FIGURE 44.14 **Life history strategies.**

Are dandelions *r*-strategists with the characteristics noted, and are bears *K*-strategists with the characteristics noted? Most often the distinctions between these two possible life strategies are not as clear-cut as they may seem.

and growth rates most of the time. Such organisms are often very good dispersers and colonizers of new habitats. Classic examples of such *opportunistic species* are bacteria, some fungi, many insects, rodents, and annual plants (Fig. 44.14, *left*).

In contrast, some environments are relatively stable and/or predictable, where populations tend to be near *K*, with minimal fluctuations in size. Resources such as food and shelter will be relatively scarce for these individuals, and those that are best able to compete will have the largest number of offspring. ***K*-selection** favors *K*-strategists, which allocate energy to their own growth and survival and to the growth and survival of their offspring. Therefore, they are usually fairly large, late to mature, have low fecundity and parity, and have a fairly long life span. Because these organisms, termed *equilibrium species*, are strong competitors, they can become established and exclude opportunistic species. They are specialists rather than colonizers and tend to become extinct when their normal way of life is destroyed. The best possible examples of *K*-strategists include long-lived plants (saguaro cacti, oaks, cypresses, and pines), birds of prey (hawks and eagles), and large mammals (whales, elephants, bears, and humans) (Fig. 44.14, *right*). Another example of a *K*-strategist is the Florida panther, the largest mammal in the Florida Everglades. It requires a very large range and produces few offspring that require parental care. Currently, the Florida panther is unable to compensate for a reduction in its range and is therefore on the verge of extinction.

Nature is actually more complex than these two possible life history patterns suggest. It now appears that our descriptions of *r*-strategist and *K*-strategist populations are at the ends of a continuum, and most populations lie somewhere in between these two extremes. For example, recall that plants have a two-generation life cycle, the sporophyte and the gametophyte. Ferns, which could be classified as *r*-strategists, distribute many spores and leave the gametophyte to fend for itself, but gymnosperms (e.g., pine trees) and angiosperms (e.g., oak trees), which could be classified as *K*-strategists, retain and protect the gametophyte. They produce seeds that contain the next sporophyte generation plus stored food. The added investment is significant, but these plants still release copious numbers of seeds.

Also, adult size is not always a determining factor for the life history pattern. For example, a cod is a rather large fish weighing up to 12 kg and measuring nearly 2 m in length—but cod release gametes in vast numbers, the zygotes form in the sea, and the parents make no further investment in developing offspring. Of the 6–7 million eggs released by a single female cod, only a few will become adult fish. Cod are considered *r*-strategists.

Check Your Progress 44.5

1. Describe the general characteristics of a *K*- and *r*-strategist.

ecology focus

When a Population Grows Too Large

White-tailed deer, which live from southern Canada to below the equator in South America, are prolific breeders. In one study, investigators found that two male and four female deer produced 160 offspring in six years. Theoretically, the number could have been 300 because a large proportion of does (female deer) breed their first year, and once they start breeding, produce about two young each year of life.

A century ago, the white-tailed deer population across eastern United States was less than half a million. Today, it is well over 200 million deer—even more than existed when Europeans first arrived to colonize America. This dramatic increase in population size can probably be attributed to a lack of predators. For one thing, hunting is tightly controlled by government agencies, and in some areas, it is banned altogether because of the danger it poses to the general public. Similarly, the natural predators of deer, such as wolves and mountain lions, are now absent from most regions. This too can be traced to a large human population that is fearful of large predators because they could possibly attack humans and domestic animals.

We like to see a mother with her fawns by the side of the road or scampering off into the woods with tails raised to show off the white underside. Or, we find it thrilling to see a large buck (male deer) with majestic antlers partially hidden in the woods (Fig. 44A). But the sad reality is that, in those areas where deer populations have become too large, the deer suffer from starvation as they deplete their own food supply. For example, after deer hunting was banned on Long Island, New York, the deer population quickly outgrew available food resources. The animals became sickly and weak and weighed so little that their ribs, vertebrae, and pelvic bones were visible through their skin.

Then, too, a very large deer population causes humans many problems. A homeowner is dismayed to see new plants decimated and evergreen trees damaged due to the munching of deer. The economic damage that large deer populations cause to agriculture, landscaping, and forestry exceeds a billion dollars per year. More alarming, a million deer-vehicle collisions take place in the U.S. each year, resulting in over a billion dollars in insurance claims, thousands of human injuries, and hundreds of human deaths. Lyme disease, transmitted by deer ticks to humans, infects over 3,000 people annually. Untreated Lyme disease can lead to debilitating arthritic symptoms.

Deer overpopulation hurts not only deer and humans, but other species as well. The forested areas that are overpopulated by deer have fewer understory plants. Furthermore, the deer selectively eat certain species of plants, while leaving others alone. This can cause long-lasting changes in the number and diversity of trees in forests, leading to a negative economic impact on logging and forestry. The number of songbirds, insects, squirrels, mice, and other animals declines with an increasing deer population. It behooves us, therefore, to learn to manage deer populations. And the good news is that in some states, such as Texas, large landowners now set aside a portion of their property for a deer herd. They improve the nutrition of the herd and restrict the harvesting of young bucks, but allow the harvesting of does. The result is a self-sustaining herd that brings them economic benefits because they charge others for the privilege of hunting on their land.

a. b. c.

FIGURE 44A White-tailed deer.
a. *Buck.* ***b.*** *Doe and fawn.* ***c.*** *Doe running away.*

44.6 Human Population Growth

The world's population has risen steadily to a present size of about 6.7 billion people (Fig. 44.15). Prior to 1750, the growth of the human population was relatively slow, but as more reproducing individuals were added, growth increased, until the curve began to slope steeply upward, indicating that the population was undergoing exponential growth. The number of people added annually to the world population peaked at about 87 million around 1990, and currently it is a little over 79 million per year. This is roughly equal to the current populations of Argentina, Ecuador, and Peru combined.

The potential for future population growth can be appreciated by considering the **doubling time,** the length of time it takes for the population size to double. Currently, the doubling time is estimated to be 52 years. Such an increase in population size would put extreme demands on our ability to produce and distribute resources. In 52 years, the world would need double the amount of food, jobs, water, energy, and so on just to maintain the present standard of living.

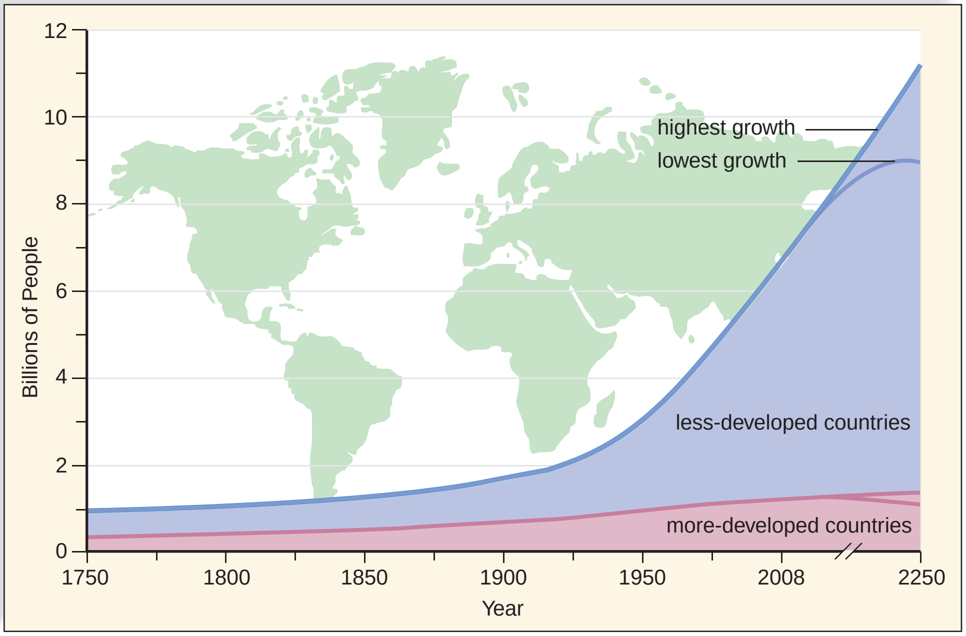
Many people are gravely concerned that the amount of time needed to add each additional billion persons to the world population has become shorter and shorter. The first billion didn't occur until 1800; the second billion was attained in 1930; the third billion in 1960; and today there are over 6 billion. The world's population may level off at 8, 10.5, or 14.2 billion, depending on the speed at which the growth rate declines. Zero population growth cannot be achieved until on the average each couple has only two children and the number of women entering their reproductive years is the same as those leaving them behind.

More-Developed Versus Less-Developed Countries

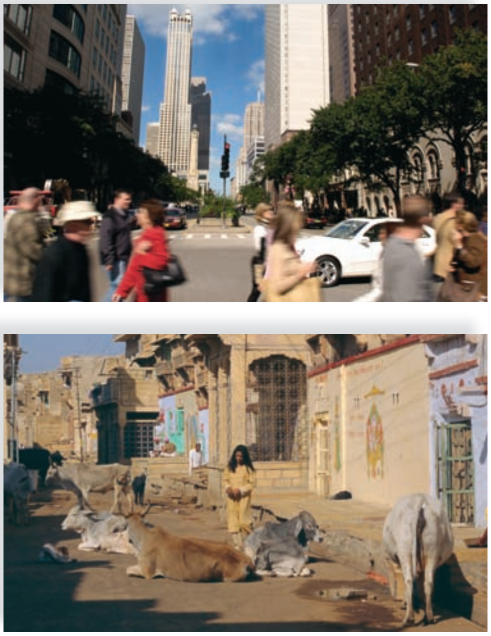
The countries of the world can be divided into two groups. In the **more-developed countries (MDCs),** typified by countries in North America, Europe, Japan, and Australia, population growth is low, and the people enjoy a good standard of living. In the **less-developed countries (LDCs),** such as certain countries in Latin America, Africa, and Asia, population growth is expanding rapidly, and the majority of people live in poverty.

The MDCs doubled their populations between 1850 and 1950. This was largely due to a decline in the death rate, the development of modern medicine, and improved socioeconomic conditions. The decline in the death rate was followed shortly thereafter by a decline in the birthrate, so that populations in the MDCs experienced only modest growth between 1950 and 1975. This sequence of events (i.e., decreased death rate followed by decreased birthrate) is termed a **demographic transition.** Yearly growth of the MDCs has now stabilized at about 0.1%.

In contrast to the other MDCs, there is no end in sight to the U.S. population growth. Although yearly growth of the U.S. population is only 0.6%, many people immigrate to the United States each year. In addition, an unusually large number of births occurred between 1946 and 1964 (called a baby boom), resulting in a large number of women still of reproductive age.



a.



b.

FIGURE 44.15 **World population growth.**

a. The world's' population size is now about 7 billion. It is predicted that the world's population size may level off at 9 billion or increase to more than 11 billion by 2250, depending on the speed with which the growth rate declines. **b.** Lifestyle of most individuals in the MDCs (*above*) is contrasted with most individuals in the LDCs (*below*).

Most of the world's population (80%) now lives in LDCs. Although the death rate began to decline steeply in the LDCs following World War II because of the importation of modern medicine from the MDCs, the birthrate remained high. The yearly growth of the LDCs peaked at 2.5% between 1960 and 1965. Since that time, a demographic transition has occurred and the death rate and the birthrate have fallen. The collective growth rate for the LDCs is now 1.5%, but many countries in sub-Saharan Africa have not participated in this decline. In some of these, women average more than five children each.

The population of the LDCs may explode from 5.5 billion today to 8 billion in 2050. Some of this increase will occur in Africa, but most will occur in Asia because the Asian population is now about 4 times the size of the African population. Asia already has 56% of the world's population living on 31% of its arable (farmable) land. Therefore, Asia is expected to experience acute water scarcity, a significant loss of biodiversity, and more urban pollution. Twelve of the world's 15 most polluted cities are in Asia.

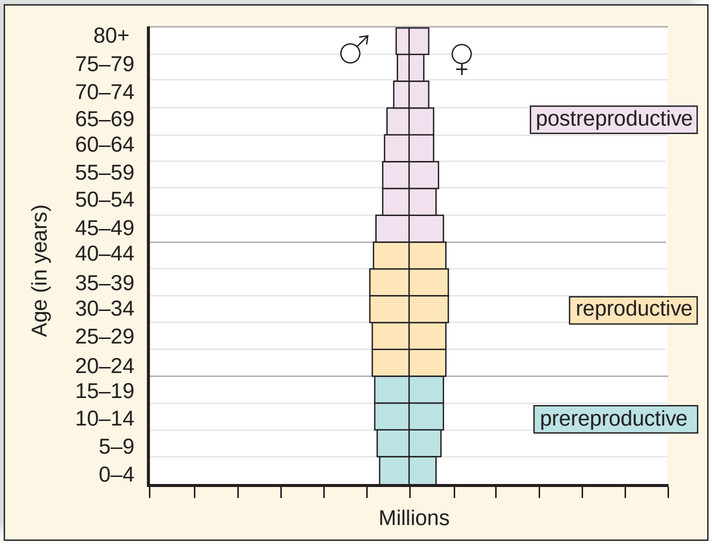
These are suggestions about how to reduce the expected population increase in the LDCs:

1. Establish and/or strengthen family planning programs. A decline in growth is seen in countries with good family planning programs supported by community leaders.
2. Use social progress to reduce the desire for large families. Providing education, raising the status of women, and reducing child mortality are social improvements that could reduce this desire.
3. Delay the onset of childbearing. This, along with wider spacing of births, could help birthrate decline.

