9** The airway must be open for exhaling to occur. If the epiglottis is up, milk entered the throat from the mouth encounters air forced out of the lungs and is carried along into the nasal cavity and out the nose. **Figure 42.11** Since enzymes are proteins, and proteins are hydrolyzed in the small intestine, the digestive enzymes in that compartment need to be resistant to enzymatic cleavage other than the cleavage required to activate them. **Figure 42.12** None. Since digestion is completed in the small intestine, tapeworms simply absorb predigested nutrients through their large body surface. **Figure 42.13** Yes. The exit of the chylomicrons involves exocytosis, an active process that consumes energy in the form of ATP. In contrast, the entry of monoglycerides and fatty acids into the cell by diffusion is a passive process that does not consume energy. **Figure 42.21** Both insulin and glucagon are involved in negative feedback circuits.

Concept Check 42.1

1. The only essential amino acids are those that an animal cannot synthesize from other molecules. **2.** Essential fatty acids are required in very small amounts. Ample quantities of these are obtained easily from milk, grains, and vegetables in the diet. Therefore, their deficiencies are rare. **3.** To identify the essential nutrient missing from an animal's diet, a researcher could supplement the diet with individual nutrients one at a time and determine which nutrient eliminates the signs of malnutrition.

Concept Check 42.2

1. A gastrovascular cavity is a digestive pouch with a single opening that functions in both ingestion and elimination; an alimentary canal is a digestive tube with a separate mouth and anus at opposite ends. **2.** As long as nutrients are within the cavity of the alimentary canal, they are in a compartment that is continuous with the outside environment via the mouth and anus and have not yet crossed a membrane to enter the body. **3.** In both cases, high-energy fuels are consumed, complex molecules are broken down into simpler ones, and waste products are eliminated. In addition, gasoline, like food, is broken down in a specialized compartment, so that surrounding structures are protected from disassembly. Finally, just as food and wastes remain outside the body in a digestive tract, neither gasoline nor its waste products enter the passenger compartment of the automobile.

Concept Check 42.3

1. Because parietal cells in the stomach pump hydrogen ions into the stomach lumen where they combine with chloride ions to form HCl, a proton pump inhibitor reduces the acidity of chyme and thus the irritation that occurs when chyme enters the esophagus. **2.** By releasing sugars from starch or glycogen in the mouth, amylase might allow us to recognize foods that provide a ready source of energy. **3.** Proteins would be denatured and digested into peptides. Further digestion, to individual amino acids, would require enzymatic secretions found in the small intestine. No digestion of carbohydrates or lipids would occur.

Concept Check 42.4

1. The increased time for transit through the alimentary canal allows for more extensive processing, and the increased surface area of the canal provides greater opportunity for absorption. **2.** A mammal's digestive system provides mutualistic microorganisms with an environment that is protected against other microorganisms by saliva and gastric juice, that is held at a constant temperature conducive to enzyme action, and that provides a steady source of nutrients. **3.** For the yogurt treatment to be effective, the bacteria from yogurt would have to establish a mutualistic relationship with the small intestine, where disaccharides are broken down and sugars are absorbed. Conditions in the small intestine are likely to be very different from those in a yogurt culture. The bacteria might be killed before they reach the small intestine, or they might not be able to grow there in sufficient numbers to aid in digestion.

Concept Check 42.5

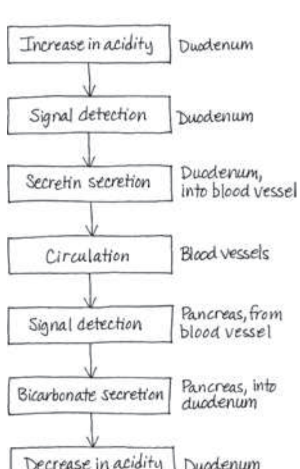
1. Over the long term, the body stores excess calories in fat, whether those calories come from fat, carbohydrate, or protein in food. **2.** In normal individuals, leptin levels decline during fasting. Individuals in the group with low levels of leptin are likely to be defective in leptin production, so leptin levels would remain low regardless of food intake. Individuals in the group with high leptin levels are likely to be defective in responding to leptin, but they still should shut off leptin production as fat stores are used up. **3.** The excess production of insulin will cause blood glucose levels to decrease below normal physiological levels. It will also trigger glycogen synthesis in the liver, further decreasing blood glucose levels. However, low blood glucose levels will stimulate the release of glucagon from alpha cells in the pancreas, which will trigger glycogen breakdown. Thus, there will be antagonistic effects in the liver.

Summary of Key Concepts Questions

42.1 Since the cofactor is necessary in all animals, those animals that do not require it in their diet must be able to synthesize it from other organic molecules. **42.2** A liquid diet containing glucose, amino acids, and other building blocks could be ingested and absorbed without the need for mechanical or chemical digestion. **42.3** The small intestine has a much larger surface area than the stomach. **42.4** The assortment of teeth in our mouth and the short length of our cecum suggest that our ancestors' digestive systems were not specialized for digesting plant material. **42.5** When mealtime arrives, nervous inputs from the brain signal the stomach to prepare to digest food through secretions and churning.

Test Your Understanding

8.



Chapter 43

Figure Questions

Figure 43.2 Although gas exchange might be improved by a steady, one-way flow of fluid, there would likely be inadequate time for food to be digested and nutrients absorbed if fluid flowed through the cavity in this manner. **Figure 43.5** Two capillary beds. The molecule of carbon dioxide would need to enter a capillary bed in the thumb before returning to the right atrium and ventricle, then travel to the lung and enter a capillary from which it could diffuse into an alveolus and be available to be exhaled. **Figure 43.8** Each feature of the ECG recording, such as the sharp upward spike, occurs once per cardiac cycle. Using the *x*-axis to measure the time in seconds between successive spikes and dividing that number by 60 would yield the heart rate as the number of cycles per minute. **Figure 43.25** The reduction in surface tension results from the presence of surfactant. Therefore, for all the infants who had died of RDS, you would expect the amount of surfactant to be near zero. For infants who had died of other causes, you would expect the amount of surfactant to be near zero for body masses less than 1,200 g but much greater than zero for body masses above 1,200 g. **Figure 43.27** Since exhalation is largely passive, the recoil of the elastic fibers in alveoli helps force air out of the lungs. When alveoli lose their elasticity, as occurs in the disease emphysema, less air is exhaled. Because more air is left in the lungs, less fresh air can be inhaled. With a smaller volume of air exchanged, there is a decrease in the partial pressure gradient that drives gas exchange. **Figure 43.28** Breathing at a rate greater than that needed to meet metabolic demand (hyperventilation) would lower blood CO_2 levels. Sensors in major blood vessels and the medulla would signal the breathing control center to decrease the rate of contraction of the diaphragm and rib muscles, decreasing the breathing rate and restoring normal CO_2 levels in the blood and other tissues. **Figure 43.29** The resulting increase in tidal volume would enhance ventilation within the lungs, increasing P_{O_2} and decreasing P_{CO_2} in the alveoli.

Concept Check 43.1

1. In both an open circulatory system and a fountain, fluid is pumped through a tube and then returns to the pump after collecting in a pool. **2.** The ability to shut off blood supply to the lungs when the animal is submerged **3.** The O_2 content would be abnormally low because some oxygen-depleted blood returned to the right atrium from the systemic circuit would mix with the oxygen-rich blood in the left atrium.

Concept Check 43.2

1. The pulmonary veins carry blood that has just passed through capillary beds in the lungs, where it accumulated O_2. The venae cavae carry blood that has just passed through capillary beds in the rest of the body, where it lost O_2 to the tissues. **2.** The delay allows the atria to empty completely, filling ventricles fully before they contract. **3.** The heart, like any other muscle, becomes stronger through regular exercise. You would expect a stronger heart to have a greater stroke volume, which would allow for the decrease in heart rate.

Concept Check 43.3

1. The large total cross-sectional area of the capillaries **2.** An increase in blood pressure and cardiac output combined with the diversion of more blood to the skeletal muscles would increase the capacity for action by increasing the rate of blood circulation and delivering more O_2 and nutrients to the skeletal muscles. **3.** Additional hearts could be used to improve blood return from the legs. However, it might be difficult to coordinate the activity of multiple hearts and to maintain adequate blood flow to hearts far from the gas exchange organs.

Concept Check 43.4

1. Secretion of erythropoietin helps increase the synthesis of red blood cells at high altitudes. **2.** Clotting factors do not initiate clotting but are essential steps in the clotting process. **3.** The chest pain results from inadequate blood flow in coronary arteries. Vasodilation promoted by nitric oxide from nitroglycerin increases blood flow, providing the heart muscle with additional oxygen and thus relieving the pain. **4.** Embryonic stem cells are pluripotent rather than multipotent, meaning that they can give rise to many rather than a few different cell types.

Concept Check 43.5

1. Their interior position helps gas exchange tissues stay moist. If the respiratory surfaces of lungs extended out into the terrestrial environment, they would quickly dry out, and diffusion of O_2 and CO_2 across these surfaces would stop. **2.** Earthworms need to keep their skin moist for gas exchange, but they need air outside this moist layer. If they stay in their waterlogged tunnels after a heavy rain, they will suffocate because they cannot get as much O_2 from water as from air. **3.** In fish, water passes over the gills in the direction opposite to that of blood flowing through the gill capillaries, maximizing the extraction of oxygen from the water along the length of the exchange surface. Similarly, in the extremities of some vertebrates, blood flows in opposite directions in neighboring veins and arteries; this countercurrent arrangement maximizes the recapture of heat from blood leaving the body core in arteries, which is important for thermoregulation in cold environments.

Concept Check 43.6

1. An increase in blood CO_2 concentration causes an increase in the rate of CO_2 diffusion into the cerebrospinal fluid, where the CO_2 combines with water to form carbonic acid. Dissociation of carbonic acid releases hydrogen ions, decreasing the pH of the cerebrospinal fluid. **2.** Increased heart rate increases the rate at which

CO_2-rich blood is delivered to the lungs, where CO_2 is removed. **3.** A hole would allow air to enter the space between the inner and outer layers of the double membrane, resulting in a condition called a pneumothorax. The two layers would no longer stick together, and the lung on the side with the hole would collapse and cease functioning.

Concept Check 43.7

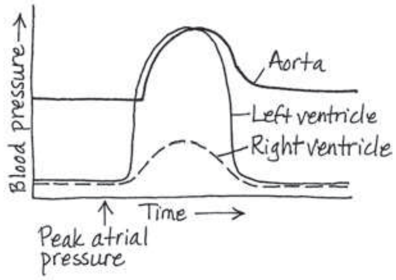
1. Differences in partial pressure between the capillaries and the surrounding tissues or medium; the net diffusion of a gas occurs from a region of higher partial pressure to a region of lower partial pressure. **2.** The Bohr shift causes hemoglobin to release more O_2 at a lower pH, such as found in the vicinity of tissues with high rates of cellular respiration and CO_2 release. **3.** The doctor is assuming that the rapid breathing is the body's response to low blood pH. Metabolic acidosis, the lowering of blood pH as a result of metabolism, can have many causes, including complications of certain types of diabetes, shock (extremely low blood pressure), and poisoning.

Summary of Key Concepts Questions

43.1 In a closed circulatory system, an ATP-driven muscular pump generally moves fluids in one direction on a scale of millimeters to meters. Exchange between cells and their environment relies on diffusion, which involves random movements of molecules. Concentration gradients of molecules across exchange surfaces can drive rapid net diffusion on a scale of 1 mm or less. **43.2** Replacement of a defective valve should increase stroke volume. A lower heart rate would therefore be sufficient to maintain the same cardiac output. **43.3** Blood pressure in the arm would fall by 25–30 mm Hg, the same difference as is normally seen between your heart and your brain. **43.4** One microliter of blood contains about 5 million erythrocytes and 5,000 leukocytes, so leukocytes make up only about 0.1% of the cells in the absence of infection. **43.5** Because CO_2 is such a small fraction of atmospheric gas (0.29 mm Hg/760 mm Hg, or less than 0.04%), the partial pressure gradient of CO_2 between the respiratory surface and the environment always strongly favors the release of CO_2 to the atmosphere. **43.6** Because the lungs do not empty completely with each breath, incoming and outgoing air mix. Lungs thus contain a mixture of fresh and stale air. **43.7** An enzyme speeds up a reaction without changing the equilibrium and without being consumed. Similarly, a respiratory pigment speeds up the exchange of gases between the body and the external environment without changing the equilibrium state and without being consumed.

Test Your Understanding

8.



Chapter 44

Figure Questions

Figure 44.13 You would expect to find these cells lining tubules where they pass through the renal medulla. Because the extracellular fluid of the renal medulla has a very high osmolarity, production of organic solutes by tubule cells in this region keeps intracellular osmolarity high, with the result that these cells maintain normal volume. **Figure 44.14** Furosemide increases urine volume. The absence of ion transport in the ascending limb leaves the filtrate too concentrated for substantial volume reduction in the distal tubule and collecting duct. **Figure 44.17** When the concentration of an ion differs across a plasma membrane, the difference in the concentration of ions inside and outside represents chemical potential energy, while the resulting difference in charge inside and outside represents electrical potential energy. **Figure 44.20** The ADH levels would likely be elevated in both sets of patients with mutations because either defect prevents the recapture of water that restores blood osmolarity to normal levels. **Figure 44.21** Arrows that would be labeled "Secretion" are the arrows indicating secretion of aldosterone, angiotensinogen, and renin.

Concept Check 44.1

1. Because the salt is moved against its concentration gradient, from low concentration (fresh water) to high concentration (blood) **2.** A freshwater osmoconformer would have body fluids too dilute to carry out life's processes. **3.** Without a layer of insulating fur, the camel must use the cooling effect of evaporative water loss to maintain body temperature, thus linking thermoregulation and osmoregulation.

Concept Check 44.2

1. Because uric acid is largely insoluble in water, it can be excreted as a semisolid paste, thereby reducing an animal's water loss. **2.** Humans produce uric acid from purine breakdown, and reducing purines in the diet often lessens the severity of gout. Birds, however, produce uric acid as a waste product of general nitrogen metabolism. They would therefore need a diet low in all nitrogen-containing compounds, not just purines.

Concept Check 44.3

1. In flatworms, ciliated cells draw interstitial fluids containing waste products into protonephridia. In earthworms, waste products pass from interstitial fluids into the coelom. From there, cilia move the wastes into metanephridia via a funnel surrounding an internal opening to the metanephridia. In insects, the Malpighian tubules pump fluids from the hemolymph, which receives waste products during exchange with cells in the course of circulation. **2.** Filtrate is formed when the glomerulus filters blood from the renal artery within Bowman's capsule. Some of the filtrate contents are recovered, enter capillaries, and exit in the renal vein; the rest remain in the filtrate and pass out of the kidney in the ureter. **3.** The presence of Na^+ and other ions (electrolytes) in the dialysate would limit the extent to which they would be removed from the filtrate during dialysis. Adjusting the electrolytes in the starting dialysate can thus lead to the restoration of proper electrolyte concentrations in the plasma. Similarly, the absence of urea and other waste products in the starting dialysate facilitates their removal from the filtrate.

Concept Check 44.4

1. The numerous nephrons and well-developed glomeruli of freshwater fishes produce urine at a high rate, while the small numbers of nephrons and smaller glomeruli of marine fishes produce urine at a low rate. **2.** The kidney medulla would absorb less water; thus, the drug would increase the amount of water lost in the urine. **3.** A decline in blood pressure in the afferent arteriole would reduce the rate of filtration by moving less material through the vessels.

Concept Check 44.5

1. Alcohol inhibits the release of ADH, causing an increase in urinary water loss and increasing the chance of dehydration. **2.** The consumption of a very large amount of water in a short period of time, coupled with an absence of solute intake, can reduce sodium levels in the blood below tolerable levels. This condition, called hyponatremia, leads to disorientation and, sometimes, respiratory distress. It has occurred in some marathon runners who drink water rather than sports drinks. (It has also caused the death of a fraternity pledge as a consequence of a water hazing ritual and the death of a contestant in a water-drinking competition.) **3.** High blood pressure

Summary of Key Concepts Questions

44.1 Water moves into a cell by osmosis when the fluid outside the cells is hypoosmotic (has a lower solute concentration than the cytosol).
44.2

Waste Attribute	Ammonia	Urea	Uric Acid
Toxicity	High	Very low	Low
Energy cost to produce	Low	Moderate	High
Water loss to excretion	High	Moderate	Low

44.3 Filtration produces a fluid for exchange processes that is free of cells and large molecules, which are of benefit to the animal and could not readily be reabsorbed. **44.4** Both types of nephrons have proximal tubules that can reabsorb nutrients, but only juxtamedullary nephrons have loops of Henle that extend deep into the renal medulla. Thus, only kidneys containing juxtamedullary nephrons can produce urine that is more concentrated than the blood. **44.5** Patients who don't produce ADH have symptoms relieved by treatment with the hormone, but many patients with diabetes insipidus lack functional receptors for ADH.

Chapter 45

Figure Questions

Figure 45.7 Newly formed sperm enter the seminal vesicle from the testis and exit via the ejaculatory duct during intercourse. Sperm enter the spermatheca after intercourse and, after storage, are released into the oviduct to fertilize an egg moving into the uterus. **Figure 45.8** When successfully courted by a second male, regardless of his genotype, about one-third of the females rid themselves of all sperm from the first mating. Thus, two-thirds retained some sperm from the first mating. We would therefore predict that two-thirds of those females would have some offspring exhibiting the small-eye phenotype of the dominant mutation carried by the males with which the females mated first. **Figure 45.11** The analysis would be informative because the polar bodies contain all of the maternal chromosomes that don't end up in the mature egg. For example, finding two copies of the disease gene in the polar bodies would indicate its absence in the egg. This method of genetic testing is sometimes carried out when oocytes collected from a female are fertilized with sperm in a laboratory dish. **Figure 45.15** The embryo normally implants about a week after conception, but it spends several days in the uterus before implanting, receiving nutrients from the endometrium. Therefore, the fertilized egg should be cultured for several days in liquid that is at normal body temperature and contains the same nutrients as those provided by the endometrium before implantation. **Figure 45.16** Testosterone can pass from fetal blood to maternal blood via the placental circulation, temporarily upsetting the hormonal balance in the mother. **Figure 45.18** Oxytocin would most likely induce labor, starting a positive-feedback loop that would direct labor to completion. Synthetic oxytocin is in fact frequently used to induce labor when prolonged pregnancy might endanger the mother or fetus.

Concept Check 45.1

1. The offspring of sexual reproduction are more genetically diverse. However, asexual reproduction can produce more offspring over multiple generations. **2.** Unlike other forms of asexual reproduction, parthenogenesis involves gamete production. By controlling whether or not haploid eggs are fertilized, species such as honeybees can readily switch between asexual and sexual reproduction. **3.** No. Owing to random assortment of chromosomes during meiosis, the offspring may receive the same copy or different copies of a particular parental chromosome from the sperm and the egg. Furthermore, genetic recombination during meiosis will result in reassortment of genes between pairs of parental chromosomes. **4.** Fragmentation occurs in both plants and animals. Also, budding in animals and the growth of adventitious from plant roots both involve emergence of new individuals from outgrowths of the parent.

Concept Check 45.2

1. Internal fertilization allows sperm to reach the egg without either gamete drying out. **2.** (a) Animals with external fertilization tend to release many gametes at once, resulting in the production of enormous numbers of zygotes. This increases the chances that some will survive to adulthood. (b) Animals with internal fertilization produce fewer offspring but generally exhibit greater care of the embryos and the young. **3.** Like the uterus of an insect, the ovary of a plant is the site of fertilization. Unlike the plant ovary, the uterus is not the site of egg production, which occurs in the insect ovary. In addition, the fertilized insect egg is expelled from the uterus, whereas the plant embryo develops within a seed in the ovary.

Concept Check 45.3

1. Viagra promotes the vasodilating action of the local regulator nitric oxide, resulting in the relaxation of smooth muscles in the blood vessels of the penis. This enhances blood flow into the erectile tissues. **2.** In humans, the secondary oocyte combines with a sperm before it finishes the second meiotic division. Thus, oogenesis is completed after, not before, fertilization. **3.** The only effect of sealing off each vas deferens is an absence of sperm in the ejaculate. Sexual response and ejaculate volume are unchanged. The cutting and sealing off of these ducts, a *vasectomy*, is a common surgical procedure for men who do not wish to produce any (more) offspring.

Concept Check 45.4

1. In the testis, FSH stimulates the Sertoli cells, which nourish developing sperm. LH stimulates the production of androgens (mainly testosterone), which in turn stimulate sperm production. In both females and males, FSH encourages the growth of cells that support and nourish developing gametes (follicle cells in females and Sertoli cells in males), and LH stimulates the production of sex hormones that promote gametogenesis (estrogens, primarily estradiol, in females and androgens, especially testosterone, in males). **2.** In estrous cycles, which occur in most female mammals, the endometrium is reabsorbed (rather than shed) if fertilization does not occur. Estrous cycles often occur just once or a few times a year, and the female is usually receptive to copulation only during the period around ovulation. Menstrual cycles are found only in humans and some other primates. They control the buildup and breakdown of the uterine lining, but not sexual receptivity. **3.** The combination of estradiol and progesterone would have a negative-feedback effect on the hypothalamus, blocking release of GnRH. This would interfere with LH secretion by the pituitary, thus preventing ovulation. This is in fact one basis of action of the most common hormonal contraceptives. **4.** In the viral replicative cycle, the production of new viral genomes is coordinated with capsid protein expression and with the production of phospholipids for viral coats. In the reproductive cycle of a human female, there is hormonally based coordination of egg maturation with the development of support tissues of the uterus.

Concept Check 45.5

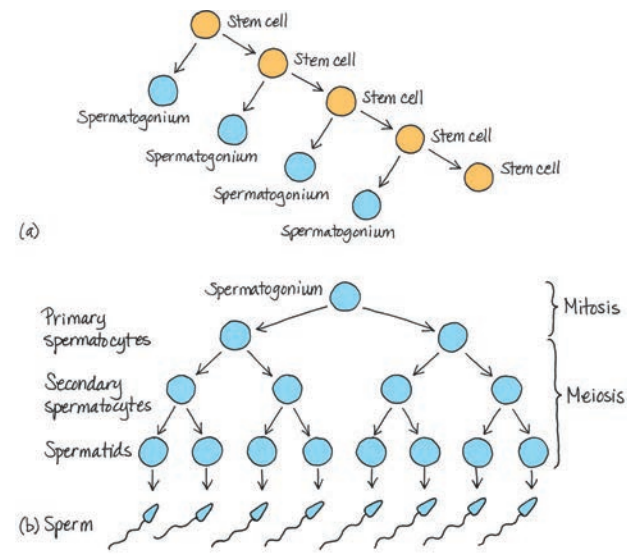
1. The secretion of hCG by the early embryo stimulates the corpus luteum to make progesterone, which helps maintain the pregnancy. During the second trimester, however, hCG production drops, the corpus luteum disintegrates, and the placenta completely takes over progesterone production. **2.** Both tubal ligation and vasectomy block the movement of gametes from the gonads to a site where fertilization could take place. **3.** The introduction of a sperm nucleus directly into an oocyte bypasses the sperm's acquisition of motility in the epididymis, its swimming to meet the egg in the oviduct, and its fusion with the egg.

Summary of Key Concepts Questions

45.1 No. Because parthenogenesis involves meiosis, the mother would pass on to each offspring a random and therefore typically distinct combination of the chromosomes she inherited from her mother and father. **45.2** None **45.3** The small size and lack of cytoplasm characteristic of a sperm are adaptations well suited to its function as a delivery vehicle for DNA. The large size and rich cytoplasmic contents of eggs support the growth and development of the embryo. **45.4** Circulating anabolic steroids mimic the feedback regulation of testosterone, turning off pituitary signaling to the testes and thereby blocking the release of signals required for spermatogenesis. **45.5** Oxygen in maternal blood diffuses from pools in the endometrium into fetal capillaries in the chorionic villi of the placenta, and from there travels throughout the circulatory system of the fetus.

Test Your Understanding

9.

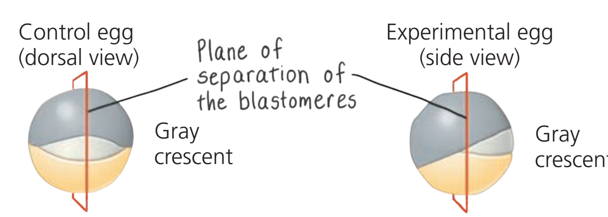


(c) The supply of stem cells would be used up, and spermatogenesis would not be able to continue.

Chapter 46

Figure Questions

Figure 46.4 You could inject the compound into an unfertilized egg, expose the egg to sperm, and see whether the fertilization envelope forms.
Figure 46.6 There would be fewer cells and they would be closer together.
Figure 46.8 (1) The blastocoel forms a single compartment that surrounds the gut, much like a doughnut surrounds a hole. (2) Ectoderm forms the outer covering of the animal, and endoderm lines the internal organs, such as the digestive tract. Mesoderm fills much of the space between these two layers.
Figure 46.19 Eight cell divisions are required to give rise to the intestinal cell closest to the mouth. **Figure 46.22** When the researchers allowed normal cortical rotation to occur, the "back-forming" determinants were activated. When they then forced the opposite rotation to occur, the back was established on the opposite side as well. Because the molecules on the normal side were already activated, forcing the opposite rotation apparently did not "cancel out" the establishment of the back side by the first rotation.
Figure 46.23 Draw It



What If? In Spemann's control, the two blastomeres were physically separated, and each grew into a whole embryo. In Roux's experiment, remnants of the dead blastomere were still contacting the live blastomere, which developed into a half-embryo. Therefore, molecules present in the dead cell's remnants may have been signaling to the live cell, inhibiting it from making all the embryonic structures. **Figure 46.24** You could inject the isolated protein (or an mRNA encoding it) into ventral cells of an earlier gastrula. If dorsal structures form on the ventral side, that would support the idea that the protein is the signaling molecule secreted or presented by the dorsal lip. You should also do a control experiment to make sure the injection process alone did not cause dorsal structures to form. **Figure 46.26** Either Sonic hedgehog mRNA or protein can serve as a marker of the ZPA. The absence of either one after removal of the AER would support your hypothesis. You could also block FGF function and see whether the ZPA formed (by looking for Sonic hedgehog).

Concept Check 46.1

1. As ion channels open in the egg's plasma membrane, the sperm enters the egg cytoplasm. Sodium ions diffuse into the egg and cause depolarization or a decrease in the membrane potential, which acts as the fast block to polyspermy. **2.** The increased Ca^{2+} concentration in the egg would cause the cortical granules to fuse with the plasma membrane, releasing their contents and causing a fertilization envelope to form, even though no sperm had entered. This would prevent fertilization. **3.** Yes. Cell signaling is important to ensure that molecules on the sperm surface bind to receptors on the egg surface to initiate signal transduction and to ensure species specificity.

Concept Check 46.2

1. The cells of the notochord migrate toward the midline of the embryo (converge), rearranging themselves so there are fewer cells across the notochord, which thus becomes longer overall (extends; see Figure 46.17). **2.** Because microfilaments would not be able to contract and decrease the size of one end of the cell, both the inward bending in the middle of the neural tube and the outward bending of the hinge regions at the edges would be blocked. Therefore, the neural tube probably would not form. **3.** Dietary intake of the vitamin folic acid dramatically reduces the frequency of neural tube defects.

Concept Check 46.3

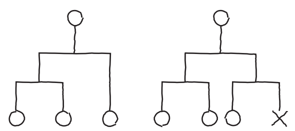
1. Axis formation establishes the location and polarity of the three axes that provide the coordinates for development. Pattern formation positions particular tissues and organs in the three-dimensional space defined by those coordinates. **2.** Morphogen gradients act by specifying cell fates across a field of cells through variation in the level of a determinant. Morphogen gradients thus act more globally than cytoplasmic determinants or inductive interactions between pairs of cells. **3.** Yes, a second embryo could develop because inhibiting BMP-4 activity would have the same effect as transplanting an organizer. **4.** Supernumerary structures would probably form towards the distal end of the limb as the apical ectodermal ridge is a major signaling center for limb development.

Summary of Key Concepts Questions

46.1 The binding of a sperm to a receptor on the egg surface is very specific and likely would not occur if the two gametes were from different species. Without sperm binding, the sperm and egg membranes would not fuse. **46.2** Apoptosis functions to eliminate structures required only in an immature form, nonfunctional cells from a pool larger than the number required, and tissues formed by a developmental program that is not adaptive for the organism as it has evolved. **46.3** Mutations that affected both limb and kidney development would be more likely to alter the function of monocilia because these organelles are important in several signaling pathways. Mutations that affected limb development but not kidney development would more likely alter a single pathway, such as Hedgehog signaling.

Test Your Understanding

8.



Chapter 47

Figure Questions

Figure 47.4 Dicer-2 binds double-stranded RNA without regard to size or sequence and then cuts that RNA into fragments, each 21 base pairs long. The Argo complex binds to double-stranded RNA fragments that are each 21 base pairs long, displaces one strand, and then uses the remaining strand to match to a particular target sequence in a single-stranded mRNA. **Figure 47.5** Cell-surface TLRs recognize molecules on the surface of pathogens, whereas TLRs in vesicles recognize internal molecules of pathogens after the pathogens are broken down. **Figure 47.7** Because the pain of a splinter stops almost immediately when you remove it from the skin, you can correctly deduce that the signals that mediate the inflammatory response are quite short-lived. **Figure 47.10** Part of the enzyme or antigen receptor provides a structural "backbone" that maintains overall shape, while interaction occurs at a surface with a close fit to the substrate or antigen. The combined effect of multiple noncovalent interactions at the active site or binding site is a high-affinity interaction of tremendous specificity. **Figure 47.13** After gene rearrangement, a lymphocyte and its daughter cells make a single version of the antigen receptor. In contrast, alternative splicing is not heritable and can give rise to diverse gene products in a single cell. **Figure 47.14** A single B cell has more than 100,000 identical antigen receptors on its surface, not four, and there are more than 1 million B cells differing in their antigen specificity, not three. **Figure 47.17** These receptors enable memory cells to present antigen on their cell surface to a helper T cell. This presentation of antigen is required to activate memory cells in a secondary immune response. **Figure 47.22** Primary response: arrows extending from Antigen (1st exposure), Antigen-presenting cell, Helper T cell, B cell, Plasma cells, Cytotoxic T cell, and Active cytotoxic T cells; secondary response: arrows extending from Antigen (2nd exposure), Memory helper T cells, Memory B cells, Memory cytotoxic T cells, Plasma cells, and Active cytotoxic T cells. **Figure 47.24** There would be no change in the results. Because the two antigen binding sites of an antibody have identical specificity, the two bacteriophages bound would have to display the same viral peptide.

Concept Check 47.1

1. Because pus contains white blood cells, fluid, and cell debris, it indicates an active and at least partially successful inflammatory response against invading pathogens. **2.** Whereas the ligand for the TLR receptor is a foreign molecule, the ligand for many signal transduction pathways is a molecule produced by the organism itself. **3.** Mounting an immune response would require recognition of some molecular feature of the wasp egg not found in the host. It might be that only some potential hosts have a receptor with the necessary specificity.

Concept Check 47.2

1. See Figure 47.9. The transmembrane regions lie within the C regions, which also form the disulfide bridges. In contrast, the antigen-binding sites are in the V regions. **2.** Generating memory cells ensures both that a receptor specific for a particular epitope will be present and that there will be more lymphocytes with this specificity than in a host that had never encountered the antigen. **3.** If each B cell produced two different light and heavy chains for its antigen receptor, different combinations would make four different receptors. If any one were self-reactive, the lymphocyte would be eliminated in the generation of self-tolerance. For this reason, many more B cells would be eliminated, and those that could respond to a foreign antigen would be less effective at doing so due to the variety of receptors (and antibodies) they express.

Concept Check 47.3

1. A child lacking a thymus would have no functional T cells. Without helper T cells to help activate B cells, the child would be unable to produce antibodies against extracellular bacteria. Furthermore, without cytotoxic T cells or helper T cells, the child's immune system would be unable to kill virus-infected cells. **2.** Since the antigen-binding site is intact, the antibody fragments could neutralize viruses and opsonize bacteria. **3.** If the handler developed immunity to proteins in the antivenin, another injection could provoke a severe immune response.

Concept Check 47.4

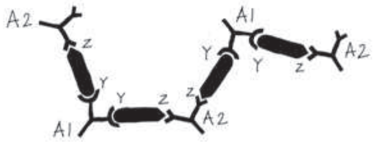
1. Unlike the polio virus, the flu virus undergoes antigenic variation very rapidly, making it difficult for the host's immune system to recognize it. Therefore, new vaccines need to be developed each year. **2.** A person with a cold is likely to produce oral and nasal secretions that facilitate viral transfer. In addition, since sickness can cause incapacitation or death, a virus that is programmed to exit the host when there is a physiological stress has the opportunity to find a new host at a time when the current host may cease to function. **3.** A person with a macrophage deficiency would have frequent infections. The causes would be poor innate responses, due to diminished phagocytosis and inflammation, and poor adaptive responses, due to the lack of macrophages to present antigens to helper T cells.

Summary of Key Concepts Questions

47.1 Lysozyme in saliva destroys bacterial cell walls; the viscosity of mucus helps trap bacteria; acidic pH in the stomach kills many bacteria; and the tight packing of cells lining the gut provides a physical barrier to infection. **47.2** Sufficient numbers of cells to mediate an innate immune response are always present, whereas an adaptive response requires selection and proliferation of an initially very small cell population specific for the infecting pathogen. **47.3** No. Immunological memory after a natural infection and that after vaccination are very similar. There may be minor differences in the particular antigens that can be recognized in a subsequent infection. **47.4** No. AIDS refers to a loss of immune function that can occur over time in an individual infected with HIV. However, certain multidrug combinations ("cocktails") or rare genetic variations usually prevent progression to AIDS in HIV-infected individuals.

Test Your Understanding

8. One possible answer:



Chapter 48

Figure Questions

Figure 48.7 Adding chloride channels would make the membrane potential less positive. Adding potassium channels would have no effect because there are no potassium ions present. **Figure 48.9** In the absence of other forces, chemical concentration gradients govern net diffusion. In this case, ions are more concentrated outside of the cell and move in when the channel opens.
Figure 48.10

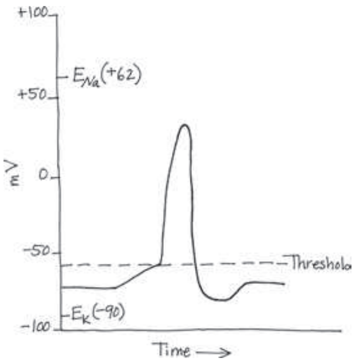


Figure 48.11

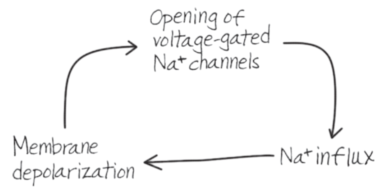


Figure 48.12

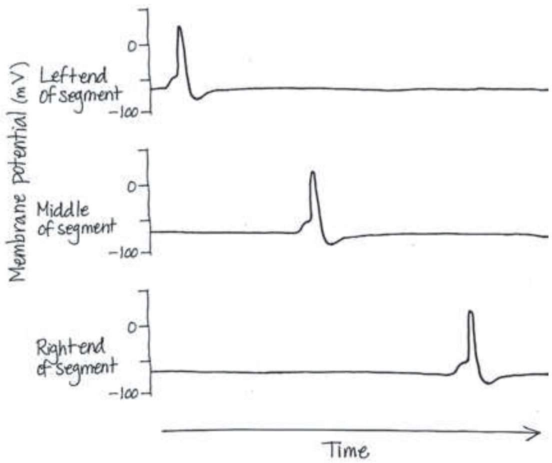


Figure 48.15 The production and transmission of action potentials would be unaffected. However, action potentials arriving at chemical synapses would be unable to trigger release of neurotransmitter. Signaling at such synapses would thus be blocked. **Figure 48.17** Summation only occurs if inputs occur simultaneously or nearly so. Thus, spatial summation, in which input is received from two different sources, is in effect also temporal summation.

Concept Check 48.1

1. Axons and dendrites extend from the cell body and function in information flow. Dendrites transfer information to the cell body, whereas axons transmit information from the cell body. A typical neuron has multiple dendrites and one axon. **2.** Sensors in your ear transmit information to your brain. There, the activity of interneurons in processing centers enables you to recognize your name. In response, signals transmitted via motor neurons cause contraction of muscles that turn your neck. **3.** Increased branching would allow control of a greater number of postsynaptic cells, enhancing coordination of responses to nervous system signals.

Concept Check 48.2

1. Ions can flow against a chemical concentration gradient if there is an opposing electrical gradient of greater magnitude. **2.** A decrease in permeability to K^+, an increase in permeability to Na^+, or both **3.** Charged dye molecules could equilibrate only if other charged molecules could also cross the membrane. If not, a membrane potential would develop that would counterbalance the chemical gradient.

Concept Check 48.3

1. A graded potential has a magnitude that varies with stimulus strength, whereas an action potential has an all-or-none magnitude that is independent of stimulus strength. **2.** Loss of the insulation provided by myelin sheaths leads to a disruption of action potential propagation along axons. Voltage-gated sodium channels are restricted to the nodes of Ranvier, and without the insulating effect of myelin, the inward current produced at one node during an action potential cannot depolarize the membrane to the threshold at the next node. **3.** Positive feedback is responsible for the rapid opening of many voltage-gated sodium channels, causing the rapid outflow of sodium ions responsible for the rising phase of the action potential. As the membrane potential becomes positive, voltage-gated potassium channels open in a form of negative feedback that helps bring about the falling phase of the action potential. **4.** The maximum frequency would decrease because the refractory period would be extended.

Concept Check 48.4

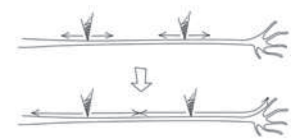
1. It can bind to different types of receptors, each triggering a specific response in postsynaptic cells. **2.** These toxins would prolong the EPSPs that acetylcholine produces because the neurotransmitter would remain longer in the synaptic cleft. **3.** Membrane depolarization, exocytosis, and membrane fusion each occur in fertilization and in neurotransmission.

Summary of Key Concepts Questions

48.1 It would prevent information from being transmitted away from the cell body along the axon. **48.2** There are very few open sodium channels in a resting neuron, so the resting potential either would not change or would become slightly more negative (hyperpolarization). **48.4** A given neurotransmitter can have many receptors that differ in their location and activity. Drugs that target receptor activity rather than neurotransmitter release or stability are therefore likely to exhibit greater specificity and potentially have fewer undesirable side effects.

Test Your Understanding

7. The activity of the sodium-potassium pump is essential to maintain the resting potential. With the pump inactivated, the sodium and potassium concentration gradients would gradually disappear, resulting in a greatly reduced resting potential. **8.** Since GABA is an inhibitory neurotransmitter in the CNS, this drug would be expected to decrease brain activity. A decrease in brain activity might be expected to slow down or reduce behavioral activity. Many sedative drugs act in this fashion. **9.** As shown in this pair of drawings, a pair of action potentials would move outward in both directions from each electrode. (Action potentials are unidirectional only if they begin at one end of an axon.) However, because of the refractory period, the two action potentials between the electrodes both stop where they meet. Thus, only one action potential reaches the synaptic terminals.



Chapter 49

Figure Questions

Figure 49.7 During swallowing, muscles along the esophagus alternately contract and relax, resulting in peristalsis. One model to explain this alternation is that each section of muscle receives nerve impulses that alternate between excitation and inhibition, just as the quadriceps and hamstring receive opposing signals in the knee-jerk reflex. **Figure 49.15** The gray areas have a different shape and pattern, indicating different planes through the brain. This fact indicates that the nucleus accumbens and the amygdala are in different planes. **Figure 49.17** The hand is shown larger than the forearm because the hand receives more innervation than the forearm for sensory input to the brain and motor output from the brain. **Figure 49.24** If the depolarization brings the membrane potential to or past threshold, it should initiate action potentials that cause dopamine release from the VTA neurons. This should mimic natural stimulation of the brain reward system, resulting in positive and perhaps pleasurable sensations.

Concept Check 49.1

1. The sympathetic division would likely be activated. It mediates the "fight-or-flight" response in stressful situations. **2.** Nerves contain bundles of axons, some that belong to motor neurons, which send signals outward from the CNS, and some that belong to sensory neurons, which bring signals into the CNS. Therefore, you would expect effects on both motor control and sensation. **3.** Neurosecretory cells of the adrenal medulla secrete the hormones epinephrine and norepinephrine in response to preganglionic input from sympathetic neurons. These hormones travel in the circulation throughout the body, triggering responses in many tissues.

Concept Check 49.2

1. The cerebral cortex on the left side of the brain initiates voluntary movement of the right side of the body. **2.** Alcohol diminishes function of the cerebellum. **3.** A coma reflects a disruption in the cycles of sleep and arousal regulated by communication between the midbrain and pons (reticular formation) and the cerebrum. You would expect this group to have damage to the midbrain, the pons, the cerebrum, or any part of the brain between these structures. Paralysis reflects an inability to carry out motor commands transmitted from the cerebrum to the spinal cord. You would expect this group to have damage to the portion of the CNS extending from the spinal cord up to but not including the midbrain and pons.

Concept Check 49.3

1. Brain damage that disrupts behavior, cognition, memory, or other functions provides evidence that the portion of the brain affected by the damage is important for the normal activity that is blocked or altered. **2.** Broca's area, which is active during the generation of speech, is located near the motor cortex, which controls skeletal muscles, including those in the face. Wernicke's area, which is active when speech is heard, is located in the posterior part of the temporal lobe, which is involved in hearing. **3.** Each cerebral hemisphere is specialized for different parts of this task—the right for face recognition and the left for language. Without an intact corpus callosum, neither hemisphere can take advantage of the other's processing abilities.

Concept Check 49.4

1. There can be an increase in the number of synapses between the neurons or an increase in the strength of existing synaptic connections. **2.** If consciousness is an emergent property resulting from the interaction of many different regions of the brain, then it is unlikely that localized brain damage will have a discrete effect on consciousness. **3.** The hippocampus is responsible for organizing newly acquired information. Without hippocampal function, the links necessary to retrieve information from the cerebral cortex will be lacking, and no functional memory, short- or long-term, will be formed.

Concept Check 49.5

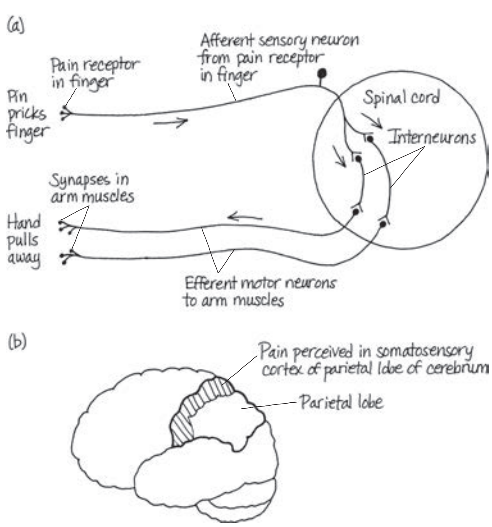
1. Both are progressive brain diseases whose risk increases with advancing age. Both result from the death of brain neurons and are associated with the accumulation of peptide or protein aggregates. **2.** The symptoms of schizophrenia can be mimicked by a drug that stimulates dopamine-releasing neurons. The brain's reward system, which is involved in drug addiction, is composed of dopamine-releasing neurons that connect the ventral tegmental area to regions in the cerebrum. Parkinson's disease results from the death of dopamine-releasing neurons. **3.** Not necessarily. It might be that the plaques, tangles, and missing regions of the brain seen at death reflect secondary effects, the consequence of other unseen changes that are actually responsible for the alterations in brain function.

Summary of Key Concepts Questions

49.1 Because reflex circuits involve only a few neurons—the simplest consist of a sensory neuron and a motor neuron—the path for information transfer is short and simple, increasing the speed of the response. **49.2** The midbrain coordinates visual reflexes; the cerebellum controls coordination of movement that depends on visual input; the thalamus serves as a routing center for visual information; and the cerebrum is essential for converting visual input to a visual image. **49.3** You would expect the right side of the body to be paralyzed because it is controlled by the left cerebral hemisphere, where language generation and interpretation are localized. **49.4** Learning a new language likely requires the maintenance of synapses that are formed during early development but are otherwise lost prior to adulthood. **49.5** Whereas amphetamine stimulates dopamine release, PCP blocks glutamate receptors, suggesting that schizophrenia does not reflect a defect in the function of just one neurotransmitter.

Test Your Understanding

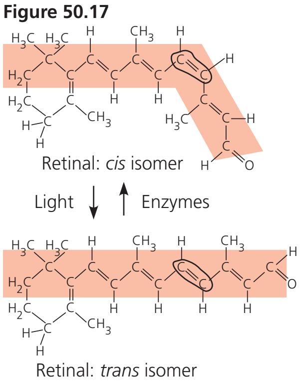
7.



Chapter 50

Figure Questions

Figure 50.17



The hydrogen (H) atoms are on the same side of the carbon-carbon double bond in the *cis* isomer and the opposite side in the *trans* isomer.

Figure 50.19 Each of the three types of cones is most sensitive to a different wavelength of light. A cone might be fully depolarized when there is light present if the light is of a wavelength far from its optimum. **Figure 50.21** In humans, an X chromosome with a defect in the red or green opsin gene is much less common than a wild-type X chromosome. Color blindness therefore typically skips a generation as the defective allele passes from an affected male to a carrier daughter and back to an affected grandson. In squirrel monkeys, no X chromosome can confer full color vision. As a result, all males are color-blind and no unusual inheritance pattern is observed. **Figure 50.23** The results of the experiment would have been identical. What matters is the activation of particular sets of neurons, not the manner in which they are activated. Any signal from a bitter cell will be interpreted by the brain as a bitter taste, regardless of the nature of the compound and the receptor involved. **Figure 50.25** Only perception. Binding of an odorant to its receptor will cause action potentials to be sent to the brain. Although an excess of that odorant might cause a diminished response through adaptation, another odorant can mask the first only at the level of perception in the brain. **Figure 50.26** Both. A muscle fiber contains many myofibrils bundled together and divided lengthwise into many sarcomeres. A sarcomere is a contractile unit made up of portions of many myofibrils, and each myofibril is a part of many sarcomeres. **Figure 50.28** Hundreds of myosin heads participate in sliding each pair of thick and thin filaments past each other. Because cross-bridge formation and breakdown are not synchronized, many myosin heads are exerting force on the thin filaments at all times during muscle contraction. **Figure 50.33** By causing all of the motor neurons that control the muscle to generate action potentials at a rate high enough to produce tetanus in all of the muscle fibers

Concept Check 50.1

1. Electromagnetic receptors in general detect only external stimuli. Nonelectromagnetic receptors, such as chemoreceptors or mechanoreceptors, can act as either internal or external sensors. **2.** The capsaicin present in the peppers activates the thermoreceptor for high temperatures. In response to the perceived high temperature, the nervous system triggers sweating to achieve evaporative cooling. **3.** You would perceive the electrical stimulus as if the sensory receptors that regulate that neuron had been activated. For example, electrical stimulation of the sensory neuron controlled by the thermoreceptor activated by menthol would likely be perceived as a local cooling.

Concept Check 50.2

1. Otoliths detect the animal's orientation with respect to gravity, providing information that is essential in environments such as the tunnel habitat of the star-nosed mole, where light cues are absent. **2.** As a sound that changes gradually from a very low to a very high pitch **3.** The stapes and the other middle ear bones transmit vibrations from the tympanic membrane to the oval window. Fusion of these bones (as occurs in a disease called otosclerosis) would block this transmission and result in hearing loss. **4.** In animals, the statoliths are extracellular. In contrast, the statoliths of plants are found within an intracellular organelle. The methods for detecting their location also differ. In animals, detection is by means of mechanoreceptors on ciliated cells. In plants, the mechanism appears to involve calcium signaling.

Concept Check 50.3

1. Planarians have ocelli that cannot form images but can sense the intensity and direction of light, providing enough information to enable the animals to find protection in shaded places. Flies have compound eyes that form images and excel at detecting movement. **2.** The person can focus on distant objects but not close objects (without glasses) because close focusing requires the lens to become almost spherical. This problem is common after age 50. **3.** The signal produced by rod and cone cells is glutamate, and their release of glutamate decreases upon exposure to light. However, a decrease in glutamate production causes other retinal cells to increase the rate at which action potentials are sent to the brain, so that the brain receives more action potentials in light than in dark. **4.** Absorption of light by retinal converts retinal from its *cis* isomer to its *trans* isomer, initiating the process of light detection. In contrast, a photon absorbed by chlorophyll does not bring about isomerization, but instead boosts an electron to a higher energy orbital, initiating the electron flow that generates ATP and NADPH.

