

## Chapter 53

# Population Ecology

### *Lecture Outline*

#### Overview: Counting Sheep

- Ecologists have been studying a population of sheep on the Scottish island of Hirta for more than 50 years.
  - These Soay sheep are the closest living relatives of domesticated sheep.
  - In 1932, the population of sheep was established on Hirta Island, where food is plentiful and predators are absent.
- The population of Soay sheep has fluctuated dramatically, sometimes changing by more than 50% from year to year.
- Why do populations of some species fluctuate greatly while others do not?
- **Population ecology** is the study of populations in relation to their environment, including biotic and abiotic influences on population density, distribution, size, and age structure.

#### Concept 53.1 Dynamic biological processes influence population density, dispersion, and demographics.

- A **population** is a group of individuals of a single species that live in the same general area.
- Members of a population rely on the same resources, are influenced by similar environmental factors, and have a high likelihood of interacting and breeding with one another.
- Populations can evolve through natural selection acting on heritable variations among individuals and changing the frequencies of various traits over time.
- Three fundamental characteristics of individuals in any population are density, dispersion, and demographics.
- Every population has a specific size and specific geographic boundaries.
- The **density** of a population is the number of individuals per unit area or volume.
- The **dispersion** of a population is the pattern of spacing among individuals within the geographic boundaries.
- Measuring the density of populations is a difficult task.
- Ecologists can count individuals, but they usually estimate population numbers.
  - It is almost always impractical to count all the individuals in a population.
- Ecologists use a variety of sampling techniques to estimate densities and total population sizes.
  - For example, ecologists might count the number of individuals in randomly located plots, calculate the average density in the samples, and extrapolate to estimate the population size in the entire area.

- Such estimates are accurate when there are many sample plots and a homogeneous habitat.
  - In other cases, instead of counting individuals, population ecologists estimate density from an index of population size, such as the number of nests, burrows, tracks, calls, or fecal droppings.
- A sampling technique that researchers commonly use to estimate wildlife populations is the **mark-recapture method**.
- Individuals are trapped and captured, marked with a tag, recorded, and then released.
- After a period of time has elapsed, traps are set again and individuals are captured and identified.
- The second capture yields both marked and unmarked individuals.
- From counts of these individuals, researchers estimate the total number of individuals in the population.
  - The mark-recapture method assumes that each marked individual has the same probability of being trapped as each unmarked individual.
  - This may not be a safe assumption because trapped individuals may be more or less likely to be trapped a second time.
- Population density results from the dynamic interplay between processes that add individuals to a population and processes that remove individuals from it.
  - Additions to a population occur through birth (including 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).
  - Immigration and emigration may represent biologically significant exchanges between populations.
- Within a population's geographic range, local densities may vary substantially.
- Variations in local density are important population characteristics, providing insight into the environmental and social interactions of individuals within a population.
- Some habitat patches are more suitable than others.
- Social interactions between members of a population may maintain patterns of spacing.
- Dispersion is *clumped* when individuals aggregate in patches.
  - Plants and fungi are often clumped where soil conditions favor germination and growth.
  - Animals may clump in favorable microenvironments (such as salamanders under a fallen log) or to facilitate mating interactions.
  - Group living may increase the effectiveness of certain predators, such as a wolf pack.
- Dispersion is *uniform* when individuals are evenly spaced.
  - For example, some plants secrete chemicals that inhibit the germination and growth of nearby competitors.
  - Animals often exhibit uniform dispersion as a result of **territoriality**, the defense of a bounded space against encroachment by others.
- In *random* dispersion, the position of each individual is independent of the others, and spacing is unpredictable.
  - Random dispersion occurs in the absence of strong attraction or repulsion among individuals in a population, or when key physical or chemical factors are relatively homogeneously distributed.