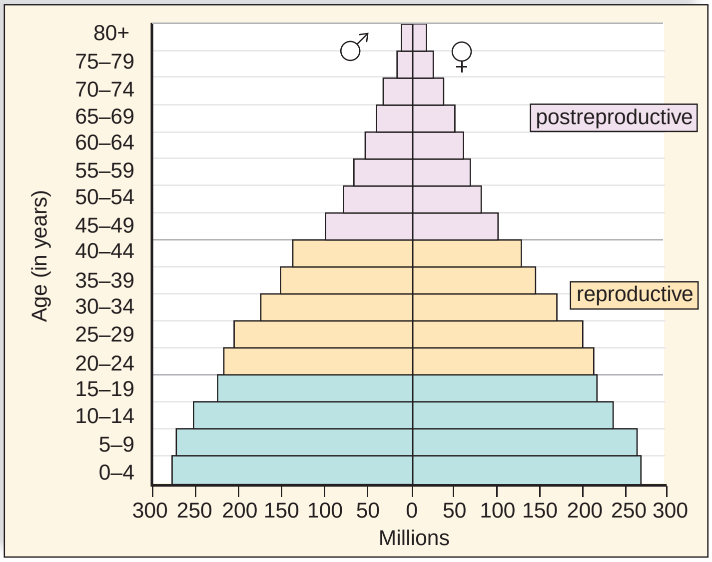
Age Distributions

The populations of the MDCs and LDCs can be divided into three age groups: prereproductive, reproductive, and postreproductive (Fig. 44.16). Currently, the LDCs are experiencing a population momentum because they have more women entering the reproductive years than older women leaving them.

Laypeople are sometimes under the impression that if each couple has two children, **zero population growth** (no increase in population size) will take place immediately. However, most countries today will continue growing due to the age structure of the population. If there are more young women entering the reproductive years than there are older women leaving them, so-called **replacement reproduction** will still result in population growth.



a. More-developed countries (MDCs)



b. Less-developed countries (LDCs)

c.

FIGURE 44.16 **Age-structure diagrams.**

The shape of these age-structure diagrams allows us to predict that (**a**) the populations of MDCs are approaching stabilization, and (**b**) the populations of LDCs will continue to increase for some time. **c.** Improved women's rights and increasing contraceptive use could change this scenario. Here a community health worker is instructing women in Bangladesh about the use of contraceptives.

Many MDCs have a stable age structure, but most LDCs have a youthful profile—a large proportion of the population is younger than 15. For example, in Nigeria, 49% of the population is under age 15. On average, Nigerian women have 5.9 children. As a result of these rates, the population of Nigeria is expected to increase from 148 million presently to 282 million in 2050. The population of the continent of Africa is projected to increase from 957 million to 2 billion between 2008 and 2050. This means that the LDC populations will still expand, even after replacement reproduction is attained. The more quickly replacement reproduction is achieved, however, the sooner zero population growth will result.

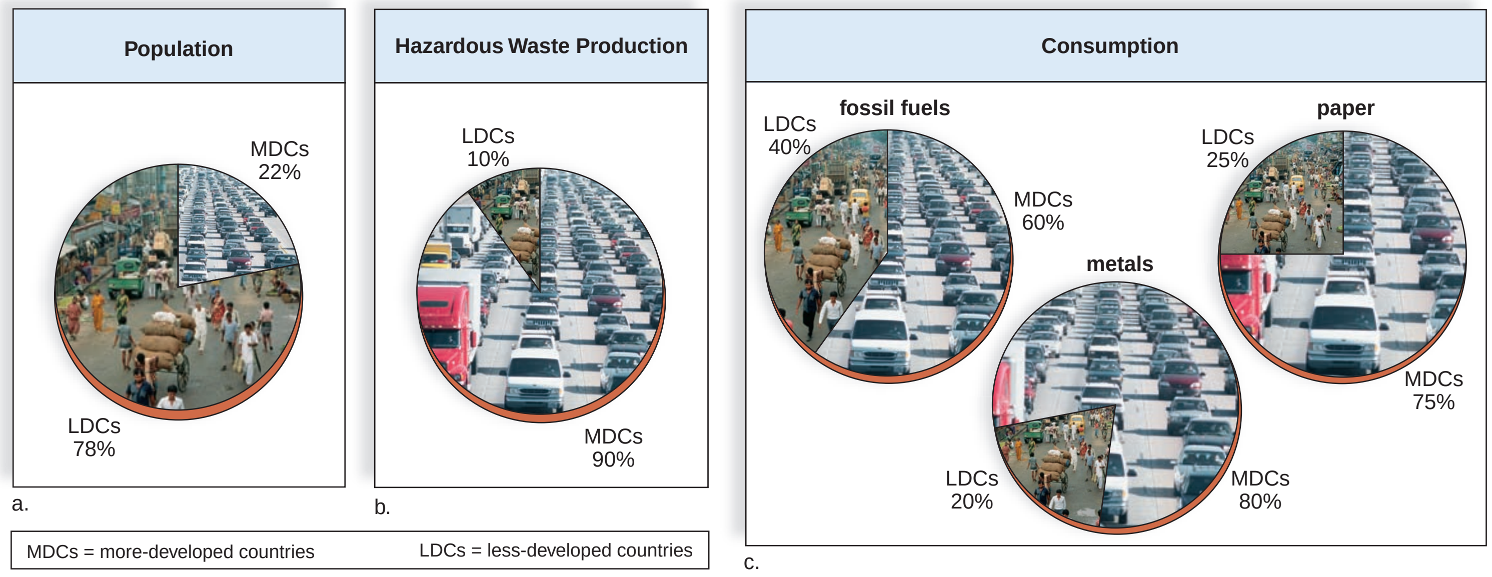


FIGURE 44.17 **Environmental impact caused by MDCs and LDCs.**

a. The combined population of MDCs is smaller than that of LDCs: The MDCs account for 22% of the world's population, and the LDCs account for 78%. **b.** MDCs produce most of the world's hazardous wastes—90% for MDCs compared with 10% for LDCs. The production of hazardous waste is tied to (**c**), the consumption of fossil fuels, metals, and paper, among other resources. The MDCs consume 60% of fossil fuels compared with 40% for the LDCs, 80% of metals compared with 20% for the LDCs, and 75% of paper compared with 25% for the LDCs.

Population Growth and Environmental Impact

Population growth is putting extreme pressure on each country's social organization, the Earth's resources, and the biosphere. Since the population of the LDCs is still growing at a significant rate, it might seem that their population increase will be the greater cause of future environmental degradation. But this is not necessarily the case because the MDCs consume a much larger proportion of the Earth's resources than do the LDCs. This consumption leads to environmental degradation, which is a major concern in itself, but the usage of these resources is disproportionate to human population growth.

Environmental Impact

The environmental impact (E.I.) of a population is measured not only in terms of population size, but also in terms of resource consumption per capita and the pollution that results because of this consumption. In other words:

E.I. = population size × resource consumption per capita
= pollution per unit of resource used

Therefore, there are two possible types of overpopulation: The first is simply due to population growth, and the second is due to increased resource consumption caused by population growth. The first type of overpopulation is more obvious in LDCs, and the second type is more obvious in MDCs because the per capita consumption is so much higher in the MDCs. For example, an average family in the United States, in terms of per capita resource consumption and waste production, is the equivalent of 30 people in India. We need to realize, therefore, that only a limited number of people can be sustained anywhere near the standard of living in the MDCs.

The current comparative environmental impact of MDCs and LDCs is shown in Figure 44.17. The MDCs account for only about one-fourth of the world population (Fig. 44.17*a*). But the MDCs account for 90% of the hazardous waste production (pollution) (Fig. 44.17*b*). Why should that be? MDCs account for much more pollution than LDCs because they consume much greater amounts of fossil fuel, metal, and paper than do LDCs, as shown in Figure 44.17*c*.

As the LDCs become more industrialized, their per capita consumption will also rise and, in some LDCs, it may nearly equal that of a more developed country. For example, China's economy is growing rapidly and, because China has such a large population (1.3 billion), it is already competing with the United States for oil and metals on the world markets. It could be that as developing countries consume more, people in the United States will adjust and learn to consume less.

Results of Environmental Impact

Consumption of resources has a negative effect on the environment. In Chapter 45, you will learn how resource consumption leads to various pollution problems and, in Chapter 47, you will learn how our increasing environmental impact may cause a mass extinction of wildlife greater than any other since the evolution of life began.

Check Your Progress **44.6**

1. Compare the population growth of the LDCs with that of the MDCs.
2. Under what circumstances can replacement reproduction still cause continued growth?
3. How will increased LDC consumption affect MDC consumption? Explain.

Connecting the Concepts

The science of ecology began when nineteenth-century naturalists studied and described the population parameters of various species. However, modern ecology has grown into much more than a simple descriptive field. Ecology, which is integral to the evolution of species, is now very much an experimental and predictive science.

Much of the success in the development of ecology as a predictive science has come from studies of populations and the creation of models that examine how populations change over time. The simplest models are based on population growth when there are unlimited resources. This results in exponential growth, a type of population growth that is rarely seen in nature for extended lengths of time. Pest species may exhibit exponential growth until they run out of resources. Because few populations exhibit exponential growth, population ecologists incorporated resource limitation into their models. The simplest models that account for limited resources result in logistic growth. Populations that exhibit logistic growth will cease growth when they reach the environmental carrying capacity.

Many modern ecological studies are concerned with identifying the factors that place limits on population growth and that set the environmental carrying capacity. A combination of careful, descriptive studies, experiments done in nature, and sophisticated models has allowed ecologists to make good predictions about which factors have the greatest influence on population growth.

The next step in the development of modern ecology has been determining how populations of different species affect one another. This is known as community ecology. Because each population in a community responds to environmental changes in slightly different ways, developing predictive models that explain how communities change has been challenging. However, ecologists are better able to predict how communities will change through time and to understand what factors influence community properties such as species number, abundance of individuals, and species interactions.

summary

44.1 Scope of Ecology

Ecology is the study of the interactions of organisms with other organisms and with the physical environment. Ecology encompasses several levels of study: organism, population, community, ecosystem, and finally the biosphere. Ecologists are particularly interested in how interactions affect the distribution, abundance, and life history strategies of organisms.

44.2 Demographics of Populations

Demographics include statistical data about a population. For example, population density is the number of individuals per unit area or volume. Distribution of individuals can be uniform, random, or clumped. A population's distribution is often determined by resources, that is, abiotic factors such as water, temperature, and availability of nutrients.

Population growth is dependent on number of births and number of deaths, immigration, and emigration. The number of births minus the number of deaths results in the rate of natural increase (growth rate). Mortality (deaths per capita) within a population can be recorded in a life table and illustrated by a survivorship curve. The pattern of population growth is reflected in the age distribution of a population, which consists of prereproductive, reproductive, and postreproductive segments. Populations that are growing exponentially have a pyramid-shaped age distribution pattern.

44.3 Population Growth Models

One model for population growth assumes that the environment offers unlimited resources. In the example given, the members of the population have discrete reproductive events, and therefore the size of next year's population is given by the equation $N_{t+1} = RN_t$. Under these conditions, exponential growth results in a J-shaped curve.

Most environments restrict growth, and exponential growth cannot continue indefinitely. Under these circumstances, an S-shaped, or logistic, growth curve results. The growth of the population is given by the equation $N/t = rN\,(K - N)/K$ for populations in which individuals have repeated reproductive events. The term $(K - N)/K$ represents the unused portion of the carrying capacity (K). When the population reaches carrying capacity, the population stops growing because environmental conditions oppose biotic potential, the maximum rate of natural increase (growth rate) for a population.

44.4 Regulation of Population Size

Population growth is limited by density-independent factors (e.g., abiotic factors such as weather) and density-dependent factors (biotic factors such as predation and competition). Other means of regulating population growth exist in some populations. For example, territoriality is possibly a means of population regulation. Other populations seem to not be regulated, and their population size fluctuates widely.

44.5 Life History Patterns

The logistic growth model has been used to suggest that the environment promotes either *r*-selection or *K*-selection. So-called *r*-selection occurs in unpredictable environments where density-independent factors affect population size. Energy is allocated to producing as many small offspring as possible. Adults remain small and do not invest in parental care of offspring. *K*-selection occurs in environments that remain relatively stable, where density-dependent factors affect population size. Energy is allocated to survival and repeated reproductive events. The adults are large and invest in parental care of offspring. Actual life histories contain trade-offs between these two patterns, and such trade-offs are subjected to natural selection.

44.6 Human Population Growth

The human population is still expanding, but deceleration has begun. It is unknown when the population size will level off, but it may occur by 2050. Substantial increases are expected in certain LDCs (less-developed countries) of Asia and also Africa. Support for family planning, human development, and delayed childbearing could help prevent the increase.

understanding the terms

age structure diagram	823
biosphere	820
biotic potential	822
carrying capacity	827
cohort	822
community	820
demographic transition	833
demography	821
density-dependent factor	828
density-independent factor	828
doubling time	833
ecology	820
ecosystem	820
exponential growth	825
habitat	820
iteroparity	824
K-selection	831
less-developed country (LDC)	833
limiting factor	821
logistic growth	826
more-developed country (MDC)	833
population	820
population density	821
population distribution	821
rate of natural increase (*r*)	822
replacement reproduction	834
resource	821
r-selection	830
semelparity	824
survivorship	822
zero population growth	834

Match the terms to these definitions:

a. ______________ Due to industrialization, a decline in the birthrate following a reduction in the death rate so that the population growth rate is lowered.

b. ______________ Group of organisms of the same species occupying a certain area and sharing a common gene pool.

c. ______________ Growth, particularly of a population, in which the increase occurs in the same manner as compound interest.

d. ______________ Largest number of organisms of a particular species that can be maintained indefinitely in a given environment.

e. ______________ Maximum population growth rate under ideal conditions.

reviewing this chapter

1. What are the various levels of ecological study? 820–21
2. What largely determines a population's density, distribution, and growth rate? 821–22
3. How does the mortality pattern and age distribution affect the growth rate? 822–24
4. What type of growth curve indicates that exponential growth is occurring? What are the environmental conditions for exponential growth? 825
5. What type of growth curve levels off because of environmental conditions? What environmental conditions are involved? 826
6. What is the carrying capacity of an area? 827
7. Are density-independent or density-dependent factors more likely to regulate population size? Why? 827–29
8. What other types of factors are involved in regulating population size? 829
9. Why would you expect the life histories of natural populations to vary and contain some characteristics that are so-called *r*-selected and some that are so-called *K*-selected? 830–31
10. What type of growth curve presently describes the growth of the human population? In what types of countries is most of this growth occurring, and how might it be curtailed? 833–34

testing yourself

Choose the best answer for each question.