Concept Check 50.4

1. Both taste cells and olfactory cells have receptor proteins in their plasma membrane that bind certain substances, leading to membrane depolarization through a signal transduction pathway involving a G protein. However, olfactory cells are sensory neurons, whereas taste cells are not. **2.** Since animals rely on chemical signals for behaviors that include finding mates, marking territories, and avoiding dangerous substances, it is adaptive for the olfactory system to have a robust response to a very small number of molecules of a particular odorant. **3.** Because the sweet, bitter, and umami tastes involve GPCR proteins but the sour taste does not, you might predict that the mutation is in a molecule that acts in the signal transduction pathway common to the different GPCRs.

Concept Check 50.5

1. In a skeletal muscle fiber, Ca^{2+} binds to the troponin complex, which moves tropomyosin away from the myosin-binding sites on actin and allows cross-bridges to form. In a smooth muscle cell, Ca^{2+} binds to calmodulin, which activates an enzyme that phosphorylates the myosin head and thus enables cross-bridge formation. **2.** *Rigor mortis*, a Latin phrase meaning "stiffness of death," results from the complete depletion of ATP in skeletal muscle. Since ATP is required to release myosin from actin and to pump Ca^{2+} out of the cytosol, muscles become chronically contracted beginning about 3–4 hours after death. **3.** A competitive inhibitor binds to the same site as the substrate for the enzyme. In contrast, the troponin and tropomyosin complex masks, but does not bind to, the myosin-binding sites on actin.

Concept Check 50.6

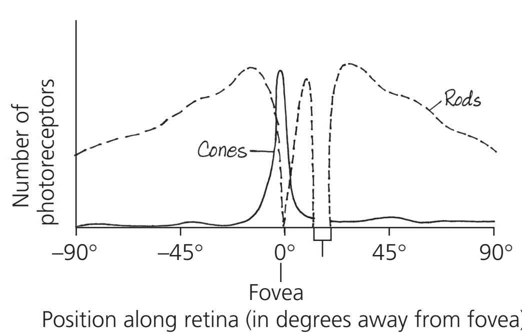
1. The main problem in swimming is drag; a fusiform body minimizes drag. The main problem in flying is overcoming gravity; wings shaped like airfoils provide lift, and adaptations such as air-filled bones reduce body mass. **2.** In modeling peristalsis you would constrict the toothpaste tube at different points along its length, using your hand to encircle the tube and squeeze concentrically. To demonstrate movement of food through the digestive tract you would want the cap off the toothpaste tube, whereas you would want the cap on to show how peristalsis contributes to worm locomotion. **3.** When you grasp the sides of the chair, you are using a contraction of the triceps to keep your arms extended against the pull of gravity on your body. As you lower yourself slowly into the chair, you gradually decrease the number of motor units in the triceps that are contracted. Contracting your biceps would jerk you down, since you would no longer be opposing gravity.

Summary of Key Concepts Questions

50.1 Nociceptors overlap with other classes of receptors in the type of stimulus they detect. They differ from other receptors only in how a particular stimulus is perceived. **50.2** Volume is encoded by the frequency of action potentials transmitted to the brain; pitch is encoded by which axons are transmitting action potentials. **50.3** The major difference is that neurons in the retina integrate information from multiple sensory receptors (photoreceptors) before transmitting information to the central nervous system. **50.4** Our olfactory sense is responsible for most of what we describe as distinct tastes. A head cold or other source of congestion blocks odorant access to receptors lining portions of the nasal cavity. **50.5** Hydrolysis of ATP is required to convert myosin to a high-energy configuration for binding to actin and to power the Ca^{2+} pump that removes cytosolic Ca^{2+} during muscle relaxation. **50.6** Human body movements rely on the contraction of muscles anchored to a rigid endoskeleton. Tendons attach muscles to bones, which in turn are composed of fibers built up from a basic organizational unit, the sarcomere. The thin and thick filaments have separate points of attachment within the sarcomere. In response to nervous system motor output, the formation and breakdown of cross-bridges between myosin heads and actin ratchet the thin and thick filaments past each other. Because the filaments are anchored, this sliding movement shortens the muscle fibers. Furthermore, because the fibers themselves are part of the muscles attached at each end to bones, muscle contraction moves bones of the body relative to each other. In this way, the structural anchoring of muscles and filaments enables muscle function, such as the bending of an elbow by contraction of the biceps.

Test Your Understanding

7.



The answer shows the actual distribution of rods and cones in the human eye. Your graph may differ, but should have the following properties: only cones at the fovea; fewer cones and more rods at both ends of the *x*-axis; no photoreceptors in the optic disk.

Chapter 51

Figure Questions

Figure 51.7 The species' distribution could be altered by dispersal limitations, the activities of people (such as a broad-scale conversion of forests to agriculture or selective harvesting), or many other factors, including those discussed later in the chapter (see Figure 51.17). **Figure 51.17** Some factors, such as fire, are relevant only for terrestrial systems. At first glance, water availability is primarily a terrestrial factor, too. However, species living along the intertidal zone of oceans or along the edge of lakes also suffer desiccation. Salinity stress is important for species in some aquatic and terrestrial systems. Oxygen availability is an important factor primarily for species in some aquatic systems and in soils and sediments.

Concept Check 51.1

1. In the tropics, high temperatures evaporate water and cause warm, moist air to rise. The rising air cools and releases much of its water as rain over the tropics. The remaining dry air descends at approximately 30° north and south, causing deserts to occur in those regions. **2.** The microclimate around the stream will be cooler, moister, and shadier than that around the unplanted agricultural field. **3.** Trees that require a long time to reach reproductive age are likely to evolve more slowly than annual plants in response to climate change, constraining the potential ability of such trees to respond to rapid climate change. **4.** Plants with C_4 photosynthesis are likely to expand their range globally as Earth's climate warms. C_4 photosynthesis minimizes photorespiration and enhances sugar production, an advantage that is especially useful in warmer regions where C_4 plants are found today.

Concept Check 51.2

1. The biggest difference between the two biomes is the higher amounts of precipitation that the forest receives. **2.** Answers will vary by location but should be based on the information and maps in Figure 51.12. How much your local area has been altered from its natural state will influence how much it reflects the expected characteristics of your biome, particularly the expected plants and animals. **3.** Northern coniferous forest is likely to replace tundra along the boundary between these biomes. To see why, note that northern coniferous forest is adjacent to tundra throughout North America, northern Europe, and Asia (see Figure 51.9) and that the temperature range for northern coniferous forest is just above that for tundra (see Figure 51.10).

Concept Check 51.3

1. Coral reefs require a solid substrate and light to grow. A rise in the sea level would reduce light penetration, making it difficult for a coral reef to thrive. **2.** Aquatic organisms either gain or lose water by osmosis if the osmolarity of their environment differs from their internal osmolarity. Water gain can cause cells to swell, and water loss can cause them to shrink. To avoid excessive changes in cell volume, organisms that live in estuaries must be able to compensate for both water gain (under freshwater conditions) and water loss (under saltwater conditions). **3.** Oxygen serves as a reactant when decomposers break down the bodies of dead algae using aerobic respiration. Following an algal bloom, there are many dead algae; hence, decomposers may use a lot of oxygen to break down the bodies of dead algae, causing the lake's oxygen levels to drop.

Concept Check 51.4

1. (a) Humans might transplant a species to a new area that it could not previously reach because of a geographic barrier. (b) Humans might eliminate a predator or herbivore species, such as sea urchins, from an area. **2.** One test would be to build a fence around a plot of land in an area that has trees of that species, excluding all deer from the plot. You could then compare the abundance of tree seedlings inside and outside the fenced plot over time. **3.** Because the ancestor of the silverswords reached isolated Hawaii early in the islands' existence, it likely faced little competition and was able to occupy many unfilled niches. The cattle egret, in contrast, arrived in the Americas only recently and has to compete with a well-established group of species. Thus, its opportunities for adaptive radiation have probably been much more limited.

Concept Check 51.5

1. Changes in how organisms interact with one another and their environment can cause evolutionary change. In turn, an evolutionary change, such as an improvement in the ability of a predator to detect its prey, can alter ecological interactions. **2.** As cod adapt to the pressure of commercial fishing by reproducing at younger ages and smaller sizes, the number of offspring they produce each year will be lower. This may cause the population to decline as time goes on, thereby further reducing the population's ability to recover. If that happened, as the population becomes smaller over time, effects of genetic drift might become increasingly important. Drift could, for example, lead to the fixation of harmful alleles, which would further hinder the ability of the cod population to recover from overfishing.

Summary of Key Concepts Questions

51.1 Because dry air would descend at the equator instead of at 30° north and south latitude (where deserts exist today), deserts would be more likely to exist along the equator (see Figure 51.3). **51.2** The dominant plants in savanna ecosystems tend to be adapted to fire and tolerant of seasonal droughts. The savanna biome is maintained by periodic fires, both natural and set by humans, but humans are also clearing savannas for agriculture and other uses. **51.3** An aphotic zone is most likely to be found in the deep waters of a lake, the oceanic pelagic zone, or the marine benthic zone. **51.4** You might arrange a flowchart that begins with abiotic limitations—first determining the physical and chemical conditions under which a species could survive—and then moves through the other factors listed in the flowchart. **51.5** Because the introduced species had few predators or parasites, it might outcompete native species and thereby increase in number and expand its range in the new location. As the introduced species increased in abundance, natural selection might cause evolution in populations of competing species, favoring individuals with traits that made them more effective competitors with the introduced species. Selection could also cause evolution in populations of potential predator or parasite species, in this case favoring individuals with traits that enabled them to take advantage of this new potential source of food. Such evolutionary changes could modify the outcome of ecological interactions, potentially leading to further evolutionary changes, and so on.

Chapter 52

Figure Questions

Figure 52.2 The fixed action pattern based on the sign stimulus of a red belly ensures that the male will chase away any invading males of his species. By chasing away such males, the defender decreases the chance that another male will fertilize eggs laid in his nesting territory. **Figure 52.5** The straight-run portion conveys two pieces of information: direction, via the angle of that run relative to the wall of the hive, and distance, via the number of waggles performed during the straight run. At a minimum, the portions between the straight runs identify the activity as a waggle dance. Since they also provide contact with workers to one side and then the other, they may ensure transmission of information to a larger number of other bees. **Figure 52.7** There should be no effect. Imprinting is an innate behavior that is carried out anew in each generation. Assuming the nest was not disturbed, the offspring of the geese imprinted on a human would imprint on the mother goose. **Figure 52.8** Perhaps the wasp doesn't use visual cues. It might also be that wasps recognize objects native to their environment, but not foreign objects, such as the pinecones. Tinbergen addressed these ideas before carrying out the pinecone study. When he swept away the pebbles and sticks around the nest, the wasps could no longer find their nests. If he shifted the natural objects in their natural arrangement, the shift in the landmarks caused a shift in the site to which the wasps returned. Finally, if natural objects around the nest site were replaced with pinecones while the wasp was in the burrow, the wasp nevertheless found her way back to the nest site. **Figure 52.10** Switching the orientations of all three grids would control for an inherent preference for or against a particular orientation. If there were no inherent preference or bias, the experiment should work equally well after the switch. **Figure 52.24** It might be that the birds require stimuli during flight to exhibit their migratory preference. If this were true, the birds would show the same orientation in the funnel experiment despite their distinct genetic programming. **Figure 52.26** It holds true for some, but not all individuals. If a parent has more than one reproductive partner, the offspring of different partners will have a coefficient of relatedness less than 0.5.

Concept Check 52.1

1. The proximate explanation for this fixed action pattern might be that nudging and rolling are released by the sign stimulus of an object outside the nest, and the behavior is carried to completion once initiated. The ultimate explanation might be that ensuring that eggs remain in the nest increases the chance of producing healthy offspring. **2.** There might be selective pressure for other prey fish to detect an injured fish because the source of the injury might threaten them as well. Among predators, there might be selection for those that are attracted to the alarm substance because they would be more likely to encounter crippled prey. Fish with adequate defenses might show no change because they have a selective advantage if they do not waste energy responding to the alarm substance. **3.** In both cases, the detection of periodic variation in the environment results in a reproductive cycle timed to environmental conditions that optimize the opportunity for success.

Concept Check 52.2

1. Natural selection would tend to favor convergence in color pattern because a predator learning to associate a pattern with a sting or bad taste would avoid all other individuals with that same color pattern, regardless of species. **2.** You might move objects around to establish an abstract rule, such as "past landmark A, the same distance as A is from the starting point," while maintaining a minimum of fixed metric relationships, that is, avoiding having the food directly adjacent to or a set distance from a landmark. As you might surmise, designing an informative experiment of this kind is not easy. **3.** Learned behavior, just like innate behavior, can contribute to reproductive isolation and thus to speciation. For example, learned bird songs contribute to species recognition during courtship, thereby helping ensure that only members of the same species mate.

Concept Check 52.3

1. Certainty of paternity is higher with external fertilization. **2.** Balancing selection could maintain the two alleles at the *forager* locus if population density fluctuated from one generation to another. At times of low population density, the energy-conserving sitter larvae (carrying the for^s allele) would be favored, while at higher population density, the more mobile Rover larvae (for^R allele) would have a selective advantage. **3.** Because females would now be present in much larger numbers than males, all three types of males should have some reproductive success. Nevertheless, since the advantage that the blue-throats rely on—a limited number of females in their territory—will be absent, the yellow-throats are likely to increase in frequency in the short term.

Concept Check 52.4

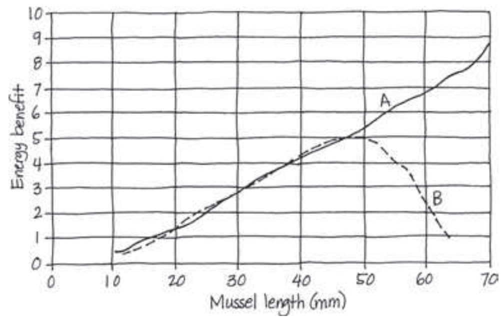
1. Because this geographic variation corresponds to differences in prey availability between two garter snake habitats, it seems likely that snakes with characteristics enabling them to feed on the abundant prey in their locale would have had increased survival and reproductive success. In this way, natural selection would have resulted in the divergent foraging behaviors. **2.** The fact that the individual shares some genes with the offspring of its sibling (in the case of humans, with the individual's niece or nephew) means that the reproductive success of that niece or nephew increases the representation of those genes in the population (selects for them). **3.** The older individual cannot be the beneficiary because he or she cannot have extra offspring. However, the cost is low for an older individual performing the altruistic act because that individual has already reproduced (but perhaps is still caring for a child or grandchild). There can therefore be selection for an altruistic act by a postreproductive individual that benefits a young relative.

Summary of Key Concepts Questions

52.1 Circannual rhythms are typically based on the cycles of light and dark in the environment. As the global climate changes, animals that migrate in response to these rhythms may shift to a location before or after local environmental conditions are optimal for reproduction and survival. **52.2** For the goose, all that is acquired is an object at which the behavior is directed. In the case of the sparrow, learning takes place that will give shape to the behavior itself. **52.3** Because feeding the female is likely to improve her reproductive success, the genes from the sacrificed male are likely to appear in a greater number of progeny. **52.4** Studying the genetic basis of these behaviors reveals that changes in a single gene can have large-scale effects on even complex behaviors.

Test Your Understanding

7.



You could measure the size of mussels that oystercatchers successfully open and compare that with the size distribution in the habitat.

Chapter 53

Figure Questions

Figure 53.4 The dispersion of the penguins would likely appear clumped as you flew over densely populated islands and sparsely populated ocean. **Figure 53.5** Ten percent (100/1,000) of the females survive to be three years old. **Figure 53.7** #109 **Figure 53.8** The population with $r = 1.0$ (blue curve) reaches 1,500 individuals in about 7.5 generations, whereas the population with $r = 0.5$ (red curve) reaches 1,500 individuals in about 14.5 generations. **Figure 53.16**

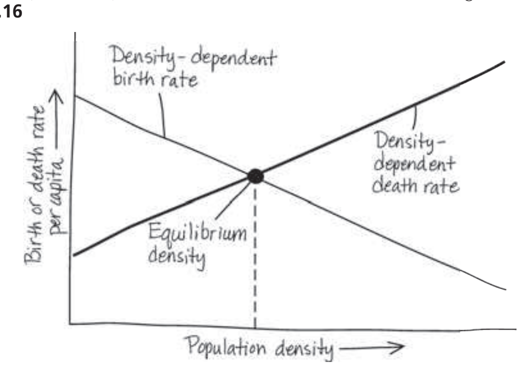
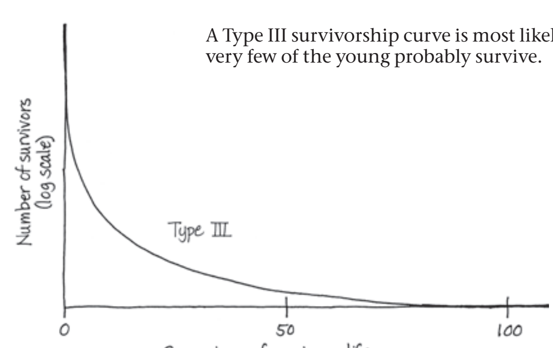


Figure 53.25 If the average ecological footprint were 8 gha per person, Earth could support about 1.5 billion people in a sustainable fashion. This estimate is obtained by dividing the total amount of Earth's productive land (11.9 billion gha) by the number of global hectares used per person (8 gha/person), which yields 1.49 billion people.

Concept Check 53.1

1.



A Type III survivorship curve is most likely because very few of the young probably survive.

2. The proportion alive at the start of year 0–1 is 485/485 = 1.0. The proportion alive at the start of year 1–2 is 218/485 = 0.449. **3.** Male sticklebacks would likely have a uniform pattern of dispersion, with antagonistic interactions maintaining a relatively constant spacing between them.

Concept Check 53.2

1. Though *r* is constant, *N*, the population size, is increasing. As *r* is applied to an increasingly large *N*, population growth (*rN*) accelerates, producing the J-shaped curve. **2.** Factors such as availability of food and other resources will slow down population growth in nature. Ecologists use the concept of unlimited growth to understand how fast populations can grow and to identify the conditions under which rapid growth can actually occur. **3.** The equation for the number of people added to the population each year is $\Delta N/\Delta t = r_{\Delta t}N$. Therefore, the net population growth in 2014 was

$$\Delta N/\Delta t = 0.005 \times 320{,}000{,}000 = 1{,}600{,}000$$

or 1.6 million people. To determine whether the population is growing exponentially, you would need to determine whether $r > 0$ and if it is constant through time (across multiple years).

Concept Check 53.3

1. When *N* (population size) is small, there are relatively few individuals producing offspring. When *N* is large, near the carrying capacity, the per capita growth rate is relatively small because it is limited by available resources. The steepest part of the logistic growth curve corresponds to a population with a number of reproducing individuals that is substantial but not yet near carrying capacity. **2.** All else being equal, you would expect a plant species to have a larger carrying capacity at the equator than at high latitudes because there is more incident sunlight near the equator. **3.** The sudden change in environmental conditions might alter the phenotypic traits favored by natural selection. Assuming the newly favored traits were encoded at least in part by genes, natural selection might alter gene frequencies in this population. In addition, a substantial drop in the carrying capacity of the population could cause the size of the population to drop considerably. If this occurred, effects of genetic drift could become more pronounced—and that in turn could lead to the fixation of harmful alleles, hindering the ability of the population to rebound in size.

Concept Check 53.4

1. Three key life history traits are when reproduction begins, how often reproduction occurs, and how many offspring are produced per reproductive episode. Organisms differ widely for each of these traits. For example, the age of first reproduction is typically 3–4 years in coho salmon compared to 30 years in loggerhead turtles. Similarly, an agave reproduces only once during its lifetime, whereas an oak tree reproduces many times. Finally, the white rhinoceros produces a single calf when it reproduces, while most insects produce many offspring each time they reproduce. **2.** By preferentially investing in the eggs it lays in the nest, the peacock wrasse increases the chance those eggs will survive. The eggs it disperses widely and does not provide care for are less likely to survive, at least some of the time, but require a lower investment by the adults. (In this sense, the adults avoid the risk of placing all their eggs in one basket.) **3.** If a parent's survival is compromised greatly by bearing young during times of stress, the animal's fitness may increase if it abandons its current young and survives to produce healthier young at a later time.

Concept Check 53.5

1. Three attributes are the size, quality, and isolation of patches. A patch that is larger or of higher quality is more likely to attract individuals and to be a source of individuals for other patches. A patch that is relatively isolated will undergo fewer exchanges of individuals with other patches. **2.** You would need to study the population for more than one cycle (longer than 10 years and probably at least 20) before having sufficient data to examine changes through time. Otherwise, it would be impossible to know whether an observed decrease in the population size reflected a long-term trend or was part of the normal cycle. **3.** In negative feedback, the output, or product, of a process slows that process. In populations that have a density-dependent birth rate, such as dune fescue grass, an accumulation of product (more individuals, resulting in a higher population density) slows the process (population growth) by decreasing the birth rate.

Concept Check 53.6

1. A bottom-heavy age structure, with a disproportionate number of young people, portends continuing growth of the population as these young people begin reproducing. In contrast, a more evenly distributed age structure predicts a more stable population size, and a top-heavy age structure predicts a decrease in population size because relatively fewer young people are reproducing. **2.** The growth rate of Earth's human population has dropped by half since the 1960s, from 2.2% in 1962 to 1.1% today. Nonetheless, the yearly increase in population size has not slowed as much because the smaller growth rate is counterbalanced by increased population size; hence, the number of additional people on Earth each year remains enormous—approximately 78 million. **3.** Each student will calculate his or her own ecological footprint. Each of us influences our ecological footprint by how we live—what we eat, how much energy we use, and the amount of waste we generate—as well as by how many children we have. Making choices that reduce our demand for resources makes our ecological footprint smaller.

Summary of Key Concepts Questions

53.1 Ecologists can potentially estimate birth rates by counting the number of young born each year, and they can estimate death rates by seeing how the number of adults changes each year. **53.2** Under the exponential model, both populations will continue to grow to infinite size, regardless of the specific value of *r* (see Figure 53.8). **53.3** There are many things you can do to increase the carrying capacity of the species, including increasing its food supply, protecting it from predators, and providing more sites for nesting or reproduction. **53.4** Ecological trade-offs are common because organisms do not have access to unlimited amounts of energy and resources. As a result, the use of energy or resources for one function (such as reproduction) can decrease the energy or resources available to support other functions (such as growth or survival). **53.5** An example of a biotic factor is disease caused by a pathogen; natural disasters, such as earthquakes and floods, are examples of abiotic factors. **53.6** Humans are unique in our potential ability to reduce global population through contraception and family planning. Humans also are capable of consciously choosing their diet and personal lifestyle, and these choices influence the number of people Earth can support.

Chapter 54

Figure Questions

Figure 54.3 Its realized and fundamental niches would be similar, unlike those of *Chthamalus*. **Figure 54.5** Individuals of a harmless species that resembled a distantly related harmful species might be attacked by predators less often than were other individuals that did not resemble the harmful species. As a result, individuals of the harmless species that resembled a harmful species would tend to contribute more offspring to the next generation than would other individuals of the harmless species. Over time, as natural selection by predators continued to favor those individuals of the harmless species that most closely resembled the harmful species, the resemblance of the harmless species to the harmful species would increase. However, selection is not the only process that could cause a harmless species to resemble a closely related harmful species. In this case, the two species could also resemble each other because they descended from a recent common ancestor and hence share many traits (including a resemblance to one another). **Figure 54.14** An increase in the abundance of carnivores that ate zooplankton might cause zooplankton abundance to drop, thereby causing phytoplankton abundance to increase. **Figure 54.15** The number of types of organisms eaten is zero for phytoplankton; one for copepods, crab-eater seals, and baleen whales; two for krill, carnivorous plankton, elephant seals, and sperm whales; three for squids, fishes, and leopard seals; and five for birds and smaller toothed whales. The two groups that both consume and are consumed by each other are fishes and squids. **Figure 54.18** The death of individuals of *Mytilus*, a dominant species, should open up space for other species and increase species richness even in the absence of *Pisaster*. **Figure 54.24** At the earliest stages of primary succession, free-living prokaryotes in the soil would reduce atmospheric N_2 to NH_3. Symbiotic nitrogen fixation could not occur until plants were present at the site. **Figure 54.28** We would expect that (a) population sizes would decrease because there would be fewer resources and less suitable habitat; (b) the extinction curve would rise more rapidly as the number of species on the island increased because small islands generally have fewer resources, less diverse habitats, and smaller population sizes; and (c) the predicted equilibrium species number would be smaller than shown in Figure 54.28. **Figure 54.31** Shrew populations in different locations and habitats might show substantial genetic variation in their susceptibility to the Lyme pathogen. As a result, there might be fewer infected ticks where shrew populations are less susceptible to the Lyme pathogen and more infected ticks where shrews are more susceptible.

Concept Check 54.1

1. The different types of symbioses are mutualism, parasitism, and commensalism. In reality, "neutral" interactions are not possible as one of the species involved in the interaction will always affect the other, even if it is to a very small extent. **2.** One of the competing species will become locally extinct because of the greater reproductive success of the more efficient competitor. **3.** By specializing in eating seeds of different plant species, individuals of the two finch species may be less likely to come into contact in the separate habitats, reinforcing a reproductive barrier to hybridization.

Concept Check 54.2

1. Species richness, the number of species in the community, and relative abundance, the proportions of the community represented by the various species, both contribute to species diversity. Compared to a community with a very high proportion of one species, one with a more even proportion of species is considered more diverse. **2.** A food chain presents a set of one-way transfers of food energy up to successively higher trophic levels. A food web documents how food chains are linked together, with many species weaving into the web at more than one trophic level. **3.** According to the bottom-up model, adding extra predators would have little effect on lower trophic levels, particularly vegetation. If the top-down model applied, increased bobcat numbers would decrease raccoon numbers, increase snake numbers, decrease mouse numbers, and increase grass biomass. **4.** A decrease in krill abundance might increase the abundance of organisms that krill eat (phytoplankton and copepods), while decreasing the abundance of organisms that eat krill (baleen whales, crabeater seals, birds, fishes, and carnivorous plankton); baleen whales and crabeater seals might be particularly at risk because they only eat krill. However, many of these possible changes could lead to other changes as well, making the overall outcome hard to predict. For example, a decrease in krill abundance could cause an increase in copepod abundance—but an increase in copepod abundance could counteract some of the other effects of decreased krill abundance (since like krill, copepods eat phytoplankton and are eaten by carnivorous plankton and fishes).

Concept Check 54.3

1. High levels of disturbance are generally so disruptive that they eliminate many species from communities, leaving the community dominated by a few tolerant species. Low levels of disturbance permit competitively dominant species to exclude other species from the community. On the other hand, moderate levels of disturbance can facilitate coexistence of a greater number of species in a community by preventing competitively dominant species from becoming abundant enough to eliminate other species from the community. **2.** Early successional species can facilitate the arrival of other species in many ways, including increasing the fertility or water-holding capacity of soils or providing shelter to seedlings from wind and intense sunlight. **3.** The absence of fire for 100 years would represent a change to a low level of disturbance. According to the intermediate disturbance hypothesis, this change should cause diversity to decline as competitively dominant species gain sufficient time to exclude less competitive species.

Concept Check 54.4

1. Ecologists propose that the greater species richness of tropical regions is the result of their longer evolutionary history and the greater solar energy input and water availability in tropical regions. **2.** Immigration of species to islands declines with distance from the mainland and increases with island area. Extinction of species is lower on larger islands and on less isolated islands. Since the number of species on islands is largely determined by the difference between rates of immigration and extinction, the number of species will be highest on large islands near the mainland and lowest on small islands far from the mainland. **3.** Because of their greater mobility, birds disperse to islands more often than snakes and lizards, so birds should have greater richness.

Concept Check 54.5

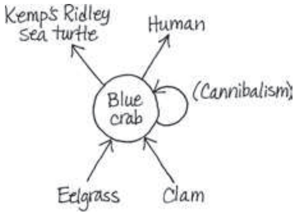
1. Pathogens are microorganisms, viruses, viroids, or prions that cause disease. **2.** To keep the rabies virus out, you could ban imports of all mammals, including pets. Potentially, you could also attempt to vaccinate all dogs in the British Isles against the virus. A more practical approach might be to quarantine all pets brought into the country that are potential carriers of the disease, the approach the British government actually takes.

Summary of Key Concepts Questions

54.1 Note: Sample answers follow; other answers could also be correct. Competition: a fox and a bobcat competing for prey. Predation: an orca eating a sea otter. Herbivory: a bison grazing in a prairie. Parasitism: a parasitoid wasp that lays its eggs on a caterpillar. Mutualism: a fungus and an alga that make up a lichen. Commensalism: a wildflower that grows in a maple forest and a maple tree. **54.2** Not necessarily if the more species-rich community is dominated by only one or a few species **54.3** Similar to clear-cutting a forest or plowing a field, some species would be present initially. As a result, the disturbance would initiate secondary succession in spite of its severe appearance. **54.4** Glaciations are major disturbances that can completely destroy communities found in temperate and polar regions. As a result, tropical communities are older than temperate or polar communities. This can cause species diversity to be high in the tropics simply because there has been more time for speciation to occur. **54.5** A keystone species is one with a pivotal ecological role. Hence, a pathogen that reduces the abundance or otherwise harms a keystone species could greatly alter the structure of the community. For example, if a novel pathogen drove a keystone species to local extinction, drastic changes in species diversity could occur.

Test Your Understanding

9. Grassland 1: $H = -(0.20 \ln 0.20 + 0.25 \ln 0.25 + 0.25 \ln 0.25 + 0.30 \ln 0.30) = 1.38$. Grassland 2: $H = -(0.80 \ln 0.80 + 0.15 \ln 0.15 + 0.05 \ln 0.05) = 0.61$. No, the application of fertilizers reduces biodiversity. **10.** Crab numbers should increase, reducing the abundance of eelgrass.



Chapter 55

Figure Questions

Figure 55.4 The blue arrow leading to *Primary consumers* could represent a grasshopper feeding on a plant. The blue arrow leading from *Primary consumers* to *Detritus* could represent the remains of a dead primary consumer (such as a grasshopper) becoming part of the detritus found in the ecosystem. The blue arrow leading from *Primary consumers* to *Secondary and tertiary consumers* could represent a bird (the secondary consumer) eating a grasshopper (the primary consumer). Finally, the blue arrow leading from *Primary consumers* to *Primary producers* could represent CO_2 released by a grasshopper in cellular respiration. **Figure 55.5** The map does not accurately reflect the productivity of wetlands, coral reefs, and coastal zones because these habitats cover areas that are too small to show up clearly on global maps. **Figure 55.6** New duck farms would add extra nitrogen and phosphorus to the water samples used in the experiment. We would expect that the extra phosphorus from these new duck farms would not alter the results (because in the original experiment, phosphorus levels were *already* so high that adding phosphorus did not increase phytoplankton growth). However, the new duck farms might increase nitrogen levels to the point where adding extra nitrogen in an experiment would not increase phytoplankton density. **Figure 55.12** The availability of water and exposure to light are other factors that may have varied across the sites. Factors such as these that are not included in the experimental design could make the results more difficult to interpret. Multiple factors can also be correlated to each other in nature, so ecologists must be careful that the factor they are studying is actually causing the observed response and is not just correlated with it. **Figure 55.13** (1) If the rate of decomposition slowed, more organic materials would be transferred from reservoir A to reservoir B; eventually, this might lead to more organic material becoming fossilized into fossil fuels. In addition, a decrease in decomposition rate would cause fewer inorganic materials to become available as nutrients in reservoir C, which would ultimately slow the rates of nutrient uptake and photosynthesis by living organisms. (2) Materials move into and out of reservoir A on a much shorter time scale than they move into reservoir B. Materials may remain in reservoir B for a very long time, or humans may remove them at a rapid pace by excavating and burning fossil fuels. **Figure 55.19** Populations evolve as organisms interact with each other and with the physical and chemical conditions of their environment. As a result, any human action that alters the environment has the potential to cause evolutionary change. In particular, since climate change has greatly affected arctic ecosystems, we would expect that climate change will cause evolution in arctic tundra populations.

Concept Check 55.1

1. Energy passes through an ecosystem, entering as sunlight and leaving as heat. It is not recycled within the ecosystem. **2.** You would need to know how much biomass the wildebeests ate from your plot and how much nitrogen was contained in that biomass. You would also need to know how much nitrogen they deposited in urine or feces. **3.** The second law states that in any energy transfer or transformation, some of the energy is dissipated to the surroundings as heat. For the ecosystem to remain intact, this "escape" of energy from the ecosystem must be offset by the continuous influx of solar radiation.

Concept Check 55.2

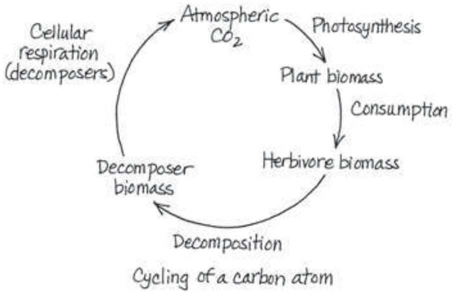
1. Only a fraction of solar radiation strikes plants or algae, only a portion of that fraction is of wavelengths suitable for photosynthesis, and much energy is lost as a result of reflection or heating of plant tissue. **2.** By manipulating the level of the factors of interest, such as phosphorus availability or soil moisture, and measuring responses by primary producers **3.** It is likely that NEP would decline after the fire. To see why, recall that $NEP = GPP - R_T$, where GPP is gross primary production and R_T is the total amount of cellular respiration in the ecosystem. By killing trees and other plants, the fire would cause GPP to decline from its pre-fire levels. In addition, as decomposers broke down the remains of trees killed by fire, the overall amount of cellular respiration (R_T) in the ecosystem could increase (because of increased cellular respiration by decomposers). **4.** The enzyme rubisco, which catalyzes the first step in the Calvin cycle, is the most abundant protein on Earth. Like all proteins, rubisco contains nitrogen, and because photosynthetic organisms require so much rubisco, they also require considerable nitrogen to make it. Phosphorus is also needed as a component of several metabolites in the Calvin cycle and as a component of both ATP and NADPH (see Figure 11.19).

Concept Check 55.3

1. 40 J; 36.4% **2.** Although the primary producers are consumed at a very rapid rate, they can grow and reproduce also at a very rapid rate. **3.** Total net primary production is 10,000 + 1,000 + 100 + 10 J = 11,110 J. This is the amount of energy theoretically available to detritivores.

Concept Check 55.4

1. For example, for the carbon cycle:



2. Removal of the trees stops nitrogen uptake from the soil, allowing nitrate to accumulate there. The nitrate is washed away by precipitation and enters the streams. **3.** Most of the nutrients in a tropical rain forest are contained in the trees, so removing the trees by logging rapidly depletes nutrients from the ecosystem. The nutrients that remain in the soil are quickly carried away into streams and groundwater by the abundant precipitation.

Concept Check 55.5

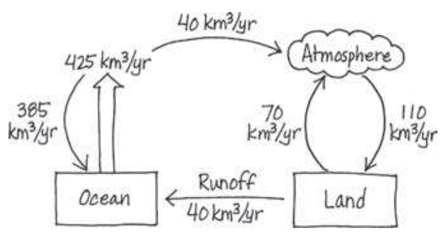
1. The main goal is to restore degraded ecosystems to a more natural state. **2.** The Kissimmee River project returns the flow of water to the original channel and restores natural flow, a self-sustaining outcome. Ecologists at the Maungatautari reserve will need to maintain the integrity of the fence indefinitely, an outcome that is not self-sustaining in the long term.

Summary of Key Concepts Questions

55.1 Because energy conversions are inefficient, with some energy inevitably lost as heat, you would expect that a given mass of primary producers would support a smaller biomass of secondary producers. **55.2** For estimates of NEP, you need to measure the respiration of all organisms in an ecosystem, not just the respiration of primary producers. In a sample of ocean water, primary producers and other organisms are usually mixed together, making their respective respirations hard to separate. **55.3** Runners use much more energy in respiration when they are running than when they are sedentary, reducing their production efficiency. **55.4** Factors other than temperature, including a shortage of water and nutrients, slow decomposition in hot deserts. **55.5** If the topsoil and deeper soil are kept separate, the engineers could return the deeper soil to the site first and then apply the more fertile topsoil to improve the success of revegetation and other restoration efforts.

Test Your Understanding

9. (a)



(b) On average, the ratio is 1, with equal amounts of water moving from the ocean to land as precipitation and moving from land to ocean in runoff.
(c) During an ice age, the amount of ocean evaporation falling on land as precipitation would be greater than the amount returning to the oceans in runoff; thus, the ratio would be >1. The difference would build up on land as ice.

Chapter 56

Figure Questions

Figure 56.4 You would need to know the complete range of the species and that it is missing across all of that range. You would also need to be certain that the species isn't hidden, as might be the case for an animal that is hibernating underground or a plant that is present in the form of seeds or spores. **Figure 56.9** The two examples are similar in that segments of DNA from the harvested samples were analyzed and compared with segments from specimens of known origin. One difference is that the whale researchers investigated relatedness at species and population levels to determine whether illegal activity had occurred, whereas the elephant investigators determined relatedness at the population level to determine the precise location of the poaching. Another difference is that mtDNA was used for the whale study, whereas nuclear DNA was used for the elephant study. The primary limitations of such approaches are the need to have (or generate) a reference database and the requirement that the organisms have sufficient variation in their DNA to reveal the relatedness of samples. **Figure 56.11** The higher the pH, the lower the acidity. Thus, the precipitation in this forest is becoming less acidic. **Figure 56.13** Answers may vary, but there are two reasons not to support transplanting additional birds. First, the Illinois population has a different genetic makeup than birds in other regions, and you would want to maintain to the greatest extent possible the frequency of beneficial genes or alleles found only in the Illinois population. Second, the translocation of birds from other states already caused the percentage of hatched eggs to increase dramatically, indicating that the transplantation of additional birds is not necessary. **Figure 56.16** The photo shows edges between forest and grassland ecosystems, grassland and river ecosystems, and grassland and lake ecosystems. **Figure 56.25** The PCB concentration increased by a factor of 4.9 from phytoplankton to zooplankton, 41.6 from phytoplankton to smelt, 8.5 from zooplankton to smelt, 4.6 from smelt to lake trout, 119.2 from smelt to herring gull eggs, and 25.7 from lake trout to herring gull eggs. **Figure 56.30** Ocean acidification reduces the availability of carbonate ions (CO_3^{2-}). Corals and many other marine organisms require carbonate ions to build their shells. Since shell-building organisms depend upon their shells for survival, scientists have predicted that ocean acidification will cause many shell-building organisms to die. In turn, increased mortality rates of organisms that build shells would cause many other changes to ecological communities. For example, increased mortality rates of corals would harm the many other species that seek protection in coral reefs or that feed upon the species living there.

Concept Check 56.1

1. The different levels of biodiversity are genetic diversity, species diversity, and ecosystem diversity. Examples of benefits would include gene-based medicines (genetic diversity), foods (species diversity), and air purification (ecosystem diversity). **2.** Habitat destruction, such as deforestation, channelizing of rivers, or conversion of natural ecosystems to agriculture or cities, deprives species of places to live. Introduced species, which are transported by humans to regions outside their native range, where they are not controlled by their natural pathogens or predators, often reduce the population sizes of native species through competition or predation. Overharvesting has reduced populations of plants and animals or driven them to extinction. Finally, global change is altering the environment to the extent that it reduces the capacity of Earth to sustain life. **3.** If both populations breed separately, then gene flow between the populations would not occur and genetic differences between them would be greater. As a result, the loss of genetic diversity would be greater than if the populations interbreed.

Concept Check 56.2

1. Reduced genetic variation decreases the capacity of a population to evolve in the face of change. **2.** The effective population size, N_e, would be $4(30 \times 10)/(30 + 10) = 30$ birds. **3.** Because millions of people use the greater Yellowstone ecosystem each year, it would be impossible to eliminate all contact between people and bears. Instead, you might try to reduce the kinds of encounters where bears are killed. You might recommend lower speed limits on roads in the park, adjust the timing or location of hunting seasons (where hunting is allowed outside the park) to minimize contact with mother bears and cubs, and provide financial incentives for livestock owners to try alternative means of protecting livestock, such as using guard dogs.

Concept Check 56.3

1. A small area supporting numerous endemic species as well as a large number of endangered and threatened species **2.** Zoned reserves may provide sustained supplies of forest products, water, hydroelectric power, educational opportunities, and income from tourism. **3.** Habitat corridors can increase the rate of movement or dispersal of organisms between habitat patches and thus the rate of gene flow between subpopulations. They thus help prevent a decrease in fitness attributable to inbreeding. They can also minimize interactions between organisms and humans as the organisms disperse; in cases involving potential predators, such as bears or large cats, minimizing such interactions is desirable.

Concept Check 56.4

1. Adding nutrients causes population explosions of algae and the organisms that feed on them. Increased respiration by algae and consumers, including detritivores, depletes the lake's oxygen, which the fish require. **2.** Decomposers are consumers that use nonliving organic matter as fuel for cellular respiration, which releases CO_2 as a by-product. Because higher temperatures lead to faster decomposition, organic matter in these soils could be decomposed to CO_2 more rapidly, thereby speeding up global warming. **3.** Reduced concentrations of ozone in the atmosphere increase the amount of UV radiation that reaches Earth's surface and the organisms living there. UV radiation can cause mutations by producing disruptive thymine dimers in DNA.

Concept Check 56.5

1. Sustainable development is an approach to development that works toward the long-term prosperity of human societies and the ecosystems that support them, which requires linking the biological sciences with the social sciences, economics, and humanities. **2.** Biophilia, our sense of connection to nature and all forms of life, may act as a significant motivation for the development of an environmental ethic that resolves not to allow species to become extinct or ecosystems to be destroyed. Such an ethic is necessary if we are to become more attentive and effective custodians of the environment. **3.** At a minimum, you would want to know the size of the population and the average reproductive rate of the individuals in it. To develop the fishery sustainably, you would seek a harvest rate that maintains the population near its original size and maximizes its harvest in the long term rather than the short term.

Summary of Key Concepts Questions

56.1 Nature provides us with many beneficial services, including a supply of reliable, clean water, the production of food and fiber, and the dilution and detoxification of our pollutants. **56.2** A more genetically diverse population is better able to withstand pressures from disease or environmental change, making it less likely to become extinct over a given period of time. **56.3** Habitat fragmentation can isolate populations, leading to inbreeding and genetic drift, and it can make populations more susceptible to local extinctions resulting from edge effects, including a change in physical conditions and an increase in competition or predation with edge-adapted species. **56.4** It's healthier to feed at a lower trophic level because biological magnification increases the concentration of toxins at higher levels. **56.5** One goal of conservation biology is to preserve as many species as possible. Sustainable approaches that maintain the quality of habitats are required for the long-term survival of organisms.

Test Your Understanding

7.

To minimize the area of forest into which the cowbirds penetrate, you should locate the road along the west edge of the reserve (since that edge abuts deforested pasture and an agricultural field). Any other location would increase the area of affected habitat. Similarly, the maintenance building should be in the southwest corner of the reserve to minimize the area susceptible to cowbirds.

Periodic Table of the Elements

Atomic number (number of protons) → 6
Element symbol → C
12.01 ← Atomic mass (number of protons plus number of neutrons averaged over all isotopes)

Metals | Metalloids | Nonmetals

Representative elements

Alkali metals (Group 1) | Alkaline earth metals (Group 2) | Halogens (Group 17) | Noble gases (Group 18)

Groups: Elements in a vertical column have the same number of electrons in their valence (outer) shell and thus have similar chemical properties.

Periods: Each horizontal row contains elements with the same total number of electron shells. Across each period, elements are ordered by increasing atomic number.