- For example, plants may grow where windblown seeds land.
- Random patterns are uncommon in nature.
- **Demography** is the study of the vital statistics of populations and how they change over time.
  - Of particular interest are birth rates and how they vary among individuals (specifically females) and death rates.
- A **life table** is an age-specific summary of the survival pattern of a population.
- 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 throughout their lifetimes until all are dead.
- To build a life table, researchers need to determine the number of individuals that die in each age group and calculate the proportion of the cohort surviving from one age to the next.
- A graphic way of representing the data in a life table is a **survivorship curve**, a plot of the numbers or proportion of individuals in a cohort of 1,000 individuals still alive at each age.
- Natural populations exhibit several patterns of survivorship.
- A Type I curve is relatively flat at the start, reflecting a low death rate in early and middle life, and drops steeply as death rates increase among older age groups.
  - Humans and many other large mammals exhibit Type I survivorship curves.
- The Type II curve is intermediate, with constant mortality over an organism's life span.
  - Many species of rodent, various invertebrates, and some annual plants show Type II survivorship curves.
- A Type III curve drops sharply at the start, reflecting very high death rates early in life, but flattens out as death rates decline for the few individuals that survive to a critical age.
  - Type III survivorship curves are associated with organisms that produce large numbers of offspring but provide little or no parental care.
  - Examples are many fishes, long-lived plants, and marine invertebrates.
- Many species fall somewhere between these basic survivorship curves or show more complex curves.
  - Some invertebrates, such as crabs, show a “stair-stepped” curve, with increased mortality during molts.
  - In birds, mortality is often high among chicks (Type II) but is fairly constant among adults (Type III).
- In populations without immigration or emigration, survivorship and reproductive rates are the two key factors determining changes in population size.
- Demographers who study sexually reproducing populations usually ignore males and focus on females because only females give birth to offspring.
- A **reproductive table** is an age-specific summary of the reproductive rates in a population, constructed by measuring the reproductive outputs of cohorts from birth until death.
- For sexual species, a reproductive table tallies the number of female offspring produced by each age group.
- The reproductive output for sexual species 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.
- Reproductive tables vary greatly from species to species.

- Squirrels have a litter of two to six young once a year for less than a decade, for example, whereas oak trees drop thousands of acorns each year for tens or hundreds of years.

### **Concept 53.2 Life history traits are products of natural selection.**

- 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 traits such as frequency of reproduction, number of offspring produced, and investment in parental care.
- The traits that affect an organism's schedule of reproduction and survival make up its **life history**.

#### ***Life histories are highly diverse, but they exhibit patterns in their variability.***

- Life histories involve three basic variables: when reproduction begins, how often the organism reproduces, and how many offspring are produced during each reproductive episode.
- Life history traits are evolutionary outcomes reflected in the development, physiology, and behavior of an organism.
- Some organisms, such as the Pacific salmon, exhibit what is known as **big-bang reproduction**, in which a salmon returns to freshwater streams to spawn and then die.
  - This pattern, known as **semelparity**, also occurs in plants such as the agave or century plant.
  - Agaves grow in arid climates with unpredictable rainfall and poor soils.
  - Agaves grow for years, accumulating nutrients in their tissues, until there is an unusually wet year. They then send up a large flowering stalk, produce seeds, and die.
  - This life history is an adaptation to the harsh desert conditions in which the agave lives.
- By contrast, some organisms produce only a few offspring during **repeated reproductive** episodes.
  - This pattern, known as **iteroparity**, is typical of lizards that produce a few large eggs annually for several years.
- What factors contribute to the evolution of semelparity versus iteroparity?
  - In other words, how much does an individual gain in reproductive success through one pattern versus the other?
- A current hypothesis answers this question based on the survival rate of the offspring and the likelihood the adult will survive to reproduce again.
- When the survival rate of offspring is low, as in highly variable or unpredictable environments, big-bang reproduction (semelparity) is favored.
  - Adults are also less likely to survive in such environments.
- Repeated reproduction (iteroparity) is favored in dependable environments, where adults are more likely to survive to breed again and competition for resources is intense.
  - In such environments, a few, well-provisioned offspring have a better chance of surviving to reproductive age.
- Oak trees and sea urchins are intermediate between the two extremes. Both live a long time, but repeatedly produce large numbers of offspring.

#### ***Limited resources mandate trade-offs between investment in reproduction and survival.***

- Life histories represent an evolutionary resolution of conflicting demands.
- Organisms may make trade-offs between survival and reproduction when resources are limited.
  - For example, red deer females have a higher mortality rate in winters that follow summers in which they reproduce.
- Selective pressures also influence the trade-off between 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 usually produce many small seeds, only a few of which reach a suitable habitat.
  - Smaller seed size may increase the chance of seedling becoming established by enabling seeds to be carried longer distances to a broader range of habitats.
  - Animals that suffer high predation rates, like quail, sardines, and mice, tend to produce many offspring.
- In other organisms, extra investment on the part of the parent greatly increases the offspring's chances of survival.
  - Walnut trees and coconut palms both have large seeds with a large store of energy and nutrients to help the seedlings become established.
  - In animals, parental care does not always end after incubation or gestation.
  - Primates provide an extended period of parental care to only a few offspring.