1. Which of these levels of ecological study involves an interaction between abiotic and biotic components?
   a. organisms
   b. populations
   c. communities
   d. ecosystem
   e. All of these are correct.
2. When phosphorus is made available to an aquatic community, the algal populations suddenly bloom. This indicates that phosphorus is
   a. a density-dependent regulating factor.
   b. a reproductive factor.
   c. a limiting factor.
   d. an *r*-selection factor.
   e. All of these are correct.
3. A J-shaped growth curve can be associated with
   a. exponential growth.
   b. biotic potential.
   c. unlimited resources.
   d. rapid population growth.
   e. All of these are correct.
4. An S-shaped growth curve
   a. occurs when resources become limited.
   b. includes an exponential growth phase.
   c. occurs in natural populations but not in laboratory ones.
   d. is subject to a sharp decline.
   e. All of these are correct.
5. If a population has a type I survivorship curve (most have a long life span), which of these would you also expect?
   a. a single reproductive event per adult
   b. overlapping generations
   c. reproduction occurring near the end of the life span
   d. a very low birthrate
   e. None of these are correct.
6. A pyramid-shaped age distribution means that
   a. the prereproductive group is the largest group.
   b. the population will grow for some time in the future.
   c. the country is more likely an LDC than an MDC.
   d. fewer women are leaving the reproductive years than entering them.
   e. All of these are correct.
7. Which of these is a density-independent regulating factor?
   a. competition
   b. predation
   c. weather
   d. resource availability
   e. the average age when childbearing begins
8. Fluctuations in population growth can correlate to changes in
   a. predation.
   b. weather.
   c. resource availability.
   d. parasitism.
   e. All of these are correct.
9. A species that has repeated reproductive events, lives a long time, but suffers a crash due to the weather is exemplifying
   a. *r*-selection.
   b. *K*-selection.
   c. a mixture of both *r*-selection and *K*-selection.
   d. density-dependent and density-independent regulation.
   e. a pyramid-shaped age structure diagram.

10. In which pair is the first included in the second?
    a. habitat—population
    b. population—community
    c. community—ecosystem
    d. ecosystem—biosphere
    e. All of these except a are correct.
11. How does population density differ from population distribution?
    a. Actually, population density is the same as population distribution.
    b. The greater the population density, the more likely that the population distribution will be clumped.
    c. Population density has nothing to do with population distribution.
    d. The less dense the population, the more likely that the population distribution will be equally spaced.
    e. Both b and c are correct.
12. Which one of these has nothing to do with a population's growth curve?
    a. exponential growth
    b. biotic potential
    c. environmental conditions
    d. rate of natural increase
    e. All of these pertain to a population's growth curve.
13. When a population is undergoing logistic growth, environmental conditions determine
    a. whether to expect exponential growth.
    b. the carrying capacity.
    c. the length of the lag phase.
    d. whether the population is subject to density-independent regulation.
    e. All of these are correct.
14. Which of these statements is correct?
    a. A life table is based on whether a population has cohorts or not.
    b. The life table supplies the information for constructing the survivorship curve.
    c. A life table, like an ideal weight table, supplies information that can keep members of a population healthy.
    d. A life table tells which ideal survivorship curve is most appropriate to a particular population.
    e. Both b and d are correct.
15. Because of the postwar baby boom, the U.S. population
    a. can never level off.
    b. presently has a pyramid-type age distribution.
    c. is subject to regulation by density-dependent factors.
    d. is more conservation-minded than before.
    e. None of these is correct.

thinking scientifically

1. In the winter moth life cycle, parasites were found to be a less important cause of mortality than cold winter weather and predators. Give an evolutionary explanation for the inefficiency of parasites in controlling population size.
2. You are a river manager charged with maintaining the flow through the use of dams so that trees, which have equilibrium life histories, can continue to grow along the river. What would you do?

bioethical issue

Population Control

The answer to how to curb the expected increase in the world's population lies in discovering how to curb the rapid population growth of the less-developed countries. In these countries, population experts have discovered what they call the "virtuous cycle." Family planning leads to healthier women, and healthier women have healthier children, and the cycle continues. Women no longer need to have many babies for only a few to survive. More education is also helpful because better-educated people are more interested in postponing childbearing and promoting women's rights. Women who have equal rights with men tend to have fewer children.

"There isn't any place where women have had the choice that they haven't chosen to have fewer children," says Beverly Winikoff at the Population Council in New York City. "Governments don't need to resort to force." Bangladesh is a case in point. Bangladesh is one of the densest and poorest countries in the world. In 1990, the birthrate was 4.9 children per woman, and now it is 3.3. This achievement was due in part to the Dhaka-based Grameen Bank, which loans small amounts of money mostly to destitute women to start a business. The bank discovered that when women start making decisions about their lives, they also start making decisions about the size of their families. Family planning within Grameen families is twice as common as the national average; in fact, those women who get a loan promise to keep their families small! Also helpful has been the network of village clinics that counsel women who want to use contraceptives. The expression "contraceptives are the best contraceptives" refers to the fact that you don't have to wait for social changes to get people to use contraceptives—the two feed back on each other.

Recently, some of the less-developed countries, faced with economic crises, have cut back on their family planning programs, and the more-developed countries have not taken up the slack. Indeed, some foreign donors have also cut back on aid—the United States by one-third. Are you in favor of foreign aid to help countries develop family planning programs? Why or why not?

Biology website

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

http://www.mhhe.com/maderbiology10

45

Community and Ecosystem Ecology

*The narrow green leaves of a Venus flytrap (*Dionaea muscipula*) end with two reddish spiked lobes on either side of a midrib. An insect, most likely a fly, is lured to the leaves because they are lined by a band of sweet-smelling nectar glands. When the fly touches a trigger hair, the trap is sprung, and the spikes of the lobes become interlocked, enclosing the insect like the bars of a jail cell. Digestive enzymes pour forth from glands on the leaf surface, breaking down the helpless victim. Carnivorous plants carry on photosynthesis, but they live in mineral-poor wetlands. Nitrogen and phosphate are absorbed from the bodies of their animal prey and not from the soil.*

The organic nutrients a Venus flytrap produces are transferred to any animal that feeds on them. Ordinarily, upon death and decomposition of organisms, inorganic nutrients are made available to plants once again. This chapter examines various types of interactions that occur among the populations of a community. It also looks at interactions with the physical environment.

The Venus flytrap, *Dionaea muscipula*, is a plant that feeds on insects.

concepts

45.1 ECOLOGY OF COMMUNITIES

- Communities are assemblages of interacting populations. Species richness and diversity characterize a community. 840–41
- A species' ecological niche is the role the species plays in its community, including its habitat and its interactions with other organisms. 841
- Community organization involves interactions among species such as competition, predation, parasitism, and mutualism. 842–48

45.2 COMMUNITY DEVELOPMENT

- Ecological succession is a change in species composition and community structure and organization over time. 850–51

45.3 DYNAMICS OF AN ECOSYSTEM

- In an ecosystem, organisms interact with one another and with the abiotic components—that is, the chemical and physical environment. 852
- Autotrophs are self-feeders: Photoautotrophs capture solar energy and produce organic nutrients. Heterotrophs, on the other hand, take in preformed organic nutrients. 852
- Ecosystems are characterized by energy flow through populations and chemical cycling within and between ecosystems. 853–54
- Energy flow between populations is represented by diagrams termed food webs and ecological pyramids. 855–56
- Biogeochemical cycles are hydrologic (water cycle), gaseous (carbon cycle, nitrogen cycle), or sedimentary (phosphorus cycle). 856–61

45.1 Ecology of Communities

Populations do not occur as single entities; they are part of a community. A **community** is an assemblage of populations of different species interacting with one another in the same environment. Communities come in different sizes, and it is sometimes difficult to decide where one community ends and another begins.

A fallen log can be considered a community because the various populations living on and within a fallen log, such as plants, fungi, worms, and insects, interact with one another and form a community. The fungi break down the log and provide food for the earthworms and insects living in and on the log. Those insects may feed on one another, too. If birds flying throughout the entire forest feed on the insects and worms living in and on the log, then they are also part of the larger forest community.

Community Structure

Two characteristics—species composition and diversity—allow us to compare communities. The species composition of a community, also known as **species richness,** is simply a listing of the various species found in that community. **Species diversity** includes both species richness and species evenness, or the relative abundance of the different species.

Species Composition

It is apparent, by comparing the photographs in Figure 45.1, that a coniferous forest has a composition different from a tropical rain forest. The narrow-leaved evergreen trees are prominent in a coniferous forest, and broad-leaved evergreen trees are numerous in a tropical rain forest. As the list of mammals demonstrates, a coniferous community and a tropical rain forest community contain different types of mammals. Ecologists comparing these two communities

a.

b.

FIGURE 45.1 **Community structure.**

Communities differ in their composition, as witnessed by their predominant plants and animals. The diversity of communities is described by the richness of species and their relative abundance. **a.** A coniferous forest. Some mammals found here are listed to the *right*. **b.** A tropical rain forest. Some mammals found here are listed to the *left*.

would go on to find differences in other plants and animals too. In the end, ecologists would conclude that not only are the species compositions of these two communities different, but the tropical rain forest has more species and, therefore, higher species richness.

Species Diversity

The *diversity* of a community goes beyond composition because it includes not only a listing of all the species in a community but also the relative abundance of each species. To take an extreme example: A forest sampled in West Virginia has 76 yellow poplar trees but only one American elm (among other species). If we were simply walking through this forest, we might miss seeing the American elm. If, instead, the forest had 36 poplar trees and 41 American elms, the forest would seem more diverse to us, and indeed it would be more diverse. The greater the species richness and the more even the distribution of the species in a community, the greater the diversity.

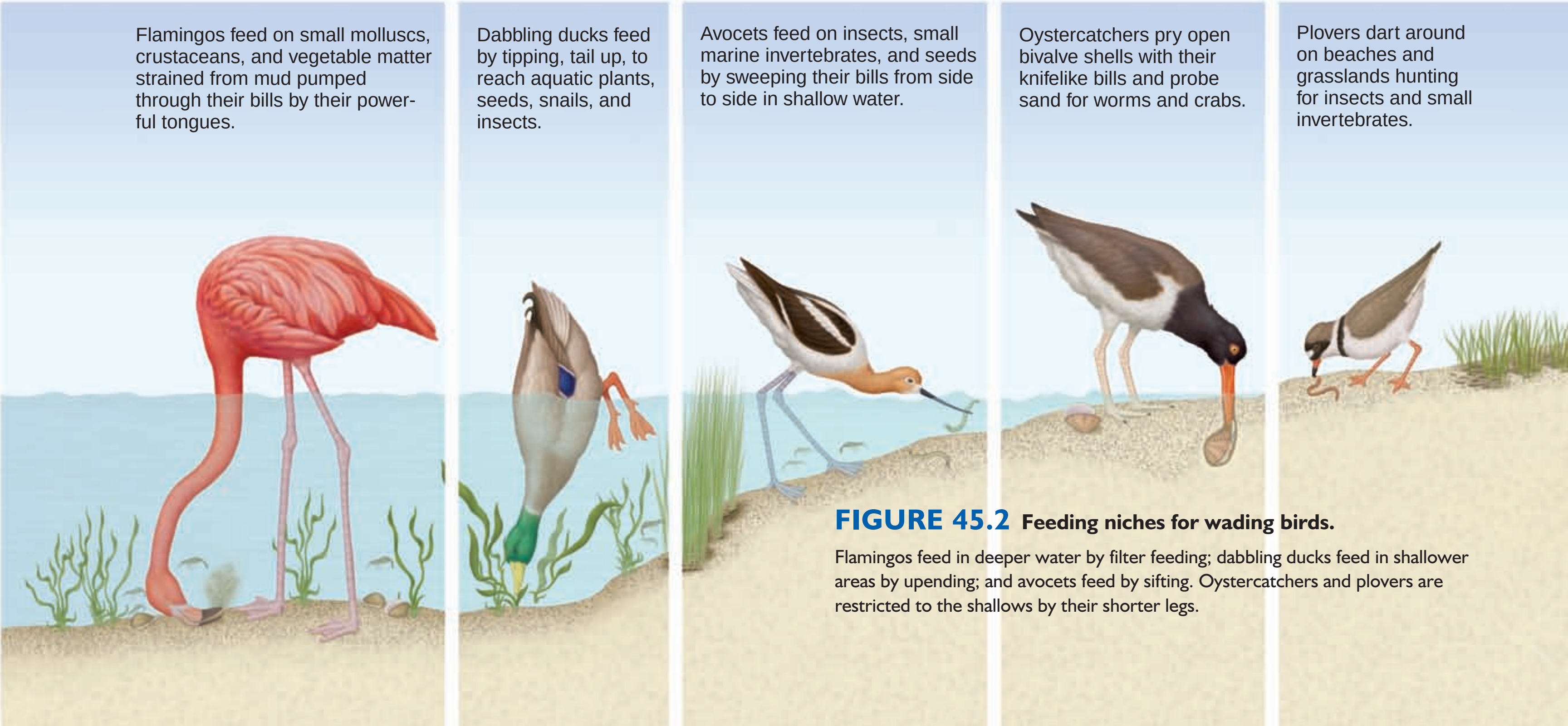
Community Interactions

This chapter examines the various types of community interactions and their importance to the structure of a community. Such interactions illustrate some of the most important evolutionary selection pressures acting on individuals. They also help us develop an understanding of how biodiversity can be preserved.

