

CHAPTER 45

Population and Community Ecology



Figure 45.1 Asian carp jump out of the water in response to electrofishing. The Asian carp in the photograph on the right were harvested from the Little Calumet River in Illinois in May, 2010, using rotenone, a toxin often used as an insecticide, in an effort to learn more about the population of the species. (credit left image: modification of work by USGS; credit right image: modification of work by Lt. David French, USCG)

INTRODUCTION Imagine sailing down a river in a small motorboat on a weekend afternoon; the water is smooth and you are enjoying the warm sunshine and cool breeze when suddenly you are hit in the head by a 20-pound silver carp. This is now a risk on many rivers and canal systems in Illinois and Missouri because of the presence of Asian carp.

This fish—actually a group of species including the silver, black, grass, and big head carp—has been farmed and eaten in China for over 1000 years. It is one of the most important aquaculture food resources worldwide. In the United States, however, Asian carp is considered a dangerous invasive species that disrupts community structure and composition to the point of threatening native species.

Chapter Outline

- 45.1 Population Demography
- 45.2 Life Histories and Natural Selection
- 45.3 Environmental Limits to Population Growth
- 45.4 Population Dynamics and Regulation
- 45.5 Human Population Growth
- 45.6 Community Ecology
- 45.7 Behavioral Biology: Proximate and Ultimate Causes of Behavior

45.1 Population Demography

By the end of this section, you will be able to do the following:

- Describe how ecologists measure population size and density
- Describe three different patterns of population distribution
- Use life tables to calculate mortality rates
- Describe the three types of survivorship curves and relate them to specific populations

Populations are dynamic entities. Populations consist all of the species living within a specific area, and populations fluctuate based on a number of factors: seasonal and yearly changes in the environment, natural disasters such as forest fires and volcanic eruptions, and competition for resources between and within species. The statistical study of population dynamics, **demography**, uses a series of mathematical tools to investigate how populations respond to changes in their biotic and abiotic environments. Many of these tools were originally designed to study human populations. For example, **life tables**, which detail the life expectancy of individuals within a population, were initially developed by life insurance companies to set insurance rates. In fact, while the term “demographics” is commonly used when discussing humans, all living populations can be studied using this approach.

Population Size and Density

The study of any population usually begins by determining how many individuals of a particular species exist, and how closely associated they are with each other. Within a particular habitat, a population can be characterized by its **population size (N)**, the total number of individuals, and its **population density**, the number of individuals within a specific area or volume. Population size and density are the two main characteristics used to describe and understand populations. For example, populations with more individuals may be more stable than smaller populations based on their genetic variability, and thus their potential to adapt to the environment. Alternatively, a member of a population with low population density (more spread out in the habitat), might have more difficulty finding a mate to reproduce compared to a population of higher density. As is shown in [Figure 45.2](#), smaller organisms tend to be more densely distributed than larger organisms.



VISUAL CONNECTION

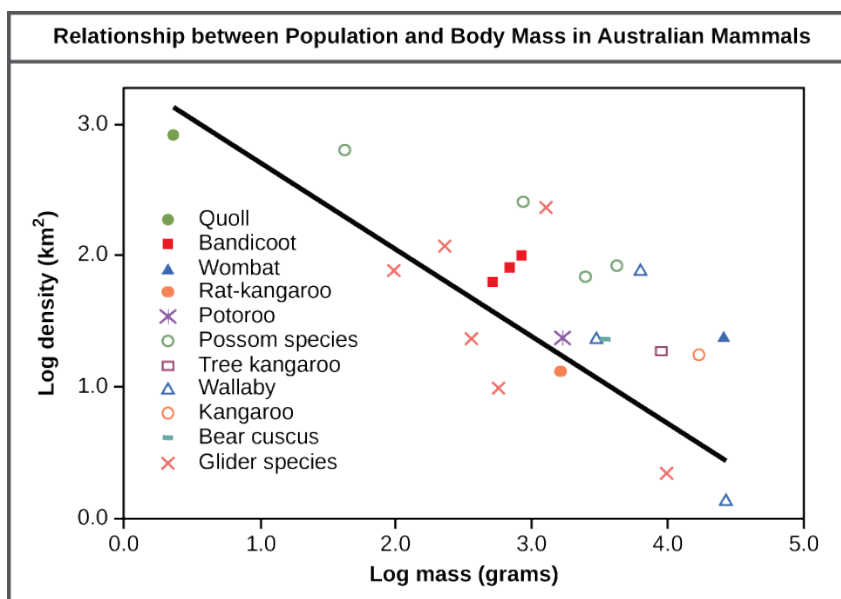


Figure 45.2 Australian mammals show a typical inverse relationship between population density and body size.

As this graph shows, population density typically decreases with increasing body size. Why do you think this

is the case?

Population Research Methods

The most accurate way to determine population size is to simply count all of the individuals within the habitat. However, this method is often not logistically or economically feasible, especially when studying large habitats. Thus, scientists usually study populations by sampling a representative portion of each habitat and using this data to make inferences about the habitat as a whole. A variety of methods can be used to sample populations to determine their size and density. For immobile organisms such as plants, or for very small and slow-moving organisms, a **quadrat** may be used (Figure 45.3). A quadrat is a way of marking off square areas within a habitat, either by staking out an area with sticks and string, or by the use of a wood, plastic, or metal square placed on the ground. After setting the quadrats, researchers then count the number of individuals that lie within their boundaries. Multiple quadrat samples are performed throughout the habitat at several random locations to estimate the population size and density within the entire habitat. The number and size of quadrat samples depends on the type of organisms under study and other factors, including the density of the organism. For example, if sampling daffodils, a 1 m² quadrat might be used. With giant redwoods, on the other hand, a larger quadrat of 100 m² might be employed. This ensures that enough individuals of the species are counted to get an accurate sample that correlates with the habitat, including areas not sampled.

