

# 53

## Population Ecology



▲ **Figure 53.1** What causes a sheep population to fluctuate in size?

### KEY CONCEPTS

- 53.1** Dynamic biological processes influence population density, dispersion, and demographics
- 53.2** The exponential model describes population growth in an idealized, unlimited environment
- 53.3** The logistic model describes how a population grows more slowly as it nears its carrying capacity
- 53.4** Life history traits are products of natural selection
- 53.5** Many factors that regulate population growth are density dependent
- 53.6** The human population is no longer growing exponentially but is still increasing rapidly

### OVERVIEW

## Counting Sheep

On the rugged Scottish island of Hirta, ecologists have been studying a population of Soay sheep for more than 50 years (**Figure 53.1**). What makes these animals worth studying for such a long time? Soay sheep are a rare and ancient breed, the closest living relative of the domesticated sheep that lived in Europe thousands of years ago. To help preserve the breed, conservationists captured sheep in 1932 on Soay Island, at the time the animals' only home, and released them on nearby Hirta. There, the sheep became valuable for a second reason: They provided an ideal opportunity to study how an isolated population of animals changes in size when food is plentiful and predators are absent. Surprisingly, ecologists found that the number of sheep on Hirta swung dramatically under these conditions, sometimes changing by more than 50% from one year to the next.

Why do populations of some species fluctuate greatly while populations of other species do not? To answer this question, we turn to the field of population ecology, the study of populations in relation to their environment. Population ecology explores how biotic and abiotic factors influence the density, distribution, size, and age structure of populations.

Our earlier study of populations in Chapter 23 emphasized the relationship between population genetics—the structure and dynamics of gene pools—and evolution. Populations evolve as natural selection acts on heritable variations among individuals, changing the frequencies of alleles and traits over time. Evolution remains a central theme as we now view populations in the context of ecology.

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

### CONCEPT 53.1

## Dynamic biological processes influence population density, dispersion, and demographics

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

Populations are often described by their boundaries and size (the number of individuals living within those boundaries). Ecologists usually begin investigating a population by defining boundaries appropriate to the organism under study

and to the questions being asked. A population's boundaries may be natural ones, as in the case of Hirta Island and its Soay sheep, or they may be arbitrarily defined by an investigator—for example, a specific county in Minnesota for a study of oak trees.

## Density and Dispersion

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

### Density: A Dynamic Perspective

In rare cases, population size and density can be determined by counting all individuals within the boundaries of the population. We could count all the Soay sheep on Hirta Island or all the sea stars in a tide pool, for instance. Large mammals that live in herds, such as buffalo or elephants, can sometimes be counted accurately from airplanes. In most cases, however, it is impractical or impossible to count all individuals in a population. Instead, ecologists use a variety of sampling techniques to estimate densities and total population sizes. For example, they might count the number of oak trees in several randomly located 100 × 100 m plots, calculate the average density in the plots, and then extend the estimate to the population size in the entire area. Such estimates are most accurate when there are many sample plots and when the habitat is fairly homogeneous. In other cases, instead of counting single organisms, population ecologists estimate density from an indicator of population size, such as the number of nests, burrows, tracks, or fecal droppings. Ecologists also use the **mark-recapture method** to estimate the size of wildlife populations (Figure 53.2).

Density is not a static property but changes as individuals are added to or removed from a population (Figure 53.3).

▼ Figure 53.2

## RESEARCH METHOD

### Determining Population Size Using the Mark-Recapture Method

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

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

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

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

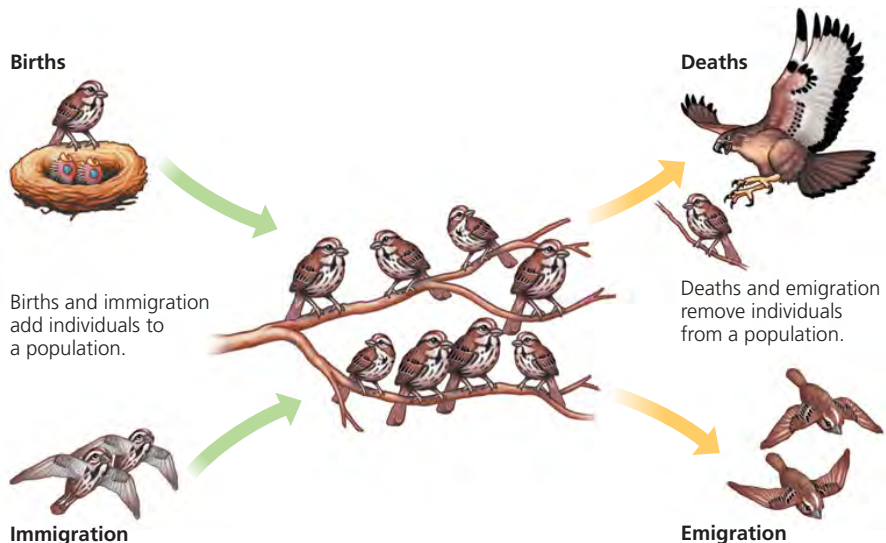
The method assumes that marked and unmarked individuals have the same probability of being captured or sampled, that the marked organisms have mixed completely back into the population, and that no individuals are born, die, immigrate, or emigrate during the resampling interval.

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

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



Hector's dolphins



▲ Figure 53.3 Population dynamics.

Additions occur through birth (which we define here to include all forms of reproduction) and **immigration**, the influx of new individuals from other areas. The factors that remove individuals from a population are death (mortality) and **emigration**, the movement of individuals out of a population and into other locations

While birth and death rates influence the density of all populations, immigration and emigration also alter the density of many populations. Long-term studies of Belding's ground squirrels (*Spermophilus beldingi*) in the vicinity of Tioga Pass, in the Sierra Nevada of California, showed that some of the squirrels moved nearly 2 km from where they were born. This long-distance movement made them immigrants to other populations. In fact, immigrants made up 1–8% of the males and 0.7–6% of the females in the study population. Although these percentages may seem small, such immigration is a meaningful biological exchange between populations over time.

### Patterns of Dispersion

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

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

A *uniform*, or evenly spaced, pattern of dispersion may result from direct interactions between individuals in the population. Some plants secrete chemicals that inhibit the germination and growth of nearby individuals that could compete for resources. Animals often exhibit uniform dispersion as a result of antagonistic social interactions, such as **territoriality**—the defense of a bounded physical space against encroachment by other individuals (Figure 53.4b). Uniform patterns are rarer than clumped patterns.

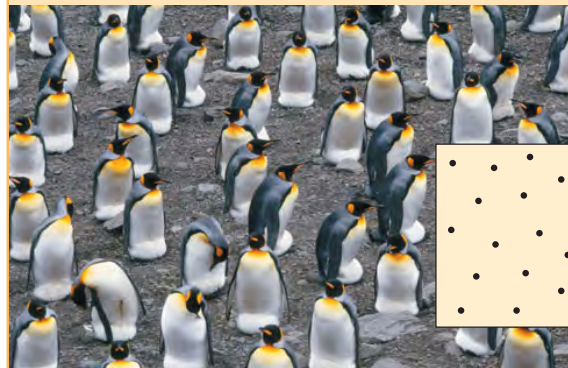
▼ **Figure 53.4** Patterns of dispersion within a population's geographic range.

(a) Clumped



Many animals, such as these sea stars, group together where food is abundant.

(b) Uniform



Birds nesting on small islands, such as these king penguins in the Falkland Islands, near the southern tip of South America, often exhibit uniform spacing, maintained by aggressive interactions between neighbors.

(c) Random



Many plants, such as these dandelions, grow from windblown seeds that land at random and later germinate.

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

In *random* dispersion (unpredictable spacing), the position of each individual in a population is independent of other individuals. This pattern occurs in the absence of strong attractions or repulsions among individuals or where key physical or chemical factors are relatively constant across the study area. Plants established by windblown seeds, such as dandelions, may be randomly distributed in a fairly uniform habitat (**Figure 53.4c**). Random patterns are not as common in nature as one might expect; most populations show at least a tendency toward a clumped distribution.

## Demographics

The factors that influence population density and dispersion patterns—ecological needs of a species, structure of the environment, and interactions among individuals within the population—also influence other characteristics of populations. **Demography** is the study of the vital statistics of populations and how they change over time. Of particular interest to demographers are birth rates and death rates. A useful way to summarize some of the vital statistics of a population is to make a life table.

### Life Tables

About a century ago, when life insurance first became available, insurance companies began to estimate how long, on average, people of a given age could be expected to live. To do this, demographers developed **life tables**, age-specific summaries of

the survival pattern of a population. Population ecologists adapted this approach to the study of populations in general.

The best way to construct a life table is to follow the fate of a **cohort**, a group of individuals of the same age, from birth until all of the individuals are dead. To build the life table, we need to determine the number of individuals that die in each age-group and to calculate the proportion of the cohort surviving from one age class to the next. Studies of the Belding's ground squirrels near Tioga Pass produced the life table in **Table 53.1**. The table reveals many things about the population. For instance, the third and eighth columns list, respectively, the proportions of females and males in the cohort that are still alive at each age. A comparison of the fifth and tenth columns reveals that males have higher death rates than females.

### Survivorship Curves

A graphic method of representing some of the data in a life table is a **survivorship curve**, a plot of the proportion or numbers in a cohort still alive at each age. As an example, let's use the data for Belding's ground squirrels in Table 53.1 to draw a survivorship curve for this population. Generally, a survivorship curve begins with a cohort of a convenient size—say, 1,000 individuals. To obtain the other points in the curve for the Belding's ground squirrel population, we multiply the proportion alive at the start of each year (the third and eighth columns of Table 53.1) by 1,000 (the hypothetical beginning cohort). The result is the number alive at the start

**Table 53.1** Life Table for Belding's Ground Squirrels (*Spermophilus beldingi*) at Tioga Pass, in the Sierra Nevada of California\*

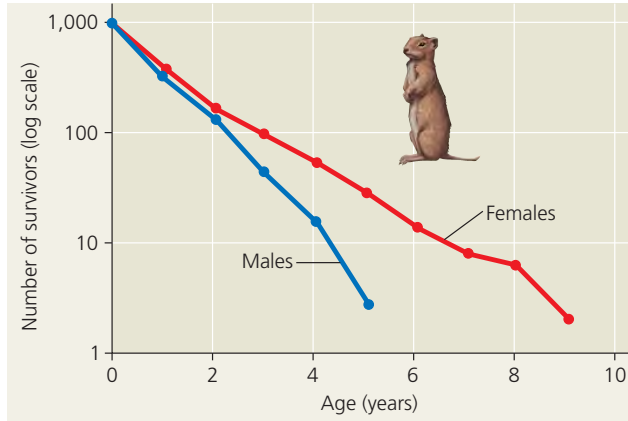
| Age (years) | FEMALES                       |                                   |                              |                         |  | MALES                         |                                   |                              |                         |  |
|-------------|-------------------------------|-----------------------------------|------------------------------|-------------------------|--|-------------------------------|-----------------------------------|------------------------------|-------------------------|--|
|             | Number Alive at Start of Year | Proportion Alive at Start of Year | Number of Deaths During Year | Death Rate <sup>†</sup> | Average Additional Life Expectancy (years) | Number Alive at Start of Year | Proportion Alive at Start of Year | Number of Deaths During Year | Death Rate <sup>†</sup> | Average Additional Life Expectancy (years) |
| 0–1         | 337                           | 1.000                             | 207                          | 0.61                    | 1.33                                       | 349                           | 1.000                             | 227                          | 0.65                    | 1.07                                       |
| 1–2         | 252 <sup>‡</sup>              | 0.386                             | 125                          | 0.50                    | 1.56                                       | 248 <sup>‡</sup>              | 0.350                             | 140                          | 0.56                    | 1.12                                       |
| 2–3         | 127                           | 0.197                             | 60                           | 0.47                    | 1.60                                       | 108                           | 0.152                             | 74                           | 0.69                    | 0.93                                       |
| 3–4         | 67                            | 0.106                             | 32                           | 0.48                    | 1.59                                       | 34                            | 0.048                             | 23                           | 0.68                    | 0.89                                       |
| 4–5         | 35                            | 0.054                             | 16                           | 0.46                    | 1.59                                       | 11                            | 0.015                             | 9                            | 0.82                    | 0.68                                       |
| 5–6         | 19                            | 0.029                             | 10                           | 0.53                    | 1.50                                       | 2                             | 0.003                             | 2                            | 1.00                    | 0.50                                       |
| 6–7         | 9                             | 0.014                             | 4                            | 0.44                    | 1.61                                       | 0                             |                                   |                              |                         |  |
| 7–8         | 5                             | 0.008                             | 1                            | 0.20                    | 1.50                                       |                               |                                   |                              |                         |  |
| 8–9         | 4                             | 0.006                             | 3                            | 0.75                    | 0.75                                       |                               |                                   |                              |                         |  |
| 9–10        | 1                             | 0.002                             | 1                            | 1.00                    | 0.50                                       |                               |                                   |                              |                         |  |

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

\*Females and males have different mortality schedules, so they are tallied separately.