Habitat and Ecological Niche

Each species occupies a particular position in the community, both in a spatial sense (where it lives) and in a functional sense (what role it plays). A particular place where a species lives and reproduces is its **habitat.** The habitat might be the forest floor, a swift stream, or the ocean's edge. The **ecological niche** is the role a species plays in its community, including its habitat and its interactions with other organisms. The niche includes the resources used to meet energy, nutrient, and survival demands. For a dragonfly larva, its habitat is a pond or lake where it eats other insects. The pond must contain vegetation where the dragonfly larva can hide from its predators, such as fish and birds. In addition, the water must be clear enough for it to see its prey and warm enough for it to be in active pursuit. Since it is difficult to study all aspects of niche, some observations focus only on one aspect, as with the birds featured in Figure 45.2. Each of these birds are specialist species because they have a limited diet, tolerate only small changes in environmental conditions, and live in a specific habitat. Other specialist species are pandas, spotted owls, and freshwater dolphins. Some species, such as raccoons, roaches, and house sparrows, are generalist with a broad range of niches. These organisms have a diversified diet, tolerate a wide range of environmental conditions, and can live in a variety of places.

Because a species' niche is affected by both abiotic factors (such as climate and habitat) and biotic factors (such as competitors, parasites, and predators), ecologists like to distinguish between the fundamental and the realized niche. The *fundamental niche* comprises all the abiotic conditions under which a species could survive when adverse biotic conditions are absent. The *realized niche* comprises those conditions under which a species does survive when adverse biotic interactions, such as competition and predation, are present. Therefore, a species' fundamental niche tends to be larger than its realized niche.



Flamingos feed on small molluscs, crustaceans, and vegetable matter strained from mud pumped through their bills by their powerful tongues.

Dabbling ducks feed by tipping, tail up, to reach aquatic plants, seeds, snails, and insects.

Avocets feed on insects, small marine invertebrates, and seeds by sweeping their bills from side to side in shallow water.

Oystercatchers pry open bivalve shells with their knifelike bills and probe sand for worms and crabs.

Plovers dart around on beaches and grasslands hunting for insects and small invertebrates.

FIGURE 45.2 Feeding niches for wading birds.

Flamingos feed in deeper water by filter feeding; dabbling ducks feed in shallower areas by upending; and avocets feed by sifting. Oystercatchers and plovers are restricted to the shallows by their shorter legs.

Competition Between Populations

Competition occurs when members of different species try to use a resource (such as light, space, or nutrients) that is in limited supply. If the resource is not in limited supply, there is no competition. In the 1930s, Russian ecologist G. F. Gause grew two species of *Paramecium* in one test tube containing a fixed amount of bacterial food. Although each population survived when grown separately, only one survived when they were grown together (Fig. 45.3). The successful *Paramecium* population had a higher biotic potential than the unsuccessful population. After observing the outcome of other similar experiments in the laboratory, ecologists formulated the **competitive exclusion principle,** which states that no two species can indefinitely occupy the same niche at the same time.

What does it take to have different ecological niches so that extinction of one species is avoided? In another laboratory experiment, Gause found that two species of *Paramecium* did continue to occupy the same tube when one species fed on bacteria at the bottom of the tube and the other fed on bacteria suspended in solution. Individuals of each species that can avoid competition have a reproductive advantage. **Resource partitioning** decreases competition between two species, leading to increased niche specialization and less niche overlap. An example of resource partitioning involves owl and hawk populations. Owls and hawks feed on similar prey (small rodents), but owls are nocturnal hunters and hawks are diurnal hunters. What could have been one niche became two more specialized niches because of a divergence of behavior.

It is possible to observe the process of niche specialization in nature. When three species of ground finches of the Galápagos Islands occur on separate islands, their beaks tend to be the same intermediate size, enabling each to feed on a wider range of seeds (Fig. 45.4). Where they co-occur, selection has favored divergence in beak size because the size of the beak affects the kinds of seeds that can be eaten. In other words, competition has led to resource partitioning and, therefore, niche specialization. The tendency for characteristics to be more divergent when populations belong to the same community than when they are isolated is termed **character displacement.** Character displacement is often used as evidence that competition and resource partitioning have taken place.

Niche specialization can be subtle. Five different species of warblers that occur in North American forests are all nearly the same size, and all feed on a type of spruce tree caterpillar. For all these species to exist, they must be avoiding direct competition. In a famous study, ecologist Robert MacArthur recorded the amount of time each of five warbler species spent in different regions of spruce canopies to determine where each species did most of its feeding (Fig. 45.5). He discovered that each species primarily used different parts of the tree canopy and, in that way, had a more specialized niche.

As another example, consider that swallows, swifts, and martins all eat flying insects and parachuting spiders. These birds even frequently fly together in mixed flocks. But each type of bird has a different nesting site and migrates at a slightly different time of year. In doing so, they are not competing for the same food source when they are feeding their young.

In all these cases of niche partitioning, we have merely assumed that what we observe today is due to competition

FIGURE 45.3

Competition between two laboratory populations of *Paramecium*.

When grown alone in pure culture, *Paramecium caudatum* and *Paramecium aurelia* exhibit sigmoidal growth. When the two species are grown together in mixed culture, *P. aurelia* is the better competitor, and *P. caudatum* dies out. Both attempted to exploit the same resources, which led to competitive exclusion.

Source: Data from G. F. Gause, *The Struggle for Existence,* 1934, Williams & Wilkins Company, Baltimore, MD.

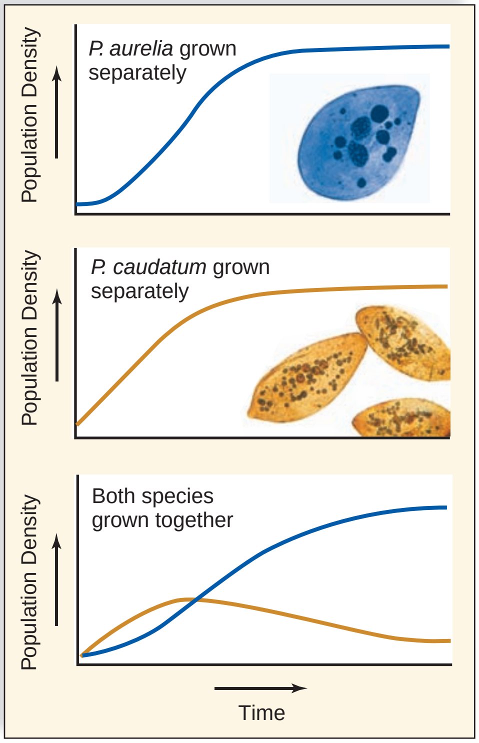
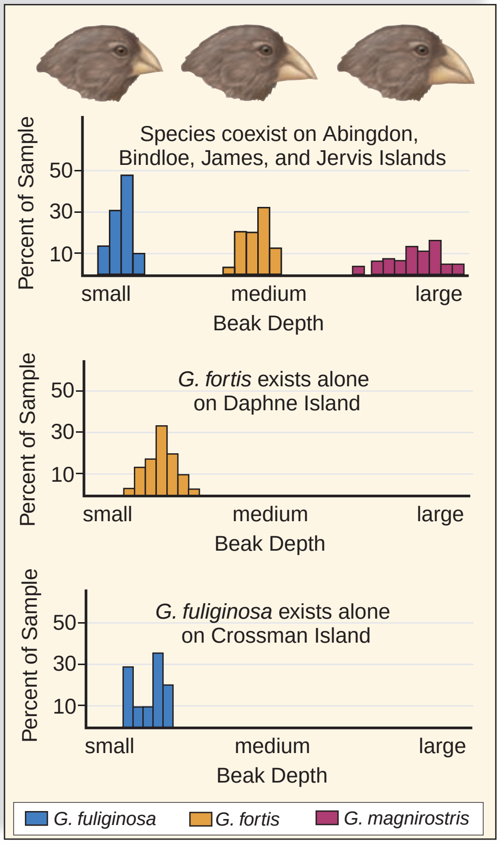


FIGURE 45.4

Character displacement in finches on the Galápagos Islands.

When *Geospiza fuliginosa, G. fortis,* and *G. magnirostris* are on the same island, their beak sizes are appropriate to eating small-, medium-, and large-sized seeds. When *G. fortis* and *G. fuliginosa* are on separate islands, their beaks have the same intermediate size, which allows them to eat seeds that vary in size.



in the past. Some ecologists are fond of saying that in doing so we have invoked the "ghosts of competition past." Are there any instances in which competition has actually been observed? Joseph Connell has studied the distribution of barnacles on the Scottish coast, where a small barnacle lives on the high part of the intertidal zone, and a large barnacle lives on the lower part (Fig. 45.6). Free-swimming larvae of both species attach themselves to rocks randomly throughout in the intertidal zone; however, in the lower zone, the large *Balanus* barnacles seem to either force the smaller *Chthamalus* individuals off the rocks or grow over them. To test his observation, Connell removed the larger barnacles and found that the smaller barnacles grew equally well on all parts of the rock. The entire intertidal zone is the fundamental niche for *Chthamalus,* but competition is restricting the range of *Chthamalus* on the rocks. *Chthamalus* is more resistant to drying out than is *Balanus;* therefore, it has an advantage that permits it to grow in the upper intertidal zone where it is exposed more often to the air. In other words, the upper intertidal zone becomes the realized niche for *Chthamalus*.

Predator-Prey Interactions

Predation occurs when one living organism, called the **predator,** feeds on another, called the **prey.** In its broadest sense, predaceous consumers include not only animals such as lions, which kill zebras, but also filter-feeding blue

FIGURE 45.5 Niche specialization among five species of coexisting warblers.

The diagrams represent spruce trees. The time each species spent in various portions of the trees was determined; each species spent more than half its time in the blue regions.

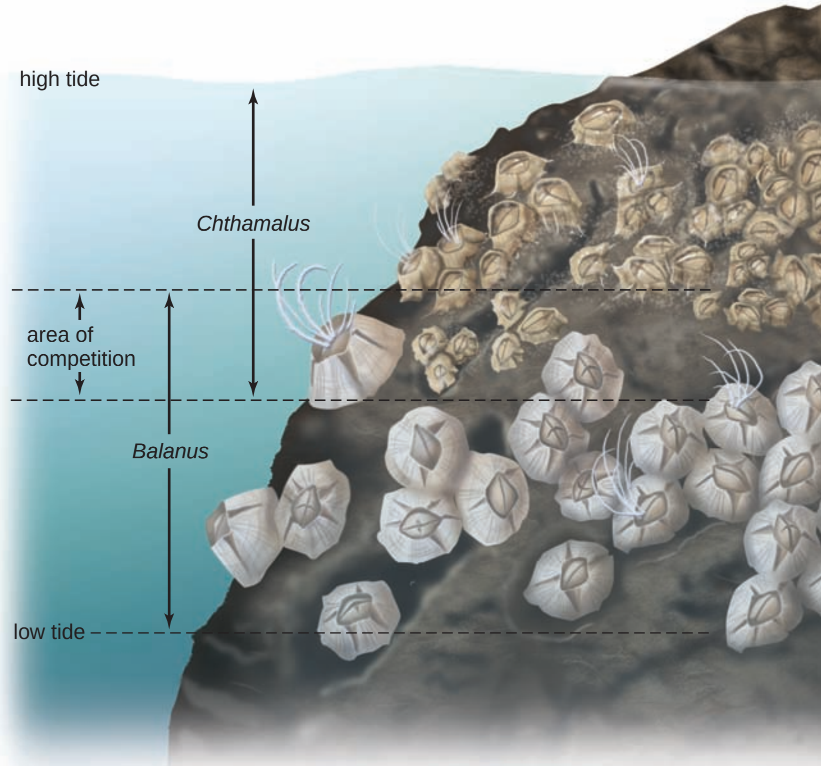


FIGURE 45.6 Competition between two species of barnacles.

Competition prevents two species of barnacles from occupying as much of the intertidal zone as possible. Both exist in the area of competition between *Chthamalus* and *Balanus*. Above this area only *Chthamalus*, a small barnacle, survives, and below it only *Balanus*, a large barnacle, survives.

whales, which strain krill from ocean waters; herbivorous deer, which browse on trees and shrubs; parasitic ticks, which suck blood from their victims; and *parasitoids*, which are wasps that lay their eggs inside the body of a host. The resulting larvae feed on the host, sometimes causing death. Parasitism can be considered a type of predation because one individual obtains nutrients from another (see page 846). Predation and parasitism are expected to increase the abundance of the predator and parasite at the expense of the abundance of the prey or host.

Predator-Prey Population Dynamics

Do predators reduce the population density of prey? In another classic experiment, G. F. Gause reared the ciliated protozoans *Paramecium caudatum* (prey) and *Didinium nasutum* (predator) together in a culture medium. He observed that *Didinium* ate all the *Paramecium* and then died of starvation. In nature, we can find a similar example. When a gardener brought prickly-pear cactus to Australia from South America, the cactus spread out of control until millions of acres were covered with nothing but cacti. The cacti were brought under control when a moth from South America, whose caterpillar feeds only on the cactus, was introduced. The caterpillar was a voracious predator on the cactus, efficiently reducing the cactus population. Now both cactus and moth are found at greatly reduced densities in Australia.

