Chapter 16 Populations

Chapter Outline

16.1 Characteristics of Populations
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16.1 Characteristics of Populations

Lesson Objectives

- Recognize that human concern about overpopulation dates to ancient Greek times.
- Explain that Cornucopians believe that technology will solve population problems.
- Connect the study of the biology of natural populations to better understand human population issues.
- Define a biological population.
- Give reasons why biologists study populations.
- Compare the importance of population size to that of population density.
- Explain how conservation biologists use Minimum Viable Population (MVP) and Population Viability Analysis (PVA).
- Explain how patchy habitats influence the distribution of individuals within a population.
- Define and explain the reasons for three patterns of dispersion within populations.
- Describe how population pyramids show the age and sex structures of populations.
- Interpret population pyramids to indicate populations' birth and death rates and life expectancy.
- Analyze the effect of age at maturity on population size.
- Explain the structure and meaning of a generalized survivorship curve.
- Compare and contrast the three basic types of survivorship curves.

Introduction

"Solving the population problem is not going to solve the problems of racism... of sexism... of religious intolerance... of war... of gross economic inequality—But if you don't solve the population problem, you're not going to solve any of those problems. Whatever problem you're interested in, you're not going to solve it unless you also solve the population problem. Whatever your cause, it's a lost cause without population control." **–Paul Ehrlich, 1996**

(From *Paul Ehrlich and the Population Bomb*, PBS video produced by Canadian biologist Dr. David Suzuki, April 26, 1996.)

What exactly is the **population problem**? How can it be solved?

Humans have shown concern for **overpopulation** since the Ancient Greeks built outposts for their expanding citizenship and delayed age of marriage for men to 30. In 1798, Thomas Malthus predicted that the human population would outgrow its food supply by the middle of the 19^{th} century. That time arrived without a Malthusian crisis, but Charles Darwin nevertheless embraced Malthus' ideas and made them the foundation of his own theory of evolution by natural selection. In a 1968 essay, *The Tragedy of the Commons*, Garrett Hardin exhorted humans to "relinquish their freedom to breed," arguing in the journal, *Science*, that "the population problem has no technical solution," but "requires a fundamental extension in morality." In 1979, the government of China instituted a "birth planning" policy, charging fines or "economic compensation fees" for families with more than one child. Others have opposing views, however. Julian Simon, professor of Business Administration and Senior Fellow at the Cato Institute, argued that *The Ultimate Resource* is population, because people and markets find solutions to any problems presented by overpopulation. A group known as **cornucopians** continues to promote the view that more is better.

FIGURE 16.1

The Chinese government mandates population control by charging "economic compensation fees" for families with more than one child.

Would you support a law forbidding you to marry until a certain age? Do you know how such a law would affect population growth? Would you limit the size of all families to one child (**Figure** 16.1)? Do you believe families should welcome as many children as possible? Should these decisions be regulated by law, or by individual choice? Clearly, the "population problem" reaches beyond biology to economics, law, morality, and religion. Although the latter subjects are beyond the scope of this text, the study of population biology can shed some light on human population issues. Let's look at what biologists have learned about natural populations. Later, we will look more closely at human populations, and compare them to populations in nature.

Measuring Populations

In biology, a **population** is a group of organisms of a single species living within a certain area. Ecologists study populations because they directly share a common gene pool. Unlike the species as a whole, members of a population form an interbreeding unit. Natural selection acts on individuals within populations, so the gene pool reflects the interaction between a population and its environment.

Biologists study populations to determine their health or stability, asking questions such as:

- Is a certain population of endangered grizzly bears growing, stable, or declining?
- Is an introduced species such as the zebra mussel or purple loosestrife growing in numbers?
- Are native populations declining because of an introduced species?
- What factors affect the growth, stability, or decline of a threatened population?

The first step in characterizing the health of a population is measuring its size. If you are studying the population of purple loosestrife plants on your block , you can probably count each individual to obtain an accurate measure of the population's size. However, measuring the population of loosestrife plants in your county would require sampling techniques, such as counting the plants in several randomly chosen small plots and then multiplying the average by the total area of your county. For secretive, highly mobile, or rare species, traps, motion-detecting cameras, or signs such as nests, burrows, tracks, or droppings allow estimates of population size.

FIGURE 16.2

Purple loosestrife plant populations show patchiness due to uneven distribution of their wetland habitats, and clumped dispersion, due to local variation in soils.

Two problems with absolute size lead ecologists to describe populations in other terms. First, because your county may not be the same size as others, the total number of individuals is less meaningful than the **population density** of individuals –the number of individuals per unit area or volume. Ecologists use population densities more often for comparisons over space or time, although total number is still important for threatened or endangered species.

Concern about threatened and endangered species has led conservationists to attempt to define **minimal viable population** size for some species. A species' **MVP** is the smallest number of individuals which can exist without extinction due to random catastrophic variations in environmental (temperature, rainfall), reproduction (birth rates or age-sex structure), or genetic diversity. In 1978, Mark Shaffer incorporated an estimate for grizzly bear MPV into the first **Population Viability Analysis (PVA)**, a model of interaction between a species and the resources on which it depends. PVAs are species-specific, and require a great deal of field data for accurate computer modeling of population dynamics. PVAs can predict the probability of extinction, focus conservation efforts, and guide plans for sustainable management.

Patterns in Populations I: in Space (or Patterns in Space)

A second problem in measuring population size relates to the distribution of individuals within the population's boundaries. If your county has extensive wetlands in the southern half, but very few in the north, a countywide population density estimate of purple loosestrife, which grows primarily in shallow freshwater pond edges, marshes, and fens, would be misleading (**Figure** 16.2). **Patchy** habitat –scattered suitable areas within population boundaries –inevitably leads to a patchy distribution of individuals within a population. On a smaller scale, plants within even a single wetland area may be **clumped or clustered** (grouped), due to soil conditions or gathering for reproduction.

The characteristic pattern of spacing of individuals within a population is **dispersion** (**Figure** 16.3). Clumped dispersion is most common, but species that compete intensely, such as cactus for water in a desert, show **uniform**, or evenly spaced, dispersion.

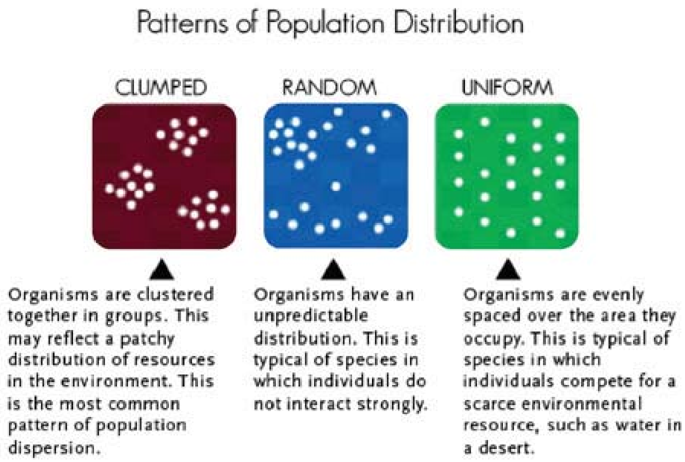


FIGURE 16.3
Populations of cacti in the desert, such as this group of cholla, show uniform, or even, dispersion due to fierce competition for water. The diagrams to the right show nearly uniform (top), random (middle), and clumped (bottom) dispersion patterns.

Other species, whose individuals do not interact strongly, show a **random**, or unpredictable, distribution. Useful measures of population density must take into account both patchiness of habitat and dispersion of individual organisms within the population's boundaries.

Age-Sex Structure of a Population

FIGURE 16.4
Grizzly bear populations include adults up to 25 or 30 years old, capable of reproducing, and young immature bears under 6 years old. Healthy populations include roughly equal proportions of each age group.

Density and dispersion describe a population's size, but size is not everything. Consider three populations of endangered grizzly bears, each containing one individual per 20 km^2, and a total of 100 individuals in 2,000 km^2.

These populations are “equal” with respect to size. One population, however, has 50 immature (non-reproducing young) bears and 50 adult bears able to reproduce. A second population has the same number of immature and adult bears, but of the 50 adults, 45 are male. The third population has 30 immature bears and 70 bears of reproductive age. Which population is healthiest (**Figure** 16.4)?

The answer is not simple, but age and sex differences between populations are significant indicators of health. Biologists concerned about a population’s future study age and sex within the population and then graph the results to show the **age-sex structure** as a **population pyramid,** although the result does not always resemble a pyramid. The X-axis in this double bar graph indicates percentage of the population, with males to the left and females to the right. The Y-axis indicates age groups from birth to old age.

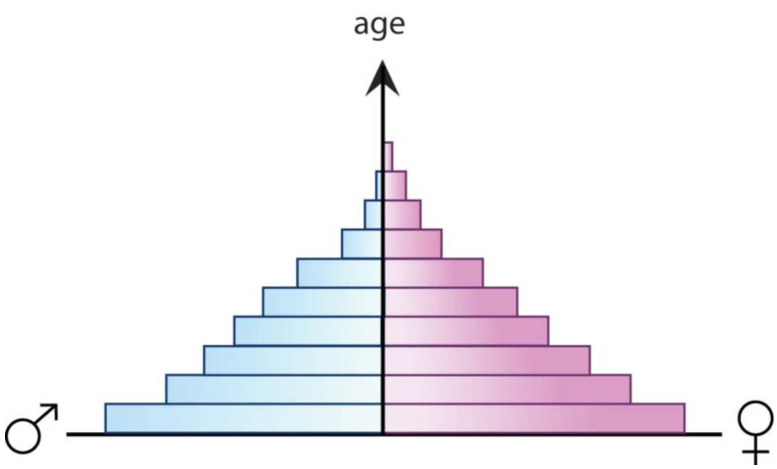


FIGURE 16.5

A generalized age-sex structure or population pyramid shows the proportion of males and females (X-axis) at each age level (Y-axis). This example shows a slightly higher proportion of females compared to males, and a much higher proportion of young individuals compared to old.

The population in the generalized example (**Figure** 16.5) contains a large proportion of young individuals, suggesting a relatively high **birth rate** (number of births per individual within the population per unit time). The bars narrow at each age interval, showing that a significant number of individuals die at every age. This relatively high **death rate** (number of deaths per individual within the population per unit time) indicates a short **life expectancy**, or average survival time for an individual. Note the slightly greater proportion of females compared to males at each age level. Careful study could determine whether the cause for this imbalance is the ratio of female to male births, or higher death rates for males throughout a shorter lifespan. You will learn in a later lesson that this pattern is characteristic of human populations in less developed countries.

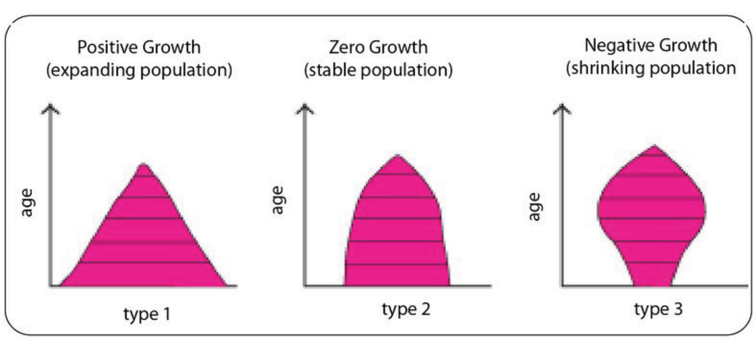


FIGURE 16.6

Age structures can reveal a population’s health. Type I, with most individuals below reproductive age, often indicates a growing population. Type II, with roughly equal proportions of the population at each age level, indicates a stable population. Type III, with more individuals at (or above!) reproductive age than young, describes a declining population.

A population's age structure may reveal its health (**Figure** 16.6). A growing population (Type I) usually has more young individuals than adults at beyond reproductive age. A stable population (Type II) often has roughly equal numbers of young members and adults. A declining population shows more adults and fewer young (Type III). Sex structure may also affect the health of a population. Sex determination in sea turtles, for example, is temperature-dependent; lower egg incubation temperatures produce males, while temperatures as little as 1-2^{o}C higher produce females (**Figure** 16.7). Some biologists predict that climate change may result in sea turtle sex structure shifts toward females, which could further endanger already threatened species. Continued monitoring of age-sex structures among sea turtles might be able to detect such changes before they become irreversible.

FIGURE 16.7

The sex of a sea turtle is determined by the temperature at which it develops –males in cooler temperatures, and females in temperatures as little as 1-2^{o}C warmer. Climate change may threaten natural sex ratios. Such changes would be reflected in changing age-sex structure pyramids.

Although it is not shown in population pyramids, an important factor affecting population size is the age at which individuals become able to reproduce (**Table** 16.1). Recall that **age at maturity** (when reproduction becomes possible) was the factor that even ancient Greeks recognized could affect population growth, when they prohibited marriage for males under the age of 30. We will return to this relationship in a later lesson, but for now, try to grasp it intuitively: if a person delays reproduction until age 30 and then has one child each year for two years, his or her **fertility** is 2. A person who has two children, one each year, beginning at age 20 also has a fertility of 2. Assume that these four children are born in the same two-year period, and that each offspring reproduces two children at the same age as his/her parent did. Sixty years after the initial four childbirths, the "delayed reproduction" individual will have 2 X 2 X 2 = 8 descendants. However, the early reproducing family will have 2 X 2 X 2 X 2 = 16 offspring –double the population increase of the first family. Do you think this could this be one way to slow human population growth?

TABLE 16.1: Number of Offspring Produced Over Time

Age at First Reproduction	Initial Reproduction	20 years later	30 years later	40 years later	60 years later
20 years	Generation 1: 2 offspring	Generation 2: 4 offspring		Generation 3: 8 offspring	Generation 4: **16**
30 years	Generation 1: 2 offspring		Generation 2: 4 offspring		Generation 3: **8**

Patterns in Populations Through Time

The characteristics of populations introduced above –birth rate, death rate, and life expectancy –interact to form several basic strategies for survival. Insurance companies began investigations into life expectancies for various groups of people –males vs. females, for example –and compiled the data in *life tables.* Biologists plot these patterns through time in **survivorship curves**, which graph the number of all individuals still living (in powers of ten, on the Y-axis) for each age (on the X-axis). The three basic types of survivorship curves are illustrated in **Figure** 16.8.