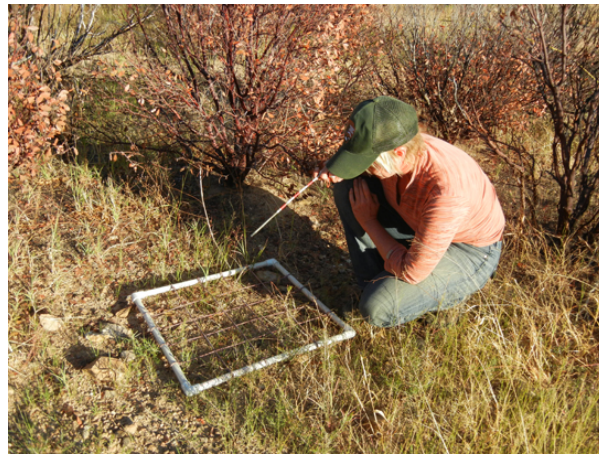


Figure 45.3 A scientist uses a quadrat to measure population size and density. (credit: NPS Sonoran Desert Network)

For mobile organisms, such as mammals, birds, or fish, scientists use a technique called **mark and recapture**. This method involves marking a sample of captured animals in some way (such as tags, bands, paint, or other body markings), and then releasing them back into the environment to allow them to mix with the rest of the population. Later, researchers collect a new sample, including some individuals that are marked (recaptures) and some individuals that are unmarked (Figure 45.4).

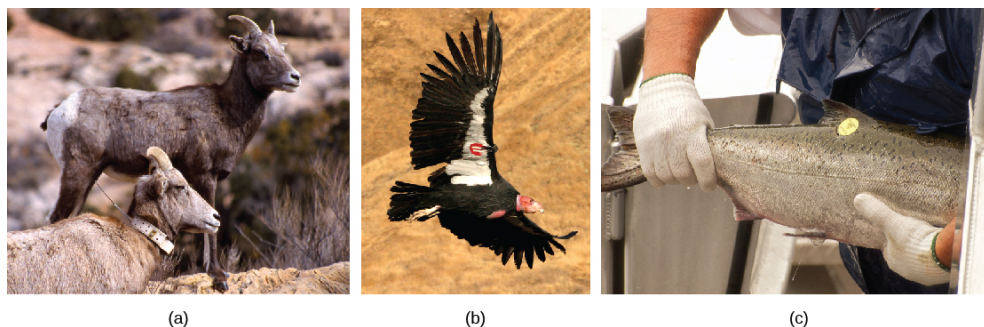


Figure 45.4 Mark and recapture is used to measure the population size of mobile animals such as (a) bighorn sheep, (b) the California condor, and (c) salmon. (credit a: modification of work by Neal Herbert, NPS; credit b: modification of work by Pacific Southwest Region USFWS; credit c: modification of work by Ingrid Taylor)

Using the ratio of marked and unmarked individuals, scientists determine how many individuals are in the sample. From this, calculations are used to estimate the total population size. This method assumes that the larger the population, the lower the percentage of tagged organisms that will be recaptured since they will have mixed with more untagged individuals. For example,

if 80 deer are captured, tagged, and released into the forest, and later 100 deer are captured and 20 of them are already marked, we can estimate the population size (N) using the following equation:

$$\frac{(\text{number marked first catch} \times \text{total number of second catch})}{\text{number marked second catch}} = N$$

Using our example, the population size would be estimated at 400.

$$\frac{(80 \times 100)}{20} = 400$$

Therefore, there are an estimated 400 total individuals in the original population.

There are some limitations to the mark and recapture method. Some animals from the first catch may learn to avoid capture in the second round, thus inflating population estimates. Alternatively, some animals may prefer to be retrapped (especially if a food reward is offered), resulting in an underestimate of population size. Also, some species may be harmed by the marking technique, reducing their survival. A variety of other techniques have been developed, including the electronic tracking of animals tagged with radio transmitters and the use of data from commercial fishing and trapping operations to estimate the size and health of populations and communities.

Species Distribution

In addition to measuring simple density, further information about a population can be obtained by looking at the distribution of the individuals. **Species dispersion patterns** (or distribution patterns) show the spatial relationship between members of a population within a habitat at a particular point in time. In other words, they show whether members of the species live close together or far apart, and what patterns are evident when they are spaced apart.

Individuals in a population can be equally spaced apart, dispersed randomly with no predictable pattern, or clustered in groups. These are known as uniform, random, and clumped dispersion patterns, respectively ([Figure 45.5](#)). Uniform dispersion is observed in plants that secrete substances inhibiting the growth of nearby individuals (such as the release of toxic chemicals by the sage plant *Salvia leucophylla*, a phenomenon called allelopathy) and in animals like the penguin that maintain a defined territory. An example of random dispersion occurs with dandelion and other plants that have wind-dispersed seeds that germinate wherever they happen to fall in a favorable environment. A clumped dispersion may be seen in plants that drop their seeds straight to the ground, such as oak trees, or in animals that live in groups (schools of fish or herds of elephants). Clumped dispersions may also be a function of habitat heterogeneity. Thus, the dispersion of the individuals within a population provides more information about how they interact with each other than does a simple density measurement. Just as lower density species might have more difficulty finding a mate, solitary species with a random distribution might have a similar difficulty when compared to social species clumped together in groups.