This raises an interesting point: The population density of the predator can be affected by the prevalence of the prey. In other words, the predator-prey relationship is actually a two-way street. In that context, consider that at first the biotic potential (maximum reproductive rate) of the prickly-pear cactus was maximized, but factors that oppose biotic potential came into play after the moth was introduced. And the biotic potential of the moth was maximized when it was first introduced, but the carrying capacity decreased after its food supply was diminished.

Sometimes, instead of remaining in a steady state, predator and prey populations first increase in size and then decrease. We can appreciate that an increase in predator population size is dependent on an increase in prey population size. But what causes a decrease in population size instead of the establishment of a steady population size? At least two possibilities account for the reduction: (1) Perhaps the biotic potential (reproductive rate) of the predator is so great that its increased numbers overconsume the prey, and then as the prey population declines, so does the predator population; or (2) perhaps the biotic potential of the predator is unable to keep pace with the prey, and the prey population overshoots the carrying capacity and suffers a crash. Now the predator population follows suit because of a lack of food. In either case, the result will be a series of peaks and valleys, with the predator population size lagging slightly behind that of the prey population.

A famous example of predator-prey cycles occurs between the snowshoe hare and the Canadian lynx, a type of small predatory cat (Fig. 45.7). The snowshoe hare is a common herbivore in the coniferous forests of North America, where it feeds on terminal twigs of various shrubs and small trees. The Canadian lynx feeds on snowshoe hares but also on ruffed grouse and spruce grouse, two types of birds. Studies have revealed that the hare and lynx populations cycle regularly, as graphed in Figure 45.7. Investigators at first assumed that the lynx brings about a decline in the hare population and that this accounts for the cycling. But others have noted that the decline in snowshoe hare abundance was accompanied by low growth and reproductive rates, which could be signs of a food shortage. Experiments were done to test whether (1) predation or (2) lack of food caused the decline in the hare population. The results suggest that both factors combined to produce a low hare population and the cycling effect.

Prey Defenses

Prey defenses are mechanisms that thwart the possibility of being eaten by a predator. Prey species have evolved a variety of mechanisms that enable them to avoid predators, including heightened senses, speed, protective armor, protective spines or thorns, tails and appendages that break off, and chemical defenses.

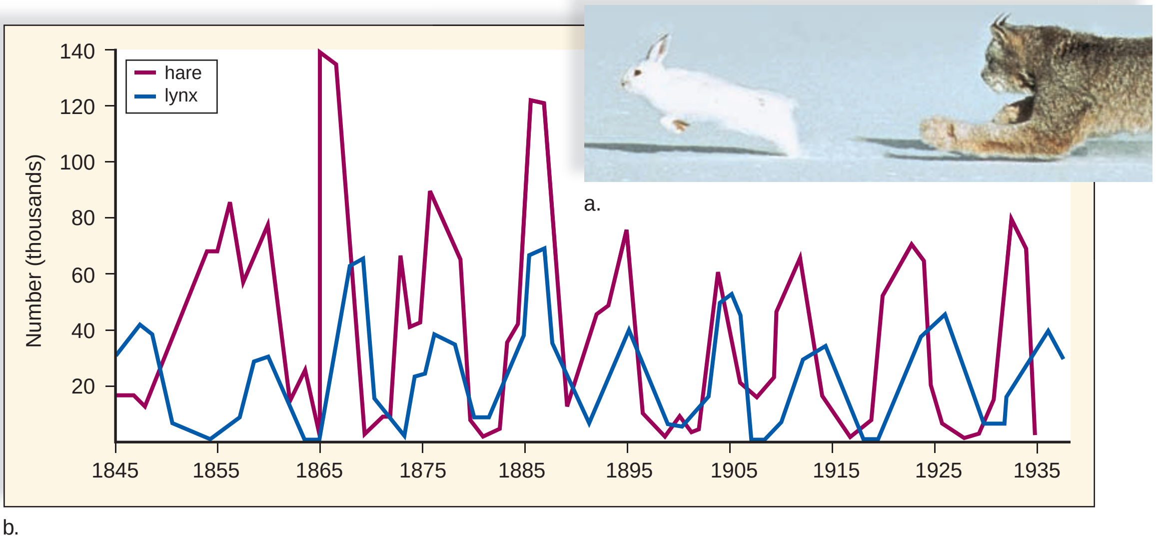


FIGURE 45.7 Predator-prey interaction between a lynx and a snowshoe hare.

a. A Canadian lynx, *Felis canadensis*, is a solitary predator. A long, strong forelimb with sharp claws grabs its main prey, the snowshoe hare, *Lepus americanus*. The lynx lives in northern forests. Its brownish gray coat blends in well against tree trunks, and its long legs enable it to walk through deep snow. **b.** The number of pelts received yearly by the Hudson Bay Company for almost 100 years shows a pattern of ten-year cycles in population densities. The snowshoe hare population reaches a peak abundance before that of the lynx by a year or more.

a. Camouflage b. Warning colorization c. Fright

FIGURE 45.8 **Antipredator defenses.**

a. Flounder is a fish that blends in with its background. **b.** The skin secretions of poison arrow frogs make them dangerous to touch. **c.** The large false head of the South American lantern fly may startle a potential predator.

One common strategy to avoid capture by a predator is **camouflage,** or the ability to blend into the background. Some animals have cryptic coloration that blends them into their surroundings. For example, flounders can take on the same coloration as their background (Fig. 45.8*a*). Many examples of protective camouflage are known: Walking sticks look like twigs; katydids look like sprouting green leaves; some caterpillars resemble bird droppings; and some insects and moths blend into the bark of trees.

Another common antipredator defense among animals is *warning coloration*, which tells the predator that the prey is potentially dangerous. As a warning to possible predators, poison arrow frogs are brightly colored (Fig. 45.8*b*). Also, many animals, including caterpillars, moths, and fishes, possess false eyespots that confuse or startle another animal. Other animals have elaborate anatomic structures that cause the *startle response*. The South American lantern fly has a large false head with false eyes, making it resemble the head of an alligator (Fig. 45.8*c*). However, antipredator defenses are not always false. A porcupine certainly looks formidable, and for good reason. Its arrowlike quills have barbs that dig into the predator's flesh and penetrate even deeper as the enemy struggles after being impaled. In the meantime, the porcupine runs away.

Association with other prey is another common strategy that may help avoid capture. Flocks of birds, schools of fish, and herds of mammals stick together as protection against predators. Baboons that detect predators visually, and antelopes that detect predators by smell, sometimes forage together, gaining double protection against stealthy predators. The gazellelike springboks of southern Africa jump stiff-legged 2–4 m into the air when alarmed. Such a jumble of shapes and motions might confuse an attacking lion, allowing the herd to escape.

Mimicry

Mimicry occurs when one species resembles another that possesses an overt antipredator defense. A mimic that lacks the defense of the organism it resembles is called a Batesian mimic (named for Henry Bates, who described the phenomenon). Once an animal experiences the defense of the model, it remembers the coloration and avoids all animals that look similar. Figure 45.9*a, b* shows two insects (flower fly and longhorn beetle) that resemble a yellow jacket wasp but lack the wasp's ability to sting. Classic examples of Batesian mimicry include the scarlet kingsnake mimicking the venomous coral snake and the viceroy butterfly mimicking the foul-tasting monarch butterfly.

There are also examples of species that have the same defense and resemble each other. Many stinging insects—bees, wasps, hornets, and bumblebees—have the familiar black and yellow bands. Once a predator has been stung by a black and yellow insect, it is wary of that color pattern in the future. Mimics that share the same protective defense are called Müllerian mimics, after Fritz Müller, who suggested that this, too, is a form of mimicry. The bumblebee in Figure 45.9*c* is a Müllerian mimic of the yellow jacket wasp because both of them can sting.

a. Flower fly b. Longhorn beetle

c. Bumblebee d. Yellow jacket

FIGURE 45.9 **Mimicry among insects.**

a. A flower fly, *Chrysotoxum*, and (**b**) a longhorn beetle, *Strophiona*, are Batesian mimics because they are incapable of stinging another animal, yet they have the same appearance as the yellow jacket wasp (**d**). **c.** The bumblebee, *Bombus*, and (**d**) the yellow jacket, *Vespula*, are Müllerian mimics because they both use stinging as a defense.

Symbiotic Relationships

Symbiotic relations are of three types, as shown in Table 45.1. Is this categorization artificial? Some biologists argue that the amount of harm or good two species do one another is dependent on what the investigator chooses to measure.

Parasitism is similar to predation in that an organism, called the **parasite,** derives nourishment from another, called the **host.** Parasitism is an example of a **symbiosis,** an association in which at least one of the species is dependent on the other (Table 45.1). Viruses, such as HIV, that reproduce inside human lymphocytes are always parasitic, and parasites occur in all of the kingdoms of life as well. Bacteria (e.g., strep infection), protists (e.g., malaria), fungi (e.g., rusts and smuts), plants (e.g., indian pipe), and animals (e.g., tapeworms and fleas) all have parasitic members. While small parasites can be endoparasites (heartworms) (Fig. 45.10), larger ones are more likely to be ectoparasites (leeches), which remain attached to the exterior of the body by means of specialized organs and appendages. The effects of parasites on the health of the host can range from slightly weakening them to actually killing them over time. When host populations are at a high density, parasites readily spread from one host to the next, causing intense infestations and a subsequent decline in host density. Parasites that do not kill their host can still play a role in reducing the host's population density because an infected host is less fertile and becomes more susceptible to another cause of death.

In addition to nourishment, host organisms also provide their parasites with a place to live and reproduce, as well as a mechanism for dispersing offspring to new hosts. Many parasites have both a primary and a secondary host. The secondary host may be a vector that transmits the parasite to the next primary host. Usually both hosts are required in order to complete the life cycle. The association between parasite and host is so intimate that parasites are often specific and even require certain species as hosts.

Commensalism

Commensalism is a symbiotic relationship between two species in which one species is benefited, and the other is neither benefited nor harmed.

FIGURE 45.10

Heartworm.

Dirofilaria immitis is a parasitic nematode spread by mosquitoes. The worms, which live in the heart and pulmonary blood artery, can cause death of the host.

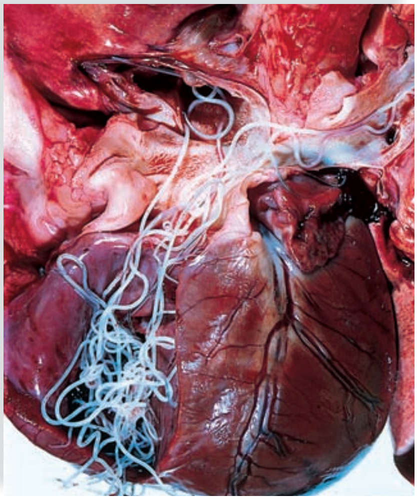


TABLE 45.1

Symbiotic Relationships

Interaction	*Expected Outcome*
Parasitism	Abundance of parasite increases, and abundance of host decreases.
Commensalism	Abundance of one species increases, and the other is not affected.
Mutualism	Abundance of both species increases.

Instances are known in which one species provides a home and/or transportation for the other species. Barnacles that attach themselves to the backs of whales and the shells of horseshoe crabs are provided with both a home and transportation. It is possible though that the movement of the host is impeded by the presence of the attached animals, and therefore some are reluctant to use these as instances of commensalism.

Epiphytes, such as Spanish moss and some species of orchids and ferns, grow in the branches of trees, where they receive light, but they take no nourishment from the trees. Instead, their roots obtain nutrients and water from the air. Clownfishes live within the waving mass of tentacles of sea anemones (Fig. 45.11). Because most fishes avoid the stinging tentacles of the anemones, clownfishes are protected from predators. Perhaps this relationship borders on mutualism, because the clownfishes actually may attract other fishes on which the anemone can feed or provide some cleaning services for the anemone.

Commensalism often turns out, on closer examination, to be an instance of either mutualism or parasitism. Cattle egrets are so named because these birds stay near cattle, which flush out their prey—insects and other animals—from vegetation. The relationship becomes mutualistic when egrets remove ectoparasites from the cattle. Remoras are fishes that attach themselves to the bellies of sharks by means of a modified dorsal fin acting as a suction cup. Remoras benefit by getting a free ride and feeding on a shark's leftovers. However, the shark benefits when remoras remove its ectoparasites.

FIGURE 45.11 **Clownfish among sea anemone's tentacles.**

If the clownfish, *Premnasa biaculeatus,* performs no service for the sea anemone, this association is a case of commensalism. If the clownfish lures other fish to be eaten by the sea anemone, this is a case of mutualism.

ecology focus

Interactions and Coevolution

Coevolution is present when two species adapt in response to selective pressure imposed by the other. Symbiosis (close association between two species), which includes parasitism, commensalism, and mutualism, is especially prone to the process of coevolution. Flowers pollinated by animals have features that attract them (see the Science Focus on pages 498–99). As an example of this type of coevolution, a butterfly-pollinated flower is often a composite, containing many individual flowers; the broad expanse provides a platform for the butterfly to land, and the butterfly has a proboscis that it in turn inserts into each tiny flower. In this case, natural selection has selected both for flat flowers and butterfly mouthparts to feed on such flowers. However, neither species would have evolved this way without the influence of the other.