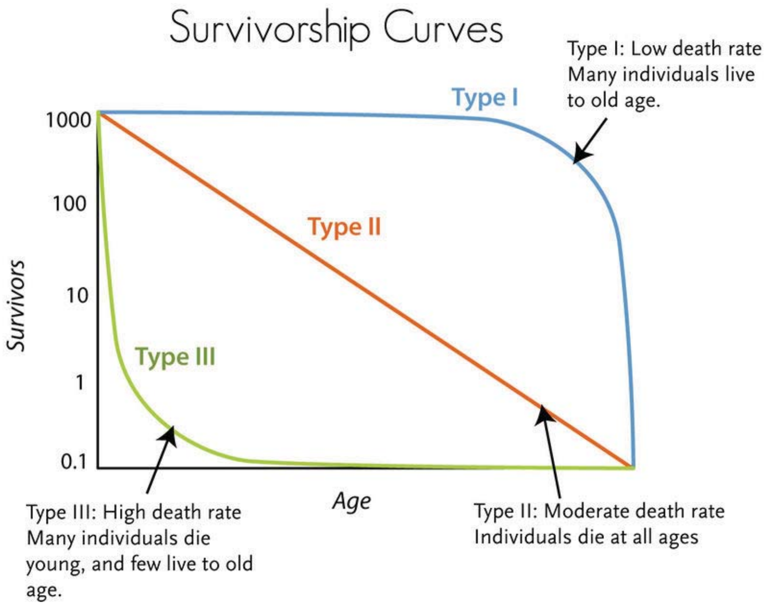


FIGURE 16.8

Survivorship curves correlate with strategies species use to adapt to various environments. Large organisms in relatively stable environments have few offspring but high levels of parental care; most individuals survive to old age (Type I). Smaller organisms in less stable environments produce many offspring but provide little parental care, and few survive to old age (Type III). Type II species show intermediate characteristics in response to a death rate which remains constant throughout life.

Species showing a Type I pattern have the highest survival rates, with most individuals living to old age. Many large animals, including humans, show this "late loss" pattern of survivorship; few offspring, high levels of parental care, and low "infant" death rates characterize Type I species. As we will see in a later lesson, human populations in rich countries fit this pattern more closely than do those in undeveloped countries.

Species with Type III survivorship patterns experience high death rates among offspring; relatively few survive to old age. Most plants and invertebrates and many fish show this "early loss" pattern. Parents invest most of the reproductive energy in high numbers of offspring to offset the high death rates, and little or no energy remains for parental care.

Species showing intermediate, Type II survivorship curves experience uniform death rates throughout their lives. Some birds and many asexual species show this "constant loss" pattern.

We'll look at these strategies more closely in the next lesson as we study how populations grow and change: population dynamics.

Lesson Summary

- Historic concern with overpopulation includes ancient Greek delay of marriage, Malthus' predictions of a resource crisis, and Darwin's use of exponential growth in his theory of natural selection.
- A group lead by Julian Simon, cornucopians, believes that more people are better, because technology and innovation will solve population problems.
- The study of the biology of natural populations can shed light on human population issues.

- In biology, a population is a group of organisms of a single species living within a certain area.
- Population size, the total number of individuals, is important for understanding endangered or threatened species, but population density is often more useful for comparing populations across time or space.

- Minimum Viable Population (MVP) and Population Viability Analysis (PVA) use extensive field data to predict best management practices for a particular species in conservation biology.

- Double bar graph population pyramids show proportions of males and females within age groups.
- Population pyramids which have wide bases indicate high birth rates and probable population growth, and decreases from one age group to the next indicate death rates and (overall) life expectancy. Populations with narrow bases indicate low birth rates and shrinking populations, and those with bases roughly equal to peaks indicate stable populations and/or low death rates.
- Delaying reproduction or increasing age to sexual maturity can decrease population growth rate, even if fertility levels remain the same.

- Patchy habitat distribution results in patchy distribution of a population throughout its boundaries.
- Dispersion of a population within its boundaries depends on intraspecies competition or cooperation.

1. Clumped distribution indicates social relationships or recent reproduction without dispersal.
2. Uniform distribution reveals competition among individuals for a limited resource.
3. Random distribution suggests little interaction among individuals.

- Survivorship curves show the number of individuals which survive (on a power-of-ten scale) at each age level.

1. Large animals, which provide few offspring with high levels of parental care, experience low death rates and long average life expectancy –a Type I pattern. This pattern is typical for humans in rich/developed countries.
2. Among plants and many invertebrates which have many offspring but little or no parental care, offspring have high death rates and relatively low average life expectancy –a Type III pattern.
3. Some birds and many asexually reproducing species have constant death rates throughout life and intermediate average life expectancy –a Type II pattern.

Review Questions

1. Compare the cornucopian perspective on human population growth to the Malthus' (sometimes called the Neo-Malthusian) view.
2. (If false, restate to make true.) Human concern about overpopulation is a recent phenomenon.
3. Define a biological population.
4. Define and compare the importance of population size vs. population density.
5. Explain how conservation biologists use Minimum Viable Population (MVP) and Population Viability Analysis (PVA).
6. How does patchy distribution differ from dispersion?
7. What types of information do population pyramids show? What kinds of inferences can you make using variations in population pyramid shape?
8. How does delaying reproduction affect population size, even if fertility remains constant?
9. Describe the three types of survivorship curves and the reproductive strategies they illustrate.
10. Apply what you have learned so far about population biology to your current understanding of human populations. Note: we will explore human populations in detail in a future lesson, so accept that your current understanding may be incomplete!

Further Reading / Supplemental Links

- http://www.estrellamountain.edu/faculty/farabee/biobk/BioBookpopecol.html

- http://www.geography.learnontheinternet.co.uk/topics/popn1.html
- http://www.census.gov/ipc/www/idb/faq.html
- http://www.biologicaldiversity.org/swcbd/species/orca/pva.pdf
- http://nationalzoo.si.edu/ConservationAndScience/EndangeredSpecies/PopViability/default.cfm

Vocabulary

age at maturity
The age at which individuals (sometimes considered only for females) become able to reproduce.

age-sex structure
A graphical depiction of proportions of males and females across all age groups within a population; also depicted as a population pyramid.

birth rate (*b*)
The number of births within a population or subgroup per unit time; in human demography, the number of childbirths per 1000 people per year.

cornucopian
A person who believes that people and markets will find solutions to any problems presented by overpopulation.

death rate (*d*)
The number of deaths within a population or subgroup per unit time; in human demography, the number of deaths per 1000 people per year.

dispersion
The pattern of spacing among individuals within a population –clumped (clustered or grouped), uniform (evenly spaced), or random (no discernible pattern).

life expectancy
Average survival time for individuals within a population.

minimum viable population
The smallest number of individuals which can exist without extinction due to chance variations in reproduction, genetics, or environment.

overpopulation
A condition in which the number of individuals in a population exceeds the carrying capacity of their environment.

population
A group of organisms of a single species living within a certain area.

population density
The number of organisms per unit area or volume.

population viability analysis
A model of interaction between a species and the resources on which it depends used in conservation biology.

survivorship curve
Graph which shows the number of all individuals still living (in powers of 10, on the Y-axis) at each age (on the X-axis).

Points to Consider

- Do you think Earth's human population has a patchy distribution? Why or why not?
- Do people show clumped, uniform, or random dispersion? Why?
- How do you think birth rates compare with death rates in the human population? Predict the shape of a population pyramid for humans.
- At this point in your study of population biology, do you consider yourself a Malthusian, following the ideas of Thomas Malthus, or a cornucopian?

16.2 Population Dynamics

Lesson Objectives

- Define population dynamics.
- Describe exponential (J-curve) growth, and explain the conditions under which it occurs.
- Explain Malthus' ideas about human population growth and their significance to evolutionary theory.
- Births and deaths: Balancing costs of reproduction and survival.
- Clarify the relationship between population growth rate, birth rate, and death rate.
- Compare trade-offs between survival and reproduction for *altricial* species to those of *precocial* and *nest parasite* species.
- Describe the relationship between age at maturity and growth rate.
- Analyze the equation for population growth rate.
- Describe several means of dispersal, and its importance to population density.
- Define migration and explain possible effects on population density and growth.
- Compare nomadism, irruption, range expansion, and colonization in terms of their effects on population density.
- Give examples of population growth patterns in nature.
- Describe logistic (S-curve) growth, and explain the conditions under which it occurs.
- Analyze the concept of carrying capacity in terms of population growth and resource availability.
- Compare and contrast density-dependent and density-independent limiting factors.
- Relate predator-prey cycles to density-dependent population control.
- Compare and contrast the adaptations and environmental characteristic of r-selected species to those of K-selected species.

Introduction

Imagine a huge bowl of your favorite potato salad, ready for a picnic on a beautiful, hot, midsummer day. The cook was careful to prepare it under strictly sanitary conditions, using fresh eggs, clean organic vegetables, and new jars of mayonnaise and mustard. Familiar with food poisoning warnings, s/he was so thorough that only a single bacterium made it into that vast amount of food. While such a scenario is highly unrealistic without authentic canning, it will serve as an example as we begin our investigation of how populations change, or **population dynamics**. Because potato salad provides an ideal environment for bacterial growth, just as your mother may have warned, we can use this single bacterial cell in the potato salad to ask:

How Do Populations Grow Under Ideal Conditions?

Given food, warm temperatures, moisture, and oxygen, a single aerobic bacterial cell can grow and divide by binary fission to become two cells in about 20 minutes. The two new cells, still under those ideal conditions, can each repeat this performance, so that after 20 more minutes, four cells constitute the population. Given this modest doubling, how many bacteria do you predict will be happily feeding on potato salad after five hours at the picnic? After you've thought about this, compare your prediction with the "data" in **Table** below.

Table 16.2: Like many populations under ideal conditions, bacteria show exponential or geometric growth. Each bacterium can undergo binary fission every 20 minutes. After 5 hours, a single bacterium can produce a population of 32,768 descendants.

TABLE 16.2:

Time (Hours and Minutes)	**Population Size** (Number of Bacteria)
0	1
20 minutes	2
40 minutes	4
1 hour	8
1 hour 20 minutes	16
1 hour 40 minutes	32
2 hours	64
2 hours 20 minutes	128
2 hours 40 minutes	256
3 hours	512
3 hours 20 minutes	1024
3 hours 40 minutes	2048
4 hours	4096
4 hours 20 minutes	8192
4 hours 40 minutes	16,384
5 hours	**32,768**

|+

Population Growth of Bacteria
Calculated for Ideal Conditions

(*Source:* CK-12 Foundation, *License:* CC-BY-SA)

Are you surprised? This phenomenal capacity for growth of living populations was first described by Thomas Robert Malthus in his 1798 *Essay on the Principle of Population.* Although Malthus focused on human populations, biologists have found that many populations are capable of this explosive reproduction, if provided with ideal conditions. This pattern of growth is **exponential**, or **geometric growth**: as the population grows larger, the rate of growth increases. If you have worked compound interest problems in math or played with numbers for estimating the interest in your savings account, you can compare the growth of a population under ideal conditions to the growth of a savings account under a constant rate of compound interest. The graph in **Figure** 16.9, using potato salad bacterial "data," shows the pattern of exponential growth: the population grows very slowly at first, but more and more rapidly as time passes.

Of course, if bacterial populations always grew exponentially, they would long ago have covered the Earth many times over. While Thomas Malthus emphasized the importance of exponential growth on population, he also stated that ideal conditions do not often exist in nature. A basic limit for all life is energy. Growth, survival, and reproduction require energy. Because energy supplies are limited, organisms must "spend" them wisely. We will end this lesson with a much more realistic model of population growth and the implications of its limits, but first, let's look more carefully at the characteristics of populations which allow them to grow.

For a discussion of exponential growth, see (**IE 1e**): http://www.youtube.com/watch?v=-3MI0ZX5WRc (10:43).

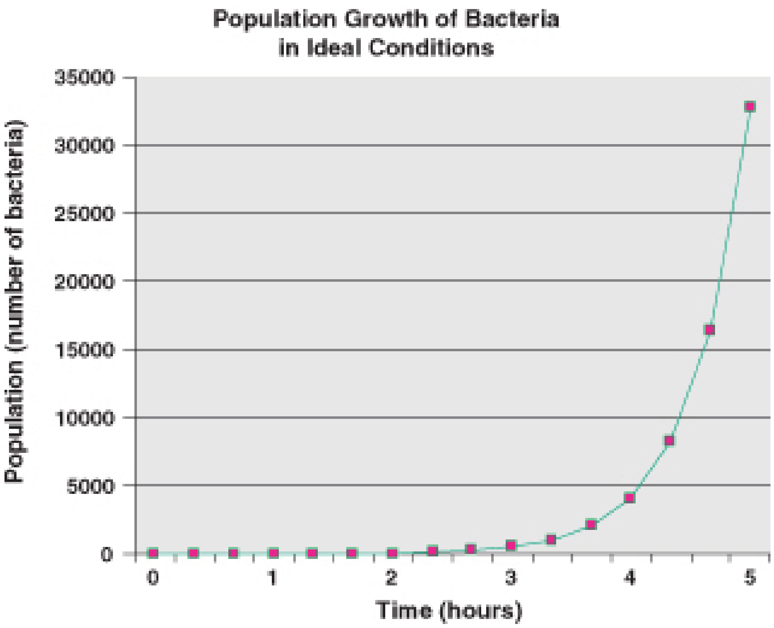
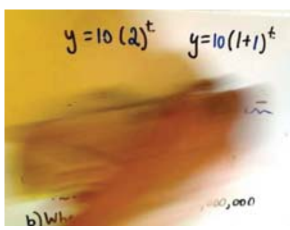


FIGURE 16.9

Exponential or geometric growth is very slow at first, but accelerates as the population grows. Because rate of growth depends on population size, growth rate increases as population increases. Most populations have the ability to grow exponentially, but such growth usually occurs only under ideal conditions that are not found in nature. Note the "J" shape of the curve.



MEDIA

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Births and Deaths: Balancing Costs of Reproduction and Survival

The **growth rate of a population** is the change in population size per member of the population per unit of time. The symbol *r* denotes growth rate. Growth rate clearly depends on **birth rate** *b,* the number of births per individual within the population per unit of time, as well a **death rate** *d,* the number of deaths per individual per unit of time. The following equation calculates growth rate, according to our preliminary understanding:

r = b –d

growth rate = birth rate –death rate

If birth rate exceeds death rate, *r* is positive and the population grows. If death rate exceeds birth rate, *r* is negative and the population declines. And if birth rate and death rate are in equilibrium, growth rate is zero, and the population remains stable. In a stable population, each individual, on the average, produces one offspring which survives long enough to reproduce itself. Mere survival is not success in the game of life; natural selection requires that survivors reproduce. As Malthus realized, nearly all species have the *potential* to grow –to reproduce many more than just a single replacement offspring. However, species vary in the strategies they use to achieve reproductive success, making trade-offs between the energy and time "costs" of survival and those of reproduction. Age at first reproduction, frequency of reproduction, number of offspring, parental care, reproductive lifespan, and offspring death rate are some of the traits which build strategies for successful reproduction.

