3. Which is true about a population's carrying capacity?
   (a) It is denoted as C.
   (b) It is usually used when studying ecosystems.
   (c) It depends on a limiting resource.
   (d) It is controlled by density-independent factors.
   (e) The population of a species cannot exceed it.

4. Which population is typically regulated by density-independent factors?
   (a) Algae
   (b) Predators
   (c) *Paramecium* bacteria
   (d) Birds
   (e) Trees

5. Which does NOT have a significant effect on the number of offspring produced by a population?
   (a) Population distribution
   (b) Sex ratio
   (c) Age structure
   (d) Population size
   (e) Carrying capacity

Module 19

Population Growth Models

Scientists often use models to help them explain how things work and to predict how things might change in the future. Population ecologists use growth models that incorporate density-dependent and density-independent factors to explain and predict changes in population size. These models are important tools for population ecologists, whether they are protecting an endangered condor population, managing a commercially harvested fish species, or controlling an insect pest. In this module we will look at several growth models and other tools for understanding changes in population size.

Learning Objectives

After reading this module you should be able to

- explain the exponential growth model of populations, which produces a J-shaped curve.
- describe how the logistic growth model incorporates a carrying capacity and produces an S-shaped curve.
- compare the reproductive strategies and survivorship curves of different species.
- explain the dynamics that occur in metapopulations.

The exponential growth model describes populations that continuously increase

Population growth models are mathematical equations that can be used to predict population size at any moment in time. In this section, we will examine one commonly used growth model.

As we saw in Gause's experiments, a population can initially grow very rapidly when its growth is not limited by scarce resources. We can define **population growth rate** as the number of offspring an individual can produce in a given time period, minus the deaths of the individual or its offspring during that same period. Under ideal conditions, with unlimited resources available, every population has a particular maximum potential for growth, which is called the **intrinsic growth rate** and denoted as ***r*.** When food is abundant, individuals have a tremendous ability to reproduce. For example, domesticated hogs (*Sus domestica*) can have litters of 10 piglets, and American bullfrogs (*Rana catesbeiana*) can lay up to 20,000 eggs. Under these ideal conditions, the probability of an individual surviving also increases. Together, a high number of births and a low number of deaths produce a high population growth rate. When conditions are less than ideal due to limited resources, a population's growth rate will be lower than its intrinsic growth rate because individuals will produce fewer offspring (or forgo breeding entirely) and the number of deaths will increase.

If we know the intrinsic growth rate of a population (r) and the number of reproducing individuals that are currently in the population (N_0), we can estimate the population's future size (N_t) after some period of time (t) has passed. The formula that allows us to estimate future population is known as the **exponential growth model**

$$N_t = N_0 e^{rt}$$

where e is the base of the natural logarithms (the e^x key on your calculator, or 2.72) and t is time. This equation tells us that, under ideal conditions, the future size of the population (N_t) depends on the current size of the population (N_0), the intrinsic growth rate of the population (r), and the amount of time (t) over which the population grows.

When populations are not limited by resources, growth can be very rapid because more births occur with each step in time. When graphed, the exponential growth model produces a **J-shaped curve,** as shown in **FIGURE 19.1**. The J-shape of the curve represents the change in a growing population over time. At first the population is so small that it cannot increase rapidly because there are few individuals present to reproduce. As the population increases, there are more reproducing individuals, and so the growth rate increases.

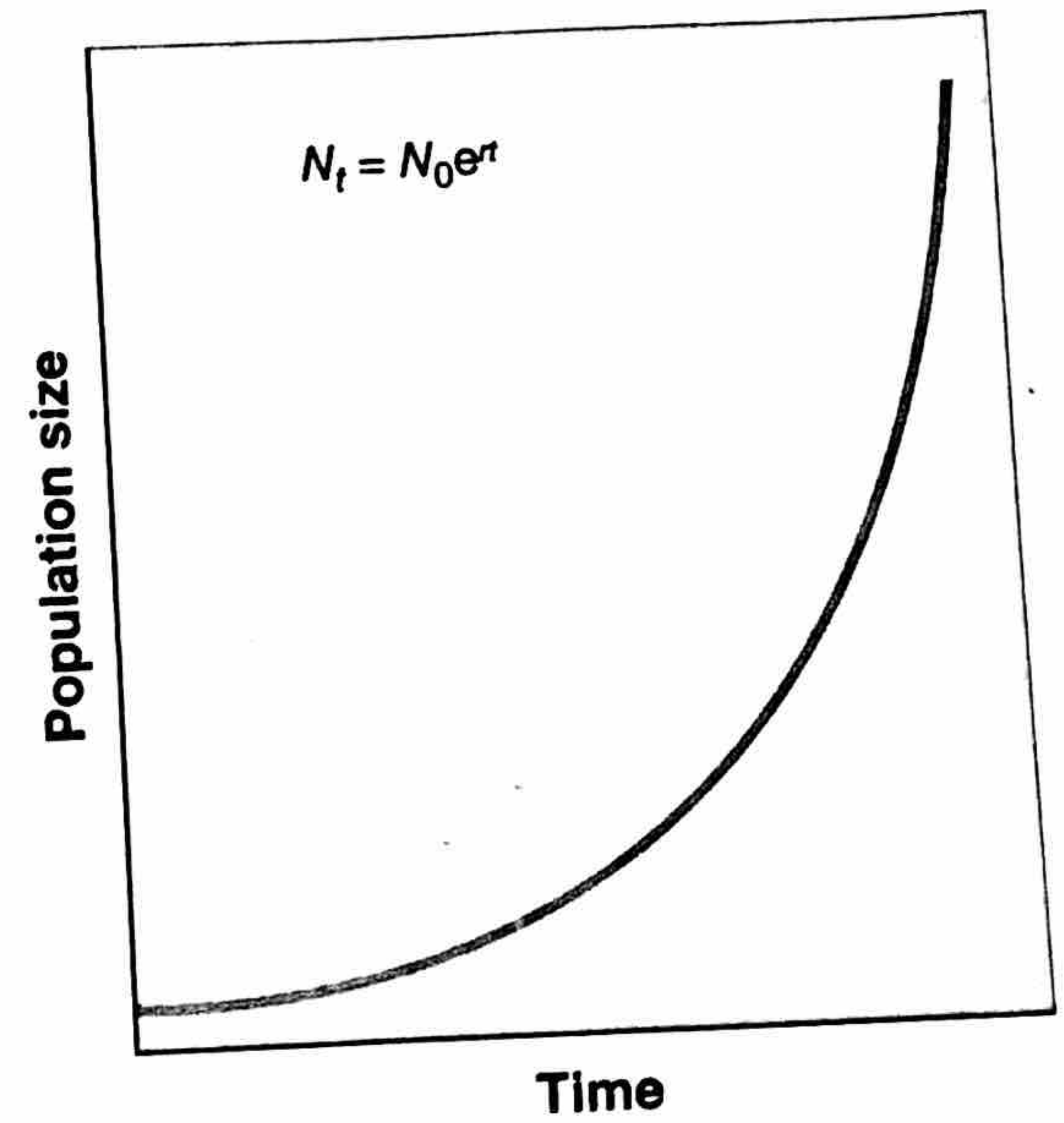

FIGURE 19.1 The exponential growth model. When populations are not limited by resources, their growth can be very rapid. More births occur with each step in time, creating a J-shaped growth curve.