<sup>†</sup>The death rate is the proportion of individuals dying during the specific time interval.

<sup>‡</sup>Includes 122 females and 126 males first captured as 1-year-olds and therefore not included in the count of squirrels age 0–1.

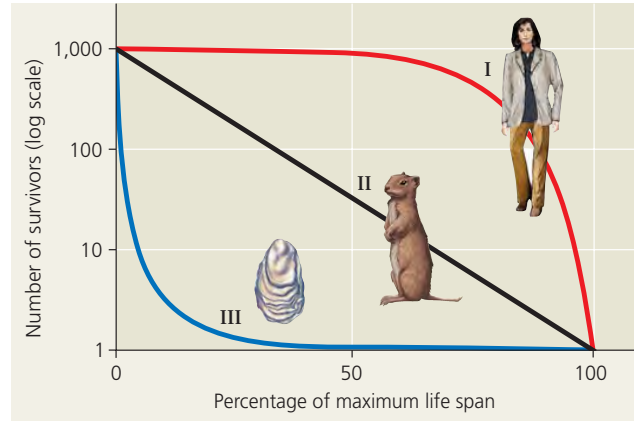


▲ **Figure 53.5 Survivorship curves for male and female Belding's ground squirrels.** The logarithmic scale on the y-axis allows the number of survivors to be visible across the entire range (2–1,000 individuals) on the graph.

of each year. Plotting these numbers versus age for female and male Belding's ground squirrels yields **Figure 53.5**. The relatively straight lines of the plots indicate relatively constant rates of death; however, male Belding's ground squirrels have a lower survival rate than females.

Figure 53.5 represents just one of many patterns of survivorship exhibited by natural populations. Though diverse, survivorship curves can be classified into three general types (**Figure 53.6**). A Type I curve is flat at the start, reflecting low death rates during early and middle life, and then drops steeply as death rates increase among older age-groups. Many large mammals, including humans, that produce few offspring but provide them with good care exhibit this kind of curve. In contrast, a Type III curve drops sharply at the start, reflecting very high death rates for the young, but flattens out as death rates decline for those few individuals that survive the early period of die-off. This type of curve is usually associated with organisms that produce very large numbers of offspring but provide little or no care, such as long-lived plants, many fishes, and most marine invertebrates. An oyster, for example, may release millions of eggs, but most larvae hatched from fertilized eggs die from predation or other causes. Those few offspring that survive long enough to attach to a suitable substrate and begin growing a hard shell tend to survive for a relatively long time. Type II curves are intermediate, with a constant death rate over the organism's life span. This kind of survivorship occurs in Belding's ground squirrels (see **Figure 53.5**) and some other rodents, various invertebrates, some lizards, and some annual plants.

Many species fall somewhere between these basic types of survivorship or show more complex patterns. In birds, mortality is often high among the youngest individuals (as in a Type III curve) but fairly constant among adults (as in a Type



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

II curve). Some invertebrates, such as crabs, may show a "stair-stepped" curve, with brief periods of increased mortality during molts, followed by periods of lower mortality when their protective exoskeleton is hard.

In populations not experiencing immigration or emigration, survivorship is one of the two key factors determining changes in population size. The other key factor determining population trends is reproductive rate.

### Reproductive Rates

Demographers who study sexually reproducing species generally ignore the males and concentrate on the females in a population because only females produce offspring. Therefore, demographers view populations in terms of females giving rise to new females. The simplest way to describe the reproductive pattern of a population is to ask how reproductive output varies with the ages of females.

A **reproductive table**, or fertility schedule, is an age-specific summary of the reproductive rates in a population. It is constructed by measuring the reproductive output of a cohort from birth until death. For a sexual species, the reproductive table tallies the number of female offspring produced by each age-group. **Table 53.2** illustrates a reproductive table for Belding's ground squirrels. Reproductive output for sexual organisms such as birds and mammals is the product of the proportion of females of a given age that are breeding and the number of female offspring of those breeding females. Multiplying these numbers gives the average number of female offspring for each female in a given age-group (the last column in **Table 53.2**). For Belding's ground squirrels, which begin to reproduce at age 1 year, reproductive output rises to a peak at 4 years of age and then falls off in older females.

**Table 53.2** Reproductive Table for Belding's Ground Squirrels at Tioga Pass

| Age (years) | Proportion of Females Weaning a Litter | Mean Size of Litters (Males + Females) | Mean Number of Females in a Litter | Average Number of Female Offspring* |
|-------------|--|--|------------------------------------|-------------------------------------|
| 0-1         | 0.00                                   | 0.00                                   | 0.00                               | 0.00                                |
| 1-2         | 0.65                                   | 3.30                                   | 1.65                               | 1.07                                |
| 2-3         | 0.92                                   | 4.05                                   | 2.03                               | 1.87                                |
| 3-4         | 0.90                                   | 4.90                                   | 2.45                               | 2.21                                |
| 4-5         | 0.95                                   | 5.45                                   | 2.73                               | 2.59                                |
| 5-6         | 1.00                                   | 4.15                                   | 2.08                               | 2.08                                |
| 6-7         | 1.00                                   | 3.40                                   | 1.70                               | 1.70                                |
| 7-8         | 1.00                                   | 3.85                                   | 1.93                               | 1.93                                |
| 8-9         | 1.00                                   | 3.85                                   | 1.93                               | 1.93                                |
| 9-10        | 1.00                                   | 3.15                                   | 1.58                               | 1.58                                |

Source: P. W. Sherman and M. L. Morton, Demography of Belding's ground squirrel, *Ecology* 65:1617-1628 (1984).  
 \*The average number of female offspring is the proportion weaning a litter multiplied by the mean number of females in a litter.

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

### CONCEPT CHECK 53.1

- DRAW IT** Each female of a particular fish species produces millions of eggs per year. Draw and label the most likely survivorship curve for this species, and explain your choice.
- WHAT IF?** As noted in Figure 53.2, an important assumption of the mark-recapture method is that marked individuals have the same probability of being captured as unmarked individuals. Describe a situation where this assumption might not be valid, and explain how the estimate of population size would be affected.
- MAKE CONNECTIONS** As shown in Figure 51.2a (p. 1119), a male stickleback fish attacks other males that invade its nesting territory. Predict the likely pattern of dispersion for male sticklebacks, and explain your reasoning.

For suggested answers, see Appendix A.

## CONCEPT 53.2

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

Populations of all species have the potential to expand greatly when resources are abundant. To appreciate the potential for population increase, consider a bacterium that can reproduce by fission every 20 minutes under ideal laboratory conditions. There would be 2 bacteria after 20 minutes, 4 after 40 minutes, and 8 after 60 minutes. If reproduction continued at this rate for a day and a half without mortality, there would be enough bacteria to form a layer 30 cm deep over the entire globe. At the other extreme, an elephant may produce only 6 offspring in a 100-year life span. Still, Charles Darwin once estimated that the descendants of a single pair of mating elephants would number 19 million within only 750 years. Darwin's estimate may not have been precisely correct, but such analyses led him to recognize the tremendous capacity for growth in all populations. Although unlimited growth does not occur for long in nature, studying population growth in an ideal, unlimited environment reveals how fast a population is capable of growing and the conditions under which rapid growth might actually occur.

#### Per Capita Rate of Increase

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

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

For simplicity here, we will ignore the effects of immigration and emigration, although a more complex formulation would certainly include these factors. We can also use mathematical notation to express this simplified relationship more concisely. If  $N$  represents population size and  $t$  represents time, then  $\Delta N$  is the change in population size and  $\Delta t$  is the time interval (appropriate to the life span or generation time of the species) over which we are evaluating population growth. (The Greek letter delta,  $\Delta$ , indicates change, such as change in time.) Using  $B$  for the number of births in the population

during the time interval and  $D$  for the number of deaths, we can rewrite the verbal equation:

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

Next, we can convert this simple model to one in which births and deaths are expressed as the average number of births and deaths per individual (per capita) during the specified time interval. The *per capita birth rate* is the number of offspring produced per unit time by an average member of the population. If, for example, there are 34 births per year in a population of 1,000 individuals, the annual per capita birth rate is  $34/1,000$ , or 0.034. If we know the annual per capita birth rate (symbolized by  $b$ ), we can use the formula  $B = bN$  to calculate the expected number of births per year in a population of any size. For example, if the annual per capita birth rate is 0.034 and the population size is 500,

$$\begin{aligned} B &= bN \\ B &= 0.034 \times 500 \\ B &= 17 \text{ per year} \end{aligned}$$

Similarly, the *per capita death rate* (symbolized by  $m$ , for mortality) allows us to calculate the expected number of deaths per unit time in a population of any size, using the formula  $D = mN$ . If  $m = 0.016$  per year, we would expect 16 deaths per year in a population of 1,000 individuals. For natural populations or those in the laboratory, the per capita birth and death rates can be calculated from estimates of population size and data in life tables and reproductive tables (for example, Tables 53.1 and 53.2).

Now we can revise the population growth equation again, this time using per capita birth and death rates rather than the numbers of births and deaths:

$$\frac{\Delta N}{\Delta t} = bN - mN$$

One final simplification is in order. Population ecologists are most interested in the *difference* between the per capita birth rate and the per capita death rate. This difference is the *per capita rate of increase*, or  $r$ :

$$r = b - m$$

The value of  $r$  indicates whether a given population is growing ( $r > 0$ ) or declining ( $r < 0$ ). **Zero population growth (ZPG)** occurs when the per capita birth and death rates are equal ( $r = 0$ ). Births and deaths still occur in such a population, of course, but they balance each other exactly.