Analyzing extreme examples can help you understand the trade-offs species must make between survival and reproductive success. Let's compare two groups of birds. Somewhat like precocious children who mature early, *precocial* birds run around to find their own food soon after hatching. Geese, ducks, and chickens use this strategy for raising their young (**Figure** 16.10). Often living and nesting on the ground, precocial species are subject to high predation rates, so few survive long enough to reproduce. Therefore, those who do reproduce lay many eggs at once, and these eggs are large. The young emerge well-developed, ready to feed and escape predators soon after hatching. Precocial species invest a great deal of energy in a large number of offspring but do not spend much energy on parental care, because even though some offspring are likely to die, others will survive long enough to reproduce.

FIGURE 16.10
Geese and ducks use a *precocial* strategy to ensure reproductive success. They invest a great deal of energy in a large number of large eggs, so that young are born well-developed and ready to fend for themselves almost immediately after hatching. Predation on goslings and ducklings is high, but this death rate is offset by a high birthrate. Overall, the population remains stable.

Contrast this precocial strategy with the opposite, *altricial* strategy used by robins and hummingbirds (**Figure** 16.11). These birds hatch helpless and naked, completely unprepared for independent life. Parents invest little energy in just a few, small eggs; hummingbirds' eggs are the smallest in the bird world, and average two per nest. However, survival of these offspring matters a great deal, because there are so few. So, parents build elaborate nests safely hidden in trees and invest a great deal of energy hunting for food around-the-clock until the young have developed enough to fledge and find food on their own.

FIGURE 16.11
Hummingbirds illustrate an *altricial* reproductive strategy. Very little energy is spent to produce two tiny eggs, but they are enclosed in a secluded nest, usually hidden in a tree. Survival of the offspring is critical because there are only two, so parents invest tremendous amounts of energy finding food for themselves and their young for nearly three weeks. This energy investment allows the offspring to develop to nearly adult size before they fledge into the world of predators and competition.

Precocial and altricial birds play by the rules of costs and benefits, each group using a different strategy. Cowbirds, however, make up their own rules, earning them the title of "parasites" in the bird world. How can a bird be a parasite? Cowbirds are altricial, but they parasitize by laying their eggs in other birds' nests, thereby escaping the high costs of parental care (**Figure** 16.12). Cowbird eggs are usually slightly larger and hatch a little sooner than the host eggs affording cowbird parents a bit of extra energy. "Early bird" hatchlings do indeed "get the worm," easily out-competing their smaller host siblings for parental food deliveries. Sometimes, they are strong enough to ungratefully oust their "sibs" from the nest. On the other hand, host parents occasionally recognize and eject the foreign egg before it hatches. Yellow warblers simply block off the offending egg (along with their own eggs) by building a new nest bottom. They then lay a new clutch of their own eggs (The eggs are not their primary energy investment). A five-"story" nest holds the record for yellow warbler (and cowbird?) determination!

FIGURE 16.12

A brown-headed cowbird egg in a phoebe's nest illustrates yet another strategy for reproductive success: invest all of your energy in a single egg, just large enough to out-compete your altricial host's eggs, and let the host parents feed your offspring! The right photo shows a male individual of this parasitic species.

Many species fall in between the extremes of precocial and altricial strategies, but all must make trade-offs between the costs of reproduction and those of surviving predation, competition, and disease, in order to ensure that at least one offspring per adult survives long enough to reproduce. It's worth reprising the survivorship curves introduced in the previous lesson to illustrate these trade-offs (**Figure** 16.13). Which curve illustrates the precocial strategy used by ducks, chickens, and grouse? Which curve demonstrates the altricial strategy of robins and hummingbirds? What shape do you think a cowbird's survivorship curve might take?

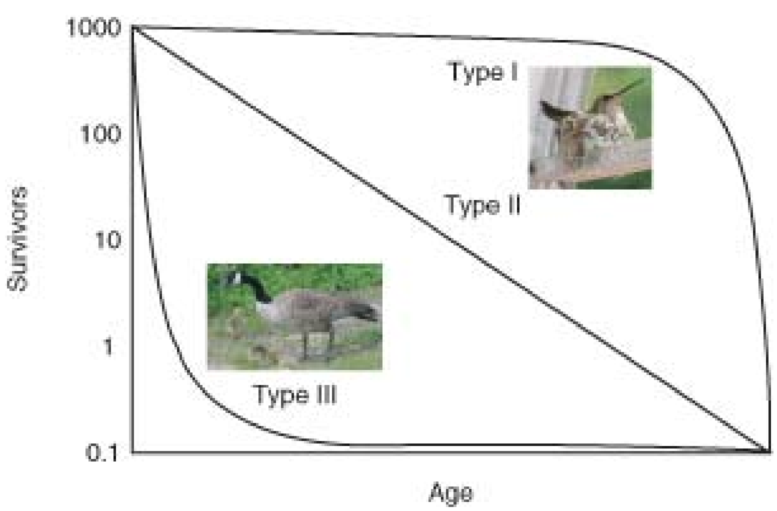

FIGURE 16.13

Survivorship curves show the various strategies for achieving population growth by adjustments in birth rate and death rate. Recall that $r = b - d$. Hummingbirds have low birth rates (*b*), but through time and energy spent on parental care and feeding, ensure high survival rates for their altricial offspring (low *d*). Geese, however, invest energy in many large eggs (high *b*) to offset high death rates from predation (*d*) among their precocial offspring.

One more strategy, introduced in the last lesson, involves variation of age at maturity. All other factors being equal (number and size of offspring, survival rates, and more), delayed reproduction lowers population growth rate. Bald eagles require five years of growth before they are able to reproduce. If they were to lay the same number of eggs during their first year, those first-year offspring and several generations of *their* offspring, as well as the parents, would be able to reproduce during that time, tremendously increasing the overall population. By delaying reproduction, bald eagles not only ensure good energy supplies for reproduction at maturity, but also limit population density to suit their large bodied, long-lived life history.

Migration and Other Movements Affect Population Densities

Populations change not only through births and deaths, but also via **immigration**, movement of individuals into a population from other areas, and **emigration**, movement of individuals out of a population. If we add per capita rates of immigration and emigration into our equation for population growth rate, it becomes:

$r = (b + i) - (d + e)$

growth rate = (birth rate + immigration rate) –(death rate + emigration rate)

Many kinds of movement adaptations regularly add to or subtract from population density.

- Most species have some means of **dispersal** –movement of offspring away from the parents. This "behavior" reduces competition within the population, promotes colonization of suitable habitat, and improves reproductive success. Some dispersal mechanisms take advantage of natural energy in the environment. For example, dandelion seeds grow "parachutes" which allow wind to carry them far from their parents –and sometimes entirely out of a population (**Figure** 16.14). For the same reason, immobile animals such as corals often produce motile larva. Mobile animals often evolve behaviors which ensure dispersal. A lone gray wolf which leaves its birth pack must find a mate and an unoccupied territory in order to reproduce; within the pack, usually only the alpha male and female have offspring. Dispersal behaviors are common in the living world; have you - as a teenage high school student, begun to feel stirrings of the wish to leave home?

FIGURE 16.14

Wind carries dandelion seeds away from their parent plants. The parachute adaptation allows for dispersal, reducing competition within the population and promoting colonization of suitable habitat.

- **Migration**, the direct, often seasonal movement of a species, is a predictable change for some animal populations. Many northern hemisphere birds, such as Swainson's Hawks (**Figure** 16.15), migrate thousands of miles southward in the fall and return north to nest in the spring in order to follow summer's long days which provide extra hunting time and a greater abundance of food.

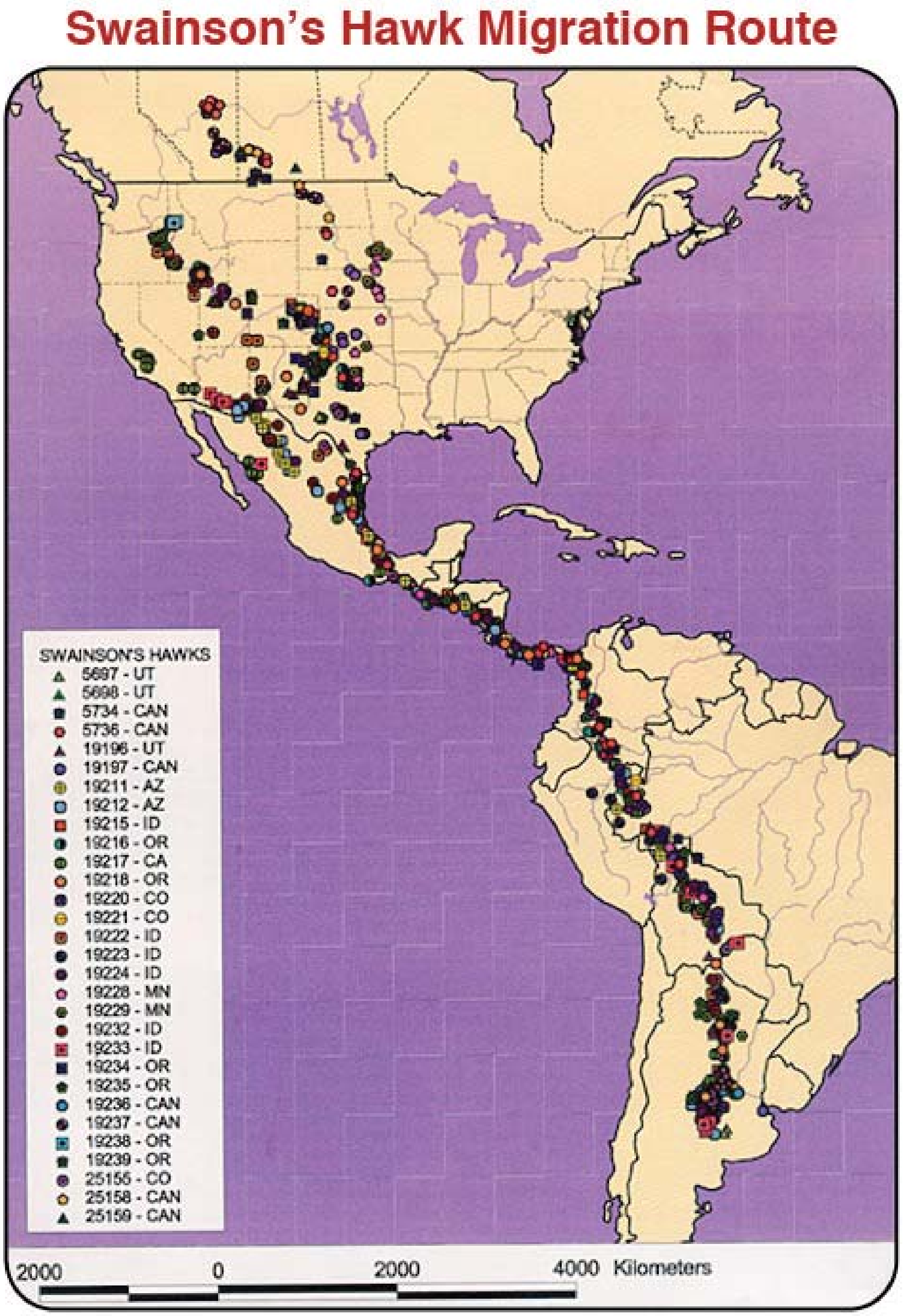

FIGURE 16.15

Entire populations of Swainson's Hawks migrate annually from North America to South America and back. Migration can affect all four factors of the growth rate equation: rates of birth, death, immigration, and emigration.

Apparently, energy benefits outweigh costs for this annual long-distance commute. Elk migrate vertically –up the mountains in spring as snow recedes and down the mountains in fall as winter advances. Monarch butterflies migrate in "shifts"; somewhat like a relay team, successive generations divide the task of moving from Mexican wintering grounds to northern summer habitats. Such migrations do not add to or subtract from populations as much as they move entire populations from one set of boundaries and environmental conditions to another. Some species, such as Peregrine Falcons, have both migratory and non-migratory forms, so their populations may grow or decline with migration. Gray Whales migrate 12,500 miles from Alaska to Mexico for calving, but at least one population limits its northward journey to the Oregon coast (**Figure** 16.16). Seasonal densities of migratory species vary considerably, but resources and environmental benefits vary as well. Migration can affect all four factors of the growth rate equation.

FIGURE 16.16
Gray Whales migrate up to 12,500 miles –further than any other mammal. At least one population stops its northward journey in Oregon; this behavior probably results in immigration and/or emigration, changing intraspecific interactions as populations merge and separate.

Other types of movement are less predictable, but still may affect population growth.

- **Nomadism**, regular, wide-ranging wandering behavior, allows some species to compensate for fluctuating food sources. Normally arctic species, Snowy Owls occasionally venture as far south as Texas, southern Russia, and northern China (**Figure** 16.17). Bohemian waxwings are notoriously nomadic, feeding on highly variable berry supplies.

- **Irruptions** or **invasions** are irregular movements, often caused by food source failures. Owls such as Great Grays and Boreals occasionally invade northern US states from their Canadian homes when rodent populations decline. Some may remain to nest following such an irruption.
- **Range expansion** involves the gradual extension of a population beyond its original boundaries. Recent examples in the US include Cardinals, now common in northern areas where they were originally absent. The Swainson's Thrush follows an indirect and unnecessarily long migration path - retracing, scientists believe, a range expansion from 10,000 years ago. **Intentional introductions** of non-native species such as the House Sparrow and **reintroductions** of extirpated species such as Peregrine Falcons throughout the Eastern US are human-initiated colonizations, which are often followed by range expansions.
- Closely related to range expansion is **colonization**, but the latter often involves newly created, or at least newly found, habitats. Illustrating both range expansion and colonization, the small red-eyed dragonfly spread throughout Europe in the late 20^{th} century and colonized Britain in 1999 (**Figure** 16.18).

Two lectures on demography (**6c**) are available at http://www.youtube.com/watch?v=3diw1Hu3auk (50:36) and http://www.youtube.com/watch?v=Wg3ESbyKbic (49:38).