Transition elements (Groups 3–12)

Period number	1 Group 1A	2 Group 2A	3 3B	4 4B	5 5B	6 6B	7 7B	8 8B	9 8B	10 8B	11 1B	12 2B	13 Group 3A	14 Group 4A	15 Group 5A	16 Group 6A	17 Group 7A	18 Group 8A
1	1 H 1.008																	2 He 4.003
2	3 Li 6.941	4 Be 9.012											5 B 10.81	6 C 12.01	7 N 14.01	8 O 16.00	9 F 19.00	10 Ne 20.18
3	11 Na 22.99	12 Mg 24.31											13 Al 26.98	14 Si 28.09	15 P 30.97	16 S 32.06	17 Cl 35.45	18 Ar 39.95
4	19 K 39.10	20 Ca 40.08	21 Sc 44.96	22 Ti 47.87	23 V 50.94	24 Cr 52.00	25 Mn 54.94	26 Fe 55.85	27 Co 58.93	28 Ni 58.69	29 Cu 63.55	30 Zn 65.38	31 Ga 69.72	32 Ge 72.64	33 As 74.92	34 Se 78.96	35 Br 79.90	36 Kr 83.80
5	37 Rb 85.47	38 Sr 87.62	39 Y 88.91	40 Zr 91.22	41 Nb 92.91	42 Mo 95.95	43 Tc (98)	44 Ru 101.1	45 Rh 102.9	46 Pd 106.4	47 Ag 107.9	48 Cd 112.4	49 In 114.8	50 Sn 118.7	51 Sb 121.8	52 Te 127.6	53 I 126.9	54 Xe 131.3
6	55 Cs 132.9	56 Ba 137.3	57* La 138.9	72 Hf 178.5	73 Ta 180.9	74 W 183.8	75 Re 186.2	76 Os 190.2	77 Ir 192.2	78 Pt 195.1	79 Au 197.0	80 Hg 200.6	81 Tl 204.4	82 Pb 207.2	83 Bi 209.0	84 Po (209)	85 At (210)	86 Rn (222)
7	87 Fr (223)	88 Ra (226)	89† Ac (227)	104 Rf (267)	105 Db (268)	106 Sg (271)	107 Bh (272)	108 Hs (277)	109 Mt (276)	110 Ds (281)	111 Rg (280)	112 Cn (285)	113 Nh (284)	114 Fl (289)	115 Mc (288)	116 Lv (293)	117 Ts (293)	118 Og (294)

*Lanthanides	58 Ce 140.1	59 Pr 140.9	60 Nd 144.2	61 Pm (145)	62 Sm 150.4	63 Eu 152.0	64 Gd 157.3	65 Tb 158.9	66 Dy 162.5	67 Ho 164.9	68 Er 167.3	69 Tm 168.9	70 Yb 173.0	71 Lu 175.0
†Actinides	90 Th 232.0	91 Pa 231.0	92 U 238.0	93 Np (237)	94 Pu (244)	95 Am (243)	96 Cm (247)	97 Bk (247)	98 Cf (251)	99 Es (252)	100 Fm (257)	101 Md (258)	102 No (259)	103 Lr (262)

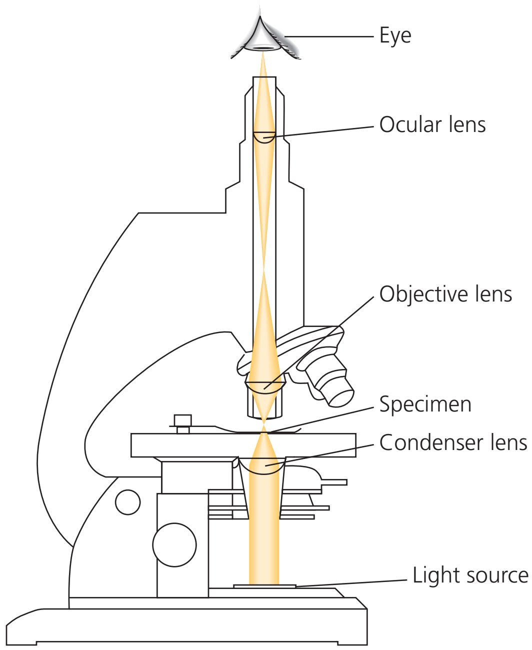
Name (Symbol)	Atomic Number	Name (Symbol)	Atomic Number	Name (Symbol)	Atomic Number	Name (Symbol)	Atomic Number	Name (Symbol)	Atomic Number
Actinium (Ac)	89	Copper (Cu)	29	Iron (Fe)	26	Osmium (Os)	76	Silicon (Si)	14
Aluminum (Al)	13	Curium (Cm)	96	Krypton (Kr)	36	Oxygen (O)	8	Silver (Ag)	47
Americium (Am)	95	Darmstadtium (Ds)	110	Lanthanum (La)	57	Palladium (Pd)	46	Sodium (Na)	11
Antimony (Sb)	51	Dubnium (Db)	105	Lawrencium (Lr)	103	Phosphorus (P)	15	Strontium (Sr)	38
Argon (Ar)	18	Dysprosium (Dy)	66	Lead (Pb)	82	Platinum (Pt)	78	Sulfur (S)	16
Arsenic (As)	33	Einsteinium (Es)	99	Lithium (Li)	3	Plutonium (Pu)	94	Tantalum (Ta)	73
Astatine (At)	85	Erbium (Er)	68	Livermorium (Lv)	116	Polonium (Po)	84	Technetium (Tc)	43
Barium (Ba)	56	Europium (Eu)	63	Lutetium (Lu)	71	Potassium (K)	19	Tellurium (Te)	52
Berkelium (Bk)	97	Fermium (Fm)	100	Magnesium (Mg)	12	Praseod`ymium (Pr)	59	Tennessine (Ts)	117
Beryllium (Be)	4	Flerovium (Fl)	114	Manganese (Mn)	25	Promethium (Pm)	61	Terbium (Tb)	65
Bismuth (Bi)	83	Fluorine (F)	9	Meitnerium (Mt)	109	Protactinium (Pa)	91	Thallium (Tl)	81
Bohrium (Bh)	107	Francium (Fr)	87	Mendelevium (Md)	101	Radium (Ra)	88	Thorium (Th)	90
Boron (B)	5	Gadolinium (Gd)	64	Mercury (Hg)	80	Radon (Rn)	86	Thulium (Tm)	69
Bromine (Br)	35	Gallium (Ga)	31	Molybdenum (Mo)	42	Rhenium (Re)	75	Tin (Sn)	50
Cadmium (Cd)	48	Germanium (Ge)	32	Moscovium (Mc)	115	Rhodium (Rh)	45	Titanium (Ti)	22
Calcium (Ca)	20	Gold (Au)	79	Neodymium (Nd)	60	Roentgenium (Rg)	111	Tungsten (W)	74
Californium (Cf)	98	Hafnium (Hf)	72	Neon (Ne)	10	Rubidium (Rb)	37	Uranium (U)	92
Carbon (C)	6	Hassium (Hs)	108	Neptunium (Np)	93	Ruthenium (Ru)	44	Vanadium (V)	23
Cerium (Ce)	58	Helium (He)	2	Nickel (Ni)	28	Rutherfordium (Rf)	104	Xenon (Xe)	54
Cesium (Cs)	55	Holmium (Ho)	67	Nihonium (Nh)	113	Samarium (Sm)	62	Ytterbium (Yb)	70
Chlorine (Cl)	17	Hydrogen (H)	1	Niobium (Nb)	41	Scandium (Sc)	21	Yttrium (Y)	39
Chromium (Cr)	24	Indium (In)	49	Nitrogen (N)	7	Seaborgium (Sg)	106	Zinc (Zn)	30
Cobalt (Co)	27	Iodine (I)	53	Nobelium (No)	102	Selenium (Se)	34	Zirconium (Zr)	40
Copernicium (Cn)	112	Iridium (Ir)	77	Oganesson (Og)	118				

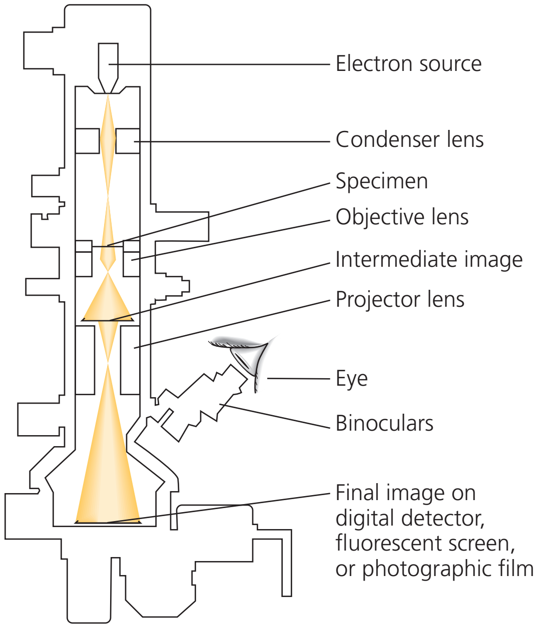
APPENDIX C The Metric System

Metric Prefixes:	10^9 = giga (G) 10^6 = mega (M) 10^3 = kilo (k)	10^{-2} = centi (c) 10^{-3} = milli (m) 10^{-6} = micro (μ)	10^{-9} = nano (n) 10^{-12} = pico (p) 10^{-15} = femto (f)

Measurement	Unit and Abbreviation	Metric Equivalent	Metric-to-English Conversion Factor	English-to-Metric Conversion Factor
Length	1 kilometer (km)	= 1,000 (10^3) meters	1 km = 0.62 mile	1 mile = 1.61 km
	1 meter (m)	= 100 (10^2) centimeters = 1,000 millimeters	1 m = 1.09 yards 1 m = 3.28 feet 1 m = 39.37 inches	1 yard = 0.914 m 1 foot = 0.305 m
	1 centimeter (cm)	= 0.01 (10^{-2}) meter	1 cm = 0.394 inch	1 foot = 30.5 cm 1 inch = 2.54 cm
	1 millimeter (mm)	= 0.001 (10^{-3}) meter	1 mm = 0.039 inch	
	1 micrometer (μm) (formerly micron, μ)	= 10^{-6} meter (10^{-3} mm)		
	1 nanometer (nm) (formerly millimicron, mμ)	= 10^{-9} meter (10^{-3} μm)		
	1 angstrom (Å)	= 10^{-10} meter (10^{-4} μm)		
Area	1 hectare (ha)	= 10,000 square meters	1 ha = 2.47 acres	1 acre = 0.405 ha
	1 square meter (m^2)	= 10,000 square centimeters	1 m^2 = 1.196 square yards 1 m^2 = 10.764 square feet	1 square yard = 0.8361 m^2 1 square foot = 0.0929 m^2
	1 square centimeter (cm^2)	= 100 square millimeters	1 cm^2 = 0.155 square inch	1 square inch = 6.4516 cm^2
Mass	1 metric ton (t)	= 1,000 kilograms	1 t = 1.103 tons	1 ton = 0.907 t
	1 kilogram (kg)	= 1,000 grams	1 kg = 2.205 pounds	1 pound = 0.4536 kg
	1 gram (g)	= 1,000 milligrams	1 g = 0.0353 ounce 1 g = 15.432 grains	1 ounce = 28.35 g
	1 milligram (mg)	= 10^{-3} gram	1 mg = approx. 0.015 grain	
	1 microgram (μg)	= 10^{-6} gram		
Volume (solids)	1 cubic meter (m^3)	= 1,000,000 cubic centimeters	1 m^3 = 1.308 cubic yards 1 m^3 = 35.315 cubic feet	1 cubic yard = 0.7646 m^3 1 cubic foot = 0.0283 m^3
	1 cubic centimeter (cm^3 or cc)	= 10^{-6} cubic meter	1 cm^3 = 0.061 cubic inch	1 cubic inch = 16.387 cm^3
	1 cubic millimeter (mm^3)	= 10^{-9} cubic meter = 10^{-3} cubic centimeter		
Volume (liquids and gases)	1 kiloliter (kL or kl)	= 1,000 liters	1 kL = 264.17 gallons	
	1 liter (L or l)	= 1,000 milliliters	1 L = 0.264 gallon 1 L = 1.057 quarts	1 gallon = 3.785 L 1 quart = 0.946 L
	1 milliliter (mL or ml)	= 10^{-3} liter = 1 cubic centimeter	1 mL = 0.034 fluid ounce 1 mL = approx. ¼ teaspoon 1 mL = approx. 15–16 drops (gtt.)	1 quart = 946 mL 1 pint = 473 mL 1 fluid ounce = 29.57 mL 1 teaspoon = approx. 5 mL
	1 microliter (μL or μl)	= 10^{-6} liter (10^{-3} milliliter)		
Pressure	1 megapascal (MPa)	= 1,000 kilopascals	1 MPa = 10 bars	1 bar = 0.1 MPa
	1 kilopascal (kPa)	= 1,000 pascals	1 kPa = 0.01 bar	1 bar = 100 kPa
	1 pascal (Pa)	= 1 newton/m^2 (N/m^2)	1 Pa = 1.0×10^{-5} bar	1 bar = 1.0×10^5 Pa
Time	1 second (s or sec)	= 1/60 minute		
	1 millisecond (ms or msec)	= 10^{-3} second		
Temperature	Degrees Celsius (°C) (0 K [Kelvin] = −273.15°C)		°F = 9/5°C + 32	°C = 5/9 (°F − 32)

APPENDIX D
A Comparison of the Light Microscope and the Electron Microscope





Light Microscope

In light microscopy, light is focused on a specimen by a glass condenser lens; the image is then magnified by an objective lens and an ocular lens for projection on the eye, digital camera, digital video camera, or photographic film.

Electron Microscope

In electron microscopy, a beam of electrons (top of the microscope) is used instead of light, and electromagnets are used instead of glass lenses. The electron beam is focused on the specimen by a condenser lens; the image is magnified by an objective lens and a projector lens for projection on a digital detector, fluorescent screen, or photographic film.

APPENDIX E Classification of Life

This appendix presents a taxonomic classification for the major extant groups of organisms discussed in this text; not all phyla are included. The classification presented here is based on the three-domain system, which assigns the two major groups of prokaryotes, bacteria and archaea, to separate domains (with eukaryotes making up the third domain).

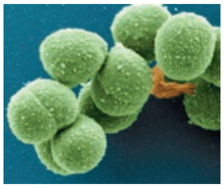
Various alternative classification schemes are discussed in Unit Five of the text. The taxonomic turmoil includes debates about the number and boundaries of kingdoms and about the alignment of the Linnaean classification hierarchy with the findings of modern cladistic analysis. In this review, asterisks (*) indicate currently recognized phyla thought by some systematists to be paraphyletic.

DOMAIN BACTERIA

- **Proteobacteria**
- **Chlamydia**
- **Spirochetes**
- **Cyanobacteria**
- **Gram-Positive Bacteria**

DOMAIN ARCHAEA

- **Euryarchaeota**
- **Thaumarchaeota**
- **Aigarchaeota**
- **Crenarchaeota**
- **Korarchaeota**



DOMAIN EUKARYA

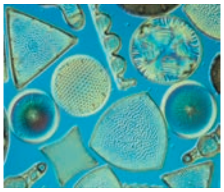
In the phylogenetic hypothesis we present in Chapter 28, major clades of eukaryotes are grouped together in the four "supergroups" listed in bold type below and on the facing page. Formerly, all the eukaryotes generally called protists were assigned to a single kingdom, Protista. However, advances in systematics have made it clear that some protists are more closely related to plants, fungi, or animals than they are to other protists. As a result, the kingdom Protista has been abandoned.

Excavata

- Diplomonadida (diplomonads)
- Parabasala (parabasalids)
- Euglenozoa (euglenozoans)
  - Kinetoplastida (kinetoplastids)
  - Euglenophyta (euglenids)

SAR

- Stramenopila (stramenopiles)
  - Chrysophyta (golden algae)
  - Phaeophyta (brown algae)
  - Bacillariophyta (diatoms)



- Alveolata (alveolates)
  - Dinoflagellata (dinoflagellates)
  - Apicomplexa (apicomplexans)
  - Ciliophora (ciliates)
- Rhizaria (rhizarians)
  - Radiolaria (radiolarians)
  - Foraminifera (forams)
  - Cercozoa (cercozoans)

Archaeplastida

- Rhodophyta (red algae)
- Chlorophyta (green algae: chlorophytes)
- Charophyta (green algae: charophytes)
- Plantae

Phylum Hepatophyta (liverworts)	Nonvascular plants (bryophytes)	
Phylum Bryophyta (mosses)		
Phylum Anthocerophyta (hornworts)		
Phylum Lycophyta (lycophytes)	Seedless vascular plants	
Phylum Monilophyta (ferns, horsetails, whisk ferns)		
Phylum Ginkgophyta (ginkgo)	Gymnosperms	Seed plants
Phylum Cycadophyta (cycads)		
Phylum Gnetophyta (gnetophytes)		
Phylum Coniferophyta (conifers)		
Phylum Anthophyta (flowering plants)	Angiosperms	

DOMAIN EUKARYA, continued

Unikonta

- Amoebozoa (amoebozoans)
  - Myxogastrida (plasmodial slime molds)
  - Dictyostelida (cellular slime molds)
  - Tubulinea (tubulinids)
  - Entamoeba (entamoebas)
- Nucleariida (nucleariids)
- Fungi
  - *Phylum Chytridiomycota (chytrids)
  - *Phylum Zygomycota (zygomycetes)
  - Phylum Glomeromycota (glomeromycetes)
  - Phylum Ascomycota (ascomycetes)
  - Phylum Basidiomycota (basidiomycetes)

- Choanoflagellata (choanoflagellates)
- Animalia
  - Phylum Porifera (sponges)
  - Phylum Ctenophora (comb jellies)
  - Phylum Cnidaria (cnidarians)
    - Medusozoa (hydrozoans, jellies, box jellies)
    - Anthozoa (sea anemones and most corals)
  - Phylum Acoela (acoel flatworms)
  - Phylum Placozoa (placozoans)
  - Lophotrochozoa (lophotrochozoans)
    - Phylum Platyhelminthes (flatworms)
      - Catenulida (chain worms)
      - Rhabditophora (planarians, flukes, tapeworms)
    - Phylum Nemertea (proboscis worms)
    - Phylum Ectoprocta (ectoprocts)
    - Phylum Brachiopoda (brachiopods)
    - Phylum Syndermata (rotifers and spiny-headed worms)
    - Phylum Cycliophora (cycliophorans)
    - Phylum Mollusca (molluscs)
      - Polyplacophora (chitons)
      - Gastropoda (gastropods)
      - Bivalvia (bivalves)
      - Cephalopoda (cephalopods)
    - Phylum Annelida (segmented worms)
      - Errantia (errantians)
      - Sedentaria (sedentarians)
  - Ecdysozoa (ecdysozoans)
    - Phylum Loricifera (loriciferans)
    - Phylum Priapula (priapulans)
    - Phylum Nematoda (roundworms)
    - Phylum Arthropoda (This survey groups arthropods into a single phylum, but some zoologists now split the arthropods into multiple phyla.)
      - Chelicerata (horseshoe crabs, arachnids)
      - Myriapoda (millipedes, centipedes)
      - Pancrustacea (crustaceans, insects)
    - Phylum Tardigrada (tardigrades)
    - Phylum Onychophora (velvet worms)
  - Deuterostomia (deuterostomes)
    - Phylum Hemichordata (hemichordates)
    - Phylum Echinodermata (echinoderms)
      - Asteroidea (sea stars, sea daisies)
      - Ophiuroidea (brittle stars)
      - Echinoides (sea urchins, sand dollars)
      - Crinoidea (sea lilies)
      - Holothuroidea (sea cucumbers)
    - Phylum Chordata (chordates)
      - Cephalochordata (cephalochordates: lancelets)
      - Urochordata (urochordates: tunicates)
      - Cyclostomata (cyclostomes)
        - Myxini (hagfishes)
        - Petromyzontida (lampreys)
      - Gnathostomata (gnathostomes)
        - Chondrichthyes (sharks, rays, chimaeras)
        - Actinopterygii (ray-finned fishes)
        - Actinistia (coelacanths)
        - Dipnoi (lungfishes)
        - Amphibia (amphibians: frogs, salamanders, caecilians)
        - Reptilia (reptiles: tuataras, lizards, snakes, turtles, crocodilians, birds)
        - Mammalia (mammals)

Vertebrates

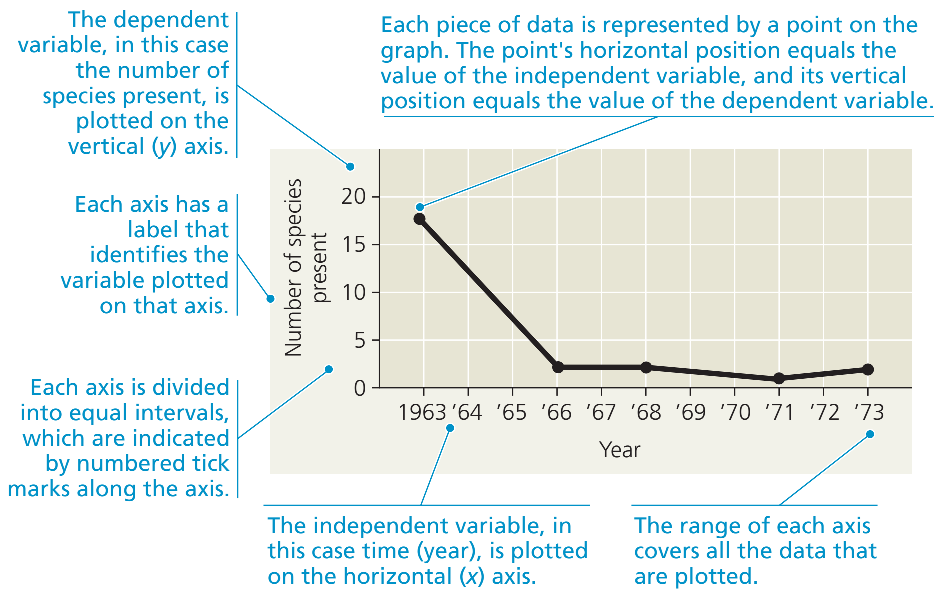
Appendix E Classification of Life

APPENDIX F Scientific Skills Review

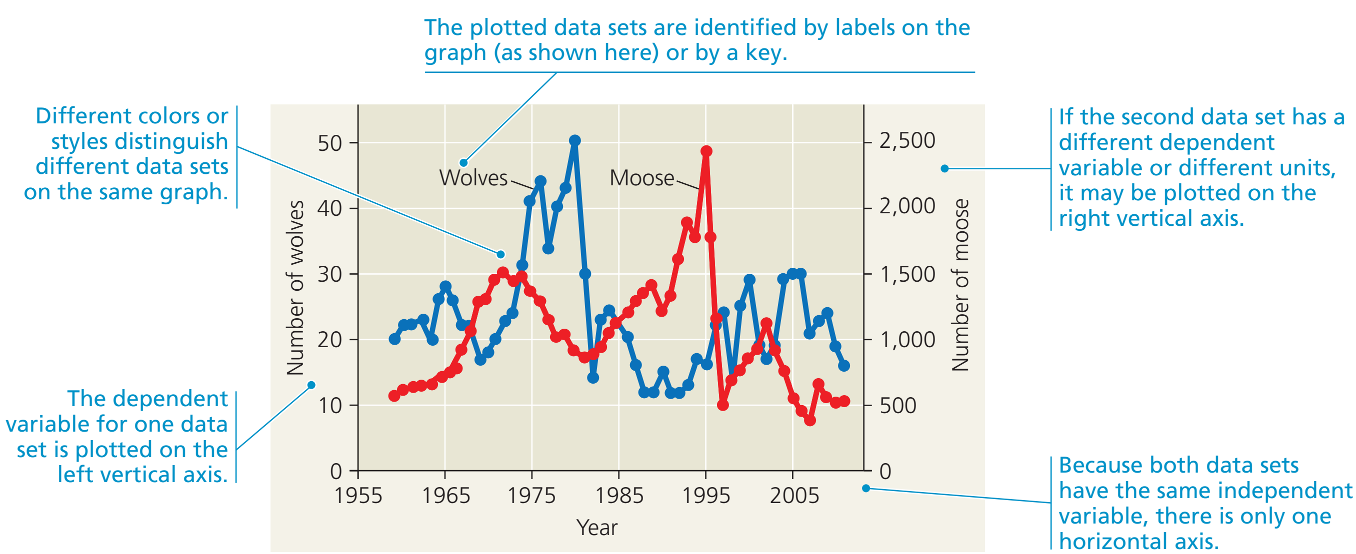
Graphs

Graphs provide a visual representation of numerical data. They may reveal patterns or trends in the data that are not easy to recognize in a table. A graph is a diagram that shows how one variable in a data set is related (or perhaps not related) to another variable. The **independent variable** is the factor that is manipulated or changed by the researchers. The **dependent variable** is the factor that the researchers are measuring in relationship to the independent variable. The independent variable is typically plotted on the *x*-axis and the dependent variable on the *y*-axis. Types of graphs that are frequently used in biology include scatter plots, line graphs, bar graphs, and histograms.

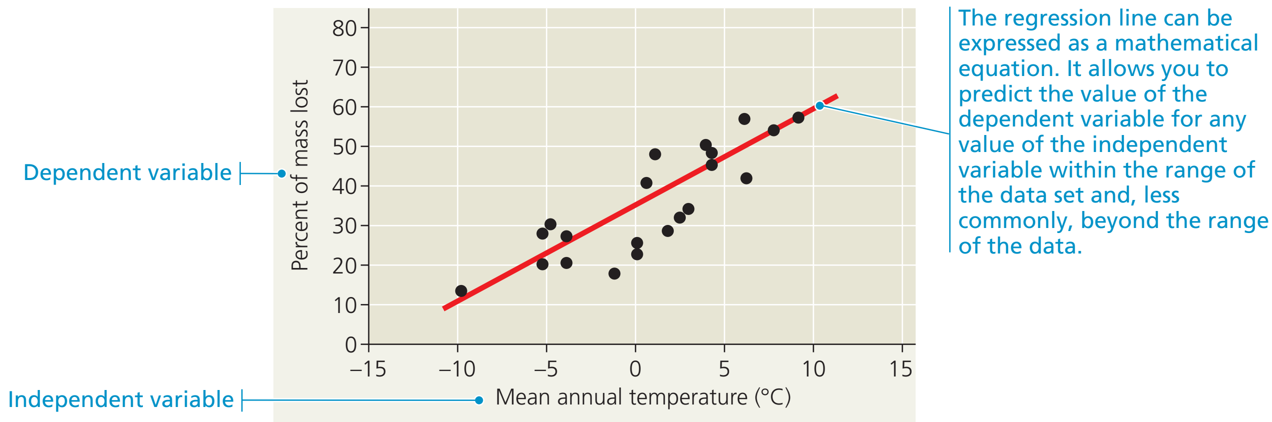
➤ A **scatter plot** is used when the data for all variables are numerical and continuous. Each piece of data is represented by a point. In a **line graph**, each data point is connected to the next point in the data set with a straight line, as in the graph to the right. (To practice making and interpreting scatter plots and line graphs, see the Scientific Skills Exercises in Chapters 2, 3, 6, 8, 11, 13, 24, 26, 34, 46, 47, 49, 50, 51, 54, and 56.)



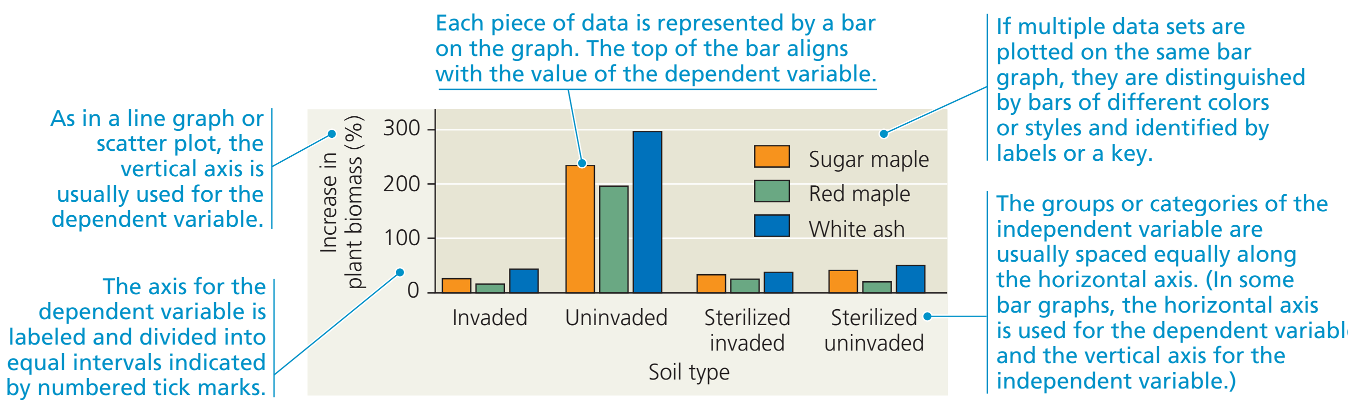
➤ Two or more data sets can be plotted on the same line graph to show how two dependent variables are related to the same independent variable. (To practice making and interpreting line graphs with two or more data sets, see the Scientific Skills Exercises in Chapters 8, 46, 47, 49, 50, 51, and 56.)



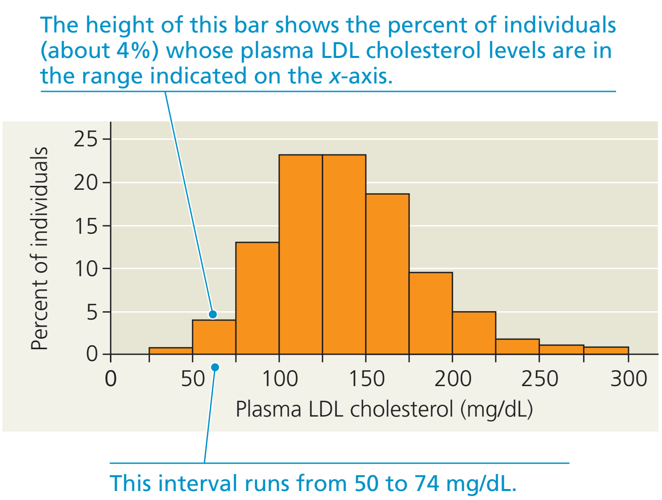
In some scatter plot graphs, a straight or curved line is drawn through the entire data set to show the general trend in the data. A straight line that mathematically best fits the data is called a *regression line*. Alternatively, a mathematical function that best fits the data may describe a curved line, often termed a *best-fit curve*. (To practice making and interpreting regression lines, see the Scientific Skills Exercises in Chapters 3, 11, and 34.)



A **bar graph** is a kind of graph in which the independent variable represents groups or nonnumerical categories and the values of the dependent variable(s) are shown by bars. (To practice making and interpreting bar graphs, see the Scientific Skills Exercises in Chapters 1, 10, 18, 21, 25, 29, 33, 35, 39, 51, 52, and 54.)



A variant of a bar graph called a **histogram** can be made for numeric data by first grouping, or "binning," the variable plotted on the *x*-axis into intervals of equal width. The "bins" may be integers or ranges of numbers. In the histogram at right, the intervals are 25 mg/dL wide. The height of each bar shows the percent (or, alternatively, the number) of experimental subjects whose characteristics can be described by one of the intervals plotted on the *x*-axis. (To practice making and interpreting histograms, see the Scientific Skills Exercises in Chapters 12, 14, and 43.)



Appendix F Scientific Skills Review

Glossary of Scientific Inquiry Terms

See Concept 1.3 for more discussion of the process of scientific inquiry.

control group In a controlled experiment, a set of subjects that lacks (or does not receive) the specific factor being tested. Ideally, the control group should be identical to the experimental group in other respects.

controlled experiment An experiment designed to compare an experimental group with a control group; ideally, the two groups differ only in the factor being tested.

data Recorded observations.

deductive reasoning A type of logic in which specific results are predicted from a general premise.

dependent variable A factor whose value is measured during an experiment to see whether it is influenced by changes in another factor (the independent variable).

experiment A scientific test. Often carried out under controlled conditions that involve manipulating one factor in a system in order to see the effects of changing that factor.

experimental group A set of subjects that has (or receives) the specific factor being tested in a controlled experiment. Ideally, the experimental group should be identical to the control group for all other factors.

hypothesis A testable explanation for a set of observations based on the available data and guided by inductive reasoning. A hypothesis is narrower in scope than a theory.

independent variable A factor whose value is manipulated or changed during an experiment to reveal possible effects on another factor (the dependent variable).

inductive reasoning A type of logic in which generalizations are based on a large number of specific observations.

inquiry The search for information and explanation, often focusing on specific questions.

model A physical or conceptual representation of a natural phenomenon.

prediction In deductive reasoning, a forecast that follows logically from a hypothesis. By testing predictions, experiments may allow certain hypotheses to be rejected.

theory An explanation that is broader in scope than a hypothesis, generates new hypotheses, and is supported by a large body of evidence.

variable A factor that varies during an experiment.

Chi-Square (χ^2) Distribution Table

To use the table, find the row that corresponds to the degrees of freedom in your data set. (The degrees of freedom is the number of categories of data minus 1.) Move along that row to the pair of values that your calculated χ^2 value lies between. Move up from those numbers to the probabilities at the top of the columns to find the probability range for your χ^2 value. A probability of 0.05 or less is generally considered significant. (To practice using the chi-square test, see the Scientific Skills Exercise in Chapter 15.)

Degrees of Freedom (df)	Probability										
	0.95	0.90	0.80	0.70	0.50	0.30	0.20	0.10	0.05	0.01	0.001
1	0.004	0.02	0.06	0.15	0.45	1.07	1.64	2.71	3.84	6.64	10.83
2	0.10	0.21	0.45	0.71	1.39	2.41	3.22	4.61	5.99	9.21	13.82
3	0.35	0.58	1.01	1.42	2.37	3.66	4.64	6.25	7.82	11.34	16.27
4	0.71	1.06	1.65	2.19	3.36	4.88	5.99	7.78	9.49	13.28	18.47
5	1.15	1.61	2.34	3.00	4.35	6.06	7.29	9.24	11.07	15.09	20.52
6	1.64	2.20	3.07	3.83	5.35	7.23	8.56	10.64	12.59	16.81	22.46
7	2.17	2.83	3.82	4.67	6.35	8.38	9.80	12.02	14.07	18.48	24.32
8	2.73	3.49	4.59	5.53	7.34	9.52	11.03	13.36	15.51	20.09	26.12
9	3.33	4.17	5.38	6.39	8.34	10.66	12.24	14.68	16.92	21.67	27.88
10	3.94	4.87	6.18	7.27	9.34	11.78	13.44	15.99	18.31	23.21	29.59

Mean and Standard Deviation

The **mean** is the sum of all data points in a data set divided by the number of data points. The mean (or average) represents a "typical" or central value around which the data points are clustered. The mean of a variable x (denoted by $\bar{x}$) is calculated from the following equation:

$$\bar{x} = \frac{1}{n}\sum_{i=1}^{n} x_i$$

In this formula, n is the number of observations, and x_i is the value of the ith observation of variable x; the "Σ" symbol indicates that the n values of x_i are to be summed. (To practice calculating the mean, see the Scientific Skills Exercises in Chapters 27, 32, and 34.)

The **standard deviation** provides a measure of the variation found in a set of data points. The standard deviation of a variable x (denoted s_x) is calculated from the following equation:

$$s = \sqrt{\frac{\sum_{i=1}^{n}(x_i - \bar{x})^2}{n-1}}$$

In this formula, n is the number of observations, x_i is the value of the ith observation of variable x, and $\bar{x}$ is the mean of x; the "Σ" symbol indicates that the n values of $(x_i - \bar{x})^2$ are to be summed. (To practice calculating standard deviation, see the Scientific Skills Exercises in Chapters 27, 32, and 34.)

Credits

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Unit One Interview Lovell A. Jones

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Unit Two Interview **top** Darren Phillips, New Mexico State University; **bottom** Elba Serrano

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College Electron Microscope Facility; **7.24c** From: Functional protofilament numbering of ciliary, flagellar, and centriolar microtubules. R. W. Linck, R. E. Stephens. *Cell Motil Cytoskeleton*. 2007 Jul; 64(7):489–95, Fig. 1B.; **7.25** From: Cross-linker system between neurofilaments, microtubules, and membranous organelles in frog axons revealed by the quick-freeze, deep-etching method. Hirokawa Nobutaka. *Journal of Cell Biology* 94(1): 129–142, 1982. Reproduced by permission of Rockefeller University Press.; **7.26a** Clara Franzini-Armstrong/University of Pennsylvania; **7.26b** M. I. Walker/Science Source; **7.26c** Michael Clayton/University of Wisconsin; **7.27** G. F. Leedale/Biophoto Associates/Science Source; **7.29** Wm. P. Wergin, courtesy of Eldon H. Newcomb; **7.30 right** Reproduced with permission from *Freeze-Etch Histology*, by L. Orci and A. Perrelet, Springer-Verlag, Heidelberg, 1975. Plate 32. Page 68. © 1975 by Springer-Verlag GmbH & Co KG; **center** From: Fine structure of desmosomes., hemidesmosomes, and an adepidermal globular layer in developing newt epidermis. DE Kelly. *Journal of Cell Biology* 1966 Jan; 28(1):51–72. Fig. 7.; **bottom** From: Low resistance junctions in crayfish. Structural changes with functional uncoupling. C. Peracchia and A. F. Dulhunty, *The Journal of Cell Biology*. 1976 Aug; 70(2 pt 1):419–39. Fig. 6. Reproduced by permission of Rockefeller University Press.; **7.31** Eye of Science/Science Source; **p. 194 vacuole** Eldon H. Newcomb; **p. 195 peroxisome** Eldon H. Newcomb; **p. 195 bottom** Susumu Nishinaga/Science Source

Chapter 8 **8.1** Bert L. de Groot; **p. 196 bottom** Crystal structure of a mammalian voltage-dependent Shaker family K^+ channel. S. B. Long, et al. *Science*. 2005 Aug 5; 309 (5736):897–903. Epub 2005 Jul 7; **p. 199 bottom** camerawithlegs/Fotolia; **8.13** Michael Abbey/Science Source; **8 Scientific Skills Exercise** teddies Photo Fun/Shutterstock; **8.19 amoeba** Biophoto Associates/Science Source; **vesicles** Don W. Fawcett/Science Source; **coated pit; coated vesicle** From: M.M. Perry and A.B. Gilbert, *Journal of Cell Science* 39: 257–272, Fig. 11 (1979). © 1979 The Company of Biologists Ltd.; **p. 212** Kristoffer Tripplaar/Alamy Stock Photo

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Chapter 12 **12.1** George von Dassow; **p. 284 bottom** Jane Stout and Claire Walczak, Indiana University, Winner of the GE Healthcare Life Sciences' 2012 Cell Imaging Competition.; **12.2a** Biophoto Associates/Science Source; **12.2b** Biology Pics/Science Source; **12.2c** Biophoto/Science Source; **12.3** John M. Murray, School for Medicine, University of Pennsylvania, Philadelphia.; **12.4** Biophoto/Science Source; **12.5 center** Biophoto/Science Source; **12.7** Conly L. Rieder; **12.8 right** J. Richard McIntosh, University of Colorado, Boulder; **left** Reproduced by permission from Matthew Schibler, from *Protoplasma* 137. © 1987: 29–44 by Springer-Verlag GmbH & Co KG; **12.10a** Don W. Fawcett/Science Source; **12.10b** Eldon H Newcomb; **12.11 left to right** Elisabeth/Pearson Education; **12.18 bottom** Guenter Albrecht-Buehler, Northwestern University, Chicago; **12.19a; 12.19b** Lan Bo Chen; **12.20 bottom right** Anne Weston/Wellcome Institute Library; **12 Scientific Skills Exercise** Mike Davidson; **p. 302 left** J.L. Carson/Newscom; **p. 302 right** Steve Gschmeissner/Science Source

Unit Three Interview **top** Denise Applewhite, Office of Communications, Princeton University; **bottom** Shirley Tilghman, Princeton University

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Chapter 28 **28.1** From: The molecular ecology of microbial eukaryotes unveils a hidden world, Moreira D, López-García P. *Trends Microbiol*. 2002 Jan;10(1):31–8. Fig. 4. Photo by Brian S. Leander and Mark Farmer.; **p. 645 bottom** Eric V. Grave/Science Source; **28 Scientific Skills Exercise** Shutterstock; **p. 648 right** Joel Mancuso, University of California, Berkeley; **p. 649 top left** M.I. Walker/Photoshot; **top right** Frank Fox/Science Source; **top right inset** David J. Patterson; **bottom left** Howard J. Spero; **bottom left inset** National Oceanic and Atmospheric Administration; **bottom right** Michael Abbey/Science Source; **28.4** Ken Ishida; **28.5** David M. Phillips/Science Source; **28.6** David J. Patterson; **28.7** Oliver Meckes/Science Source; **28.8** David J. Patterson; **28.9** Centers for Disease Control and Prevention; **28.10** Steve Gschmeissner/Science Source; **28.11** Stephen Durr; **28.12** Colin Bates; **28.13** J. R. Waaland/Biological Photo Service; **28.14** Guy Brugerolle; **28.15a** Virginia Institute of Marine Science; **28.15b** Science Source; **28.16** Masamichi Aikawa; **28.17a** M. I. Walker/Science Source; **28.18** Robert Brons/Biological Photo Service; **28.19** Nature Picture Library; **28.20** Eva Nowack; **28.21a** D. P. Wilson; Eric Hosking; David Hosking/Science Source; **28.21b** Michael Guiry; **28.21c** Biophoto Associates/Science Source; **28.21d** David Murray/Dorling Kindersley, Ltd.; **28.22a** M. I. Walker/Science Source; **28.22b** Laurie Campbell/Photoshot License Limited; **28.22c** David L. Ballantine; **28.23** William L. Dentler; **28.25** Ken Hickman; **28.26 left, bottom** Robert Kay; **28.27** Kevin Carpenter and Patrick Keeling; **28.28** Dave Clarke Photography/Alamy Stock Photo; **p. 669** Greg Antipa/Biophoto Associates/Science Source

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Dave Clarke/Zoological Society of London; **right** The U.S. Bureau of Fisheries; **33.23** Fredrik Pleijel; **33.24** Wolcott Henry/National Geographic Creative/Getty Images; **33.25** Astrid Michler, Hanns-Frieder Michler/Science Source; **33.26** Photoshot; **33.27** London Scientific Films/Oxford Scientific/Getty Images; **33.28** Power and Syred/Science Source; **33.29** Dan Cooper; **33.30** Stephen Paddock; **33.32** Mark Newman/Frank Lane Picture Agency; **33.33 top** Tim Flach/The Image Bank/Getty Images; **center** Andrew Syred/Science Source; **bottom** Reinhard Hölzl/Imagebroker/AGE Fotostock; **33.34** Tim Flach/The Image Bank/Getty Images; **33.35a** PREMAPHOTOS/Nature Picture Library; **33.35b** Tom McHugh/Science Source; **33.37** Maximilian Weinzierl/Alamy Stock Photo; **33.38** Peter Herring/Image Quest Marine; **33.39** Peter Parks/Image Quest Marine; **33.41** Meul/ARCO/Nature Picture Library; **33.42a** Cathy Keifer/Shutterstock; **33.42b** Cathy Keifer/Shutterstock; **33.42c** Jim Zipp/Science Source; **33.42d** Cathy Keifer/Shutterstock; **33.42e** Cathy Keifer/Shutterstock; **33.43 bristletail** Kevin Murphy; **silverfish** Perry Babin; **weevil** PREMAPHOTOS/Nature Picture Library; **red tachinid** Bruce Marlin; **wasp** John Cancalosi/Nature Picture Library; **hummingbird** Hans Christoph Kappel/Nature Picture Library; **homopteran** Dante Fenolio/Science Source; **katydid** Chris Mattison/Alamy Stock Photo; **33.44** Andrey Nekrasov/Image Quest Marine; **33.45** Daniel Janies; **33.46** Jeff Rotman/Science Source; **33.47** Louise Murray/Robert Harding World Imagery; **33.48** Jurgen Freund/Nature Picture Library; **33.49** Hal Beral/Corbis; **p. 769** Lucy Arnold

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Chapter 36 **36.1** Dennis Frates/Alamy Stock Photo; **p. 836 bottom** Bjorn Svensson/Science Source; **36.3a** Rolf Rutishauser; **36.3b** Rolf Rutishauser; **p. 842** Nigel Cattlin/Science Source; **36.8** Holger Herlyn, University of Mainz, Germany; **inset** Benjamin Blonder and David Elliott; **36.10** Scott Camazine/Science Source; **36.13a; 36.13b** Power and Syred/Science Source; **36.15 ocotillo** Gerald Holmes, California Polytechnic State University at San Luis Obispo, Bugwood.org; **inset** Steven Baskauf, Nature Conservancy Tennessee Chapter Headquarters; **leafless ocotillo** Kate Shane, Southwest School of Botanical Medicine; **oleander cross section** Natalie Bronstein; **oleander** Andrew de Lory/Dorling Kindersley, Ltd.; **baobab tree** Ryan Faas/Alamy Stock Photo; **36.18 left, center, right** M. H. Zimmerman, from P. B. Tomlinson, Harvard University; **36.19** From: A coiled-coil interaction mediates cauliflower mosaic virus cell-to-cell movement. L. Stavolone et al. *Proc Natl Acad Sci U S A*. 2005 Apr 26;102(17):6219-24. Fig. 5C.; **p. 856** Catalin Petolea/Alamy Stock Photo

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Chapter 46 **46.1** Brad Smith/Stamps School of Art & Design, University of Michigan; **p. 1073 bottom** Oxford Scientific/Getty Images; **46.4abcd** From: Methods for quantitating sea urchin sperm-egg binding. V D Vacquier and J E Payne. *Exp Cell Res*. 1973 Nov; 82(1):227-35.; **46.4efgh** From: Wave of Free Calcium at Fertilization in the Sea Urchin Egg Visualized with Fura-2. M. Hafner et al. *Cell Motil. Cytoskel.*, 1988; 9:271-277; **46.6a-d** George von Dassow; **46.7 top** Jurgen Berger; **bottom** Andrew J. Ewald; **46.8a** Charles A. Ettensohn; **46.13b** Alejandro Díaz Díez/AGE Fotostock/Alamy Stock Photo; **46.14 left** Huw Williams; **right** Thomas Poole; **46.15b** Keith Wheeler/Science Source; **46.18b left** Hiroki Nishida; **right** Hiroki Nishida; **46.19** Medical Research Council; **46.20 & 21** MDC Biology Sinsheimer Labs; **46.24** From: Dorsal-ventral patterning and neural induction in *Xenopus* embryos. E. M. De Robertis and H. Kuroda. *Annu Rev Cell Dev Biol*. 2004;20:285-308. Fig. 1.; **46.25a** Kathryn W. Tosney; **46.26** Dennis Summerbell; **p. 1096** James Gerholdt/Getty Images

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Appendix A Figure 5.11 Wallace/Sanders/Ferl, *Biology: The Science of Life*, 3rd Ed., ©1991. Reprinted and electronically reproduced by permission of Pearson Education, Inc., Upper Saddle River, New Jersey.

Glossary

Pronunciation Key

ā	ace
a/ah	ash
ch	chose
ē	meet
e/eh	bet
g	game
ī	ice
i	hit
ks	box
kw	quick
ng	song
ō	robe
o	ox
oy	boy
s	say
sh	shell
th	thin
ū	boot
u/uh	up
z	zoo

′ = primary accent
′ = secondary accent

5′ cap A modified form of guanine nucleotide added onto the 5′ end of a pre-mRNA molecule.

ABC hypothesis A model of flower formation identifying three classes of organ identity genes that direct formation of the four types of floral organs.

abiotic (ā′-bī-ot′-ik) Nonliving; referring to the physical and chemical properties of an environment.

abortion The termination of a pregnancy in progress.

abscisic acid (ABA) (ab-sis′-ik) A plant hormone that slows growth, often antagonizing the actions of growth hormones. Two of its many effects are to promote seed dormancy and facilitate drought tolerance.

absorption The third stage of food processing in animals: the uptake of small nutrient molecules by an organism's body.

absorption spectrum The range of a pigment's ability to absorb various wavelengths of light; also a graph of such a range.

abyssal zone (uh-bis′-ul) The part of the ocean's benthic zone between 2,000 and 6,000 m deep.

acanthodian (ak′-an-thō′-dē-un) Any of a group of ancient jawed aquatic vertebrates from the Silurian and Devonian periods.

accessory fruit A fruit, or assemblage of fruits, in which the fleshy parts are derived largely or entirely from tissues other than the ovary.

acclimatization (uh-klī′-muh-tī -zā′-shun) Physiological adjustment to a change in an environmental factor.

acetyl CoA Acetyl coenzyme A; the entry compound for the citric acid cycle in cellular respiration, formed from a two-carbon fragment of pyruvate attached to a coenzyme.

acetylcholine (as′-uh-til-kō′-lēn) One of the most common neurotransmitters; functions by binding to receptors and altering the permeability of the postsynaptic membrane to specific ions, either depolarizing or hyperpolarizing the membrane.

acid A substance that increases the hydrogen ion concentration of a solution.

acoelomate (uh-sē′-lō-māt) A solid-bodied animal lacking a cavity between the gut and outer body wall.

acquired immunodeficiency syndrome (AIDS) The symptoms and signs present during the late stages of HIV infection, defined by a specified reduction in the number of T cells and the appearance of characteristic secondary infections.

acrosomal reaction (ak′-ruh-sōm′-ul) The discharge of hydrolytic enzymes from the acrosome, a vesicle in the tip of a sperm, when the sperm approaches or contacts an egg.

acrosome (ak′-ruh-sōm) A vesicle in the tip of a sperm containing hydrolytic enzymes and other proteins that help the sperm reach the egg.

actin (ak′-tin) A globular protein that links into chains, two of which twist helically about each other, forming microfilaments (actin filaments) in muscle and other kinds of cells.

action potential An electrical signal that propagates (travels) along the membrane of a neuron or other excitable cell as a nongraded (all-or-none) depolarization.

action spectrum A graph that profiles the relative effectiveness of different wavelengths of radiation in driving a particular process.

activation energy The amount of energy that reactants must absorb before a chemical reaction will start; also called free energy of activation.

activator A protein that binds to DNA and stimulates gene transcription. In prokaryotes, activators bind in or near the promoter; in eukaryotes, activators generally bind to control elements in enhancers.

active immunity Long-lasting immunity conferred by the action of B cells and T cells and the resulting B and T memory cells specific for a pathogen. Active immunity can develop as a result of natural infection or immunization.

active site The specific region of an enzyme that binds the substrate and that forms the pocket in which catalysis occurs.

active transport The movement of a substance across a cell membrane against its concentration or electrochemical gradient, mediated by specific transport proteins and requiring an expenditure of energy.

adaptation Inherited characteristic of an organism that enhances its survival and reproduction in a specific environment.

adaptive evolution Evolution that results in a better match between organisms and their environment.

adaptive immunity A vertebrate-specific defense that is mediated by B lymphocytes (B cells) and T lymphocytes (T cells) and that exhibits specificity, memory, and self-nonself recognition; also called acquired immunity.

adaptive radiation Period of evolutionary change in which groups of organisms form many new species whose adaptations allow them to fill different ecological roles in their communities.

addition rule A rule of probability stating that the probability of any one of two or more mutually exclusive events occurring can be determined by adding their individual probabilities.

adenosine triphosphate *See* ATP (adenosine triphosphate).

adenylyl cyclase (uh-den′-uh-lil) An enzyme that converts ATP to cyclic AMP in response to an extracellular signal.

adhesion The clinging of one substance to another, such as water to plant cell walls by means of hydrogen bonds.

adipose tissue A connective tissue that insulates the body and serves as a fuel reserve; contains fat-storing cells called adipose cells.

adrenal gland (uh-drē′-nul) One of two endocrine glands located adjacent to the kidneys in mammals. Endocrine cells in the outer portion (cortex) respond to adrenocorticotropic hormone (ACTH) by secreting steroid hormones that help maintain homeostasis during long-term stress. Neurosecretory cells in the central portion (medulla) secrete epinephrine and norepinephrine in response to nerve signals triggered by short-term stress.

aerobic respiration A catabolic pathway for organic molecules, using oxygen (O_2) as the final electron acceptor in an electron transport chain and ultimately producing ATP. This is the most efficient catabolic pathway and is carried out in most eukaryotic cells and many prokaryotic organisms.

age structure The relative number of individuals of each age in a population.

aggregate fruit A fruit derived from a single flower that has more than one carpel.