Coevolution also occurs between predators and prey. For example, a cheetah sprints forward to catch its prey, and this behavior selects for those gazelles that are fast enough to avoid capture. Over generations, the adaptation of the prey (a great running speed, in this case) may very well put selective pressure on the predator for an adaptation to the prey's defense mechanism. Hence, an evolutionary "arms race" can develop. The process of coevolution has been studied in the cuckoo, a social parasite that reproduces at the expense of other bird species by laying its eggs in their nests. It is a strange sight to see a small bird feeding a cuckoo nestling several times its size. How did this strange happening develop? Investigators discovered that in order to "trick" a host bird, the adult cuckoo has to (1) lay an egg that mimics the host's egg, (2) lay its egg very rapidly (only 10 seconds are required) in the afternoon while the host is away from the nest, and (3) leave most of the hosts' eggs in the nest because hosts will desert a nest that has only one egg in it. (The cuckoo chick hatches first and is adapted to removing any other eggs in the nest [Fig. 45A*a*].) At this stage in the arms race, the cuckoo appears to have the upper hand, but the host birds may very well next evolve a way to distinguish the cuckoo from their own young.

Coevolution can take many forms. In the case of *Plasmodium,* the cause of malaria, the sexual portion of the life cycle occurs within mosquitoes (the vector), and the asexual portion occurs in humans. The human immune system uses surface proteins to detect pathogens, and *Plasmodium* has numerous genes for surface proteins, and it is capable of changing these surface proteins repeatedly. In this way, it stays one step ahead of the host's immune system. A similar capability of HIV has added to the difficulty of producing an AIDS vaccine.

The relationship between parasite and host can even include the ability of parasites to seemingly manipulate the behavior of their hosts in self-serving ways. Ants infected with the lance fluke (but not those uninfected) mysteriously cling to blades of grass with their mouthparts. There, the infected ants are eaten by grazing sheep, and the flukes are transmitted to the next host in their life cycle. Similarly, when snails of the genus *Succinea* are parasitized by worms of the genus *Leucochloridium,* they are eaten by birds. As the worms mature, they invade the snail's eyestalks, making them resemble edible caterpillars. Now the birds eat the snails, and the parasites release their eggs, which complete development inside the urinary tracts of birds.

The traditional view was that as host and parasite coevolved, each would become more tolerant of the other since, if the opposite occurred, the parasite would soon run out of hosts. Parasites could first become commensal, or harmless to the host. Then, given enough time, the parasite and host might even become mutualists. In fact, the evolution of the eukaryotic cell by endosymbiosis is predicated on the supposition that bacteria took up residence inside a larger cell, and then the parasite and cell became mutualists.

However, this argument is too teleological for some; after all, no organism is capable of "looking ahead" at its evolutionary fate. Rather, if an aggressive parasite could transmit more of itself in less time than a benign one, aggressiveness would be favored by natural selection. On the other hand, other factors, such as the life cycle of the host, can determine whether aggressiveness is beneficial or not. For example, a benign parasite of newts will do better than an aggressive one. Why? Because newts take up solitary residence outside ponds in the forest for six years, and parasites have to wait that long before they are likely to meet up with another potential host. If a parasite kills its host before it can reach another, it not only has lost its food source, but also its home.

FIGURE 45A Social parasitism.
a. *The cuckoo,* Cuculus, *is a social parasite of the reed warbler,* Acrocephalus. *A cuckoo chick is heaving the eggs of its host out of the nest.* ***b.*** *Its own egg* (see inset) *mimics and is accepted by the host as its own.*

Mutualism

Mutualism is a symbiotic relationship in which both members benefit. As with other symbiotic relationships, it is possible to find numerous examples among all organisms. Bacteria that reside in the human intestinal tract acquire food, but they also provide us with vitamins, molecules we are unable to synthesize for ourselves. Termites would not be able to digest wood if not for the protozoans that inhabit their intestinal tracts and digest cellulose. Mycorrhizae are mutualistic associations between the roots of plants and fungal hyphae. The hyphae improve the uptake of nutrients for the plant, protect the plant's roots against pathogens, and produce plant growth hormones. In return, the plant provides the fungus with carbohydrates. Some sea anemones make their home on the backs of crabs. The crab uses the stinging tentacles of the sea anemone to gather food and to protect itself; the sea anemone gets a free ride that allows it greater access to food than other anemones. Lichens can grow on rocks because their fungal member conserves water and leaches minerals that are provided to the algal partner, which photosynthesizes and provides organic food for both populations. However, it's been suggested that the fungus is parasitic, at least to a degree, on the algae.

In tropical America, the bullhorn acacia tree is adapted to provide a home for ants of the species *Pseudomyrmex ferruginea*. Unlike other acacias, this species has swollen thorns with a hollow interior, where ant larvae can grow and develop. In addition to housing the ants, acacias provide them with food. The ants feed from nectaries at the base of the leaves and eat fat- and protein-containing nodules called Beltian bodies, found at the tips of the leaves. The ants constantly protect the plant from herbivores and other plants that might shade it because, unlike other ants, they are active 24 hours a day.

The relationship between plants and their pollinators, mentioned previously, is a good example of mutualism. Perhaps the relationship began when herbivores feasted on pollen. The provision of nectar by the plant may have spared the pollen and, at the same time, allowed the animal to become an agent of pollination. By now, pollinator mouthparts are adapted to gathering the nectar of a particular plant species, and this species is dependent on the pollinator for dispersing pollen (see pages 498–99). The mutualistic relationships between flowers and their pollinators are examples of coevolution.

FIGURE 45.12

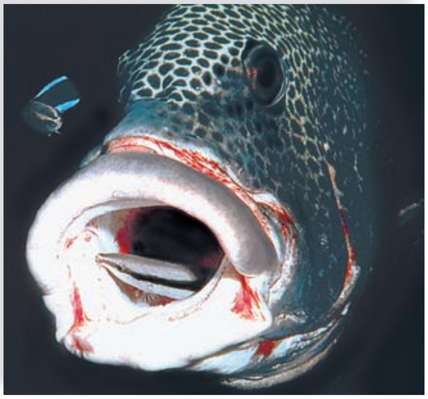
Clark's nutcrackers.

Mutualism can take many forms, such as when birds like Clark's nutcrackers feed on but also disperse the seeds of whitebark pine trees.

FIGURE 45.13

Cleaning symbiosis.

A cleaner wrasse, *Labroides dimidiatus*, in the mouth of a spotted sweetlip, *Plectorhincus chaetodontoides*, is feeding off parasites. Does this association improve the health of the sweetlip, or is the sweetlip being exploited? Investigation is under way.



The outcome of mutualism is an intricate web of species interdependencies critical to the community. For example, in areas of the western United States, the branches and cones of whitebark pine are turned upward, meaning that the seeds do not fall to the ground when the cones open. Birds called Clark's nutcrackers eat the seeds of whitebark pine trees and store them in the ground (Fig. 45.12). Therefore, Clark's nutcrackers are critical seed dispersers for the trees. Also, grizzly bears find the stored seeds and consume them. Whitebark pine seeds do not germinate unless their seed coats are exposed to fire. When natural forest fires in the area are suppressed, whitebark pine trees decline in number, and so do Clark's nutcrackers and grizzly bears. When lightning-ignited fires are allowed to burn, or prescribed burning is used in the area, the whitebark pine populations increase, as do the populations of Clark's nutcrackers and grizzly bears.

Cleaning symbiosis is a symbiotic relationship in which crustaceans, fish, and birds act as cleaners for a variety of vertebrate clients. Large fish in coral reefs line up at cleaning stations and wait their turn to be cleaned by small fish that even enter the mouths of the large fish (Fig. 45.13). Whether cleaning symbiosis is an example of mutualism has been questioned because of the lack of experimental data. If clients respond to tactile stimuli by remaining immobile while cleaners pick at them, then cleaners may be exploiting this response by feeding on host tissues, as well as on ectoparasites.

Check Your Progress 45.1

1. What is the difference between an organism's habitat and niche?
2. What two factors can cause predator and prey populations to cycle in a predictable manner?
3. Give examples to show mutualism can be involved when one population feeds off another.

science focus

Island Biogeography Pertains to Biodiversity

Would you expect larger coral reefs to have a greater number of species, called species richness, than smaller coral reefs? The area (space) occupied by a community can have a profound effect on its biodiversity. American ecologists Robert MacArthur and E. O. Wilson developed a general **model of island biogeography** to explain and predict the effects of (1) distance from the mainland and (2) size of an island on community diversity.

Imagine two new islands that, as yet, contain no species at all. One of these islands is near the mainland, and one is far from the mainland (Fig. 45B*a*). Which island will receive more immigrants from the mainland? Most likely, the near one because it's easier for immigrants to get there. Similarly, imagine two islands that differ in size (Fig. 45B*b*). Which island will be able to support a greater number of species? The large one, because its greater amount of resources can support more populations, while species on the smaller island may eventually face extinction due to scarce resources. MacArthur and Wilson studied the biodiversity on many island chains, including the West Indies, and discovered that species richness does correlate positively with island distance from mainland and island size. They developed a model of island biogeography that takes into account both factors. An equilibrium is reached when the rate of species immigration matches the rate of species extinction due to limited space (Fig. 45B*c*). Notice that the equilibrium point is highest for a large island that is near the mainland. The equilibrium could be dynamic (new species keep on arriving, and new extinctions keep on occurring), or the composition of the community could remain steady unless disturbed.

Biodiversity

Conservationists note that the trends graphed in Figure 45B*c* in particular apply to their work because humans often create preserved areas surrounded by farms, towns, and cities, or even water. For example, in Panama, Barro Colorado Island (BCI) was created in the 1910s when a river was dammed to form a lake. As predicted by the model of island biogeography, BCI lost species because it was a small island that had been cut off from the mainland. Among the species that became extinct were the top predators on the island, namely the jaguar, puma, and ocelot. Thereafter, medium-sized terrestrial mammals, such as the coatimundi, increased in number. Because the coatimundi is an avid predator of bird eggs and nestlings, soon there were fewer bird species on BCI, even though the island is large enough to support them.

The model of island biogeography suggests that the larger the conserved area, the better the chance of preserving more species. Is it possible to increase the amount of space without using more area? Two possibilities come to mind. If the environment has patches, it has a greater number of habitats—and thus greater diversity. As gardeners, we are urged to create patches in our yards if we wish to attract more butterflies and birds! One way to introduce patchiness is through stratification, the use of layers. Just as a high-rise apartment building allows more human families to live in an area, so can stratification within a community provide more and different types of living space for different species.

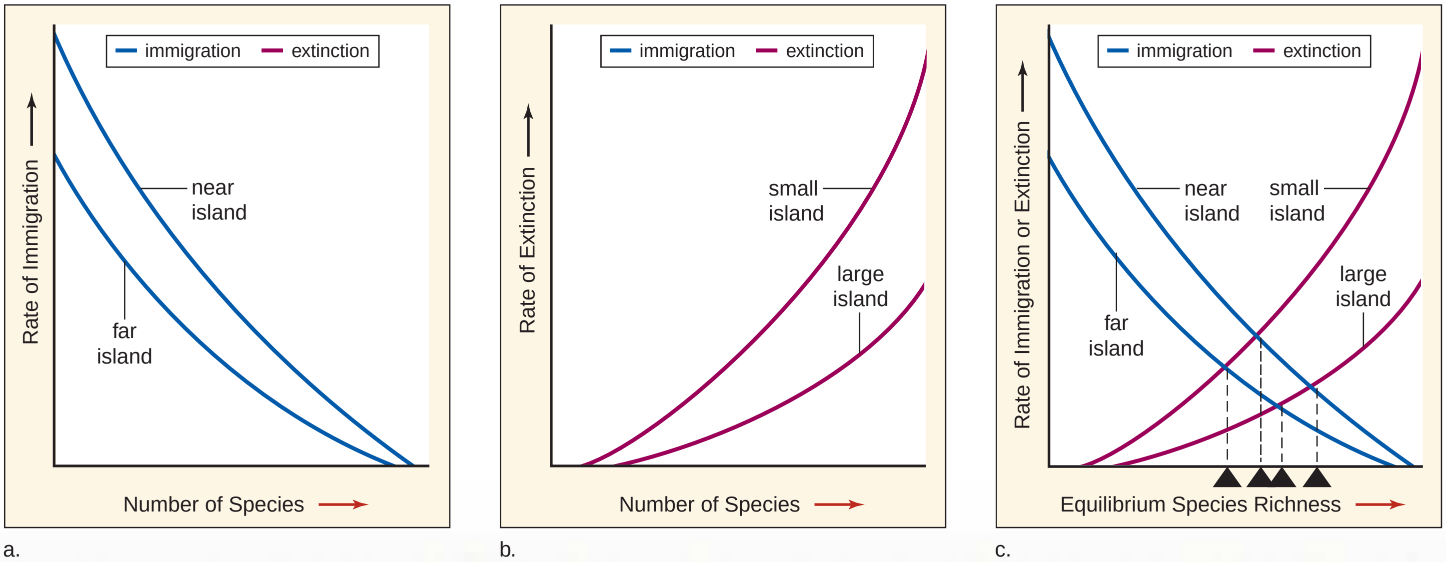


FIGURE 45B Species richness.
a. *An island near the mainland will have a higher immigration rate than an island far from the mainland.* ***b.*** *A small island will have a higher extinction rate than a large island.* ***c.*** *The balance between immigration and extinction for four possible types of islands. A large island that is near the mainland will have a higher equilibrium species richness than the other types of islands.*

FIGURE 45.14

Secondary succession.

This example of secondary succession occurred in a former cornfield in New Jersey on the east coast of the United States. **a.** During the first year, only the remains of corn plants are seen. **b.** During the second year, wild grasses have invaded the area. **c.** By the fifth year, the grasses look more mature, and sedges have joined them. **d.** During the tenth year, there are goldenrod plants, shrubs (blackberry), and juniper trees. **e.** After 20 years, the juniper trees are mature, and there are also birch and maple trees in addition to the blackberry shrubs.

a. First year

b. Second year

45.2 Community Development

Each community has a history that can be surveyed over a short time period or even over geological time. We know that the distribution of life has been influenced by dynamic changes occurring during the history of Earth. We have previously discussed how continental drift contributed to various mass extinctions that have occurred in the past. For example, when the continents joined to form the supercontinent Pangaea, many forms of marine life became extinct. Or, when the continents drifted toward the poles, immense glaciers drew water from the oceans and even chilled once-tropical lands. During an ice age, glaciers moved southward, and then in between ice ages, glaciers retreated, changing the environment and allowing life to colonize the land once again. Over time, complex communities evolved. Many ecologists, however, try to observe changes as they occur during much shorter timescales.