One way to think about exponential growth in a population is to compare it to the growth of a bank account where N_0 is the account balance and r is the interest rate. Let's say you put \$1,000 in a bank account at an annual interest rate of 5 percent. After 1 year the new balance in the account would be:

$$N_t = \$1{,}000 \times e^{(0.05 \times 1)}$$

$$N_t = \$1{,}051.27$$

In the second year, the balance in the account would be:

$$N_t = \$1{,}000 \times e^{(0.05 \times 2)}$$

$$N_t = \$1{,}105.17$$

In the tenth year, the account would grow to a balance of \$1,648.72. Moving forward to the twentieth year,

Population growth models Mathematical equations that can be used to predict population size at any moment in time.

Population growth rate The number of offspring an individual can produce in a given time period, minus the deaths of the individual or its offspring during the same period.

Intrinsic growth rate (*r*) The maximum potential for growth of a population under ideal conditions with unlimited resources.

Exponential growth model ($N_t = N_0 e^{rt}$) A growth model that estimates a population's future size (N_t) after a period of time (t), based on the intrinsic growth rate (r) and the number of reproducing individuals currently in the population (N_0).

J-shaped curve The curve of the exponential growth model when graphed.

the same 5 percent interest rate would produce a balance of $2,718.28.

Applying an annual rate of growth to an increasing amount, whether money in a bank account or a population of organisms, produces rapid growth over time. Exponential growth is density independent because the value will grow by the same percentage every year. "Do the Math: Calculating Exponential Growth" gives a step-by-step example to show how this principle works in populations.

The exponential growth model is an excellent starting point for understanding population growth. Indeed, there is solid evidence that real populations—even small ones—can grow exponentially, at least initially. However, no population can experience exponential growth indefinitely. In Gause's experiments with *Paramecium*, the two populations initially grew exponentially until they approached the carrying capacity of their test-tube environment, at which point their growth slowed and eventually leveled off to reflect the amount of food that was added daily. We now turn to another model that gives a more complete view of population growth.

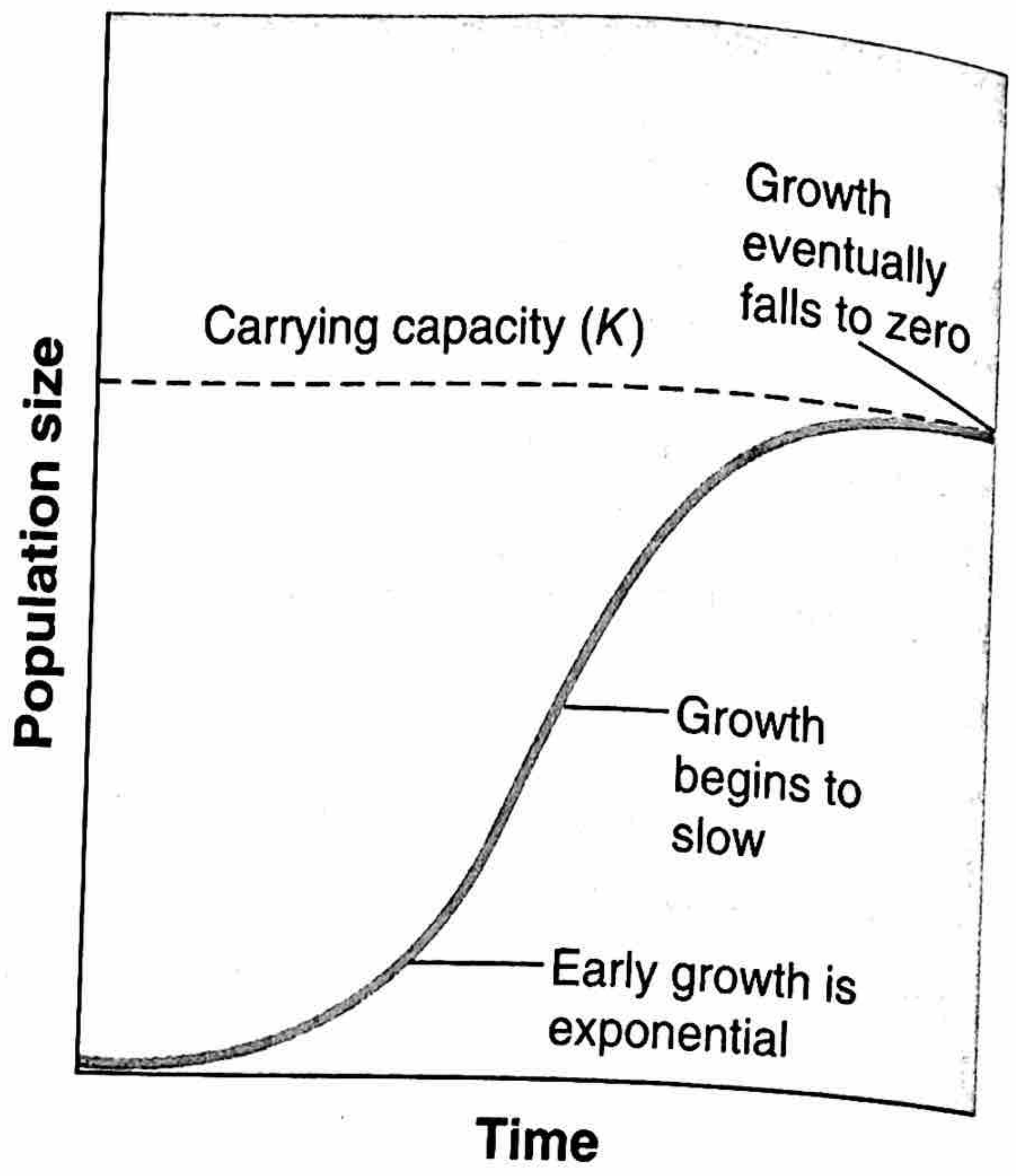

FIGURE 19.2 The logistic growth model. A small population initially experiences exponential growth. As the population becomes larger, however, resources become scarcer, and the growth rate slows. When the population size reaches the carrying capacity of the environment, growth stops. As a result, the pattern of population growth follows an S-shaped curve.