**Concept 53.3 The exponential model describes population growth in an idealized, unlimited environment.**

- All populations have a tremendous capacity for growth.
- Unlimited population increase does not occur indefinitely for any species, however, either in the laboratory or in nature.
- The study of population growth in an idealized, unlimited environment reveals the capacity of species for increase and the conditions in which that capacity may be expressed.
- Imagine a hypothetical population living in an ideal, unlimited environment.
- For simplicity's sake, we ignore immigration and emigration and define a change in population size during a fixed time interval using the following verbal equation:

$$\text{Change in population size during time interval} = \text{Births during time interval} - \text{Deaths during time interval}$$

- Using mathematical notation, we can express this 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.
  - We can rewrite the verbal equation as

$$\Delta N / \Delta t = B - D$$

where  $B$  is the number of births during the time interval and  $D$  is the number of deaths.

- We can convert this simple model into one in which births and deaths are expressed as the average number of births and deaths per individual during the specified time period.
- The *per capita birth rate* is the number of offspring produced per unit time by an average member of the population.

- For example, if there are 34 births per year in a population of 1,000 individuals, the annual per capita birth rate is  $34/1000$ , or 0.034.
- If we know the annual per capita birth rate (expressed as  $b$ ), we can use the formula  $B = bN$  to calculate the expected number of births per unit time in a population of any size.
- Similarly, knowing the *per capita death rate* (symbolized by  $d$ ) allows us to calculate the expected number of deaths per unit time in a population of any size using the formula  $D = dN$ .
  - If  $d = 0.016$  per year, we would expect 16 deaths per year in a population of 1,000 individuals.
- Now we can revise the population growth equation, using per capita birth and death rates:
 
$$\Delta N/\Delta t = bN - dN$$
- Population ecologists are most interested in the differences between the per capita birth rate and the per capita death rate.
- This difference is the *per capita rate of increase*, or  $r$ , which equals  $b - d$ .
- The value of  $r$  indicates whether a population is growing ( $r > 0$ ) or declining ( $r < 0$ ).
- If  $r = 0$ , then there is **zero population growth (ZPG)**.
  - Births and deaths still occur, but they balance exactly.
- Using the per capita rate of increase, we rewrite the equation for the change in population size as
 
$$\Delta N/\Delta t = rN$$
- Ecologists use differential calculus to express population growth *instantaneously*, as the growth rate at a particular instant in time:
 
$$dN/dt = r_{\text{inst}}N$$
 where  $r_{\text{inst}}$  is the instantaneous per capita rate of increase.
- Population growth under ideal conditions is called **exponential population growth**.
  - Under these conditions, we may assume the maximum growth rate for the population ( $r_{\text{max}}$ ), called the *intrinsic rate of increase*.
- The equation for exponential population growth is
 
$$dN/dt = r_{\text{max}}N$$
- The size of a population that is growing exponentially increases at a constant rate, resulting in a J-shaped growth curve when the population size is plotted over time.
  - Although the maximum *rate* of increase is constant, the population accumulates more new individuals per unit of time when it is large.
  - As a result, the curve gets steeper over time.
- A population with a high intrinsic rate of increase grows faster than one with a lower rate of increase.
- J-shaped curves are characteristic of populations that are introduced into a new or unfilled environment or whose numbers have been drastically reduced by a catastrophic event and are rebounding.

**Concept 53.4 The logistic growth model describes how a population grows more slowly as it nears its carrying capacity.**

- Typically, resources are limited and, as population density increases, each individual has access to an increasingly smaller share of available resources.
- Ultimately, there is a limit to the number of individuals that can occupy a habitat.
- Ecologists define **carrying capacity** ( $K$ ) as the maximum stable population size that a particular environment can support.
  - Carrying capacity is not fixed but varies over space and time with the abundance of limiting resources.
- Energy limitations often determine the carrying capacity, although other factors, such as shelters, refuges from predators, nutrient availability, water, and suitable nesting sites, can all be limiting.
- If individuals cannot obtain sufficient resources to reproduce, then the per capita birth rate  $b$  declines.
- If individuals cannot find and consume enough energy to maintain themselves, or if disease or parasitism increases with density, then the per capita death rate  $d$  increases.
- A decrease in  $b$  or an increase in  $d$  results in a lower per capita rate of increase  $r$ .

