chapter 6

Population and Community Ecology

New England Forests Come Full Circle

When the Pilgrims arrived in Massachusetts in 1620, they found immense areas of undisturbed temperate seasonal forest containing a variety of tree species, including sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), white pine (*Pinus strobus*), and eastern hemlock (*Tsuga canadensis*). Over the next 200 years, settlers cut down most of the trees to clear land for farming and housing. This deforestation peaked in the 1800s, at which point up to 80 percent of all New England forests had been cleared. Between 1850 and 1950, however, many people abandoned their New England farms to take jobs in the growing textile industry. Others moved to the Midwest, where farmland was more fertile and considerably less expensive.

What happened to the former farmland is a testament to the resilience of the forest ecosystem. The transformation began shortly after the farmers left. Seeds of grasses and wildflowers were carried to the abandoned fields by birds or blown there by the wind. Within a year, the fields were carpeted with a large variety of plant species. Eventually, a single group of plants—the goldenrods—came to dominate the fields by growing taller and outcompeting other species of plants for sunlight. The other species remained in the fields, but they were not very abundant. Nevertheless, the dominance of the goldenrods was short-lived.

> The old stone walls that are so common in the New England countryside are the only evidence that this forest was once farmland.

Goldenrods and other wildflowers play an important part in old-field communities because they support a diverse group of plant-eating insects. Some of these herbivorous insects are generalists that feed on a wide range of plant species, while others specialize on only a small number of plant species. The number of individuals of each insect species varies from year to year, and occasionally some species experience very large population increases, or outbreaks. One such species is a leaf beetle (*Microrhopala vittata*) that specializes in eating goldenrods. Periodic outbreaks of this species in the abandoned fields of New England dramatically reduced goldenrod populations. With fewer goldenrods, other plant species could compete and prosper.

The complex interactions among populations of goldenrods, insects, and other species created an ever-changing ecosystem. For example, as the leaf beetle population increased in the community, so did the populations of predators and parasites that fed on them. As these predators and parasites reduced the population of leaf beetles, the goldenrod population began to rebound. As the goldenrods surged, they once again caused other plant species to decline in numbers.

Over time, tree seeds arrived and tree seedlings began to grow, which changed the species composition of the old fields once again. One species in particular, the fast-growing white pine, eventually came to dominate. The pine trees cast so much shade that the goldenrods and other sunlight-loving plant species could not survive.

White pines dominated the old-field communities until humans began harvesting them for lumber in the 1900s. Just as the reduction of goldenrod populations made room for other plant species, logging of the white pines made room for broadleaf tree species. Two of these broadleaf species, American beech and sugar maple, are dominant in New England forests today. The New England fields that had been abandoned earlier were slowly transformed into communities that resemble the original forests of centuries ago, with a mix of pines, hemlocks, and broadleaf trees. The old stone walls that are so common in the New England countryside are the only evidence that this forest was once farmland.

The story of the New England forests shows us that populations can increase or decrease dramatically over time. It also illustrates how species interactions within a community can alter species abundance. Finally, it demonstrates how human activity can alter the distribution and diversity of species within an ecosystem.

Sources:
W. P. Carson and R. B. Root, Herbivory and plant species coexistence: Community regulation by an outbreaking phytophagous insect, *Ecological Monographs* 70 (2000): 73–99; T. Wessels, *Reading the Forested Landscape* (Countryman Press, 1997).

A New England forest is a wonderful reminder of the intricate complexity of the natural world. As we saw in this account, there are clear patterns in the distribution and abundance of species over space and time. Understanding the factors that generate these patterns can help us find ways to preserve global biodiversity. These factors include the ways in which populations increase and decrease in size and how species interact in ecological communities. In this chapter, we will examine the factors that help determine the abundance and distribution of populations. We will then look at interactions among species that live within ecological communities and how these interactions further determine whether a species can persist in a particular location on Earth. Finally, we will examine how ecological communities change over time.

module

18 The Abundance and Distribution of Populations

Complexity in the natural world ranges from a single individual to all of the biotic and abiotic components of Earth. In this module, we will begin by broadly examining the different levels of complexity in nature and then narrow our focus to the population level. We will consider the characteristics of populations and then discuss factors that determine how populations increase and decrease over time.

Learning Objectives

After reading this module you should be able to

- explain how nature exists at several levels of complexity.
- discuss the characteristics of populations.
- contrast the effects of density-dependent and density-independent factors on population growth.