The logistic growth model describes populations that experience a carrying capacity

While the exponential growth model describes a continuously increasing population that grows at a fixed rate, populations do not experience exponential growth indefinitely. For this reason, ecologists have modified the exponential growth model to incorporate environmental limits on population growth, including limiting resources. The **logistic growth model** describes a population whose growth is initially exponential, but slows as the population approaches the carrying capacity of the environment (K). As we can see in FIGURE 19.2, if a population starts out small, its growth can be very rapid. As the population size nears about one-half of the carrying capacity, however, population growth begins to slow. As the population size approaches the carrying capacity, the population stops growing. When graphed, the logistic growth model produces an **S-shaped curve.** We observed this pattern in Gause's *Paramecium* experiments: At the carrying capacity, the populations stopped growing and remained at a constant size (see Figure 18.3).

The logistic growth model is used to predict the growth of populations that are subject to density-dependent constraints as the population grows, such as increased competition for food, water, or nest sites. Because density-independent factors such as hurricanes and floods are inherently unpredictable, the logistic growth model does not account for them.

One of the assumptions of the logistic growth model is that the number of offspring produced depends on the current population size and the carrying capacity of the environment. However, many species of mammals mate during the fall or winter, and the number of offspring that develop depends on the food supply at the time of mating. Because these offspring are not actually born until the following spring, there is a risk that food availability will not match the new population size. If there is less food available in the spring than needed to feed the offspring, the population will experience an **overshoot** by becoming larger than the environment's carrying capacity. As a result of this overshoot, there will not be enough food for all the individuals in the population, and the population will experience a **die-off,** which is a rapid population decline due to death.

The reindeer (*Rangifer tarandus*) population on St. Paul Island in Alaska is a good example of this pattern. As you can see in FIGURE 19.3, a small population of 25 reindeer that was introduced to the island in 1910 grew exponentially until it reached more than 2,000

Logistic growth model A growth model that describes a population whose growth is initially exponential, but slows as the population approaches the carrying capacity of the environment.

S-shaped curve The shape of the logistic growth model when graphed.

Overshoot When a population becomes larger than the environment's carrying capacity.

Die-off A rapid decline in a population due to death.

do the math

Calculating Exponential Growth

Consider a population of rabbits that has an initial population size of 10 individuals ($N_0 = 10$). Let's assume that the intrinsic rate of growth for a rabbit is $r = 0.5$ (or 50 percent), which means that each rabbit produces a net increase of 0.5 rabbits each year. With this information, we can predict the size of the rabbit population 2 years from now:

$$N_t = N_0 e^{rt}$$
$$N_t = 10 \times e^{0.5 \times 2}$$
$$N_t = 10 \times e^1$$
$$N_t = 10 \times (2.72)^1$$
$$N_t = 10 \times 2.72$$
$$N_t = 27 \text{ rabbits}$$

We can then ask how large the rabbit population will be after 4 years:

$$N_t = 10 \times e^{0.5 \times 4}$$
$$N_t = 10 \times e^2$$
$$N_t = 10 \times (2.72)^2$$
$$N_t = 10 \times 7.4$$
$$N_t = 74 \text{ rabbits}$$

We can also project the size of the rabbit population 10 years from now:

$$N_t = 10 \times e^{0.5 \times 10}$$
$$N_t = 10 \times e^5$$
$$N_t = 10 \times (2.72)^5$$
$$N_t = 10 \times 148.9$$
$$N_t = 1{,}489 \text{ rabbits}$$

Your Turn Now assume that the intrinsic rate of growth is 1.0 for rabbits. Calculate the predicted size of the rabbit population after 1, 5, and 10 years. Create a graph that shows the growth curves for an intrinsic rate of growth at 0.5, as calculated above, and an intrinsic rate of growth at 1.0. (Note that you will need to use your calculator to complete this problem.)

individuals in 1938. After 1938, the population crashed to only 8 animals, most likely because the reindeer ran out of food.