FIGURE 16.17

Normally arctic species, Snowy Owls occasionally wander as far south as Texas, southern Russia, and northern China. This nomadic behavior allows them to feed on prey which have unpredictable fluctuations in population density.

FIGURE 16.18

Small red-eyed dragonflies expanded their range throughout northwest Europe in the late 20^{th} century and colonized Britain in 1999.

MEDIA

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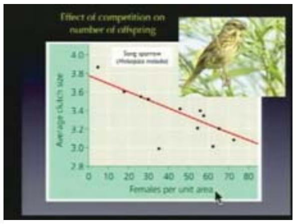

MEDIA

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How Do Populations Grow in Nature?

You learned above that populations can grow exponentially if conditions are ideal. While exponential growth occurs when populations move into new or unfilled environments or rebound after catastrophes, most organisms do not live in ideal conditions very long, if at all. Let's look at some data for populations growing under more realistic conditions.

Biologist Georgyi Gause studied the population growth of two species of *Paramecium* in laboratory cultures. Both species grew exponentially at first, as Malthus predicted. However, as each population increased, rates of growth slowed and eventually leveled off. Each species reached a different maximum, due to differences in size of individuals and space and nutrient needs, but both showed the same, S-shaped growth pattern. **Figures** 16.19 Paramecium Graph, 16.20 Sheep in Tasmania Graph, and 16.21 Population Growth Graph according to Malthus' and Verhulst's models show this growth pattern graphically as an S-shaped curve.

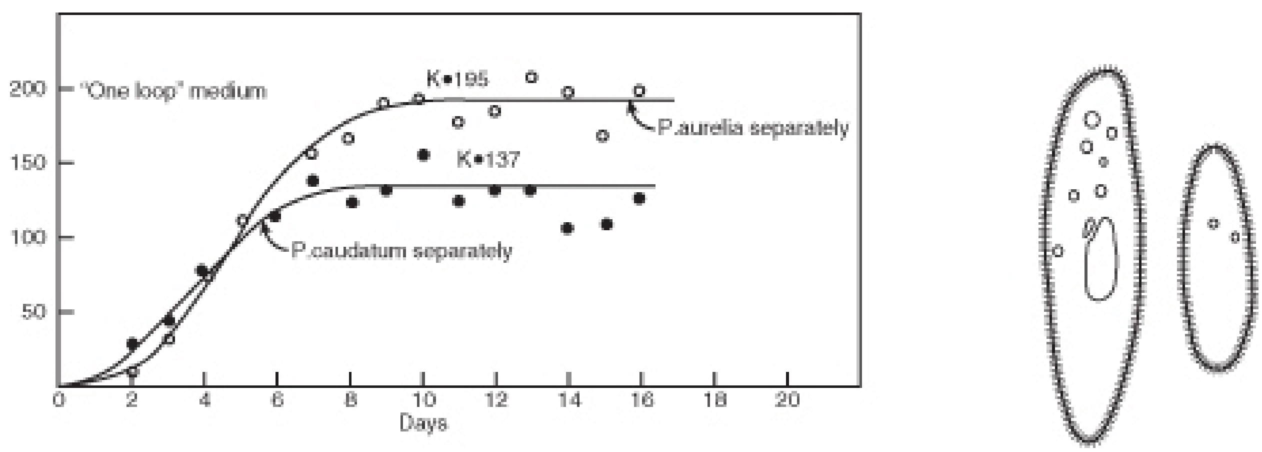

FIGURE 16.19

Two species of Paramecium illustrate logistic growth, with different plateaus due to differences in size and space and nutrient requirements. The growth pattern resembles and is often called an S-curve. Slow but exponential growth at low densities is followed by faster growth and then leveling.

Perhaps even more realistic is the growth of a sheep population, observed after the introduction of fourteen sheep to the island of Tasmania in 1800. Like the lab *Paramecia*, the sheep population at first grew exponentially. However, over the next 20 years, the population sharply declined by 1/3. Finally, the number of sheep increased slowly to a plateau. The general shape of the growth curve matched the S-shape of Paramecium growth, except that the sheep "overshot" their plateau at first.

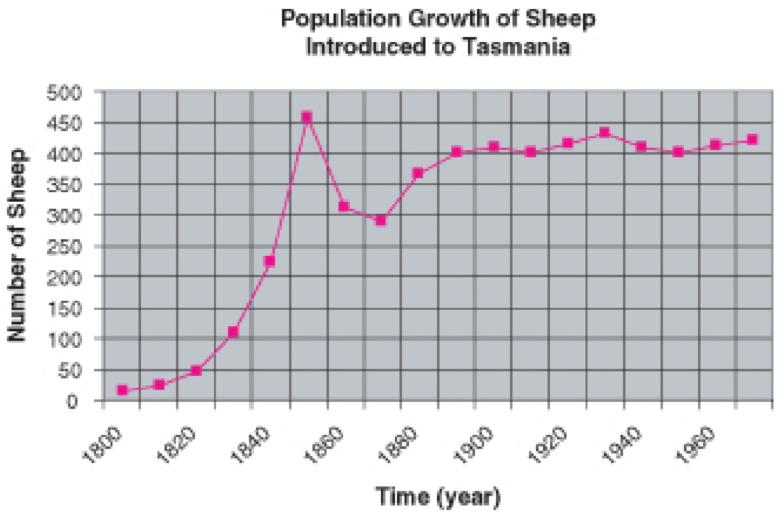

FIGURE 16.20

Sheep introduced to Tasmania show logistic growth, except that they overshoot their carrying capacity before stabilizing.

As Malthus realized, no population can maintain exponential growth indefinitely. Inevitably, **limiting factors** such as reduced food supply or space lower birth rates, increase death rates, or lead to emigration, and lower the population growth rate. After reading Malthus' work in 1938, Pierre Verhulst derived a mathematical model of population growth which closely matches the S-curves observed under realistic conditions. In this **logistic (S-curve) model**, growth rate is proportional to the size of the population but also to the amount of available resources. At higher population densities, limited resources lead to competition and lower growth rates. Eventually, the growth rate declines to zero and the population becomes stable.

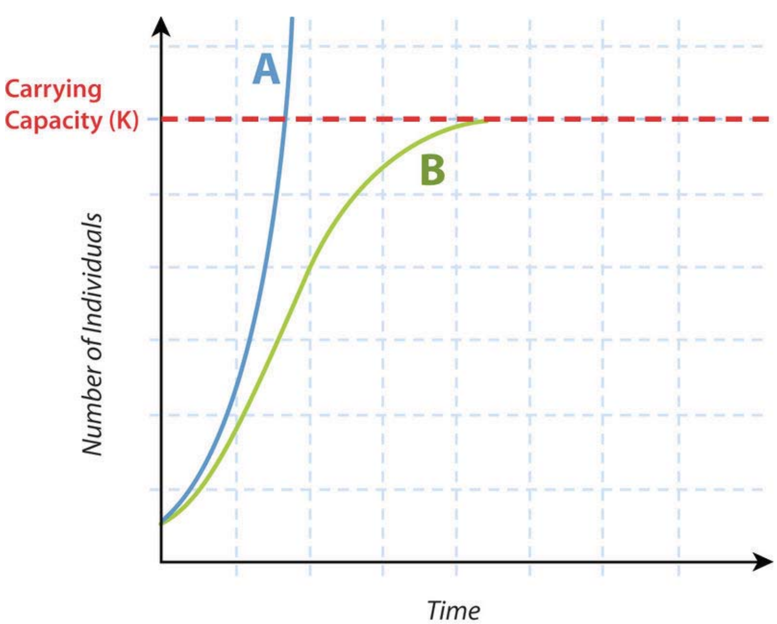

FIGURE 16.21

Growth of populations according to Malthus' exponential model (A) and Verhulst's logistic model (B). Both models assume that population growth is proportional to population size, but the logistic model also assumes that growth depends on available resources. A models growth under ideal conditions and shows that all populations have a capacity to grow infinitely large. B limits exponential growth to low densities; at higher densities, competition for resources or other limiting factors inevitably cause growth rate to slow to zero. At that point, the population reaches a stable plateau, the carrying capacity (K).

The logistic model describes population growth for many populations in nature. Some, like the sheep in Tasmania, "overshoot" the plateau before stabilizing, and some fluctuate wildly above and below a plateau average. A few may crash and disappear. However, the plateau itself has become a foundational concept in population biology known as **carrying capacity (K)**. Carrying capacity is the maximum population size that a particular environment can support without habitat degradation. Limiting factors determine carrying capacity, and often these interact. In the next section, we will explore in more detail the kinds of factors which restrict populations to specific carrying capacities and some adaptations that limit growth.

Limits to Population Growth

A **limiting factor** is a property of a population's environment –living or nonliving –which controls the process of population growth. Biologists have identified two major types of limiting factors: Density-dependent factors and Density-independent factors.

- **Density-dependent factors** promote **intraspecific competition** –competition between members of the same population for the same resource –as the population grows and becomes more crowded. Density-dependent limiting factors have the potential to control population size. Consider food supply as an example. When population density is low, amount of food per individual is high, and birth rates are high. As density increases, food supply per individual decline and birth rates drop, causing growth rate to decline. Eventually, food shortages may lead to increased death rates and a negative growth rate, lowering population size. Lower population size means more food per individual, and the population begins to grow again, reaching or temporarily overshooting the carrying capacity. Food supply in this instance is a regulatory limiting factor, because it keeps the population at equilibrium. Density-dependent limiting factors may include:
- Light
- Water, nutrients/minerals, or oxygen
- Waste, or the ability of an ecosystem to recycle nutrients and/or waste
- Predation by predators which feed preferentially on more abundant prey
- Disease and/or parasites
- Space, with or without territorial behaviors, or nesting sites
- Temperature
- Aggressive behaviors, often combined with stress and effects on immune systems

Let's look at two examples in detail, to emphasize the importance of density-dependent regulation of growth. First, waste products build up with increasing population density. Most environments have some capacity for recycling of wastes, but sometimes rapid population growth means that natural environmental systems can't keep up. An interesting - if not completely natural - example is the growth of yeast populations through fermentation in the making of wine. Alcohol is a waste product for the yeast, even though it is the point of the process as far as we're concerned. As the yeast population grows, alcohol builds up; but alcohol is toxic –to yeast as well as to humans –and after the concentration reaches 13%, increased death rates doom the yeast population. Therefore, no naturally fermented wine contains more than 13% alcohol.

- A second density-dependent limiting factor is predation. Predators kill and eat their prey, of course, so predation increases prey death rate and can cause negative growth rates –population decline. If predators have multiple types of prey, and switch their feeding to specific prey only when they are abundant, predators may regulate prey population size. However, especially in northern climates, predators often specialize on a single prey species. Goshawks, for example, feed primarily on ruffed grouse, and Canada Lynx depend on snowshoe hares (**Figure** 16.22). If predation causes a significant decline in the prey population, starving predators may experience their own (delayed) decrease in population as a result of lower birth rates or increased death rates. The result is a **predator-prey cycle**; both populations rise and fall, with predator populations trailing prey (**Figure** 16.23).

Goshawks play the game with a little twist; when ruffed grouse populations in their Canadian conifer forest homes decline, they migrate southward. Grouse populations show ten-year cycles; note that the goshawk counts from Hawk

FIGURE 16.22
Populations of snowshoe hare (left) and their Canada Lynx predator (right) show repeating cycles, with predator population changes trailing those of their prey.

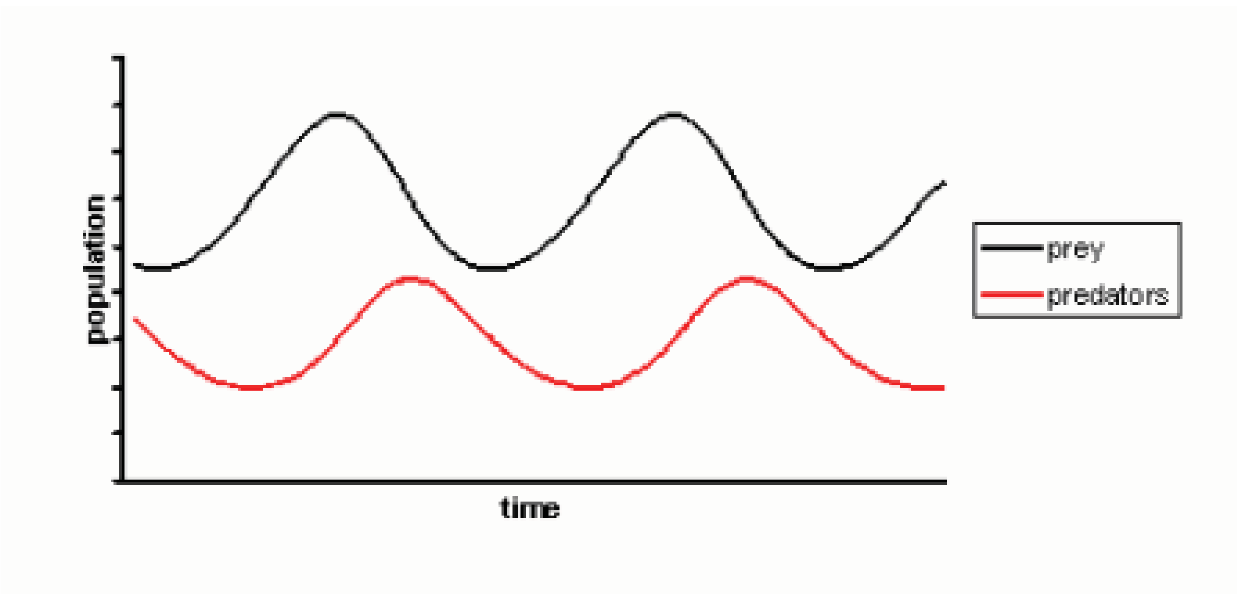

FIGURE 16.23
Repeating cycles of growth and decline characterize population dynamic interactions between some pairs of predator and prey species.

Ridge in Duluth, Minnesota show ten-year "invasions" which correspond to prey population lows in Canada (**Figure** 16.24).

All of these factors have the potential to lower birth rates or increase death/emigration rates via increased intraspecific competition at higher population densities. Many natural populations are kept at or below carrying capacity by one or a complex interaction among several of the above limiting factors.