Nature exists at several levels of complexity

As FIGURE 18.1 shows, the environment around us exists at a series of increasingly complex levels: individuals, populations, communities, ecosystems, and the biosphere. The simplest level is the individual—a single organism. As we saw in Chapter 5, natural selection operates at the level of the individual because it is the individual that must survive and reproduce.

The second level of complexity is a *population*. A **population** is composed of all individuals that belong to the same species and live in a given area at a particular time. Evolution occurs at the level of the population. Scientists who study populations are also interested in the factors that cause the number of individuals to increase or decrease. As we saw in Chapter 1, the boundaries of a population are rarely clear and may be set arbitrarily by scientists. For example, depending on what we want to learn, we might study the entire population of white-tailed deer in North America, or we might focus on the deer that live within a single state, or even within a single forest.

The third level of complexity is the *community*. A **community** incorporates all of the populations of organisms within a given area. Like those of a population, the boundaries of a community may be defined by the state or federal agency responsible for managing it. Scientists who study communities are generally interested in how species interact with one another. In Chapter 4, we saw that terrestrial communities can be grouped into biomes that contain plants with similar

Population The individuals that belong to the same species and live in a given area at a particular time.

Community All of the populations of organisms within a given area.

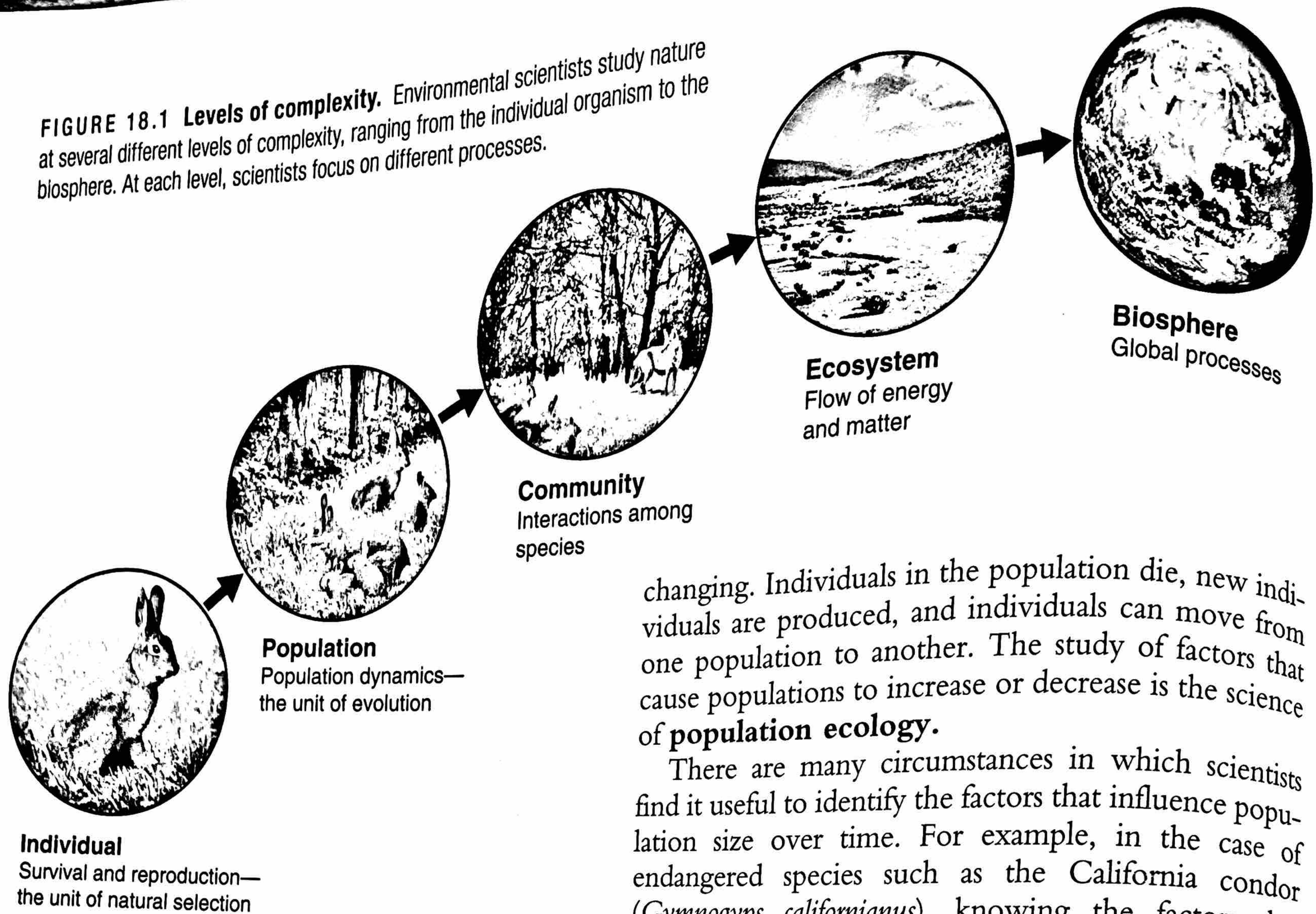

FIGURE 18.1 Levels of complexity. Environmental scientists study nature at several different levels of complexity, ranging from the individual organism to the biosphere. At each level, scientists focus on different processes.

growth forms. However, the actual composition of tree species varies from community to community. While the temperate seasonal forests of the eastern United States and Europe experience similar patterns of temperature and precipitation, they contain different tree species.

Communities exist within an ecosystem, which consists of all of the biotic and abiotic components in a particular location. Ecosystem ecologists study flows of energy and matter, such as the cycling of nutrients through the system.