AIDS (acquired immunodeficiency syndrome) The symptoms and signs present during the late stages of HIV infection, defined by a specified reduction in the number of T cells and the appearance of characteristic secondary infections.

alcohol fermentation Glycolysis followed by the reduction of pyruvate to ethyl alcohol, regenerating NAD^+ and releasing carbon dioxide.

alga (plural, **algae**) A general term for any species of photosynthetic protist, including both unicellular and multicellular forms. Algal species are included in three eukaryote supergroups (Excavata, SAR, and Archaeplastida).

alimentary canal (al′-uh-men′-tuh-rē) A complete digestive tract, consisting of a tube running between a mouth and an anus.

alkaline vent A deep-sea hydrothermal vent that releases water that is warm (40–90°C) rather than hot and that has a high pH (is basic). These vents consist of tiny pores lined with iron and other catalytic minerals that some scientists hypothesize might have been the location of the earliest abiotic synthesis of organic compounds.

allele (uh-lē′-ul) Any of the alternative versions of a gene that may produce distinguishable phenotypic effects.

allopatric speciation (al′-uh-pat′-rik) The formation of new species in populations that are geographically isolated from one another.

allopolyploid (al′-ō-pol′-ē-ployd) A fertile individual that has more than two chromosome sets as a result of two different species interbreeding and combining their chromosomes.

allosteric regulation The binding of a regulatory molecule to a protein at one site that affects the function of the protein at a different site.

alpha (α) helix (al′-fuh hē′-liks) A coiled region constituting one form of the secondary structure of proteins, arising from a specific pattern of hydrogen bonding between atoms of the polypeptide backbone (not the side chains).

alternation of generations A life cycle in which there is both a multicellular diploid form, the sporophyte, and a multicellular haploid form, the gametophyte; characteristic of plants and some algae.

alternative RNA splicing A type of eukaryotic gene regulation at the RNA-processing level in which different mRNA molecules are produced from the same primary transcript, depending on which RNA segments are treated as exons and which as introns.

altruism (al′-trū-iz-um) Selflessness; behavior that reduces an individual's fitness while increasing the fitness of another individual.

alveolates (al-vē′-uh-lets) One of the three major subgroups for which the SAR eukaryotic supergroup is named. This clade arose by secondary endosymbiosis, and its members have membrane-enclosed sacs (alveoli) located just under the plasma membrane.

alveolus (al-vē′-uh-lus) (plural, **alveoli**) One of the dead-end air sacs where gas exchange occurs in a mammalian lung.

Alzheimer's disease (alts′-hī-merz) An age-related dementia (mental deterioration) characterized by confusion and memory loss.

amino acid (uh-mēn′-ō) An organic molecule possessing both a carboxyl and an amino group. Amino acids serve as the monomers of polypeptides.

amino group (uh-mēn′-ō) A chemical group consisting of a nitrogen atom bonded to two hydrogen atoms; can act as a base in solution, accepting a hydrogen ion and acquiring a charge of 1 + .

aminoacyl-tRNA synthetase An enzyme that joins each amino acid to the appropriate tRNA.

ammonia A small, toxic molecule (NH_3) produced by nitrogen fixation or as a metabolic waste product of protein and nucleic acid metabolism.

ammonite A member of a group of shelled cephalopods that were important marine predators for hundreds of millions of years until their extinction at the end of the Cretaceous period (65.5 million years ago).

amniocentesis (am′-nē-ō-sen-tē′-sis) A technique associated with prenatal diagnosis in which amniotic fluid is obtained by aspiration from a needle inserted into the uterus. The fluid and the fetal cells it contains are analyzed to detect certain genetic and congenital defects in the fetus.

amniote (am′-nē-ōt) A member of a clade of tetrapods named for a key derived character, the amniotic egg, which contains specialized membranes, including the fluid-filled amnion, that protect the embryo. Amniotes include mammals as well as birds and other reptiles.

amniotic egg An egg that contains specialized membranes that function in protection, nourishment, and gas exchange. The amniotic egg was a major evolutionary innovation, allowing embryos to develop on land in a fluid-filled sac, thus reducing the dependence of tetrapods on water for reproduction.

amoeba (uh-mē′-buh) A protist characterized by the presence of pseudopodia.

amoebocyte (uh-mē′-buh-sīt′) An amoeba-like cell that moves by pseudopodia and is found in most animals. Depending on the species, it may digest and distribute food, dispose of wastes, form skeletal fibers, fight infections, or change into other cell types.

amoebozoan (uh-mē′-buh-zō′-an) A protist in a clade that includes many species with lobe- or tube-shaped pseudopodia.

amphibian A member of the clade of tetrapods that includes salamanders, frogs, and caecilians.

amphipathic (am′-fē-path′-ik) Having both a hydrophilic region and a hydrophobic region.

amplification The strengthening of stimulus energy during transduction.

amygdala (uh-mig′-duh-luh) A structure in the temporal lobe of the vertebrate brain that has a major role in the processing of emotions.

amylase (am′-uh-lās′) An enzyme that hydrolyzes starch (a glucose polymer from plants) and glycogen (a glucose polymer from animals) into smaller polysaccharides and the disaccharide maltose.

anabolic pathway (an′-uh-bol′-ik) A metabolic pathway that consumes energy to synthesize a complex molecule from simpler molecules.

anaerobic respiration (an-er-ō′-bik) A catabolic pathway in which inorganic molecules other than oxygen accept electrons at the "downhill" end of electron transport chains.

analogous Having characteristics that are similar because of convergent evolution, not homology.

analogy (an-al′-uh-jē) Similarity between two species that is due to convergent evolution rather than to descent from a common ancestor with the same trait.

anaphase The fourth stage of mitosis, in which the chromatids of each chromosome have separated and the daughter chromosomes are moving to the poles of the cell.

anatomy The structure of an organism.

anchorage dependence The requirement that a cell must be attached to a substratum in order to initiate cell division.

androgen (an′-drō-jen) Any steroid hormone, such as testosterone, that stimulates the development and maintenance of the male reproductive system and secondary sex characteristics.

aneuploidy (an′-yū-ploy′-dē) A chromosomal aberration in which one or more chromosomes are present in extra copies or are deficient in number.

angiosperm (an′-jē-ō-sperm) A flowering plant, which forms seeds inside a protective chamber called an ovary.

anhydrobiosis (an-hī′-drō-bī-ō′-sis) A dormant state involving loss of almost all body water.

animal pole The point at the end of an egg in the hemisphere where the least yolk is concentrated; opposite of vegetal pole.

anion (an′-ī-on) A negatively charged ion.

anterior Pertaining to the front, or head, of a bilaterally symmetrical animal.

anterior pituitary A portion of the pituitary gland that develops from nonneural tissue; consists of endocrine cells that synthesize and secrete several tropic and nontropic hormones.

anther In an angiosperm, the terminal pollen sac of a stamen, where pollen grains containing sperm-producing male gametophytes form.

antheridium (an-thuh-rid′-ē-um) (plural, **antheridia**) In plants, the male gametangium, a moist chamber in which gametes develop.

anthropoid (an′-thruh-poyd) A member of a primate group made up of the monkeys and the apes (gibbons, orangutans, gorillas, chimpanzees, bonobos, and humans).

antibody A protein secreted by plasma cells (differentiated B cells) that binds to a particular antigen; also called immunoglobulin. All antibodies have the same Y-shaped structure and in their monomer form consist of two identical heavy chains and two identical light chains.

anticodon (an′-tī-kō′-don) A nucleotide triplet at one end of a tRNA molecule that base-pairs with a particular complementary codon on an mRNA molecule.

antidiuretic hormone (ADH) (an′-tī-dī-yū-ret′-ik) A peptide hormone, also called vasopressin, that promotes water retention by the kidneys. Produced in the hypothalamus and released from the posterior pituitary, ADH also functions in the brain.

antigen (an′-ti-jen) A substance that elicits an immune response by binding to receptors of B or T cells.

antigen presentation (an′-ti-jen) The process by which an MHC molecule binds to a fragment of an intracellular protein antigen and carries it to the cell surface, where it is displayed and can be recognized by a T cell.

antigen-presenting cell (an′-ti-jen) A cell that upon ingesting pathogens or internalizing pathogen proteins generates peptide fragments that are bound by class II MHC molecules and subsequently displayed on the cell surface to T cells. Macrophages, dendritic cells, and B cells are the primary antigen-presenting cells.

antigen receptor (an′-ti-jen) The general term for a surface protein, located on B cells and T cells, that binds to antigens, initiating adaptive immune responses. The antigen receptors on B cells are called B cell receptors, and the antigen receptors on T cells are called T cell receptors.

antiparallel Referring to the arrangement of the sugar-phosphate backbones in a DNA double helix (they run in opposite 5′ S 3′ directions).

aphotic zone (ā′-fō′-tik) The part of an ocean or lake beneath the photic zone, where light does not penetrate sufficiently for photosynthesis to occur.

apical bud (ā′-pik-ul) A bud at the tip of a plant stem; also called a terminal bud.

apical dominance (ā′-pik-ul) Tendency for growth to be concentrated at the tip of a plant shoot because the apical bud partially inhibits axillary bud growth.

apical ectodermal ridge (AER) (ā′-pik-ul) A thickened area of ectoderm at the tip of a limb bud that promotes outgrowth of the limb bud.

apical meristem (ā′-pik-ul mār′-uh-stem) A localized region at a growing tip of a plant body where one or more cells divide repeatedly. The dividing cells of an apical meristem enable the plant to grow in length.

apicomplexan (ap′-ē-kom-pleks′-un) A group of alveolate protists, this clade includes many species that parasitize animals. Some apicomplexans cause human disease.

apomixis (ap′-uh-mik′-sis) The ability of some plant species to reproduce asexually through seeds without fertilization by a male gamete.

apoplast (ap′-ō-plast) Everything external to the plasma membrane of a plant cell, including cell walls, intercellular spaces, and the space within dead structures such as xylem vessels and tracheids.

apoptosis (ā-puh-tō′-sus) A type of programmed cell death, which is brought about by activation of enzymes that break down many chemical components in the cell.

aposematic coloration (ap′-ō-si-mat′-ik) The bright warning coloration of many animals with effective physical or chemical defenses.

appendix A small, finger-like extension of the vertebrate cecum; contains a mass of white blood cells that contribute to immunity.

aquaporin A channel protein in a cellular membrane that specifically facilitates osmosis, the diffusion of free water across the membrane.

aqueous solution (ā′-kwē-us) A solution in which water is the solvent.

arachnid A member of a subgroup of the major arthropod clade Chelicerata. Arachnids have six pairs of appendages, including four pairs of walking legs, and include spiders, scorpions, ticks, and mites.

arbuscular mycorrhiza (ar-bus′-kyū-lur mī′-kō-rī′-zuh) Association of a fungus with a plant root system in which the fungus causes the invagination of the host (plant) cells' plasma membranes.

arbuscular mycorrhizal fungus (ar-bus′-kyū-lur) A symbiotic fungus whose hyphae grow through the cell wall of plant roots and extend into the root cell (enclosed in tubes formed by invagination of the root cell plasma membrane).

arbuscules Specialized branching hyphae that are found in some mutualistic fungi and exchange nutrients with living plant cells.

Archaea (ar′-kē′-uh) One of two prokaryotic domains, the other being Bacteria.

Archaeplastida (ar′-kē-plas′-tid-uh) One of four supergroups of eukaryotes proposed in a current hypothesis of the evolutionary history of eukaryotes. This monophyletic group, which includes red algae, green algae, and plants, descended from an ancient protistan ancestor that engulfed a cyanobacterium. *See also* Excavata, SAR, and Unikonta.

archegonium (ar-ki-gō′-nē-um) (plural, **archegonia**) In plants, the female gametangium, a moist chamber in which gametes develop.

archenteron (ar-ken′-tuh-ron) The endoderm-lined cavity, formed during gastrulation, that develops into the digestive tract of an animal.

archosaur (ar′-kō-sōr) A member of the reptilian group that includes crocodiles, alligators and dinosaurs, including birds.

arteriole (ar-ter′-ē-ōl) A vessel that conveys blood between an artery and a capillary bed.

artery A vessel that carries blood away from the heart to organs throughout the body.

arthropod A segmented ecdysozoan with a hard exoskeleton and jointed appendages. Familiar examples include insects, spiders, millipedes, and crabs.

artificial selection The selective breeding of domesticated plants and animals to encourage the occurrence of desirable traits.

ascocarp The fruiting body of a sac fungus (ascomycete).

ascomycete (as′-kuh-mī′-sēt) A member of the fungal phylum Ascomycota, commonly called sac fungus. The name comes from the saclike structure in which the spores develop.

ascus (plural, **asci**) A saclike spore capsule located at the tip of a dikaryotic hypha of a sac fungus.

asexual reproduction The generation of offspring from a single parent that occurs without the fusion of gametes. In most cases, the offspring are genetically identical to the parent.

A site One of a ribosome's three binding sites for tRNA during translation. The A site holds the tRNA carrying the next amino acid to be added to the polypeptide chain. (A stands for aminoacyl tRNA.)

assisted migration The translocation of a species to a favorable habitat beyond its native range for the purpose of protecting the species from human-caused threats.

associative learning The acquired ability to associate one environmental feature (such as a color) with another (such as danger).

atherosclerosis A cardiovascular disease in which fatty deposits called plaques develop in the inner walls of the arteries, obstructing the arteries and causing them to harden.

atom The smallest unit of matter that retains the properties of an element.

atomic mass The total mass of an atom, numerically equivalent to the mass in grams of 1 mole of the atom. (For an element with more than one isotope, the atomic mass is the average mass of the naturally occurring isotopes, weighted by their abundance.)

atomic nucleus An atom's dense central core, containing protons and neutrons.

atomic number The number of protons in the nucleus of an atom, unique for each element and designated by a subscript.

ATP (adenosine triphosphate) (a-den′-ō-sēn trī-fos′-fāt) An adenine-containing nucleoside triphosphate that releases free energy when its phosphate bonds are hydrolyzed. This energy is used to drive endergonic reactions in cells.

ATP synthase A complex of several membrane proteins that functions in chemiosmosis with adjacent electron transport chains, using the energy of a hydrogen ion (proton) concentration gradient to make ATP. ATP synthases are found in the inner mitochondrial membranes of eukaryotic cells and in the plasma membranes of prokaryotes.

atrial natriuretic peptide (ANP) (ā′-trē-ul na′-trē-yū-ret′-ik) A peptide hormone secreted by cells of the atria of the heart in response to high blood pressure. ANP's effects on the kidney alter ion and water movement and reduce blood pressure.

atrioventricular (AV) node A region of specialized heart muscle tissue between the left and right atria where electrical impulses are delayed for about 0.1 second before spreading to both ventricles and causing them to contract.

atrioventricular (AV) valve A heart valve located between each atrium and ventricle that prevents a backflow of blood when the ventricle contracts.

atrium (ā′-trē-um) (plural, **atria**) A chamber of the vertebrate heart that receives blood from the veins and transfers blood to a ventricle.

autocrine Referring to a secreted molecule that acts on the cell that secreted it.

autoimmune disease An immunological disorder in which the immune system turns against self.

autonomic nervous system (ot′-ō-nom′-ik) An efferent branch of the vertebrate peripheral nervous system that regulates the internal environment; consists of the sympathetic, parasympathetic, and enteric divisions.

autopolyploid (ot′-ō-pol′-ē-ployd) An individual that has more than two chromosome sets that are all derived from a single species.

autosome (ot′-ō-sōm) A chromosome that is not directly involved in determining sex; not a sex chromosome.

autotroph (ot′-ō-trōf) An organism that obtains organic food molecules without eating other organisms or substances derived from other organisms. Autotrophs use energy from the sun or from oxidation of inorganic substances to make organic molecules from inorganic ones.

auxin (ôk′-sin) A term that primarily refers to indoleacetic acid (IAA), a natural plant hormone that has a variety of effects, including cell elongation, root formation, secondary growth, and fruit growth.

axillary bud (ak′-sil-ār-ē) A structure that has the potential to form a lateral shoot, or branch. The bud appears in the angle formed between a leaf and a stem.

axon (ak′-son) A typically long extension, or process, of a neuron that carries nerve impulses away from the cell body toward target cells.

B cells The lymphocytes that complete their development in the bone marrow and become effector cells for the humoral immune response.

Bacteria One of two prokaryotic domains, the other being Archaea.

bacteriophage (bak-tēr′-ē-ō-fāj) A virus that infects bacteria; also called a phage.

bacteroid A form of the bacterium *Rhizobium* contained within the vesicles formed by the root cells of a root nodule.

balancing selection Natural selection that maintains two or more phenotypic forms in a population.

bar graph A graph in which the independent variable represents groups or nonnumerical categories and the values of the dependent variable(s) are shown by bars.

bark All tissues external to the vascular cambium, consisting mainly of the secondary phloem and layers of periderm.

Barr body A dense object lying along the inside of the nuclear envelope in cells of female mammals, representing a highly condensed, inactivated X chromosome.

basal angiosperm A member of one of three clades of early-diverging lineages of extant flowering plants. Examples are *Amborella*, water lilies, and star anise and its relatives.

basal body (bā′-sul) A eukaryotic cell structure consisting of a "9 + 0" arrangement of microtubule triplets. The basal body may organize the microtubule assembly of a cilium or flagellum and is structurally very similar to a centriole.

basal metabolic rate (BMR) The metabolic rate of a resting, fasting, and nonstressed endotherm at a comfortable temperature.

basal taxon In a specified group of organisms, a taxon whose evolutionary lineage diverged early in the history of the group.

base A substance that reduces the hydrogen ion concentration of a solution.

basidiocarp Elaborate fruiting body of a dikaryotic mycelium of a club fungus.

basidiomycete (buh-sid′-ē-ō-mī′-sēt) A member of the fungal phylum Basidiomycota, commonly called club fungus. The name comes from the club-like shape of the basidium.

basidium (plural, **basidia**) (buh-sid′-ē-um, buh-sid′-ē-ah) A reproductive appendage that produces sexual spores on the gills of mushrooms (club fungi).

Batesian mimicry (bāt′-zē-un mim′-uh-krē) A type of mimicry in which a harmless species resembles an unpalatable or harmful species to which it is not closely related.

behavior Individually, an action carried out by muscles or glands under control of the nervous system in response to a stimulus; collectively, the sum of an animal's responses to external and internal stimuli.

behavioral ecology The study of the evolution of and ecological basis for animal behavior.

benign tumor A mass of abnormal cells with specific genetic and cellular changes such that the cells are not capable of surviving at a new site and generally remain at the site of the tumor's origin.

benthic zone The bottom surface of an aquatic environment.

benthos (ben′-thōz) The communities of organisms living in the benthic zone of an aquatic biome.

beta (β) pleated sheet One form of the secondary structure of proteins in which the polypeptide chain folds back and forth. Two regions of the chain lie parallel to each other and are held together by hydrogen bonds between atoms of the polypeptide backbone (not the side chains).

beta oxidation A metabolic sequence that breaks fatty acids down to two-carbon fragments that enter the citric acid cycle as acetyl CoA.

bicoid A maternal effect gene that codes for a protein responsible for specifying the anterior end in *Drosophila melanogaster*.

bilateral symmetry Body symmetry in which a central longitudinal plane divides the body into two equal but opposite halves.

bilaterian (bī′-luh-ter′-ē-uhn) A member of a clade of animals with bilateral symmetry and three germ layers.

bile A mixture of substances that is produced in the liver and stored in the gallbladder; enables formation of fat droplets in water as an aid in the digestion and absorption of fats.

binary fission A method of asexual reproduction in single-celled organisms in which the cell grows to roughly double its size and then divides into two cells. In prokaryotes, binary fission does not involve mitosis, but in single-celled eukaryotes that undergo binary fission, mitosis is part of the process.

binomial A common term for the two-part, latinized format for naming a species, consisting of the genus and specific epithet; also called a binomen.

biodiversity hot spot A relatively small area with numerous endemic species and a large number of endangered and threatened species.

bioenergetics (1) The overall flow and transformation of energy in an organism. (2) The study of how energy flows through organisms.

biofilm A surface-coating colony of one or more species of prokaryotes that engage in metabolic cooperation.

biofuel A fuel produced from biomass.

biogeochemical cycle Any of the various chemical cycles, which involve both biotic and abiotic components of ecosystems.

biogeography The scientific study of the past and present geographic distributions of species.

bioinformatics The use of computers, software, and mathematical models to process and integrate biological information from large data sets.

biological augmentation An approach to restoration ecology that uses organisms to add essential materials to a degraded ecosystem.

biological clock An internal timekeeper that controls an organism's biological rhythms. The biological clock marks time with or without environmental cues but often requires signals from the environment to remain tuned to an appropriate period. *See also* circadian rhythm.

biological magnification A process in which retained substances become more concentrated at each higher trophic level in a food chain.

biological species concept Definition of a species as a group of populations whose members have the potential to interbreed in nature and produce viable, fertile offspring but do not produce viable, fertile offspring with members of other such groups.

biology The scientific study of life.

biomanipulation An approach that applies the top-down model of community organization to alter ecosystem characteristics. For example, ecologists can prevent algal blooms and eutrophication by altering the density of higher-level consumers in lakes instead of by using chemical treatments.

biomass The total mass of organic matter comprising a group of organisms in a particular habitat.

biome (bī′-ōm) Any of the world's major ecosystem types, often classified according to the predominant vegetation for terrestrial biomes and the physical environment for aquatic biomes and characterized by adaptations of organisms to that particular environment.

bioremediation The use of organisms to detoxify and restore polluted and degraded ecosystems.

biosphere The entire portion of Earth inhabited by life; the sum of all the planet's ecosystems.

biotechnology The manipulation of organisms or their components to produce useful products.

biotic (bī-ot′-ik) Pertaining to the living factors—the organisms—in an environment.

bipolar disorder A depressive mental illness characterized by swings of mood from high to low; also called manic-depressive disorder.

birth control pill A hormonal contraceptive that inhibits ovulation, retards follicular development, or alters a woman's cervical mucus to prevent sperm from entering the uterus.

blade (1) A leaflike structure of a seaweed that provides most of the surface area for photosynthesis. (2) The flattened portion of a typical leaf.

blastocoel (blas′-tuh-sēl) The fluid-filled cavity that forms in the center of a blastula.

blastocyst (blas′-tuh-sist) The blastula stage of mammalian embryonic development, consisting of an inner cell mass, a cavity, and an outer layer, the trophoblast. In humans, the blastocyst forms 1 week after fertilization.

blastomere An early embryonic cell arising during the cleavage stage of an early embryo.

blastopore (blas′-tō-pōr) In a gastrula, the opening of the archenteron that typically develops into the anus in deuterostomes and the mouth in protostomes.

blastula (blas′-tyū-luh) A hollow ball of cells that marks the end of the cleavage stage during early embryonic development in animals.

blood A connective tissue with a fluid matrix called plasma in which red blood cells, white blood cells, and cell fragments called platelets are suspended.

blue-light photoreceptor A type of light receptor in plants that initiates a variety of responses, such as phototropism and slowing of hypocotyl elongation.

body cavity A fluid- or air-filled space between the digestive tract and the body wall.

body plan In multicellular eukaryotes, a set of morphological and developmental traits that are integrated into a functional whole—the living organism.

Bohr shift A lowering of the affinity of hemoglobin for oxygen, caused by a drop in pH. It facilitates the release of oxygen from hemoglobin in the vicinity of active tissues.

bolus A lubricated ball of chewed food.

bone A connective tissue consisting of living cells held in a rigid matrix of collagen fibers embedded in calcium salts.

book lung An organ of gas exchange in spiders, consisting of stacked plates contained in an internal chamber.

bottleneck effect Genetic drift that occurs when the size of a population is reduced, as by a natural disaster or human actions. Typically, the surviving population is no longer genetically representative of the original population.

bottom-up model A model of community organization in which mineral nutrients influence community organization by controlling plant or phytoplankton numbers, which in turn control herbivore numbers, which in turn control predator numbers.

Bowman's capsule (bō′-munz) A cup-shaped receptacle in the vertebrate kidney that is the initial, expanded segment of the nephron, where filtrate enters from the blood.

brachiopod (bra′-kē-uh-pod′) A marine lophophorate with a shell divided into dorsal and ventral halves; also called lamp shells.

brain Organ of the central nervous system where information is processed and integrated.

brainstem A collection of structures in the vertebrate brain, including the midbrain, the pons, and the medulla oblongata; functions in homeostasis, coordination of movement, and conduction of information to higher brain centers.

branch point The representation on a phylogenetic tree of the divergence of two or more taxa from a common ancestor. A branch point is usually shown as a dichotomy in which a branch representing the ancestral lineage splits (at the branch point) into two branches, one for each of the two descendant lineages.

brassinosteroid A steroid hormone in plants that has a variety of effects, including inducing cell elongation, retarding leaf abscission, and promoting xylem differentiation.

breathing Ventilation of the lungs through alternating inhalation and exhalation.

bronchiole (brong′-kē-ōl′) A fine branch of the bronchi that transports air to alveoli.

bronchus (brong′-kus) (plural, **bronchi**) One of a pair of breathing tubes that branch from the trachea into the lungs.

brown alga A multicellular, photosynthetic protist with a characteristic brown or olive color that results from carotenoids in its plastids. Most brown algae are marine, and some have a plantlike body.

bryophyte (brī′-uh-fīt) An informal name for a moss, liverwort, or hornwort; a nonvascular plant that lives on land but lacks some of the terrestrial adaptations of vascular plants.

buffer A solution that contains a weak acid and its corresponding base. A buffer minimizes changes in pH when acids or bases are added to the solution.

bulk feeder An animal that eats relatively large pieces of food.

bulk flow The movement of a fluid due to a difference in pressure between two locations.

bundle-sheath cell In C_4 plants, a type of photosynthetic cell arranged into tightly packed sheaths around the veins of a leaf.

C_3 plant A plant that uses the Calvin cycle for the initial steps that incorporate CO_2 into organic material, forming a three-carbon compound as the first stable intermediate.

C_4 plant A plant in which the Calvin cycle is preceded by reactions that incorporate CO_2 into a four-carbon compound, the end product of which supplies CO_2 for the Calvin cycle.

calcitonin (kal′-si-tō′-nin) A hormone secreted by the thyroid gland that lowers blood calcium levels by promoting calcium deposition in bone and calcium excretion from the kidneys; nonessential in adult humans.

callus A mass of dividing, undifferentiated cells growing at the site of a wound or in culture.

calorie (cal) The amount of heat energy required to raise the temperature of 1 g of water by 1°C; also the amount of heat energy that 1 g of water releases when it cools by 1°C. The Calorie (with a capital C), usually used to indicate the energy content of food, is a kilocalorie.

Calvin cycle The second of two major stages in photosynthesis (following the light reactions), involving fixation of atmospheric CO_2 and reduction of the fixed carbon into carbohydrate.

Cambrian explosion A relatively brief time in geologic history when many present-day phyla of animals first appeared in the fossil record. This burst of evolutionary change occurred about 535–525 million years ago and saw the emergence of the first large, hard-bodied animals.

CAM plant A plant that uses crassulacean acid metabolism, an adaptation for photosynthesis in arid conditions. In this process, CO_2 entering open stomata during the night is converted to organic acids, which release CO_2 for the Calvin cycle during the day, when stomata are closed.

canopy The uppermost layer of vegetation in a terrestrial biome.

capillary (kap′-il-ār′-ē) A microscopic blood vessel that penetrates the tissues and consists of a single layer of endothelial cells that allows exchange between the blood and interstitial fluid.

capillary bed (kap′-il-ār′-ē) A network of capillaries in a tissue or organ.

capsid The protein shell that encloses a viral genome. It may be rod-shaped, polyhedral, or more complex in shape.

capsule (1) In many prokaryotes, a dense and well-defined layer of polysaccharide or protein that surrounds the cell wall and is sticky, protecting the cell and enabling it to adhere to substrates or other cells. (2) The sporangium of a bryophyte (moss, liverwort, or hornwort).

carbohydrate (kar′-bō-hī′-drāt) A sugar (monosaccharide) or one of its dimers (disaccharides) or polymers (polysaccharides).

carbon fixation The initial incorporation of carbon from CO_2 into an organic compound by an autotrophic organism (a plant, another photosynthetic organism, or a chemoautotrophic prokaryote).

carbonyl group (kar′-buh-nil) A chemical group present in aldehydes and ketones and consisting of a carbon atom double-bonded to an oxygen atom.

carboxyl group (kar-bok′-sil) A chemical group present in organic acids and consisting of a single carbon atom double-bonded to an oxygen atom and also bonded to a hydroxyl group.

cardiac cycle (kar′-dē-ak) The alternating contractions and relaxations of the heart.

cardiac muscle (kar′-dē-ak) A type of striated muscle that forms the contractile wall of the heart. Its cells are joined by intercalated disks that relay the electrical signals underlying each heartbeat.

cardiac output (kar′-dē-ak) The volume of blood pumped per minute by each ventricle of the heart.

cardiovascular system A closed circulatory system with a heart and branching network of arteries, capillaries, and veins. The system is characteristic of vertebrates.

carnivore An animal that mainly eats other animals.

carotenoid (kuh-rot′-uh-noyd′) An accessory pigment, either yellow or orange, in the chloroplasts of plants and in some prokaryotes. By absorbing wavelengths of light that chlorophyll cannot, carotenoids broaden the spectrum of colors that can drive photosynthesis.

carpel (kar′-pul) The ovule-producing reproductive organ of a flower, consisting of the stigma, style, and ovary.

carrier In genetics, an individual who is heterozygous at a given genetic locus for a recessively inherited disorder. The heterozygote is generally phenotypically normal for the disorder but can pass on the recessive allele to offspring.

carrying capacity The maximum population size that can be supported by the available resources, symbolized as *K*.

cartilage (kar′-til-ij) A flexible connective tissue with an abundance of collagenous fibers embedded in chondroitin sulfate.

Casparian strip (ka-spār′-ē-un) A water-impermeable ring of wax in the endodermal cells of plants that blocks the passive flow of water and solutes into the stele by way of cell walls.

catabolic pathway (kat′-uh-bol′-ik) A metabolic pathway that releases energy by breaking down complex molecules to simpler molecules.

catalysis (kuh-ta′-luh-sis) A process by which a chemical agent called a catalyst selectively increases the rate of a reaction without being consumed by the reaction.

catalyst (kat′-uh-list) A chemical agent that selectively increases the rate of a reaction without being consumed by the reaction.

cation (cat′-ī′-on) A positively charged ion.

cation exchange (cat′-ī′-on) A process in which positively charged minerals are made available to a plant when hydrogen ions in the soil displace mineral ions from the clay particles.

cecum (sē′-kum) (plural, **ceca**) The blind pouch forming one branch of the large intestine.

cell Life's fundamental unit of structure and function; the smallest unit of organization that can perform all activities required for life.

cell body The part of a neuron that houses the nucleus and most other organelles.

cell cycle An ordered sequence of events in the life of a cell, from its origin in the division of a parent cell until its own division into two. The eukaryotic cell cycle is composed of interphase (including G_1, S, and G_2 phases) and M phase (including mitosis and cytokinesis).

cell cycle control system A cyclically operating set of molecules in the eukaryotic cell that both triggers and coordinates key events in the cell cycle.

cell division The reproduction of cells.

cell fractionation The disruption of a cell and separation of its parts by centrifugation at successively higher speeds.

cell-mediated immune response The branch of adaptive immunity that involves the activation of cytotoxic T cells, which defend against infected cells.

cell plate A membrane-bounded, flattened sac located at the midline of a dividing plant cell, inside which the new cell wall forms during cytokinesis.

cellular respiration The catabolic pathways of aerobic and anaerobic respiration, which break down organic molecules and use an electron transport chain for the production of ATP.

cellulose (sel′-yū-lōs) A structural polysaccharide of plant cell walls, consisting of glucose monomers joined by β glycosidic linkages.

cell wall A protective layer external to the plasma membrane in the cells of plants, prokaryotes, fungi, and some protists. Polysaccharides such as cellulose (in plants and some protists), chitin (in fungi), and peptidoglycan (in bacteria) are important structural components of cell walls.

central nervous system (CNS) The portion of the nervous system where signal integration occurs; in vertebrate animals, the brain and spinal cord.

central vacuole In a mature plant cell, a large membranous sac with diverse roles in growth, storage, and sequestration of toxic substances.

centriole (sen′-trē-ōl) A structure in the centrosome of an animal cell composed of a cylinder of microtubule triplets arranged in a "9 + 0" pattern. A centrosome has a pair of centrioles.

centromere (sen′-trō-mēr) In a duplicated chromosome, the region on each sister chromatid where it is most closely attached to its sister chromatid by proteins that bind to the centromeric DNA. Other proteins condense the chromatin in that region, so it appears as a narrow "waist" on the duplicated chromosome. (An unduplicated chromosome has a single centromere, identified by the proteins bound there.)

centrosome (sen′-trō-sōm) A structure present in the cytoplasm of animal cells that functions as a microtubule-organizing center and is important during cell division. A centrosome has two centrioles.

cercozoan An amoeboid or flagellated protist that feeds with threadlike pseudopodia.

cerebellum (sār′-ruh-bel′-um) Part of the vertebrate hindbrain located dorsally; functions in unconscious coordination of movement and balance.

cerebral cortex (suh-rē′-brul) The surface of the cerebrum; the largest and most complex part of the mammalian brain, containing nerve cell bodies of the cerebrum; the part of the vertebrate brain most changed through evolution.

cerebrum (suh-rē′-brum) The dorsal portion of the vertebrate forebrain, composed of right and left hemispheres; the integrating center for memory, learning, emotions, and other highly complex functions of the central nervous system.

cervix (ser′-viks) The neck of the uterus, which opens into the vagina.

chaparral A scrubland biome of dense, spiny evergreen shrubs found at midlatitudes along coasts where cold ocean currents circulate offshore; characterized by mild, rainy winters and long, hot, dry summers.

chaperonin (shap′-er-ō′-nin) A protein complex that assists in the proper folding of other proteins.

character An observable heritable feature that may vary among individuals.

character displacement The tendency for characteristics to be more divergent in sympatric populations of two species than in allopatric populations of the same two species.

checkpoint A control point in the cell cycle where stop and go-ahead signals can regulate the cycle.

chelicera (kē-lih′-suh-ruh) (plural, **chelicerae**) One of a pair of clawlike feeding appendages characteristic of chelicerates.

chelicerate (kē-lih-suh′-rāte) An arthropod that has chelicerae and a body divided into a cephalothorax and an abdomen. Living chelicerates include sea spiders, horseshoe crabs, scorpions, ticks, and spiders.

chemical bond An attraction between two atoms, resulting from a sharing of outer-shell electrons or the presence of opposite charges on the atoms. The bonded atoms gain complete outer electron shells.

chemical energy Energy available in molecules for release in a chemical reaction; a form of potential energy.

chemical equilibrium In a chemical reaction, the state in which the rate of the forward reaction equals the rate of the reverse reaction, so that the relative concentrations of the reactants and products do not change with time.

chemical reaction The making and breaking of chemical bonds, leading to changes in the composition of matter.

chemiosmosis (kem′-ē-oz-mō′-sis) An energy-coupling mechanism that uses energy stored in the form of a hydrogen ion gradient across a membrane to drive cellular work, such as the synthesis of ATP. Under aerobic conditions, most ATP synthesis in cells occurs by chemiosmosis.

chemoautotroph (kē′-mō-ot′-ō-trōf) An organism that obtains energy by oxidizing inorganic substances and needs only carbon dioxide as a carbon source.

chemoheterotroph (kē′-mō-het′-er-ō-trōf) An organism that requires organic molecules for both energy and carbon.

chemoreceptor A sensory receptor that responds to a chemical stimulus, such as a solute or an odorant.

chiasma (plural, **chiasmata**) (kī-az′-muh, kī-az′-muh-tuh) The X-shaped, microscopically visible region where crossing over has occurred earlier in prophase I between homologous nonsister chromatids. Chiasmata become visible after synapsis ends, with the two homologs remaining associated due to sister chromatid cohesion.

chitin (kī′-tin) A structural polysaccharide, consisting of amino sugar monomers, found in many fungal cell walls and in the exoskeletons of all arthropods.

chlorophyll (klōr′-ō-fil) A green pigment located in membranes within the chloroplasts of plants and algae and in the membranes of certain prokaryotes. Chlorophyll *a* participates directly in the light reactions, which convert solar energy to chemical energy.

chlorophyll *a* (klōr′-ō-fil) A photosynthetic pigment that participates directly in the light reactions, which convert solar energy to chemical energy.

chlorophyll *b* (klōr′-ō-fil) An accessory photosynthetic pigment that transfers energy to chlorophyll *a*.

chloroplast (klōr′-ō-plast) An organelle found in plants and photosynthetic protists that absorbs sunlight and uses it to drive the synthesis of organic compounds from carbon dioxide and water.

choanocyte (kō-an′-uh-sīt) A flagellated feeding cell found in sponges. Also called a collar cell, it has a collar-like ring that traps food particles around the base of its flagellum.

cholesterol (kō-les′-tuh-rol) A steroid that forms an essential component of animal cell membranes and acts as a precursor molecule for the synthesis of other biologically important steroids, such as many hormones.

chondrichthyan (kon-drik′-thē-an) A member of the clade Chondrichthyes, vertebrates with skeletons made mostly of cartilage, such as sharks and rays.

chordate A member of the phylum Chordata, animals that at some point during their development have a notochord; a dorsal, hollow nerve cord; pharyngeal slits or clefts; and a muscular, post-anal tail.

chorionic villus sampling (CVS) (kōr′-ē-on′-ik vil′-us) A technique associated with prenatal diagnosis in which a small sample of the fetal portion of the placenta is removed for analysis to detect certain genetic and congenital defects in the fetus.

chromatin (krō′-muh-tin) The complex of DNA and proteins that makes up eukaryotic chromosomes. When the cell is not dividing, chromatin exists in its dispersed form, as a mass of very long, thin fibers that are not visible with a light microscope.

chromosome (krō′-muh-sōm) A cellular structure consisting of one DNA molecule and associated protein molecules. (In some contexts, such as genome sequencing, the term may refer to the DNA alone.) A eukaryotic cell typically has multiple, linear chromosomes, which are located in the nucleus. A prokaryotic cell often has a single, circular chromosome, which is found in the nucleoid, a region that is not enclosed by a membrane. *See also* chromatin.

chromosome theory of inheritance (krō′-muh-sōm) A basic principle in biology stating that genes are located at specific positions (loci) on chromosomes and that the behavior of chromosomes during meiosis accounts for inheritance patterns.

chylomicron (kī′-lō-mī′-kron) A lipid transport globule composed of fats mixed with cholesterol and coated with proteins.

chyme (kīm) The mixture of partially digested food and digestive juices formed in the stomach.

chytrid (kī′-trid) A member of the fungal phylum Chytridiomycota, mostly aquatic fungi with flagellated zoospores that represent an early-diverging fungal lineage.

ciliate (sil′-ē-it) A type of protist that moves by means of cilia.

cilium (sil′-ē-um) (plural, **cilia**) A short appendage containing microtubules in eukaryotic cells. A motile cilium is specialized for locomotion or moving fluid past the cell; it is formed from a core of nine outer doublet microtubules and two inner single microtubules (the "9 + 2" arrangement) ensheathed in an extension of the plasma membrane. A primary cilium is usually nonmotile and plays a sensory and signaling role; it lacks the two inner microtubules (the "9 + 0" arrangement).

circadian rhythm (ser-kā′-dē-un) A physiological cycle of about 24 hours that persists even in the absence of external cues.

***cis-trans* isomer** One of several compounds that have the same molecular formula and covalent bonds between atoms but differ in the spatial arrangements of their atoms owing to the inflexibility of double bonds; formerly called a geometric isomer.

citric acid cycle A chemical cycle involving eight steps that completes the metabolic breakdown of glucose molecules begun in glycolysis by oxidizing acetyl CoA (derived from pyruvate) to carbon dioxide; occurs within the mitochondrion in eukaryotic cells and in the cytosol of prokaryotes; together with pyruvate oxidation, the second major stage in cellular respiration.

clade (klād) A group of species that includes an ancestral species and all of its descendants. A clade is equivalent to a monophyletic group.

cladistics (kluh-dis′-tiks) An approach to systematics in which organisms are placed into groups called clades based primarily on common descent.

class In Linnaean classification, the taxonomic category above the level of order.

cleavage (1) The process of cytokinesis in animal cells, characterized by pinching of the plasma membrane. (2) The succession of rapid cell divisions without significant growth during early embryonic development that converts the zygote to a ball of cells.

cleavage furrow The first sign of cleavage in an animal cell; a shallow groove around the cell in the cell surface near the old metaphase plate.

climate The long-term prevailing weather conditions at a given place.

climate change A directional change in temperature, precipitation, or other aspect of the global climate that lasts for three decades or more.

climograph A plot of the temperature and precipitation in a particular region.

clitoris (klit′-uh-ris) An organ at the upper intersection of the labia minora that engorges with blood and becomes erect during sexual arousal.

cloaca (klō-ā′-kuh) A common opening for the digestive, urinary, and reproductive tracts found in many nonmammalian vertebrates but in few mammals.

clonal selection The process by which an antigen selectively binds to and activates only those lymphocytes bearing receptors specific for the antigen. The selected lymphocytes proliferate and differentiate into a clone of effector cells and a clone of memory cells specific for the stimulating antigen.

clone (1) A lineage of genetically identical individuals or cells. (2) In popular usage, an individual that is genetically identical to another individual. (3) As a verb, to make one or more genetic replicas of an individual or cell. *See also* gene cloning.

cloning vector In genetic engineering, a DNA molecule that can carry foreign DNA into a host cell and replicate there. Cloning vectors include plasmids and bacterial artificial chromosomes (BACs), which move recombinant DNA from a test tube back into a cell, and viruses that transfer recombinant DNA by infection.

closed circulatory system A circulatory system in which blood is confined to vessels and is kept separate from the interstitial fluid.

cnidocyte (nī′-duh-sīt) A specialized cell unique to the phylum Cnidaria; contains a capsule-like organelle housing a coiled thread that, when discharged, explodes outward and functions in prey capture or defense.

cochlea (kok′-lē-uh) The complex, coiled organ of hearing that contains the organ of Corti.

coding strand Nontemplate strand of DNA, which has the same sequence as the mRNA except it has thymine (T) instead of uracil (U).

codominance The situation in which the phenotypes of both alleles are exhibited in the heterozygote because both alleles affect the phenotype in separate, distinguishable ways.

codon (kō′-don) A three-nucleotide sequence of DNA or mRNA that specifies a particular amino acid or termination signal; the basic unit of the genetic code.

coefficient of relatedness The fraction of genes that, on average, are shared by two individuals.

coelom (sē′-lōm) A body cavity lined by tissue derived only from mesoderm.

coelomate (sē′-lō-māt) An animal that possesses a true coelom (a body cavity lined by tissue completely derived from mesoderm).

coenocytic fungus (sē′-no-si′-tic) A fungus that lacks septa and hence whose body is made up of a continuous cytoplasmic mass that may contain hundreds or thousands of nuclei.

coenzyme (kō-en′-zīm) An organic molecule serving as a cofactor. Most vitamins function as coenzymes in metabolic reactions.

coevolution The joint evolution of two interacting species, each in response to selection imposed by the other.

cofactor Any nonprotein molecule or ion that is required for the proper functioning of an enzyme. Cofactors can be permanently bound to the active site or may bind loosely and reversibly, along with the substrate, during catalysis.

cognition The process of knowing that may include awareness, reasoning, recollection, and judgment.

cognitive map A neural representation of the abstract spatial relationships between objects in an animal's surroundings.

cohesion The linking together of like molecules, often by hydrogen bonds.

cohesion-tension hypothesis The leading explanation of the ascent of xylem sap. It states that transpiration exerts pull on xylem sap, putting the sap under negative pressure, or tension, and that the cohesion of water molecules transmits this pull along the entire length of the xylem from shoots to roots.

cohort A group of individuals of the same age in a population.

coleoptile (kō′-lē-op′-tul) The covering of the young shoot of the embryo of a grass seed.

coleorhiza (kō′-lē-uh-rī′-zuh) The covering of the young root of the embryo of a grass seed.

collagen A glycoprotein in the extracellular matrix of animal cells that forms strong fibers, found extensively in connective tissue and bone; the most abundant protein in the animal kingdom.

collecting duct The location in the kidney where processed filtrate, called urine, is collected from the renal tubules.

collenchyma cell (kō-len′-kim-uh) A flexible plant cell type that occurs in strands or cylinders that support young parts of the plant without restraining growth.

colon (kō′-len) The largest section of the vertebrate large intestine; functions in water absorption and formation of feces.

commensalism (kuh-men′-suh-lizm) A $+/0$ ecological interaction in which one organism benefits but the other is neither helped nor harmed.

communication In animal behavior, a process involving transmission of, reception of, and response to signals. The term is also used in connection with other organisms, as well as individual cells of multicellular organisms.

community All the organisms that inhabit a particular area; an assemblage of populations of different species living close enough together for potential interaction.

community ecology The study of how interactions between species affect community structure and organization.

companion cell A type of plant cell that is connected to a sieve-tube element by many plasmodesmata and whose nucleus and ribosomes may serve one or more adjacent sieve-tube elements.

competition A −/− interaction that occurs when individuals of different species compete for a resource that limits the survival and reproduction of each species.

competitive exclusion The concept that when populations of two similar species compete for the same limited resources, one population will use the resources more efficiently and have a reproductive advantage that will eventually lead to the elimination of the other population.

competitive inhibitor A substance that reduces the activity of an enzyme by entering the active site in place of the substrate, whose structure it mimics.

complement system A group of about 30 blood proteins that may amplify the inflammatory response, enhance phagocytosis, or directly lyse extracellular pathogens.

complementary DNA (cDNA) A double-stranded DNA molecule made *in vitro* using mRNA as a template and the enzymes reverse transcriptase and DNA polymerase. A cDNA molecule corresponds to the exons of a gene.

complete dominance The situation in which the phenotypes of the heterozygote and dominant homozygote are indistinguishable.

complete flower A flower that has all four basic floral organs: sepals, petals, stamens, and carpels.

complete metamorphosis The transformation of a larva into an adult that looks very different, and often functions very differently in its environment, than the larva.

compound A substance consisting of two or more different elements combined in a fixed ratio.

compound eye A type of multifaceted eye in insects and crustaceans consisting of up to several thousand light-detecting, focusing ommatidia.

concentration gradient A region along which the density of a chemical substance increases or decreases.

conception The fertilization of an egg by a sperm in humans.

cone A cone-shaped cell in the retina of the vertebrate eye, sensitive to color.

conformer An animal for which an internal condition conforms to (changes in accordance with) changes in an environmental variable.

conidium (plural, **conidia**) A haploid spore produced at the tip of a specialized hypha in ascomycetes during asexual reproduction.

conifer A member of the largest gymnosperm phylum. Most conifers are cone-bearing trees, such as pines and firs.

conjugation (kon′-jū-gā′-shun) (1) In prokaryotes, the direct transfer of DNA between two cells that are temporarily joined. When the two cells are members of different species, conjugation results in horizontal gene transfer. (2) In ciliates, a sexual process in which two cells exchange haploid micronuclei but do not reproduce.

connective tissue Animal tissue that functions mainly to bind and support other tissues, having a sparse population of cells scattered through an extracellular matrix.

conodont An early, soft-bodied vertebrate with prominent eyes and dental elements.

conservation biology The integrated study of ecology, evolutionary biology, physiology, molecular biology, and genetics to sustain biological diversity at all levels.

consumer An organism that feeds on producers, other consumers, or nonliving organic material.

contraception The deliberate prevention of pregnancy.

contractile vacuole A membranous sac that helps move excess water out of certain freshwater protists.

control element A segment of noncoding DNA that helps regulate transcription of a gene by serving as a binding site for a transcription factor. Multiple control elements are present in a eukaryotic gene's enhancer.

control group In a controlled experiment, a set of subjects that lacks (or does not receive) the specific factor being tested. Ideally, the control group should be identical to the experimental group in other respects.

controlled experiment An experiment designed to compare an experimental group with a control group; ideally, the two groups differ only in the factor being tested.

convergent evolution The evolution of similar features in independent evolutionary lineages.

convergent extension A process in which the cells of a tissue layer rearrange themselves in such a way that the sheet of cells becomes narrower (converges) and longer (extends).

cooperativity A kind of allosteric regulation whereby a shape change in one subunit of a protein caused by substrate binding is transmitted to all the other subunits, facilitating binding of additional substrate molecules to those subunits.

coral reef Typically a warm-water, tropical ecosystem dominated by the hard skeletal structures secreted primarily by corals. Some coral reefs also exist in cold, deep waters.

corepressor A small molecule that binds to a bacterial repressor protein and changes the protein's shape, allowing it to bind to the operator and switch an operon off.

cork cambium (kam′-bē-um) A cylinder of meristematic tissue in woody plants that replaces the epidermis with thicker, tougher cork cells.

corpus callosum (kor′-pus kuh-lō′-sum) The thick band of nerve fibers that connects the right and left cerebral hemispheres in mammals, enabling the hemispheres to process information together.

corpus luteum (kor′-pus lū′-tē-um) A secreting tissue in the ovary that forms from the collapsed follicle after ovulation and produces progesterone.

cortex (1) The outer region of cytoplasm in a eukaryotic cell, lying just under the plasma membrane, that has a more gel-like consistency than the inner regions due to the presence of multiple microfilaments. (2) In plants, ground tissue that is between the vascular tissue and dermal tissue in a root or eudicot stem.

cortical nephron In mammals and birds, a nephron with a loop of Henle located almost entirely in the renal cortex.

cotransport The coupling of the "downhill" diffusion of one substance to the "uphill" transport of another against its own concentration gradient.

cotyledon (kot′-uh-lē′-dun) A seed leaf of an angiosperm embryo. Some species have one cotyledon, others two.

countercurrent exchange The exchange of a substance or heat between two fluids flowing in opposite directions. For example, blood in a fish gill flows in the opposite direction of water passing over the gill, maximizing diffusion of oxygen into and carbon dioxide out of the blood.

countercurrent multiplier system A countercurrent system in which energy is expended in active transport to facilitate exchange of materials and generate concentration gradients.

covalent bond (kō-vā′-lent) A type of strong chemical bond in which two atoms share one or more pairs of valence electrons.

crassulacean acid metabolism (CAM) (crass-yū-lā′-shen) An adaptation for photosynthesis in arid conditions, first discovered in the family Crassulaceae. In this process, a plant takes up CO_2 and incorporates it into a variety of organic acids at night; during the day, CO_2 is released from organic acids for use in the Calvin cycle.