- **Density-independent factors** can also limit populations, but they seldom regulate populations because they act irregularly, regardless of the population's density. Populations limited by density-independent factors seldom reach carrying capacity. Weather is a good example. Agaves (Century Plants) reproduce once at the end of a long lifespan (**Figure** 16.25). The average lifespan is about 25 years rather than a full century, but an individual's lifespan depends at least in part on erratic rainfall. Agaves will reproduce only after rainfall

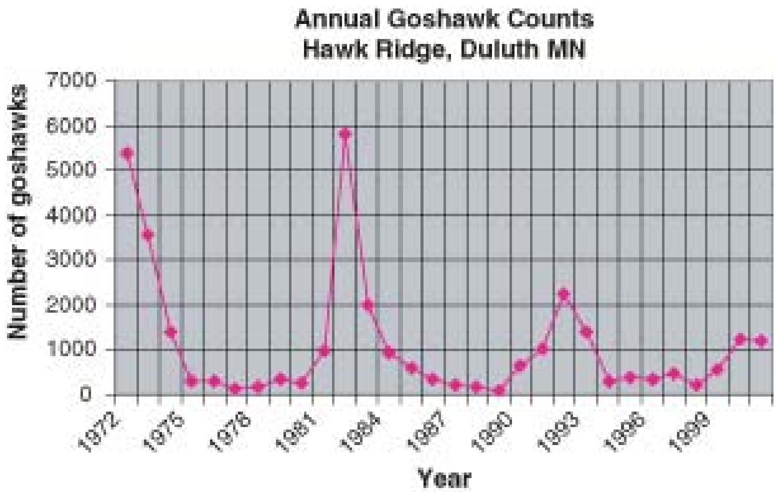

FIGURE 16.24
The pattern of migration of goshawks observed at Hawk Ridge in Duluth, Minnesota, shows irruptions which correspond to low points in cycles of their Canadian prey populations (ruffed grouse). Such cycles are the result of density-dependent interactions between predator and prey. Predators cause increased death rates in prey populations, especially at high prey densities. When prey populations crash as a result of predation, predators are stressed and some (such as lynx) decline. Others, such as the goshawk, irrupt southward in search of higher-density populations.

allows sufficient growth –however long that takes. Eventually, a wet season will bring about a single episode of flowering and the production of a huge number of seeds. Their growth and eventual reproduction will, in turn, depend on erratic rainfall. The density-independent factor rainfall limits birth rate, which in turn limits growth rate, but because of its unpredictability, it cannot regulate Agave populations.

Other density-independent limiting factors include human activities:

- *Pesticides and herbicides*: For example, DDT thinned the eggshells of Peregrine Falcons, reducing their birthrates and leading to their extirpation from the eastern half of North America.
- *Habitat destruction*: Conversion of prairies and grasslands worldwide drastically reduced populations of Burrowing Owls in North America and Giant Pandas in China.

To conclude our discussion of population dynamics, let's look at two sets of adaptations related to the logistic growth curve which describe the growth of most populations. These should remind you of the survival patterns we discussed earlier in this lesson. Recall that for logistic growth, ***r*** is the **growth rate** of the population, and ***K*** is the **carrying capacity**.

- Scientists have found that species adapted to unstable or unpredictable environments are usually limited by density-independent factors to population densities considerably lower than carrying capacity. Such environments favor adaptations which maximize growth rates: early maturity, small size, high numbers of small offspring, single episodes of reproduction, short life expectancy, and the ability to disperse widely. Because populations are usually far below carrying capacity, crowding is minimal, so these species invest little energy in competitive adaptations. Survivorship curves (**Figure** 16.13) are Type III, with high early death rates. Such species are said to be **r-selected** –that is, selected for rapid growth. Weed species are often *r*-selected for colonization and rapid population of disturbed or newly created habitats such as roadsides, abandoned fields, mudslides, or lava flows. Jack pine trees are *r*-selected species which "pioneer" clear areas immediately after forest fires. They grow quickly in hot, dry soils and release seeds from cones which are opened only by fire –reproducing and dispersing seeds at just the right, if unpredictable, time (**Figure** 16.26).

- Whereas density-independent factors limit **r-selected species** in unpredictable environments, **K-selected species** are adapted to stable environments and regulated by density-dependent factors. Stable environments support

FIGURE 16.25
Each Century Plant reproduces only once during its long lifespan. This strategy allows it to gather sufficient water over a number of years in an environment where rainfall is scarce and unpredictable. Then, during an especially wet season, the plant produces a huge number of seeds and dies. Does the Century Plant's pattern remind you of the salmon's life cycle?

K-selected populations at or near carrying capacity, at which point crowding leads to significant intraspecific competition. Such environments favor adaptations for efficient resource utilization which confer competitive ability. K-selected individuals often grow slowly to large size, live long, and delay but repeat reproduction of fewer offspring. They may provide extensive parental care because they can count on environmental stability and survival of these relatively few offspring. Survivorship curves resemble the Type I pattern: long life expectancy and relatively low death rates in the stable environment. Maple trees are K-selected "climax" species which grow slowly in their own shade and reproduce relatively large seeds over a number of years throughout their relatively long lifespan (**Figure** 16.27).

Characteristics of r-selected and K-selected species are compared in **Table** 16.3.

TABLE 16.3:

	r- Selected Species	K-Selected Species
Environment	Unstable	Stable
Type of Regulating Factors	Density-independent	Density-dependent
Organism Size	Small	Large
Maturity	Early	Late

TABLE 16.3: (continued)

	r- Selected Species	K-Selected Species
Number of Offspring	Many	Few
Energy used to make each Individual	Low	High
Average Life Expectancy	Short	Long
Number of Reproductive Events per Individual	Once	Many times
Survivorship	Type III: only a few individuals live long lives	Type I or II: most individuals live long lives

FIGURE 16.26
Jack pines show r-selected adaptations to an unpredictable (density-independent) limiting factor: fire. Cones (bottom image) open to release many tiny seeds only at high temperatures. The trees (top image) grow quickly in the open, bare areas left by forest fires, so are often called "pioneer" species.

FIGURE 16.27
Maple trees show K-selected adaptations to a predictable shade environment they help to create. Maples release relatively large seeds annually, and offspring grow slowly but steadily in the shaded, rich soil of their parents. Maples experience significant intraspecific competition, and their populations tend to be limited by density-dependent factors. Because maple forests tend to persist for long periods because they can grow in their own shade, they are often called "climax" species.

In conclusion, all populations eventually reach limits, at or below carrying capacities for the ecosystems in which they live. Some have adaptations for rapid growth, but the unpredictable environments in which they live inflict high death rates. Others live in stable environments where death rates are relatively low, but their populations are high, so individuals must spend energy on costly competitive strategies in order to gather scarce sunlight, nutrients, or water - or fight disease or predation. Many species live between these extremes, but all populations have limits.

Lesson Summary

- The ways in which populations change are called population dynamics.

1. Populations have the potential to grow exponentially, at least under ideal conditions.
2. Exponential growth begins with slow growth, but as population increases, growth rate increases.
3. J-curves depict the pattern of exponential population growth.
4. Malthus first described exponential growth for the human population and predicted that humans would outgrow their food resources, leading to widespread famine or war.

- If birth rate (plus immigration) exceeds death rate (plus emigration), a population grows. If death rate exceeds birth rate, the population declines. And if birth rate and death rate are in equilibrium, growth rate is zero and the population remains stable.
- In a stable population, each individual (on the average) produces one offspring which survives long enough to reproduce itself.
- *Altricial* species have a few undeveloped offspring but invest a great deal of energy in parental care. *Precocial* species invest energy in a large number of well-developed offspring, but little in parental care.
- The earlier species begin to reproduce, the faster their population grows, with all other factors being equal.

- Dispersal moves offspring away from parents, reducing intraspecific competition.
- Migration, seasonal movement of populations, can affect all four components of population growth rate.
- Regular wandering behavior (nomadism) adapts specific populations to fluctuating food supplies.
- Irruption, range expansion, and colonization have irregular, unpredictable effects on population growth.

- Few populations in nature grow exponentially. No population can continue such growth indefinitely.
- The logistic (S-curve) model best describes the growth of many populations in nature.
- In the logistic model, growth rate depends on both population size and availability of resources. Growth is slow at first, but as size increases, growth accelerates. At higher densities, limited resources cause growth rate to decline, and populations stabilize at carrying capacity.

- A limiting factor is a property of a population's environment which restricts population growth.
- Density-dependent limiting factors lower birth rates or increase death/emigration rates via increased intraspecific competition at higher population densities.
- Many natural populations are kept at or below carrying capacity by one or a complex interaction among several density-dependent limiting factors, such as competition, predation, or disease.
- Density-independent factors, such as rainfall, drought, or pollution, can also limit populations, but they seldom regulate populations because they act irregularly, regardless of the population's density.
- Cycles of growth and decline limit some predator and prey populations.
- Density-independent factors limit *r*-selected species in unpredictable environments, while K-selected species are adapted to stable environments and regulated by density-dependent factors.

Review Questions

1. Explain Malthus' ideas about population growth and their significance to evolutionary theory.
2. Compare exponential(J-curve)growth to logistic(S-curve)growth, and explain the conditions under which each occurs in nature.
3. Summarize the equation for population growth rate, and explain each factor.
4. Compare survival and reproduction in *altricial* species to the same factors for *precocial* species.
5. How might delaying age of childbirth prevent the need to limit family size, as China has done?
6. Give examples of dispersal and migration, and how they affect populations.
7. Define carrying capacity and explain its importance to population growth.
8. Compare and contrast density-dependent and density-independent limiting factors.
9. Relate predator-prey cycles to density-dependent population control.
10. Compare and contrast the adaptations and environmental characteristics typical of r-selected species to those of K-selected species.

Further Reading / Supplemental Links

- http://www.estrellamountain.edu/faculty/farabee/biobk/BioBookpopecol.html
- http://www.geography.learnontheinternet.co.uk/topics/popn1.html
- http://curriculum.calstatela.edu/courses/builders/lessons/less/biomes/breeding.html
- http://www.bestfootforward.com/
- http://www.footprintnetwork.org/gfn_sub.php?content=footprint_overview
- http://www.panda.org/news_facts/publications/living_planet_report/index.cfm
- http://www.worldchanging.com/archives/006904.html
- http://lca.jrc.ec.europa.eu/lcainfohub/introduction.vm
- http://www.ilea.org/leaf/richard2002.html

Vocabulary

altricial
Refers to a pattern of growth and development in organisms which are incapable of moving around on their own soon after hatching or being born.

birth rate (*b*)
Number of births within a population or subgroup per unit time; in human demography, the number of childbirths per 1000 people per year.

carrying capacity (k)
The maximum population size that a particular environment can support without habitat degradation.

colonization
Movement of a population into a newly created or newly found area.

death rate (*d*)
Number of deaths within a population or subgroup per unit time; in human demography, the number of deaths per 1000 people per year.

density-dependent factor
Factor which has the potential to control population size because its effects are proportional to population density.

density-independent factor
Factor which may affect population size or density but cannot control it.

dispersal
Movement of offspring away from parents, resulting in reduced competition within the population and more effective colonization of suitable habitat.

emigration (*e*)
Movement of individuals out of a population's range.

exponential model (geometric or J-curve)
A model of population growth which assumes that growth rate increases as population size increases.

immigration (*i*)
Movement of individuals into a population's range from other areas.

intraspecific competition
Competition between members of the same population for the same resource.

irruption (invasion)
Irregular movements, often caused by food source failures.

K-selected species
A species which has adaptations which maximize efficient utilization of resources, conferring competitive strength near or at carrying capacity.

limiting factor
A property of a population's environment –living or nonliving –which controls the process of population growth.

logistic (S-curve)
A model of population growth which assumes that the rate of growth is proportional to both population size and availability of resources.

migration
The direct, often seasonal movement of a species or population.

nomadism
Regular, wide-ranging wandering behavior, which allows some species to compensate for fluctuating food supplies.

population
A group of organisms of a single species living within a certain area.

population dynamics
Changes in population size and structure.

population growth rate (*r*)
The change in population size per member of the population per unit time.

precocial
Refers to species in which the young are relatively mature and mobile from the moment of birth or hatching.

predator-prey cycle
Regular, repeating increases and decreases in a prey population followed by corresponding changes in its predator's population.

r-selected species
Species which has adaptations which maximize growth rate, *r*.

range expansion
The gradual extension of a population beyond its original boundaries.

Points to Consider

- Why do you think Malthus' predictions of widespread famine and war have not (yet?) been realized? Do you think his ideas make sense for the future?
- Are humans altricial or precocial? Why?
- In your opinion, could delaying age of first childbirth help solve human population problems?
- How important do you think dispersal, range expansion, or immigration are for human populations?
- Do you think humans have more r-selected adaptations, or K-selected adaptations?
- Do you think Earth has a carrying capacity for humans? If so, what kinds of limiting factors determine that carrying capacity?

16.3 Human Population Growth: Doomsday, Cornucopia, or Somewhere in Between?

Lesson Objectives

- Contrast the Neo-Malthusian or "limits to growth" and cornucopian or "technological fix" views of human population growth.
- Compare the overall pattern of human population growth to the J-curve (exponential) and S-curve (logistic) models.
- Analyze the factors which have influenced human population growth from our beginnings 200,000 years ago to 1804, when we first reached the one billion mark.
- Describe the four stages of human population growth as outlined by the demographic transition model.
- Evaluate the demographic transition model as it applies to European population growth in the late 18th and 19th centuries.
- Evaluate the demographic transition model as it applies to less developed countries.
- Apply the demographic transition model to recent changes in developed countries.
- Using age-sex structures, contrast population growth in developed countries to growth in undeveloped countries.
- Explain the concept of replacement fertility rate.
- Discuss the implications of Stage 5 population dynamics.
- Know and understand predictions for future worldwide human population growth.
- Analyze limiting factors and technological advances which may contribute to a carrying capacity of Earth for the human population.
- Explore the concept of sustainability as a goal for economic, social, and environmental decision-making.
- Explain the tool of ecological footprint analysis as a means of evaluating the sustainability of lifestyles for individuals, countries and the world.
- Calculate your ecological footprint and compare it to averages for your country and the world.
- Recognize our human potential to make decisions which could direct future population growth.
- Explore some options for social, political and cultural change, and environmental conservation which could help to balance population dynamics and resource utilization.

Introduction

Hundreds of stone figures measuring up to 10 meters tall and weighing up to 87 tons overlook a low-diversity grassland on Easter Island in the Pacific Ocean (**Figure** 16.28). The food sources, woody trees, and rope-yielding plants which helped to build and transport these statues over five hundred years ago are gone.

Pollen analyses suggest that the island was totally forested at least until 1200 CE, but that by 1650 the forests had entirely disappeared. Middens (waste dump sites) show a sudden disappearance of sea bird and fish bones, suggesting that wood for canoes was no longer available. Sediments reveal that half of native plant species had become extinct. Later fire pits indicate the possibility of cannibalism.