Ecological Succession

Communities are subject to disturbances that can range in severity from a storm blowing down a patch of trees, to a beaver damming a pond, to a volcanic eruption. We know from observation that following these disturbances, we'll see changes in the plant and animal communities over time; often, we'll wind up with the same kind of community with which we started.

Ecological succession is a change involving a series of species replacements in a community. *Primary succession* occurs in areas where there is no soil formation, such as following a volcanic eruption or a glacial retreat. Wind, water, and other abiotic factors start the formation of soil from exposed rock. *Secondary succession* occurs in areas where soil is present, as when a cultivated field, such as a cornfield in New Jersey, returns to a natural state (Fig. 45.14). This is disturbance-based succession. Notice that the progression changes from grasses to shrubs to a mixture of shrubs and trees.

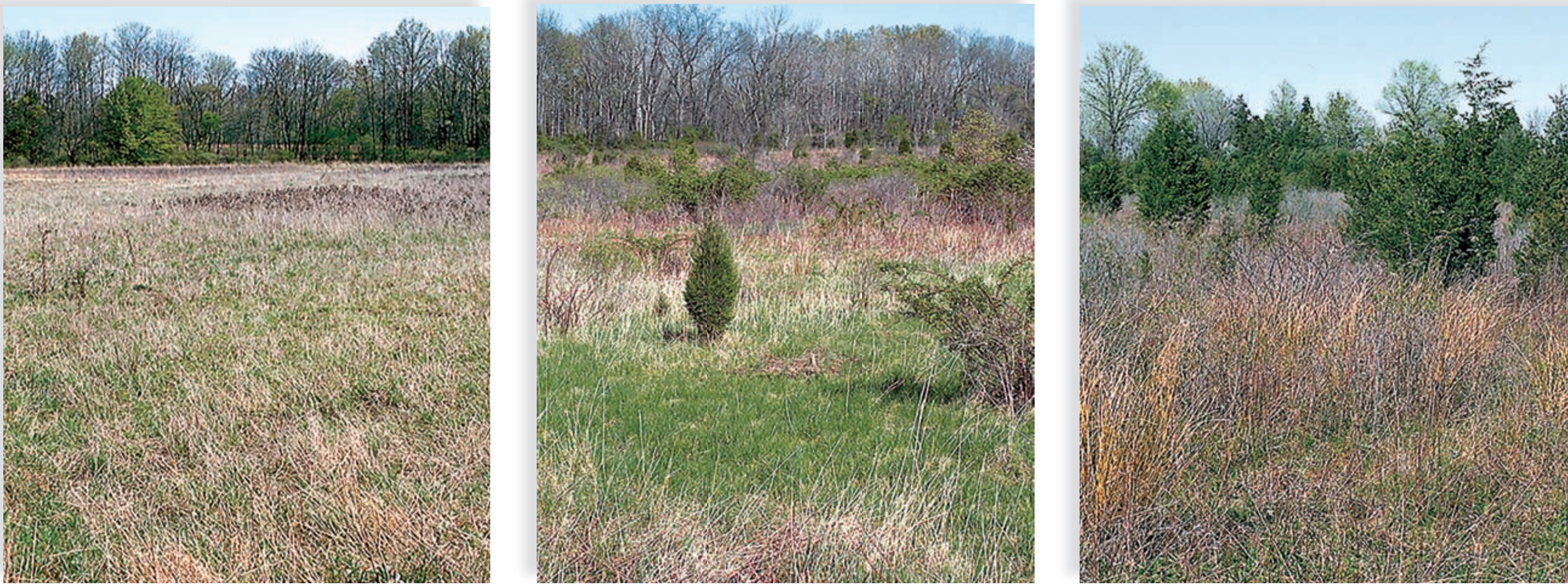
The first species to begin secondary succession are called **pioneer species**—that is, plants that are invaders of disturbed areas—and then the area progresses through the series of stages described in Figure 45.15. Again, we observe a series that begins with small, short-lived species and proceeds through stages of species of mixed sizes and life spans, until finally there are only large, long-lived species of trees. Ecologists have tried to determine the processes and mechanisms by which the changes described in Figures 45.14 and 45.15 take place—and whether these processes always have the same "end point" of community composition and diversity.

Models About Succession

In 1916, F. E. Clements proposed that succession in a particular area will always lead to the same type of community, which he called a **climax community.** He hypothesized that climate, in particular, determined whether succession resulted in a desert, a type of grassland, or a particular type of forest. This is the reason, he said, that coniferous forests occur in northern latitudes, deciduous forests in temperate zones, and tropical rain forests in the tropics. Secondarily, he hypothesized that soil conditions might also affect the results. Shallow, dry soil might produce a grassland where otherwise a forest might be expected, or the rich soil of a riverbank might produce a woodland where a prairie is expected.

Further, Clements hypothesized that each stage facilitated the invasion and replacement by organisms of the next stage. Shrubs can't grow on dunes until dune grass has caused soil to develop. Similarly, in the example given in Figure 45.15, shrubs can't arrive until grasses have made the soil suitable for them. Each successive community prepares the way for the next, so that grass-shrub-forest development occurs in a sequential way. Therefore, in what is sometimes called "climax theory," this is known as the *facilitation model* of succession.

Aside from this facilitation model, there is also an *inhibition model*. That model predicts that colonists hold onto



c. Fifth year

d. Tenth year

e. Twentieth year

their space and inhibit the growth of other plants until the colonists die or are damaged. Still another model, called the *tolerance model*, predicts that different types of plants can colonize an area at the same time. Sheer chance determines which seeds arrive first, and successional stages may simply reflect the length of time it takes species to mature. This alone could account for the herb-shrub-forest development that is often seen (Fig. 45.15). The length of time it takes for trees to develop might give the impression that there is a recognizable series of plant communities, from the simple to the complex. In reality, succession does occur, and the models mentioned here are probably not mutually exclusive, but a mixture of multiple, complex processes.

Although it may not have been apparent to early ecologists, we now recognize that the most outstanding characteristic of natural communities is their dynamic nature. Also, it seems obvious to us now that the most complex communities most likely consist of habitat patches that are at various stages of succession. Each successional stage has its own mix of plants and animals, and if a sample of all stages is present, community diversity is greatest. Further, we do not know if succession continues to certain end points, because the process may not be complete anywhere on the face of the Earth.

Check Your Progress 45.2

1. Several different hypothesis (models) are available to explain succession. Does this mean that ecological succession doesn't occur?

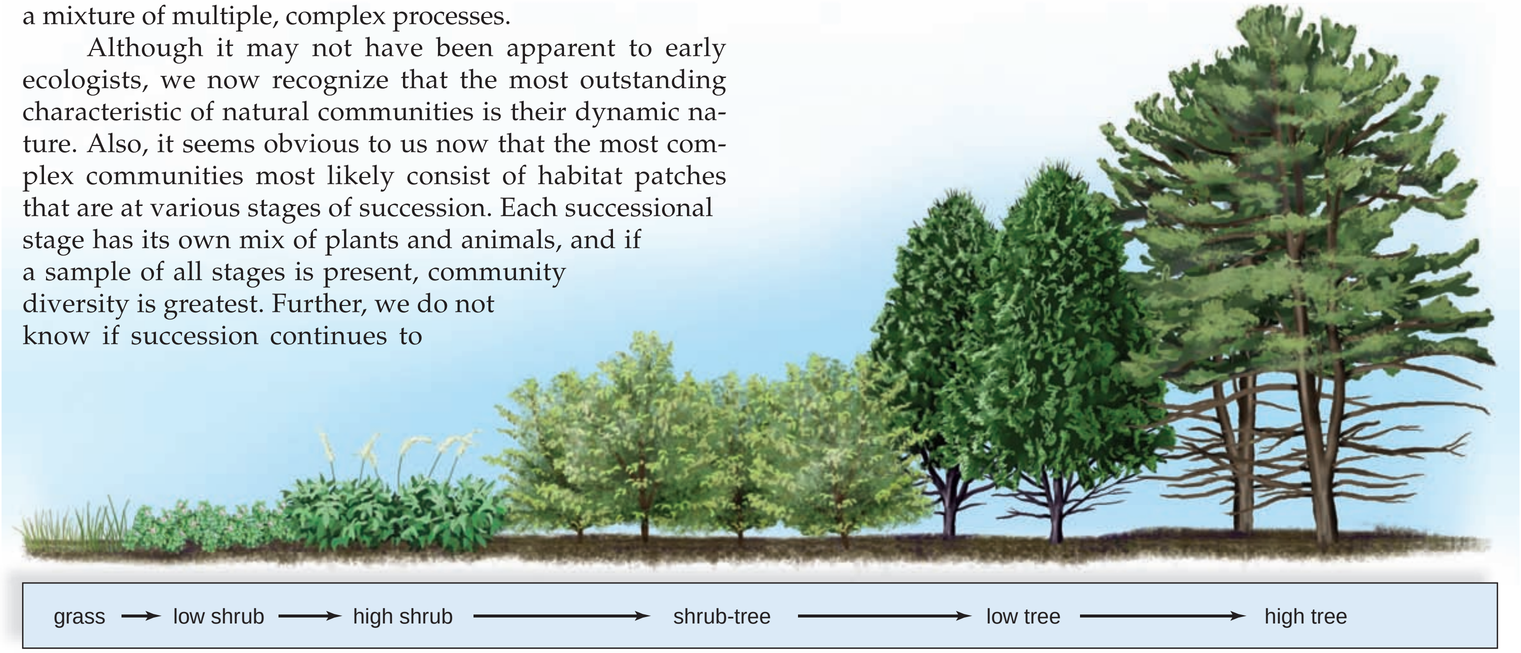


FIGURE 45.15 **Secondary succession in a forest.**

In secondary succession in a large conifer plantation in central New York State, certain species are common to particular stages. However, the process of regrowth shows approximately the same stages as secondary succession from a cornfield (see Fig. 45.14).

45.3 Dynamics of an Ecosystem

In an **ecosystem,** populations interact among themselves and with the physical environment. The abiotic components of an ecosystem are the nonliving components such as the atmosphere, water, and soil. The biotic components are living things that can be categorized according to their food source (Fig. 45.16).

Autotrophs

Autotrophs require only inorganic nutrients and an outside energy source to produce organic nutrients for their own use and for all the other members of a community. They are called **producers** because they produce food. Autotrophs include photosynthetic organisms such as land plants and algae. They possess chlorophyll and carry on photosynthesis in freshwater and marine habitats. Algae make up the phytoplankton, which are photosynthesizing organisms suspended in water. Green plants are the dominant photosynthesizers on land.

Some autotrophic bacteria are chemosynthetic. They obtain energy by oxidizing inorganic compounds such as ammonia, nitrites, and sulfides, and they use this energy to synthesize organic compounds. Chemoautotrophs have been found to support communities in some caves and also at hydrothermal vents along deep-sea oceanic ridges where sunlight is unavailable.

Heterotrophs

Heterotrophs need a preformed source of organic nutrients as they acquire food from a different (*hetero*) source. They are called **consumers** because they consume food that was generated by a producer. **Herbivores** are animals that graze directly on plants or algae. In terrestrial habitats, insects are small herbivores; antelopes and bison are large herbivores. In aquatic habitats, zooplankton are small herbivores; fishes and manatees are large herbivores. **Carnivores** feed on other animals; birds that feed on insects are carnivores, and so are hawks that feed on birds and small mammals. **Omnivores** are animals that feed on both plants and animals. Chickens, raccoons, and humans are omnivores. Some animals are scavengers, such as vultures and jackals, which eat the carcasses of dead animals.

Detritivores are organisms that feed on detritus, which is decomposing particles of organic matter. Marine fan worms filter detritus from the water, while clams take it from the substratum. Earthworms, some beetles, termites, and ants are all terrestrial detritivores. Bacteria and fungi, including mushrooms, are decomposers; they acquire nutrients by breaking down dead organic matter, including animal wastes. **Decomposers** perform a valuable service because they release inorganic substances that are taken up by plants once more. Otherwise, plants would be completely dependent only on physical processes, such as the release of minerals from rocks, to supply them with inorganic nutrients.

a. Producers

b. Herbivores

c. Carnivores

d. Decomposers

FIGURE 45.16 **Biotic components.**

a. Diatoms and green plants are photoautotrophs. **b.** Caterpillars and rabbits are herbivores. **c.** Spiders and osprey are carnivores. **d.** Bacteria and mushrooms are decomposers.

Energy Flow and Chemical Cycling

A diagram of all the biotic components of an ecosystem illustrates that every ecosystem is characterized by two fundamental phenomena: energy flow and chemical cycling (Fig. 45.17). Energy flow begins when producers absorb solar energy, and chemical cycling begins when producers take in inorganic nutrients from the physical environment. Thereafter, via photosynthesis, producers make organic nutrients (food) directly for themselves and indirectly for the other populations of the ecosystem. Energy flows through an ecosystem via photosynthesis because as organic nutrients pass from one component of the ecosystem to another, such as when an herbivore eats a plant or a carnivore eats an herbivore, only a portion of the original amount of energy is transferred. Eventually, the energy dissipates into the environment as heat. Therefore, the vast majority of ecosystems cannot exist without a continual supply of solar energy.