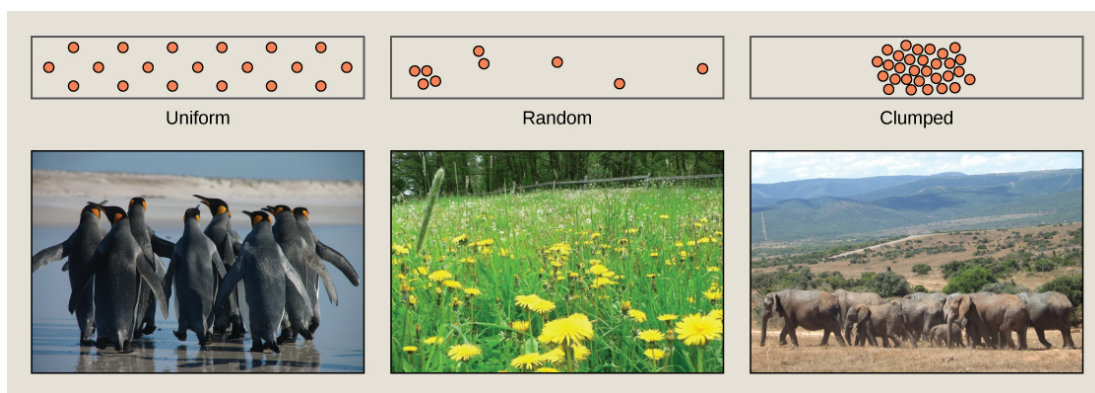


Figure 45.5 Species may have uniform, random, or clumped distribution. Territorial birds such as penguins tend to have uniform distribution. Plants such as dandelions with wind-dispersed seeds tend to be randomly distributed. Animals such as elephants that travel in groups exhibit clumped distribution. (credit a: modification of work by Ben Tubby; credit b: modification of work by Rosendahl; credit c: modification of work by Rebecca Wood)

Demography

While population size and density describe a population at one particular point in time, scientists must use demography to

study the dynamics of a population. Demography is the statistical study of population changes over time: birth rates, death rates, and life expectancies. Each of these measures, especially birth rates, may be affected by the population characteristics described above. For example, a large population size results in a higher birth rate because more potentially reproductive individuals are present. In contrast, a large population size can also result in a higher death rate because of competition, disease, and the accumulation of waste. Similarly, a higher population density or a clumped dispersion pattern results in more potential reproductive encounters between individuals, which can increase birth rate. Lastly, a female-biased sex ratio (the ratio of males to females) or **age structure** (the proportion of population members at specific age ranges) composed of many individuals of reproductive age can increase birth rates.

In addition, the demographic characteristics of a population can influence how the population grows or declines over time. If birth and death rates are equal, the population remains stable. However, the population size will increase if birth rates exceed death rates; the population will decrease if birth rates are less than death rates. Life expectancy is another important factor; the length of time individuals remain in the population impacts local resources, reproduction, and the overall health of the population. These demographic characteristics are often displayed in the form of a life table.

Life Tables

Life tables provide important information about the life history of an organism. Life tables divide the population into age groups and often sexes, and show how long a member of that group is likely to live. They are modeled after actuarial tables used by the insurance industry for estimating human life expectancy. Life tables may include the probability of individuals dying before their next birthday (i.e., their **mortality rate**), the percentage of surviving individuals dying at a particular age interval, and their life expectancy at each interval. An example of a life table is shown in [Table 45.1](#) from a study of Dall mountain sheep, a species native to northwestern North America. Notice that the population is divided into age intervals (column A). The mortality rate (per 1000), shown in column D, is based on the number of individuals dying during the age interval (column B) divided by the number of individuals surviving at the beginning of the interval (Column C), multiplied by 1000.

$$\text{mortality rate} = \frac{\text{number of individuals dying}}{\text{number of individuals surviving}} \times 1000$$

For example, between ages three and four, 12 individuals die out of the 776 that were remaining from the original 1000 sheep. This number is then multiplied by 1000 to get the mortality rate per thousand.

$$\text{mortality rate} = \frac{12}{776} \times 1000 \approx 15.5$$

As can be seen from the mortality rate data (column D), a high death rate occurred when the sheep were between 6 and 12 months old, and then increased even more from 8 to 12 years old, after which there were few survivors. The data indicate that if a sheep in this population were to survive to age one, it could be expected to live another 7.7 years on average, as shown by the life expectancy numbers in column E.