CRISPR-Cas9 system A technique for editing genes in living cells, involving a bacterial protein called Cas9 associated with a guide RNA complementary to a gene sequence of interest.

crista (plural, **cristae**) (kris′-tuh, kris′-tē) An infolding of the inner membrane of a mitochondrion. The inner membrane houses electron transport chains and molecules of the enzyme catalyzing the synthesis of ATP (ATP synthase).

critical load The amount of added nutrient, usually nitrogen or phosphorus, that can be absorbed by plants without damaging ecosystem integrity.

crop rotation The practice of growing different crops in succession on the same land chiefly to preserve the productive capacity of the soil.

cross-fostering study A behavioral study in which the young of one species are placed in the care of adults from another species.

crossing over The reciprocal exchange of genetic material between nonsister chromatids during prophase I of meiosis.

cross-pollination In angiosperms, the transfer of pollen from an anther of a flower on one plant to the stigma of a flower on another plant of the same species.

cryptic coloration Camouflage that makes a potential prey difficult to spot against its background.

culture A system of information transfer through social learning or teaching that influences the behavior of individuals in a population.

cuticle (kyū′-tuh-kul) (1) A waxy covering on the surface of stems and leaves that prevents desiccation in terrestrial plants. (2) A tough coat that covers the body of a nematode.

cyclic AMP (cAMP) Cyclic adenosine monophosphate, a ring-shaped molecule made from ATP that is a common intracellular signaling molecule (second messenger) in eukaryotic cells. It is also a regulator of some bacterial operons.

cyclic electron flow A route of electron flow during the light reactions of photosynthesis that involves only one photosystem and that produces ATP but not NADPH or O_2.

cyclin (sī′-klin) A cellular protein that occurs in a cyclically fluctuating concentration and that plays an important role in regulating the cell cycle.

cyclin-dependent kinase (Cdk) (sī′-klin) A protein kinase that is active only when attached to a particular cyclin.

cyclostome (sī′-cluh-stōm) Member of one of the two main clades of vertebrates; cyclostomes lack jaws and include lampreys and hagfishes. *See also* gnathostome.

cystic fibrosis (sis′-tik fī-brō′-sis) A human genetic disorder caused by a recessive allele for a chloride channel protein; characterized by an excessive secretion of mucus and consequent vulnerability to infection; fatal if untreated.

cytochrome (sī′-tō-krōm) An iron-containing protein that is a component of electron transport chains in the mitochondria and chloroplasts of eukaryotic cells and the plasma membranes of prokaryotic cells.

cytokinesis (sī′-tō-kuh-nē′-sis) The division of the cytoplasm to form two separate daughter cells immediately after mitosis, meiosis I, or meiosis II.

cytokinin (sī′-tō-kī′-nin) Any of a class of related plant hormones that retard aging and act in concert with auxin to stimulate cell division, influence the pathway of differentiation, and control apical dominance.

cytoplasm (sī′-tō-plaz-um) The contents of the cell bounded by the plasma membrane; in eukaryotes, the portion exclusive of the nucleus.

cytoplasmic determinant A maternal substance, such as a protein or RNA, that when placed into an egg influences the course of early development by regulating the expression of genes that affect the developmental fate of cells.

cytoplasmic streaming A circular flow of cytoplasm, involving interactions of myosin and actin filaments, that speeds the distribution of materials within cells.

cytoskeleton A network of microtubules, microfilaments, and intermediate filaments that extend throughout the cytoplasm and serve a variety of mechanical, transport, and signaling functions.

cytosol (sī′-tō-sol) The semifluid portion of the cytoplasm.

cytotoxic T cell A type of lymphocyte that, when activated, kills infected cells as well as certain cancer cells and transplanted cells.

dalton A measure of mass for atoms and subatomic particles; the same as the atomic mass unit, or amu.

data Recorded observations.

day-neutral plant A plant in which flower formation is not controlled by photoperiod or day length.

decomposer An organism that absorbs nutrients from nonliving organic material such as corpses, fallen plant material, and the wastes of living organisms and converts them to inorganic forms; a detritivore.

deductive reasoning A type of logic in which specific results are predicted from a general premise.

de-etiolation The changes a plant shoot undergoes in response to sunlight; also known informally as greening.

dehydration reaction A chemical reaction in which two molecules become covalently bonded to each other with the removal of a water molecule.

deletion (1) A deficiency in a chromosome resulting from the loss of a fragment through breakage. (2) A mutational loss of one or more nucleotide pairs from a gene.

demographic transition In a stable population, a shift from high birth and death rates to low birth and death rates.

demography The study of changes over time in the vital statistics of populations, especially birth rates and death rates.

denaturation (dē-nā′-chur-ā′-shun) In proteins, a process in which a protein loses its native shape due to the disruption of weak chemical bonds and interactions, thereby becoming biologically inactive; in DNA, the separation of the two strands of the double helix. Denaturation occurs under extreme (noncellular) conditions of pH, salt concentration, or temperature.

dendrite (den′-drīt) One of usually numerous, short, highly branched extensions of a neuron that receive signals from other neurons.

dendritic cell An antigen-presenting cell, located mainly in lymphatic tissues and skin, that is particularly efficient in presenting antigens to helper T cells, thereby initiating a primary immune response.

density The number of individuals per unit area or volume.

density dependent Referring to any characteristic that varies with population density.

density-dependent inhibition The phenomenon observed in normal animal cells that causes them to stop dividing when they come into contact with one another.

density independent Referring to any characteristic that is not affected by population density.

deoxyribonucleic acid (DNA) (dē-ok′-sē-rī′-bō-nū-klā′-ik) A nucleic acid molecule, usually a double-stranded helix, in which each polynucleotide strand consists of nucleotide monomers with a deoxyribose sugar and the nitrogenous bases adenine (A), cytosine (C), guanine (G), and thymine (T); capable of being replicated and determining the inherited structure of a cell's proteins.

deoxyribose (dē-ok′-si-rī′-bōs) The sugar component of DNA nucleotides, having one fewer hydroxyl group than ribose, the sugar component of RNA nucleotides.

dependent variable A factor whose value is measured during an experiment or other test to see whether it is influenced by changes in another factor (the independent variable).

depolarization A change in a cell's membrane potential such that the inside of the membrane is made less negative relative to the outside. For example, a neuron membrane is depolarized if a stimulus decreases its voltage from the resting potential of $-70\,\text{mV}$ in the direction of zero voltage.

dermal tissue system The outer protective covering of plants.

desert A terrestrial biome characterized by very low precipitation.

desmosome A type of intercellular junction in animal cells that functions as a rivet, fastening cells together.

determinate cleavage A type of embryonic development in protostomes that rigidly casts the developmental fate of each embryonic cell very early.

determinate growth A type of growth characteristic of most animals and some plant organs, in which growth stops after a certain size is reached.

determination The progressive restriction of developmental potential in which the possible fate of each cell becomes more limited as an embryo develops. At the end of determination, a cell is committed to its fate.

detritivore (deh-trī′-tuh-vōr) A consumer that derives its energy and nutrients from nonliving organic material such as corpses, fallen plant material, and the wastes of living organisms; a decomposer.

detritus (di-trī′-tus) Dead organic matter.

deuteromycete (dū′-tuh-rō-mī′-sēt) Traditional classification for a fungus with no known sexual stage.

deuterostome development (dū′-tuh-rō-stōm′) In animals, a developmental mode distinguished by the development of the anus from the blastopore; often also characterized by radial cleavage and by the body cavity forming as outpockets of mesodermal tissue.

Deuterostomia (dū′-tuh-rō-stōm′-ē-uh) One of the three main lineages of bilaterian animals. *See also* Ecdysozoa and Lophotrochozoa.

development The events involved in an organism's changing gradually from a simple to a more complex or specialized form.

diabetes mellitus (dī′-uh-bē′-tis mel′-uh-tus) An endocrine disorder marked by an inability to maintain glucose homeostasis. The type 1 form results from autoimmune destruction of insulin-secreting cells; treatment usually requires daily insulin injections. The type 2 form most commonly results from reduced responsiveness of target cells to insulin; obesity and lack of exercise are risk factors.

diacylglycerol (DAG) (dī-a′-sil-glis′-er-ol) A second messenger produced by the cleavage of the phospholipid PIP_2 in the plasma membrane.

diaphragm (dī′-uh-fram′) (1) A sheet of muscle that forms the bottom wall of the thoracic cavity in mammals. Contraction of the diaphragm pulls air into the lungs. (2) A dome-shaped rubber cup fitted into the upper portion of the vagina before sexual intercourse. It serves as a physical barrier to the passage of sperm into the uterus.

diapsid (dī-ap′-sid) A member of an amniote clade distinguished by a pair of holes on each side of the skull. Diapsids include the lepidosaurs and archosaurs.

diastole (dī-as′-tō-lē) The stage of the cardiac cycle in which a heart chamber is relaxed and fills with blood.

diastolic pressure Blood pressure in the arteries when the ventricles are relaxed.

diatom Photosynthetic protist in the stramenopile clade; diatoms have a unique glass-like wall made of silicon dioxide embedded in an organic matrix.

dicot A term traditionally used to refer to flowering plants that have two embryonic seed leaves, or cotyledons. Recent molecular evidence indicates that dicots do not form a clade; species once classified as dicots are now grouped into eudicots, magnoliids, and several lineages of basal angiosperms.

differential gene expression The expression of different sets of genes by cells with the same genome.

differentiation The process by which a cell or group of cells becomes specialized in structure and function.

diffusion The random thermal motion of particles of liquids, gases, or solids. In the presence of a concentration or electrochemical gradient, diffusion results in the net movement of a substance from a region where it is more concentrated to a region where it is less concentrated.

digestion The second stage of food processing in animals: the breaking down of food into molecules small enough for the body to absorb.

dihybrid (dī′-hī′-brid) An organism that is heterozygous with respect to two genes of interest. All the offspring from a cross between parents doubly homozygous for different alleles are dihybrids. For example, parents of genotypes *AABB* and *aabb* produce a dihybrid of genotype *AaBb*.

dihybrid cross (dī′-hī′-brid) A cross between two organisms that are each heterozygous for both of the characters being followed (or the self-pollination of a plant that is heterozygous for both characters).

dikaryotic (dī′-kār-ē-ot′-ik) Referring to a fungal mycelium with two haploid nuclei per cell, one from each parent.

dinoflagellate (dī′-nō-flaj′-uh-let) A member of a group of mostly unicellular photosynthetic algae with two flagella situated in perpendicular grooves in cellulose plates covering the cell.

dinosaur A member of an extremely diverse clade of reptiles varying in body shape, size, and habitat. Birds are the only extant dinosaurs.

dioecious (dī-ē′-shus) In plant biology, having the male and female reproductive parts on different individuals of the same species.

diploblastic Having two germ layers.

diploid cell (dip′-loyd) A cell containing two sets of chromosomes (2*n*), one set inherited from each parent.

diplomonad A protist that has modified mitochondria, two equal-sized nuclei, and multiple flagella.

directional selection Natural selection in which individuals at one end of the phenotypic range survive or reproduce more successfully than do other individuals.

disaccharide (dī-sak′-uh-rīd) A double sugar, consisting of two monosaccharides joined by a glycosidic linkage formed by a dehydration reaction.

dispersal The movement of individuals or gametes away from their parent location. This movement sometimes expands the geographic range of a population or species.

dispersion The pattern of spacing among individuals within the boundaries of a population.

disruptive selection Natural selection in which individuals on both extremes of a phenotypic range survive or reproduce more successfully than do individuals with intermediate phenotypes.

distal tubule In the vertebrate kidney, the portion of a nephron that helps refine filtrate and empties it into a collecting duct.

disturbance A natural or human-caused event that changes a biological community and usually removes organisms from it. Disturbances, such as fires and storms, play a pivotal role in structuring many communities.

disulfide bridge A strong covalent bond formed when the sulfur of one cysteine monomer bonds to the sulfur of another cysteine monomer.

DNA (deoxyribonucleic acid) (dē-ok′-sē-rī′-bō-nū-klā′-ik) A nucleic acid molecule, usually a double-stranded helix, in which each polynucleotide strand consists of nucleotide monomers with a deoxyribose sugar and the nitrogenous bases adenine (A), cytosine (C), guanine (G), and thymine (T); capable of being replicated and determining the inherited structure of a cell's proteins.

DNA cloning The production of multiple copies of a specific DNA segment.

DNA ligase (lī′-gās) A linking enzyme essential for DNA replication; catalyzes the covalent bonding of the 3′ end of one DNA fragment (such as an Okazaki fragment) to the 5′ end of another DNA fragment (such as a growing DNA chain).

DNA methylation The presence of methyl groups on the DNA bases (usually cytosine) of plants, animals, and fungi. (The term also refers to the process of adding methyl groups to DNA bases.)

DNA microarray assay A method to detect and measure the expression of thousands of genes at one time. Tiny amounts of a large number of single-stranded DNA fragments representing different genes are fixed to a glass slide and tested for hybridization with samples of labeled cDNA.

DNA polymerase (puh-lim′-er-ās) An enzyme that catalyzes the elongation of new DNA (for example, at a replication fork) by the addition of nucleotides to the 3′ end of an existing chain. There are several different DNA polymerases; DNA polymerase III and DNA polymerase I play major roles in DNA replication in *E. coli*.

DNA replication The process by which a DNA molecule is copied; also called DNA synthesis.

DNA sequencing Determining the complete nucleotide sequence of a gene or DNA segment.

DNA technology Techniques for sequencing and manipulating DNA.

domain (1) A taxonomic category above the kingdom level. The three domains are Archaea, Bacteria, and Eukarya. (2) A discrete structural and functional region of a protein.

dominant allele An allele that is fully expressed in the phenotype of a heterozygote.

dominant species A species with substantially higher abundance or biomass than other species in a community. Dominant species exert a powerful control over the occurrence and distribution of other species.

dormancy A condition typified by extremely low metabolic rate and a suspension of growth and development.

dorsal Pertaining to the top of an animal with radial or bilateral symmetry.

dorsal lip The region above the blastopore on the dorsal side of the amphibian embryo.

double bond A double covalent bond; the sharing of two pairs of valence electrons by two atoms.

double circulation A circulatory system consisting of separate pulmonary and systemic circuits, in which blood passes through the heart after completing each circuit.

double fertilization A mechanism of fertilization in angiosperms in which two sperm cells unite with two cells in the female gametophyte (embryo sac) to form the zygote and endosperm.

double helix The form of native DNA, referring to its two adjacent antiparallel polynucleotide strands wound around an imaginary axis into a spiral shape.

Down syndrome A human genetic disease usually caused by the presence of an extra chromosome 21; characterized by developmental delays and heart and other defects that are generally treatable or non-life-threatening.

Duchenne muscular dystrophy (duh-shen′) A human genetic disease caused by a sex-linked recessive allele; characterized by progressive weakening and a loss of muscle tissue.

duodenum (dū′-uh-dēn′-um) The first section of the small intestine, where chyme from the stomach mixes with digestive juices from the pancreas, liver, and gallbladder as well as from gland cells of the intestinal wall.

duplication An aberration in chromosome structure due to fusion with a fragment from a homologous chromosome, such that a portion of a chromosome is duplicated.

dynein (dī′-nē-un) In cilia and flagella, a large motor protein extending from one microtubule doublet to the adjacent doublet. ATP hydrolysis drives changes in dynein shape that lead to bending of cilia and flagella.

E site One of a ribosome's three binding sites for tRNA during translation. The E site is the place where discharged tRNAs leave the ribosome. (E stands for exit.)

Ecdysozoa (ek′-dē-sō-zō′-uh) One of the three main lineages of bilaterian animals; many ecdysozoans are molting animals. *See also* Deuterostomia and Lophotrochozoa.

echinoderm (i-kī′-nō-derm) A slow-moving or sessile marine deuterostome with a water vascular system and, in larvae, bilateral symmetry. Echinoderms include sea stars, brittle stars, sea urchins, feather stars, and sea cucumbers.

ecological footprint The aggregate land and water area required by a person, city, or nation to produce all of the resources it consumes and to absorb all of the waste it generates.

ecological niche (nich) The sum of a species' use of the biotic and abiotic resources in its environment.

ecological species concept Definition of a species in terms of ecological niche, the sum of how members of the species interact with the nonliving and living parts of their environment.

ecological succession Transition in the species composition of a community following a disturbance; establishment of a community in an area virtually barren of life.

ecology The study of how organisms interact with each other and their environment.

ecosystem All the organisms in a given area as well as the abiotic factors with which they interact; one or more communities and the physical environment around them.

ecosystem ecology The study of energy flow and the cycling of chemicals among the various biotic and abiotic components in an ecosystem.

ecosystem engineer An organism that influences community structure by causing physical changes in the environment.

ecosystem service A function performed by an ecosystem that directly or indirectly benefits humans.

ecotone The transition from one type of habitat or ecosystem to another, such as the transition from a forest to a grassland.

ectoderm (ek′-tō-durm) The outermost of the three primary germ layers in animal embryos; gives rise to the outer covering and, in some phyla, the nervous system, inner ear, and lens of the eye.

ectomycorrhiza (plural, **ectomycorrhizae**) (ek′-tō-mī′-kō-rī′-zuh, ek′-tō-mī′-kō-rī′-zē) Association of a fungus with a plant root system in which the fungus surrounds the roots but does not cause invagination of the host (plant) cell's plasma membrane.

ectomycorrhizal fungus A symbiotic fungus that forms sheaths of hyphae over the surface of plant roots and also grows into extracellular spaces of the root cortex.

ectoparasite A parasite that feeds on the external surface of a host.

ectopic Occurring in an abnormal location.

ectoproct A sessile, colonial lophophorate; also called a bryozoan.

ectothermic Referring to organisms for which external sources provide most of the heat for temperature regulation.

Ediacaran biota (ē′-dē-uh-keh′-run bī-ō′-tuh) An early group of macroscopic, soft-bodied, multicellular eukaryotes known from fossils that range in age from 635 million to 535 million years old.

effective population size An estimate of the size of a population based on the numbers of females and males that successfully breed; generally smaller than the total population.

effector A pathogen-encoded protein that cripples the host's innate immune system.

effector cell (1) A muscle cell or gland cell that carries out the body's response to stimuli as directed by signals from the brain or other processing center of the nervous system. (2) A lymphocyte that has undergone clonal selection and is capable of mediating an adaptive immune response.

egg The female gamete.

ejaculation The propulsion of sperm from the epididymis through the muscular vas deferens, ejaculatory duct, and urethra.

electrocardiogram (ECG or EKG) A record of the electrical impulses that travel through heart muscle during the cardiac cycle.

electrochemical gradient The diffusion gradient of an ion, which is affected by both the concentration difference of an ion across a membrane (a chemical force) and the ion's tendency to move relative to the membrane potential (an electrical force).

electrogenic pump An active transport protein that generates voltage across a membrane while pumping ions.

electromagnetic receptor A receptor of electromagnetic energy, such as visible light, electricity, or magnetism.

electromagnetic spectrum The entire spectrum of electromagnetic radiation, ranging in wavelength from less than a nanometer to more than a kilometer.

electron A subatomic particle with a single negative electrical charge and a mass about 1/2,000 that of a neutron or proton. One or more electrons move around the nucleus of an atom.

electron microscope (EM) A microscope that uses magnets to focus an electron beam on or through a specimen, resulting in a practical resolution that is 100-fold greater than that of a light microscope using standard techniques. A transmission electron microscope (TEM) is used to study the internal structure of thin sections of cells. A scanning electron microscope (SEM) is used to study the fine details of cell surfaces.

electron shell An energy level of electrons at a characteristic average distance from the nucleus of an atom.

electron transport chain A sequence of electron carrier molecules (membrane proteins) that shuttle electrons down a series of redox reactions that release energy used to make ATP.

electronegativity The attraction of a given atom for the electrons of a covalent bond.

electroporation A technique to introduce recombinant DNA into cells by applying a brief electrical pulse to a solution containing the cells. The pulse creates temporary holes in the cells' plasma membranes, through which DNA can enter.

element Any substance that cannot be broken down to any other substance by chemical reactions.

elimination The fourth and final stage of food processing in animals: the passing of undigested material out of the body.

embryo sac (em′-brē-ō) The female gametophyte of angiosperms, formed from the growth and division of the megaspore into a multicellular structure that typically has eight haploid nuclei.

embryonic lethal A mutation with a phenotype leading to death of an embryo or larva.

embryophyte Alternate name for land plants that refers to their shared derived trait of multicellular, dependent embryos.

emergent properties New properties that arise with each step upward in the hierarchy of life, owing to the arrangement and interactions of parts as complexity increases.

emigration The movement of individuals out of a population.

enantiomer (en-an′-tē-ō-mer) One of two compounds that are mirror images of each other and that differ in shape due to the presence of an asymmetric carbon.

endangered species A species that is in danger of extinction throughout all or a significant portion of its range.

endemic (en-dem′-ik) Referring to a species that is confined to a specific geographic area.

endergonic reaction (en′-der-gon′-ik) A nonspontaneous chemical reaction in which free energy is absorbed from the surroundings.

endocrine gland (en′-dō-krin) A ductless gland that secretes hormones directly into the interstitial fluid, from which they diffuse into the bloodstream.

endocrine system (en′-dō-krin) In animals, the internal system of communication involving hormones, the ductless glands that secrete hormones, and the molecular receptors on or in target cells that respond to hormones; functions in concert with the nervous system to effect internal regulation and maintain homeostasis.

endocytosis (en′-dō-sī-tō′-sis) Cellular uptake of biological molecules and particulate matter via formation of vesicles from the plasma membrane.

endoderm (en′-dō-durm) The innermost of the three primary germ layers in animal embryos; lines the archenteron and gives rise to the liver, pancreas, lungs, and the lining of the digestive tract in species that have these structures.

endodermis In plant roots, the innermost layer of the cortex that surrounds the vascular cylinder.

endomembrane system The collection of membranes inside and surrounding a eukaryotic cell, related either through direct physical contact or by the transfer of membranous vesicles; includes the plasma membrane, the nuclear envelope, the smooth and rough endoplasmic reticulum, the Golgi apparatus, lysosomes, vesicles, and vacuoles.

endometriosis (en′-dō-mē-trē-ō′-sis) The condition resulting from the presence of endometrial tissue outside of the uterus.

endometrium (en′-dō-mē′-trē-um) The inner lining of the uterus, which is richly supplied with blood vessels.

endoparasite A parasite that lives within a host.

endophyte A harmless fungus, or occasionally another organism, that lives between cells of a plant part or multicellular alga.

endoplasmic reticulum (ER) (en′-dō-plaz′-mik ruh-tik′-yū-lum) An extensive membranous network in eukaryotic cells, continuous with the outer nuclear membrane and composed of ribosome-studded (rough) and ribosome-free (smooth) regions.

endorphin (en-dōr′-fin) Any of several hormones produced in the brain and anterior pituitary that inhibit pain perception.

endoskeleton A hard skeleton buried within the soft tissues of an animal.

endosperm In angiosperms, a nutrient-rich tissue formed by the union of a sperm with two polar nuclei during double fertilization. The endosperm provides nourishment to the developing embryo in angiosperm seeds.

endospore A thick-coated, resistant cell produced by some bacterial cells when they are exposed to harsh conditions.

endosymbiont theory The theory that mitochondria and plastids, including chloroplasts, originated as prokaryotic cells engulfed by a host cell. The engulfed cell and its host cell then evolved into a single organism. *See also* endosymbiosis.

endosymbiosis A relationship between two species in which one organism lives inside the cell or cells of another organism. *See also* endosymbiont theory.

endothelium (en′-dō-thē′-lē-um) The simple squamous layer of cells lining the lumen of blood vessels.

endothermic Referring to organisms that are warmed by heat generated by their own metabolism. This heat usually maintains a relatively stable body temperature higher than that of the external environment.

endotoxin A toxic component of the outer membrane of certain gram-negative bacteria that is released only when the bacteria die.

energetic hypothesis The concept that the length of a food chain is limited by the inefficiency of energy transfer along the chain.

energy The capacity to cause change, especially to do work (to move matter against an opposing force).

energy coupling In cellular metabolism, the use of energy released from an exergonic reaction to drive an endergonic reaction.

enhancer A segment of eukaryotic DNA containing multiple control elements, usually located far from the gene whose transcription it regulates.

enteric nervous system A distinct network of neurons that exerts direct and partially independent control over the digestive tract, pancreas, and gallbladder.

entropy A measure of molecular disorder, or randomness.

enzyme (en′-zīm) A macromolecule serving as a catalyst, a chemical agent that increases the rate of a reaction without being consumed by the reaction. Most enzymes are proteins.

enzyme-substrate complex (en′-zīm) A temporary complex formed when an enzyme binds to its substrate molecule(s).

epicotyl (ep′-uh-kot′-ul) In an angiosperm embryo, the embryonic axis above the point of attachment of the cotyledon(s) and below the first pair of miniature leaves.

epidemic A widespread outbreak of a disease.

epidermis (1) The dermal tissue system of nonwoody plants, usually consisting of a single layer of tightly packed cells. (2) The outermost layer of cells in an animal.

epididymis (ep′-uh-did′-uh-mus) A coiled tubule located adjacent to the mammalian testis where sperm are stored.

epigenetic inheritance Inheritance of traits transmitted by mechanisms that do not involve the nucleotide sequence.

epinephrine (ep′-i-nef′-rin) A catecholamine that, when secreted as a hormone by the adrenal medulla, mediates "fight-or-flight" responses to short-term stresses; also released by some neurons as a neurotransmitter; also called adrenaline.

epiphyte (ep′-uh-fīt) A plant that nourishes itself but grows on the surface of another plant for support, usually on the branches or trunks of trees.

epistasis (ep′-i-stā′-sis) A type of gene interaction in which the phenotypic expression of one gene alters that of another independently inherited gene.

epithelial tissue (ep′-uh-thē′-lē-ul) Sheets of tightly packed cells that line organs and body cavities as well as external surfaces.

epithelium An epithelial tissue.

epitope A small, accessible region of an antigen to which an antigen receptor or antibody binds.

equilibrium potential (E_{ion}) The magnitude of a cell's membrane voltage at equilibrium; calculated using the Nernst equation.

erythrocyte (eh-rith′-ruh-sīt) A blood cell that contains hemoglobin, which transports oxygen; also called a red blood cell.

erythropoietin (EPO) (eh-rith′-rō-poy′-uh-tin) A hormone that stimulates the production of erythrocytes. It is secreted by the kidney when body tissues do not receive enough oxygen.

esophagus (eh-sof′-uh-gus) A muscular tube that conducts food, by peristalsis, from the pharynx to the stomach.

essential amino acid An amino acid that an animal cannot synthesize itself and must be obtained from food in prefabricated form.

essential element A chemical element required for an organism to survive, grow, and reproduce.

essential fatty acid An unsaturated fatty acid that an animal needs but cannot make.

essential nutrient A substance that an organism cannot synthesize from any other material and therefore must absorb in preassembled form.

estradiol (es′-truh-dī′-ol) A steroid hormone that stimulates the development and maintenance of the female reproductive system and secondary sex characteristics; the major estrogen in mammals.

estrogen (es′-trō-jen) Any steroid hormone, such as estradiol, that stimulates the development and maintenance of the female reproductive system and secondary sex characteristics.

estrous cycle (es′-trus) A reproductive cycle characteristic of female mammals except humans and certain other primates, in which the endometrium is reabsorbed in the absence of pregnancy and sexual response occurs only during a mid-cycle point known as estrus.

estuary The area where a freshwater stream or river merges with the ocean.

ethylene (eth′-uh-lēn) A gaseous plant hormone involved in responses to mechanical stress, programmed cell death, leaf abscission, and fruit ripening.

etiolation Plant morphological adaptations for growing in darkness.

euchromatin (yū-krō′-muh-tin) The less condensed form of eukaryotic chromatin that is available for transcription.

eudicot (yū-dī′-kot) A member of a clade that contains the vast majority of flowering plants that have two embryonic seed leaves, or cotyledons.

euglenid (yū′-glen-id) A protist, such as *Euglena* or its relatives, characterized by an anterior pocket from which one or two flagella emerge.

euglenozoan A member of a diverse clade of flagellated protists that includes predatory heterotrophs, photosynthetic autotrophs, and pathogenic parasites.

Eukarya (yū-kar′-ē-uh) The domain that includes all eukaryotic organisms.

eukaryotic cell (yū′-ker-ē-ot′-ik) A type of cell with a membrane-enclosed nucleus and membrane-enclosed organelles. Organisms with eukaryotic cells (protists, plants, fungi, and animals) are called eukaryotes.

eumetazoan (yū′-met-uh-zō′-un) A member of a clade of animals with true tissues. All animals except sponges and a few other groups are eumetazoans.

eurypterid (yur-ip′-tuh-rid) An extinct carnivorous chelicerate; also called a water scorpion.

Eustachian tube (yū-stā′-shun) The tube that connects the middle ear to the pharynx.

eutherian (yū-thēr′-ē-un) Placental mammal; mammal whose young complete their embryonic development within the uterus, joined to the mother by the placenta.

eutrophic lake (yū-trōf′-ik) A lake that has a high rate of biological productivity supported by a high rate of nutrient cycling.

eutrophication A process by which nutrients, particularly phosphorus and nitrogen, become highly concentrated in a body of water, leading to increased growth of organisms such as algae or cyanobacteria.

evaporative cooling The process in which the surface of an object becomes cooler during evaporation, a result of the molecules with the greatest kinetic energy changing from the liquid to the gaseous state.

evapotranspiration The total evaporation of water from an ecosystem, including water transpired by plants and evaporated from a landscape, usually measured in millimeters and estimated for a year.

evo-devo Evolutionary developmental biology; a field of biology that compares developmental processes of different multicellular organisms to understand how these processes have evolved and how changes can modify existing organismal features or lead to new ones.

evolution Descent with modification; the idea that living species are descendants of ancestral species that were different from the present-day ones; also defined more narrowly as the change in the genetic composition of a population from generation to generation.

evolutionary tree A branching diagram that reflects a hypothesis about evolutionary relationships among groups of organisms.

Excavata (ex′-kuh-vah′-tuh) One of four supergroups of eukaryotes proposed in a current hypothesis of the evolutionary history of eukaryotes. Excavates have unique cytoskeletal features, and some species have an "excavated" feeding groove on one side of the cell body. *See also* SAR, Archaeplastida, and Unikonta.

excitatory postsynaptic potential (EPSP) An electrical change (depolarization) in the membrane of a postsynaptic cell caused by the binding of an excitatory neurotransmitter from a presynaptic cell to a postsynaptic receptor; makes it more likely for a postsynaptic cell to generate an action potential.

excretion The disposal of nitrogen-containing metabolites and other waste products.

exergonic reaction (ek′-ser-gon′-ik) A spontaneous chemical reaction in which there is a net release of free energy.

exocytosis (ek′-sō-sī-tō′-sis) The cellular secretion of biological molecules by the fusion of vesicles containing them with the plasma membrane.

exon A sequence within a primary transcript that remains in the RNA after RNA processing; also refers to the region of DNA from which this sequence was transcribed.

exoskeleton A hard encasement on the surface of an animal, such as the shell of a mollusc or the cuticle of an arthropod, that provides protection and points of attachment for muscles.

exotoxin (ek′-sō-tok′-sin) A toxic protein that is secreted by a prokaryote or other pathogen and that produces specific symptoms, even if the pathogen is no longer present.

expansin Plant enzyme that breaks the cross-links (hydrogen bonds) between cellulose microfibrils and other cell wall constituents, loosening the wall's fabric.

experiment A scientific test. Often carried out under controlled conditions that involve manipulating one factor in a system in order to see the effects of changing that factor.

experimental group A set of subjects that has (or receives) the specific factor being tested in a controlled experiment. Ideally, the experimental group should be identical to the control group for all other factors.

exploitation A +/− ecological interaction in which one species benefits by feeding on the other species, which is harmed. Exploitative interactions include predation, herbivory, and parasitism.

exponential population growth Growth of a population in an ideal, unlimited environment, represented by a J-shaped curve when population size is plotted over time.

expression vector A cloning vector that contains a highly active bacterial promoter just upstream of a restriction site where a eukaryotic gene can be inserted, allowing the gene to be expressed in a bacterial cell. Expression vectors are also available that have been genetically engineered for use in specific types of eukaryotic cells.

extinction vortex A downward population spiral in which inbreeding and genetic drift combine to cause a small population to shrink and, unless the spiral is reversed, become extinct.

extracellular matrix (ECM) The meshwork surrounding animal cells, consisting of glycoproteins, polysaccharides, and proteoglycans synthesized and secreted by cells.

extraembryonic membrane One of four membranes (yolk sac, amnion, chorion, and allantois) located outside the embryo that support the developing embryo in reptiles and mammals.

extreme halophile An organism that lives in a highly saline environment, such as the Great Salt Lake or the Dead Sea.

extreme thermophile An organism that thrives in hot environments (often 60–80°C or hotter).

extremophile An organism that lives in environmental conditions so extreme that few other species can survive there. Extremophiles include extreme halophiles ("salt lovers") and extreme thermophiles ("heat lovers").

F_1 generation The first filial, hybrid (heterozygous) offspring arising from a parental (P generation) cross.

F_2 generation The offspring resulting from interbreeding (or self-pollination) of the hybrid F_1 generation.

facilitated diffusion The passage of molecules or ions down their electrochemical gradient across a biological membrane with the assistance of specific transmembrane transport proteins, requiring no energy expenditure.

facultative anaerobe (fak′-ul-tā′-tiv an′-uh-rōb) An organism that makes ATP by aerobic respiration if oxygen is present but that switches to anaerobic respiration or fermentation if oxygen is not present.

family In Linnaean classification, the taxonomic category above genus.

fast-twitch fiber A muscle fiber used for rapid, powerful contractions.

fat A lipid consisting of three fatty acids linked to one glycerol molecule; also called a triacylglycerol or triglyceride.

fate map A territorial diagram of embryonic development that displays the future derivatives of individual cells and tissues.

fatty acid A carboxylic acid with a long carbon chain. Fatty acids vary in length and in the number and location of double bonds; three fatty acids linked to a glycerol molecule form a fat molecule, also called triacylglycerol or triglyceride.

feces (fē′-sēz) The wastes of the digestive tract.

feedback inhibition A method of metabolic control in which the end product of a metabolic pathway acts as an inhibitor of an enzyme within that pathway.

feedback regulation The regulation of a process by its output or end product.

fermentation A catabolic process that makes a limited amount of ATP from glucose (or other organic molecules) without an electron transport chain and that produces a characteristic end product, such as ethyl alcohol or lactic acid.

fertilization (1) The union of haploid gametes to produce a diploid zygote. (2) The addition of mineral nutrients to the soil.

fetus (fē′-tus) A developing mammal that has all the major structures of an adult. In humans, the fetal stage lasts from the 9th week of gestation until birth.

F factor In bacteria, the DNA segment that confers the ability to form pili for conjugation and associated functions required for the transfer of DNA from donor to recipient. The F factor may exist as a plasmid or be integrated into the bacterial chromosome.

fiber A lignified cell type that reinforces the xylem of angiosperms and functions in mechanical support; a slender, tapered sclerenchyma cell that usually occurs in bundles.

fibroblast (fī′-brō-blast) A type of cell in loose connective tissue that secretes the protein ingredients of the extracellular fibers.

fibronectin An extracellular glycoprotein secreted by animal cells that helps them attach to the extracellular matrix.

filament In an angiosperm, the stalk portion of the stamen, the pollen-producing reproductive organ of a flower.

filter feeder An animal that feeds by using a filtration mechanism to strain small organisms or food particles from its surroundings.

filtrate Cell-free fluid extracted from the body fluid by the excretory system.

filtration In excretory systems, the extraction of water and small solutes, including metabolic wastes, from the body fluid.

fimbria (plural, **fimbriae**) A short, hairlike appendage of a prokaryotic cell that helps it adhere to the substrate or to other cells.

first law of thermodynamics The principle of conservation of energy: Energy can be transferred and transformed, but it cannot be created or destroyed.

fission The separation of an organism into two or more individuals of approximately equal size.

fixed action pattern In animal behavior, a sequence of unlearned acts that is essentially unchangeable and, once initiated, usually carried to completion.

flaccid (flas′-id) Limp. Lacking turgor (stiffness or firmness), as in a plant cell in surroundings where there is a tendency for water to leave the cell. (A walled cell becomes flaccid if it has a higher water potential than its surroundings, resulting in the loss of water.)

flagellum (fluh-jel′-um) (plural, **flagella**) A long cellular appendage specialized for locomotion. Like motile cilia, eukaryotic flagella have a core with nine outer doublet microtubules and two inner single microtubules (the "9 + 2" arrangement) ensheathed in an extension of the plasma membrane. Prokaryotic flagella have a different structure.

florigen A flowering signal, probably a protein, that is made in leaves under certain conditions and that travels to the shoot apical meristems, inducing them to switch from vegetative to reproductive growth.

flower In an angiosperm, a specialized shoot with up to four sets of modified leaves, bearing structures that function in sexual reproduction.

fluid feeder An animal that lives by sucking nutrient-rich fluids from another living organism.

fluid mosaic model The currently accepted model of cell membrane structure, which envisions the membrane as a mosaic of protein molecules drifting laterally in a fluid bilayer of phospholipids.

follicle (fol′-uh-kul) A microscopic structure in the ovary that contains the developing oocyte and secretes estrogens.

follicle-stimulating hormone (FSH) (fol′-uh-kul) A tropic hormone that is produced and secreted by the anterior pituitary and that stimulates the production of eggs by the ovaries and sperm by the testes.

food chain The pathway along which food energy is transferred from trophic level to trophic level, beginning with producers.

food vacuole A membranous sac formed by phagocytosis of microorganisms or particles to be used as food by the cell.

food web The interconnected feeding relationships in an ecosystem.

foot (1) The portion of a bryophyte sporophyte that gathers sugars, amino acids, water, and minerals from the parent gametophyte via transfer cells. (2) One of the three main parts of a mollusc; a muscular structure usually used for movement. *See also* mantle and visceral mass.

foraging The seeking and obtaining of food.

foram (foraminiferan) An aquatic protist that secretes a hardened shell containing calcium carbonate and extends pseudopodia through pores in the shell.

forebrain One of three ancestral and embryonic regions of the vertebrate brain; develops into the thalamus, hypothalamus, and cerebrum.

fossil A preserved remnant or impression of an organism that lived in the past.

founder effect Genetic drift that occurs when a few individuals become isolated from a larger population and form a new population whose gene pool composition is not reflective of that of the original population.

fovea (fō′-vē-uh) The place on the retina at the eye's center of focus, where cones are highly concentrated.

F plasmid The plasmid form of the F factor.

fragmentation A means of asexual reproduction whereby a single parent breaks into parts that regenerate into whole new individuals.

frameshift mutation A mutation occurring when nucleotides are inserted in or deleted from a gene and the number inserted or deleted is not a multiple of three, resulting in the improper grouping of the subsequent nucleotides into codons.

free energy The portion of a biological system's energy that can perform work when temperature and pressure are uniform throughout the system. The change in free energy of a system (ΔG) is calculated by the equation $\Delta G = \Delta H - T\Delta S$, where ΔH is the change in enthalpy (in biological systems, equivalent to total energy), ΔT is the absolute temperature, and ΔS is the change in entropy.

frequency-dependent selection Selection in which the fitness of a phenotype depends on how common the phenotype is in a population.

fruit A mature ovary of a flower. The fruit protects dormant seeds and often functions in their dispersal.

functional group A specific configuration of atoms commonly attached to the carbon skeletons of organic molecules and involved in chemical reactions.

fusion In evolutionary biology, a process in which gene flow between two species that can form hybrid offspring weakens barriers to reproduction between the species. This process causes their gene pools to become increasingly alike and can cause the two species to fuse into a single species.

G_0 phase A nondividing state occupied by cells that have left the cell cycle, sometimes reversibly.

G_1 phase The first gap, or growth phase, of the cell cycle, consisting of the portion of interphase before DNA synthesis begins.

G_2 phase The second gap, or growth phase, of the cell cycle, consisting of the portion of interphase after DNA synthesis occurs.

gallbladder An organ that stores bile and releases it as needed into the small intestine.

game theory An approach to evaluating alternative strategies in situations where the outcome of a particular strategy depends on the strategies used by other individuals.

gametangium (gam′-uh-tan′-jē-um) (plural, **gametangia**) Multicellular plant structure in which gametes are formed. Female gametangia are called archegonia, and male gametangia are called antheridia.

gamete (gam′-ēt) A haploid reproductive cell, such as an egg or sperm, that is formed by meiosis or is the descendant of cells formed by meiosis. Gametes unite during sexual reproduction to produce a diploid zygote.

gametogenesis (guh-mē′-tō-gen′-uh-sis) The process by which gametes are produced.

gametophore (guh-mē′-tō-fōr) The mature gamete-producing structure of a moss gametophyte.

gametophyte (guh-mē′-tō-fīt) In organisms (plants and some algae) that have alternation of generations, the multicellular haploid form that produces haploid gametes by mitosis. The haploid gametes unite and develop into sporophytes.

ganglion (gan′-glē-uhn) (plural, **ganglia**) A cluster (functional group) of nerve cell bodies.

gap junction A type of intercellular junction in animal cells, consisting of proteins surrounding a pore that allows the passage of materials between cells.

gas exchange The uptake of molecular oxygen from the environment and the discharge of carbon dioxide to the environment.

gastric juice A digestive fluid secreted by the stomach.

gastrovascular cavity A central cavity with a single opening in the body of certain animals, including cnidarians and flatworms, that functions in both the digestion and distribution of nutrients.

gastrula (gas′-trū-luh) An embryonic stage in animal development encompassing the formation of three layers: ectoderm, mesoderm, and endoderm.

gastrulation (gas′-trū-lā′-shun) In animal development, a series of cell and tissue movements in which the blastula-stage embryo folds inward, producing a three-layered embryo, the gastrula.

gated channel A transmembrane protein channel that opens or closes in response to a particular stimulus.

gated ion channel A gated channel for a specific ion. The opening or closing of such channels may alter a cell's membrane potential.

gel electrophoresis (ē-lek′-trō-fōr-ē′-sis) A technique for separating nucleic acids or proteins on the basis of their size and electrical charge, both of which affect their rate of movement through an electric field in a gel made of agarose or another polymer.

gene A discrete unit of hereditary information consisting of a specific nucleotide sequence in DNA (or RNA, in some viruses).

gene annotation Analysis of genomic sequences to identify protein-coding genes and determine the function of their products.

gene cloning The production of multiple copies of a gene.

gene drive A process that biases inheritance such that a particular allele is more likely to be inherited than are other alleles, causing the favored allele to spread (be "driven") through the population.

gene expression The process by which information encoded in DNA directs the synthesis of proteins or, in some cases, RNAs that are not translated into proteins and instead function as RNAs.

gene flow The transfer of alleles from one population to another, resulting from the movement of fertile individuals or their gametes.

gene pool The aggregate of all copies of every type of allele at all loci in every individual in a population. The term is also used in a more restricted sense as the aggregate of alleles for just one or a few loci in a population.

gene therapy The introduction of genes into an afflicted individual for therapeutic purposes.

genetic drift A process in which chance events cause unpredictable fluctuations in allele frequencies from one generation to the next. Effects of genetic drift are most pronounced in small populations.

genetic engineering The direct manipulation of genes for practical purposes.

genetic map An ordered list of genetic loci (genes or other genetic markers) along a chromosome.

genetic profile An individual's unique set of genetic markers, detected most often today by PCR or, previously, by electrophoresis and nucleic acid probes.

genetic recombination General term for the production of offspring with combinations of traits that differ from those found in either parent.

genetic variation Differences among individuals in the composition of their genes or other DNA segments.

genetically modified organism (GMO) An organism that has acquired one or more genes by artificial means; also called a transgenic organism.

genetics The scientific study of heredity and hereditary variation.

genome (jē′-nōm) The genetic material of an organism or virus; the complete complement of an organism's or virus's genes along with its noncoding nucleic acid sequences.

genome-wide association study (jē′-nōm) A large-scale analysis of the genomes of many people having a certain phenotype or disease, with the aim of finding genetic markers that correlate with that phenotype or disease.

genomic imprinting (juh-nō′-mik) A phenomenon in which expression of an allele in offspring depends on whether the allele is inherited from the male or female parent.

genomics (juh-nō′-miks) The systematic study of whole sets of genes (or other DNA) and their interactions within a species, as well as genome comparisons between species.

genotype (jē′-nō-tīp) The genetic makeup, or set of alleles, of an organism.

genus (jē′-nus) (plural, **genera**) A taxonomic category above the species level, designated by the first word of a species' two-part scientific name.

geologic record A standard time scale dividing Earth's history into time periods, grouped into four eons—Hadean, Archaean, Proterozoic, and Phanerozoic—and further subdivided into eras, periods, and epochs.

germ layer One of the three main layers in a gastrula that will form the various tissues and organs of an animal body.

gestation (jes-tā′-shun) *See* pregnancy.

gibberellin (jib′-uh-rel′-in) Any of a class of related plant hormones that stimulate growth in the stem and leaves, trigger the germination of seeds and breaking of bud dormancy, and (with auxin) stimulate fruit development.

glans The rounded structure at the tip of the clitoris or penis that is involved in sexual arousal.

glia (glial cells) Cells of the nervous system that support, regulate, and augment the functions of neurons.

global ecology The study of the functioning and distribution of organisms across the biosphere and how the regional exchange of energy and materials affects them.

glomeromycete (glō′-mer-ō-mī′-sēt) A member of the fungal phylum Glomeromycota, characterized by a distinct branching form of mycorrhizae called arbuscular mycorrhizae.

glomerulus (glō-mār′-yū-lus) A ball of capillaries surrounded by Bowman's capsule in the nephron and serving as the site of filtration in the vertebrate kidney.

glucocorticoid A steroid hormone that is secreted by the adrenal cortex and that influences glucose metabolism and immune function.

glucagon (glū′-kuh-gon) A hormone secreted by the pancreas that raises blood glucose levels. It promotes glycogen breakdown and release of glucose by the liver.

glyceraldehyde 3-phosphate (G3P) (glis′-er-al′-de-hīd) A three-carbon carbohydrate that is the direct product of the Calvin cycle; it is also an intermediate in glycolysis.

glycogen (glī′-kō-jen) An extensively branched glucose storage polysaccharide found in the liver and muscle of animals; the animal equivalent of starch.

glycolipid A lipid with one or more covalently attached carbohydrates.

glycolysis (glī-kol′-uh-sis) A series of reactions that ultimately splits glucose into pyruvate. Glycolysis occurs in almost all living cells, serving as the starting point for fermentation or cellular respiration.

glycoprotein A protein with one or more covalently attached carbohydrates.

glycosidic linkage A covalent bond formed between two monosaccharides by a dehydration reaction.

gnathostome (na′-thu-stōm) Member of one of the two main clades of vertebrates; gnathostomes have jaws and include sharks and rays, ray-finned fishes, coelacanths, lungfishes, amphibians, reptiles, and mammals. *See also* cyclostome.

golden alga A biflagellated, photosynthetic protist named for its color, which results from its yellow and brown carotenoids.

Golgi apparatus (gol′-jē) An organelle in eukaryotic cells consisting of stacks of flat membranous sacs that modify, store, and route products of the endoplasmic reticulum and synthesize some products, notably noncellulose carbohydrates.

gonad (gō′-nad) A male or female gamete-producing organ.

G protein A GTP-binding protein that relays signals from a plasma membrane signal receptor, known as a G protein-coupled receptor, to other signal transduction proteins inside the cell.