***Ecologists can modify the mathematical model to incorporate changes in the growth rate as the population size nears the carrying capacity.***

- In the **logistic population growth** model, the per capita rate of increase declines as the carrying capacity is reached.
- Mathematically, we start with the equation for exponential growth 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 accommodate and  $(K - N)/K$  is the fraction of  $K$  that is still available for population growth.
- By multiplying the intrinsic rate of increase  $r_{\max}$  by  $(K - N)/K$ , we modify the growth rate of the population as  $N$  increases:
 
$$dN/dt = r_{\max}N[(K - N)/K]$$
- When  $N$  is small compared to  $K$ , the term  $(K - N)/K$  is large and the per capita rate of increase is close to the intrinsic rate of increase.
- When  $N$  is large and resources are limiting,  $N$  approaches  $K$ . The term  $(K - N)/K$  is small and so is the rate of population growth.
- Population growth is greatest when the population is approximately half of the carrying capacity.
  - At this population size, there are many reproducing individuals, and the per capita rate of increase remains relatively high.
- The logistic model of population growth produces a sigmoid (S-shaped) growth curve when  $N$  is plotted over time.
- New individuals are added to the population most rapidly at intermediate population sizes, when there is not only a substantial breeding population but also lots of available space and other resources in the population.
- *Why* does the population growth rate slow as  $N$  approaches  $K$ ? Population growth slows as the birth rate  $b$  decreases or the death rate  $d$  increases.

***How well does the logistic growth model fit the growth of real populations?***

- The growth of laboratory populations of some organisms fits an S-shaped curve fairly well.

- These populations are grown in a constant environment without predators or competitors.
- Some of the basic assumptions built into the logistic growth model do not apply to all populations, however.
- The logistic growth model assumes that populations adjust instantaneously and approach the carrying capacity smoothly.
  - In most natural populations, there is a lag time before the negative effects of increasing population are realized.
  - Populations may overshoot their carrying capacity before settling down to a relatively stable density.
  - Some populations fluctuate greatly, making it difficult to define the carrying capacity.
- The logistic growth model assumes that, regardless of the population density, each individual added to the population has the same negative effect on the population growth rate.
  - Some populations show an *Allee effect*, in which individuals may have a more difficult time surviving or reproducing if the population is too small.
  - Animals may not be able to find mates in the breeding season at small population sizes.
  - A plant may be protected in a clump of individuals but vulnerable to excessive wind if it stands alone.
- The logistic population growth model provides a basis from which ecologists can consider how real populations grow and how to construct more complex models.
  - The model is useful in conservation biology for estimating how rapidly a particular population might increase after it has been reduced to a small size, or for estimating sustainable harvest rates for fish or wildlife populations.
  - Conservation biologists can use the model to estimate the lower critical size below which populations of certain species may become extinct.
- The logistic growth model predicts different per capita growth rates for populations of low or high density relative to the carrying capacity of the environment.
  - At high densities, each individual has few resources available, and the population grows slowly.
  - At low densities, per capita resources are abundant, and the population can grow rapidly.
- Different life history features are favored under low and high population densities.
- At high population density, selection favors adaptations that enable organisms to survive and reproduce using few resources.
  - Competitive ability and efficient use of resources should be favored in populations that are at or near their carrying capacity.
  - These are traits associated with iteroparity.
- At low population density, adaptations that promote rapid reproduction, such as the production of numerous, small offspring, should be favored.
  - These are traits associated with semelparity.
- Ecologists have attempted to connect these differences in favored traits at different population densities with the logistic model of population growth.
- Selection for life history traits that are sensitive to population density is known as **K-selection**, or density-dependent selection.

- $K$ -selection tends to maximize population size and operates in populations living at a density near  $K$ .
- Selection for life history traits that maximize reproductive success at low densities is known as  **$r$ -selection**, or density-independent selection.
  - $r$ -selection tends to maximize  $r$ , the per capita rate of increase, and occurs in environments in which population densities fluctuate well below  $K$  or when individuals face little competition.
    - Such conditions are often found in disturbed habitats.