Life Table of Dall Mountain Sheep¹

Age interval (years)	Number dying in age interval out of 1000 born	Number surviving at beginning of age interval out of 1000 born	Mortality rate per 1000 alive at beginning of age interval	Life expectancy or mean lifetime remaining to those attaining age interval
0-0.5	54	1000	54.0	7.06
0.5-1	145	946	153.3	--
1-2	12	801	15.0	7.7
2-3	13	789	16.5	6.8

Table 45.1 This life table of *Ovis dalli* shows the number of deaths, number of survivors, mortality rate, and life expectancy at

¹Data Adapted from Edward S. Deevey, Jr., "Life Tables for Natural Populations of Animals," *The Quarterly Review of Biology* 22, no. 4 (December 1947):

Age interval (years)	Number dying in age interval out of 1000 born	Number surviving at beginning of age interval out of 1000 born	Mortality rate per 1000 alive at beginning of age interval	Life expectancy or mean lifetime remaining to those attaining age interval
3-4	12	776	15.5	5.9
4-5	30	764	39.3	5.0
5-6	46	734	62.7	4.2
6-7	48	688	69.8	3.4
7-8	69	640	107.8	2.6
8-9	132	571	231.2	1.9
9-10	187	439	426.0	1.3
10-11	156	252	619.0	0.9
11-12	90	96	937.5	0.6
12-13	3	6	500.0	1.2
13-14	3	3	1000	0.7

Table 45.1 This life table of *Ovis dalli* shows the number of deaths, number of survivors, mortality rate, and life expectancy at each age interval for the Dall mountain sheep.

Survivorship Curves

Another tool used by population ecologists is a **survivorship curve**, which is a graph of the number of individuals surviving at each age interval plotted versus time (usually with data compiled from a life table). These curves allow us to compare the life histories of different populations (Figure 45.6). Humans and most primates exhibit a Type I survivorship curve because a high percentage of offspring survive their early and middle years—death occurs predominantly in older individuals. These types of species usually have small numbers of offspring at one time, and they give a high amount of parental care to them to ensure their survival. Birds are an example of an intermediate or Type II survivorship curve because birds die more or less equally at each age interval. These organisms also may have relatively few offspring and provide significant parental care. Trees, marine invertebrates, and most fishes exhibit a Type III survivorship curve because very few of these organisms survive their younger years; however, those that make it to an old age are more likely to survive for a relatively long period of time. Organisms in this category usually have a very large number of offspring, but once they are born, little parental care is provided. Thus these offspring are “on their own” and vulnerable to predation, but their sheer numbers assure the survival of enough individuals to perpetuate the species.

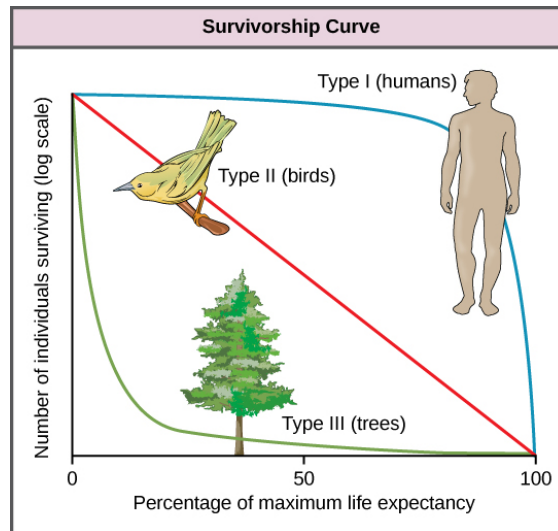


Figure 45.6 Survivorship curves show the distribution of individuals in a population according to age. Humans and most mammals have a Type I survivorship curve because death primarily occurs in the older years. Birds have a Type II survivorship curve, as death at any age is equally probable. Trees have a Type III survivorship curve because very few survive the younger years, but after a certain age, individuals are much more likely to survive.

45.2 Life Histories and Natural Selection

By the end of this section, you will be able to do the following:

- Describe how life history patterns are influenced by natural selection
- Explain different life history patterns and how different reproductive strategies affect species' survival

A species' **life history** describes the series of events over its lifetime, such as how resources are allocated for growth, maintenance, and reproduction. Life history traits affect the life table of an organism. A species' life history is genetically determined and shaped by the environment and natural selection.

Life History Patterns and Energy Budgets

Energy is required by all living organisms for their growth, maintenance, and reproduction; at the same time, energy is often a major limiting factor in determining an organism's survival. Plants, for example, acquire energy from the sun via photosynthesis, but must expend this energy to grow, maintain health, and produce energy-rich seeds to produce the next generation. Animals have the additional burden of using some of their energy reserves to acquire food. Furthermore, some animals must expend energy caring for their offspring. Thus, all species have an **energy budget**: they must balance energy intake with their use of energy for metabolism, reproduction, parental care, and energy storage (such as bears building up body fat for winter hibernation).

Parental Care and Fecundity

Fecundity is the potential reproductive capacity of an individual within a population. In other words, fecundity describes how many offspring could ideally be produced if an individual has as many offspring as possible, repeating the reproductive cycle as soon as possible after the birth of the offspring. In animals, fecundity is inversely related to the amount of parental care given to an individual offspring. Species, such as many marine invertebrates, that produce many offspring usually provide little if any care for the offspring (they would not have the energy or the ability to do so anyway). Most of their energy budget is used to produce many tiny offspring. Animals with this strategy are often self-sufficient at a very early age. This is because of the energy tradeoff these organisms have made to maximize their evolutionary fitness. Because their energy is used for producing offspring instead of parental care, it makes sense that these offspring have some ability to be able to move within their environment and find food and perhaps shelter. Even with these abilities, their small size makes them extremely vulnerable to predation, so the production of many offspring allows enough of them to survive to maintain the species.