Using the per capita rate of increase, we can now rewrite the equation for change in population size as

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

Remember that this equation is for a discrete, or fixed, time interval (often one year, as in the previous example) and does

not include immigration or emigration. Most ecologists prefer to use differential calculus to express population growth *instantaneously*, as growth rate at a particular instant in time:

$$\frac{dN}{dt} = r_{\text{inst}}N$$

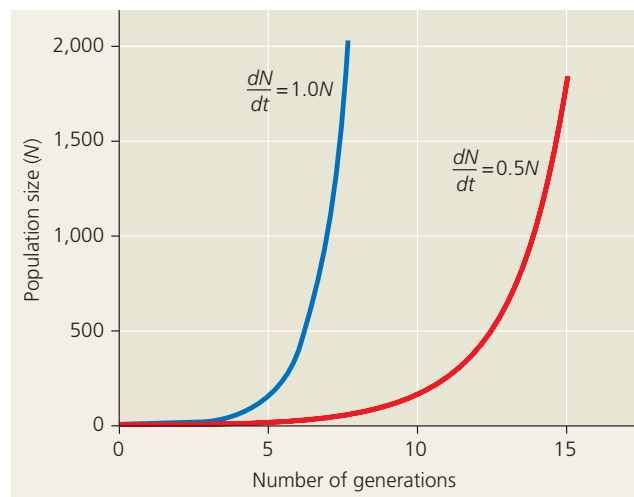
In this case  $r_{\text{inst}}$  is simply the instantaneous per capita rate of increase. If you have not yet studied calculus, don't be intimidated by the form of the last equation; it is similar to the previous one, except that the time intervals  $\Delta t$  are very short and are expressed in the equation as  $dt$ . In fact, as  $\Delta t$  becomes shorter, the discrete  $r$  approaches the instantaneous  $r_{\text{inst}}$  in value.

## Exponential Growth

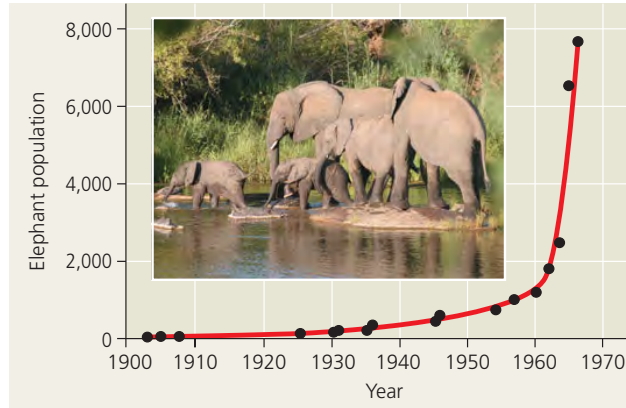
Earlier we described a population whose members all have access to abundant food and are free to reproduce at their physiological capacity. Population increase under these ideal conditions is called **exponential population growth**, also known as geometric population growth. Under these conditions, the per capita rate of increase may assume the maximum rate for the species, denoted as  $r_{\text{max}}$ . The equation for exponential population growth is

$$\frac{dN}{dt} = r_{\text{max}}N$$

The size of a population that is growing exponentially increases at a constant rate, resulting eventually in a J-shaped growth curve when population size is plotted over time (**Figure 53.7**). Although the maximum *rate* of increase is constant, the population accumulates more new individuals per unit of time when it is large than when it is small; thus, the



▲ **Figure 53.7 Population growth predicted by the exponential model.** This graph compares growth in two populations with different values of  $r_{\text{max}}$ . Increasing the value of  $r_{\text{max}}$  from 0.5 to 1.0 increases the rate of rise in population size over time, as reflected by the relative slopes of the curves at any given population size.



▲ **Figure 53.8** Exponential growth in the African elephant population of Kruger National Park, South Africa.

curves in Figure 53.7 get progressively steeper over time. This occurs because population growth depends on  $N$  as well as  $r_{\max}$ , and larger populations experience more births (and deaths) than small ones growing at the same per capita rate. It is also clear from Figure 53.7 that a population with a higher maximum rate of increase ( $dN/dt = 1.0N$ ) will grow faster than one with a lower rate of increase ( $dN/dt = 0.5N$ ).

The J-shaped curve of exponential growth is characteristic of some populations that are introduced into a new environment or whose numbers have been drastically reduced by a catastrophic event and are rebounding. For example, the population of elephants in Kruger National Park, South Africa, grew exponentially for approximately 60 years after they were first protected from hunting (Figure 53.8). The increasingly large number of elephants eventually caused enough damage to vegetation in the park that a collapse in their food supply was likely. To protect other species and the park ecosystem before that happened, park managers began limiting the elephant population by using birth control and exporting elephants to other countries.

### CONCEPT CHECK 53.2

1. Explain why a constant rate of increase ( $r_{\max}$ ) for a population produces a growth graph that is J-shaped.
2. Where is exponential growth by a plant population more likely—in an area where a forest was destroyed by fire or in a mature, undisturbed forest? Why?
3. **WHAT IF?** In 2009, the United States had a population of about 307 million people. If there were 14 births and 8 deaths per 1,000 people, what was the country's net population growth that year (ignoring immigration and emigration, which are substantial)? Do you think the United States is currently experiencing exponential population growth? Explain.

For suggested answers, see Appendix A.

## CONCEPT 53.3

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

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

Crowding and resource limitation can have a profound effect on population growth rate. If individuals cannot obtain sufficient resources to reproduce, the per capita birth rate ( $b$ ) will decline. If they cannot consume enough energy to maintain themselves or if disease or parasitism increases with density, the per capita death rate ( $m$ ) may increase. A decrease in  $b$  or an increase in  $m$  results in a lower per capita rate of increase ( $r$ ).

### The Logistic Growth Model

We can modify our mathematical model to incorporate changes in growth rate as the population size nears the carrying capacity. In the **logistic population growth** model, the per capita rate of increase approaches zero as the carrying capacity is reached.

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

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

When  $N$  is small compared to  $K$ , the term  $(K - N)/K$  is close to 1, and the per capita rate of increase,  $r_{\max}(K - N)/K$ , approaches the maximum rate of increase. But when  $N$  is large and resources are limiting, then  $(K - N)/K$  is close to 0, and the per capita rate of increase is small. When  $N$  equals  $K$ , the population stops



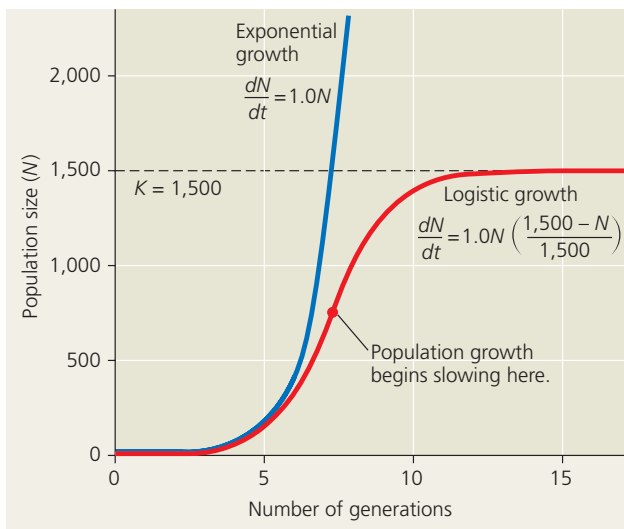
**Table 53.3** Logistic Growth of a Hypothetical Population ( $K = 1,500$ )

| Population Size ( $N$ ) | Maximum Rate of Increase ( $r_{\max}$ ) | $\frac{K - N}{K}$ | Per Capita Rate of Increase: $r_{\max} \left( \frac{K - N}{K} \right)$ | Population Growth Rate:* $r_{\max} N \left( \frac{K - N}{K} \right)$ |
|-------------------------|---|-------------------|--|--|
| 25                      | 1.0                                     | 0.98              | 0.98   | +25  |
| 100                     | 1.0                                     | 0.93              | 0.93   | +93  |
| 250                     | 1.0                                     | 0.83              | 0.83   | +208   |
| 500                     | 1.0                                     | 0.67              | 0.67   | +333   |
| 750                     | 1.0                                     | 0.50              | 0.50   | +375   |
| 1,000                   | 1.0                                     | 0.33              | 0.33   | +333   |
| 1,500                   | 1.0                                     | 0.00              | 0.00   | 0  |

\*Rounded to the nearest whole number.

growing. **Table 53.3** shows calculations of population growth rate for a hypothetical population growing according to the logistic model, with  $r_{\max} = 1.0$  per individual per year. Notice that the overall population growth rate is highest, +375 individuals per year, when the population size is 750, or half the carrying capacity. At a population size of 750, the per capita rate of increase remains relatively high (one-half the maximum rate), but there are more reproducing individuals ( $N$ ) in the population than at lower population sizes.

As shown in **Figure 53.9**, the logistic model of population growth produces a sigmoid (S-shaped) growth curve when  $N$



**▲ Figure 53.9** Population growth predicted by the logistic model. The rate of population growth decreases as population size ( $N$ ) approaches the carrying capacity ( $K$ ) of the environment. The red line shows logistic growth in a population where  $r_{\max} = 1.0$  and  $K = 1,500$  individuals. For comparison, the blue line illustrates a population continuing to grow exponentially with the same  $r_{\max}$ .

is plotted over time (the red line). New individuals are added to the population most rapidly at intermediate population sizes, when there is not only a breeding population of substantial size, but also lots of available space and other resources in the environment. The population growth rate decreases dramatically as  $N$  approaches  $K$ .

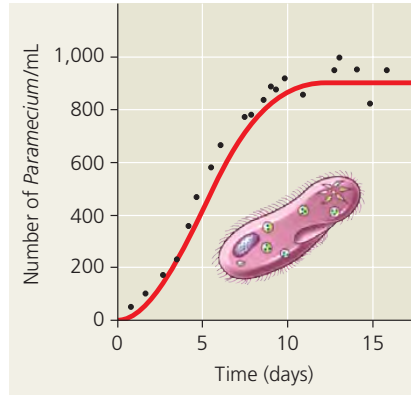
Note that we haven't said anything yet about *why* the population growth rate decreases as  $N$  approaches  $K$ . For a population's growth rate to decrease, the birth rate  $b$  must decrease, the death rate  $m$  must increase, or both. Later in the chapter, we will consider some of the factors affecting these rates, including the presence of disease, predation, and limited amounts of food and other resources.

## The Logistic Model and Real Populations

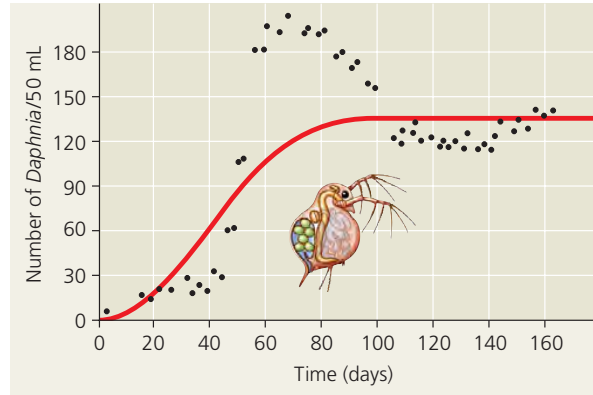
The growth of laboratory populations of some small animals, such as beetles and crustaceans, and of some microorganisms, such as bacteria, *Paramecium*, and yeasts, fits an S-shaped curve fairly well under conditions of limited resources (**Figure 53.10a**). These populations are grown in a constant environment lacking predators and competing species that may reduce growth of the populations, conditions that rarely occur in nature.