Jared Diamond, in his book *Collapse: How Societies Choose to Fail or Succeed,* examines this bleak scene and other past societies and concludes that doomed civilizations share eight traits which contribute to their collapse. Seven of the eight traits are rooted in overpopulation relative to environmental carrying capacity. Diamond considers Easter

FIGURE 16.28
Easter Island today is a low-diversity grassland nearly devoid of the food sources, woody trees, and rope-yielding plants which helped to build and transport these 10-meter stone statues. Jared Diamond suggests that overpopulation and overexploitation of resources led to the collapse of a once-thriving Easter Island society, and that Easter Island is "Earth writ small" –a warning to the world.

Island to be "Earth writ small" –a warning that this island's environmental devastation could foreshadow a similar fate for our planet. He encourages humans to learn from earlier collapses to conserve the forest, soil, water, animal, fish, photosynthetic, atmospheric, and energy resources upon which our human lives depend. A large group of people sometimes known as **"Neo-Malthusians"** join Diamond in his belief that human population growth cannot continue without dire consequences.

Julian Simon and a group dubbed **"cornucopians"** see the human condition differently. Named for the mythical Greek "horn of plenty" which supplied endless food and drink magically, cornucopians believe that the Earth can provide an almost limitless abundance of natural resources, that few natural limits to growth exist, and that technology can solve or overcome population-induced resource scarcity and environmental degradation. Larger human population (within an appropriate political environment) is the answer to the problems of population growth, according to Simon.

Are you, like Diamond and Malthus before him, a "doomster"? Or do you join Simon as a "boomster"? Most "doomsters" and "boomsters" share the belief that we are responsible for managing problems related to population growth. Let's use our understanding of **population** biology to study the human population. Our goal will be to shed light on the decisions we –the only species able to consider and alter our rates of birth and death –make about future population growth.

The past two lessons have shown how populations in nature grow. You have learned that all populations have the *potential* to grow **exponentially** (**J-curve** pattern of growth), but that exponential growth is limited to ideal conditions, which are rare in nature. In nature, competition for limited resources or unpredictable, density-independent limiting factors restrict populations to densities at or below carrying capacities (**S-curve** growth pattern). Some populations grow smoothly to a stable carrying capacity, but others overshoot that density and may crash before rebuilding to a relatively stable level. A few crash to extinction. In unstable environments, some populations establish cycles of population growth and decline. Unstable environments favor adaptations for rapid growth (**r-selected species**), and stable environments favor adaptations for efficient use of resources (**K-selected species**).

Where do humans fit? Are we built for growth –or conditioned for efficient use of resources? Does our growth pattern resemble a J, or an S? Are we in danger of extinction? What exactly is our "population problem," and what can we do to solve it?

Early Human Population Growth

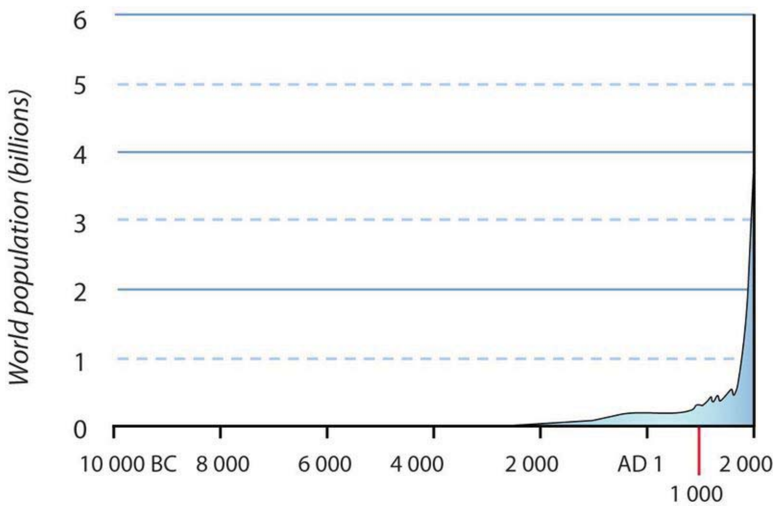

FIGURE 16.29
The growth of the world's human population (using estimates by scholars in the field for the time before census data) shows a classic J shape on this 12,000-year scale. Can you distinguish the decline due to "black death" in the early middle ages?

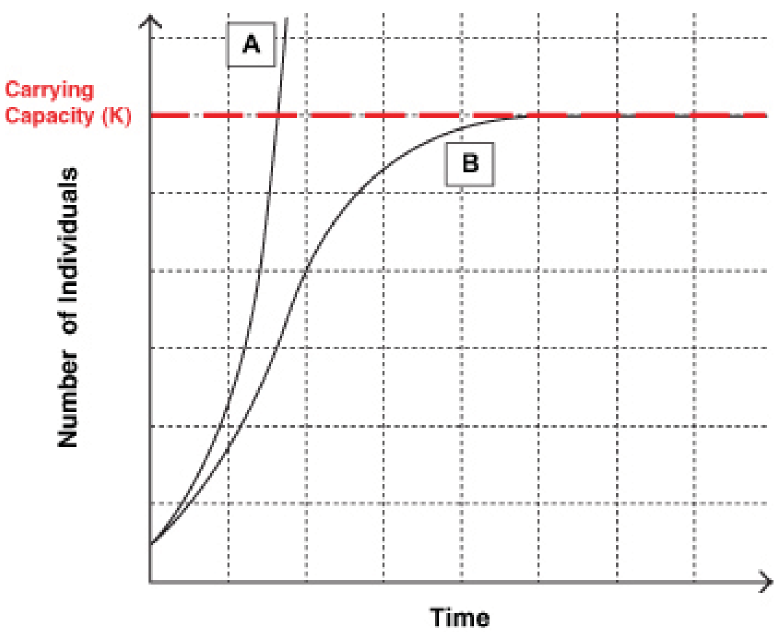

FIGURE 16.30
Growth of populations according to Malthus' exponential model (A) and Verhulst's logistic model (B). Both models assume that population growth is proportional to population size, but the logistic model also assumes that growth depends on available resources. A model's growth under ideal conditions shows that all populations have a capacity to grow infinitely large. B limits exponential growth to low densities; at higher densities, competition for resources or other limiting factors inevitably cause growth rate to slow to zero. At that point, the population reaches a stable plateau, or the **carrying capacity**.

Let's begin by looking at the data. Worldwide human population from 10,000 BCE through today is graphed in **Figure** 16.29. The theoretical J (exponential) and **S (logistic) growth** curves are reviewed in **Figure** 16.30. Overall, our growth resembles exponential growth (the J curve), increasing very slowly at first, but later growing at accelerating rates which show no sign of nearing carrying capacity. We appear to be *r*-selected for rapid growth; indeed, some have described humans as the most successful "weed species" Earth has ever seen as we are fast growing, rapidly dispersing, and colonize habitats from pole to pole. If Earth has a carrying capacity for humans, it is not yet visible in our growth curve –at least on this scale.

However, closer study of human population dynamics reveals more complexity. Different countries show different patterns of population growth today, and history shows varying patterns of growth across time. The history of human population growth can be divided into four stages. Today's countries show snapshot views of these stages. In this section, we will look at early human population growth.

As scientists currently understand human history, *Homo sapiens* arose about 200,000 years ago in Africa. Living as nomadic hunter-gatherers, we migrated to Eurasia and Australia about 40,000 years ago and into the Americas 30,000 years later. Throughout this period, both birth rates and death rates were probably high –as much as 5%. Our human population grew slowly as we spread throughout the world, out-competing other hominid species with our apparently superior reproductive and competitive adaptations. Ice ages, warming periods, and volcanic eruptions were density-independent factors which severely limited our population growth. For example, a "supervolcanic" eruption at Toba in Sumatra 74,000 years ago covered India and Pakistan with more than 5 feet of ash, causing 6 years of nuclear winter, a thousand-year ice age, and the death of up to 99% of the humans living at the time!

With the invention of agriculture 10,000 years ago, we began to develop settled civilizations and trade. Disease associated with animal domestication and city living increased death rates, but reliable food supplies, shared child-care, and division of labor increased birth rates. These effects may have offset each other; slow and uneven growth probably continued. However, the development of agriculture, like many advances in technology, almost certainly raised carrying capacity.

Beginning about 6000 years ago, political states evolved, cooperated or competed, and sometimes waged war. Empires formed, connecting previously independent populations. In the Middle Ages, technology advanced, and the 17^{th} century brought the Scientific Revolution. Throughout this long period of human history, death rates and birth rates continued to be high. **Density-independent factors** such as drought and the "little ice age" combined with **density-dependent factors** such as disease to keep death rates high and variable. The "black death" of the mid-fourteenth century killed as many as 75 million people worldwide and the disease is one of the very few events whose effects are visible in any graph of human population growth (**Figures** 16.29, 16.31). Birth rates continued at a high level throughout early human history. Carrying capacity rose with major advances in technology, as humans modified the environment by irrigating land, building cities, and transporting animals, plants, and products. The overall result was slow growth and a young population. By 1804 CE, the world's human population had reached 1 billion.

Demographic Transition

Major changes in human population growth began during the 18^{th} century, but they affected different regions at different times. We will first consider Europe, and later compare Europe to other regions of the world. In 18^{th} century Europe, seed planters, improved ploughs, threshing machines, crop rotation, and selective breeding of animals led to major growth in food supplies, so death rates due to starvation declined. With increasing understanding of the causes of disease, people improved water supplies, sewers, and personal hygiene –and lowered death rates even more. The Industrial Revolution of the 19^{th} century developed new sources of energy, such as coal and electricity. These further increased the efficiency of new agricultural machines and promoted the development of new forms of transportation, mainly railroads, which improved distribution of food. Death rates fell –particularly for those 5 to 10 years of age, allowing many more children to survive to reproduce. The pattern of human survivorship shifted toward a Type III curve.

Although death rates fell, birth rates remained at earlier levels. The gap between birth and death rates increased, and population growth began to accelerate (remember that $r = b - d$). Although this change did not happen uniformly throughout the world, it was soon reflected in world population levels: it took 200,000 years for the human population to grow to 1 billion, but only 123 years to grow to 2 billion!

Demographic transition theory holds that human populations pass through four stages of growth (**Figure** 16.32).

- Early human history, with its slow, uneven growth maintained by high rates of birth and death, illustrates Stage 1 (**Figure** 16.31 Human Population Growth 8000 BC to 1800 AD, but compare to section "1" of

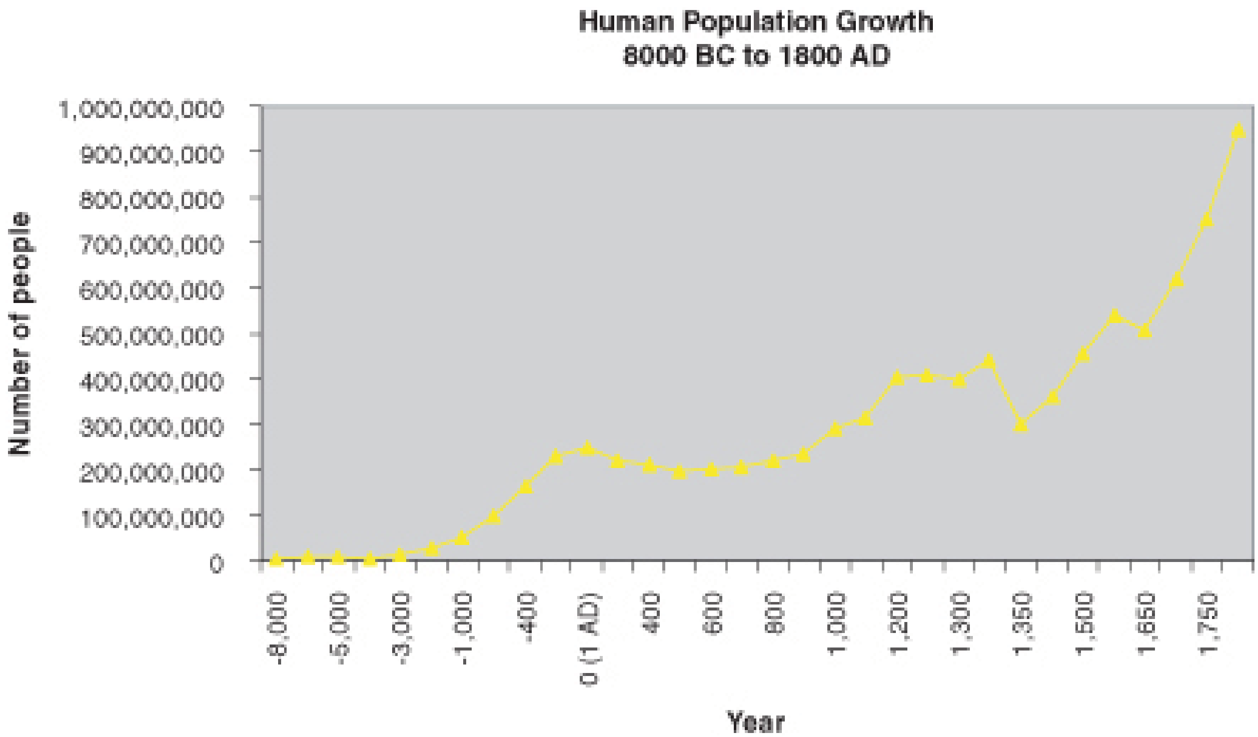

FIGURE 16.31

Early human populations showed slow, uneven growth. At this scale, the negative effect of increased death rate due to the "black plague" during the mid-fourteenth century is clear.