Animal species that have few offspring during a reproductive event usually give extensive parental care, devoting much of their energy budget to these activities, sometimes at the expense of their own health. This is the case with many mammals, such as humans, kangaroos, and pandas. The offspring of these species are relatively helpless at birth and need to develop before they

achieve self-sufficiency.

Plants with low fecundity produce few energy-rich seeds (such as coconuts and chestnuts) with each having a good chance to germinate into a new organism; plants with high fecundity usually have many small, energy-poor seeds (like orchids) that have a relatively poor chance of surviving. Although it may seem that coconuts and chestnuts have a better chance of surviving, the energy tradeoff of the orchid is also very effective. It is a matter of where the energy is used, for large numbers of seeds or for fewer seeds with more energy.

Early versus Late Reproduction

The timing of reproduction in a life history also affects species survival. Organisms that reproduce at an early age have a greater chance of producing offspring, but this is usually at the expense of their growth and the maintenance of their health.

Conversely, organisms that start reproducing later in life often have greater fecundity or are better able to provide parental care, but they risk that they will not survive to reproductive age. Examples of this can be seen in fishes. Small fish, like guppies, use their energy to reproduce rapidly, but never attain the size that would give them defense against some predators. Larger fish, like the bluegill or shark, use their energy to attain a large size, but do so with the risk that they will die before they can reproduce or at least reproduce to their maximum. These different energy strategies and tradeoffs are key to understanding the evolution of each species as it maximizes its fitness and fills its niche. In terms of energy budgeting, some species “blow it all” and use up most of their energy reserves to reproduce early before they die. Other species delay having reproduction to become stronger, more experienced individuals and to make sure that they are strong enough to provide parental care if necessary.

Single versus Multiple Reproductive Events

Some life history traits, such as fecundity, timing of reproduction, and parental care, can be grouped together into general strategies that are used by multiple species. **Semelparity** occurs when a species reproduces only once during its lifetime and then dies. Such species use most of their resource budget during a single reproductive event, sacrificing their health to the point that they do not survive. Examples of semelparity are bamboo, which flowers once and then dies, and the Chinook salmon ([Figure 45.7a](#)), which uses most of its energy reserves to migrate from the ocean to its freshwater nesting area, where it reproduces and then dies. Scientists have posited alternate explanations for the evolutionary advantage of the Chinook’s post-reproduction death: a programmed suicide caused by a massive release of corticosteroid hormones, presumably so the parents can become food for the offspring, or simple exhaustion caused by the energy demands of reproduction; these are still being debated.

Iteroparity describes species that reproduce repeatedly during their lives. Some animals are able to mate only once per year, but survive multiple mating seasons. The pronghorn antelope is an example of an animal that goes into a seasonal estrus cycle (“heat”): a hormonally induced physiological condition preparing the body for successful mating ([Figure 45.7b](#)). Females of these species mate only during the estrus phase of the cycle. A different pattern is observed in primates, including humans and chimpanzees, which may attempt reproduction at any time during their reproductive years, even though their menstrual cycles make pregnancy likely only a few days per month during ovulation ([Figure 45.7c](#)).



Figure 45.7 The (a) Chinook salmon mates once and dies. The (b) pronghorn antelope mates during specific times of the year during its reproductive life. Primates, such as humans and (c) chimpanzees, may mate on any day, independent of ovulation. (credit a: modification of work by Roger Tabor, USFWS; credit b: modification of work by Mark Gocke, USDA; credit c: modification of work by “Shiny Things”/Flickr)

LINK TO LEARNING

Play this [interactive PBS evolution-based mating game \(http://openstax.org/l/mating_game\)](http://openstax.org/l/mating_game) to learn more about reproductive strategies.



EVOLUTION CONNECTION

Energy Budgets, Reproductive Costs, and Sexual Selection in *Drosophila*

Research into how animals allocate their energy resources for growth, maintenance, and reproduction has used a variety of experimental animal models. Some of this work has been done using the common fruit fly, *Drosophila melanogaster*. Studies have shown that not only does reproduction have a cost as far as how long male fruit flies live, but also fruit flies that have already mated several times have limited sperm remaining for reproduction. Fruit flies maximize their last chances at reproduction by selecting optimal mates.

In a 1981 study, male fruit flies were placed in enclosures with either virgin or inseminated females. The males that mated with virgin females had shorter life spans than those in contact with the same number of inseminated females with which they were unable to mate. This effect occurred regardless of how large (indicative of their age) the males were. Thus, males that did not mate lived longer, allowing them more opportunities to find mates in the future.

More recent studies, performed in 2006, show how males select the female with which they will mate and how this is affected by previous matings (Figure 45.8).² Males were allowed to select between smaller and larger females. Findings showed that larger females had greater fecundity, producing twice as many offspring per mating as the smaller females did. Males that had previously mated, and thus had lower supplies of sperm, were termed “resource-depleted,” while males that had not mated were termed “non-resource-depleted.” The study showed that although non-resource-depleted males preferentially mated with larger females, this selection of partners was more pronounced in the resource-depleted males. Thus, males with depleted sperm supplies, which were limited in the number of times that they could mate before they replenished their sperm supply, selected larger, more fecund females, thus maximizing their chances for offspring. This study was one of the first to show that the physiological state of the male affected its mating behavior in a way that clearly maximizes its use of limited reproductive resources.