Some of the basic assumptions built into the logistic model clearly do not apply to all populations. The logistic model assumes that populations adjust instantaneously to growth and approach carrying capacity smoothly. In reality, there is often a delay before the negative effects of an increasing population are realized. If food becomes limiting for a population, for instance, reproduction will decline eventually, but females may use their energy reserves to continue reproducing for a short time. This may cause the population to overshoot its carrying capacity temporarily, as shown for the water fleas in **Figure 53.10b**. If the population then drops below carrying capacity, there will be a delay in population growth until the increased number of offspring are actually born. Still other populations fluctuate greatly, making it difficult even to define carrying capacity. We will examine some possible reasons for such fluctuations later in the chapter.

In addition to the assumption that populations adjust instantaneously to growth, the logistic model is based on another assumption—that regardless of population density, each individual added to a population has the same negative effect on population growth rate. However, some populations show an *Allee effect* (named after W. C. Allee, of the University of Chicago, who first described it), in which individuals may have a more difficult time surviving or reproducing if the population size is too small. For example, a single plant may be damaged by excessive wind if it is standing alone, but it would be protected in a clump of individuals.



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



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

◀ **Figure 53.10** How well do these populations fit the logistic growth model?

The logistic model is a useful starting point for thinking about how populations grow and for constructing more complex models. The model is also important in conservation biology for predicting how rapidly a particular population might increase in numbers after it has been reduced to a small size and for estimating sustainable harvest rates for wildlife populations. Conservation biologists can use the model to estimate the critical size below which populations of certain organisms, such as the northern subspecies of the white rhinoceros (*Ceratotherium simum*), may become extinct (Figure 53.11). Like any useful starting hypothesis, the logistic model has stimulated research that has led to a better understanding of the subject: in this case, the factors affecting population growth.



▲ **Figure 53.11** White rhinoceros mother and calf. The two animals pictured here are members of the southern subspecies, which has a population of more than 10,000 individuals. The northern subspecies is critically endangered, with a population of fewer than 15 known individuals.

### CONCEPT CHECK 53.3

1. Explain why a population that fits the logistic growth model increases more rapidly at intermediate size than at relatively small and large sizes.
2. **WHAT IF?** Add rows to Table 53.3 for three cases where  $N > K$ , specifically,  $N = 1,600$ ,  $1,750$ , and  $2,000$ . What is the population growth rate in each case? In which portion of Figure 53.10b is the *Daphnia* population changing in a way that corresponds to the values you calculated?
3. **MAKE CONNECTIONS** Concept 19.3, pp. 390–393, discusses viruses that are pathogens of animals and plants. How might the presence of such pathogens alter the carrying capacity of a population? Explain.

For suggested answers, see Appendix A.

### CONCEPT 53.4

#### Life history traits are products of natural selection

**EVOLUTION** Natural selection favors traits that improve an organism's chances of survival and reproductive success. In every species, there are trade-offs between survival and reproductive traits such as frequency of reproduction, number of offspring (number of seeds produced by plants; litter or clutch size for animals), and investment in parental care. The traits that affect an organism's schedule of reproduction and survival make up its **life history**. A life history entails three main variables: when reproduction begins (the age at first reproduction or age at maturity), how often the organism reproduces, and how many offspring are produced per reproductive episode.

With the important exception of humans, which we will consider later in the chapter, organisms do not choose consciously when to reproduce or how many offspring to have. Rather, organisms' life history traits are evolutionary outcomes reflected in their development, physiology, and behavior.

## Evolution and Life History Diversity

The fundamental idea that evolution accounts for the diversity of life is manifest in a broad range of life histories found in nature. The Pacific salmon, for example, hatches in the headwaters of a stream and then migrates to the open ocean, where it requires one to four years to mature. The salmon eventually returns to the freshwater stream to spawn, producing thousands of eggs in a single reproductive opportunity before it dies. This "one-shot" pattern of big-bang reproduction, or **semelparity** (from the Latin *semel*, once, and *parere*, to beget), also occurs in some plants, such as the agave, or "century plant" (Figure 53.12). Agaves generally grow in arid climates with unpredictable rainfall and poor soils. An agave grows for years, accumulating nutrients in its tissues, until there is an unusually wet year. It then sends up a large flowering stalk, produces seeds, and dies. This life history is an adaptation to the agave's harsh desert environment.

In contrast to semelparity is **iteroparity** (from the Latin *iterare*, to repeat), or repeated reproduction. In iteroparity, organisms produce relatively few but large offspring each time they reproduce, and they provision the offspring better. Some lizards, for example, produce a few large, nutrient-containing eggs annually beginning in their second year of life.

What factors contribute to the evolution of semelparity versus iteroparity? A current hypothesis suggests that there are two critical factors: the survival rate of the offspring and the likelihood that the adult will survive to reproduce again. Where the survival rate of offspring is low, typically in highly variable or unpredictable environments, the prediction is that semelparity will be favored. Adults are also less likely to survive in such environments, so producing large numbers of offspring should increase the probability that at least some of those offspring will survive. Iteroparity may be favored in



◀ **Figure 53.12** An agave (*Agave americana*), an example of big-bang reproduction. The leaves of the plant are visible at the base of the giant flowering stalk, which is produced only at the end of the agave's life.

more dependable environments, where adults are more likely to survive to breed again and where competition for resources may be intense. In such cases, a few relatively large, well-provisioned offspring should have a better chance of surviving until they can reproduce.

Nature abounds with life histories that are intermediate between the two extremes of semelparity and iteroparity. Oak trees and sea urchins, for example, can live a long time but repeatedly produce relatively large numbers of offspring.

## "Trade-offs" and Life Histories

No organism could produce as many offspring as a semelparous species and provision them as well as an iteroparous species. There is a trade-off between reproduction and survival. Figure 53.13 describes a study of European kestrels that demonstrated a survival cost to parents that care for a large

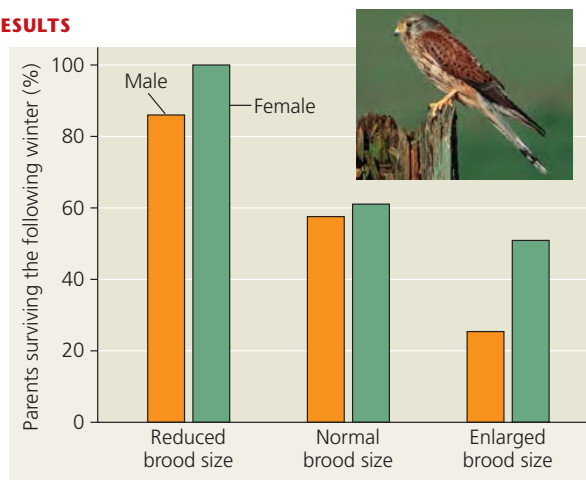
▼ **Figure 53.13**

## INQUIRY

### How does caring for offspring affect parental survival in kestrels?

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

#### RESULTS



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

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

**WHAT IF?** The males of some bird species provide no parental care. If this were true for the European kestrel, how would the experimental results differ from those shown above?

number of young. In another study, in Scotland, researchers found that female red deer that reproduced in a given summer were more likely to die the next winter than were females that did not reproduce.

Selective pressures influence the trade-off between the number and size of offspring. Plants and animals whose young are subject to high mortality rates often produce large numbers of relatively small offspring. Plants that colonize disturbed environments, for example, usually produce many small seeds, only a few of which may reach a suitable habitat. Small size may also increase the chance of seedling establishment by enabling the seeds to be carried longer distances to a broader range of habitats (Figure 53.14a). Animals that suffer high predation rates, such as quail, sardines, and mice, also tend to produce large numbers of offspring.

In other organisms, extra investment on the part of the parent greatly increases the offspring's chances of survival. Walnut and Brazil nut trees provision large seeds with nutrients that help the seedlings become established (Figure 53.14b). Primates generally bear only one or two offspring at a time; parental care and an extended period of learning in the first several years of life are very important to offspring fitness. Such provisioning and extra care can be especially important in habitats with high population densities.

Ecologists have attempted to connect differences in favored traits at different population densities with the logistic growth model discussed in Concept 53.3. Selection for traits that are sensitive to population density and are favored at high densities is known as **K-selection**, or density-dependent selection. In contrast, selection for traits that maximize reproductive success in uncrowded environments (low densities) is called **r-selection**, or density-independent selection. These names follow from the variables of the logistic equation. *K*-selection is said to operate in populations living at a density near the limit imposed by their resources (the carrying capacity, *K*), where competition among individuals is stronger. Mature trees growing in an old-growth forest are an example of *K*-selected organisms. In contrast, *r*-selection is said to maximize *r*, the per capita rate of increase, and occurs in environments in which population densities are well below carrying capacity or individuals face little competition. Such conditions are often found in disturbed habitats. Weeds growing in an abandoned agricultural field are an example of *r*-selected organisms.

The concepts of *K*- and *r*-selection represent two extremes in a range of actual life histories. The framework of *K*- and *r*-selection, grounded in the idea of carrying capacity, has helped ecologists to propose alternative hypotheses of life history evolution. These alternative hypotheses, in turn, have stimulated more thorough study of how factors such as disturbance, stress, and the frequency of opportunities for successful reproduction affect the evolution of life histories. They have also forced ecologists to address the important question we alluded to earlier: *Why* does population growth



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



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

▲ Figure 53.14 Variation in the size of seed crops in plants.

rate decrease as population size approaches carrying capacity? Answering this question is the focus of the next section.

### CONCEPT CHECK 53.4

1. Consider two rivers: One is spring fed and has a constant water volume and temperature year-round; the other drains a desert landscape and floods and dries out at unpredictable intervals. Which river would you predict is more likely to support many species of iteroparous animals? Why?
2. In the fish called the peacock wrasse (*Symphodus tinca*), females disperse some of their eggs widely and lay other eggs in a nest. Only the latter receive parental care. Explain the trade-offs in reproduction that this behavior illustrates.
3. **WHAT IF?** Mice that experience stress such as a food shortage will sometimes abandon their young. Explain how this behavior might have evolved in the context of reproductive trade-offs and life history.

For suggested answers, see Appendix A.

## CONCEPT 53.5

### Many factors that regulate population growth are density dependent

What environmental factors keep populations from growing indefinitely? Why are some populations fairly stable in size, while others, such as the Soay sheep on Hirta Island, are not?

Population regulation is an area of ecology that has many practical applications. Farmers may want to reduce the abundance of insect pests or stop the growth of an invasive weed that is spreading rapidly. Conservation ecologists need to know what environmental factors create favorable feeding or breeding habitats for endangered species, such as the white rhinoceros and the whooping crane. Management programs based on population-regulating factors have helped prevent the extinction of many endangered species.

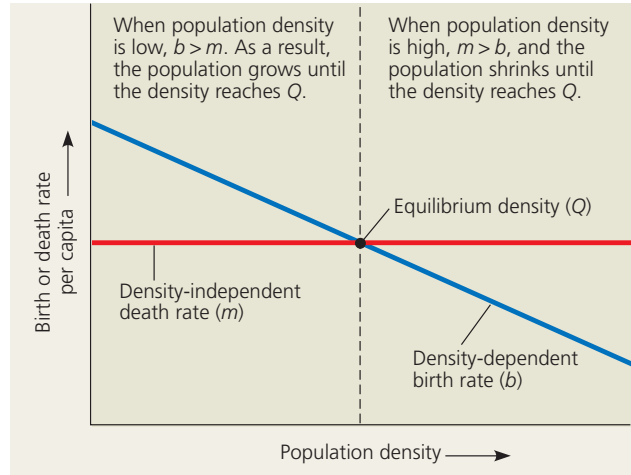
### Population Change and Population Density

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

A birth rate or death rate that does *not* change with population density is said to be **density independent**. In a classic study of population regulation, Andrew Watkinson and John Harper, of the University of Wales, found that the mortality of dune fescue grass (*Vulpia membranacea*) is mainly due to physical factors that kill similar proportions of a local population, regardless of its density. For example, drought stress that arises when the roots of the grass are uncovered by shifting sands is a density-independent factor. In contrast, a death rate that rises as population density rises is said to be **density dependent**, as is a birth rate that falls with rising density. Watkinson and Harper found that reproduction by dune fescue declines as population density increases, in part because water or nutrients become more scarce. Thus, the key factors regulating birth rate in this population are density dependent, while death rate is largely regulated by density-independent factors. **Figure 53.15** shows how the combination of density-dependent reproduction and density-independent mortality can stop population growth, leading to an equilibrium population density in species such as dune fescue.