G protein-coupled receptor (GPCR) A signal receptor protein in the plasma membrane that responds to the binding of a signaling molecule by activating a G protein. Also called a G protein-linked receptor.

graded potential In a neuron, a shift in the membrane potential that has an amplitude proportional to signal strength and that decays as it spreads.

Gram stain A staining method that distinguishes between two different kinds of bacterial cell walls; may be used to help determine medical response to an infection.

gram-negative Describing the group of bacteria that have a cell wall that is structurally more complex and contains less peptidoglycan than the cell wall of gram-positive bacteria. Gram-negative bacteria are often more toxic than gram-positive bacteria.

gram-positive Describing the group of bacteria that have a cell wall that is structurally less complex and contains more peptidoglycan than the cell wall of gram-negative bacteria. Gram-positive bacteria are usually less toxic than gram-negative bacteria.

granum (gran′-um) (plural, **grana**) A stack of membrane-bounded thylakoids in the chloroplast. Grana function in the light reactions of photosynthesis.

gravitropism (grav′-uh-trō′-pizm) A response of a plant or animal to gravity.

gray matter Regions of clustered neuron cell bodies within the CNS.

green alga A photosynthetic protist, named for green chloroplasts that are similar in structure and pigment composition to the chloroplasts of plants. Green algae are a paraphyletic group; some members are more closely related to plants than they are to other green algae.

greenhouse effect The warming of Earth due to the atmospheric accumulation of carbon dioxide and certain other gases, which absorb reflected infrared radiation and reradiate some of it back toward Earth.

gross primary production (GPP) The total primary production of an ecosystem.

ground tissue system Plant tissues that are neither vascular nor dermal, fulfilling a variety of functions, such as storage, photosynthesis, and support.

growth factor (1) A protein that must be present in the extracellular environment (culture medium or animal body) for the growth and normal development of certain types of cells. (2) A local regulator that acts on nearby cells to stimulate cell proliferation and differentiation.

growth hormone (GH) A hormone that is produced and secreted by the anterior pituitary and that has both direct (nontropic) and tropic effects on a wide variety of tissues.

guard cells The two cells that flank the stomatal pore and regulate the opening and closing of the pore.

gustation The sense of taste.

guttation The exudation of water droplets from leaves, caused by root pressure in certain plants.

gymnosperm (jim′-nō-sperm) A vascular plant that bears naked seeds—seeds not enclosed in protective chambers.

hagfish Marine jawless vertebrates that have highly reduced vertebrae and a skull made of cartilage; most hagfishes are bottom-dwelling scavengers.

hair cell A mechanosensory cell that alters output to the nervous system when hairlike projections on the cell surface are displaced.

half-life The amount of time it takes for 50% of a sample of a radioactive isotope to decay.

halophile *See* extreme halophile.

Hamilton's rule The principle that for natural selection to favor an altruistic act, the benefit to the recipient, devalued by the coefficient of relatedness, must exceed the cost to the altruist.

haploid cell (hap′-loyd) A cell containing only one set of chromosomes (n).

Hardy-Weinberg equilibrium The state of a population in which frequencies of alleles and genotypes remain constant from generation to generation, provided that only Mendelian segregation and recombination of alleles are at work.

heart A muscular pump that uses metabolic energy to elevate the hydrostatic pressure of the circulatory fluid (blood or hemolymph). The fluid then flows down a pressure gradient through the body and eventually returns to the heart.

heart attack The damage or death of cardiac muscle tissue resulting from prolonged blockage of one or more coronary arteries.

heart murmur A hissing sound that most often results from blood squirting backward through a leaky valve in the heart.

heart rate The frequency of heart contraction (in beats per minute).

heat Thermal energy in transfer from one body of matter to another.

heat of vaporization The quantity of heat a liquid must absorb for 1 g of it to be converted from the liquid to the gaseous state.

heat-shock protein A protein that helps protect other proteins during heat stress. Heat-shock proteins are found in plants, animals, and microorganisms.

heavy chain One of the two types of polypeptide chains that make up an antibody molecule and B cell receptor; consists of a variable region, which contributes to the antigen-binding site, and a constant region.

helicase An enzyme that untwists the double helix of DNA at replication forks, separating the two strands and making them available as template strands.

helper T cell A type of T cell that, when activated, secretes cytokines that promote the response of B cells (humoral response) and cytotoxic T cells (cell-mediated response) to antigens.

hemoglobin (hē′-mō-glō′-bin) An iron-containing protein in red blood cells that reversibly binds oxygen.

hemolymph (hē′-mō-limf′) In invertebrates with an open circulatory system, the body fluid that bathes tissues.

hemophilia (hē′-muh-fil′-ē-uh) A human genetic disease caused by a sex-linked recessive allele resulting in the absence of one or more blood-clotting proteins; characterized by excessive bleeding following injury.

hepatic portal vein A large vessel that conveys nutrient-laden blood from the small intestine to the liver, which regulates the blood's nutrient content.

herbivore (hur′-bi-vōr′) An animal that mainly eats plants or algae.

herbivory An interaction in which an organism eats part of a plant or alga.

heredity The transmission of traits from one generation to the next.

hermaphrodite (hur-maf′-ruh-dīt′) An individual that functions as both male and female in sexual reproduction by producing both sperm and eggs.

hermaphroditism (hur-maf′-rō-dī-tizm) A condition in which an individual has both female and male gonads and functions as both a male and a female in sexual reproduction by producing both sperm and eggs.

heterochromatin (het′-er-ō-krō′-muh-tin) Eukaryotic chromatin that remains highly compacted during interphase and is generally not transcribed.

heterochrony (het′-uh-rok′-ruh-nē) Evolutionary change in the timing or rate of an organism's development.

heterocyst (het′-er-ō-sist) A specialized cell that engages in nitrogen fixation in some filamentous cyanobacteria; also called a heterocyte.

heterokaryon (het′-er-ō-kār′-ē-un) A fungal mycelium that contains two or more haploid nuclei per cell.

heteromorphic (het′-er-ō-mōr′-fik) Referring to a condition in the life cycle of plants and certain algae in which the sporophyte and gametophyte generations differ in morphology.

heterosporous (het-er-os′-pōr-us) Referring to a plant species that has two kinds of spores: microspores, which develop into male gametophytes, and megaspores, which develop into female gametophytes.

heterotroph (het′-er-ō-trōf) An organism that obtains organic food molecules by eating other organisms or substances derived from them.

heterozygote An organism that has two different alleles for a gene (encoding a character).

heterozygote advantage Greater reproductive success of heterozygous individuals compared with homozygotes; tends to preserve variation in a gene pool.

heterozygous (het′-er-ō-zī′-gus) Having two different alleles for a given gene.

hibernation A long-term physiological state in which metabolism decreases, the heart and respiratory system slow down, and body temperature is maintained at a lower level than normal.

high-density lipoprotein (HDL) A particle in the blood made up of thousands of cholesterol molecules and other lipids bound to a protein. HDL scavenges excess cholesterol.

hindbrain One of three ancestral and embryonic regions of the vertebrate brain; develops into the medulla oblongata, pons, and cerebellum.

histamine (his′-tuh-mēn) A substance released by mast cells that causes blood vessels to dilate and become more permeable in inflammatory and allergic responses.

histogram A variant of a bar graph that is made for numeric data by first grouping, or "binning," the variable plotted on the *x*-axis into intervals of equal width. The "bins" may be integers or ranges of numbers. The height of each bar shows the percent or number of experimental subjects whose characteristics can be described by one of the intervals plotted on the *x*-axis.

histone (his′-tōn) A small protein with a high proportion of positively charged amino acids that binds to the negatively charged DNA and plays a key role in chromatin structure.

histone acetylation (his′-tōn) The attachment of acetyl groups to certain amino acids of histone proteins.

HIV (human immunodeficiency virus) The infectious agent that causes AIDS. HIV is a retrovirus.

holdfast A rootlike structure that anchors a seaweed.

homeobox (hō′-mē-ō-boks′) A 180-nucleotide sequence within homeotic genes and some other developmental genes that is widely conserved in animals. Related sequences occur in plants and yeasts.

homeostasis (hō′-mē-ō-stā′-sis) The steady-state physiological condition of the body.

homeotic gene (hō-mē-o′-tik) Any of the master regulatory genes that control placement and spatial organization of body parts in animals, plants, and fungi by controlling the developmental fate of groups of cells.

hominin (hō′-mi-nin) A group consisting of humans and the extinct species that are more closely related to us than to chimpanzees.

homologous chromosomes (or homologs) (hō-mol′-uh-gus) A pair of chromosomes of the same length, centromere position, and staining pattern that possess genes for the same characters at corresponding loci. One homologous chromosome is inherited from the organism's father, the other from the mother. Also called a homologous pair.

homologous pair *See* homologous chromosomes.

homologous structures (hō-mol′-uh-gus) Structures in different species that are similar because of common ancestry.

homologs *See* homologous chromosomes.

homology (hō-mol′-ō-jē) Similarity in characteristics resulting from a shared ancestry.

homoplasy (hō′-muh-play′-zē) A similar (analogous) structure or molecular sequence that has evolved independently in two species.

homosporous (hō-mos′-puh-rus) Referring to a plant species that has a single kind of spore, which typically develops into a bisexual gametophyte.

homozygote An organism that has a pair of identical alleles for a gene (encoding a character).

homozygous (hō′-mō-zī′-gus) Having two identical alleles for a given gene.

horizontal gene transfer The transfer of genes from one genome to another through mechanisms such as transposable elements, plasmid exchange, viral activity, and perhaps fusions of different organisms.

hormone In multicellular organisms, one of many types of secreted chemicals that are formed in specialized cells, travel in body fluids, and act on specific target cells in other parts of the organism, changing the target cells' functioning.

hornwort A small, herbaceous, nonvascular plant that is a member of the phylum Anthocerophyta.

host The larger participant in a symbiotic relationship, often providing a home and food source for the smaller symbiont.

host range The limited number of species whose cells can be infected by a particular virus.

Human Genome Project An international collaborative effort to map and sequence the DNA of the entire human genome.

human immunodeficiency virus (HIV) The infectious agent that causes AIDS (acquired immunodeficiency syndrome). HIV is a retrovirus.

humoral immune response (hyū′-mer-ul) The branch of adaptive immunity that involves the activation of B cells and that leads to the production of antibodies, which defend against bacteria and viruses in body fluids.

humus (hyū′-mus) Decomposing organic material that is a component of topsoil.

Huntington's disease A human genetic disease caused by a dominant allele; characterized by uncontrollable body movements and degeneration of the nervous system; usually fatal 10 to 20 years after the onset of symptoms.

hybrid Offspring that results from the mating of individuals from two different species or from two true-breeding varieties of the same species.

hybrid zone A geographic region in which members of different species meet and mate, producing at least some offspring of mixed ancestry.

hybridization In genetics, the mating, or crossing, of two true-breeding varieties.

hydration shell The sphere of water molecules around a dissolved ion.

hydrocarbon An organic molecule consisting only of carbon and hydrogen.

hydrogen bond A type of weak chemical bond that is formed when the slightly positive hydrogen atom of a polar covalent bond in one molecule is attracted to the slightly negative atom of a polar covalent bond in another molecule or in another region of the same molecule.

hydrogen ion A single proton with a charge of $1+$. The dissociation of a water molecule (H_2O) leads to the generation of a hydroxide ion (OH^-) and a hydrogen ion (H^+); in water, H^+ is not found alone but associates with a water molecule to form a hydronium ion.

hydrolysis (hī-drol′-uh-sis) A chemical reaction that breaks bonds between two molecules by the addition of water; functions in disassembly of polymers to monomers.

hydronium ion A water molecule that has an extra proton bound to it; H_3O^+, commonly represented as H^+.

hydrophilic (hī′-drō-fil′-ik) Having an affinity for water.

hydrophobic (hī′-drō-fō′-bik) Having no affinity for water; tending to coalesce and form droplets in water.

hydrophobic interaction (hī′-drō-fō′-bik) A type of weak chemical interaction caused when molecules that do not mix with water coalesce to exclude water.

hydroponic culture A method in which plants are grown in mineral solutions rather than in soil.

hydrostatic skeleton A skeletal system composed of fluid held under pressure in a closed body compartment; the main skeleton of most cnidarians, flatworms, nematodes, and annelids.

hydrothermal vent An area on the seafloor where heated water and minerals from Earth's interior gush into the seawater, producing a dark, hot, oxygen-deficient environment. The producers in a hydrothermal vent community are chemoautotrophic prokaryotes.

hydroxide ion A water molecule that has lost a proton; OH^-.

hydroxyl group (hī-drok′-sil) A chemical group consisting of an oxygen atom joined to a hydrogen atom. Molecules possessing this group are soluble in water and are called alcohols.

hyperpolarization A change in a cell's membrane potential such that the inside of the membrane becomes more negative relative to the outside. Hyperpolarization reduces the chance that a neuron will transmit a nerve impulse.

hypersensitive response A plant's localized defense response to a pathogen, involving the death of cells around the site of infection.

hypertension A disorder in which blood pressure remains abnormally high.

hypertonic Referring to a solution that, when surrounding a cell, will cause the cell to lose water.

hypha (plural, **hyphae**) (hī′-fuh, hī′-fē) One of many connected filaments that collectively make up the mycelium of a fungus.

hypocotyl (hī′-puh-cot′-ul) In an angiosperm embryo, the embryonic axis below the point of attachment of the cotyledon(s) and above the radicle.

hypothalamus (hī′-pō-thal′-uh-mus) The ventral part of the vertebrate forebrain; functions in maintaining homeostasis, especially in coordinating the endocrine and nervous systems; secretes hormones of the posterior pituitary and releasing factors that regulate the anterior pituitary.

hypothesis (hī-poth′-uh-sis) A testable explanation for a set of observations based on the available data and guided by inductive reasoning. A hypothesis is narrower in scope than a theory.

hypotonic Referring to a solution that, when surrounding a cell, will cause the cell to take up water.

imbibition The uptake of water by a seed or other structure, resulting in swelling.

immigration The influx of new individuals into a population from other areas.

immune system An organism's system of defenses against agents that cause disease.

immunization The process of generating a state of immunity by artificial means. In vaccination, an inactive or weakened form of a pathogen is administered, inducing B and T cell responses and immunological memory. In passive immunization, antibodies specific for a particular pathogen are administered, conferring immediate but temporary protection.

immunoglobulin (Ig) (im′-yū-nō-glob′-yū-lin) *See* antibody.

imprinting In animal behavior, the formation at a specific stage in life of a long-lasting behavioral response to a specific individual or object. *See also* genomic imprinting.

inclusive fitness The total effect an individual has on proliferating its genes by producing its own offspring and by providing aid that enables other close relatives to increase production of their offspring.

incomplete dominance The situation in which the phenotype of heterozygotes is intermediate between the phenotypes of individuals homozygous for either allele.

incomplete flower A flower in which one or more of the four basic floral organs (sepals, petals, stamens, or carpels) are either absent or nonfunctional.

incomplete metamorphosis A type of development in certain insects, such as grasshoppers, in which the young (called nymphs) resemble adults but are smaller and have different body proportions. The nymph goes through a series of molts, each time looking more like an adult, until it reaches full size.

independent variable A factor whose value is manipulated or changed during an experiment to reveal possible effects on another factor (the dependent variable).

indeterminate cleavage A type of embryonic development in deuterostomes in which each cell produced by early cleavage divisions retains the capacity to develop into a complete embryo.

indeterminate growth A type of growth characteristic of plants, in which the organism continues to grow as long as it lives.

induced fit Caused by entry of the substrate, the change in shape of the active site of an enzyme so that it binds more snugly to the substrate.

inducer A specific small molecule that binds to a bacterial repressor protein and changes the repressor's shape so that it cannot bind to an operator, thus switching an operon on.

induction A process in which a group of cells or tissues influences the development of another group through close-range interactions.

inductive reasoning A type of logic in which generalizations are based on a large number of specific observations.

inflammatory response An innate immune defense triggered by physical injury or infection of tissue involving the release of substances that promote swelling, enhance the infiltration of white blood cells, and aid in tissue repair and destruction of invading pathogens.

inflorescence A group of flowers tightly clustered together.

ingestion The first stage of food processing in animals: the act of eating.

ingroup A species or group of species whose evolutionary relationships are being examined in a given analysis.

inhibitory postsynaptic potential (IPSP) An electrical change (usually hyperpolarization) in the membrane of a postsynaptic neuron caused by the binding of an inhibitory neurotransmitter from a presynaptic cell to a postsynaptic receptor; makes it more difficult for a postsynaptic neuron to generate an action potential.

innate behavior Animal behavior that is developmentally fixed and under strong genetic control. Innate behavior is exhibited in virtually the same form by all individuals in a population despite internal and external environmental differences during development and throughout their lifetimes.

innate immunity A form of defense common to all animals that is active immediately upon exposure to a pathogen and that is the same whether or not the pathogen has been encountered previously.

inner cell mass An inner cluster of cells at one end of a mammalian blastocyst that subsequently develops into the embryo proper and some of the extraembryonic membranes.

inner ear One of the three main regions of the vertebrate ear; includes the cochlea (which in turn contains the organ of Corti) and the semicircular canals.

inositol trisphosphate (IP_3) (in-ō′-suh-tol) A second messenger that functions as an intermediate between certain signaling molecules and a subsequent second messenger, Ca^{2+}, by causing a rise in cytoplasmic Ca^{2+} concentration.

inquiry The search for information and explanation, often focusing on specific questions.

insertion A mutation involving the addition of one or more nucleotide pairs to a gene.

***in situ* hybridization** A technique using nucleic acid hybridization with a labeled probe to detect the location of a specific mRNA in an intact organism.

insulin (in′-suh-lin) A hormone secreted by pancreatic beta cells that lowers blood glucose levels. It promotes the uptake of glucose by most body cells and the synthesis and storage of glycogen in the liver and also stimulates protein and fat synthesis.

integral protein A transmembrane protein with hydrophobic regions that extend into and often completely span the hydrophobic interior of the membrane and with hydrophilic regions in contact with the aqueous solution on one or both sides of the membrane (or lining the channel in the case of a channel protein).

integrin (in′-tuh-grin) In animal cells, a transmembrane receptor protein with two subunits that interconnects the extracellular matrix and the cytoskeleton.

integument (in-teg′-yū-ment) Layer of sporophyte tissue that contributes to the structure of an ovule of a seed plant.

integumentary system The outer covering of a mammal's body, including skin, hair, and nails, claws, or hooves.

interferon (in′-ter-fēr′-on) A protein that has antiviral or immune regulatory functions. For example, interferons secreted by virus-infected cells help nearby cells resist viral infection.

intermediate disturbance hypothesis The concept that moderate levels of disturbance can foster greater species diversity than low or high levels of disturbance.

intermediate filament A component of the cytoskeleton that includes filaments intermediate in size between microtubules and microfilaments.

interneuron An association neuron; a nerve cell within the central nervous system that forms synapses with sensory and/or motor neurons and integrates sensory input and motor output.

internode A segment of a plant stem between the points where leaves are attached.

interphase The period in the cell cycle when the cell is not dividing. During interphase, cellular metabolic activity is high, chromosomes and organelles are duplicated, and cell size may increase. Interphase often accounts for about 90% of the cell cycle.

intersexual selection A form of natural selection in which individuals of one sex (usually the females) are choosy in selecting their mates from the other sex; also called mate choice.

interspecific interaction A relationship between individuals of two or more species in a community.

interstitial fluid The fluid filling the spaces between cells in most animals.

intertidal zone The shallow zone of the ocean adjacent to land and between the high- and low-tide lines.

intrasexual selection A form of natural selection in which there is direct competition among individuals of one sex for mates of the opposite sex.

intrinsic rate of increase (*r*) In population models, the per capita rate at which an exponentially growing population increases in size at each instant in time.

introduced species A species moved by humans, either intentionally or accidentally, from its native location to a new geographic region; also called non-native or exotic species.

intron (in′-tron) A noncoding, intervening sequence within a primary transcript that is removed from the transcript during RNA processing; also refers to the region of DNA from which this sequence was transcribed.

invasive species A species, often introduced by humans, that takes hold outside its native range.

inversion An aberration in chromosome structure resulting from reattachment of a chromosomal fragment in a reverse orientation to the chromosome from which it originated.

invertebrate An animal without a backbone. Invertebrates make up 95% of animal species.

***in vitro* fertilization (IVF)** (vē′-trō) Fertilization of oocytes in laboratory containers followed by artificial implantation of the early embryo in the mother's uterus.

***in vitro* mutagenesis** A technique used to discover the function of a gene by cloning it, introducing specific changes into the cloned gene's sequence, reinserting the mutated gene into a cell, and studying the phenotype of the mutant.

ion (ī′-on) An atom or group of atoms that has gained or lost one or more electrons, thus acquiring a charge.

ion channel (ī′-on) A transmembrane protein channel that allows a specific ion to diffuse across the membrane down its concentration or electrochemical gradient.

ionic bond (ī-on′-ik) A chemical bond resulting from the attraction between oppositely charged ions.

ionic compound (ī-on′-ik) A compound resulting from the formation of an ionic bond; also called a salt.

iris The colored part of the vertebrate eye, formed by the anterior portion of the choroid.

isomer (ī′-sō-mer) One of two or more compounds that have the same numbers of atoms of the same elements but different structures and hence different properties.

isomorphic Referring to alternating generations in plants and certain algae in which the sporophytes and gametophytes look alike, although they differ in chromosome number.

isotonic (ī′-sō-ton′-ik) Referring to a solution that, when surrounding a cell, causes no net movement of water into or out of the cell.

isotope (ī′-sō-tōp′) One of several atomic forms of an element, each with the same number of protons but a different number of neutrons, thus differing in atomic mass.

iteroparity Reproduction in which adults produce offspring over many years; also called repeated reproduction.

jasmonate Any of a class of plant hormones that regulate a wide range of developmental processes in plants and play a key role in plant defense against herbivores.

joule (J) A unit of energy: 1 J = 0.239 cal; 1 cal = 4.184 J.

juxtaglomerular apparatus (JGA) (juks′-tuh-gluh-mār′-yū-ler) A specialized tissue in nephrons that releases the enzyme renin in response to a drop in blood pressure or volume.

juxtamedullary nephron In mammals and birds, a nephron with a loop of Henle that extends far into the renal medulla.

karyogamy (kār′-ē-og′-uh-mē) In fungi, the fusion of haploid nuclei contributed by the two parents; occurs as one stage of sexual reproduction, preceded by plasmogamy.

karyotype (kār′-ē-ō-tīp) A display of the chromosome pairs of a cell arranged by size and shape.

keystone species A species that is not necessarily abundant in a community yet exerts strong control on community structure by the nature of its ecological role or niche.

kidney In vertebrates, one of a pair of excretory organs where blood filtrate is formed and processed into urine.

kilocalorie (kcal) A thousand calories; the amount of heat energy required to raise the temperature of 1 kg of water by 1°C.

kinetic energy (kuh-net′-ik) The energy associated with the relative motion of objects. Moving matter can perform work by imparting motion to other matter.

kinetochore (kuh-net′-uh-kōr) A structure of proteins attached to the centromere that links each sister chromatid to the mitotic spindle.

kinetoplastid A protist, such as a trypanosome, that has a single large mitochondrion that houses an organized mass of DNA.

kingdom A taxonomic category, the second broadest after domain.

kin selection Natural selection that favors altruistic behavior by enhancing the reproductive success of relatives.

***K*-selection** Selection for life history traits that are sensitive to population density; also called density-dependent selection.

labia majora A pair of thick, fatty ridges that encloses and protects the rest of the vulva.

labia minora A pair of slender skin folds that surrounds the openings of the vagina and urethra.

lacteal (lak′-tē-ul) A tiny lymph vessel extending into the core of an intestinal villus and serving as the destination for absorbed chylomicrons.

lactic acid fermentation Glycolysis followed by the reduction of pyruvate to lactate, regenerating NAD^+ with no release of carbon dioxide.

lagging strand A discontinuously synthesized DNA strand that elongates by means of Okazaki fragments, each synthesized in a $5' \rightarrow 3'$ direction away from the replication fork.

lamprey Any of the jawless vertebrates with highly reduced vertebrae that live in freshwater and marine environments. Almost half of extant lamprey species are parasites that feed by clamping their round, jawless mouth onto the flank of a live fish; nonparasitic lampreys are suspension feeders that feed only as larvae.

lancelet A member of the clade Cephalochordata, small blade-shaped marine chordates that lack a backbone.

landscape An area containing several different ecosystems linked by exchanges of energy, materials, and organisms.

landscape ecology The study of how the spatial arrangement of habitat types affects the distribution and abundance of organisms and ecosystem processes.

large intestine The portion of the vertebrate alimentary canal between the small intestine and the anus; functions mainly in water absorption and the formation of feces.

larva (lar′-vuh) (plural, **larvae**) A free-living, sexually immature form in some animal life cycles that may differ from the adult animal in morphology, nutrition, and habitat.

larynx (lār′-inks) The portion of the respiratory tract containing the vocal cords; also called the voice box.

lateralization Segregation of functions in the cortex of the left and right cerebral hemispheres.

lateral line system A mechanoreceptor system consisting of a series of pores and receptor units along the sides of the body in fishes and aquatic amphibians; detects water movements made by the animal itself and by other moving objects.

lateral meristem (mār′-uh-stem) A meristem that thickens the roots and shoots of woody plants. The vascular cambium and cork cambium are lateral meristems.

lateral root A root that arises from the pericycle of an established root.

law of conservation of mass A physical law stating that matter can change form but cannot be created or destroyed. In a closed system, the mass of the system is constant.

law of independent assortment Mendel's second law, stating that each pair of alleles segregates, or assorts, independently of each other pair during gamete formation; applies when genes for two characters are located on different pairs of homologous chromosomes or when they are far enough apart on the same chromosome to behave as though they are on different chromosomes.

law of segregation Mendel's first law, stating that the two alleles in a pair segregate (separate from each other) into different gametes during gamete formation.

leading strand The new complementary DNA strand synthesized continuously along the template strand toward the replication fork in the mandatory $5' \rightarrow 3'$ direction.

leaf The main photosynthetic organ of vascular plants.

leaf primordium (plural, **primordia**) A finger-like projection along the flank of a shoot apical meristem, from which a leaf arises.

learning The modification of behavior as a result of specific experiences.

lens The structure in an eye that focuses light rays onto the photoreceptors.

lenticel (len′-ti-sel) A small raised area in the bark of stems and roots that enables gas exchange between living cells and the outside air.

lepidosaur (leh-pid′-uh-sōr) A member of the reptilian group that includes lizards, snakes, and two species of New Zealand animals called tuataras.

leukocyte (lū′-kō-sīt′) A blood cell that functions in fighting infections; also called a white blood cell.

lichen The mutualistic association between a fungus and a photosynthetic alga or cyanobacterium.

life cycle The generation-to-generation sequence of stages in the reproductive history of an organism.

life history The traits that affect an organism's schedule of reproduction and survival.

life table A summary of the age-specific survival and reproductive rates of individuals in a population.

ligament A fibrous connective tissue that joins bones together at joints.

ligand (lig′-und) A molecule that binds specifically to another molecule, usually a larger one.

ligand-gated ion channel (lig′-und) A transmembrane protein containing a pore that opens or closes as it changes shape in response to a signaling molecule (ligand), allowing or blocking the flow of specific ions; also called an ionotropic receptor.

light chain One of the two types of polypeptide chains that make up an antibody molecule and B cell receptor; consists of a variable region, which contributes to the antigen-binding site, and a constant region.

light-harvesting complex A complex of proteins associated with pigment molecules (including chlorophyll *a*, chlorophyll *b*, and carotenoids) that captures light energy and transfers it to reaction-center pigments in a photosystem.

light microscope (LM) An optical instrument with lenses that refract (bend) visible light to magnify images of specimens.

light reactions The first of two major stages in photosynthesis (preceding the Calvin cycle). These reactions, which occur on the thylakoid membranes of the chloroplast or on membranes of certain prokaryotes, convert solar energy to the chemical energy of ATP and NADPH, releasing oxygen in the process.

lignin (lig′-nin) A strong polymer embedded in the cellulose matrix of the secondary cell walls of vascular plants that provides structural support in terrestrial species.

limiting nutrient An element that must be added for production to increase in a particular area.

limnetic zone In a lake, the well-lit, open surface waters far from shore.

linear electron flow A route of electron flow during the light reactions of photosynthesis that involves both photosystems (I and II) and produces ATP, NADPH, and O_2. The net electron flow is from H_2O to $NADP^+$.

line graph A graph in which each data point is connected to the next point in the data set with a straight line.

linkage map A genetic map based on the frequencies of recombination between markers during crossing over of homologous chromosomes.

linked genes Genes located close enough together on a chromosome that they tend to be inherited together.

lipid (lip′-id) Any of a group of large biological molecules, including fats, phospholipids, and steroids, that mix poorly, if at all, with water.

littoral zone In a lake, the shallow, well-lit waters close to shore.

liver A large internal organ in vertebrates that performs diverse functions, such as producing bile, maintaining blood glucose level, and detoxifying poisonous chemicals in the blood.

liverwort A small, herbaceous, nonvascular plant that is a member of the phylum Hepatophyta.

loam The most fertile soil type, made up of roughly equal amounts of sand, silt, and clay.

lobe-fin Member of a clade of osteichthyans having rod-shaped muscular fins. The group includes coelacanths, lungfishes, and tetrapods.

local regulator A secreted molecule that influences cells near where it is secreted.

locomotion Active motion from place to place.

locus (lō′-kus) (plural, **loci**) (lō′-sī) A specific place along the length of a chromosome where a given gene is located.

logistic population growth Population growth that levels off as population size approaches carrying capacity.

long-day plant A plant that flowers (usually in late spring or early summer) only when the light period is longer than a critical length.

long noncoding RNA (lncRNA) An RNA between 200 and hundreds of thousands of nucleotides in length that does not code for protein but is expressed at significant levels.

long-term memory The ability to hold, associate, and recall information over one's lifetime.

long-term potentiation (LTP) An enhanced responsiveness to an action potential (nerve signal) by a receiving neuron.

loop of Henle (hen′-lē) The hairpin turn, with a descending and ascending limb, between the proximal and distal tubules of the vertebrate kidney; functions in water and salt reabsorption.

lophophore (lof′-uh-fōr) In some lophotrochozoan animals, including brachiopods, a crown of ciliated tentacles that surround the mouth and function in feeding.

Lophotrochozoa (lo-phah′-truh-kō-zō′-uh) One of the three main lineages of bilaterian animals; lophotrochozoans include organisms that have lophophores or trochophore larvae. *See also* Deuterostomia and Ecdysozoa.

low-density lipoprotein (LDL) A particle in the blood made up of thousands of cholesterol molecules and other lipids bound to a protein. LDL transports cholesterol from the liver for incorporation into cell membranes.

lung An infolded respiratory surface of a terrestrial vertebrate, land snail, or spider that connects to the atmosphere by narrow tubes.

luteinizing hormone (LH) (lū′-tē-uh-nī′-zing) A tropic hormone that is produced and secreted by the anterior pituitary and that stimulates ovulation in females and androgen production in males.

lycophyte (lī′-kuh-fīt) An informal name for a member of the phylum Lycophyta, which includes club mosses, spike mosses, and quillworts.

lymph The colorless fluid, derived from interstitial fluid, in the lymphatic system of vertebrates.

lymph node An organ located along a lymph vessel. Lymph nodes filter lymph and contain cells that attack viruses and bacteria.

lymphatic system A system of vessels and nodes, separate from the circulatory system, that returns fluid, proteins, and cells to the blood.

lymphocyte A type of white blood cell that mediates immune responses. The two main classes are B cells and T cells.

lysogenic cycle (lī′-sō-jen′-ik) A type of phage replicative cycle in which the viral genome becomes incorporated into the bacterial host chromosome as a prophage, is replicated along with the chromosome, and does not kill the host.

lysosome (lī′-suh-sōm) A membrane-enclosed sac of hydrolytic enzymes found in the cytoplasm of animal cells and some protists.

lysozyme (lī′-sō-zīm) An enzyme that destroys bacterial cell walls; in mammals, it is found in sweat, tears, and saliva.

lytic cycle (lit′-ik) A type of phage replicative cycle resulting in the release of new phages by lysis (and death) of the host cell.

macroevolution Evolutionary change above the species level. Examples of macroevolutionary change include the origin of a new group of organisms through a series of speciation events and the impact of mass extinctions on the diversity of life and its subsequent recovery.

macromolecule A giant molecule formed by the joining of smaller molecules, usually by a dehydration reaction. Polysaccharides, proteins, and nucleic acids are macromolecules.

macronutrient An essential element that an organism must obtain in relatively large amounts. *See also* micronutrient.

macrophage (mak′-rō-fāj) A phagocytic cell present in many tissues that functions in innate immunity by destroying microbes and in acquired immunity as an antigen-presenting cell.

magnoliid A member of the angiosperm clade that is most closely related to the combined eudicot and monocot clades. Extant examples are magnolias, laurels, and black pepper plants.

major depressive disorder A mood disorder characterized by feelings of sadness, lack of self-worth, emptiness, or loss of interest in nearly all things.

major histocompatibility complex (MHC) molecule A host protein that functions in antigen presentation. Foreign MHC molecules on transplanted tissue can trigger T cell responses that may lead to rejection of the transplant.

malignant tumor A cancerous tumor containing cells that have significant genetic and cellular changes and are capable of invading and surviving in new sites. Malignant tumors can impair the functions of one or more organs.

Malpighian tubule (mal-pig′-ē-un) A unique excretory organ of insects that empties into the digestive tract, removes nitrogenous wastes from the hemolymph, and functions in osmoregulation.

mammal A member of the clade Mammalia, amniotes that have hair and mammary glands (glands that produce milk).

mammary gland An exocrine gland that secretes milk for nourishing the young. Mammary glands are characteristic of mammals.

mantle One of the three main parts of a mollusc; a fold of tissue that drapes over the mollusc's visceral mass and may secrete a shell. *See also* foot and visceral mass.

mantle cavity A water-filled chamber that houses the gills, anus, and excretory pores of a mollusc.

map unit A unit of measurement of the distance between genes. One map unit is equivalent to a 1% recombination frequency.

marine benthic zone The ocean floor.

mark-recapture method A sampling technique used to estimate the size of animal populations.

marsupial (mar-sū′-pē-ul) A mammal, such as a koala, kangaroo, or opossum, whose young complete their embryonic development inside a maternal pouch called the marsupium.

mass extinction The elimination of a large number of species throughout Earth, the result of global environmental changes.

mass number The total number of protons and neutrons in an atom's nucleus.

mate-choice copying Behavior in which individuals in a population copy the mate choice of others, apparently as a result of social learning.

maternal effect gene A gene that, when mutant in the mother, results in a mutant phenotype in the offspring, regardless of the offspring's genotype. Maternal effect genes, also called egg-polarity genes, were first identified in *Drosophila melanogaster*.

matter Anything that takes up space and has mass.

maximum likelihood As applied to DNA sequence data, a principle that states that when considering multiple phylogenetic hypotheses, one should take into account the hypothesis that reflects the most likely sequence of evolutionary events, given certain rules about how DNA changes over time.

maximum parsimony A principle that states that when considering multiple explanations for an observation, one should first investigate the simplest explanation that is consistent with the facts.

mean The sum of all data points in a data set divided by the number of data points.

mechanoreceptor A sensory receptor that detects physical deformation in the body's environment associated with pressure, touch, stretch, motion, or sound.

medulla oblongata (meh-dul′-uh ob′-long-go′-tuh) The lowest part of the vertebrate brain, commonly called the medulla; a swelling of the hindbrain anterior to the spinal cord that controls autonomic, homeostatic functions, including breathing, heart and blood vessel activity, swallowing, digestion, and vomiting.

medusa (plural, **medusae**) (muh-dū′-suh) The floating, flattened, mouth-down version of the cnidarian body plan. The alternate form is the polyp.

megapascal (MPa) (meg′-uh-pas-kal′) A unit of pressure equivalent to about 10 atmospheres of pressure.

megaphyll (meh′-guh-fil) A leaf with a highly branched vascular system, found in almost all vascular plants other than lycophytes. *See also* microphyll.

megaspore A spore from a heterosporous plant species that develops into a female gametophyte.

meiosis (mī-ō′-sis) A modified type of cell division in sexually reproducing organisms consisting of two rounds of cell division but only one round of DNA replication. It results in cells with half the number of chromosome sets as the original cell.

meiosis I (mī-ō′-sis) The first division of a two-stage process of cell division in sexually reproducing organisms that results in cells with half the number of chromosome sets as the original cell.

meiosis II (mī-ō′-sis) The second division of a two-stage process of cell division in sexually reproducing organisms that results in cells with half the number of chromosome sets as the original cell.

melanocyte-stimulating hormone (MSH) A hormone produced and secreted by the anterior pituitary with multiple activities, including regulating the behavior of pigment-containing cells in the skin of some vertebrates.

melatonin A hormone that is secreted by the pineal gland and that is involved in the regulation of biological rhythms and sleep.

membrane potential The difference in electrical charge (voltage) across a cell's plasma membrane due to the differential distribution of ions. Membrane potential affects the activity of excitable cells and the transmembrane movement of all charged substances.

memory cell One of a clone of long-lived lymphocytes, formed during the primary immune response, that remains in a lymphoid organ until activated by exposure to the same antigen that triggered its formation. Activated memory cells mount the secondary immune response.

menopause The cessation of ovulation and menstruation marking the end of a human female's reproductive years.

menstrual cycle (men′-strū-ul) In humans and certain other primates, the periodic growth and shedding of the uterine lining that occurs in the absence of pregnancy.

menstruation The shedding of portions of the endometrium during a uterine (menstrual) cycle.

meristem (mār′-uh-stem) Plant tissue that remains embryonic as long as the plant lives, allowing for indeterminate growth.

meristem identity gene (mār′-uh-stem) A plant gene that promotes the switch from vegetative growth to flowering.

mesoderm (mez′-ō-derm) The middle primary germ layer in a triploblastic animal embryo; develops into the notochord, the lining of the coelom, muscles, skeleton, gonads, kidneys, and most of the circulatory system in species that have these structures.

mesohyl (mez′-ō-hīl) A gelatinous region between the two layers of cells of a sponge.

mesophyll (mez′-ō-fil) Leaf cells specialized for photosynthesis. In C_3 and CAM plants, mesophyll cells are located between the upper and lower epidermis; in C_4 plants, they are located between the bundle-sheath cells and the epidermis.

messenger RNA (mRNA) A type of RNA, synthesized using a DNA template, that attaches to ribosomes in the cytoplasm and specifies the primary structure of a protein. (In eukaryotes, the primary RNA transcript must undergo RNA processing to become mRNA.)

metabolic pathway A series of chemical reactions that either builds a complex molecule (anabolic pathway) or breaks down a complex molecule to simpler molecules (catabolic pathway).

metabolic rate The total amount of energy an animal uses in a unit of time.

metabolism (muh-tab′-uh-lizm) The totality of an organism's chemical reactions, consisting of catabolic and anabolic pathways, which manage the material and energy resources of the organism.

metagenomics The collection and sequencing of DNA from a group of species, usually an environmental sample of microorganisms. Computer software sorts partial sequences and assembles them into genome sequences of individual species making up the sample.

metamorphosis (met′-uh-mōr′-fuh-sis) A developmental transformation that turns an animal larva into either an adult or an adult-like stage that is not yet sexually mature.

metanephridium (met′-uh-nuh-frid′-ē-um) (plural, **metanephridia**) An excretory organ found in many invertebrates that typically consists of tubules connecting ciliated internal openings to external openings.

metaphase The third stage of mitosis, in which the spindle is complete and the chromosomes, attached to microtubules at their kinetochores, are all aligned at the metaphase plate.

metaphase plate An imaginary structure located at a plane midway between the two poles of a cell in metaphase on which the centromeres of all the duplicated chromosomes are located.

metapopulation A group of spatially separated populations of one species that interact through immigration and emigration.

metastasis (muh-tas′-tuh-sis) The spread of cancer cells to locations distant from their original site.

methanogen (meth-an′-ō-jen) An organism that produces methane as a waste product of the way it obtains energy. All known methanogens are in domain Archaea.

methyl group A chemical group consisting of a carbon bonded to three hydrogen atoms. The methyl group may be attached to a carbon or to a different atom.

microbiome The collection of microorganisms living in or on an organism's body, along with their genetic material.

microclimate Climate patterns on a very fine scale, such as the specific climatic conditions underneath a log.

microevolution Evolutionary change below the species level; change in the allele frequencies in a population over generations.

microfilament A cable composed of actin proteins in the cytoplasm of almost every eukaryotic cell, making up part of the cytoskeleton and acting alone or with myosin to cause cell contraction; also called an actin filament.

micronutrient An essential element that an organism needs in very small amounts. *See also* macronutrient.

microphyll (mī′-krō-fil) A small, usually spine-shaped leaf supported by a single strand of vascular tissue, found only in lycophytes.

micropyle A pore in the integuments of an ovule.

microRNA (miRNA) A small, single-stranded RNA molecule, generated from a double-stranded RNA precursor. The miRNA associates with one or more proteins in a complex that can degrade or prevent translation of an mRNA with a complementary sequence.

microspore A spore from a heterosporous plant species that develops into a male gametophyte.

microtubule A hollow rod composed of tubulin proteins that makes up part of the cytoskeleton in all eukaryotic cells and is found in cilia and flagella.

microvillus (plural, **microvilli**) One of many fine, finger-like projections of the epithelial cells in the lumen of the small intestine that increase its surface area.

midbrain One of three ancestral and embryonic regions of the vertebrate brain; develops into sensory integrating and relay centers that send sensory information to the cerebrum.

middle ear One of three main regions of the vertebrate ear; in mammals, a chamber containing three small bones (the malleus, incus, and stapes) that convey vibrations from the eardrum to the oval window.

middle lamella (luh-mel′-uh) In plants, a thin layer of adhesive extracellular material, primarily pectins, found between the primary walls of adjacent young cells.

migration A regular, long-distance change in location.

mineral In nutrition, a simple nutrient that is inorganic and therefore cannot be synthesized in the body.

mineralocorticoid A steroid hormone secreted by the adrenal cortex that regulates salt and water homeostasis.

minimum viable population (MVP) The smallest population size at which a species is able to sustain its numbers and survive.

mismatch repair The cellular process that uses specific enzymes to remove and replace incorrectly paired nucleotides.

missense mutation A nucleotide-pair substitution that results in a codon that codes for a different amino acid.

mitochondrial matrix The compartment of the mitochondrion enclosed by the inner membrane and containing enzymes and substrates for the citric acid cycle, as well as ribosomes and DNA.

mitochondrion (mī′-tō-kon′-drē-un) (plural, **mitochondria**) An organelle in eukaryotic cells that serves as the site of cellular respiration; uses oxygen to break down organic molecules and synthesize ATP.

mitosis (mī-tō′-sis) A process of nuclear division in eukaryotic cells conventionally divided into five stages: prophase, prometaphase, metaphase, anaphase, and telophase. Mitosis conserves chromosome number by allocating replicated chromosomes equally to each of the daughter nuclei.

mitotic (M) phase The phase of the cell cycle that includes mitosis and cytokinesis.

mitotic spindle An assemblage of microtubules and associated proteins that is involved in the movement of chromosomes during mitosis.

mixotroph An organism that is capable of both photosynthesis and heterotrophy.

model A physical or conceptual representation of a natural phenomenon.

model organism A particular species chosen for research into broad biological principles because it is representative of a larger group and usually easy to grow in a lab.

molarity A common measure of solute concentration, referring to the number of moles of solute per liter of solution.

mold Informal term for a fungus that grows as a filamentous fungus, producing haploid spores by mitosis and forming a visible mycelium.

mole (mol) The number of grams of a substance that equals its molecular or atomic mass in daltons; a mole contains Avogadro's number of the molecules or atoms in question.

molecular clock A method for estimating the time required for a given amount of evolutionary change, based on the observation that some regions of genomes evolve at constant rates.

molecular mass The sum of the masses of all the atoms in a molecule; sometimes called molecular weight.

molecule Two or more atoms held together by covalent bonds.

molting A process in ecdysozoans in which the exoskeleton is shed at intervals, allowing growth by the production of a larger exoskeleton.

monilophyte An informal name for a member of the phylum Monilophyta, which includes ferns, horsetails, and whisk ferns and their relatives.

monoclonal antibody (mon′-ō-klōn′-ul) Any of a preparation of antibodies that have been produced by a single clone of cultured cells and thus are all specific for the same epitope.

monocot A member of a clade consisting of flowering plants that have one embryonic seed leaf, or cotyledon.

monogamous (muh-nog′-uh-mus) Referring to a type of relationship in which one male mates with just one female.

monohybrid An organism that is heterozygous with respect to a single gene of interest. All the offspring from a cross between parents homozygous for different alleles are monohybrids. For example, parents of genotypes *AA* and *aa* produce a monohybrid of genotype *Aa*.

monohybrid cross A cross between two organisms that are heterozygous for the character being followed (or the self-pollination of a heterozygous plant).

monomer (mon′-uh-mer) The subunit that serves as the building block of a polymer.

monophyletic (mon′-ō-fī-let′-ik) Pertaining to a group of taxa that consists of a common ancestor and all of its descendants. A monophyletic taxon is equivalent to a clade.

monosaccharide (mon′-ō-sak′-uh-rīd) The simplest carbohydrate, active alone or serving as a monomer for disaccharides and polysaccharides. Also called simple sugars, monosaccharides have molecular formulas that are generally some multiple of CH_2O.

monosomic Referring to a diploid cell that has only one copy of a particular chromosome instead of the normal two.

monotreme An egg-laying mammal, such as a platypus or echidna. Like all mammals, monotremes have hair and produce milk, but they lack nipples.

morphogen A substance, such as Bicoid protein in *Drosophila*, that provides positional information in the form of a concentration gradient along an embryonic axis.

morphogenesis (mōr′-fō-jen′-uh-sis) The development of the form of an organism and its structures.

morphological species concept Definition of a species in terms of measurable anatomical criteria.

moss A small, herbaceous, nonvascular plant that is a member of the phylum Bryophyta.

motor neuron A nerve cell that transmits signals from the brain or spinal cord to muscles or glands.

motor protein A protein that interacts with cytoskeletal elements and other cell components, producing movement of the whole cell or parts of the cell.

motor system An efferent branch of the vertebrate peripheral nervous system composed of motor neurons that carry signals to skeletal muscles in response to external stimuli.

motor unit A single motor neuron and all the muscle fibers it controls.

movement corridor A series of small clumps or a narrow strip of quality habitat (usable by organisms) that connects otherwise isolated patches of quality habitat.

MPF Maturation-promoting factor (or M-phase-promoting factor); a protein complex required for a cell to progress from late interphase to mitosis. The active form consists of cyclin and a protein kinase.

mucus A viscous and slippery mixture of glycoproteins, cells, salts, and water that moistens and protects the membranes lining body cavities that open to the exterior.

Müllerian mimicry (myū-lār′-ē-un mim′-uh-krē) Reciprocal mimicry by two unpalatable species.

multifactorial Referring to a phenotypic character that is influenced by multiple genes and environmental factors.

multigene family A collection of genes with similar or identical sequences, presumably of common origin.

multiple fruit A fruit derived from an entire inflorescence.

multiplication rule A rule of probability stating that the probability of two or more independent events occurring together can be determined by multiplying their individual probabilities.

muscle tissue Tissue consisting of long muscle cells that can contract, either on its own or when stimulated by nerve impulses.

mutagen (myū′-tuh-jen) A chemical or physical agent that interacts with DNA and can cause a mutation.

mutation (myū-tā′-shun) A change in the nucleotide sequence of an organism's DNA or in the DNA or RNA of a virus.

mutualism (myū′-chū-ul-izm) A +/+ ecological interaction that benefits each of the interacting species.

mycelium (mī-sē′-lē-um) The densely branched network of hyphae in a fungus.

mycorrhiza (plural, **mycorrhizae**) (mī′-kō-rī′-zuh, mī′-kō-rī′-zē) A mutualistic association of plant roots and fungus.

mycosis (mī-kō′-sis) General term for a fungal infection.

myelin sheath (mī′-uh-lin) Wrapped around the axon of a neuron, an insulating coat of cell membranes from Schwann cells or oligodendrocytes. It is interrupted by nodes of Ranvier, where action potentials are generated.

myofibril (mī′-ō-fī′-bril) A longitudinal bundle in a muscle cell (fiber) that contains thin filaments of actin and regulatory proteins and thick filaments of myosin.

myoglobin (mī′-uh-glō′-bin) An oxygen-storing, pigmented protein in muscle cells.

myosin (mī′-uh-sin) A type of motor protein that associates into filaments that interact with actin filaments to cause cell contraction.

myriapod (mir′-ē-uh-pod′) A terrestrial arthropod with many body segments and one or two pairs of legs per segment. Millipedes and centipedes are the two major groups of living myriapods.