	Ratio large/small females mated
Non sperm-depleted	8 ± 5
Sperm-depleted	15 ± 5

Figure 45.8 Male fruit flies that had previously mated (sperm-depleted) picked larger, more fecund females more often than those that had not mated (non-sperm-depleted). This change in behavior causes an increase in the efficiency of a limited reproductive resource: sperm.

These studies demonstrate two ways in which the energy budget is a factor in reproduction. First, energy expended on mating may reduce an animal's lifespan, but by this time they have already reproduced, so in the context of natural selection this early death is not of much evolutionary importance. Second, when resources such as sperm (and the energy needed to replenish it) are low, an organism's behavior can change to give them the best chance of passing their genes on to the next generation. These changes in behavior, so important to evolution, are studied in a discipline known as behavioral biology, or ethology, at the interface between population biology and psychology.

45.3 Environmental Limits to Population Growth

By the end of this section, you will be able to do the following:

- Explain the characteristics of and differences between exponential and logistic growth patterns
- Give examples of exponential and logistic growth in natural populations
- Describe how natural selection and environmental adaptation led to the evolution of particular life history patterns

Although life histories describe the way many characteristics of a population (such as their age structure) change over time in a general way, population ecologists make use of a variety of methods to model population dynamics mathematically. These more

²Adapted from Phillip G. Byrne and William R. Rice, “Evidence for adaptive male mate choice in the fruit fly *Drosophila melanogaster*,” *Proc Biol Sci.* 273, no. 1589 (2006): 917–922, doi: 10.1098/rspb.2005.3372.

precise models can then be used to accurately describe changes occurring in a population and better predict future changes. Certain long-accepted models are now being modified or even abandoned due to their lack of predictive ability, and scholars strive to create effective new models.

Exponential Growth

Charles Darwin, in his theory of natural selection, was greatly influenced by the English clergyman Thomas Malthus. Malthus published a book in 1798 stating that populations with unlimited natural resources grow very rapidly, and then population growth decreases as resources become depleted. This accelerating pattern of increasing population size is called **exponential growth**.

The best example of exponential growth is seen in bacteria. Bacteria reproduce by prokaryotic fission. This division takes about an hour for many bacterial species. If 1000 bacteria are placed in a large flask with an unlimited supply of nutrients (so the nutrients will not become depleted), after an hour, there is one round of division and each organism divides, resulting in 2000 organisms—an increase of 1000. In another hour, each of the 2000 organisms will double, producing 4000, an increase of 2000 organisms. After the third hour, there should be 8000 bacteria in the flask, an increase of 4000 organisms. The important concept of exponential growth is the accelerating **population growth rate**—the number of organisms added in each reproductive generation—that is, it is increasing at a greater and greater rate. After 1 day and 24 of these cycles, the population would have increased from 1000 to more than 16 billion. When the population size, N , is plotted over time, a **J-shaped growth curve** is produced (Figure 45.9).

The bacteria example is not representative of the real world where resources are limited. Furthermore, some bacteria will die during the experiment and thus not reproduce, lowering the growth rate. Therefore, when calculating the growth rate of a population, the **death rate (D)** (number organisms that die during a particular time interval) is subtracted from the **birth rate (B)** (number organisms that are born during that interval). This is shown in the following formula:

$$\frac{\Delta N \text{ (change in number)}}{\Delta T \text{ (change in time)}} = B \text{ (birth rate)} - D \text{ (death rate)}$$

The birth rate is usually expressed on a per capita (for each individual) basis. Thus, B (birth rate) = bN (the per capita birth rate “ b ” multiplied by the number of individuals “ N ”) and D (death rate) = dN (the per capita death rate “ d ” multiplied by the number of individuals “ N ”). Additionally, ecologists are interested in the population at a particular point in time, an infinitely small time interval. For this reason, the terminology of differential calculus is used to obtain the “instantaneous” growth rate, replacing the *change* in number and time with an instant-specific measurement of number and time.

$$\frac{dN}{dT} = bN - dN = (b - d)N$$

Notice that the “ d ” associated with the first term refers to the derivative (as the term is used in calculus) and is different from the death rate, also called “ d .” The difference between birth and death rates is further simplified by substituting the term “ r ” (intrinsic rate of increase) for the relationship between birth and death rates:

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

The value “ r ” can be positive, meaning the population is increasing in size; or negative, meaning the population is decreasing in size; or zero, where the population’s size is unchanging, a condition known as **zero population growth**. A further refinement of the formula recognizes that different species have inherent differences in their intrinsic rate of increase (often thought of as the potential for reproduction), even under ideal conditions. Obviously, a bacterium can reproduce more rapidly and have a higher intrinsic rate of growth than a human. The maximal growth rate for a species is its **biotic potential, or r_{\max}** , thus changing the equation to:

$$\frac{dN}{dT} = r_{\max}N$$

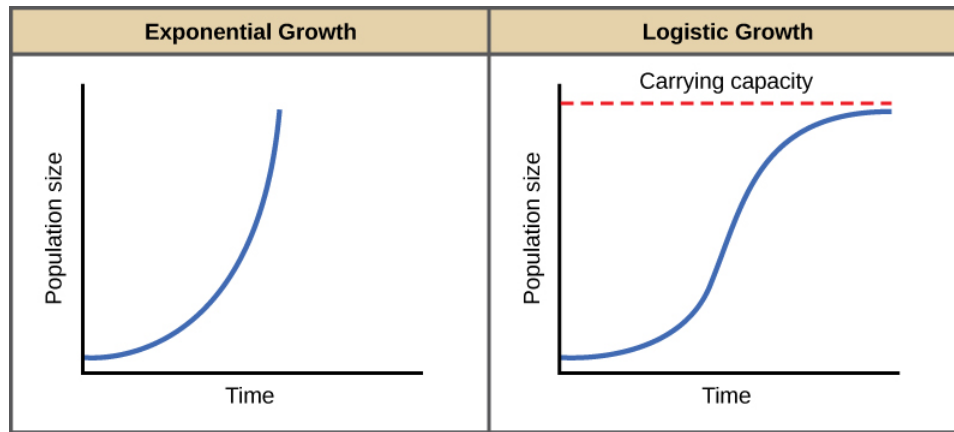


Figure 45.9 When resources are unlimited, populations exhibit exponential growth, resulting in a J-shaped curve. When resources are limited, populations exhibit logistic growth. In logistic growth, population expansion decreases as resources become scarce, and it levels off when the carrying capacity of the environment is reached, resulting in an S-shaped curve.

Logistic Growth

Exponential growth is possible only when infinite natural resources are available; this is not the case in the real world. Charles Darwin recognized this fact in his description of the “struggle for existence,” which states that individuals will compete (with members of their own or other species) for limited resources. The successful ones will survive to pass on their own characteristics and traits (which we know now are transferred by genes) to the next generation at a greater rate (natural selection). To model the reality of limited resources, population ecologists developed the **logistic growth** model.

Carrying Capacity and the Logistic Model

In the real world, with its limited resources, exponential growth cannot continue indefinitely. Exponential growth may occur in environments where there are few individuals and plentiful resources, but when the number of individuals gets large enough, resources will be depleted, slowing the growth rate. Eventually, the growth rate will plateau or level off (Figure 45.9). This population size, which represents the maximum population size that a particular environment can support, is called the **carrying capacity**, or K .

The formula we use to calculate logistic growth adds the carrying capacity as a moderating force in the growth rate. The expression “ $K - N$ ” indicates how many individuals may be added to a population at a given stage, and “ $K - N$ ” divided by “ K ” is the fraction of the carrying capacity available for further growth. Thus, the exponential growth model is restricted by this factor to generate the logistic growth equation:

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

Notice that when N is very small, $(K - N)/K$ becomes close to K/K or 1, and the right side of the equation reduces to $r_{\max}N$, which means the population is growing exponentially and is not influenced by carrying capacity. On the other hand, when N is large, $(K - N)/K$ comes close to zero, which means that population growth will be slowed greatly or even stopped. Thus, population growth is greatly slowed in large populations by the carrying capacity K . This model also allows for the population of a negative population growth, or a population decline. This occurs when the number of individuals in the population exceeds the carrying capacity (because the value of $(K - N)/K$ is negative).

A graph of this equation yields an **S-shaped curve** (Figure 45.9), and it is a more realistic model of population growth than exponential growth. There are three different sections to an S-shaped curve. Initially, growth is exponential because there are few individuals and ample resources available. Then, as resources begin to become limited, the growth rate decreases. Finally, growth levels off at the carrying capacity of the environment, with little change in population size over time.

Role of Intraspecific Competition

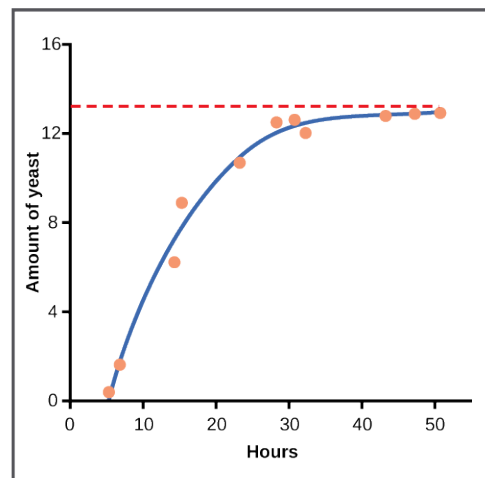
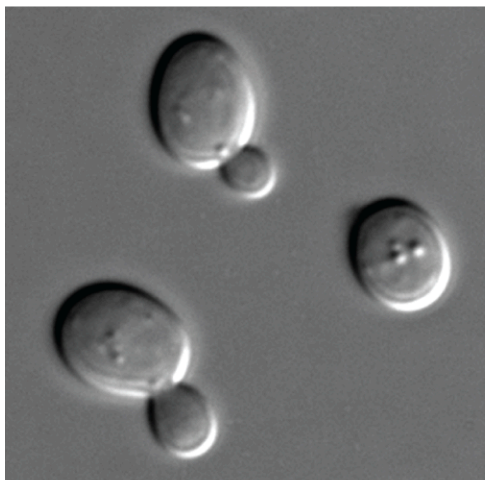
The logistic model assumes that every individual within a population will have equal access to resources and, thus, an equal chance for survival. For plants, the amount of water, sunlight, nutrients, and the space to grow are the important resources, whereas in animals, important resources include food, water, shelter, nesting space, and mates.