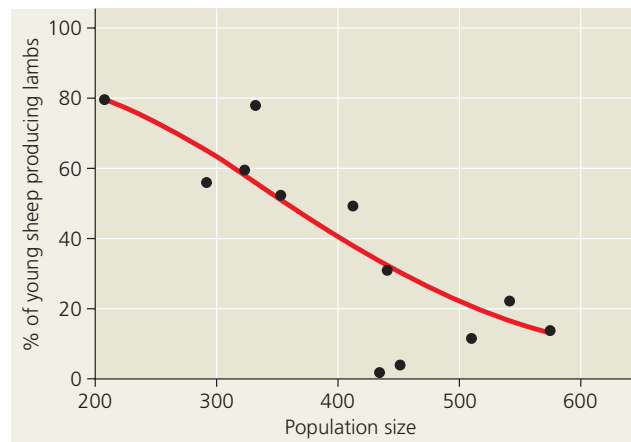
### Mechanisms of Density-Dependent Population Regulation

Biology's unifying theme of *feedback regulation* (see Chapter 1) applies to population dynamics. Without some type of negative feedback between population density and the rates of



**▲ Figure 53.15 Determining equilibrium for population density.** This simple model considers only birth and death rates. (Immigration and emigration rates are assumed to be either zero or equal.) In this example, the birth rate changes with population density, while the death rate is constant. At the equilibrium density ( $Q$ ), the birth and death rates are equal.

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



**▲ Figure 53.16 Decreased reproduction at high population densities.** Reproduction by young Soay sheep on Hirta Island drops dramatically as population size increases.

birth and death, a population would never stop growing. Density-dependent regulation provides that feedback, halting population growth through mechanisms that reduce birth rates or increase death rates. For example, on Hirta Island, Soay sheep compete for food and other resources. Ecologists have closely monitored sheep density and reproduction for many years. The strongest density-dependent reduction in birth rates appears in young sheep, typically 1-year-olds giving birth for the first time (**Figure 53.16**). Competition and several other mechanisms of density-dependent population regulation are described in **Figure 53.17**, on pages 1183–1184.

▼ Figure 53.17

## Exploring Mechanisms of Density-Dependent Regulation

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

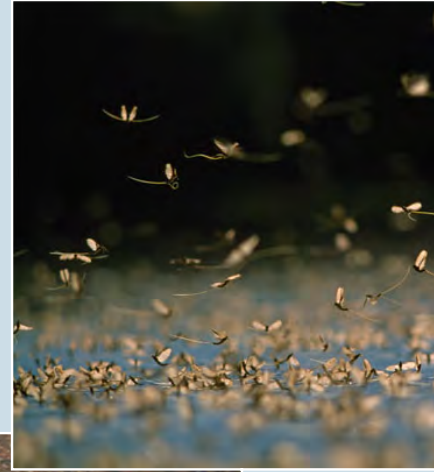
### Competition for Resources

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



### Predation

Predation can be an important cause of density-dependent mortality if a predator captures more food as the population density of the prey increases. As a prey population builds up, predators may also feed preferentially on that species. Some fish species, such as the cutthroat trout (*Oncorhynchus clarkii*), concentrate for a few days on a particular insect species that is emerging from its aquatic larval stage and then switch to another prey species when it becomes more abundant.



### Toxic Wastes

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



5  $\mu$ m

### Intrinsic Factors

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



## Exploring Mechanisms of Density-Dependent Regulation

### Territoriality

Territoriality can limit population density when space becomes the resource for which individuals compete. Cheetahs (*Acinonyx jubatus*) use a chemical marker in urine to warn other cheetahs of their territorial boundaries. Australasian gannets (*Morus serrator*) defend their territories when nesting by calling and pecking at one another. Maintaining a territory increases the likelihood that an animal will capture enough food to reproduce. The presence of surplus, or nonbreeding, individuals is a good indication that territoriality is restricting population growth.



### Disease

If the transmission rate of a particular disease depends on a certain level of crowding in a population, then the disease's impact is density dependent. In humans, respiratory diseases such as influenza (flu) and tuberculosis are caused by pathogens that spread through the air when an infected person sneezes or coughs. Both diseases strike a greater percentage of people in densely populated cities than in rural areas.



These various examples of population regulation by negative feedback show how increased densities cause population growth rates to decline by affecting reproduction, growth, and survival. But though negative feedback helps explain why populations stop growing, it does not address why some populations fluctuate dramatically while others remain relatively stable. That is the topic we address next.

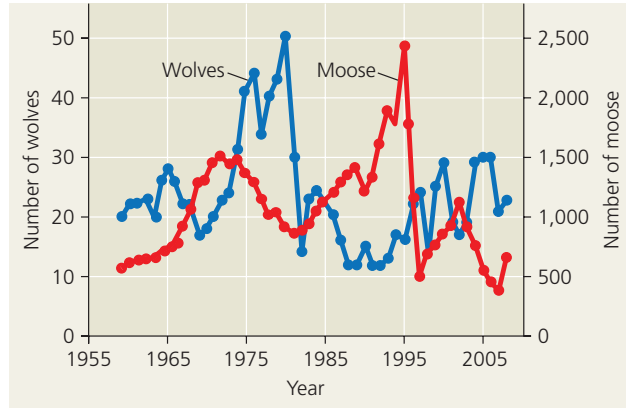
### Population Dynamics

All populations for which we have long-term data show some fluctuation in size. Such population fluctuations from year to year or place to place, called **population dynamics**, are influenced by many factors and in turn affect other species, including our own. For example, fluctuations in fish populations influence seasonal harvests of commercially important species. The study of population dynamics focuses on the complex interactions between biotic and abiotic factors that cause variation in population sizes.

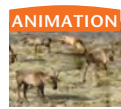
### Stability and Fluctuation

Populations of large mammals were once thought to remain relatively stable over time, but long-term studies have challenged that idea. The number of Soay sheep on Hirta Island fluctuates greatly, rising or falling by more than half from one year to the next. What causes the size of this population to change so dramatically? Harsh weather, particularly cold, wet winters, can weaken the sheep and reduce food availability, decreasing the size of the population. When sheep numbers are high, other factors, such as an increase in the density of parasites, also cause the population to shrink. Conversely, when sheep numbers are low and the weather is mild, food is readily available and the population grows quickly.

Like the Soay sheep population on Hirta, the moose population on Isle Royale in Lake Superior also fluctuates over time. In the case of the moose, predation is an additional factor that regulates the population. Moose from the mainland colonized



▲ **Figure 53.18** Fluctuations in moose and wolf populations on Isle Royale, 1959–2008.



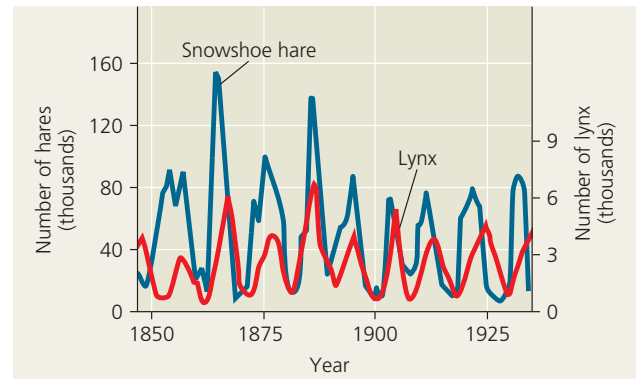
**BioFlix** Visit the Study Area at [www.masteringbiology.com](http://www.masteringbiology.com) for the BioFlix® 3-D Animation on Population Ecology.

the island around 1900 by walking across the frozen lake. Wolves, which rely on moose for most of their food, followed around 1950. Because the lake has not frozen over in recent years, both populations have been isolated from immigration and emigration. Despite this isolation, the moose population experienced two major increases and collapses during the last 50 years (Figure 53.18). The first collapse coincided with a peak in the numbers of wolves from 1975 to 1980. The second collapse, around 1995, coincided with harsh winter weather, which increased the energy needs of the animals and made it harder for the moose to find food under the deep snow.

### Population Cycles: Scientific Inquiry

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

One striking example of population cycles is the roughly 10-year cycling of snowshoe hares (*Lepus americanus*) and lynx (*Lynx canadensis*) in the far northern forests of Canada and Alaska. Lynx are predators that specialize in preying on snowshoe hares, so lynx numbers might be expected to rise and fall with the numbers of hares (Figure 53.19). But why do hare numbers rise and fall in approximately 10-year cycles? Three main hypotheses have been proposed. First, the cycles may be caused by food shortage during winter. Hares eat the terminal twigs of small shrubs such as willow and birch in winter, although why this food supply might cycle in 10-year intervals is uncertain. Second, the cycles may be due to predator-prey interactions. Many predators other than lynx



▲ **Figure 53.19** Population cycles in the snowshoe hare and lynx. Population counts are based on the number of pelts sold by trappers to the Hudson Bay Company.

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

eat hares, and they may overexploit their prey. Third, the size of the hare population may vary with sunspot activity, which also undergoes cyclic changes. When sunspot activity is low, slightly less atmospheric ozone is produced, and slightly more UV radiation reaches Earth's surface. In response, plants produce more UV-blocking chemicals and fewer chemicals that deter herbivores, increasing the quality of the hares' food.

Let's consider the evidence for these three hypotheses. If hare cycles are due to winter food shortage, then they should stop if extra food is provided to a field population. Researchers conducted such experiments in the Yukon for 20 years—over two hare cycles. They found that hare populations in the areas with extra food increased about threefold in density but continued to cycle in the same way as the unfed control populations. Thus, food supplies alone do not cause the hare cycle shown in Figure 53.19, so we can reject the first hypothesis.

Using radio collars, ecologists tracked individual hares to determine why they died. Predators killed almost 90% of the hares in such studies, and none of the hares appeared to have died of starvation. These data support the second hypothesis. When ecologists excluded predators from one area with electric fences and also excluded predators and provided food in another area, they found that the hare cycle is driven largely by excessive predation but that food availability also plays an important role, particularly in the winter. Better-fed hares may be more likely to escape from predators.



To test the third hypothesis, ecologists compared the timing of hare cycles with sunspot activity, which has a cycle of approximately 11 years. As predicted, periods of low sunspot activity were followed by peaks in the hare population. The results of all of these experiments suggest that both predation and sunspot activity regulate the cycling of hare numbers and that food availability plays a less important role.

The availability of prey is the major factor influencing population changes for predators such as lynx, great-horned owls, and weasels, each of which depends heavily on a single prey species. When prey become scarce, predators often turn on one another. Coyotes kill both foxes and lynx, and great-horned owls kill smaller birds of prey as well as weasels, accelerating the collapse of the predator populations. Long-term experimental studies help to unravel the causes of such population cycles.