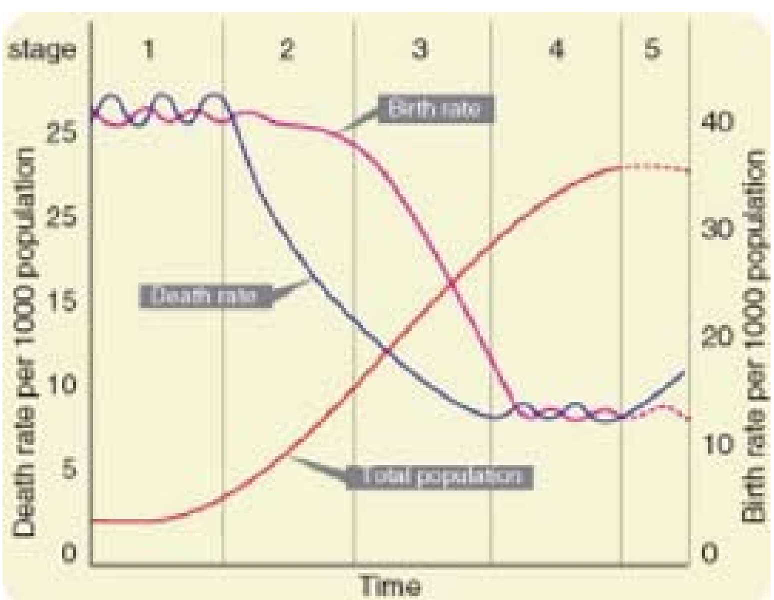

FIGURE 16.32

Demographic transition theory proposes that human populations pass through four or five predictable stages of population growth. The 1st and 4th stages are relatively stable, in the first stage because b and d are both high, and in the last because b and d are both low. The key to the theory (disputed by some) is this: once death rates fall due to industrialization and technology, birth rates will follow (the Transition, Stages 2 and 3). Because the theory is based on observations of developed countries, some people dispute its universality.

Figure 16.32).

- Stage 2, just discussed for Europe, involves a significant drop in death rate *not matched by an increase in birth rate*, resulting in an increasingly rapid rise in population –exponential growth.
- In Stage 3, according to the theory, changes in technology and society lead to a decline in birth rate:

1. The decline in child mortality and improvement in agriculture leads rural families to realize they no longer need to have as many children.
2. Agricultural improvements shift more people to urban areas and reduce the need for children.
3. Compulsory education removes children from the work force but adds to the cost of raising them.
4. Increasing education and employment of women reduces their time for and interest in having children.
5. Birth control methods expand.
6. Later marriage and delayed childbearing further lower birth rate.

Eventually, according to demographic transition theory, falling birth rates approach already-diminished death rates, and population growth begins to level off.

- In Stage 4, birth rates equal death rates, r = zero, and populations become stable.

This somewhat idealistic theory suggests that societies pass through predictable changes which lead to population growth patterns resembling the logistic or S curve. As we have seen (Figure 1), world population growth does not (yet?) show Stages 3 or 4. However, individual countries appear to be at different stages along the continuum; some have reached Stage 4 and a few even require the addition of a 5th stage.

Recent Population Growth

Death rates have fallen throughout the world, so that no country today is considered to remain in Stage 1. Countries appear to vary with respect to the timing of Stages 2 and 3. Many less developed countries remain in Stage 2, including Yemen, Afghanistan, Bhutan, Laos, and part of Sub-Saharan Africa.

Angola's age structure (**Figure** 16.33) reveals accelerating Stage 2 growth. Widest at its base, the structure indicates many youths who will survive to reproduce at their parents' high **fertility** rates because death rates are declining. Some countries, particularly those in regions of Africa which have been devastated by AIDS, appear stalled in Stage 2 due to disease and stagnant development. The demographic transition model may not prove to fit population growth in developing countries. Poor, low-income people in undeveloped countries have the highest birth rates. If demographic transition requires wealth and education, the world's unequal distribution of development and resources may mean that these high birth rates will merely maintain exponential growth, rather than precipitate the social change associated with industrialization.

However, many countries appear to have begun the shift to Stage 3. Fertility rates have dropped 40% throughout much of South America, the Middle East, and the Pacific Islands. Countries such as India, Bangladesh, and Zimbabwe have lowered birth rates between 25-40%, and others such as Pakistan, Saudi Arabia, and Haiti have reduced fertility to 10-25% of earlier rates. Populations in most of these countries are beginning to level off, although resistance to change in the social factors which reduce birthrate may delay or prevent this response. Ecologist Garrett Hardin has pointed out that voluntary birth control selects against people who use it; by itself, voluntary control is unlikely to limit population growth.

High levels of industrialization and development have led to **replacement** (or lower) **fertility rates** in most of Europe, the United States, Canada, Australia, Brazil, China, and Thailand. China, Brazil, and Thailand passed through demographic transition extremely rapidly due to rapid economic and social changes. Replacement fertility includes 2 children to replace parents and a fraction of a child to make up for early mortality and at-birth sex ratio differences. Because mortality rates vary, replacement fertility rate ranges from 2.5 to 3.3 in poor countries,

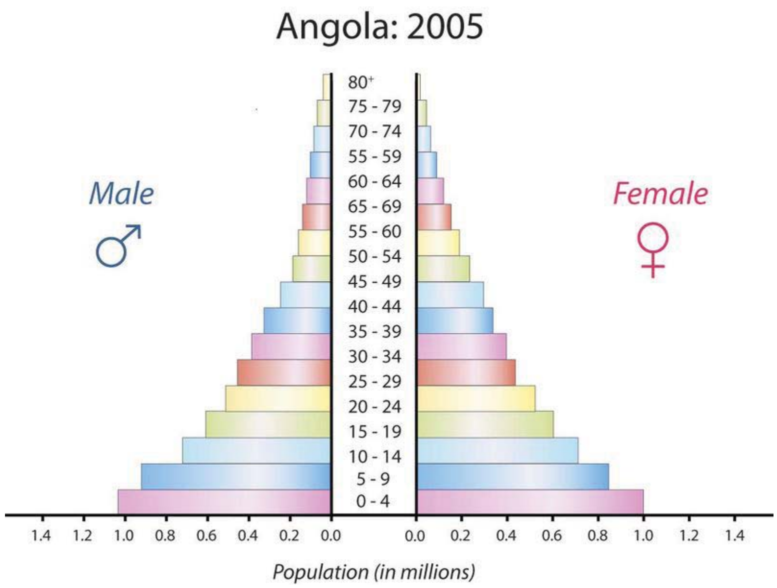

FIGURE 16.33

Angola's population pyramid reflects Stage 2 growth: The wide bars at its base show the many youths who will survive to reproduce at their parent's high fertility rates because death rates (small steps moving up the pyramid) are declining.

but averages 2.1 in developed countries. Globally, replacement fertility is 2.33 children per woman. In Stage 3 countries, populations will eventually stabilize if replacement fertility continues. However, many - including the US –continue to grow rapidly due to the "youth bulges" of exponential Stage 2 growth. The age structures of China and the US (**Figure** 16.34) show demographic transition, but also youth bulges which will mean continuing growth for some time.

Some countries have lowered birthrates below death rates so that *r* is actually negative. Japan, Germany, Italy, Spain, Portugal, and Greece are not producing enough children to replace their parents; populations in some of the southern European countries have already begun to decline. Top-heavy age structures for Spain and Japan are shown in **Figure** 16.35. In countries such as Russia, negative growth emerged suddenly from economic and political crises which caused emigration, declining fertility, and increased male mortality, rather than from development and wealth as the transition model predicts. Negative growth rates pose economic threats: growth-dependent industries decline, and the burden of a large aging, economically dependent population falls on a smaller group of young workers. These shrinking population conditions are sometimes referred to as **Stage 5** of the demographic transition.

Future Population Growth: Does Earth Have a Carrying Capacity for Humans?

As of September 2007, the world's human population stood at about 6.7 billion, growing by 211,090 people each day. Historically, we didn't hit the one-billion mark until 1804 (having begun 200,000 years earlier), but we needed just 12 years to grow by our last billion. Projections by the United Nations and the U.S. Census Bureau predict that by 2050, Earth will host 9.4 billion people; other estimates project that the earth will host 10 to 11 billion people by 2050.

See http://www.youtube.com/watch?v=4BbkQiQyaYc (7:31) for an animation of world population growth.

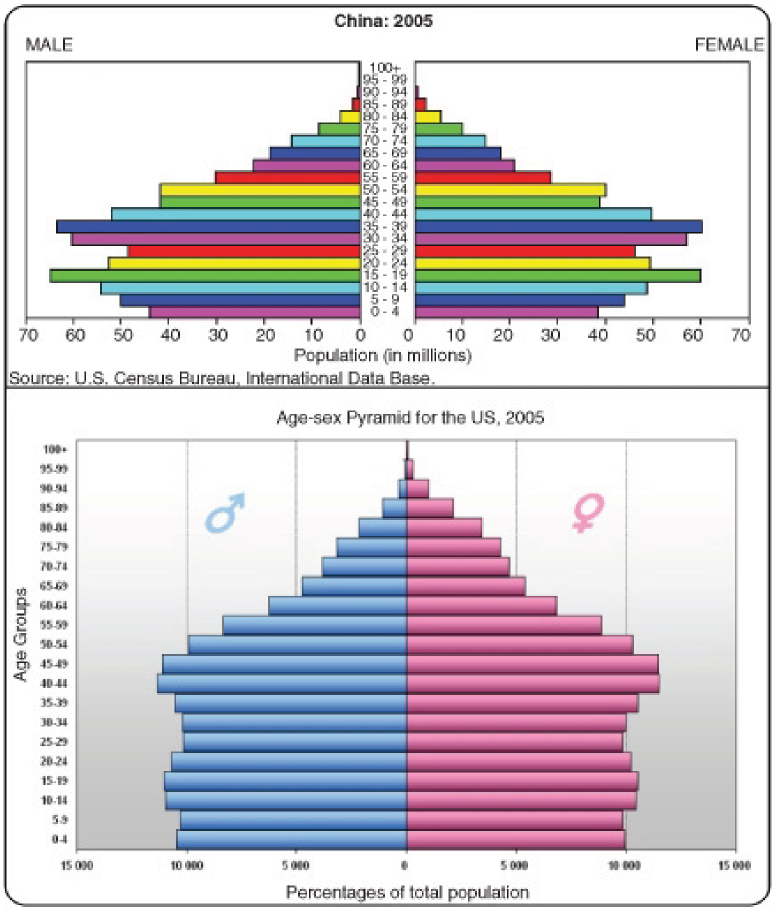

FIGURE 16.34

Population pyramids for China (above) and the U.S. (below) show decreased birth rates which suggest they have reached Stage 3 of the demographic transition model. Both countries show a population bulge remaining from Stage 2 exponential growth, so populations will continue to grow for a number of years. Eventually, if birth rates remain at replacement levels, populations will stabilize in Stage 4.

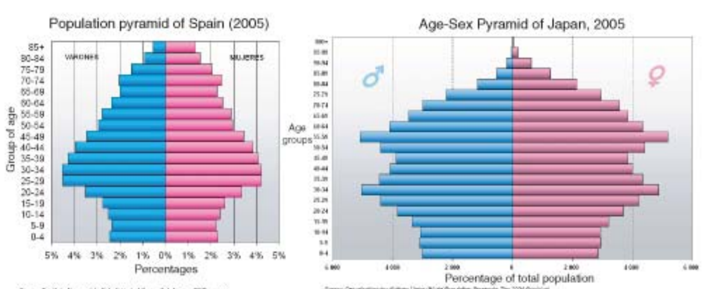

FIGURE 16.35

The top-heavy age structures for Spain and Japan show declining populations due to birth rates which have fallen below already-low death rates. Unless significant immigration occurs, these countries may suffer negative economic effects, such as decline in growth-dependent industries. The burden of a large aging, economically dependent population may fall on a smaller group of young workers.

MEDIA

Click image to the left for more content.

Cornucopians welcome such growth, believing more people are better for technology and innovation. The demographic transition model predicts that when all nations are industrialized, the human population will eventually reach a stable level –a carrying capacity of sorts. However, many scientists believe that humans have already overshot the carrying capacity of Earth for our unique levels of resource exploitation and habitat alteration. They and other Neo-Malthusians predict that resource depletion and environmental degradation will eventually lead to famine, epidemics, or war –a Malthusian crisis.

Does Earth have a carrying capacity for humans? Recall that carrying capacity is the maximum population size that a particular environment can support without habitat degradation. Ideally, carrying capacity matches population size to resource availability. Although the human population is clearly continuing to grow, many scientists believe that we over-consume resources and exceed the environment's capacity to cycle nutrients and process waste. They believe that multiple factors will contribute to a crisis in which disease, starvation, or global conflict will cause a population crash or even extinction:

- Our current *agricultural system*, globally transformed by the **Green Revolution** of the mid-20^{th} century, depends heavily on nonrenewable fossil fuels for fertilizers, pesticides, and irrigation. Ecologist and agriculturalist David Pimentel predicts that to avert disaster, the U.S. must reduce its population to a maximum of 200 million (we are now above 300 million –see the "pop clock" **Figure** 16.36), and the world population must drop to 1/3 its current level. Distribution of food has long been a problem and today has some rather ironic consequences: A 2006 MSNBC report claimed, "There are an estimated 800 million undernourished people and more than a billion considered overweight worldwide."

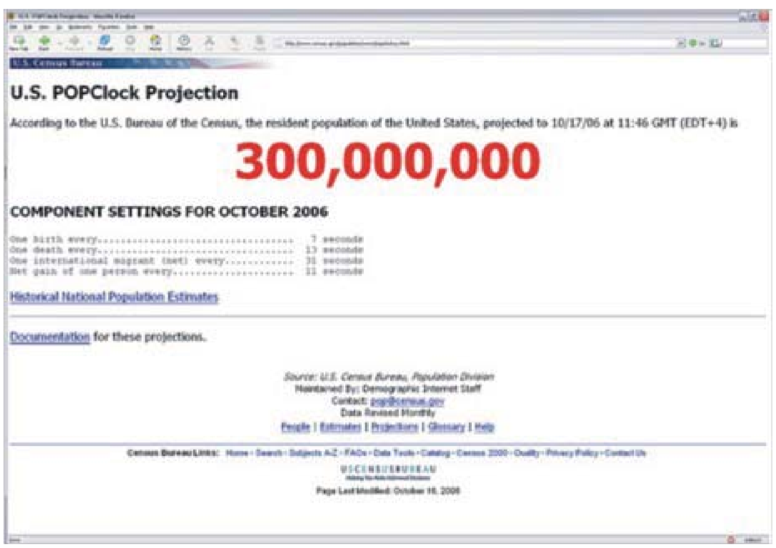

FIGURE 16.36

The U.S. population passed 300 million on October 17, 2006. Agriculturalist David Pimentel believes the U.S. must lower its population by 1/3 to prevent a crisis caused by inability to continue our fossil fuel-dependent agricultural practices. U.S. and World Population Clocks are maintained by the U.S. Census Bureau online at:

- Both developing and developed countries depend almost entirely on *petroleum* to fuel industrialization and transportation, as well as agriculture. In 1956, geophysicist Marion Hubbert predicted that world oil production would peak about half a century into the future and then decline, initiating a global crisis. Predictions about the consequences of **Peak Oil** range from successful development of alternative fuels, to collapse of the global industrialized economy, to intense nationalism and war. Some analysts, such as energy banker Matthew Simmons, believe that the Peak has already occurred (**Figure** 16.37). Others, like energy industry consultants Wood McKenzie, believe we will not reach the peak for another ten years. The difference does not seem significant, but ten years would allow more time for development of alternative fuels and institution of conservation measures.