The largest and most complex system environmental scientists study is the biosphere, which incorporates all of Earth's ecosystems. Scientists who study the biosphere are interested in the movement of air, water, and heat around the globe.

Populations have distinctive characteristics

When we study nature at the level of the population, one of the first things that becomes apparent is that populations are dynamic—that is, they are constantly changing. Individuals in the population die, new individuals are produced, and individuals can move from one population to another. The study of factors that cause populations to increase or decrease is the science of **population ecology**.

There are many circumstances in which scientists find it useful to identify the factors that influence population size over time. For example, in the case of endangered species such as the California condor (*Gymnogyps californianus*), knowing the factors that affect its population size has helped us to implement measures that improve its survival and reproduction. Similarly, knowing the factors that influence the population size of a pest species can help us control it. For instance, population ecologists are currently studying the emerald ash borer (*Agrilus planipennis*), an insect from Asia that was accidentally introduced to the American Midwest and is causing the widespread death of ash trees. Once we understand the population ecology of this destructive insect, we can begin to explore and develop strategies to control or eradicate it.

To understand how populations change over time, we must first examine the basic characteristics of populations. These characteristics are *size, density, distribution, sex ratio,* and *age structure*.

Population ecology The study of factors that cause populations to increase or decrease.

Population size (*N*) The total number of individuals within a defined area at a given time.

Population Size

Population size (*N*) is the total number of individuals within a defined area at a given time. For example, the California condor once ranged throughout California and the southwestern United States. Over the past 2 centuries, however, a combination of poaching, poisoning, and accidents (such as flying into electric power lines) greatly reduced the population's size. By 1987, only 22 birds remained in the wild. Scientists realized that the species was nearing extinction and decided to capture all the wild birds and start a captive breeding program in zoos. As a result of these captive breeding programs and other conservation efforts, the condor population size had increased to more than 437 birds by 2014.