### Immigration, Emigration, and Metapopulations

So far, our discussion of population dynamics has focused mainly on the contributions of births and deaths. However, immigration and emigration also influence populations. When a population becomes crowded and resource competition increases (see Figure 53.16), emigration often increases. In the slime mold *Dictyostelium discoideum*, single-celled individuals (called amoebas) group together when food is scarce and form a “slug” containing thousands of cells (see Figure 28.25). This multicellularity likely evolved in part because slugs can produce a fruiting body that is raised off the forest floor, allowing the spores to disperse relatively long distances. New work shows an additional advantage of multicellularity in *Dictyostelium* (Figure 53.20). Aggregating improved emigration and foraging: *Dictyostelium* slugs traveled across stretches of soil much better than single amoebas did, and amoebas that separated from slugs reached soil patches and food that solitary amoebas did not.

Immigration and emigration are particularly important when a number of local populations are linked, forming a **metapopulation**. Immigration and emigration link the Belding’s ground squirrel population we discussed earlier to other populations of the species, all of which make up a metapopulation.

Local populations in a metapopulation can be thought of as occupying discrete patches of suitable habitat in a sea of otherwise unsuitable habitat. Such patches vary in size, quality, and isolation from other patches, factors that influence how many individuals move among the populations. Patches with many individuals can supply more emigrants to other patches. If one population becomes extinct, the patch it occupied can be recolonized by immigrants from another population.

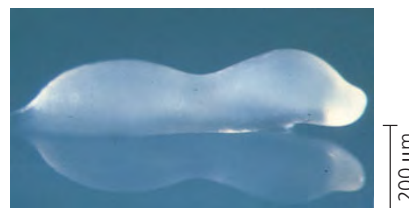
The Glanville fritillary (*Melitaea cinxia*) illustrates the movement of individuals between populations. This butterfly is found in about 500 meadows across the Åland Islands of Finland, but its potential habitat in the islands is much

▼ Figure 53.20

## INQUIRY

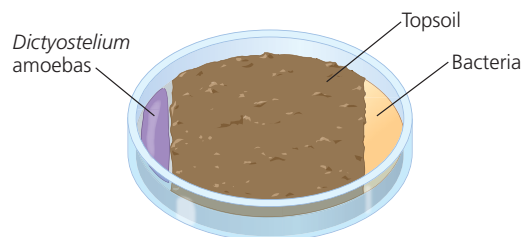
### How does food availability affect emigration and foraging in a cellular slime mold?

**EXPERIMENT** Jennie Kuzdzal-Fick and colleagues at Rice University, in Texas, examined whether multicellular “slugs” of the protist *Dictyostelium discoideum* were more successful than single cells (called amoebas) of that species at crossing soil and finding bacteria to feed on.



*Dictyostelium discoideum* slug

The researchers placed a 6-cm-wide layer of sterilized topsoil on a dish containing agar, pipetted *Dictyostelium* amoebas onto the agar on one side of the topsoil, and added bacteria to the other side.



In one set of dishes, the amoebas were wild-type cells, which are capable of aggregating into slugs; in another set of dishes, the amoebas were mutants that cannot aggregate.

**RESULTS** Slugs traveled farther across the soil than amoebas did. The researchers also found that amoebas that sloughed off (separated from) the slugs reached areas that solitary amoebas could not reach.

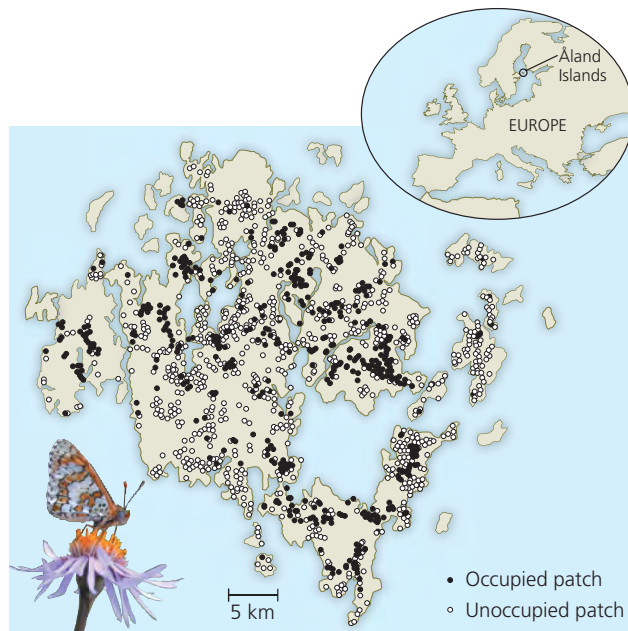
**CONCLUSION** An advantage of multicellularity in *Dictyostelium* is improved emigration and foraging.

**SOURCE** J. J. Kuzdzal-Fick et al., Exploiting new terrain: an advantage to sociality in the slime mold *Dictyostelium discoideum*, *Behavioral Ecology* 18:433–437 (2007).

**WHAT IF?** Even in cases of severe resource depletion, *Dictyostelium* amoebas do not always aggregate into slugs. Suggest one potential disadvantage of aggregation for a *Dictyostelium* population.

larger, approximately 4,000 suitable patches. New populations of the butterfly regularly appear and existing populations become extinct, constantly shifting the locations of the 500 colonized patches (Figure 53.21). The species persists in a balance of extinctions and recolonizations.

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



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

### CONCEPT CHECK 53.5

1. Describe three attributes of habitat patches that could affect population density and rates of immigration and emigration.
2. **WHAT IF?** Suppose you were studying a species that has a population cycle of about ten years. How long would you need to study the species to determine if its population size were declining? Explain.
3. **MAKE CONNECTIONS** Concept 40.2, p. 861, describes negative feedback as a process that regulates biological systems. Explain how the density-dependent birth rate of dune fescue grass exemplifies negative feedback.

For suggested answers, see Appendix A.

### CONCEPT 53.6

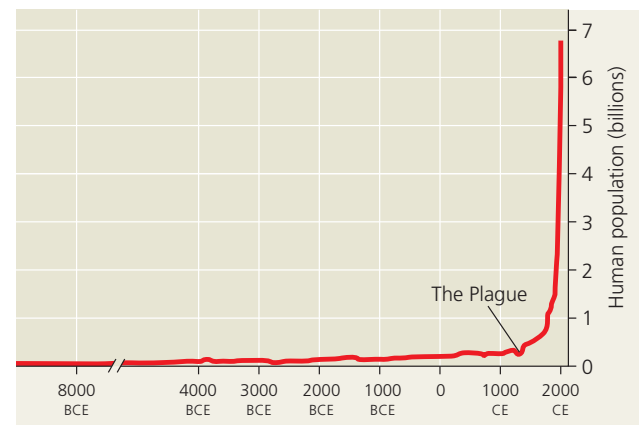
## The human population is no longer growing exponentially but is still increasing rapidly

In the last few centuries, the human population has grown at an unprecedented rate, more like the elephant population in Kruger National Park (see Figure 53.8) than the fluctuating populations we considered in Concept 53.5. No population can grow indefinitely, however. In this section of the chapter, we'll apply the concepts of population dynamics to the specific case of the human population.

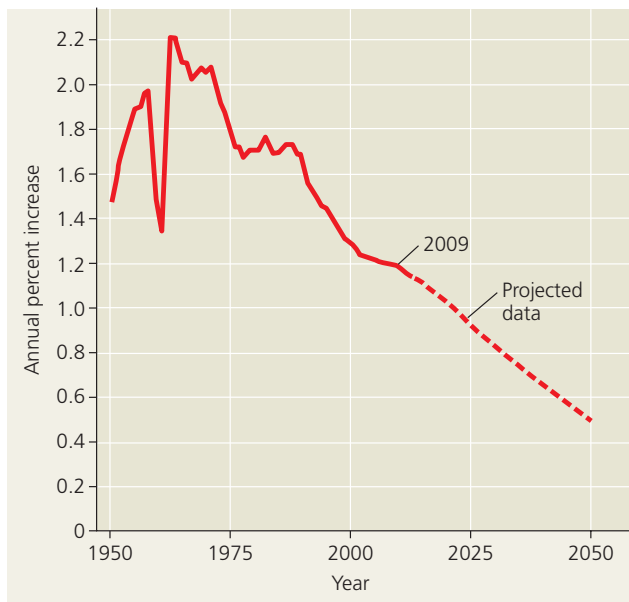
## The Global Human Population

The exponential growth model in Figure 53.7 approximates the human population explosion over the last four centuries (**Figure 53.22**). Ours is a singular case; no other population of large animals has likely ever sustained so much growth for so long. The human population increased relatively slowly until about 1650, at which time approximately 500 million people inhabited Earth. Our population doubled to 1 billion within the next two centuries, doubled again to 2 billion by 1930, and doubled still again by 1975 to more than 4 billion. The global population is now more than 6.8 billion people and is increasing by about 79 million each year. Currently the population grows by more than 200,000 people each day, the equivalent of adding a city the size of Amarillo, Texas, or Kitchener, Ontario. At this rate, it takes only about four years to add the equivalent of another United States to the world population. Population ecologists predict a population of 7.8–10.8 billion people on Earth by the year 2050.

Though the global population is still growing, the *rate* of growth did begin to slow during the 1960s (**Figure 53.23**, on the next page). The annual rate of increase in the global population peaked at 2.2% in 1962; by 2009, it had declined to 1.2%. Current models project a continued decline in the annual growth rate to roughly 0.5% by 2050, a rate that would still add 45 million more people per year if the population climbs to a projected 9 billion. The reduction in growth rate over the past four decades shows that the human population has departed from true exponential growth, which assumes a constant rate. This departure is the result of fundamental changes in population dynamics due to diseases, including AIDS, and to voluntary population control.



**▲ Figure 53.22 Human population growth (data as of 2009).** The global human population has grown almost continuously throughout history, but it skyrocketed after the Industrial Revolution. Though it is not apparent at this scale, the rate of population growth has slowed in recent decades, mainly as a result of decreased birth rates throughout the world.



▲ **Figure 53.23 Annual percent increase in the global human population (data as of 2009).** The sharp dip in the 1960s is due mainly to a famine in China in which about 60 million people died.

### Regional Patterns of Population Change

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

Zero population growth = High birth rate – High death rate

or

Zero population growth = Low birth rate – Low death rate

The movement from high birth and death rates toward low birth and death rates, which tends to accompany industrialization and improved living conditions, is called the **demographic transition**. In Sweden, this transition took about 150 years, from 1810 to 1960, when birth rates finally approached death rates. In Mexico, where the human population is still growing rapidly, the transition is projected to take until at least 2050. Demographic transition is associated with an increase in the quality of health care and sanitation as well as improved access to education, especially for women.

After 1950, death rates declined rapidly in most developing countries, but birth rates have declined in a more variable manner. The fall in birth rate has been most dramatic in China. In 1970, the Chinese birth rate predicted an average of 5.9 children per woman per lifetime (total fertility rate); by 2009, largely because of the government’s strict one-child policy, the expected total fertility rate was 1.8 children. In some countries of Africa, the transition to lower birth rates has also

been rapid, though birth rates remain high in most of sub-Saharan Africa. In India, birth rates have fallen more slowly.