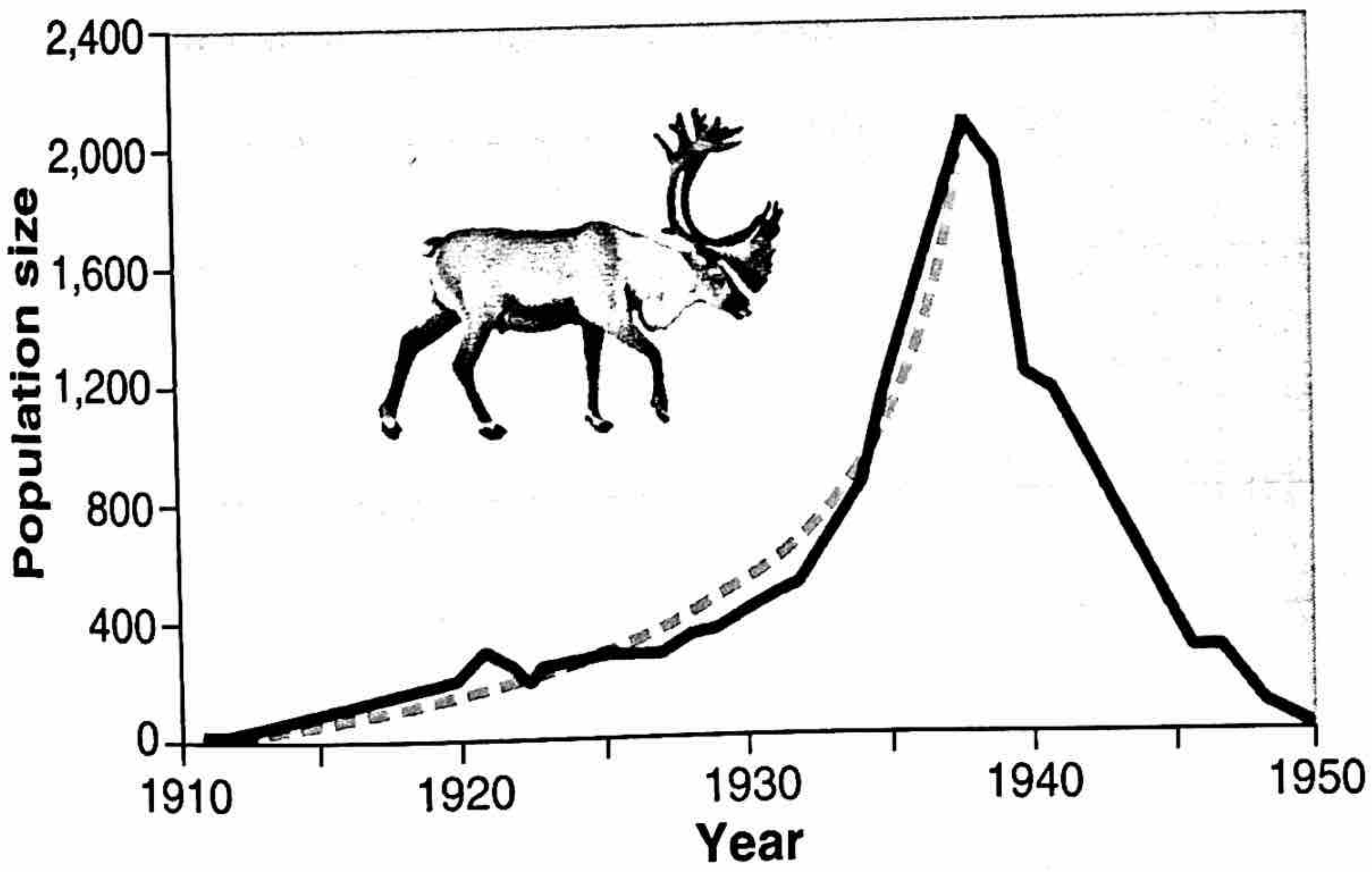

FIGURE 19.3 Growth and decline of a reindeer population. Humans introduced 25 reindeer to St. Paul Island, Alaska, in 1910. The population initially experienced rapid growth (blue line) that approximated a J-shaped exponential growth curve (orange line). In 1938, the population crashed, probably because the animals exhausted the food supply. *(Data from V. B. Scheffer, "The rise and fall of a reindeer herd," Scientific Monthly (1951): 356–362.)*

Such die-offs can take a population well below the carrying capacity of the environment. In subsequent cycles of reproduction, the population may grow large again. FIGURE 19.4 illustrates the recurring cycle of overshoots and die-offs that causes populations to oscillate around the carrying capacity. In many cases, these oscillations decline over time and approach the carrying capacity.

So far we have considered only how populations are limited by resources such as food, water, and the

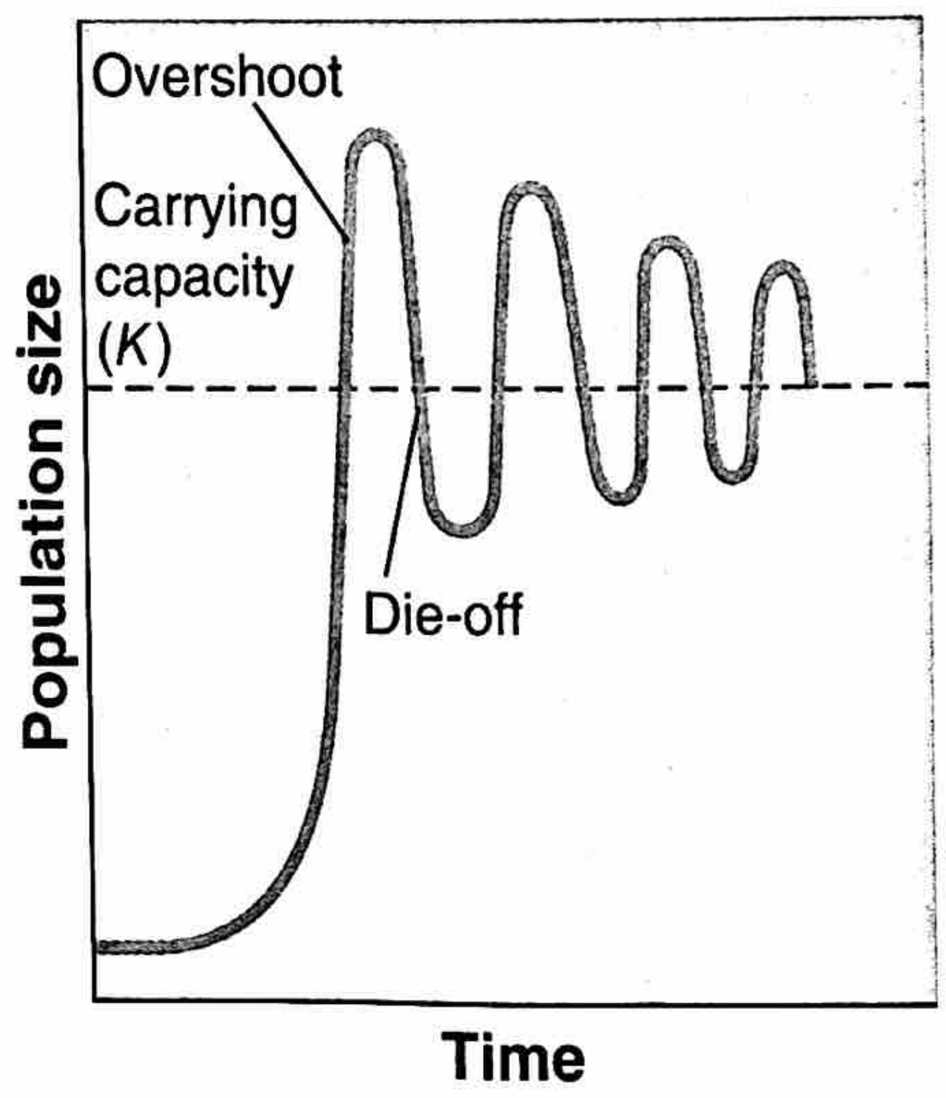

FIGURE 19.4 Population oscillations. Some populations experience recurring cycles of overshoots and die-offs that lead to a pattern of oscillations around the carrying capacity of their environment.