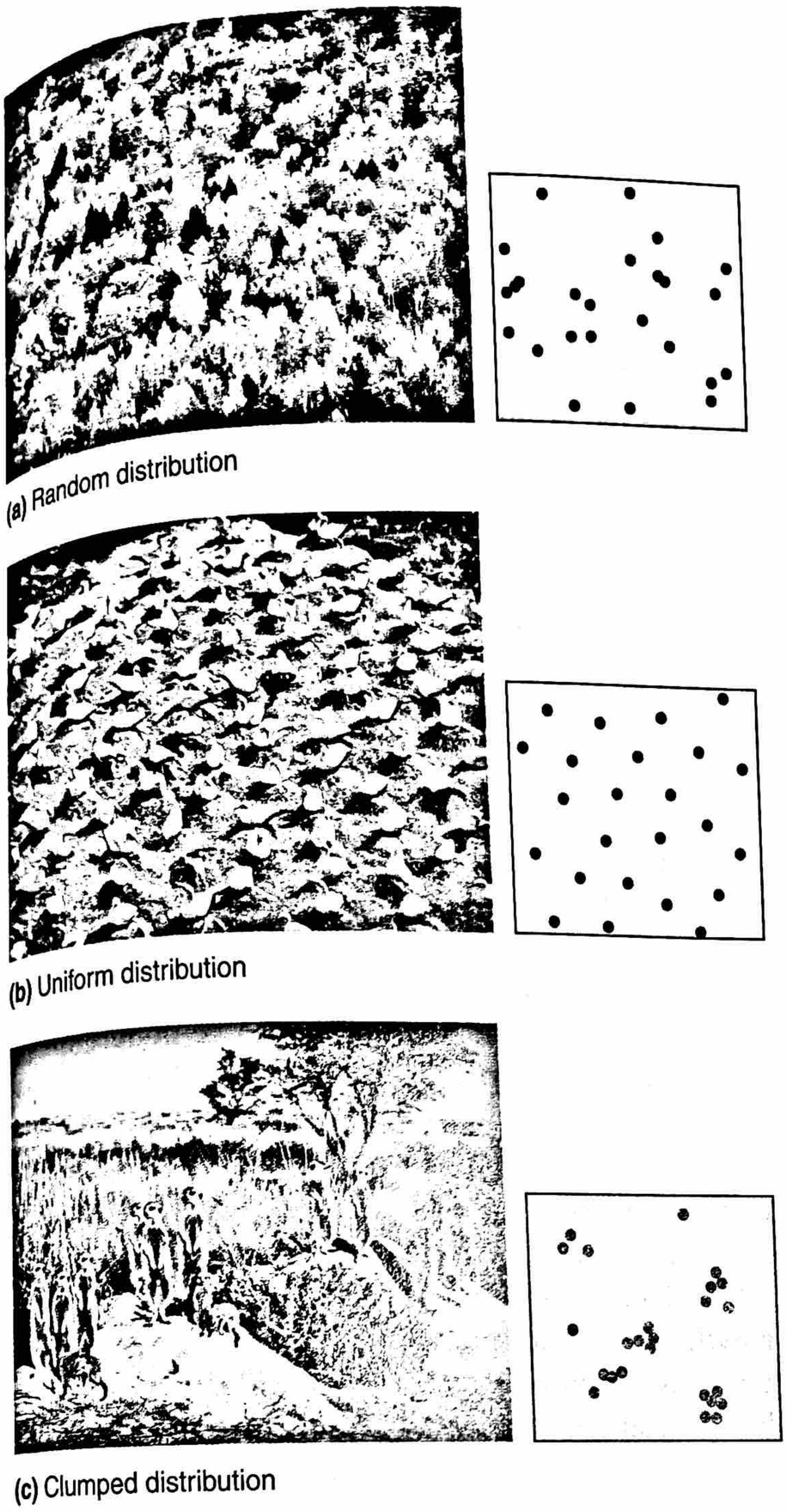

FIGURE 18.2 Population distributions. Populations in nature distribute themselves in three ways. (a) Many of the tree species in this New England forest are randomly distributed, with no apparent pattern in the locations of individuals. (b) Territorial nesting birds, such as these Australasian gannets (Morus serrator), exhibit a uniform distribution, in which all individuals maintain a similar distance from one another. (c) Many pairs of eyes are better than one at detecting approaching predators. The clumped distribution of these meerkats (*Suricata suricatta*) provides them with extra protection. *(a: David R. Frazier Photolibrary, Inc./Science Source; b: Michael Thompson/Earth Scenes/ Animals Animals; c: Clem Haagner/ARDEA)*

Population Density

Population density is the number of individuals per unit area (or volume, in the case of aquatic organisms) at a given time. Knowing a population's density, in addition to its size, can help scientists estimate whether a species is rare or abundant. For example, the density of coyotes (*Canis latrans*) in some parts of Texas might be only 1 per square kilometer, but in other parts of the state it might be as high as 12 per square kilometer. Scientists also study population density to determine whether a population in a particular location is so dense that it might outstrip its food supply.

Population density can be a particularly useful measure for wildlife managers who must set hunting or fishing limits on a species. For example, managers may divide the entire population of an animal species that is hunted or fished into management zones. Management zones may be designated political areas, such as counties, or areas with natural boundaries, such as the major water bodies in a state. Wildlife managers might offer more hunting or fishing permits for zones with a high-density population and fewer permits for zones with a low-density population.

Population Distribution

In addition to population size and density, population ecologists are interested in how a population occupies space. **Population distribution** is a description of how individuals are distributed with respect to one another. FIGURE 18.2 shows three types of population distributions. In some populations, such as a population of trees in a natural forest, the distribution of individuals is *random* (Figure 18.2a). In other words, there is no pattern to the locations where the individual trees grow.