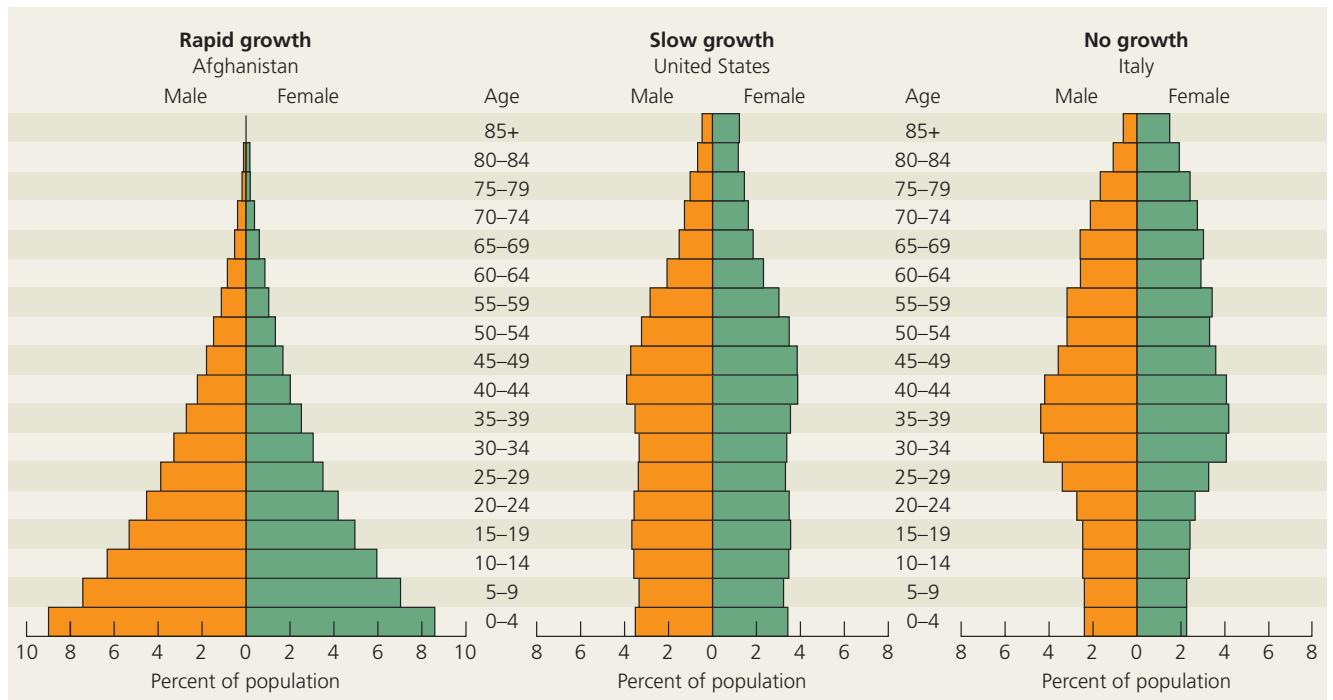
How do such variable birth rates affect the growth of the world’s population? In industrialized nations, populations are near equilibrium (growth rate about 0.1% per year), with reproductive rates near the replacement level (total fertility rate = 2.1 children per female). In many industrialized countries, including Canada, Germany, Japan, and the United Kingdom, total reproductive rates are in fact *below* replacement. These populations will eventually decline if there is no immigration and if the birth rate does not change. In fact, the population is already declining in many eastern and central European countries. Most of the current global population growth (1.2% per year) is concentrated in less industrialized countries, where about 80% of the world’s people now live.

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

### Age Structure

Another important demographic variable in present and future growth trends is a country’s **age structure**, the relative number of individuals of each age in the population. Age structure is commonly graphed as “pyramids” like those in **Figure 53.24**. For Afghanistan, the pyramid is bottom-heavy, skewed toward young individuals who will grow up and perhaps sustain the explosive growth with their own reproduction. The age structure for the United States is relatively even until the older, postreproductive ages, except for a bulge that corresponds to the “baby boom” that lasted for about two decades after the end of World War II. Even though couples born during those years have had an average of fewer than two children, the nation’s overall birth rate still exceeds the death rate because some “boomers” and most of the boomers’ offspring are still of reproductive age. Moreover, although the current total reproductive rate in the United States is 2.1 children per woman—approximately replacement rate—the population is projected to grow slowly through 2050 as a result of immigration. For Italy, the pyramid has a small base, indicating that individuals younger than reproductive age are relatively underrepresented in the population. This situation contributes to the projection of a population decrease in Italy.

Age-structure diagrams not only predict a population’s growth trends but can also illuminate social conditions. Based on the diagrams in Figure 53.24, we can predict, for

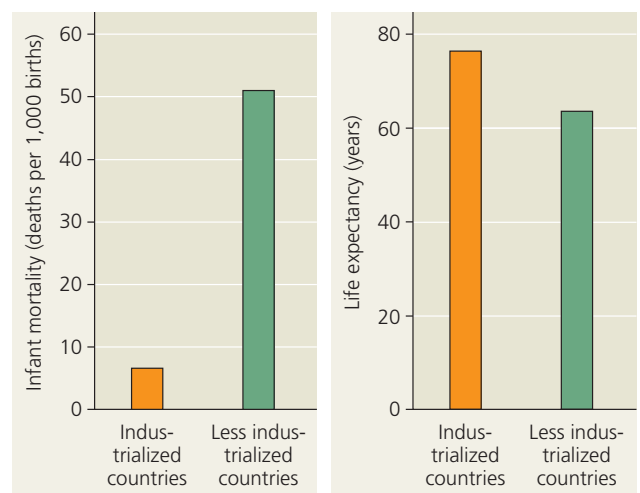


▲ **Figure 53.24 Age-structure pyramids for the human population of three countries (data as of 2009).** The annual growth rate was approximately 2.6% in Afghanistan, 1.0% in the United States, and 0.0% in Italy.

instance, that employment and education opportunities will continue to be a significant problem for Afghanistan in the foreseeable future. The large number of young people entering the Afghan population could also be a source of continuing social and political unrest, particularly if their needs and aspirations are not met. In Italy and the United States, a decreasing proportion of younger working-age people will soon be supporting an increasing population of retired “boomers.” In the United States, this demographic feature has made the future of Social Security and Medicare a major political issue. Understanding age structures can help us plan for the future.

### Infant Mortality and Life Expectancy

*Infant mortality*, the number of infant deaths per 1,000 live births, and *life expectancy at birth*, the predicted average length of life at birth, vary widely among different human populations. These differences reflect the quality of life faced by children at birth and influence the reproductive choices parents make. If infant mortality is high, then parents are likely to have more children to ensure that some reach adulthood. **Figure 53.25** contrasts average infant mortality and life expectancy in the industrialized and less industrialized countries of the world in 2008. While these averages are markedly different, they do not capture the broad range of the human condition. In 2008, for example, the infant mortality rate was 155 (15.5%) in Afghanistan but only 3 (0.3%) in Japan, while



▲ **Figure 53.25 Infant mortality and life expectancy at birth in industrialized and less industrialized countries (data as of 2008).**

life expectancy at birth was 44 years in Afghanistan and 82 years in Japan. Although global life expectancy has been increasing since about 1950, it has recently dropped in a number of regions, including countries of the former Soviet Union and in sub-Saharan Africa. In these regions, social upheaval, decaying infrastructure, and infectious diseases such as AIDS and tuberculosis are reducing life expectancy. In the African

country of Angola, for instance, life expectancy in 2008 was approximately 38 years, about half of that in Japan, Sweden, Italy, and Spain.

## Global Carrying Capacity

No ecological question is more important than the future size of the human population. The projected worldwide population size depends on assumptions about future changes in birth and death rates. As we noted earlier, population ecologists project a global population of approximately 7.8–10.8 billion people in 2050. In other words, without some catastrophe, an estimated 1–4 billion people will be added to the population in the next four decades because of the momentum of population growth. But just how many humans can the biosphere support? Will the world be overpopulated in 2050? Is it *already* overpopulated?

### Estimates of Carrying Capacity

For over three centuries, scientists have attempted to estimate the human carrying capacity of Earth. The first known estimate, 13.4 billion people, was made in 1679 by Anton van Leeuwenhoek, the discoverer of protists (see Chapter 28). Since then, estimates have varied from less than 1 billion to more than 1,000 billion (1 trillion), with an average of 10–15 billion.

Carrying capacity is difficult to estimate, and scientists use different methods to produce their estimates. Some current researchers use curves like that produced by the logistic equation (see Figure 53.9) to predict the future maximum of the human population. Others generalize from existing “maximum” population density and multiply this number by the area of habitable land. Still others base their estimates on a single limiting factor, such as food, and consider variables such as the amount of available farmland, the average yield of crops, the prevalent diet—vegetarian or meat based—and the number of calories needed per person per day.

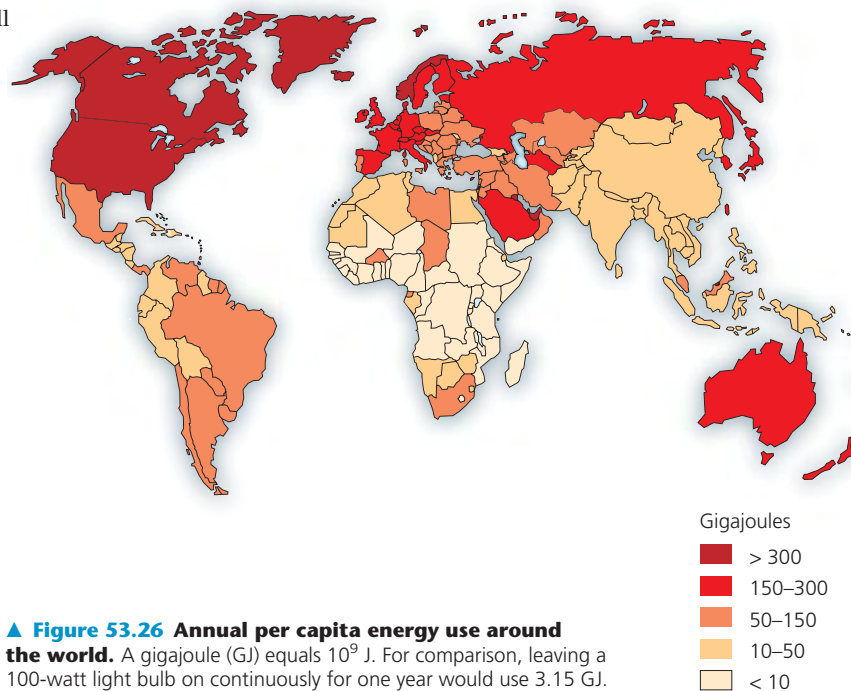
### Limits on Human Population Size

A more comprehensive approach to estimating the carrying capacity of Earth is to recognize that humans have multiple constraints: We need food, water, fuel, building materials, and other resources, such as clothing and transportation. The **ecological footprint** concept summarizes the aggregate land and water area required by each person, city, or nation to produce all the resources it consumes and to absorb all the waste it generates. One way to estimate the eco-

logical footprint of the entire human population is to add up all the ecologically productive land on the planet and divide by the population. This calculation yields approximately 2 hectares (ha) per person (1 ha = 2.47 acres). Reserving some land for parks and conservation means reducing this allotment to 1.7 ha per person—the benchmark for comparing actual ecological footprints. Anyone who consumes resources that require more than 1.7 ha to produce is said to be using an unsustainable share of Earth’s resources. A typical ecological footprint for a person in the United States is about 10 ha.