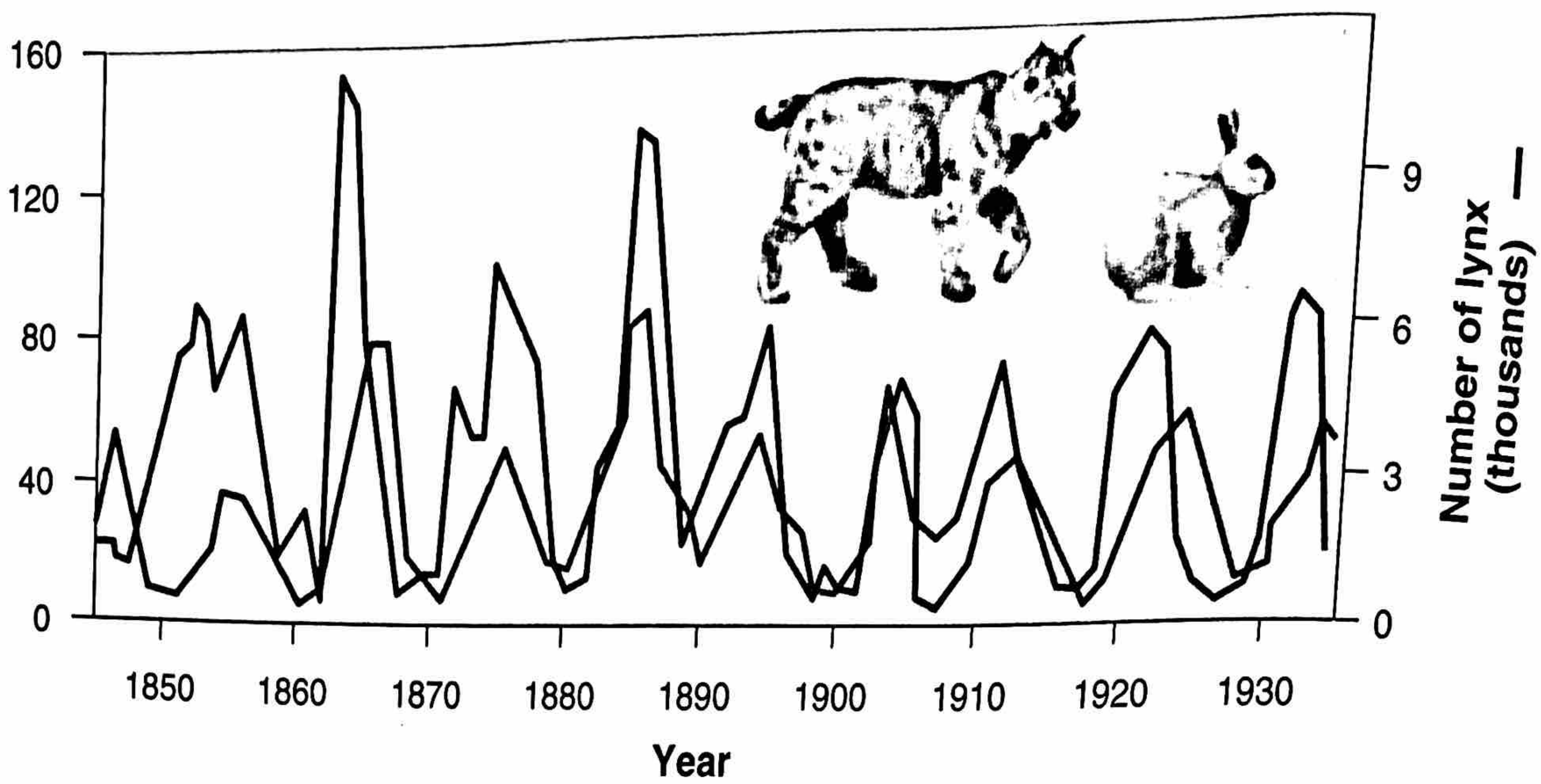

FIGURE 19.5 Population oscillations in lynx and hares. Both lynx and hares exhibit repeated oscillations of abundance, with the lynx population peaking 1 to 2 years after the hare population. When hares are not abundant, there is plenty of food, which allows the hare population to increase. As the hare population increases, there are more hares for lynx to eat, so then the lynx population increases. As the hare population becomes very abundant, they start to run out of food and the hare population dies off. As hares become less abundant, the lynx population subsequently dies off. With less predation and more food once again available, the hare population increases again, and the cycle repeats. *(Data from Hudson's Bay Company)*

availability of nest sites. Predation may play an important additional role in limiting population growth. A classic example is the relationship between snowshoe hares (*Lepus americanus*) and lynx (*Lynx canadensis*) that prey on them in North America. Trapping records from the Hudson's Bay Company, which purchased hare and lynx pelts for nearly 90 years in Canada, indicate that the populations of both species cycle over time. **FIGURE 19.5** shows how this interaction works. The lynx population peaks 1 or 2 years after the hare population peaks. As the hare population increases, it provides more prey for the lynx, and thus the lynx population begins to grow. As the hare population reaches a peak, food for hares becomes scarce, and the hare population dies off. The decline in hares leads to a subsequent decline in the lynx population. Because the low lynx numbers reduce predation, the hare population increases again.

A similar case of predator control of prey populations has been observed on Isle Royale, Michigan, an island in Lake Superior. Wolves (*Canis lupus*) and moose (*Alces alces*) have coexisted on Isle Royale for several decades. Starting in 1981, the wolf population declined sharply, probably as a result of a deadly canine virus. As wolf predation on moose declined, the moose population grew rapidly until it ran out of food and experienced a large die-off that began in 1995. **FIGURE 19.6** shows the changes in both populations over a period of more than 50 years.

K-selected species A species with a low intrinsic growth rate that causes the population to increase slowly until it reaches carrying capacity.

Species have different reproductive strategies and distinct survivorship curves

Population size most commonly increases through reproduction. Population ecologists have identified a range of reproductive strategies in nature.