NAD^+ The oxidized form of nicotinamide adenine dinucleotide, a coenzyme that can accept electrons, becoming NADH. NADH temporarily stores electrons during cellular respiration.

NADH The reduced form of nicotinamide adenine dinucleotide that temporarily stores electrons during cellular respiration. NADH acts as an electron donor to the electron transport chain.

$NADP^+$ The oxidized form of nicotinamide adenine dinucleotide phosphate, an electron carrier that can accept electrons, becoming NADPH. NADPH temporarily stores energized electrons produced during the light reactions.

NADPH The reduced form of nicotinamide adenine dinucleotide phosphate; temporarily stores energized electrons produced during the light reactions. NADPH acts as "reducing power" that can be passed along to an electron acceptor, reducing it.

natural killer cell A type of white blood cell that can kill tumor cells and virus-infected cells as part of innate immunity.

natural selection A process in which individuals that have certain inherited traits tend to survive and reproduce at higher rates than other individuals because of those traits.

negative feedback A form of regulation in which accumulation of an end product of a process slows the process; in physiology, a primary mechanism of homeostasis, whereby a change in a variable triggers a response that counteracts the initial change.

negative pressure breathing A breathing system in which air is pulled into the lungs.

nematocyst (nem′-uh-tuh-sist′) In a cnidocyte of a cnidarian, a capsule-like organelle containing a coiled thread that when discharged can penetrate the body wall of the prey.

nephron (nef′-ron) The tubular excretory unit of the vertebrate kidney.

neritic zone The shallow region of the ocean overlying the continental shelf.

nerve A fiber composed primarily of the bundled axons of neurons.

nervous system In animals, the fast-acting internal system of communication involving sensory receptors, networks of nerve cells, and connections to muscles and glands that respond to nerve signals; functions in concert with the endocrine system to effect internal regulation and maintain homeostasis.

nervous tissue Tissue made up of neurons and supportive cells.

net ecosystem production (NEP) The gross primary production of an ecosystem minus the energy used by all autotrophs and heterotrophs for respiration.

net primary production (NPP) The gross primary production of an ecosystem minus the energy used by the producers for respiration.

neural crest In vertebrates, a region located along the sides of the neural tube where it pinches off from the ectoderm. Neural crest cells migrate to various parts of the embryo and form pigment cells in the skin and parts of the skull, teeth, adrenal glands, and peripheral nervous system.

neural tube A tube of infolded ectodermal cells that runs along the anterior-posterior axis of a vertebrate, just dorsal to the notochord. It will give rise to the central nervous system.

neurohormone A molecule that is secreted by a neuron, travels in body fluids, and acts on specific target cells, changing their functioning.

neuron (nyūr′-on) A nerve cell; the fundamental unit of the nervous system, having structure and properties that allow it to conduct signals by taking advantage of the electrical charge across its plasma membrane.

neuronal plasticity The capacity of a nervous system to change with experience.

neuropeptide A relatively short chain of amino acids that serves as a neurotransmitter.

neurotransmitter A molecule that is released from the synaptic terminal of a neuron at a chemical synapse, diffuses across the synaptic cleft, and binds to the postsynaptic cell, triggering a response.

neutral variation Genetic variation that does not provide a selective advantage or disadvantage.

neutron A subatomic particle having no electrical charge (electrically neutral), with a mass of about 1.7×10^{-24}g, found in the nucleus of an atom.

neutrophil The most abundant type of white blood cell. Neutrophils are phagocytic and tend to self-destruct as they destroy foreign invaders, limiting their life span to a few days.

nitric oxide (NO) A gas produced by many types of cells that functions as a local regulator and as a neurotransmitter.

nitrogen cycle The natural process by which nitrogen, either from the atmosphere or from decomposed organic material, is converted by soil bacteria to compounds assimilated by plants. This incorporated nitrogen is then taken in by other organisms and subsequently released, acted on by bacteria, and made available again to the nonliving environment.

nitrogen fixation The conversion of atmospheric nitrogen (N_2) to ammonia (NH_3). Biological nitrogen fixation is carried out by certain prokaryotes, some of which have mutualistic relationships with plants.

nociceptor (nō′-si-sep′-tur) A sensory receptor that responds to noxious or painful stimuli; also called a pain receptor.

node A point along the stem of a plant at which leaves are attached.

node of Ranvier (ron′-vē-ā′) Gap in the myelin sheath of certain axons where an action potential may be generated. In saltatory conduction, an action potential is regenerated at each node, appearing to "jump" along the axon from node to node.

nodule A swelling on the root of a legume. Nodules are composed of plant cells that contain nitrogen-fixing bacteria of the genus *Rhizobium*.

noncompetitive inhibitor A substance that reduces the activity of an enzyme by binding to a location remote from the active site, changing the enzyme's shape so that the active site no longer effectively catalyzes the conversion of substrate to product.

nondisjunction An error in meiosis or mitosis in which members of a pair of homologous chromosomes or a pair of sister chromatids fail to separate properly from each other.

nonequilibrium model A model that maintains that communities change constantly after being buffeted by disturbances.

nonpolar covalent bond A type of covalent bond in which electrons are shared equally between two atoms of similar electronegativity.

nonsense mutation A mutation that changes an amino acid codon to one of the three stop codons, resulting in a shorter and usually nonfunctional protein.

norepinephrine A catecholamine that is chemically and functionally similar to epinephrine and acts as a hormone or neurotransmitter; also called noradrenaline.

northern coniferous forest A terrestrial biome characterized by long, cold winters and dominated by cone-bearing trees.

no-till agriculture A plowing technique that minimally disturbs the soil, thereby reducing soil loss.

notochord (nō′-tuh-kord′) A longitudinal, flexible rod made of tightly packed mesodermal cells that runs along the anterior-posterior axis of a chordate in the dorsal part of the body.

nuclear envelope In a eukaryotic cell, the double membrane that surrounds the nucleus, perforated with pores that regulate traffic with the cytoplasm. The outer membrane is continuous with the endoplasmic reticulum.

nuclear lamina A netlike array of protein filaments that lines the inner surface of the nuclear envelope and helps maintain the shape of the nucleus.

nucleariid A member of a group of unicellular, amoeboid protists that are more closely related to fungi than they are to other protists.

nuclease An enzyme that cuts DNA or RNA, either removing one or a few bases or hydrolyzing the DNA or RNA completely into its component nucleotides.

nucleic acid (nū-klā′-ik) A polymer (polynucleotide) consisting of many nucleotide monomers; serves as a blueprint for proteins and, through the actions of proteins, for all cellular activities. The two types are DNA and RNA.

nucleic acid hybridization (nū-klā′-ik) The base pairing of one strand of a nucleic acid to the complementary sequence on a strand from *another* nucleic acid molecule.

nucleic acid probe (nū-klā′-ik) In DNA technology, a labeled single-stranded nucleic acid molecule used to locate a specific nucleotide sequence in a nucleic acid sample. Molecules of the probe hydrogen-bond to the complementary sequence wherever it occurs; radioactive, fluorescent, or other labeling of the probe allows its location to be detected.

nucleoid (nū′-klē-oyd) A non-membrane-enclosed region in a prokaryotic cell where its chromosome is located.

nucleolus (nū-klē′-ō-lus) (plural, **nucleoli**) A specialized structure in the nucleus, consisting of chromosomal regions containing ribosomal RNA (rRNA) genes along with ribosomal proteins imported from the cytoplasm; site of rRNA synthesis and ribosomal subunit assembly. *See also* ribosome.

nucleosome (nū′-klē-ō-sōm′) The basic, bead-like unit of DNA packing in eukaryotes, consisting of a segment of DNA wound around a protein core composed of two copies of each of four types of histone.

nucleotide (nū-klē-ō-tīd′) The building block of a nucleic acid, consisting of a five-carbon sugar covalently bonded to a nitrogenous base and one to three phosphate groups.

nucleotide excision repair (nū′-klē-ō-tīd′) A repair system that removes and then correctly replaces a damaged segment of DNA using the undamaged strand as a guide.

nucleotide-pair substitution (nū′-klē-ō-tīd′) A type of point mutation in which one nucleotide in a DNA strand and its partner in the complementary strand are replaced by another pair of nucleotides.

nucleus (1) An atom's central core, containing protons and neutrons. (2) The organelle of a eukaryotic cell that contains the genetic material in the form of chromosomes, made up of chromatin. (3) A cluster of neurons.

nutrition The process by which an organism takes in and makes use of food substances.

obligate aerobe (ob′-lig-et ār′-ōb) An organism that requires oxygen for cellular respiration and cannot live without it.

obligate anaerobe (ob′-lig-et an′-uh-rōb) An organism that carries out only fermentation or anaerobic respiration. Such organisms cannot use oxygen and in fact may be poisoned by it.

ocean acidification The process by which the pH of the ocean is lowered (made more acidic) when excess CO_2 dissolves in seawater and forms carbonic acid (H_2CO_3).

oceanic pelagic zone Most of the ocean's waters far from shore, constantly mixed by ocean currents.

odorant A molecule that can be detected by sensory receptors of the olfactory system.

Okazaki fragment (ō′-kah-zah′-kē) A short segment of DNA synthesized away from the replication fork on a template strand during DNA replication. Many such segments are joined together to make up the lagging strand of newly synthesized DNA.

olfaction The sense of smell.

oligodendrocyte A type of glial cell that forms insulating myelin sheaths around the axons of neurons in the central nervous system.

oligotrophic lake A nutrient-poor, clear lake with few phytoplankton.

ommatidium (ōm′-uh-tid′-ē-um) (plural, **ommatidia**) One of the facets of the compound eye of arthropods and some polychaete worms.

omnivore An animal that regularly eats animals as well as plants or algae.

oncogene (on′-kō-jēn) A gene found in viral or cellular genomes that is involved in triggering molecular events that can lead to cancer.

oocyte (ō′-uh-sīt) A cell in the female reproductive system that differentiates to form an egg.

oogenesis (ō′-uh-jen′-uh-sis) The process in the ovary that results in the production of female gametes.

oogonium (ō′-uh-gō′-nē-em) (plural, **oogonia**) A cell that divides mitotically to form oocytes.

open circulatory system A circulatory system in which fluid called hemolymph bathes the tissues and organs directly and there is no distinction between the circulating fluid and the interstitial fluid.

operator In bacterial and phage DNA, a sequence of nucleotides near the start of an operon to which an active repressor can attach. The binding of the repressor prevents RNA polymerase from attaching to the promoter and transcribing the genes of the operon.

operculum (ō-per′-kyuh-lum) In aquatic osteichthyans, a protective bony flap that covers and protects the gills.

operon (op′-er-on) A unit of genetic function found in bacteria and phages, consisting of a promoter, an operator, and a coordinately regulated cluster of genes whose products function in a common pathway.

opisthokont (uh-pis′-thuh-kont′) A member of an extremely diverse clade of eukaryotes that includes fungi, animals, and several closely related groups of protists.

opposable thumb A thumb that can touch the ventral surface (fingerprint side) of the fingertip of all four fingers of the same hand with its own ventral surface.

opsin A membrane protein bound to a light-absorbing pigment molecule.

optimal foraging model The basis for analyzing behavior as a compromise between feeding costs and feeding benefits.

oral cavity The mouth of an animal.

orbital The three-dimensional space where an electron is found 90% of the time.

order In Linnaean classification, the taxonomic category above the level of family.

organ A specialized center of body function composed of several different types of tissues.

organelle (ōr-guh-nel′) Any of several membrane-enclosed structures with specialized functions, suspended in the cytosol of eukaryotic cells.

organic chemistry The study of carbon compounds (organic compounds).

organ identity gene A plant homeotic gene that uses positional information to determine which emerging leaves develop into which types of floral organs.

organism An individual living thing, consisting of one or more cells.

organismal ecology The branch of ecology concerned with the morphological, physiological, and behavioral ways in which individual organisms meet the challenges posed by their biotic and abiotic environments.

organ of Corti (kor′-tē) The actual hearing organ of the vertebrate ear, located in the floor of the cochlear duct in the inner ear; contains the receptor cells (hair cells) of the ear.

organogenesis (ōr-gan′-ō-jen′-uh-sis) The process in which organ rudiments develop from the three germ layers after gastrulation.

organ system A group of organs that work together in performing vital body functions.

origin of replication Site where the replication of a DNA molecule begins, consisting of a specific sequence of nucleotides.

orthologous genes Homologous genes that are found in different species because of speciation.

osculum (os′-kyuh-lum) A large opening in a sponge that connects the spongocoel to the environment.

osmoconformer An animal that is isoosmotic with its environment.

osmolarity (oz′-mō-lār′-uh-tē) Solute concentration expressed as molarity.

osmoregulation Regulation of solute concentrations and water balance by a cell or organism.

osmoregulator An animal that controls its internal osmolarity independent of the external environment.

osmosis (oz-mō′-sis) The diffusion of free water across a selectively permeable membrane.

osteichthyan (os′-tē-ik′-thē-an) A member of a vertebrate clade with jaws and mostly bony skeletons.

outer ear One of the three main regions of the ear in reptiles (including birds) and mammals; made up of the auditory canal and, in many birds and mammals, the pinna.

outgroup A species or group of species from an evolutionary lineage that is known to have diverged before the lineage that contains the group of species being studied. An outgroup is selected so that its members are closely related to the group of species being studied, but not as closely related as any study-group members are to each other.

oval window In the vertebrate ear, a membrane-covered gap in the skull bone, through which sound waves pass from the middle ear to the inner ear.

ovarian cycle (ō-vār′-ē-un) The cyclic recurrence of the follicular phase, ovulation, and the luteal phase in the mammalian ovary, regulated by hormones.

ovary (ō′-vuh-rē) (1) In flowers, the portion of a carpel in which the egg-containing ovules develop. (2) In animals, the structure that produces female gametes and reproductive hormones.

oviduct (ō′-vuh-duct) A tube passing from the ovary to the vagina in invertebrates or to the uterus in vertebrates, where it is also called a fallopian tube.

oviparous (ō-vip′-uh-rus) Referring to a type of development in which young hatch from eggs laid outside the mother's body.

ovoviviparous (ō′-vō-vī-vip′-uh-rus) Referring to a type of development in which young hatch from eggs that are retained in the mother's uterus.

ovulation The release of an egg from an ovary. In humans, an ovarian follicle releases an egg during each uterine (menstrual) cycle.

ovule (o′-vyūl) A structure that develops within the ovary of a seed plant and contains the female gametophyte.

oxidation The complete or partial loss of electrons from a substance involved in a redox reaction.

oxidative phosphorylation (fos′-fōr-uh-lā′-shun) The production of ATP using energy derived from the redox reactions of an electron transport chain; the third major stage of cellular respiration.

oxidizing agent The electron acceptor in a redox reaction.

oxytocin (ok′-si-tō′-sen) A hormone produced by the hypothalamus and released from the posterior pituitary. It induces contractions of the uterine muscles during labor and causes the mammary glands to eject milk during nursing.

***p53* gene** A tumor-suppressor gene that codes for a specific transcription factor that promotes the synthesis of proteins that inhibit the cell cycle.

paedomorphosis (pē′-duh-mōr′-fuh-sis) The retention in an adult organism of the juvenile features of its evolutionary ancestors.

pain receptor A sensory receptor that responds to noxious or painful stimuli; also called a nociceptor.

paleoanthropology The study of human origins and evolution.

paleontology (pā′-lē-un-tol′-ō-jē) The scientific study of fossils.

pancreas (pan′-krē-us) A gland with exocrine and endocrine tissues. The exocrine portion functions in digestion, secreting enzymes and an alkaline solution into the small intestine via a duct; the ductless endocrine portion functions in homeostasis, secreting the hormones insulin and glucagon into the blood.

pancrustacean A member of a diverse arthropod clade that includes lobsters, crabs, barnacles and other crustaceans, as well as insects and their six-legged terrestrial relatives.

pandemic A global epidemic.

Pangaea (pan-jē′-uh) The supercontinent that formed near the end of the Paleozoic era, when plate movements brought all the landmasses of Earth together.

parabasalid A protist, such as a trichomonad, with modified mitochondria.

paracrine Referring to a secreted molecule that acts on a neighboring cell.

paralogous genes Homologous genes that are found in the same genome as a result of gene duplication.

paraphyletic (pār′-uh-fī-let′-ik) Pertaining to a group of taxa that consists of a common ancestor and some, but not all, of its descendants.

parareptile A basal group of reptiles, consisting mostly of large, stocky quadrupedal herbivores. Parareptiles died out in the late Triassic period.

parasite (pār′-uh-sīt) An organism that feeds on the cell contents, tissues, or body fluids of another species (the host) while in or on the host organism. Parasites harm but usually do not kill their host.

parasitism (pār′-uh-sit-izm) A +/− ecological interaction in which one organism, the parasite, benefits by feeding upon another organism, the host, which is harmed; some parasites live within the host (feeding on its tissues), while others feed on the host's external surface.

parasympathetic division One of three divisions of the autonomic nervous system; generally enhances body activities that gain and conserve energy, such as digestion and reduced heart rate.

parathyroid gland One of four small endocrine glands, embedded in the surface of the thyroid gland, that secrete parathyroid hormone.

parathyroid hormone (PTH) A hormone secreted by the parathyroid glands that raises blood calcium level by promoting calcium release from bone and calcium retention by the kidneys.

parenchyma cell (puh-ren′-ki-muh) A relatively unspecialized plant cell type that carries out most of the metabolism, synthesizes and stores organic products, and develops into a more differentiated cell type.

parental type An offspring with a phenotype that matches one of the true-breeding parental (P generation) phenotypes; also refers to the phenotype itself.

Parkinson's disease A progressive brain disease characterized by difficulty in initiating movements, slowness of movement, and rigidity.

parthenogenesis (par′-thuh-nō′-jen′-uh-sis) A form of asexual reproduction in which females produce offspring from unfertilized eggs.

partial pressure The pressure exerted by a particular gas in a mixture of gases (for instance, the pressure exerted by oxygen in air).

passive immunity Short-term immunity conferred by the transfer of antibodies, as occurs in the transfer of maternal antibodies to a fetus or nursing infant.

passive transport The diffusion of a substance across a biological membrane with no expenditure of energy.

pathogen An organism or virus that causes disease.

pathogen-associated molecular pattern (PAMP) A molecular sequence that is specific to a certain pathogen.

pattern formation The development of a multicellular organism's spatial organization, the arrangement of organs and tissues in their characteristic places in three-dimensional space.

peat Extensive deposits of partially decayed organic material often formed primarily from the wetland moss *Sphagnum*.

pedigree A diagram of a family tree with conventional symbols, showing the occurrence of heritable characters in parents and offspring over multiple generations.

pelagic zone The open-water component of aquatic biomes.

penis The copulatory structure of male mammals.

PEP carboxylase An enzyme that adds CO_2 to phosphoenolpyruvate (PEP) to form oxaloacetate in mesophyll cells of C_4 plants. It acts prior to photosynthesis.

pepsin An enzyme present in gastric juice that begins the hydrolysis of proteins.

pepsinogen The inactive form of pepsin secreted by chief cells located in gastric pits of the stomach.

peptide bond The covalent bond between the carboxyl group on one amino acid and the amino group on another, formed by a dehydration reaction.

peptidoglycan (pep′-tid-ō-glī′-kan) A type of polymer in bacterial cell walls consisting of modified sugars cross-linked by short polypeptides.

perception The interpretation of sensory system input by the brain.

pericycle The outermost layer in the vascular cylinder, from which lateral roots arise.

periderm (pār′-uh-derm′) The protective coat that replaces the epidermis in woody plants during secondary growth, formed of the cork and cork cambium.

peripheral nervous system (PNS) The sensory and motor neurons that connect to the central nervous system.

peripheral protein A protein loosely bound to the surface of a membrane or to part of an integral protein and not embedded in the lipid bilayer.

peristalsis (pār′-uh-stal′-sis) (1) Alternating waves of contraction and relaxation in the smooth muscles lining the alimentary canal that push food along the canal. (2) A type of movement on land produced by rhythmic waves of muscle contractions passing from front to back, as in many annelids.

peristome (pār′-uh-stōme′) A ring of interlocking, tooth-like structures on the upper part of a moss capsule (sporangium), often specialized for gradual spore discharge.

peritubular capillary One of the tiny blood vessels that form a network surrounding the proximal and distal tubules in the kidney.

peroxisome (puh-rok′-suh-sōm′) An organelle containing enzymes that transfer hydrogen atoms from various substrates to oxygen (O_2), producing and then degrading hydrogen peroxide (H_2O_2).

petal A modified leaf of a flowering plant. Petals are the often colorful parts of a flower that advertise it to insects and other pollinators.

petiole (pet′-ē-ōl) The stalk of a leaf, which joins the leaf to a node of the stem.

P generation The true-breeding (homozygous) parent individuals from which F_1 hybrid offspring are derived in studies of inheritance; P stands for "parental."

pH A measure of hydrogen ion concentration equal to $-\log[H^+]$ and ranging in value from 0 to 14.

phage (fāj) A virus that infects bacteria; also called a bacteriophage.

phagocytosis (fag′-ō-sī-tō′-sis) A type of endocytosis in which large particulate substances or small organisms are taken up by a cell. It is carried out by some protists and by certain immune cells of animals (in mammals, mainly macrophages, neutrophils, and dendritic cells).

pharyngeal cleft (fuh-rin′-jē-ul) In chordate embryos, one of the grooves that separate a series of arches along the outer surface of the pharynx and may develop into a pharyngeal slit.

pharyngeal slit (fuh-rin′-jē-ul) In chordate embryos, one of the slits that form from the pharyngeal clefts and open into the pharynx, later developing into gill slits in many vertebrates.

pharynx (fār′-inks) (1) An area in the vertebrate throat where air and food passages cross. (2) In flatworms, the muscular tube that protrudes from the ventral side of the worm and ends in the mouth.

phase change (1) A shift from one developmental phase to another. (2) In plants, a morphological change that arises from a transition in shoot apical meristem activity.

phenotype (fē′-nō-tīp) The observable physical and physiological traits of an organism, which are determined by its genetic makeup.

pheromone (fār′-uh-mōn) In animals and fungi, a small molecule released into the environment that functions in communication between members of the same species. In animals, it acts much like a hormone in influencing physiology and behavior.

phloem (flō′-em) Vascular plant tissue consisting of living cells arranged into elongated tubes that transport sugar and other organic nutrients throughout the plant.

phloem sap (flō′-em) The sugar-rich solution carried through a plant's sieve tubes.

phosphate group A chemical group consisting of a phosphorus atom bonded to four oxygen atoms; important in energy transfer.

phospholipid (fos′-fō-lip′-id) A lipid made up of glycerol joined to two fatty acids and a phosphate group. The hydrocarbon chains of the fatty acids act as nonpolar, hydrophobic tails, while the rest of the molecule acts as a polar, hydrophilic head. Phospholipids form bilayers that function as biological membranes.

phosphorylated intermediate (fos′-fōr-uh-lā′-ted) A molecule (often a reactant) with a phosphate group covalently bound to it, making it more reactive (less stable) than the unphosphorylated molecule.

phosphorylation cascade (fos′-fōr-uh-lā′-shun) A series of chemical reactions during cell signaling mediated by enzymes (kinases), in which each kinase in turn phosphorylates and activates another, ultimately leading to phosphorylation of many proteins.

photic zone (fō′-tic) The narrow top layer of an ocean or lake, where light penetrates sufficiently for photosynthesis to occur.

photoautotroph (fō′-tō-ot′-ō-trōf) An organism that harnesses light energy to drive the synthesis of organic compounds from carbon dioxide.

photoheterotroph (fō′-tō-het′-er-ō-trōf) An organism that uses light to generate ATP but must obtain carbon in organic form.

photomorphogenesis Effects of light on plant morphology.

photon (fō′-ton) A quantum, or discrete quantity, of light energy that behaves as if it were a particle.

photoperiodism (fō′-tō-pēr′-ē-ō-dizm) A physiological response to photoperiod, the interval in a 24-hour period during which an organism is exposed to light. An example of photoperiodism is flowering.

photophosphorylation (fō′-tō-fos′-fōr-uh-lā′-shun) The process of generating ATP from ADP and phosphate by means of chemiosmosis, using a proton-motive force generated across the thylakoid membrane of the chloroplast or the membrane of certain prokaryotes during the light reactions of photosynthesis.

photoreceptor An electromagnetic receptor that detects the radiation known as visible light.

photorespiration A metabolic pathway that consumes oxygen and ATP, releases carbon dioxide, and decreases photosynthetic output. Photorespiration generally occurs on hot, dry, bright days, when stomata close and the O_2/CO_2 ratio in the leaf increases, favoring the binding of O_2 rather than CO_2 by rubisco.

photosynthesis (fō′-tō-sin′-thi-sis) The conversion of light energy to chemical energy that is stored in sugars or other organic compounds; occurs in plants, algae, and certain prokaryotes.

photosystem A light-capturing unit located in the thylakoid membrane of the chloroplast or in the membrane of some prokaryotes, consisting of a reaction-center complex surrounded by numerous light-harvesting complexes. There are two types of photosystems, I and II; they absorb light best at different wavelengths.

photosystem I (PS I) A light-capturing unit in a chloroplast's thylakoid membrane or in the membrane of some prokaryotes; it has two molecules of P700 chlorophyll *a* at its reaction center.

photosystem II (PS II) One of two light-capturing units in a chloroplast's thylakoid membrane or in the membrane of some prokaryotes; it has two molecules of P680 chlorophyll *a* at its reaction center.

phototropism (fō′-tō-trō′-pizm) Growth of a plant shoot toward or away from light.

phyllotaxy (fil′-uh-tak′-sē) The pattern of leaf attachment to the stem of a plant.

phylogenetic tree A branching diagram that represents a hypothesis about the evolutionary history of a group of organisms.

phylogeny (fī-loj′-uh-nē) The evolutionary history of a species or group of related species.

phylum (fī′-lum) (plural, **phyla**) In Linnaean classification, the taxonomic category above class.

physiology The processes and functions of an organism.

phytochrome (fī′-tuh-krōm) A type of light receptor in plants that mostly absorbs red light and regulates many plant responses, such as seed germination and shade avoidance.

phytoremediation An emerging technology that seeks to reclaim contaminated areas by taking advantage of some plant species' ability to extract heavy metals and other pollutants from the soil and to concentrate them in easily harvested portions of the plant.

pilus (plural, **pili**) (pī′-lus, pī′-lī) In bacteria, a structure that links one cell to another at the start of conjugation; also called a sex pilus or conjugation pilus.

pineal gland (pī′-nē-ul) A small gland on the dorsal surface of the vertebrate forebrain that secretes the hormone melatonin.

pinocytosis (pī′-nō-sī-tō′-sis) A type of endocytosis in which the cell ingests extracellular fluid and its dissolved solutes.

pistil A single carpel (a simple pistil) or a group of fused carpels (a compound pistil).

pith Ground tissue that is internal to the vascular tissue in a stem; in many monocot roots, parenchyma cells that form the central core of the vascular cylinder.

pituitary gland (puh-tū′-uh-tār′-ē) An endocrine gland at the base of the hypothalamus; consists of a posterior lobe, which stores and releases two hormones produced by the hypothalamus, and an anterior lobe, which produces and secretes many hormones that regulate diverse body functions.

placenta (pluh-sen′-tuh) A structure in the uterus of a pregnant eutherian mammal that nourishes the fetus with the mother's blood supply; formed from the uterine lining and embryonic membranes.

placoderm A member of an extinct group of fishlike vertebrates that had jaws and were enclosed in a tough outer armor.

planarian A free-living flatworm found in ponds and streams.

plasma (plaz′-muh) The liquid matrix of blood in which the blood cells are suspended.

plasma membrane (plaz′-muh) The membrane at the boundary of every cell that acts as a selective barrier, regulating the cell's chemical composition.

plasmid (plaz′-mid) A small, circular, double-stranded DNA molecule that carries accessory genes separate from those of a bacterial chromosome; in DNA cloning, plasmids are used as vectors carrying up to about 10,000 base pairs (10 kb) of DNA. Plasmids are also found in some eukaryotes, such as yeasts.

plasmodesma (plaz′-mō-dez′-muh) (plural, **plasmodesmata**) An open channel through the cell wall that connects the cytoplasm of adjacent plant cells, allowing water, small solutes, and some larger molecules to pass between the cells.

plasmogamy (plaz-moh′-guh-mē) In fungi, the fusion of the cytoplasm of cells from two individuals; occurs as one stage of sexual reproduction, followed later by karyogamy.

plasmolysis (plaz-mol′-uh-sis) A phenomenon in walled cells in which the cytoplasm shrivels and the plasma membrane pulls away from the cell wall; occurs when the cell loses water to a hypertonic environment.

plastid One of a family of closely related organelles that includes chloroplasts, chromoplasts, and amyloplasts. Plastids are found in cells of photosynthetic eukaryotes.

plate tectonics The theory that the continents are part of great plates of Earth's crust that float on the hot, underlying portion of the mantle. Movements in the mantle cause the continents to move slowly over time.

platelet A pinched-off cytoplasmic fragment of a specialized bone marrow cell. Platelets circulate in the blood and are important in blood clotting.

pleiotropy (plī′-o-truh-pē) The ability of a single gene to have multiple effects.

pluripotent Describing a cell that can give rise to many, but not all, parts of an organism.

point mutation A change in a single nucleotide pair of a gene.

polar covalent bond A covalent bond between atoms that differ in electronegativity. The shared electrons are pulled closer to the more electronegative atom, making it slightly negative and the other atom slightly positive.

polar molecule A molecule (such as water) with an uneven distribution of charges in different regions of the molecule.

polarity A lack of symmetry; structural differences in opposite ends of an organism or structure, such as the root end and shoot end of a plant.

pollen grain In seed plants, a structure consisting of the male gametophyte enclosed within a pollen wall.

pollen tube A tube that forms after germination of the pollen grain and that functions in the delivery of sperm to the ovule.

pollination (pol′-uh-nā′-shun) The transfer of pollen to the part of a seed plant containing the ovules, a process required for fertilization.

poly-A tail A sequence of 50–250 adenine nucleotides added onto the 3′ end of a pre-mRNA molecule.

polygamous Referring to a type of relationship in which an individual of one sex mates with several of the other.

polygenic inheritance (pol′-ē-jen′-ik) An additive effect of two or more genes on a single phenotypic character.

polymer (pol′-uh-mer) A long molecule consisting of many similar or identical monomers linked together by covalent bonds.

polymerase chain reaction (PCR) (puh-lim′-uh-rās) A technique for amplifying DNA *in vitro* by incubating it with specific primers, a heat-resistant DNA polymerase, and nucleotides.

polynucleotide (pol′-ē-nū′-klē-ō-tīd) A polymer consisting of many nucleotide monomers in a chain. The nucleotides can be those of DNA or RNA.

polyp The sessile variant of the cnidarian body plan. The alternate form is the medusa.

polypeptide (pol′-ē-pep′-tīd) A polymer of many amino acids linked together by peptide bonds.

polyphyletic (pol′-ē-fī-let′-ik) Pertaining to a group of taxa that includes distantly related organisms but does not include their most recent common ancestor.

polyploidy (pol′-ē-ploy′-dē) A chromosomal alteration in which the organism possesses more than two complete chromosome sets. It is the result of an accident of cell division.

polyribosome (polysome) (pol′-ē-rī′-buh-sōm′) A group of several ribosomes attached to, and translating, the same messenger RNA molecule.

polysaccharide (pol′-ē-sak′-uh-rīd) A polymer of many monosaccharides, formed by dehydration reactions.

polyspermy The fertilization of an egg by more than one sperm.

polytomy (puh-lit′-uh-mē) In a phylogenetic tree, a branch point from which more than two descendant taxa emerge. A polytomy indicates that the evolutionary relationships between the descendant taxa are not yet clear.

pons A portion of the brain that participates in certain automatic, homeostatic functions, such as regulating the breathing centers in the medulla.

population A group of individuals of the same species that live in the same area and interbreed, producing fertile offspring.

population dynamics The study of how complex interactions between biotic and abiotic factors influence variations in population size.

population ecology The study of populations in relation to their environment, including environmental influences on population density and distribution, age structure, and variations in population size.

positional information Molecular cues that control pattern formation in an animal or plant embryonic structure by indicating a cell's location relative to the organism's body axes. These cues elicit a response by genes that regulate development.

positive feedback A form of regulation in which an end product of a process speeds up that process; in physiology, a control mechanism in which a change in a variable triggers a response that reinforces or amplifies the change.

positive interaction A +/+ or +/0 ecological interaction in which at least one of the interacting species benefits and neither is harmed; positive interactions include mutualism and commensalism.

positive pressure breathing A breathing system in which air is forced into the lungs.

posterior Pertaining to the rear, or tail end, of a bilaterally symmetrical animal.

posterior pituitary An extension of the hypothalamus composed of nervous tissue that secretes oxytocin and antidiuretic hormone made in the hypothalamus; a temporary storage site for these hormones.

postzygotic barrier (pōst′-zī-got′-ik) A reproductive barrier that prevents hybrid zygotes produced by two different species from developing into viable, fertile adults.

potential energy The energy that matter possesses as a result of its location or spatial arrangement (structure).

predation An interaction between species in which one species, the predator, eats the other, the prey.

prediction In deductive reasoning, a forecast that follows logically from a hypothesis. By testing predictions, experiments may allow certain hypotheses to be rejected.

pregnancy The condition of carrying one or more embryos in the uterus; also called gestation.

prepuce (prē′-pyūs) A fold of skin covering the head of the clitoris or penis.

pressure potential (ψ_P) A component of water potential that consists of the physical pressure on a solution, which can be positive, zero, or negative.

prezygotic barrier (prē′-zī-got′-ik) A reproductive barrier that impedes mating between species or hinders fertilization if interspecific mating is attempted.

primary cell wall In plants, a relatively thin and flexible layer that surrounds the plasma membrane of a young cell.

primary consumer An herbivore; an organism that eats plants or other autotrophs.

primary electron acceptor In the thylakoid membrane of a chloroplast or in the membrane of some prokaryotes, a specialized molecule that shares the reaction-center complex with a pair of chlorophyll *a* molecules and that accepts an electron from them.

primary growth Growth produced by apical meristems, lengthening stems and roots.

primary immune response The initial adaptive immune response to an antigen, which appears after a lag of about 10–17 days.

primary meristems The three meristematic derivatives (protoderm, procambium, and ground meristem) of an apical meristem.

primary oocyte (ō′-uh-sīt) An oocyte prior to completion of meiosis I.

primary producer An autotroph, usually a photosynthetic organism. Collectively, autotrophs make up the trophic level of an ecosystem that ultimately supports all other levels.

primary production The amount of light energy converted to chemical energy (organic compounds) by the autotrophs in an ecosystem during a given time period.

primary structure The level of protein structure referring to the specific linear sequence of amino acids.

primary succession A type of ecological succession that occurs in an area where there were originally no organisms present and where soil has not yet formed.

primary transcript An initial RNA transcript from any gene; also called pre-mRNA when transcribed from a protein-coding gene.

primase An enzyme that joins RNA nucleotides to make a primer during DNA replication, using the parental DNA strand as a template.

primer A short polynucleotide with a free 3′ end, bound by complementary base pairing to the template strand and elongated with DNA nucleotides during DNA replication.

prion An infectious agent that is a misfolded version of a normal cellular protein. Prions appear to increase in number by converting correctly folded versions of the protein to more prions.

problem solving The cognitive activity of devising a method to proceed from one state to another in the face of real or apparent obstacles.

producer An organism that produces organic compounds from CO_2 by harnessing light energy (in photosynthesis) or by oxidizing inorganic chemicals (in chemosynthetic reactions carried out by some prokaryotes).

product A material resulting from a chemical reaction.

production efficiency The percentage of energy stored in assimilated food that is not used for respiration or eliminated as waste.

progesterone A steroid hormone that contributes to the menstrual cycle and prepares the uterus for pregnancy; the major progestin in mammals.

progestin Any steroid hormone with progesterone-like activity.

prokaryotic cell (prō′-kār′-ē-ot′-ik) A type of cell lacking a membrane-enclosed nucleus and membrane-enclosed organelles. Organisms with prokaryotic cells (bacteria and archaea) are called prokaryotes.

prolactin A hormone produced and secreted by the anterior pituitary with a great diversity of effects in different vertebrate species. In mammals, it stimulates growth of and milk production by the mammary glands.

prometaphase The second stage of mitosis, in which the nuclear envelope fragments and the spindle microtubules attach to the kinetochores of the chromosomes.

promoter A specific nucleotide sequence in the DNA of a gene that binds RNA polymerase, positioning it to start transcribing RNA at the appropriate place.

prophage (prō′-fāj) A phage genome that has been inserted into a specific site on a bacterial chromosome.

prophase The first stage of mitosis, in which the chromatin condenses into discrete chromosomes visible with a light microscope, the mitotic spindle begins to form, and the nucleolus disappears but the nucleus remains intact.

prostaglandin (pros′-tuh-glan′-din) One of a group of modified fatty acids that are secreted by virtually all tissues and that perform a wide variety of functions as local regulators.

prostate gland (pros′-tāt) A gland in human males that secretes an acid-neutralizing component of semen.

protease (prō′-tē-āz) An enzyme that digests proteins by hydrolysis.

protein (prō′-tēn) A biologically functional molecule consisting of one or more polypeptides folded and coiled into a specific three-dimensional structure.

protein kinase (prō′-tēn kī′-nās) An enzyme that transfers phosphate groups from ATP to a protein, thus phosphorylating the protein.

protein phosphatase (prō′-tēn fos′-fuh-tās) An enzyme that removes phosphate groups from (dephosphorylates) proteins, often functioning to reverse the effect of a protein kinase.

proteoglycan (prō′-tē-ō-glī′-kan) A large molecule consisting of a small core protein with many carbohydrate chains attached, found in the extracellular matrix of animal cells. A proteoglycan may consist of up to 95% carbohydrate.

proteome The entire set of proteins expressed by a given cell, tissue, or organism.

proteomics (prō′-tē-ō′-miks) The systematic study of sets of proteins and their properties, including their abundance, chemical modifications, and interactions.

protist An informal term applied to any eukaryote that is not a plant, animal, or fungus. Most protists are unicellular, though some are colonial or multicellular.

protocell An abiotic precursor of a living cell that had a membrane-like structure and that maintained an internal chemistry different from that of its surroundings.

proton (prō′-ton) A subatomic particle with a single positive electrical charge, with a mass of about 1.7×10^{-24}g, found in the nucleus of an atom.

protonema (prō′-tuh-nē′-muh) (plural, **protonemata**) A mass of green, branched, one-cell-thick filaments produced by germinating moss spores.

protonephridium (prō′-tō-nuh-frid′-ē-um) (plural, **protonephridia**) An excretory system, such as the flame bulb system of flatworms, consisting of a network of tubules lacking internal openings.

proton-motive force (prō′-ton) The potential energy stored in the form of a proton electrochemical gradient, generated by the pumping of hydrogen ions (H^+) across a biological membrane during chemiosmosis.

proton pump (prō′-ton) An active transport protein in a cell membrane that uses ATP to transport hydrogen ions out of a cell against their concentration gradient, generating a membrane potential in the process.

proto-oncogene (prō′-tō-on′-kō-jēn) A normal cellular gene that has the potential to become an oncogene.

protoplast The living part of a plant cell, which also includes the plasma membrane.

protostome development In animals, a developmental mode distinguished by the development of the mouth from the blastopore; often also characterized by spiral cleavage and by the body cavity forming when solid masses of mesoderm split.

provirus A viral genome that is permanently inserted into a host genome.

proximal tubule In the vertebrate kidney, the portion of a nephron immediately downstream from Bowman's capsule that conveys and helps refine filtrate.

pseudocoelomate (sū′-dō-sē′-lō-māt) An animal whose body cavity is lined by tissue derived from mesoderm and endoderm.

pseudogene (sū′-dō-jēn) A DNA segment that is very similar to a real gene but does not yield a functional product; a DNA segment that formerly functioned as a gene but has become inactivated in a particular species because of mutation.

pseudopodium (sū′-dō-pō′-dē-um) (plural, **pseudopodia**) A cellular extension of amoeboid cells used in moving and feeding.

P site One of a ribosome's three binding sites for tRNA during translation. The P site holds the tRNA carrying the growing polypeptide chain. (P stands for peptidyl tRNA.)

pterosaur Winged reptile that lived during the Mesozoic era.

pulse The rhythmic bulging of the artery walls with each heartbeat.

punctuated equilibria In the fossil record, long periods of apparent stasis, in which a species undergoes little or no morphological change, interrupted by relatively brief periods of sudden change.

Punnett square A diagram used in the study of inheritance to show the predicted genotypic results of random fertilization in genetic crosses between individuals of known genotype.

pupil The opening in the iris, which admits light into the interior of the vertebrate eye. Muscles in the iris regulate its size.

purine (pyū′-rēn) One of two types of nitrogenous bases found in nucleotides, characterized by a six-membered ring fused to a five-membered ring. Adenine (A) and guanine (G) are purines.

pyrimidine (puh-rim′-uh-dēn) One of two types of nitrogenous bases found in nucleotides, characterized by a six-membered ring. Cytosine (C), thymine (T), and uracil (U) are pyrimidines.

quantitative character A heritable feature that varies continuously over a range rather than in an either-or fashion.

quaternary structure (kwot′-er-nār′-ē) The particular shape of a complex, aggregate protein, defined by the characteristic three-dimensional arrangement of its constituent subunits, each a polypeptide.

radial cleavage A type of embryonic development in deuterostomes in which the planes of cell division that transform the zygote into a ball of cells are either parallel or perpendicular to the vertical axis of the embryo, thereby aligning tiers of cells one above the other.

radial symmetry Symmetry in which the body is shaped like a pie or barrel (lacking a left side and a right side) and can be divided into mirror-imaged halves by any plane through its central axis.

radicle An embryonic root of a plant.

radioactive isotope An isotope (an atomic form of a chemical element) that is unstable; the nucleus decays spontaneously, giving off detectable particles and energy.

radiolarian A protist, usually marine, with a shell generally made of silica and pseudopodia that radiate from the central body.

radiometric dating A method for determining the absolute age of rocks and fossils, based on the half-life of radioactive isotopes.

radula A straplike scraping organ used by many molluscs during feeding.

***ras* gene** A gene that codes for Ras, a G protein that relays a growth signal from a growth factor receptor on the plasma membrane to a cascade of protein kinases, ultimately resulting in stimulation of the cell cycle.

ratite (rat′-īt) A member of the group of flightless birds.

ray-finned fish A member of the clade Actinopterygii, aquatic osteichthyans with fins supported by long, flexible rays, including tuna, bass, and herring.

reabsorption In excretory systems, the recovery of solutes and water from filtrate.

reactant A starting material in a chemical reaction.

reaction-center complex A complex of proteins associated with a special pair of chlorophyll *a* molecules and a primary electron acceptor. Located centrally in a photosystem, this complex triggers the light reactions of photosynthesis. Excited by light energy, the pair of chlorophylls donates an electron to the primary electron acceptor, which passes an electron to an electron transport chain.

reading frame On an mRNA, the triplet grouping of ribonucleotides used by the translation machinery during polypeptide synthesis.

receptacle The base of a flower; the part of the stem that is the site of attachment of the floral organs.

reception In cellular communication, the first step of a signaling pathway in which a signaling molecule is detected by a receptor molecule on or in the cell.

receptor-mediated endocytosis (en′-dō-sī-tō′-sis) The movement of specific molecules into a cell by the infolding of vesicles containing proteins with receptor sites specific to the molecules being taken in; enables a cell to acquire bulk quantities of specific substances.

receptor potential An initial response of a receptor cell to a stimulus, consisting of a change in voltage across the receptor membrane proportional to the stimulus strength.

receptor tyrosine kinase (RTK) A receptor protein spanning the plasma membrane, the cytoplasmic (intracellular) part of which can catalyze the transfer of a phosphate group from ATP to a tyrosine on another protein. Receptor tyrosine kinases often respond to the binding of a signaling molecule by dimerizing and then phosphorylating a tyrosine on the cytoplasmic portion of the other receptor in the dimer.

recessive allele An allele whose phenotypic effect is not observed in a heterozygote.

reciprocal altruism Altruistic behavior between unrelated individuals, whereby the altruistic individual benefits in the future when the beneficiary reciprocates.

recombinant chromosome A chromosome created when crossing over combines DNA from two parents into a single chromosome.

recombinant DNA molecule A DNA molecule made *in vitro* with segments from different sources.

recombinant type (recombinant) An offspring whose phenotype differs from that of the true-breeding P generation parents; also refers to the phenotype itself.

rectum The terminal portion of the large intestine, where the feces are stored prior to elimination.

red alga A photosynthetic protist, named for its color, which results from a red pigment that masks the green of chlorophyll. Most red algae are multicellular and marine.

redox reaction (rē′-doks) A chemical reaction involving the complete or partial transfer of one or more electrons from one reactant to another; short for **red**uction-**ox**idation reaction.

reducing agent The electron donor in a redox reaction.

reduction The complete or partial addition of electrons to a substance involved in a redox reaction.

reflex An automatic reaction to a stimulus, mediated by the spinal cord or lower brain.

refractory period (rē-frakt′-ōr-ē) The short time immediately after an action potential in which the neuron cannot respond to another stimulus, owing to the inactivation of voltage-gated sodium channels.

regulator An animal for which mechanisms of homeostasis moderate internal changes in a particular variable in the face of external fluctuation of that variable.

regulatory gene A gene that codes for a protein, such as a repressor, that controls the transcription of another gene or group of genes.

reinforcement In evolutionary biology, a process in which natural selection strengthens prezygotic barriers to reproduction, thus reducing the chances of hybrid formation. Such a process is likely to occur only if hybrid offspring are less fit than members of the parent species.

relative abundance The proportional abundance of different species in a community.

relative fitness The contribution an individual makes to the gene pool of the next generation, relative to the contributions of other individuals in the population.

renal cortex The outer portion of the vertebrate kidney.

renal medulla The inner portion of the vertebrate kidney, beneath the renal cortex.

renal pelvis The funnel-shaped chamber that receives processed filtrate from the vertebrate kidney's collecting ducts and is drained by the ureter.

renin-angiotensin-aldosterone system (RAAS) A hormone cascade pathway that helps regulate blood pressure and blood volume.

repetitive DNA Nucleotide sequences, usually noncoding, that are present in many copies in a eukaryotic genome. The repeated units may be short and arranged tandemly (in series) or long and dispersed in the genome.

replication fork A Y-shaped region on a replicating DNA molecule where the parental strands are being unwound and new strands are being synthesized.

repressor A protein that inhibits gene transcription. In prokaryotes, repressors bind to the DNA in or near the promoter. In eukaryotes, repressors may bind to control elements within enhancers, to activators, or to other proteins in a way that blocks activators from binding to DNA.

reproductive isolation The existence of biological factors (barriers) that impede members of two species from producing viable, fertile offspring.

reptile A member of the clade of amniotes that includes tuataras, lizards, snakes, turtles, crocodilians, and birds.

reservoir In biogeochemical cycles, location of a chemical element, consisting of either organic or inorganic materials that are either available for direct use by organisms or unavailable as nutrients.

residual volume The amount of air that remains in the lungs after forceful exhalation.

resource partitioning The division of environmental resources by coexisting species such that the niche of each species differs by one or more significant factors from the niches of all coexisting species.

respiratory pigment A protein that transports oxygen in blood or hemolymph.

response (1) In cellular communication, the change in a specific cellular activity brought about by a transduced signal from outside the cell. (2) In feedback regulation, a physiological activity triggered by a change in a variable.

resting potential The membrane potential characteristic of a nonconducting excitable cell, with the inside of the cell more negative than the outside.

restriction enzyme An endonuclease (type of enzyme) that recognizes and cuts DNA molecules foreign to a bacterium (such as phage genomes). The enzyme cuts at specific nucleotide sequences (restriction sites).

restriction fragment A DNA segment that results from the cutting of DNA by a restriction enzyme.

restriction site A specific sequence on a DNA strand that is recognized and cut by a restriction enzyme.

retina (ret′-i-nuh) The innermost layer of the vertebrate eye, containing photoreceptor cells (rods and cones) and neurons; transmits images formed by the lens to the brain via the optic nerve.

retinal The light-absorbing pigment in rods and cones of the vertebrate eye.

retrotransposon (re′-trō-trans-pō′-zon) A transposable element that moves within a genome by means of an RNA intermediate, a transcript of the retrotransposon DNA.

retrovirus (re′-trō-vī′-rus) An RNA virus that replicates by transcribing its RNA into DNA and then inserting the DNA into a cellular chromosome; an important class of cancer-causing viruses.

reverse transcriptase (tran-skrip′-tās) An enzyme encoded by certain viruses (retroviruses) that uses RNA as a template for DNA synthesis.

reverse transcriptase–polymerase chain reaction (RT-PCR) A technique for determining expression of a particular gene. It uses reverse transcriptase and DNA polymerase to synthesize cDNA from all the mRNA in a sample and then subjects the cDNA to PCR amplification using primers specific for the gene of interest.

rhizarians (rī-za′-rē-uhns) One of the three major subgroups for which the SAR eukaryotic supergroup is named. Many species in this clade are amoebas characterized by threadlike pseudopodia.

rhizobacterium A soil bacterium whose population size is much enhanced in the rhizosphere, the soil region close to a plant's roots.

rhizoid (rī′-zoyd) A long, tubular single cell or filament of cells that anchors bryophytes to the ground. Unlike roots, rhizoids are not composed of tissues, lack specialized conducting cells, and do not play a primary role in water and mineral absorption.

rhizosphere The soil region close to plant roots and characterized by a high level of microbiological activity.

rhodopsin (rō-dop′-sin) A visual pigment consisting of retinal and opsin. Upon absorbing light, the retinal changes shape and dissociates from the opsin.

ribonucleic acid (RNA) (rī′-bō-nū-klā′-ik) A type of nucleic acid consisting of a polynucleotide made up of nucleotide monomers with a ribose sugar and the nitrogenous bases adenine (A), cytosine (C), guanine (G), and uracil (U); usually single-stranded; functions in protein synthesis, in gene regulation, and as the genome of some viruses.

ribose The sugar component of RNA nucleotides.

ribosomal RNA (rRNA) (rī′-buh-sō′-mul) RNA molecules that, together with proteins, make up ribosomes; the most abundant type of RNA.

ribosome (rī′-buh-sōm) A complex of rRNA and protein molecules that functions as a site of protein synthesis in the cytoplasm; consists of a large and a small subunit. In eukaryotic cells, each subunit is assembled in the nucleolus. *See also* nucleolus.

ribozyme (rī′-buh-zīm) An RNA molecule that functions as an enzyme, such as an intron that catalyzes its own removal during RNA splicing.