**Concept 53.5 Many factors that regulate population growth are density-dependent.**

- Why do all populations eventually stop growing?
  - What environmental factors stop a population from growing indefinitely?
  - Why do some populations show radical fluctuations in size over time, while others remain relatively stable?
- Population *regulation* is an area of ecology with many practical applications.
  - A farmer may want to reduce the abundance of an agricultural pest.
  - A conservation ecologist may need to know what environmental factors create a favorable feeding or breeding habitat for an endangered species.
- The first step in answering these questions is to examine the effects of increased population density on rates of birth, death, immigration, and emigration.
- A birth rate or death rate that does *not* change with population density is **density-independent**.
  - For example, mortality of dune fescue grass is due to physical factors that kill a similar proportion of a local population regardless of density.
- A death rate that increases or a birth rate that falls as population density rises is said to be **density-dependent**.
  - Reproduction by dune fescue declines as the population density increases, due to greater seed herbivory.
- In dune fescue, the factors that regulate birth rate are density-dependent, whereas the death rate is regulated by density-independent factors.

***Negative feedback prevents unlimited population growth.***

- Density-dependent regulation provides negative feedback on population growth, operating through mechanisms that help to reduce birth rates and increase death rates.
- In crowded populations, increasing population density increases competition for declining nutrients and other resources, thus reducing reproductive output.
  - On Hirta Island, the effects of increasing density reduce the birth rate most strongly for the youngest sheep, one-year-old juveniles.
- In animal populations, territoriality may limit density.
  - In this case, space is the resource for which individuals compete.
  - Oceanic birds often nest on rocky islands to avoid predators. Beyond a certain population density, additional birds cannot find a suitable nesting spot and do not reproduce.
  - The presence of nonbreeding individuals in a population is an indication that territoriality is restricting population growth.

- Population density can also influence the health and thus the survival of organisms.
  - As crowding increases, the transmission rate of a disease may increase.
  - If the transmission rate of a disease depends on a certain level of crowding in a population, then the disease's impact may be density-dependent.
  - Tuberculosis, caused by bacteria that spread through the air when an infected person coughs or sneezes, affects a higher percentage of people living in high-density cities than in rural areas.
- Predation may be an important cause of density-dependent mortality for a prey species if a predator encounters and captures more food as the population density of the prey increases.
  - As a prey population builds up, predators may feed preferentially on that species, consuming a higher percentage of individuals.
  - For example, trout may concentrate for a few days on a particular species of insect that is emerging from its aquatic larval stage, and then switch prey as another insect species becomes more abundant.
- The accumulation of toxic wastes can contribute to density-dependent regulation of population size.
  - In laboratory cultures of microorganisms, metabolic by-products accumulate as populations grow, poisoning the organisms within this limited artificial environment.
  - For example, as a yeast population increases, the yeast accumulate alcohol during fermentation.
  - Yeast can withstand an alcohol concentration of only approximately 13% before they begin to die.
- For some animal species, intrinsic (physiological) rather than extrinsic (environmental) factors appear to regulate population size.
  - White-footed mice individuals become more aggressive as population size increases, even when food and shelter are provided in abundance.
  - Eventually the mouse population ceases to grow.
  - These behavioral changes may be due to hormonal changes caused by stress, which delay sexual maturation and depress the immune system.

***All populations for which data are available show some fluctuation in numbers.***

- The study of **population dynamics** focuses on the complex interactions between biotic and abiotic factors that cause variations in population size.
- Populations of large mammals, such as deer and moose, were once thought to remain relatively stable over time, but long-term studies have challenged that view.
- The numbers of Soay sheep on Hirta Island may rise or fall by more than 50% from one year to the next.
- What causes the size of this population to change so dramatically? The most important factor appears to be the weather.
  - Harsh weather, particularly cold, wet winters, weakens the sheep and decreases food availability, thus reducing 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.

- A long-term population study has found that the moose population on Isle Royale in Lake Superior also fluctuates over time.
- Predation plays an important role in regulating the moose population.
  - Moose from the mainland colonized the island in around 1900. Wolves followed 50 years later.
  - In recent years, both populations have been isolated from immigration and emigration.
  - The moose population experienced two major increases and collapses during the last 45 years.
  - The first collapse coincided with a peak in the wolf population from 1975 to 1980.
  - The second collapse in 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.