In other populations, such as a population of trees in a plantation, the distribution of individuals is uniform, or evenly spaced (Figure 18.2b). Uniform distributions are common among territorial animals, such as nesting birds that defend areas of similar sizes around their nests. Uniform distributions are also observed among plants that produce toxic chemicals to prevent other plants of the same species from growing close to them.

In still other populations, the distribution of individuals is *clumped* (Figure 18.2c). Clumped distributions, which are common among schooling fish, flocking birds, and herding mammals, are often observed when living in large groups provides enhanced feeding opportunities or protection from predators.

Population Sex Ratio

The **sex ratio** of a population is the ratio of males to females. In most sexually reproducing species, the sex ratio is usually close to 50:50, although sex ratios can be far from equal in some species. In fig wasps, for example, there may be as many as 20 females for every male. Because the number of offspring produced is

Population density The number of individuals per unit area at a given time.

Population distribution A description of how individuals are distributed with respect to one another.

Sex ratio The ratio of males to females in a population.

primarily a function of how many females there are in the population, knowing a population's sex ratio helps scientists estimate the number of offspring a population will produce in the next generation.

Population Age Structure

Many populations are composed of individuals of varying ages. A population's **age structure** describes how many individuals fit into particular age categories. Knowing a population's age structure helps ecologists predict how rapidly a population can grow. For instance, a population with a large proportion of old individuals no longer capable of reproducing, or with a large proportion of individuals too young to reproduce, will produce far fewer offspring than a population that has a large proportion of individuals of reproductive age.

Population size is affected by density-dependent and density-independent factors

Factors that influence population size can be classified as *density dependent* or *density independent*. We will look at each type in turn.

Density-dependent Factors

In 1932, Russian biologist Georgii Gause conducted a set of experiments that demonstrated that food supply can control population growth. Gause monitored population growth in two species of *Paramecium* (a type of single-celled aquatic organism) living under ideal conditions in test tubes. Each day he added a constant amount of food. As the graph in **FIGURE 18.3a** shows, both species of *Paramecium* initially experienced rapid population growth, but over time the rate of growth began to slow. Eventually, the two population sizes reached a plateau and remained there for the rest of the experiment.

Gause suspected that *Paramecium* population growth was limited by food supply. To test this hypothesis, he conducted a second experiment in which he doubled the amount of food he added to the test tubes. Again, both species of *Paramecium* experienced rapid population growth early in the experiment, and the rate of growth, again, slowed over time. However, as Figure 18.3b shows, their maximum population sizes were approximately double those observed in the first experiment.

Gause's results confirmed that food is a *limiting resource* for *Paramecium*. A **limiting resource** is a resource that a population cannot live without and that occurs in quantities lower than the population would require to increase in size. If a limiting resource decreases, so does the size of a population that depends on it. For terrestrial plant populations, water and nutrients such as nitrogen and phosphorus are common limiting resources. For animal populations, food, water, and nest sites are common limiting resources.

Factors such as food that influence an individual's probability of survival and its amount of reproduction in a manner that depends on the size of the population are called **density-dependent factors.** For example, because a smaller population requires less total food, food scarcity will have little or no effect on the survival and reproduction of individuals in a small population but it will have large negative effects on a large population.

In Gause's *Paramecium* experiments, population growth slowed as population size increased because there was a limit to how many individuals the food supply could sustain. This limit to the number of individuals that can exist in a population is called the **carrying capacity** of the environment and is denoted as ***K*.** Knowing the carrying capacity for a species and its limiting resource helps us predict how many individuals an environment can sustain.

Density-independent Factors

Whereas density-dependent factors affect an individual's probability of survival and amount of reproduction differently depending on whether the population is large or small, **density-independent factors** have the same effect on an individual's probability of survival and amount of reproduction regardless of the population size. A tornado, for example, can uproot and kill a large number of trees in an area. However, a given tree's probability of being killed does not depend on whether it resides in a forest with a high or low density of other trees. Other density-independent factors include hurricanes, floods, fires, volcanic eruptions, and other climatic events. An individual's likelihood of mortality increases during such an event regardless of whether the population happens to be at a low or high density.

Age structure A description of how many individuals fit into particular age categories in a population.

Limiting resource A resource that a population cannot live without and that occurs in quantities lower than the population would require to increase in size.

Density-dependent factor A factor that influences an individual's probability of survival and reproduction in a manner that depends on the size of the population.

Carrying capacity (*K*) The limit of how many individuals in a population the environment can sustain.

Density-independent factor A factor that has the same effect on an individual's probability of survival and the amount of reproduction at any population size.