Ecologists sometimes calculate ecological footprints using other currencies besides land area, such as energy use. Average energy use differs greatly for a person in developed and developing nations (Figure 53.26). A typical person in the United States, Canada, or Norway consumes roughly 30 times the energy that a person in central Africa does. Moreover, fossil fuels, such as oil, coal, and natural gas, are the source of 80% or more of the energy used in most developed nations. As you will see in Chapter 56, this unsustainable reliance on fossil fuels is changing Earth’s climate and increasing the amount of waste that each of us produces. Ultimately, the combination of resource use per person and population density determines our global ecological footprint.

We can only speculate about Earth’s ultimate carrying capacity for the human population and about what factors will eventually limit our growth. Perhaps food will be the main limiting factor. Malnutrition and famine are common in some regions, but they result mainly from the unequal distribution of food rather than from inadequate production. So far, technological improvements in agriculture have allowed



food supplies to keep up with global population growth. However, the principles of energy flow through ecosystems (which you read about in Chapter 55) tell us that environments can support a larger number of herbivores than carnivores. If everyone ate as much meat as the wealthiest people in the world, less than half of the present world population could be fed by current food harvests.

Perhaps we humans will eventually be limited by suitable space. Certainly, as our population grows, the conflict over how space is utilized will intensify, and agricultural land will be developed for housing. There seem to be few limits, however, on how closely humans can be crowded together, as long as adequate food and water are provided to us and space is available to dispose of our wastes.

Humans could also run out of nonrenewable resources, such as certain metals and fossil fuels. The demands of many populations have already far exceeded the local and even regional supplies of one renewable resource—fresh water. More than 1 billion people do not have access to sufficient water to meet their basic sanitation needs. The human population may also be limited by the capacity of the environment to absorb its wastes. If so, then Earth's current human occupants could lower the planet's long-term carrying capacity for future generations.

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

### CONCEPT CHECK 53.6

1. How does a human population's age structure affect its growth rate?
2. How has the growth of Earth's human population changed in recent decades? Answer in terms of growth rate and the number of people added each year.
3. **WHAT IF?** What choices can you make to influence your own ecological footprint?

For suggested answers, see Appendix A.

## 53 CHAPTER REVIEW

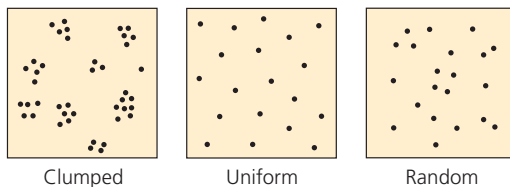
### SUMMARY OF KEY CONCEPTS

#### CONCEPT 53.1

**Dynamic biological processes influence population density, dispersion, and demographics (pp. 1170–1175)**

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

Patterns of dispersion



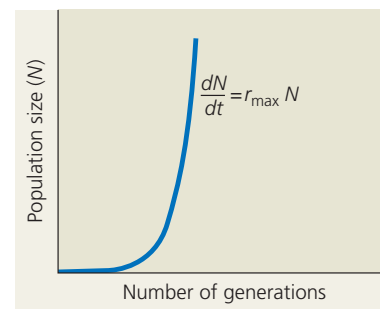
- Populations increase from births and **immigration** and decrease from deaths and **emigration**. **Life tables**, **survivorship curves**, and **reproductive tables** summarize specific trends in **demography**.

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

#### CONCEPT 53.2

**The exponential model describes population growth in an idealized, unlimited environment (pp. 1175–1177)**

- If immigration and emigration are ignored, a population's growth rate (the per capita rate of increase) equals its birth rate minus its death rate.
- The **exponential growth** equation  $dN/dt = r_{\max}N$  represents a population's potential growth in an unlimited environment, where  $r_{\max}$  is the maximum per capita rate of increase and  $N$  is the number of individuals in the population.

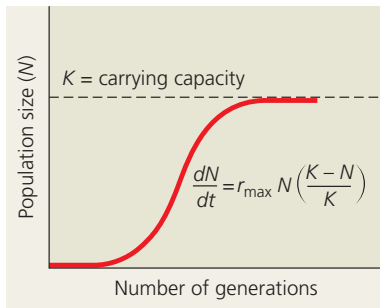


**?** Suppose one population has an  $r_{\max}$  that is twice as large as the  $r_{\max}$  of another population. What is the maximum size that both populations will reach over time, based on the exponential model?

### CONCEPT 53.3

The logistic model describes how a population grows more slowly as it nears its carrying capacity (pp. 1177–1179)

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



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

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

### CONCEPT 53.4

Life history traits are products of natural selection (pp. 1179–1181)

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

? What two factors likely contribute to the evolution of semelparity versus iteroparity?

### CONCEPT 53.5

Many factors that regulate population growth are density dependent (pp. 1182–1187)

- In **density-dependent** population regulation, death rates rise and birth rates fall with increasing density. In **density-independent** population regulation, birth and death rates do not vary with density.
- Density-dependent changes in birth and death rates curb population increase through negative feedback and can eventually stabilize a population near its carrying capacity. Density-dependent limiting factors include intraspecific competition for limited food or space, increased predation, disease, stress due to crowding, and buildup of toxic substances.
- Because changing environmental conditions periodically disrupt them, all populations exhibit some size fluctuations. Many

populations undergo regular boom-and-bust cycles that are influenced by complex interactions between biotic and abiotic factors. A **metapopulation** is a group of populations linked by immigration and emigration.

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

### CONCEPT 53.6

The human population is no longer growing exponentially but is still increasing rapidly (pp. 1187–1191)

- Since about 1650, the global human population has grown exponentially, but within the last 50 years, the rate of growth has fallen by nearly half. Differences in **age structure** show that while some nations' populations are growing rapidly, those of others are stable or declining in size. Infant mortality rates and life expectancy at birth differ markedly between industrialized and less industrialized countries.
- The carrying capacity of Earth for humans is uncertain. **Ecological footprint** is the aggregate land and water area needed to produce all the resources a person or group of people consume and to absorb all of their wastes. It is one measure of how close we are to the carrying capacity of Earth. With a world population of more than 6.8 billion people, we are already using many resources in an unsustainable manner.

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

## TEST YOUR UNDERSTANDING

### LEVEL 1: KNOWLEDGE/COMPREHENSION

1. Population ecologists follow the fate of same-age cohorts to
  - a. determine a population's carrying capacity.
  - b. determine the birth rate and death rate of each group in a population.
  - c. determine if a population is regulated by density-dependent processes.
  - d. determine the factors that regulate the size of a population.
  - e. determine if a population's growth is cyclic.
2. A population's carrying capacity
  - a. may change as environmental conditions change.
  - b. can be accurately calculated using the logistic growth model.
  - c. generally remains constant over time.
  - d. increases as the per capita growth rate ( $r$ ) decreases.
  - e. can never be exceeded.
3. Scientific study of the population cycles of the snowshoe hare and its predator, the lynx, has revealed that
  - a. the prey population is controlled by predators alone.
  - b. hares and lynx are so mutually dependent that each species cannot survive without the other.
  - c. multiple biotic and abiotic factors contribute to the cycling of the hare and lynx populations.
  - d. both hare and lynx populations are regulated mainly by abiotic factors.
  - e. the hare population is  $r$ -selected and the lynx population is  $K$ -selected.
4. Based on current growth rates, Earth's human population in 2012 will be closest to
  - a. 2 million.
  - b. 3 billion.
  - c. 4 billion.
  - d. 7 billion.
  - e. 10 billion.

5. A recent study of ecological footprints concluded that
  - a. Earth's carrying capacity for humans is about 10 billion.
  - b. Earth's carrying capacity would increase if per capita meat consumption increased.
  - c. current demand by industrialized countries for resources is much smaller than the ecological footprint of those countries.
  - d. it is not possible for technological improvements to increase Earth's carrying capacity for humans.
  - e. the ecological footprint of the United States is large because per capita resource use is high.

### LEVEL 2: APPLICATION/ANALYSIS

6. The observation that members of a population are uniformly distributed suggests that
  - a. the size of the area occupied by the population is increasing.
  - b. resources are distributed unevenly.
  - c. the members of the population are competing for access to a resource.
  - d. the members of the population are neither attracted to nor repelled by one another.
  - e. the density of the population is low.
7. According to the logistic growth equation
 
$$\frac{dN}{dt} = r_{\max}N \frac{(K - N)}{K}$$
  - a. the number of individuals added per unit time is greatest when  $N$  is close to zero.
  - b. the per capita growth rate ( $r$ ) increases as  $N$  approaches  $K$ .
  - c. population growth is zero when  $N$  equals  $K$ .
  - d. the population grows exponentially when  $K$  is small.
  - e. the birth rate ( $b$ ) approaches zero as  $N$  approaches  $K$ .
8. Which pair of terms most accurately describes life history traits for a stable population of wolves?
  - a. semelparous;  $r$ -selected
  - b. semelparous;  $K$ -selected
  - c. iteroparous;  $r$ -selected
  - d. iteroparous;  $K$ -selected
  - e. iteroparous;  $N$ -selected
9. During exponential growth, a population always
  - a. grows by thousands of individuals.
  - b. grows at its maximum per capita rate.
  - c. quickly reaches its carrying capacity.
  - d. cycles through time.
  - e. loses some individuals to emigration.
10. Which of the following statements about human population in industrialized countries is *incorrect*?
  - a. Life history is  $r$ -selected.
  - b. Average family size is relatively small.
  - c. The population has undergone the demographic transition.
  - d. The survivorship curve is Type I.
  - e. Age distribution is relatively uniform.

### LEVEL 3: SYNTHESIS/EVALUATION

11. **DRAW IT** To estimate which age cohort in a population of females produces the most female offspring, you need information about the number of offspring produced per capita within that cohort and the number of individuals alive in the

cohort. Make this estimate for Belding's ground squirrels by multiplying the number of females alive at the start of the year (column 2 in Table 53.1) by the average number of female offspring produced per female (column 5 in Table 53.2). Draw a bar graph with female age in years on the  $x$ -axis (0–1, 1–2, and so on) and total number of female offspring produced for each age cohort on the  $y$ -axis. Which cohort of female Belding's ground squirrels produces the most female young?

### 12. EVOLUTION CONNECTION

Write a paragraph contrasting the conditions that favor the evolution of semelparous (one-time) reproduction versus iteroparous (repeated) reproduction.

### 13. SCIENTIFIC INQUIRY

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

### 14. SCIENCE, TECHNOLOGY, AND SOCIETY

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

### 15. WRITE ABOUT A THEME

**Environmental Interactions** In a short essay (100–150 words), identify the factor or factors in Figure 53.17 that you think may ultimately be most important for density-dependent population regulation in humans, and explain your reasoning.

For selected answers, see Appendix A.

**MasteringBIOLOGY** [www.masteringbiology.com](http://www.masteringbiology.com)

#### 1. MasteringBiology® Assignments

**BioFlix** Tutorial Population Ecology

Tutorial Population Ecology: Logistic Growth

**Activities** Techniques for Estimating Population Density and Size • Investigating Survivorship Curves • Modeling Population Growth • Human Population Growth • Human Population Growth and Regulation • Analyzing Age-Structure Pyramids • GraphIt!: Age Pyramids and Population Growth

**Questions** Student Misconceptions • Reading Quiz • Multiple Choice • End-of-Chapter

#### 2. eText

Read your book online, search, take notes, highlight text, and more.

#### 3. The Study Area

Practice Tests • Cumulative Test • **BioFlix** 3-D Animations • MP3 Tutor Sessions • Videos • Activities • Investigations • Lab Media • Audio Glossary • Word Study Tools • Art