***Some populations undergo regular boom-and-bust cycles.***

- Some populations show cyclic population changes.
  - Small herbivorous mammals such as voles and lemmings tend to have 3- to 4-year cycles.
  - Ruffed grouse and ptarmigan have 9- to 11-year cycles.
- A striking example of population cycles is the 10-year cycles of lynx and snowshoe hare in northern Canada and Alaska.
- Lynx are specialist predators of snowshoe hares, so it is not surprising that lynx numbers vary with the numbers of hares.
- Why do hare numbers rise and fall in 10-year cycles? There are three main hypotheses.
  1. The cycles may be caused by food shortages during the winter.
  2. The cycles may be due to predator-prey interactions.
  3. The cycles may vary with changes in sunspot activity.
- If hare population cycles are due to winter food shortages, as the first hypothesis suggests, they should stop if extra food is added to a field population.
- Researchers conducted such an experiment over 20 years.
  - They found that hare population densities increased about threefold in areas that had extra food, so the carrying capacity of a habitat for hares can clearly be increased by adding food.
  - The populations of lynx and hares continued to cycle, however, so food supplies alone do not cause the hare cycles.
  - The first hypothesis can be rejected.
- To test the second hypothesis, field ecologists placed radio collars on hares to find them as they die and determine the cause of death.
  - Ninety percent of dead hares were killed by predators; none appear to have died of starvation.
  - These data support the second hypothesis.
- Ecologists excluded predators from one area and excluded predators *and* added food to another area.
  - They found that the hare cycle is driven largely by predation but that food availability also plays an important role, especially in winter.
  - Perhaps better-fed hares are more likely to escape from predators.
- To test the third hypothesis, ecologists compared the timing of hare cycles and sunspot activity.

- When sunspot activity is low, slightly less ozone is produced in the atmosphere, and slightly more ultraviolet radiation reaches Earth's surface.
- In response, plants produce more chemicals that act as sunscreens and fewer chemicals that deter herbivores, thus increasing the quality of the hares' food.
- The researchers found that periods of low sunspot activity were followed by peaks in the hare population.
- All of these experiments suggest that both predation and sunspot activity regulate 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, which depend 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, thus accelerating the collapse of the predator populations.
- Long-term experimental studies continue to help unravel the complex causes of these population cycles.

***Local populations can be linked to form a metapopulation.***

- Immigration and emigration can also influence populations, particularly when a group of populations is linked together to form a **metapopulation**.
- In a sense, local populations in a metapopulation occupy discrete patches of suitable habitat within a sea of unsuitable habitat.
  - The patches vary in size, quality, and isolation from other patches, influencing how 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 metapopulation concept 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.

**Concept 53.6 The human population is no longer growing exponentially, but it is still increasing rapidly.**

- The concepts of population dynamics can be applied to the specific case of the human population.
- It is unlikely that any other population of large animals has ever sustained so much population growth for so long.
- The human population increased relatively slowly until about 1650, when approximately 500 million people inhabited Earth.
- Since then, human population numbers have doubled three times.
- The global population is now more than 6.6 billion people and is increasing by about 75 million each year, or 200,000 people each day.
- Population ecologists predict a population of 7.8–10.8 billion people on Earth by 2050.

- Although the global population is still growing, the *rate* of growth began to slow during the 1960s.
  - The rate of increase in the global population peaked at 2.2% in 1962.
  - By 2005, the rate of increase had declined to 1.15%.
  - Current models project a decline in the overall growth rate to just over 0.4% by 2050.
- Human population growth has departed from true exponential growth, which assumes a constant rate.
- The declines are the result of fundamental changes in population dynamics due to diseases such as AIDS and voluntary population control.