In the real world, phenotypic variation among individuals within a population means that some individuals will be better adapted to their environment than others. The resulting competition between population members of the same species for resources is termed **intraspecific competition** (intra- = “within”; -specific = “species”). Intraspecific competition for resources may not affect populations that are well below their carrying capacity—resources are plentiful and all individuals can obtain what they need. However, as population size increases, this competition intensifies. In addition, the accumulation of waste products can reduce an environment’s carrying capacity.

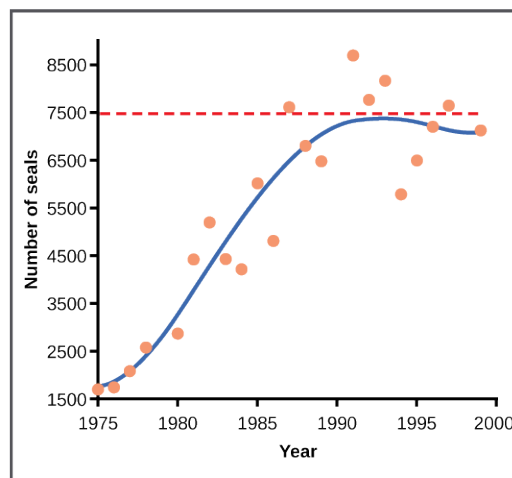
Examples of Logistic Growth

Yeast, a microscopic fungus used to make bread and alcoholic beverages, exhibits the classical S-shaped curve when grown in a test tube (Figure 45.10a). Its growth levels off as the population depletes the nutrients. In the real world, however, there are variations to this idealized curve. Examples in wild populations include sheep and harbor seals (Figure 45.10b). In both examples, the population size exceeds the carrying capacity for short periods of time and then falls below the carrying capacity afterwards. This fluctuation in population size continues to occur as the population oscillates around its carrying capacity. Still, even with this oscillation, the logistic model is confirmed.

VISUAL CONNECTION



(a)



(b)

Figure 45.10 (a) Yeast grown in ideal conditions in a test tube show a classical S-shaped logistic growth curve, whereas (b) a natural population of seals shows real-world fluctuation.

If the major food source of the seals declines due to pollution or overfishing, which of the following would likely occur?

- a. The carrying capacity of seals would decrease, as would the seal population.
- b. The carrying capacity of seals would decrease, but the seal population would remain the same.
- c. The number of seal deaths would increase but the number of births would also increase, so the population size would remain the same.
- d. The carrying capacity of seals would remain the same, but the population of seals would decrease.

45.4 Population Dynamics and Regulation

By the end of this section, you will be able to do the following:

- Give examples of how the carrying capacity of a habitat may change
- Compare and contrast density-dependent growth regulation and density-independent growth regulation, giving examples
- Give examples of exponential and logistic growth in wild animal populations
- Describe how natural selection and environmental adaptation leads to the evolution of particular life-history patterns

The logistic model of population growth, while valid in many natural populations and a useful model, is a simplification of real-world population dynamics. Implicit in the model is that the carrying capacity of the environment does not change, which is not the case. The carrying capacity varies annually: for example, some summers are hot and dry whereas others are cold and wet. In many areas, the carrying capacity during the winter is much lower than it is during the summer. Also, natural events such as earthquakes, volcanoes, and fires can alter an environment and hence its carrying capacity. Additionally, populations do not usually exist in isolation. They engage in **interspecific competition**: that is, they share the environment with other species competing for the same resources. These factors are also important to understanding how a specific population will grow.

Nature regulates population growth in a variety of ways. These are grouped into **density-dependent** factors, in which the density of the population at a given time affects growth rate and mortality, and **density-independent** factors, which influence mortality in a population regardless of population density. Note that in the former, the effect of the factor on the population depends on the density of the population at onset. Conservation biologists want to understand both types because this helps them manage populations and prevent extinction or overpopulation.

Density-Dependent Regulation

Most density-dependent factors are biological in nature (biotic), and include predation, inter- and intraspecific competition, accumulation of waste, and diseases such as those caused by parasites. Usually, the denser a population is, the greater its mortality rate. For example, during intra- and interspecific competition, the reproductive rates of the individuals will usually be lower, reducing their population's rate of growth. In addition, low prey density increases the mortality of its predator because it has more difficulty locating its food source.

An example of density-dependent regulation is shown in [Figure 45.11](#) with results from a study focusing on the giant intestinal roundworm (*Ascaris lumbricoides*), a parasite of humans and other mammals.³ Denser populations of the parasite exhibited lower fecundity: they contained fewer eggs. One possible explanation for this is that females would be smaller in more dense populations (due to limited resources) and that smaller females would have fewer eggs. This hypothesis was tested and disproved in a 2009 study which showed that female weight had no influence.⁴ The actual cause of the density-dependence of fecundity in this organism is still unclear and awaiting further investigation.

³N.A. Croll et al., "The Population Biology and Control of *Ascaris lumbricoides* in a Rural Community in Iran." *Transactions of the Royal Society of Tropical Medicine and Hygiene* 76, no. 2 (1982): 187-197, doi:10.1016/0035-9203(82)90272-3.

⁴Martin Walker et al., "Density-Dependent Effects on the Weight of Female *Ascaris lumbricoides* Infections of Humans and its Impact on Patterns of Egg Production." *Parasites & Vectors* 2, no. 11 (February 2009), doi:10.1186/1756-3305-2-11.