Only a portion of the organic nutrients made by producers is passed on to consumers because plants use organic molecules to fuel their own cellular respiration. Similarly, only a small percentage of nutrients consumed by lower-level consumers, such as herbivores, is available to higher-level consumers, or carnivores. As Figure 45.18 demonstrates, a certain amount of the food eaten by an herbivore is never digested and is eliminated as feces. Metabolic nitrogenous wastes are excreted as urine. Of the assimilated energy, a large portion is used during cellular respiration for the production of ATP and thereafter becomes heat. Only the remaining energy, which is converted into increased body weight or additional offspring, becomes available to carnivores.

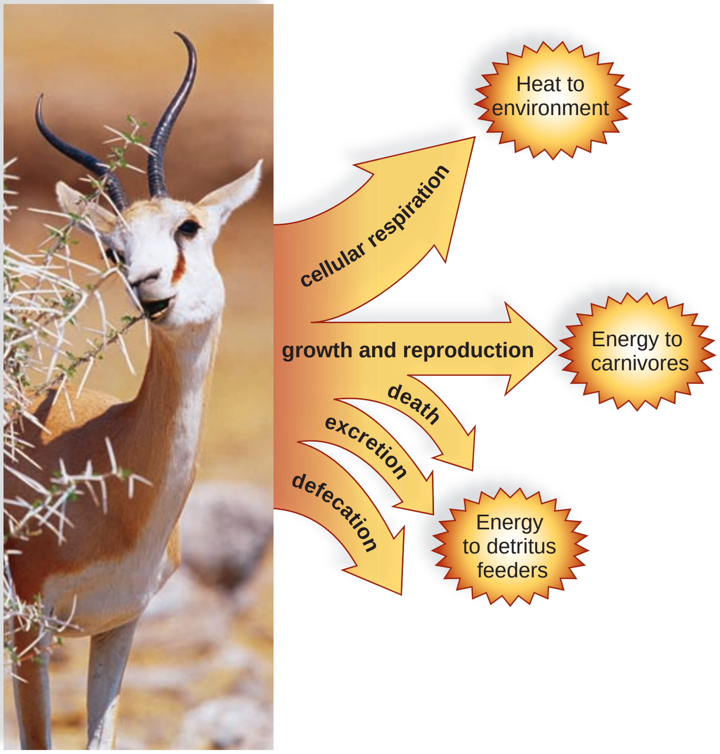


FIGURE 45.18 **Energy balances.**

Only about 10% of the food energy taken in by an herbivore is passed on to carnivores. A large portion goes to detritus feeders via defecation, excretion, and death, and another large portion is used for cellular respiration.

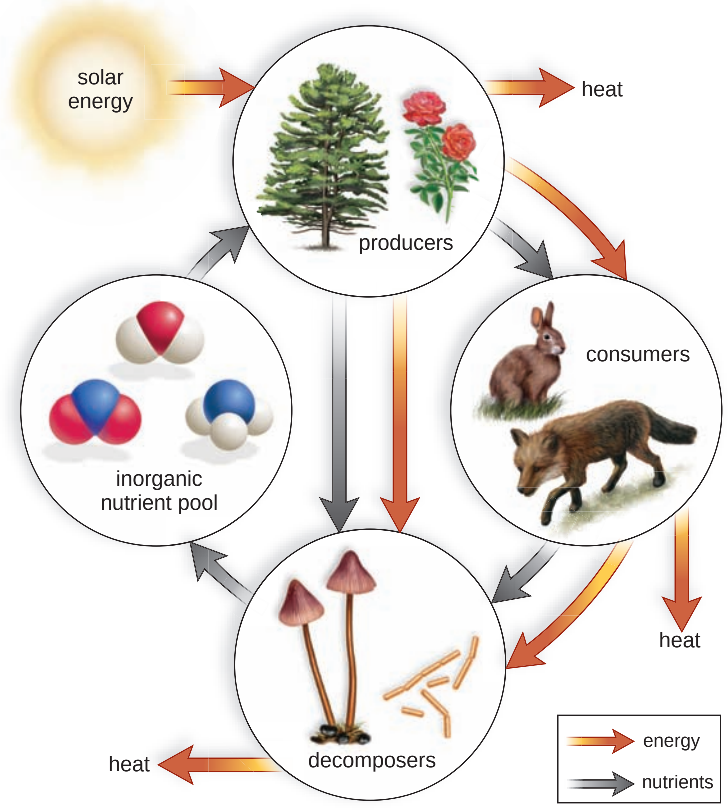


FIGURE 45.17 **Nature of an ecosystem.**

Chemicals cycle, but energy flows through an ecosystem. As energy transformations repeatedly occur, all the energy derived from the sun eventually dissipates as heat.

The elimination of feces and urine by a heterotroph, and indeed the death of all organisms, does not mean that organic nutrients are lost to an ecosystem. Instead, they represent the organic nutrients made available to decomposers. Decomposers convert the organic nutrients, such as glucose, back into inorganic chemicals, such as carbon dioxide and water, and release them to the soil or atmosphere. When these inorganic chemicals are absorbed by producers from the atmosphere or soil, these chemicals have completed their cycle within an ecosystem.

The laws of thermodynamics support the concept that energy flows through an ecosystem. The first law states that energy can neither be created nor destroyed. This explains why ecosystems are dependent on a continual outside source of energy, usually solar energy, which is used by photosynthesizers to produce organic nutrients. The second law states that, with every transformation, some energy is degraded into a less available form such as heat. Because plants carry on cellular respiration, for example, only about 55% of the original energy absorbed by plants is available to an ecosystem.

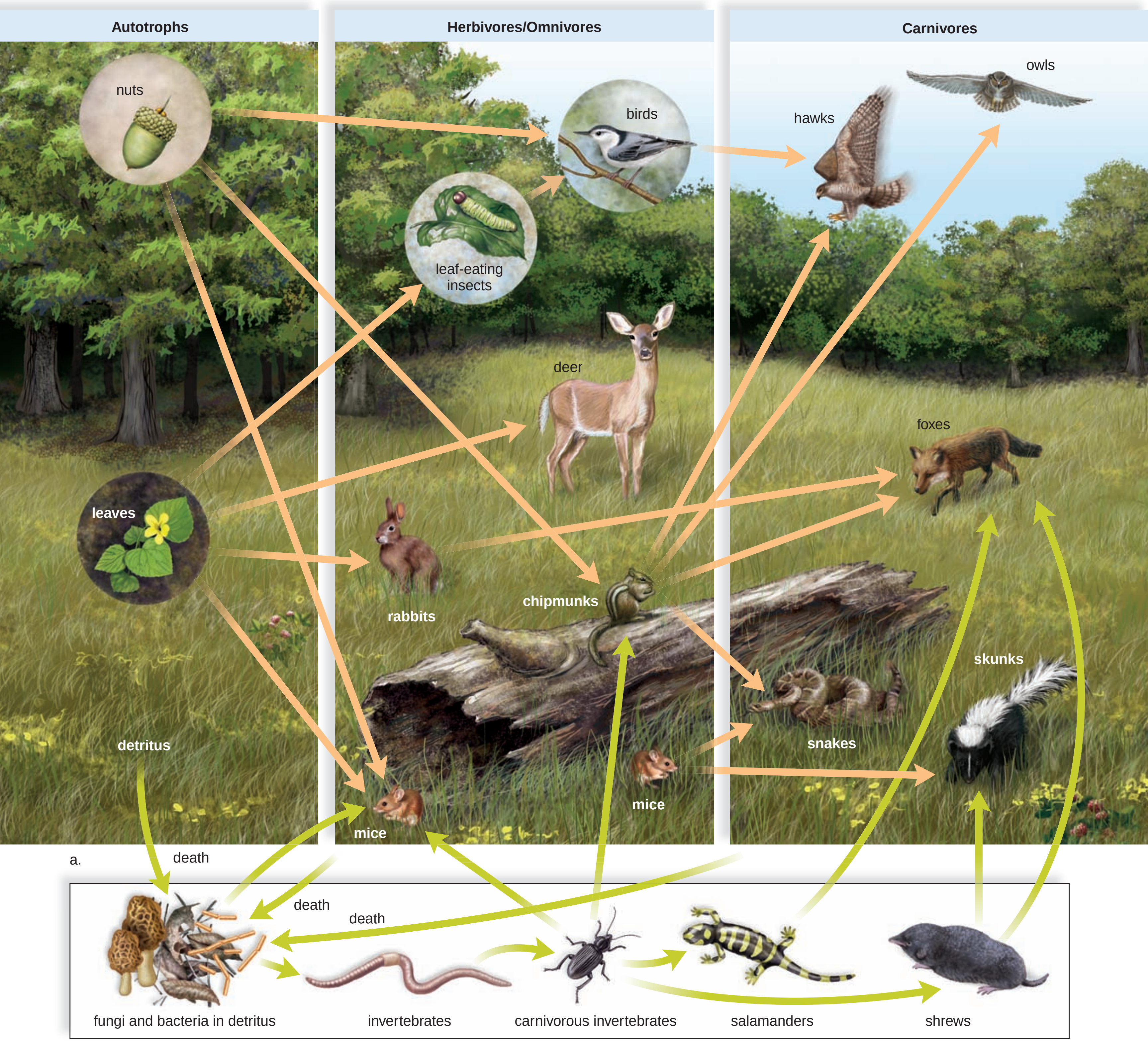


FIGURE 45.19 **Grazing and detrital food web.**

Food webs are descriptions of who eats whom. **a.** Tan arrows illustrate possible grazing food webs. For example, birds, which feed on nuts, may be eaten by a hawk. Autotrophs such as the tree are producers (first trophic, or feeding, level), the first series of animals are primary consumers (second trophic level), and the next group of animals are secondary consumers (third trophic level). **b.** Green arrows illustrate possible detrital food webs, which begin with detritus—the bacteria and fungi of decay and the remains of dead organisms. A large portion of these remains are from the grazing food web illustrated in (**a**). The organisms in the detrital food web are sometimes fed on by animals in the grazing food web, as when robins feed on earthworms. Thus, the grazing food web and the detrital food web are connected to one another.

Energy Flow

The principles discussed previously in this chapter can now be applied to an actual ecosystem—a forest of 132,000 m^2 in New Hampshire. The various interconnecting paths of energy flow are represented by a **food web,** a diagram that describes trophic (feeding) relationships. Figure 45.19*a* is a grazing food web because it begins with a producer, specifically the oak tree depicted. Insects in the form of caterpillars feed on leaves, while mice, rabbits, and deer feed on leaf tissue at or near the ground. Birds, chipmunks, and mice feed on fruits and nuts, but they are in fact omnivores because they also feed on caterpillars. These herbivores and omnivores all provide food for a number of different carnivores.

Figure 45.19*b* is a detrital food web, which begins with detritus. Detritus is food for soil organisms such as earthworms. Earthworms are in turn fed on by carnivorous invertebrates, and they may be eaten by shrews or salamanders. Because the members of a detrital food web may become food for aboveground carnivores, the detrital and grazing food webs are joined.

We naturally tend to think that aboveground plants such as trees are the largest storage form of organic matter and energy, but this is not necessarily the case. In this particular forest, the organic matter lying on the forest floor and mixed into the soil contains over twice as much energy as the leaf matter of living trees. Therefore, more energy in a forest may be funneling through the detrital food web than through the grazing food web.

Trophic Levels

The arrangement of the species in Figure 45.19 suggests that organisms are linked to one another in a straight line, according to feeding relationships, or who eats whom. Diagrams that show a single path of energy flow in an ecosystem are called **food chains.** For example, in the grazing food web, we could find this grazing food chain:

leaves ⟶ caterpillars ⟶ birds ⟶ hawks

And in the detrital food web, we could find this detrital food chain:

detritus ⟶ earthworms ⟶ salamanders

A **trophic level** is a level of nourishment within a food web or chain. In the grazing food web in Figure 45.19*a*, going from left to right, the green plants are producers (first trophic level), the first series of animals are primary consumers (second trophic level), and the next group of animals are secondary consumers (third trophic level).

Ecological Pyramids

The shortness of food chains can be attributed to the loss of energy between trophic levels. In general, only about 10% of the energy of one trophic level is available to the next trophic level. Therefore, if an herbivore population consumes 1,000 kg of plant material, only about 100 kg is converted to body tissue of an herbivore, 10 kg to first-level carnivores, and 1 kg to second-level carnivores. The so-called 10% rule explains why few carnivores can be supported in a food web. The flow of energy with large losses between successive trophic levels is sometimes depicted as an **ecological pyramid** (Fig. 45.20).

Energy losses between trophic levels also result in pyramids based on the number of organisms or the amount of biomass at each trophic level. When constructing such pyramids, problems arise, however. For example, in Figure 45.19, each tree would contain numerous caterpillars; therefore, there would be more herbivores than autotrophs! The explanation, of course, has to do with size. An autotroph can be as tiny as a microscopic alga or as big as a beech tree; similarly, an herbivore can be as small as a caterpillar or as large as an elephant.

Pyramids of biomass eliminate size as a factor because **biomass** is the number of organisms multiplied by the dry weight of the organic matter within one organism. The biomass of the producers is expected to be greater than the biomass of the herbivores, and that of the herbivores is expected to be greater than that of the carnivores. In aquatic ecosystems, such as some lakes and open seas where algae are the only producers, the herbivores may have a greater biomass than the producers when their measurements are taken because the algae are consumed at a high rate. Such

FIGURE 45.20 **Ecological pyramid.**

The biomass, or dry weight (g/m^2), for trophic levels in a grazing food web in a bog at Silver Springs, Florida. There is a sharp drop in biomass between the producer level and herbivore level, which is consistent with the common knowledge that the detrital food web plays a significant role in bogs.