***Population dynamics vary widely from region to region.***

- To maintain population stability, a regional human population can exist in one of two configurations:
  - Zero population growth = High birth rates – High death rates
  - Zero population growth = Low birth rates – Low death rates
- The movement from the first toward the second state is called the **demographic transition**.
- After 1950, mortality rates have declined rapidly in most developing countries.
- Birth rates have declined in a more variable manner.
  - The fall in birth rate has been most dramatic in China, where the total fertility rate (number of children per woman per lifetime) fell from an average of 5.9 children in 1970 to 1.7 children in 2004.
  - In some countries of Africa, the transition to lower birth rates has also been rapid, although birth rates remain high in most of sub-Saharan Africa.
  - In India, birth rates have fallen more slowly.
- In the developed nations, populations are near equilibrium (growth rate of about 0.1% per year), with reproductive rates near the replacement level (total fertility rate of 2.1 children per woman).
- In many developed nations, the reproductive rates are in fact *below* the replacement level.
  - These populations will eventually decline without immigration and a rise in the birth rate.
  - The population is already declining in many eastern and central European countries.
- Most population growth is concentrated in developing countries, where 80% of the world's people 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.
  - Delayed marriage and reproduction help to decrease population growth rates and move a society toward zero population growth.
- World leaders continue to disagree about how much support should be provided for global family planning efforts.

***One important demographic variable is a country's age structure.***

- **Age structure**, the relative number of individuals of each age, is illustrated as a pyramid showing the percentage of the population at each age.
- Age structures differ greatly from nation to nation.
- Age structure diagrams can predict a population's growth trends and future social conditions.

- 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.
- Although global life expectancy has been increasing since about 1950, more recently it has dropped in a number of regions, including countries of the former Soviet Union and in sub-Saharan Africa.
  - In these regions, the combination of social upheaval, decaying infrastructure, and infectious diseases such as AIDS and tuberculosis is reducing life expectancy.

***Estimating Earth's carrying capacity for humans is a complex problem.***

- Predictions of the size of the human population vary from 7.8 to 10.8 billion people by 2050.
  - How many humans can the biosphere support?
  - Will the world be overpopulated in 2050? Is it *already* overpopulated?
- For more than three centuries, scientists have attempted to estimate the carrying capacity of Earth for humans.
  - Estimates have ranged from fewer than 1 billion to more than 1 trillion, with an average of 10–15 billion.
- Carrying capacity is difficult to estimate, and scientists have used different methods to obtain their answers.
  - Some use curves like those produced by the logistic growth equation to predict the future maximum human population size.
  - Others generalize from the existing “maximum” population density and multiply by the area of habitable land.
  - Other estimates are based on a single limiting factor, usually food, and consider many variables, including 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.
- In calculating the carrying capacity of humans, scientists must consider multiple constraints. Humans need food, water, fuel, building materials, and other resources, such as clothing and transportation.
- The concept of an **ecological footprint** summarizes the aggregate land and water area appropriated by each person, city, or nation to produce all the resources it consumes and to absorb all the waste it generates.
  - If the area of all the ecologically productive land on Earth is divided by the global human population, the result is about 2 hectares (ha) per person.
  - 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 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.
- For instance, the amount of photosynthesis that occurs on Earth is finite, constrained by the land and sea area and by the sun's radiation.

- Scientists determined the extent to which people around the world consume seven types of photosynthetic products: plant foods, wood for building and fuel, paper, fiber, meat, milk, and eggs (the last three based on estimates of how much plant material goes into their production).
  - Areas with high population densities, such as China and India, have high consumption rates.
  - Areas with much lower population densities but higher per capita consumption, such as parts of the United States and Europe, have equally high consumption rates.
- The combination of population density and resource use per person determines our global ecological footprint.
- Food may be the main factor that will determine Earth's ultimate carrying capacity for the human population.
  - Malnutrition and famine result mainly from unequal distribution of food rather than inadequate production.
  - So far, technological improvements in agriculture have enabled food supplies to keep up with global population growth.
- Perhaps we will eventually be limited by suitable space, like the gannets on oceanic islands.
  - As our population grows, conflict over space 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 and space is available to dispose of their waste.
- 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—water.
  - More than 1 billion people do not have access to sufficient water to meet their basic sanitation needs.
- Perhaps the human population will eventually be limited by the capacity of the environment to absorb its wastes.
  - In such cases, Earth's current human occupants could lower the planet's long-term carrying capacity for future generations.
- Some optimists have suggested that because of our ability to develop technology, human population growth has no practical limits.
  - Technology has undoubtedly increased Earth's carrying capacity for humans, but no population can continue to grow indefinitely.
- There is no single, agreed-on carrying capacity for humans on Earth.
- How many people our planet can sustain depends on their quality of life and the distribution of wealth across people and nations.
- Humans can decide whether zero population growth will be attained through social changes based on human choices or through increased mortality due to resource limitations, plagues, war, and environmental degradation.