RNA interference (RNAi) A mechanism for silencing the expression of specific genes. In RNAi, double-stranded RNA molecules that match the sequence of a particular gene are processed into siRNAs that either block translation or trigger the degradation of the gene's messenger RNA. This happens naturally in some cells, and can be carried out in laboratory experiments as well.

RNA polymerase An enzyme that links ribonucleotides into a growing RNA chain during transcription, based on complementary binding to nucleotides on a DNA template strand.

RNA processing Modification of RNA primary transcripts, including splicing out of introns, joining together of exons, and alteration of the 5′ and 3′ ends.

RNA sequencing (RNA-seq) (RNA-sēk) A method of analyzing large sets of RNAs that involves making cDNAs and sequencing them.

RNA splicing After synthesis of a eukaryotic primary RNA transcript, the removal of portions of the transcript (introns) that will not be included in the mRNA and the joining together of the remaining portions (exons).

rod A rodlike cell in the retina of the vertebrate eye, sensitive to low light intensity.

root An organ in vascular plants that anchors the plant and enables it to absorb water and minerals from the soil.

root cap A cone of cells at the tip of a plant root that protects the apical meristem.

root hair A tiny extension of a root epidermal cell, growing just behind the root tip and increasing surface area for absorption of water and minerals.

root pressure Pressure exerted in the roots of plants as the result of osmosis, causing exudation from cut stems and guttation of water from leaves.

root system All of a plant's roots, which anchor it in the soil, absorb and transport minerals and water, and store food.

rooted Describing a phylogenetic tree that contains a branch point (often, the one farthest to the left) representing the most recent common ancestor of all taxa in the tree.

rough ER That portion of the endoplasmic reticulum with ribosomes attached.

round window In the mammalian ear, the point of contact where vibrations of the stapes create a traveling series of pressure waves in the fluid of the cochlea.

R plasmid A bacterial plasmid carrying genes that confer resistance to certain antibiotics.

***r*-selection** Selection for life history traits that maximize reproductive success in uncrowded environments; also called density-independent selection.

rubisco (rū-bis′-kō) Ribulose bisphosphate (RuBP) carboxylase-oxygenase, the enzyme that normally catalyzes the first step of the Calvin cycle (the addition of CO_2 to RuBP). When excess O_2 is present or CO_2 levels are low, rubisco can bind oxygen, resulting in photorespiration.

ruminant (rūh′-muh-nent) A cud-chewing animal, such as a cow or sheep, with multiple stomach compartments specialized for an herbivorous diet.

salicylic acid (sal′-i-sil′-ik) A signaling molecule in plants that may be partially responsible for activating systemic acquired resistance to pathogens.

salivary gland A gland associated with the oral cavity that secretes substances that lubricate food and begin the process of chemical digestion.

salt A compound resulting from the formation of an ionic bond; also called an ionic compound.

saltatory conduction (sol′-tuh-tōr′-ē) Rapid transmission of a nerve impulse along an axon, resulting from the action potential jumping from one node of Ranvier to another, skipping the myelin-sheathed regions of membrane.

SAR One of four supergroups of eukaryotes proposed in a current hypothesis of the evolutionary history of eukaryotes. This supergroup contains a large, extremely diverse collection of protists from three major subgroups: stramenopiles, alveolates, and rhizarians. *See also* Excavata, Archaeplastida, and Unikonta.

sarcomere (sar′-kō-mēr) The fundamental, repeating unit of striated muscle, delimited by the Z lines.

sarcoplasmic reticulum (SR) (sar′-kō-plaz′-mik ruh-tik′-yū-lum) A specialized endoplasmic reticulum that regulates the calcium concentration in the cytosol of muscle cells.

saturated fatty acid A fatty acid in which all carbons in the hydrocarbon tail are connected by single bonds, thus maximizing the number of hydrogen atoms that are attached to the carbon skeleton.

savanna A tropical grassland biome with scattered individual trees and large herbivores and maintained by occasional fires and drought.

scaffolding protein A type of large relay protein to which several other relay proteins are simultaneously attached, increasing the efficiency of signal transduction.

scanning electron microscope (SEM) A microscope that uses an electron beam to scan the surface of a sample, coated with metal atoms, to study details of its topography.

scatter plot A graph in which each piece of data is represented by a point. A scatter plot is used when the data for all variables are numerical and continuous.

schizophrenia (skit′-suh-frē′-nē-uh) A severe mental disturbance characterized by psychotic episodes in which patients have a distorted perception of reality.

Schwann cell A type of glial cell that forms insulating myelin sheaths around the axons of neurons in the peripheral nervous system.

science An approach to understanding the natural world.

scion (sī′-un) The twig grafted onto the stock when making a graft.

sclereid (sklār′-ē-id) A short, irregular sclerenchyma cell in nutshells and seed coats. Sclereids are scattered throughout the parenchyma of some plants.

sclerenchyma cell (skluh-ren′-kim-uh) A rigid, supportive plant cell type usually lacking a protoplast and possessing thick secondary walls strengthened by lignin at maturity.

scrotum A pouch of skin outside the abdomen that houses the testes; functions in maintaining the testes at the lower temperature required for spermatogenesis.

second law of thermodynamics The principle stating that every energy transfer or transformation increases the entropy of the universe. Usable forms of energy are at least partly converted to heat.

second messenger A small, nonprotein, water-soluble molecule or ion, such as a calcium ion (Ca^{2+}) or cyclic AMP, that relays a signal to a cell's interior in response to a signaling molecule bound by a signal receptor protein.

secondary cell wall In plant cells, a strong and durable matrix that is often deposited in several laminated layers around the plasma membrane and provides protection and support.

secondary consumer A carnivore that eats herbivores.

secondary endosymbiosis A process in eukaryotic evolution in which a heterotrophic eukaryotic cell engulfed a photosynthetic eukaryotic cell, which survived in a symbiotic relationship inside the heterotrophic cell.

secondary growth Growth produced by lateral meristems, thickening the roots and shoots of woody plants.

secondary immune response The adaptive immune response elicited on second or subsequent exposures to a particular antigen. The secondary immune response is more rapid, of greater magnitude, and of longer duration than the primary immune response.

secondary oocyte (ō′-uh-sīt) An oocyte that has completed meiosis I.

secondary production The amount of chemical energy in consumers' food that is converted to their own new biomass during a given time period.

secondary structure Regions of repetitive coiling or folding of the polypeptide backbone of a protein due to hydrogen bonding between constituents of the backbone (not the side chains).

secondary succession A type of succession that occurs where an existing community has been cleared by some disturbance that leaves the soil or substrate intact.

secretion (1) The discharge of molecules synthesized by a cell. (2) The active transport of wastes and certain other solutes from the body fluid into the filtrate in an excretory system.

seed An adaptation of some terrestrial plants consisting of an embryo packaged along with a store of food within a protective coat.

seed coat A tough outer covering of a seed, formed from the outer coat of an ovule. In a flowering plant, the seed coat encloses and protects the embryo and endosperm.

seedless vascular plant An informal name for a plant that has vascular tissue but lacks seeds. Seedless vascular plants form a paraphyletic group that includes the phyla Lycophyta (club mosses and their relatives) and Monilophyta (ferns and their relatives).

selective permeability A property of biological membranes that allows them to regulate the passage of substances across them.

self-incompatibility The ability of a seed plant to reject its own pollen and sometimes the pollen of closely related individuals.

semelparity (seh′-mel-pār′-i-tē) Reproduction in which an organism produces all of its offspring in a single event; also called big-bang reproduction.

semen (sē′-mun) The fluid that is ejaculated by the male during orgasm; contains sperm and secretions from several glands of the male reproductive tract.

semicircular canals A three-part chamber of the inner ear that functions in maintaining equilibrium.

semiconservative model Type of DNA replication in which the replicated double helix consists of one old strand, derived from the parental molecule, and one newly made strand.

semilunar valve A valve located at each exit of the heart, where the aorta leaves the left ventricle and the pulmonary artery leaves the right ventricle.

seminal vesicle (sem′-i-nul ves′-i-kul) A gland in males that secretes a fluid component of semen that lubricates and nourishes sperm.

seminiferous tubule (sem′-i-nif′-er-us) A highly coiled tube in the testis in which sperm are produced.

senescence (se-nes′-ens) The growth phase in a plant or plant part (as a leaf) from full maturity to death.

sensitive period A limited phase in an animal's development when learning of particular behaviors can take place; also called a critical period.

sensor In homeostasis, a receptor that detects a stimulus.

sensory adaptation The tendency of sensory neurons to become less sensitive when they are stimulated repeatedly.

sensory neuron A nerve cell that receives information from the internal or external environment and transmits signals to the central nervous system.

sensory reception The detection of a stimulus by sensory cells.

sensory receptor A specialized structure or cell that responds to a stimulus from an animal's internal or external environment.

sensory transduction The conversion of stimulus energy to a change in the membrane potential of a sensory receptor cell.

sepal (sē′-pul) A modified leaf in angiosperms that helps enclose and protect a flower bud before it opens.

septum (plural, **septa**) One of the cross-walls that divide a fungal hypha into cells. Septa generally have pores large enough to allow ribosomes, mitochondria, and even nuclei to flow from cell to cell.

serial endosymbiosis A hypothesis for the origin of eukaryotes consisting of a sequence of endosymbiotic events in which mitochondria, chloroplasts, and perhaps other cellular structures were derived from small prokaryotes that had been engulfed by larger cells.

set point In homeostasis in animals, a value maintained for a particular variable, such as body temperature or solute concentration.

seta (sē′-tuh) (plural, **setae**) The elongated stalk of a bryophyte sporophyte.

sex chromosome A chromosome responsible for determining the sex of an individual.

sex-linked gene A gene located on either sex chromosome. Most sex-linked genes are on the X chromosome and show distinctive patterns of inheritance; there are very few genes on the Y chromosome.

sexual dimorphism (dī-mōr′-fizm) Differences between the secondary sex characteristics of males and females of the same species.

sexual reproduction Reproduction arising from fusion of two gametes.

sexual selection A process in which individuals with certain inherited characteristics are more likely than other individuals of the same sex to obtain mates.

Shannon diversity An index of community diversity symbolized by H and represented by the equation $H = -(p_A \ln p_A + p_B \ln p_B + p_C \ln p_C + \cdots)$, where A, B, C ... are species, p is the relative abundance of each species, and ln is the natural logarithm.

shared ancestral character A character, shared by members of a particular clade, that originated in an ancestor that is not a member of that clade.

shared derived character An evolutionary novelty that is unique to a particular clade.

shoot system The aerial portion of a plant body, consisting of stems, leaves, and (in angiosperms) flowers.

short tandem repeat (STR) Simple sequence DNA containing multiple tandemly repeated units of two to five nucleotides. Variations in STRs act as genetic markers in STR analysis, used to prepare genetic profiles.

short-day plant A plant that flowers (usually in late summer, fall, or winter) only when the light period is shorter than a critical length.

short-term memory The ability to hold information, anticipations, or goals for a time and then release them if they become irrelevant.

sickle-cell disease A recessively inherited human blood disorder in which a single nucleotide change in the α-globin gene causes hemoglobin to aggregate, changing red blood cell shape and causing multiple symptoms in afflicted individuals.

sieve plate An end wall in a sieve-tube element, which facilitates the flow of phloem sap in angiosperm sieve tubes.

sieve-tube element A living cell that conducts sugars and other organic nutrients in the phloem of angiosperms; also called a sieve-tube member. Connected end to end, they form sieve tubes.

sign stimulus An external sensory cue that triggers a fixed action pattern by an animal.

signal In animal behavior, transmission of a stimulus from one animal to another. The term is also used in the context of communication in other kinds of organisms and in cell-to-cell communication in all multicellular organisms.

signal peptide A sequence of about 20 amino acids at or near the leading (amino) end of a polypeptide that targets it to the endoplasmic reticulum or other organelles in a eukaryotic cell.

signal-recognition particle (SRP) A protein-RNA complex that recognizes a signal peptide as it emerges from a ribosome and helps direct the ribosome to the endoplasmic reticulum (ER) by binding to a receptor protein on the ER.

signal transduction The linkage of a mechanical, chemical, or electromagnetic stimulus to a specific cellular response.

signal transduction pathway A series of steps linking a mechanical, chemical, or electrical stimulus to a specific cellular response.

silent mutation A nucleotide-pair substitution that has no observable effect on the phenotype; for example, within a gene, a mutation that results in a codon that codes for the same amino acid.

simple fruit A fruit derived from a single carpel or several fused carpels.

simple sequence DNA A DNA sequence that contains many copies of tandemly repeated short sequences.

single bond A single covalent bond; the sharing of a pair of valence electrons by two atoms.

single circulation A circulatory system consisting of a single pump and circuit, in which blood passes from the sites of gas exchange to the rest of the body before returning to the heart.

single-lens eye The camera-like eye found in some jellies, polychaete worms, spiders, and many molluscs.

single nucleotide polymorphism (SNP) (snip) A single base-pair site in a genome where nucleotide variation is found in at least 1% of the population.

single-strand binding protein A protein that binds to the unpaired DNA strands during DNA replication, stabilizing them and holding them apart while they serve as templates for the synthesis of complementary strands of DNA.

sinoatrial (SA) node (sī′-nō-ā′-trē-uhl) A region in the right atrium of the heart that sets the rate and timing at which all cardiac muscle cells contract; the pacemaker.

sister chromatids Two copies of a duplicated chromosome attached to each other by proteins at the centromere and, sometimes, along the arms. While joined, two sister chromatids make up one chromosome. Chromatids are eventually separated during mitosis or meiosis II.

sister taxa Groups of organisms that share an immediate common ancestor and hence are each other's closest relatives.

skeletal muscle A type of striated muscle that is generally responsible for the voluntary movements of the body.

sliding-filament model The idea that muscle contraction is based on the movement of thin (actin) filaments along thick (myosin) filaments, shortening the sarcomere, the basic unit of muscle organization.

slow-twitch fiber A muscle fiber that can sustain long contractions.

small interfering RNA (siRNA) One of multiple small, single-stranded RNA molecules generated by cellular machinery from a long, linear, double-stranded RNA molecule. The siRNA associates with one or more proteins in a complex that can degrade or prevent translation of an mRNA with a complementary sequence.

small intestine The longest section of the alimentary canal, so named because of its small diameter compared with that of the large intestine; the principal site of the enzymatic hydrolysis of food macromolecules and the absorption of nutrients.

smooth ER That portion of the endoplasmic reticulum that is free of ribosomes.

smooth muscle A type of muscle lacking the striations of skeletal and cardiac muscle because of the uniform distribution of myosin filaments in the cells; responsible for involuntary body activities.

social learning Modification of behavior through the observation of other individuals.

sociobiology The study of social behavior based on evolutionary theory.

sodium-potassium pump A transport protein in the plasma membrane of animal cells that actively transports sodium out of the cell and potassium into the cell.

soil horizon A soil layer with physical characteristics that differ from those of the layers above or beneath.

solute (sol′-yūt) A substance that is dissolved in a solution.

solute potential (ψ_S) A component of water potential that is proportional to the molarity of a solution and that measures the effect of solutes on the direction of water movement; also called osmotic potential, it can be either zero or negative.

solution A liquid that is a homogeneous mixture of two or more substances.

solvent The dissolving agent of a solution. Water is the most versatile solvent known.

somatic cell (sō-mat′-ik) Any cell in a multicellular organism except a sperm or egg or their precursors.

somite One of a series of blocks of mesoderm that exist in pairs just lateral to the notochord in a vertebrate embryo.

soredium (suh-rē′-dē-um) (plural, **soredia**) In lichens, a small cluster of fungal hyphae with embedded algae.

sorus (plural, **sori**) A cluster of sporangia on a fern sporophyll. Sori may be arranged in various patterns, such as parallel lines or dots, which are useful in fern identification.

spatial learning The establishment of a memory that reflects the environment's spatial structure.

speciation (spē′-sē-ā′-shun) An evolutionary process in which one species splits into two or more species.

species (spē′-sēz) A population or group of populations whose members have the potential to interbreed in nature and produce viable, fertile offspring but do not produce viable, fertile offspring with members of other such groups.

species-area curve (spē′-sēz) The biodiversity pattern that shows that the larger the geographic area of a community is, the more species it has.

species diversity (spē′-sēz) The number and relative abundance of species in a biological community.

species richness (spē′-sēz) The number of species in a biological community.

specific heat The amount of heat that must be absorbed or lost for 1 g of a substance to change its temperature by 1°C.

spectrophotometer An instrument that measures the proportions of light of different wavelengths absorbed and transmitted by a pigment solution.

sperm The male gamete.

spermatheca (sper′-muh-thē′-kuh) (plural, **spermathecae**) In many insects, a sac in the female reproductive system where sperm are stored.

spermatogenesis (sper-ma′-tō-gen′-uh-sis) The continuous and prolific production of mature sperm in the testis.

spermatogonium (sper-ma′-tō-gō′-nē-um) (plural, **spermatogonia**) A cell that divides mitotically to form spermatocytes.

S phase The synthesis phase of the cell cycle; the portion of interphase during which DNA is replicated.

sphincter (sfink′-ter) A ringlike band of muscle fibers that controls the size of an opening in the body, such as the passage between the esophagus and the stomach.

spiral cleavage A type of embryonic development in protostomes in which the planes of cell division that transform the zygote into a ball of cells are diagonal to the vertical axis of the embryo. As a result, the cells of each tier sit in the grooves between cells of adjacent tiers.

spliceosome (splī′-sō-sōm) A large complex made up of proteins and RNA molecules that splices RNA by interacting with the ends of an RNA intron, releasing the intron and joining the two adjacent exons.

spongocoel (spon′-jō-sēl) The central cavity of a sponge.

spontaneous process A process that occurs without an overall input of energy; a process that is energetically favorable.

sporangium (spōr-an′-jē-um) (plural, **sporangia**) A multicellular organ in fungi and plants in which meiosis occurs and haploid cells develop.

spore (1) In the life cycle of a plant or alga undergoing alternation of generations, a haploid cell produced in the sporophyte by meiosis. A spore can divide by mitosis to develop into a multicellular haploid individual, the gametophyte, without fusing with another cell. (2) In fungi, a haploid cell, produced either sexually or asexually, that produces a mycelium after germination.

sporocyte (spō′-ruh-sīt) A diploid cell within a sporangium that undergoes meiosis and generates haploid spores; also called a spore mother cell.

sporophyll (spō′-ruh-fil) A modified leaf that bears sporangia and hence is specialized for reproduction.

sporophyte (spō-ruh-fīt·) In organisms (plants and some algae) that have alternation of generations, the multicellular diploid form that results from the union of gametes. Meiosis in the sporophyte produces haploid spores that develop into gametophytes.

sporopollenin (spōr-uh-pol′-eh-nin) A durable polymer that covers exposed zygotes of charophyte algae and forms the walls of plant spores, preventing them from drying out.

stability In evolutionary biology, a term referring to a hybrid zone in which hybrids continue to be produced; this causes the hybrid zone to be "stable" in the sense of persisting over time.

stabilizing selection Natural selection in which intermediate phenotypes survive or reproduce more successfully than do extreme phenotypes.

stamen (stā′-men) The pollen-producing reproductive organ of a flower, consisting of an anther and a filament.

standard deviation A measure of the variation found in a set of data points.

standard metabolic rate (SMR) Metabolic rate of a resting, fasting, and nonstressed ectotherm at a particular temperature.

starch A storage polysaccharide in plants, consisting entirely of glucose monomers joined by glycosidic linkages.

start point In transcription, the nucleotide position on the promoter where RNA polymerase begins synthesis of RNA.

statocyst (stat′-uh-sist′) A type of mechanoreceptor that functions in equilibrium in invertebrates by use of statoliths, which stimulate hair cells in relation to gravity.

statolith (stat′-uh-lith′) (1) In plants, a specialized plastid that contains dense starch grains and may play a role in detecting gravity. (2) In invertebrates, a dense particle that settles in response to gravity and is found in sensory organs that function in equilibrium.

stele (stēl) The vascular tissue of a stem or root.

stem A vascular plant organ consisting of an alternating system of nodes and internodes that support the leaves and reproductive structures.

stem cell Any relatively unspecialized cell that can produce, during a single division, two identical daughter cells or two more specialized daughter cells that can undergo further differentiation, or one cell of each type.

steroid A type of lipid characterized by a carbon skeleton consisting of four fused rings with various chemical groups attached.

sticky end A single-stranded end of a double-stranded restriction fragment.

stigma (plural, **stigmata**) The sticky part of a flower's carpel, which receives pollen grains.

stimulus In feedback regulation, a fluctuation in a variable that triggers a response.

stipe A stemlike structure of a seaweed.

stock The plant that provides the root system when making a graft.

stoma (stō′-muh) (plural, **stomata**) A microscopic pore surrounded by guard cells in the epidermis of leaves and stems that allows gas exchange between the environment and the interior of the plant.

stomach An organ of the digestive system that stores food and performs preliminary steps of digestion.

Stramenopiles (strah′-men-ō′-pē-lēs) One of the three major subgroups for which the SAR eukaryotic supergroup is named. This clade arose by secondary endosymbiosis and includes diatoms and brown algae.

stratum (strah′-tum) (plural, **strata**) A rock layer formed when new layers of sediment cover older ones and compress them.

strigolactone Any of a class of plant hormones that inhibit shoot branching, trigger the germination of parasitic plant seeds, and stimulate the association of plant roots with mycorrhizal fungi.

strobilus (strō-bī′-lus) (plural, **strobili**) The technical term for a cluster of sporophylls known commonly as a cone, found in most gymnosperms and some seedless vascular plants.

stroke The death of nervous tissue in the brain, usually resulting from rupture or blockage of arteries in the head.

stroke volume The volume of blood pumped by a heart ventricle in a single contraction.

stroma (strō′-muh) The dense fluid within the chloroplast surrounding the thylakoid membrane and containing ribosomes and DNA; involved in the synthesis of organic molecules from carbon dioxide and water.

stromatolite Layered rock that results from the activities of prokaryotes that bind thin films of sediment together.

structural isomer One of two or more compounds that have the same molecular formula but differ in the covalent arrangements of their atoms.

style The stalk of a flower's carpel, with the ovary at the base and the stigma at the top.

substrate The reactant on which an enzyme works.

substrate feeder An animal that lives in or on its food source, eating its way through the food.

substrate-level phosphorylation The enzyme-catalyzed formation of ATP by direct transfer of a phosphate group to ADP from an intermediate substrate in catabolism.

sugar sink A plant organ that is a net consumer or storer of sugar. Growing roots, shoot tips, stems, and fruits are examples of sugar sinks supplied by phloem.

sugar source A plant organ in which sugar is being produced by either photosynthesis or the breakdown of starch. Mature leaves are the primary sugar sources of plants.

sulfhydryl group A chemical group consisting of a sulfur atom bonded to a hydrogen atom.

summation A phenomenon of neural integration in which the membrane potential of the postsynaptic cell is determined by the combined effect of EPSPs or IPSPs produced in rapid succession at one synapse or simultaneously at different synapses.

suprachiasmatic nucleus (SCN) (sūp′-ruh-kē′-as-ma-tik) A group of neurons in the hypothalamus of mammals that functions as a biological clock.

surface tension A measure of how difficult it is to stretch or break the surface of a liquid. Water has a high surface tension because of the hydrogen bonding of surface molecules.

surfactant A substance secreted by alveoli that decreases surface tension in the fluid that coats the alveoli.

survivorship curve A plot of the number of members of a cohort that are still alive at each age; one way to represent age-specific mortality.

suspension feeder An animal that feeds by removing suspended food particles from the surrounding medium by a capture, trapping, or filtration mechanism.

sustainable agriculture Long-term productive farming methods that are environmentally safe.

sustainable development Development that meets the needs of people today without limiting the ability of future generations to meet their needs.

swim bladder In aquatic osteichthyans, an air sac that enables the animal to control its buoyancy in the water.

symbiont (sim′-bē-ont) The smaller participant in a symbiotic relationship, living in or on the host.

symbiosis An ecological relationship between organisms of two different species that live together in direct and intimate contact.

sympathetic division One of three divisions of the autonomic nervous system; generally increases energy expenditure and prepares the body for action.

sympatric speciation (sim-pat′-rik) The formation of new species in populations that live in the same geographic area.

symplast In plants, the continuum of cytoplasm connected by plasmodesmata between cells.

synapse (sin′-aps) The junction where a neuron communicates with another cell across a narrow gap via a neurotransmitter or an electrical coupling.

synapsid (si-nap′-sid) A member of an amniote clade distinguished by a single hole on each side of the skull. Synapsids include the mammals.

synapsis (si-nap′-sis) The pairing and physical connection of one duplicated chromosome to its homolog during prophase I of meiosis.

synaptonemal (si-nap′-tuh-nē′-muhl) **complex** A zipper-like structure composed of proteins, which connects a chromosome to its homolog tightly along their lengths during part of prophase I of meiosis.

systematics A scientific discipline focused on classifying organisms and determining their evolutionary relationships.

systemic acquired resistance A defensive response in infected plants that helps protect healthy tissue from pathogenic invasion.

systemic circuit The branch of the circulatory system that supplies oxygenated blood to and carries deoxygenated blood away from organs and tissues throughout the body.

systems biology An approach to studying biology that aims to model the dynamic behavior of whole biological systems based on a study of the interactions among the system's parts.

systole (sis′-tō-lē) The stage of the cardiac cycle in which a heart chamber contracts and pumps blood.

systolic pressure Blood pressure in the arteries during contraction of the ventricles.

taproot A main vertical root that develops from an embryonic root and gives rise to lateral (branch) roots.

tastant Any chemical that stimulates the sensory receptors in a taste bud.

taste bud A collection of modified epithelial cells on the tongue or in the mouth that are receptors for taste in mammals.

TATA box A DNA sequence in eukaryotic promoters crucial in forming the transcription initiation complex.

taxis (tak′-sis) An oriented movement toward or away from a stimulus.

taxon (plural, **taxa**) A named taxonomic unit at any given level of classification.

taxonomy (tak-son′-uh-mē) A scientific discipline concerned with naming and classifying the diverse forms of life.

Tay-Sachs disease A human genetic disease caused by a recessive allele for a dysfunctional enzyme, leading to accumulation of certain lipids in the brain. Seizures, blindness, and degeneration of motor and mental performance usually become manifest a few months after birth, followed by death within a few years.

T cells The class of lymphocytes that mature in the thymus; they include both effector cells for the cell-mediated immune response and helper cells required for both branches of adaptive immunity.

technology The application of scientific knowledge for a specific purpose, often involving industry or commerce but also including uses in basic research.

telomere (tel′-uh-mēr) The tandemly repetitive DNA at the end of a eukaryotic chromosome's DNA molecule. Telomeres protect the organism's genes from being eroded during successive rounds of replication. *See also* repetitive DNA.

telophase The fifth and final stage of mitosis, in which daughter nuclei are forming and cytokinesis has typically begun.

temperate broadleaf forest A biome located throughout midlatitude regions where there is sufficient moisture to support the growth of large, broadleaf deciduous trees.

temperate grassland A terrestrial biome that exists at midlatitude regions and is dominated by grasses and forbs.

temperate phage A phage that is capable of replicating by either a lytic or lysogenic cycle.

temperature A measure in degrees of the average kinetic energy (thermal energy) of the atoms and molecules in a body of matter.

template strand The DNA strand that provides the pattern, or template, for ordering, by complementary base pairing, the sequence of nucleotides in an RNA transcript.

tendon A fibrous connective tissue that attaches muscle to bone.

terminator In bacteria, a sequence of nucleotides in DNA that marks the end of a gene and signals RNA polymerase to release the newly made RNA molecule and detach from the DNA.

territoriality A behavior in which an animal defends a bounded physical space against encroachment by other individuals, usually of its own species.

tertiary consumer (ter′-shē-ār′-ē) A carnivore that eats other carnivores.

tertiary structure (ter′-shē-ār′-ē) The overall shape of a protein molecule due to interactions of amino acid side chains, including hydrophobic interactions, ionic bonds, hydrogen bonds, and disulfide bridges.

test In foram protists, a porous shell that consists of a single piece of organic material hardened with calcium carbonate.

testcross Breeding an organism of unknown genotype with a homozygous recessive individual to determine the unknown genotype. The ratio of phenotypes in the offspring reveals the unknown genotype.

testis (plural, **testes**) The male reproductive organ, or gonad, in which sperm and reproductive hormones are produced.

testosterone A steroid hormone required for development of the male reproductive system, spermatogenesis, and male secondary sex characteristics; the major androgen in mammals.

tetanus (tet′-uh-nus) The maximal, sustained contraction of a skeletal muscle, caused by a very high frequency of action potentials elicited by continual stimulation.

tetrapod A vertebrate clade whose members have limbs with digits. Tetrapods include mammals, amphibians, and birds and other reptiles.

thalamus (thal′-uh-mus) An integrating center of the vertebrate forebrain. Neurons with cell bodies in the thalamus relay neural input to specific areas in the cerebral cortex and regulate what information goes to the cerebral cortex.

theory An explanation that is broader in scope than a hypothesis, generates new hypotheses, and is supported by a large body of evidence.

thermal energy Kinetic energy due to the random motion of atoms and molecules; energy in its most random form. *See also* heat.

thermocline A narrow stratum of abrupt temperature change in the ocean and in many temperate-zone lakes.

thermodynamics (ther′-mō-dī-nam′-iks) The study of energy transformations that occur in a collection of matter. *See also* first law of thermodynamics and second law of thermodynamics.

thermophile *See* extreme thermophile.

thermoreceptor A receptor stimulated by either heat or cold.

thermoregulation The maintenance of internal body temperature within a tolerable range.

theropod A member of a group of dinosaurs that were bipedal carnivores.

thick filament A filament composed of staggered arrays of myosin molecules; a component of myofibrils in muscle fibers.

thigmomorphogenesis (thig′-mō-mor′-phō-gen′-uh-sis) A response in plants to chronic mechanical stimulation, resulting from increased ethylene production. An example is thickening stems in response to strong winds.

thigmotropism (thig-mō′-truh-pizm) A directional growth of a plant in response to touch.

thin filament A filament consisting of two strands of actin and two strands of regulatory protein coiled around one another; a component of myofibrils in muscle fibers.

threatened species A species that is considered likely to become endangered in the foreseeable future.

threshold The potential that an excitable cell membrane must reach for an action potential to be initiated.

thrombus A fibrin-containing clot that forms in a blood vessel and blocks the flow of blood.

thylakoid (thī′-luh-koyd) A flattened, membranous sac inside a chloroplast. Thylakoids often exist in stacks called grana that are interconnected; their membranes contain molecular "machinery" used to convert light energy to chemical energy.

thymus (thī′-mus) A small organ in the thoracic cavity of vertebrates where maturation of T cells is completed.

thyroid gland An endocrine gland, located on the ventral surface of the trachea, that secretes two iodine-containing hormones, triiodothyronine (T_3) and thyroxine (T_4), as well as calcitonin.

thyroid hormone Either of two iodine-containing hormones (triiodothyronine and thyroxine) that are secreted by the thyroid gland and that help regulate metabolism, development, and maturation in vertebrates.

thyroxine (T_4) One of two iodine-containing hormones that are secreted by the thyroid gland and that help regulate metabolism, development, and maturation in vertebrates.

tidal volume The volume of air a mammal inhales and exhales with each breath.

tight junction A type of intercellular junction between animal cells that prevents the leakage of material through the space between cells.

tissue An integrated group of cells with a common structure, function, or both.

tissue system One or more tissues organized into a functional unit connecting the organs of a plant.

Toll-like receptor (TLR) A membrane receptor on a phagocytic white blood cell that recognizes fragments of molecules common to a set of pathogens.

tonicity The ability of a solution surrounding a cell to cause that cell to gain or lose water.

top-down model A model of community organization in which predation influences community organization by controlling herbivore numbers, which in turn control plant or phytoplankton numbers, which in turn control nutrient levels; also called the trophic cascade model.

topoisomerase A protein that breaks, swivels, and rejoins DNA strands. During DNA replication, topoisomerase helps to relieve strain in the double helix ahead of the replication fork.

topsoil A mixture of particles derived from rock, living organisms, and decaying organic material (humus).

torpor A physiological state in which activity is low and metabolism decreases.

totipotent (tō′-tuh-pōt′-ent) Describing a cell that can give rise to all parts of the embryo and adult, as well as extraembryonic membranes in species that have them.

trace element An element indispensable for life but required in extremely minute amounts.

trachea (trā′-kē-uh) The portion of the respiratory tract that passes from the larynx to the bronchi; also called the windpipe.

tracheal system In insects, a system of branched, air-filled tubes that extends throughout the body and carries oxygen directly to cells.

tracheid (trā′-kē-id) A long, tapered water-conducting cell found in the xylem of nearly all vascular plants. Functioning tracheids are no longer living.

trait One of two or more detectable variants in a genetic character.

***trans* fat** An unsaturated fat, formed artificially during hydrogenation of oils, containing one or more *trans* double bonds.

transcription The synthesis of RNA using a DNA template.

transcription factor A regulatory protein that binds to DNA and affects transcription of specific genes.

transcription initiation complex The completed assembly of transcription factors and RNA polymerase bound to a promoter.

transcription unit A region of DNA that is transcribed into an RNA molecule.

transduction A process in which phages (viruses) carry bacterial DNA from one bacterial cell to another. When these two cells are members of different species, transduction results in horizontal gene transfer. *See also* signal transduction.

transfer RNA (tRNA) An RNA molecule that functions as a translator between nucleic acid and protein languages by picking up a specific amino acid and carrying it to the ribosome, where the tRNA recognizes the appropriate codon in the mRNA.

transformation (1) The process by which a cell in culture acquires the ability to divide indefinitely, similar to the division of cancer cells. (2) A change in genotype and phenotype due to the assimilation of external DNA by a cell. When the external DNA is from a member of a different species, transformation results in horizontal gene transfer.

transgenic Pertaining to an organism whose genome contains DNA introduced from another organism of the same or a different species.

translation The synthesis of a polypeptide using the genetic information encoded in an mRNA molecule. There is a change of "language" from nucleotides to amino acids.

translocation (1) An aberration in chromosome structure resulting from attachment of a chromosomal fragment to a nonhomologous chromosome. (2) During protein synthesis, the third stage in the elongation cycle, when the RNA carrying the growing polypeptide moves from the A site to the P site on the ribosome. (3) The transport of organic nutrients in the phloem of vascular plants.

transmission electron microscope (TEM) A microscope that passes an electron beam through very thin sections stained with metal atoms and is primarily used to study the internal structure of cells.

transpiration The evaporative loss of water from a plant.

transport epithelium One or more layers of specialized epithelial cells that carry out and regulate solute movement.

transport protein A transmembrane protein that helps a certain substance or class of closely related substances to cross the membrane.

transport vesicle A small membranous sac in a eukaryotic cell's cytoplasm carrying molecules produced by the cell.

transposable element A segment of DNA that can move within the genome of a cell by means of a DNA or RNA intermediate; also called a transposable genetic element.

transposon A transposable element that moves within a genome by means of a DNA intermediate.

transverse (T) tubule An infolding of the plasma membrane of skeletal muscle cells.

triacylglycerol (trī-as′-ul-glis′-uh-rol) A lipid consisting of three fatty acids linked to one glycerol molecule; also called a fat or triglyceride.

trichome An epidermal cell that is a highly specialized, often hairlike outgrowth on a plant shoot.

triple response A plant growth maneuver in response to mechanical stress, involving slowing of stem elongation, thickening of the stem, and a curvature that causes the stem to start growing horizontally.

triplet code A genetic information system in which a series of three-nucleotide-long words specifies a sequence of amino acids for a polypeptide chain.

triploblastic Possessing three germ layers: the endoderm, mesoderm, and ectoderm. All bilaterian animals are triploblastic.

trisomic Referring to a diploid cell that has three copies of a particular chromosome instead of the normal two.

trochophore larva (trō′-kuh-fōr) Distinctive larval stage observed in some lophotrochozoan animals, including some annelids and molluscs.

trophic efficiency The percentage of production transferred from one trophic level to the next higher trophic level.

trophic structure The different feeding relationships in an ecosystem, which determine the route of energy flow and the pattern of chemical cycling.

trophoblast The outer epithelium of a mammalian blastocyst. It forms the fetal part of the placenta, supporting embryonic development but not forming part of the embryo proper.

tropical dry forest A terrestrial biome characterized by relatively high temperatures and precipitation overall but with a pronounced dry season.

tropical rain forest A terrestrial biome characterized by relatively high precipitation and temperatures year-round.

tropics Latitudes between 23.5° north and south.

tropism A growth response that results in the curvature of whole plant organs toward or away from stimuli due to differential rates of cell elongation.

tropomyosin The regulatory protein that blocks the myosin-binding sites on actin molecules.

troponin complex The regulatory proteins that control the position of tropomyosin on the thin filament.

true-breeding Referring to organisms that produce offspring of the same variety over many generations of self-pollination.

tubal ligation A means of sterilization in which a woman's two oviducts (fallopian tubes) are tied closed and a segment of each is removed to prevent eggs from reaching the uterus.

tube foot One of numerous extensions of an echinoderm's water vascular system. Tube feet function in locomotion and feeding.

tumor-suppressor gene A gene whose protein product inhibits cell division, thereby preventing the uncontrolled cell growth that contributes to cancer.

tundra A terrestrial biome at the extreme limits of plant growth. At the northernmost limits, it is called arctic tundra, and at high altitudes, where plant forms are limited to low shrubby or matlike vegetation, it is called alpine tundra.

tunicate A member of the clade Urochordata, sessile marine chordates that lack a backbone.

turgid (ter′-jid) Swollen or distended, as in plant cells. (A walled cell becomes turgid if it has a lower water potential than its surroundings, resulting in entry of water.)

turgor pressure The force directed against a plant cell wall after the influx of water and swelling of the cell due to osmosis.

turnover The mixing of waters as a result of changing water-temperature profiles in a lake.

twin study A behavioral study in which researchers compare the behavior of identical twins raised apart with that of identical twins raised in the same household.

tympanic membrane Another name for the eardrum, the membrane between the outer and middle ear.

Unikonta (yū′-ni-kon′-tuh) One of four supergroups of eukaryotes proposed in a current hypothesis of the evolutionary history of eukaryotes. This clade, which is supported by studies of myosin proteins and DNA, consists of amoebozoans and opisthokonts. *See also* Excavata, SAR, and Archaeplastida.

unsaturated fatty acid A fatty acid that has one or more double bonds between carbons in the hydrocarbon tail. Such bonding reduces the number of hydrogen atoms attached to the carbon skeleton.

urban ecology The study of organisms and their environment in urban and suburban settings.

urea A soluble nitrogenous waste produced in the liver by a metabolic cycle that combines ammonia with carbon dioxide.

ureter (yū-rē′-ter) A duct leading from the kidney to the urinary bladder.

urethra (yū-rē′-thruh) A tube that releases urine from the mammalian body near the vagina in females and through the penis in males; also serves in males as the exit tube for the reproductive system.

uric acid A product of protein and purine metabolism and the major nitrogenous waste product of insects, land snails, and many reptiles. Uric acid is relatively nontoxic and largely insoluble in water.

urinary bladder The pouch where urine is stored prior to elimination.

uterine cycle The cyclic changes in the endometrium (uterine lining) of mammals that occur in the absence of pregnancy. In certain primates, including humans, the uterine cycle is a menstrual cycle.

uterus A female organ where eggs are fertilized and/or development of the young occurs.

vaccine A harmless variant or derivative of a pathogen that stimulates a host's immune system to mount defenses against the pathogen.

vacuole (vak′-yū-ōl′) A membrane-bounded vesicle whose specialized function varies in different kinds of cells.

vagina Part of the female reproductive system between the uterus and the outside opening; the birth canal in mammals. During copulation, the vagina accommodates the male's penis and receives sperm.

valence The bonding capacity of a given atom; the number of covalent bonds that an atom can form, which usually equals the number of unpaired electrons in its outermost (valence) shell.

valence electron An electron in the outermost electron shell.

valence shell The outermost energy shell of an atom, containing the valence electrons involved in the chemical reactions of that atom.

van der Waals interactions Weak attractions between molecules or parts of molecules that result from transient local partial charges.

variable A factor that varies in an experiment.

variation Differences between members of the same species.

vas deferens In mammals, the tube in the male reproductive system in which sperm travel from the epididymis to the urethra.

vasa recta The capillary system in the kidney that serves the loop of Henle.

vascular cambium A cylinder of meristematic tissue in woody plants that adds layers of secondary vascular tissue called secondary xylem (wood) and secondary phloem.

vascular plant A plant with vascular tissue. Vascular plants include all living plant species except liverworts, mosses, and hornworts.

vascular tissue Plant tissue consisting of cells joined into tubes that transport water and nutrients throughout the plant body.

vascular tissue system A transport system formed by xylem and phloem throughout a vascular plant. Xylem transports water and minerals; phloem transports sugars, the products of photosynthesis.

vasectomy The cutting and sealing of each vas deferens to prevent sperm from entering the urethra.

vasoconstriction A decrease in the diameter of blood vessels caused by contraction of smooth muscles in the vessel walls.

vasodilation An increase in the diameter of blood vessels caused by relaxation of smooth muscles in the vessel walls.

vasopressin *See* antidiuretic hormone (ADH).

vector An organism that transmits pathogens from one host to another.

vegetal pole The point at the end of an egg in the hemisphere where most yolk is concentrated; opposite of animal pole.

vegetative propagation Asexual reproduction in plants that is facilitated or induced by humans.

vegetative reproduction Asexual reproduction in plants.

vein (1) In animals, a vessel that carries blood toward the heart. (2) In plants, a vascular bundle in a leaf.

ventilation The flow of air or water over a respiratory surface.

ventral Pertaining to the underside, or bottom, of an animal with radial or bilateral symmetry.

ventricle (ven′-tri-kul) (1) A heart chamber that pumps blood out of the heart. (2) A space in the vertebrate brain, filled with cerebrospinal fluid.

venule (ven′-yūl) A vessel that conveys blood between a capillary bed and a vein.

vernalization The use of cold treatment to induce a plant to flower.

vertebrate A chordate animal with vertebrae, the series of bones that make up the backbone.

vesicle (ves′-i-kul) A membranous sac in the cytoplasm of a eukaryotic cell.

vessel A continuous water-conducting micropipe found in most angiosperms and a few nonflowering vascular plants.

vessel element A short, wide water-conducting cell found in the xylem of most angiosperms and a few nonflowering vascular plants. Dead at maturity, vessel elements are aligned end to end to form micropipes called vessels.

vestigial structure A feature of an organism that is a historical remnant of a structure that served a function in the organism's ancestors.

villus (plural, **villi**) (1) A finger-like projection of the inner surface of the small intestine. (2) A finger-like projection of the chorion of the mammalian placenta. Large numbers of villi increase the surface areas of these organs.

viral envelope A membrane, derived from membranes of the host cell, that cloaks the capsid, which in turn encloses a viral genome.

virulent phage A phage that replicates only by a lytic cycle.

virus An infectious particle incapable of replicating outside of a cell, consisting of an RNA or DNA genome surrounded by a protein coat (capsid) and, for some viruses, a membranous envelope.

visceral mass One of the three main parts of a mollusc; the part containing most of the internal organs. *See also* foot and mantle.

visible light That portion of the electromagnetic spectrum that can be detected as various colors by the human eye, ranging in wavelength from about 380 nm to about 750 nm.

vital capacity The maximum volume of air that a mammal can inhale and exhale with each breath.

vitamin An organic molecule required in the diet in very small amounts. Many vitamins serve as coenzymes or parts of coenzymes.

viviparous (vī-vip′-uh-rus) Referring to a type of development in which the young are born alive after having been nourished in the uterus by blood from the placenta.

voltage-gated ion channel A specialized ion channel that opens or closes in response to changes in membrane potential.

vulva Collective term for the female external genitalia.

water potential (ψ) The physical property predicting the direction in which water will flow, governed by solute concentration and applied pressure.

water vascular system A network of hydraulic canals unique to echinoderms that branches into extensions called tube feet, which function in locomotion and feeding.

wavelength The distance between crests of waves, such as those of the electromagnetic spectrum.

wetland A habitat that is inundated by water at least some of the time and that supports plants adapted to water-saturated soil.

white matter Tracts of axons within the CNS.

whole-genome shotgun approach Procedure for genome sequencing in which the genome is randomly cut into many overlapping short segments that are sequenced; computer software then assembles the complete sequence.

wild type The phenotype most commonly observed in natural populations; also refers to the individual with that phenotype.

wilting The drooping of leaves and stems as a result of plant cells becoming flaccid.

wobble Flexibility in the base-pairing rules in which the nucleotide at the 5′ end of a tRNA anticodon can form hydrogen bonds with more than one kind of base in the third position (3′ end) of a codon.

xerophyte (zir′-ō-fīt′) A plant adapted to an arid climate.

X-linked gene A gene located on the X chromosome; such genes show a distinctive pattern of inheritance.

X-ray crystallography A technique used to study the three-dimensional structure of molecules. It depends on the diffraction of an X-ray beam by the individual atoms of a crystallized molecule.

xylem (zī′-lum) Vascular plant tissue consisting mainly of tubular dead cells that conduct most of the water and minerals upward from the roots to the rest of the plant.

xylem sap (zī′-lum) The dilute solution of water and minerals carried through vessels and tracheids.

yeast Single-celled fungus. Yeasts reproduce asexually by binary fission or by the pinching of small buds off a parent cell. Many fungal species can grow both as yeasts and as a network of filaments; relatively few species grow only as yeasts.

yolk Nutrients stored in an egg.

zero population growth (ZPG) A period of stability in population size, when additions to the population through births and immigration are balanced by subtractions through deaths and emigration.

zona pellucida The extracellular matrix surrounding a mammalian egg.

zoned reserve An extensive region that includes areas relatively undisturbed by humans surrounded by areas that have been changed by human activity and are used for economic gain.

zone of polarizing activity (ZPA) A block of mesoderm located just under the ectoderm where the posterior side of a limb bud is attached to the body; required for proper pattern formation along the anterior-posterior axis of the limb.

zoonotic pathogen A disease-causing agent that is transmitted to humans from other animals.

zoospore Flagellated spore found in chytrid fungi and some protists.

zygomycete (zī′-guh-mī′-sēt) A member of the fungal phylum Zygomycota, characterized by the formation of a sturdy structure called a zygosporangium during sexual reproduction.

zygosporangium (zī′-guh-spōr-an′-jē-um) (plural, **zygosporangia**) In zygomycete fungi, a sturdy multinucleate structure in which karyogamy and meiosis occur.

zygote (zī′-gōt) The diploid cell produced by the union of haploid gametes during fertilization; a fertilized egg.

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