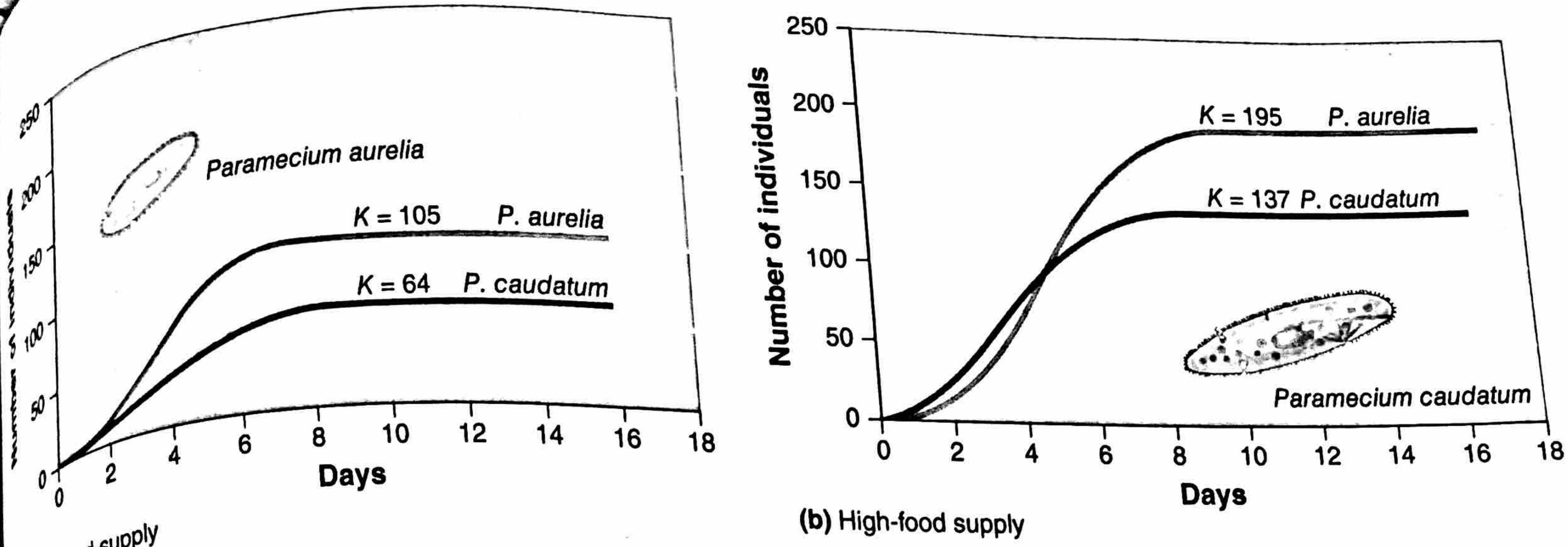

FIGURE 18.3 Gause's experiments. (a) Under low-food conditions, the population sizes of two species of *Paramecium* initially increased rapidly, but then leveled off as their food supply became limiting. (b) When twice as much food was provided, both species attained population sizes that were nearly twice as large, but they again leveled off. *(Data from Gause, 1932)*

Bird populations are often regulated by density-independent factors. For example, in the United Kingdom, a particularly cold winter can freeze the surfaces of ponds, making amphibians and fish inaccessible to wading birds such as herons. With their food supply no longer available, herons would have an increased risk of starving to death, regardless of whether the heron population is at a low or a high density.

module

18

REVIEW

In this module, we learned that nature exists at a series of different levels of complexity, which include individuals, populations, communities, and ecosystems. We then examined the level of the population and observed that populations possess a number of characteristics that can be used to describe them, including their abundance and distribution. Finally, we discussed how density-dependent factors can regulate populations more strongly as populations grow whereas density-independent factors can regulate populations at any population size. In the next module, we will see how scientists use mathematical models of populations to obtain insights into how populations change in abundance over time.

Module 18 AP® Review Questions

1. Which is the correct order of ecological levels from basic to complex?
   (a) Individual, population, ecosystem, biosphere, community
   (b) Individual, community, ecosystem, population, biosphere
   (c) Individual, population, community, ecosystem, biosphere
   (d) Ecosystem, biosphere, community, population, individual
   (e) Individual, population, community, biosphere, ecosystem

2. Population distribution is
   (a) often clumped in response to predation.
   (b) used by wildlife managers when regulating hunting and fishing.
   (c) measured relative to other species.
   (d) uniform in most tree species.
   (e) important when estimating the number of offspring expected.