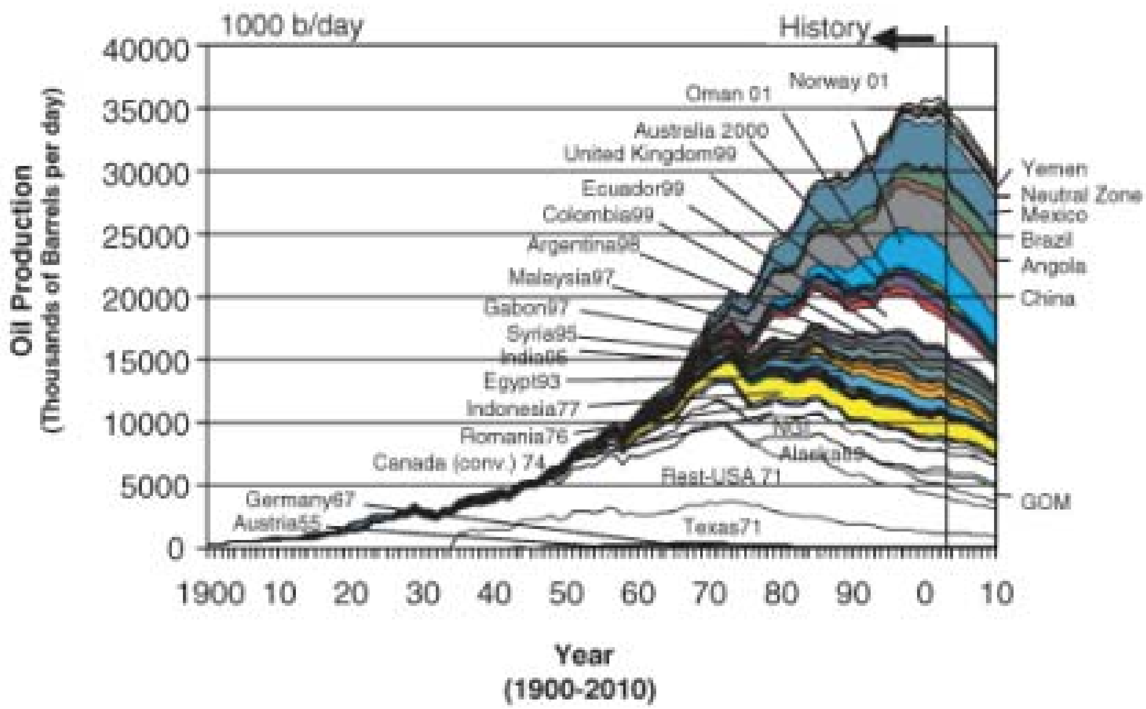

FIGURE 16.37

Oil production outside OPEC and former Soviet Union countries has already peaked, according to oil industry data bases for 2003 and 2004.

- **Fresh water supplies** are declining due to pollution and overuse. According to the United Nations, 2.6 billion people lack water for sanitation, and 1.1 billion have inadequate supplies of safe drinking water. Irrigation and overuse have seriously reduced groundwater supplies, and water pollution threatens biodiversity as well as human sources. Waterborne diseases and lack of water for sanitation cause up to 80% of human illness. Growing populations, of course, will worsen this water crisis.
- **Habitat destruction** due to agriculture, urban sprawl, and mining is the number one cause of extinction today, precipitating a biodiversity crisis. The World Resources Institute estimates that agriculture has displaced 1/3 of all temperate and tropical forests and $\frac{1}{4}$ of all grasslands; in the U.S., less than 2% of native prairie ecosystems remain. Stephen Hawking calculates that continuation of the last 200 years' rate of population growth would have us all standing shoulder-to-shoulder, literally.
- Burning fossil fuels has brought about **atmospheric change**.

Sulfur and nitrogen emissions cause acid rain, which destroys fish, lakes, forests, and limestone structures. CO_2 emissions lead to global warming. Earth's surface air temperatures have risen 0.74°C (1.33°F) during the last 100 years, and will continue to rise by 1.1 to 6.4 °C (2.0 to 11.5 °F) by 2100, according to the Intergovernmental Panel on Climate Change (IPCC).

Food, oil, water, land, and air crises support the idea that our human population has already grown beyond carrying capacity with respect to environmental degradation. As world population continues to grow, what can we do to avert famine, disease, or war? How can we prevent a crash? What should be our goal?

Fortunately, individuals, organizations, and governments are beginning to address these problems. The concept of **sustainability** as a goal for human activities may hold promise for economic, social, and environmental decision-making. Although the term is recent, the concept is clearly expressed in the Great Law of the Iroquois Confederacy: A sustainable activity or state can be maintained indefinitely, without compromising resources for the future. Sustainability of products and services considers complete life cycles –raw materials, manufacturing, transportation/distribution, use and re-use, maintenance, recycling and ultimate disposal. All phases must address conservation of natural and human resources and also biodiversity. Many people believe current population and lifestyles are not sustainable. Unequal distribution of resources suggests that developing countries may accelerate pressure on resources in order to improve their own lifestyles.

A preliminary tool for estimating sustainability is an **ecological footprint** analysis. Your ecological footprint is the amount of land area you would need to sustain your current lifestyle. Footprint analysis considers the resources you consume and the pollution you generate, and then calculates the amount of land which would be needed to produce equivalent *renewable* resources and process associated with waste. Air, land, water, food, and energy resources are all incorporated into the model. You can estimate your own footprint online (see Links at the end of the lesson) and compare it to that of countries throughout the world (**Figure** 16.38). Note that the average U.S. footprint is 12 times that of India, 24 times that of Somalia, and 4.4 times the world average. The last figure is worth expressing in another way: to provide everyone alive today with our western lifestyle, we'd need 4 or 5 backup planets.

To date, there is no overall agreement on a carrying capacity of Earth for humans, but many people are concerned about population growth, resource depletion and environmental degradation. Joel E. Cohen, in his book *How many people can the earth support*? summarizes three potential responses to the "population problem" identified at the beginning of the chapter. All three can contribute to the ultimate solution.

1. *"Make a bigger pie."* Use technology and innovation to create, conserve, and distribute resources.
2. *"Put fewer forks on the table."* Through birth control and cultural change, reduce both population size and lifestyle expectations.
3. *"Teach better manners."* Transform political and social structures toward the goal of social justice.

The human population, like all populations, has the capacity to reproduce exponentially and yet must live within a finite world. Unique among animals, however, we can utilize technology, cultural planning, and values in decisions which influence our future welfare. Which tools would you choose? What decisions will you help to make?

Lesson Summary

- According to Neo-Malthusians, the worldwide human population may have already passed Earth's carrying capacity in terms of environmental degradation, resource depletion, and unbalanced distribution of food, wealth, and development. More people will increase the danger of famine or war.
- According to the cornucopians, technology and innovation can solve any problems which arise due to human population growth. The more people, the better.

- The demographic transition model suggests that human populations pass through four stages of population growth:

Stage 1: Growth is slow and uneven, because high death rate offsets high birth rate.
Stage 2: Development and sanitation reduce death rates, so populations grow exponentially.
Stage 3: With industrialization, urbanization and contraception, births fall, and growth begins to decline.

Country	Ecological Footprint (global hectares per person)
Worldwide	2.2
Africa	1.1
Australia	6.6
Canada	7.6
China	1.6
European Union	4.8
Findhorn, Scotland, Ecovillage	2.56
Haiti	0.6
India	0.8
Japan	4.4
United States	9.6
Somalia	0.4

FIGURE 16.38

Ecological footprints measure the amount of land area required to sustain (produce replacement resources and assimilate waste) particular lifestyles. Note the 24-fold difference between citizens of Somalia and those of the US. One U.S. acre is equal to 0.405 hectares.

Stage 4: Eventually, birth rate equals death rate, growth rate is zero, and the population stabilizes.

- Because this model uses late 18^{th} and 19^{th} century European data, it correlates closely with demographic transitions throughout developed nations into the 20^{th} century, but may not fit undeveloped countries.

- No country remains in Stage 1.
- A number of poor, undeveloped countries remain in stage 2; age pyramids show large youth populations.
- Many countries have entered Stage 3, with some lowering fertility rates by as much as 40%, but pyramid "youth bulges" mean they continue to grow.
- Replacement fertility varies from country to country because death rates vary.
- A few countries have reduced fertility rates below replacement and are shrinking in population.
- Shrinking countries may for a time experience economic difficulties related to an aging population.

- In September 2007, world population stood at about 6.7 billion, growing by 211,090 people each day.
- The last billion-person increase took only 12 years.

- Despite recent declines in birthrate in some developed countries, the human population will continue to increase at least until a peak in 2050 of 9.4 billion people or more.
- Many scientists believe that we humans have already overshot the carrying capacity of Earth if resource exploitation and habitat alteration are considered.
- Five factors which many believe already limit sustainable human population size are:

1. Agricultural dependence on nonrenewable fossil fuels for fertilizers, pesticides, and irrigation.
2. Dependence of industry and transportation on a finite fossil fuel supply, which has already peaked.
3. Decline in freshwater resources due to pollution and overuse.
4. Habitat destruction due to urban sprawl and agriculture, and a consequent biodiversity crisis.
5. Atmospheric changes such as acid rain and global warming –both consequences of increased fossil fuel burning.

- The concept of sustainability may hold promise for economic, social, and environmental decisions.
- Sustainability of products and services considers complete life cycles from raw materials to disposal.
- A tool for estimating sustainability is the ecological footprint.

1. The average U.S. footprint is 12 times India's, 24 times Somalia's, and 4.4 times the world average.
2. Were all people to adopt a U.S. lifestyle, we would need 4 or 5 planets to supply resources and dispose of waste sustainably.

- Potential solutions to the problems of population growth are summarized by Joel E. Cohen:

1. Create new and conserve existing resources –the technological "fix."
2. Lower population size and lifestyle expectations –cultural change.
3. Distribute resources equitably –social justice.

Review Questions

1. Describe the *overall* pattern of human population growth, beginning with our origins 200,000 years ago and compare it to the exponential and logistic models.
2. Compare the factors that influenced human population growth up to the first 1 billion mark to those which controlled growth of the last billion.
3. Summarize the 5 stages of the demographic transition model in terms of *b, d,* and *r.*
4. Explain the problems with the original, four-stage demographic transition model of human population growth. Give examples of each.
5. Explain why replacement fertility must exceed 2 children per female.
6. Use the "pop clock" links at the end of the chapter to look up the current US and world populations. Compare these to predictions for 2050 made by the UN and U.S. Census Bureau. Why do many people consider these numbers to be above Earth's carrying capacity?
7. Summarize 5 environmental effects of human activity which may act as limiting factors for population growth. How many of these relate to our use of fossil fuels, and why is this a problem?
8. Explain how ecological footprints measure sustainability, and compare them for developed and undeveloped nations.
9. Explain what Joel E. Cohen meant by suggesting that "a bigger pie," "fewer forks," and "manners" are needed to address the problems of overpopulation.
10. Consider what you know about resource limitations, population distribution, levels of consumption, technology, poverty, economics, political realities, religious views, and different human perspectives on the earth.

Choose and describe 3 changes you believe would be most successful in solving the problems of worldwide population growth –and 3 changes you believe would be least successful. Support each change with reasons why you think it would be more or less effective.

Further Reading / Supplemental Links

- Joel E. Cohen, *How Many People Can the Earth Support?* Norton, 532 pp, 1995.
- http://www.bradshawfoundation.com/journey
- http://desip.igc.org/mapanim.html
- http://www.eoearth.org/article/Human_population_explosion
- http://www.globalchange.umich.edu/globalchange2/current/lectures/human_pop/human_pop.html
- http://www.census.gov/main/www/popclock.html
- http://www.bestfootforward.com/
- http://www.footprintnetwork.org/gfn_sub.php?content=footprint_overview
- http://www.panda.org/news_facts/publications/living_planet_report/index.cfm
- http://www.worldchanging.com/archives/006904.html
- http://lca.jrc.ec.europa.eu/lcainfohub/introduction.vm
- http://www.ilea.org/leaf/richard2002.html

Vocabulary

carrying capacity
The maximum population size that a particular environment can support without habitat degradation.

cornucopian
A person who believes that people and markets will find solutions to any problems presented by overpopulation.

demographic transition theory
Theory that proposes that human populations pass through 4 or 5 predictable stages of population growth.

density-dependent factor
Factor which has the potential to control population size because its effects are proportional to population density.

density-independent factor
Factor which may affect population size or density but cannot control it.

ecological footprint
The amount of land area needed to sustain a particular lifestyle, matching its resource consumption and pollution to necessary renewable resource production and waste assimilation.

exponential model (geometric or J-curve)
A model of population growth which assumes that growth rate increases as population size increases.

k-selected species
Species which have adaptations which maximize efficient utilization of resources, conferring competitive strength near or at carrying capacity.

logistic (S-curve)
A model of population growth which assumes that the rate of growth is proportional to both population size and availability of resources.

Neo-Malthusians
Individuals who believe that human population growth cannot continue without dire consequences.

population
A group of organisms of a single species living within a certain area.

r-selected species
Species which have adaptations which maximize growth rate, *r*.

replacement fertility
The number of births per female required to maintain current population levels; includes 2 children to replace the parents and a fraction of a child extra to make up for early mortality and sex ratio differences at birth.

Points to Consider

- Now that you have studied some of the data on human population growth, return to the questions in the introduction to this lesson and consider whether or not your answers have changed.

1. Are we built for growth –or for efficient use of resources?
2. Does our growth pattern resemble a J, or an S? Why?
3. Do you think Earth has a carrying capacity for humans?
4. Do you think we are we in danger of extinction?
5. What exactly is our “population problem,” and what do you think we should do to solve it?

- Jared Diamond, reflecting on the fates of past societies facing problems of sustainability, in Collapse: How Societies Choose to Fail or Succeed (2005), p. 522, says: "Two types of choices seem to me to have been crucial in tipping ... outcomes towards success or failure: long-term planning, and willingness to reconsider core values. On reflection, we can also recognize the crucial role of these same two choices for the outcomes of our individual lives." Do you think the worldwide human population will be able to make these choices wisely?

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