K-selected Species

***K*-selected species** are species that have a low intrinsic growth rate that causes the population to increase

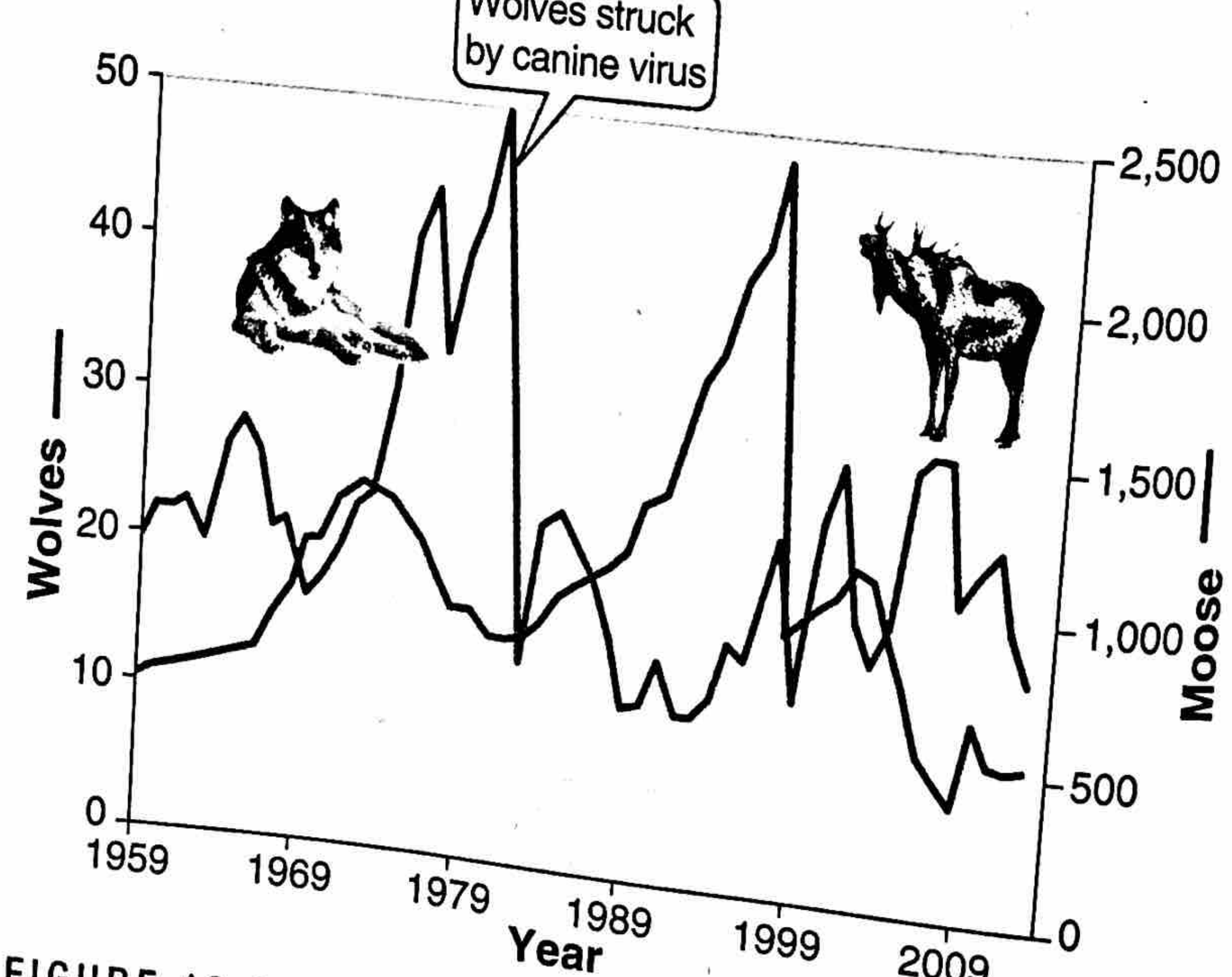

FIGURE 19.6 Predator control of prey populations. As the population of wolves on Isle Royale succumbed to a canine virus, their moose prey experienced a dramatic population increase. *(Data from J. A. Vucetich and R. O. Peterson, Ecological Studies of Wolves on Isle Royale: Annual Report 2007–2008, School of Forest Resources and Environmental Science, Michigan Technological University.)*

slowly until it reaches the carrying capacity of the environment. As a result, the abundance of *K*-selected species is determined by the carrying capacity, and their population fluctuations are small. The name "*K*-selected species" refers to the fact that these populations commonly exist close to their carrying capacity, denoted as *K* in population models.

K-selected species have certain traits in common. For instance, *K*-selected animals are typically large organisms that reach reproductive maturity relatively late, produce a few, large offspring, and provide substantial parental care. Elephants, for example, do not become reproductively mature until they are 13 years old, breed only once every 2 to 4 years, and produce only one calf at a time. Large mammals and most birds are *K*-selected species. For environmental scientists interested in biodiversity management or protection, the slow growth of *K*-selected species poses a challenge; in practical terms, it means that an endangered *K*-selected species cannot respond quickly to efforts to save it from extinction.

TABLE 19.1 Traits of *K*-selected and *r*-selected species

Trait	*K*-selected species	*r*-selected species
Life span	Long	Short
Time to reproductive maturity	Long	Short
Number of reproductive events	Few	Many
Number of offspring	Few	Many
Size of offspring	Large	Small
Parental care	Present	Absent
Population growth rate	Slow	Fast
Population regulation	Density dependent	Density independent
Population dynamics	Stable, near carrying capacity	Highly variable

r-selected Species

At the opposite end of the spectrum from *K*-selected species, ***r*-selected species** have a high intrinsic growth rate that often leads to population overshoots and die-offs. Such populations reproduce often and produce large numbers of offspring. The name *r*-selected species refers to the fact that the intrinsic growth rate is designated as *r* in population models. In contrast to *K*-selected species, populations of *r*-selected species do not typically remain near their carrying capacity, but instead exhibit rapid population growth that is often followed by overshoots and die-offs. Among animals, *r*-selected species tend to be small organisms that reach reproductive maturity relatively early, reproduce frequently, produce many small offspring, and provide little or no parental care. House mice (*Mus musculus*), for example, become reproductively mature at 6 weeks of age, can breed every 5 weeks, and produce up to a dozen offspring at a time. Other *r*-selected organisms include small fishes, many insect species, and weedy plant species. Many organisms that humans consider to be pests, such as cockroaches, dandelions, and rats, are *r*-selected species.

TABLE 19.1 summarizes the traits of *K*-selected and *r*-selected species. These two categories represent opposite ends of a wide spectrum of reproductive strategies. Most species fall somewhere in between these two extremes, and many exhibit combinations of traits from the two extremes. For example, tuna and redwood trees are both long-lived species that take a long time to reach reproductive maturity. Once they do, however, they produce millions of small offspring that receive no parental care.

In addition to different reproductive strategies, species have distinct patterns of survival over the life span of individuals. These patterns can be plotted on a graph as **survivorship curves,** as shown in FIGURE 19.7. There are three basic types of survivorship curves. A **type I survivorship curve** has high survival throughout most of the life span, but then individuals start to die in large numbers as they approach old age. Species with type I curves include *K*-selected species such as elephants, whales, and humans. In contrast, a **type II survivorship curve** has a relatively constant decline in survivorship throughout most of the life span. Species with a type II curve include corals and squirrels. A **type III survivorship curve** has low survivorship early in life with few individuals reaching adulthood. Species with type III curves include *r*-selected species such as mosquitoes and dandelions.

***r*-selected species** A species that has a high intrinsic growth rate, which often leads to population overshoots and die-offs.

Survivorship curve A graph that represents the distinct patterns of species survival as a function of age.

Type I survivorship curve A pattern of survival over time in which there is high survival throughout most of the life span, but then individuals start to die in large numbers as they approach old age.

Type II survivorship curve A pattern of survival over time in which there is a relatively constant decline in survivorship throughout most of the life span.

Type III survivorship curve A pattern of survival over time in which there is low survivorship early in life with few individuals reaching adulthood.

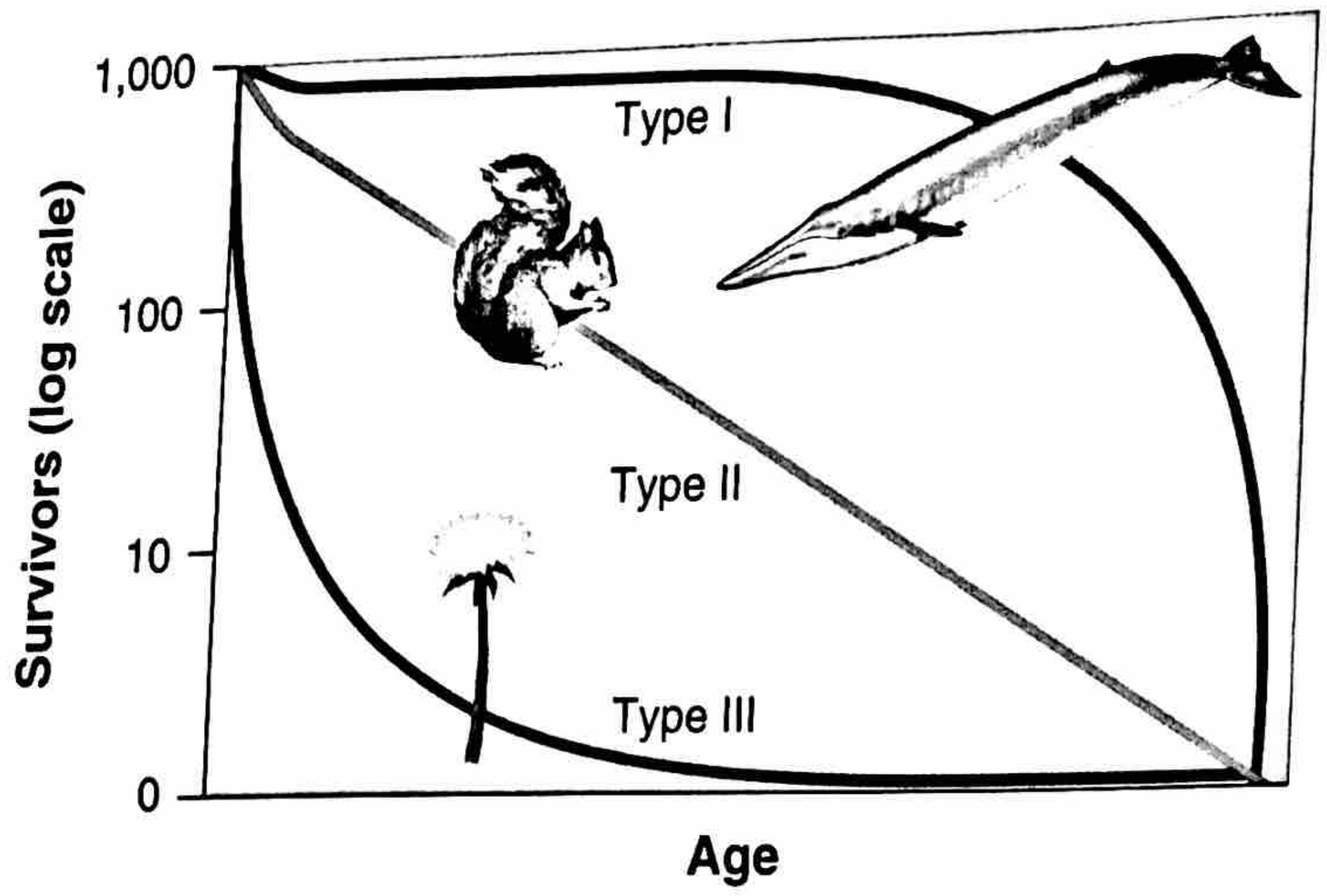

FIGURE 19.7 Survivorship curves. Different species have distinct patterns of survivorship over the life span. Species range from exhibiting excellent survivorship until old age (type I curve) to exhibiting a relatively constant decline in survivorship over time (type II curve) to having very low rates of survivorship early in life (type III curve). *K*-selected species tend to exhibit type I curves, whereas *r*-selected species tend to exhibit type III curves.

Interconnected populations form metapopulations

Cougars (*Puma concolor*)—also called mountain lions or pumas—once lived throughout North America but, because of habitat destruction and overhunting, they are now found primarily in the remote mountain ranges of the western United States. In New Mexico, cougar populations are distributed in patches of mountainous habitat scattered across the desert landscape. These mountain habitats allow the cats to avoid human activities and provide them with reliable sources of water and of prey such as mule deer (*Odocoileus hemionus*).

Because areas of desert separate the cougar's mountain habitats, we can consider the cougars of each mountain range to be a distinct population. Each population has its own dynamics based on local abiotic conditions and prey availability: Large mountain ranges support large cougar populations and smaller mountain ranges support smaller cougar populations. As FIGURE 19.8 shows, cougars sometimes move between mountain ranges, often using strips of natural habitat that connect the separated populations. Strips of natural habitat that connect populations are known as **corridors** and provide some connectedness among the populations. A group of spatially distinct populations that are connected by occasional movements of individuals between them is called a **metapopulation.**

The connectedness among the populations within a metapopulation is an important part of each population's overall persistence. Small populations are more likely than large ones to go extinct. As we have seen, small populations contain relatively little genetic variation and therefore may not be able to adapt to changing environmental conditions. Small populations can also experience *inbreeding depression.* **Inbreeding depression** occurs when individuals with similar genotypes— typically relatives—breed with each other and produce offspring that have an impaired ability to survive and reproduce. This impaired ability occurs when each parent carries one copy of a harmful mutation in his or her genome. When the parents breed, some of their offspring receive two copies of the harmful mutation and, as a result, have poor chances of survival and successful reproduction.

Small populations are also more vulnerable than large populations to catastrophes such as particularly harsh winters that drive down their populations to critically low numbers. In a metapopulation, occasional immigrants from larger nearby populations can add to the size of a small population and introduce new genetic diversity, both of which help reduce the risk of extinction.

Metapopulations can also provide a species with some protection against threats such as diseases. A disease could cause a population living in a single large habitat patch to go extinct. But if a population living in an isolated habitat patch is part of a much larger metapopulation, then, while a disease could wipe out that isolated population, immigrants from other populations could later recolonize the patch and help the species to persist.

Because many habitats are naturally patchy across the landscape, many species are part of metapopulations. For instance, numerous species of butterflies specialize on plants with patchy distributions. Some amphibians live in isolated wetlands, but occasionally disperse to other wetlands. The number of species that exist as metapopulations is growing because human activities have fragmented habitats, dividing single large populations into several smaller populations. Identifying and managing metapopulations is thus an increasingly important part of protecting biodiversity.

Corridor Strips of natural habitat that connect populations.

Metapopulation A group of spatially distinct populations that are connected by occasional movements of individuals between them.

Inbreeding depression When individuals with similar genotypes—typically relatives—breed with each other and produce offspring that have an impaired ability to survive and reproduce.

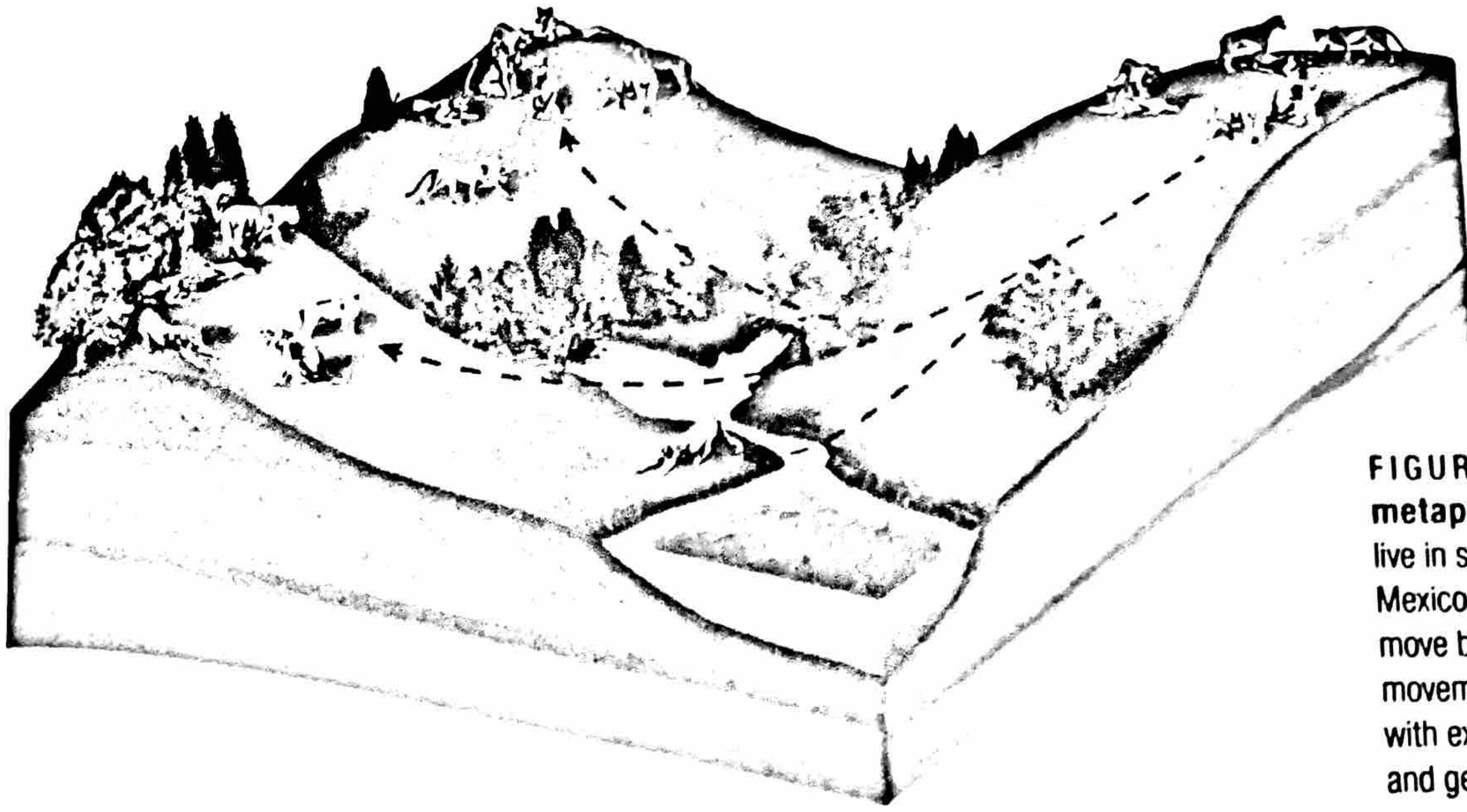

FIGURE 19.8 A cougar metapopulation. Populations of cougars live in separate mountain ranges in New Mexico. Occasionally, however, individuals move between mountain ranges. These movements can recolonize mountain ranges with extinct populations and add individuals and genetic diversity to existing populations.

module

19

REVIEW

In this module, we examined population growth models, which help us understand population increases and decreases. Exponential growth models are the simplest because they assume unlimited resources. Logistic growth models are more realistic because they incorporate a carrying capacity and the associated density-dependent factors that occur in natural populations. By varying assumptions of growth models, we see that a population can overshoot its carrying capacity and experience a die-off. Populations can also oscillate due to predator-prey interactions. Populations can be characterized as either *K*-selected or *r*-selected and have unique types of survivorship curves. Finally, we have seen that a species can exist as a metapopulation composed of multiple, interconnected populations. In the next module, we will move from the population level to the community level and examine how species interactions help to determine which species can persist in natural communities.

Module 19 AP® Review Questions

1. The intrinsic growth rate of a population
   (a) occurs at the population's carrying capacity.
   (b) depends on the limiting resources of the population.
   (c) increases as the population size increases.
   (d) only occurs under ideal conditions.
   (e) decreases as the population size increases.

2. Population growth using the exponential growth model
   (a) increases at a constant rate.
   (b) applies to most populations only after a long time.
   (c) has an increasing intrinsic growth rate.
   (d) represents ideal conditions that rarely occur in natural populations.
   (e) incorporates the carrying capacity of the population.

3. An *r*-selected species characteristically has
   (a) a type I survivorship curve.
   (b) few offspring.
   (c) a population near carrying capacity.
   (d) significant parental care.
   (e) a fast population growth rate.

4. Which is true of a population overshoot?
   (a) It occurs when reproduction quickly responds to changes in food supply.
   (b) It is followed by a die-off.
   (c) It is most likely to be experienced by *K*-selected species.
   (d) It rarely occurs in species with type III survivorship curves.
   (e) It occurs when a species stops growing after reaching the carrying capacity.