

Concept 53.1: Biological processes influence population density, dispersion, and demographics

- A **population** is a group of individuals of a single species living in the same general area
- Populations are described by their boundaries and size

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Turtle Tracks

- Population ecology explores how biotic and abiotic factors influence density, distribution, size, and age structure of populations
- For example, the number of loggerhead turtle hatchlings that survive their first journey to the ocean is affected by both biotic and abiotic factors

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Figure 53.1



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Figure 53.1a



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Density and Dispersion

- Density** is the number of individuals per unit area or volume
- Dispersion** is the pattern of spacing among individuals within the boundaries of the population

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Density: A Dynamic Perspective

- In most cases, it is impractical or impossible to count all individuals in a population
- Sampling techniques can be used to estimate densities and total population sizes
- Population size can be estimated by either extrapolation from small samples, an index of population size (e.g., number of nests), or the **mark-recapture method**

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Determining Population Size Using the Mark-recapture method

- Scientists capture, tag, and release a random sample of individuals (s) in a population
- Marked individuals are given time to mix back into the population
- Scientists capture a second sample of individuals (n), and note how many of them are marked (x)
- Population size (N) is estimated by $N = \frac{sn}{x}$

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Figure 53.2



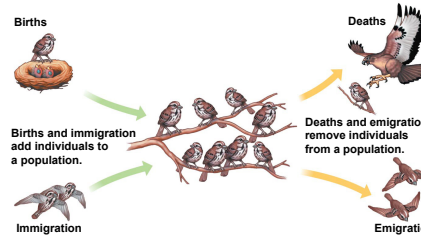
Hector's dolphins

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- Density is the result of an interplay between processes that add individuals to a population and those that remove individuals
- Immigration** is the influx of new individuals from other areas
- Emigration** is the movement of individuals out of a population

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Figure 53.3



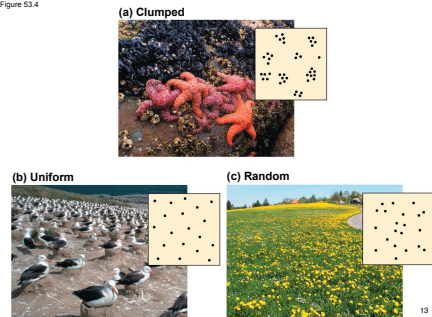
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Patterns of Dispersion

- Environmental and social factors influence the spacing of individuals in a population
- In a clumped dispersion, individuals aggregate in patches
- A clumped dispersion may be influenced by resource availability and behavior

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Figure 53.4



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Figure 53.4a



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Figure 53.4b



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Video: Flapping Geese



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Video: Albatross Courtship Ritual



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Video: Prokaryotic Flagella



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- A uniform dispersion is one in which individuals are evenly distributed
- It may be influenced by social interactions such as **territoriality**, the defense of a bounded space against other individuals

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- In a random dispersion, the position of each individual is independent of other individuals
- It occurs in the absence of strong attractions or repulsions

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Demographics

- **Demography** is the study of the vital statistics of a population and how they change over time
- Death rates and birth rates are of particular interest to demographers

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Life Tables

- A **life table** is an age-specific summary of the survival pattern of a population
- It is best made by following the fate of a **cohort**, a group of individuals of the same age
- The life table of Belding's ground squirrels reveals many things about this population
 - For example, it provides data on the proportions of males and females alive at each age

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Table 53.1

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

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

Source: P. W. Sherman and M. L. Martin, Demography of Belding's ground squirrel, *Ecology* 65:1417-1428 (1984).
¹ Males and females have different mortality schedules, so they are tallied separately.
² The death rate is the proportion of individuals dying during the specific time interval.
 *Includes 122 females and 136 males first captured as 1-year-olds and therefore not included in the rest of squirrel age 0-1.

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Table 53.1a
Table 53.1 Life Table for Belding's Ground Squirrels

Age (years)	FEMALES				
	Number Alive at Start of Year	Proportion Alive at Start of Year	Number of Deaths During Year	Death Rate ¹	Average Additional Life Expectancy (years)
0-1	337	1.000	207	0.61	1.33
1-2	252 ²	0.386	125	0.50	1.56
2-3	127	0.197	60	0.47	1.60
3-4	67	0.106	32	0.48	1.59
4-5	35	0.054	16	0.46	1.59
5-6	19	0.029	10	0.53	1.50
6-7	9	0.014	4	0.44	1.61
7-8	5	0.008	1	0.20	1.50
8-9	4	0.006	3	0.75	0.75
9-10	1	0.002	1	1.00	0.50

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Table 53.1b

Table 53.1 Life Table for Belding's Ground Squirrels

Age (years)	MALES				
	Number Alive at Start of Year	Proportion Alive at Start of Year	Number of Deaths During Year	Death Rate ¹	Average Additional Life Expectancy (years)
0-1	349	1.000	227	0.65	1.07
1-2	248 ²	0.350	140	0.56	1.12
2-3	108	0.152	74	0.69	0.93
3-4	34	0.048	23	0.68	0.89
4-5	11	0.015	9	0.82	0.68
5-6	2	0.003	2	1.00	0.50
6-7	0				

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Table 53.1c



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Table 53.1d



Researchers working with a Belding's ground squirrel

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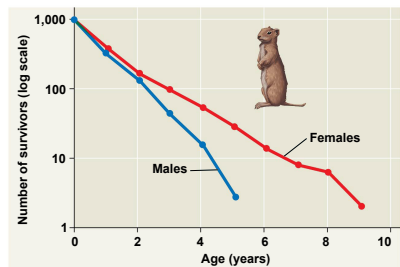
Survivorship Curves

- A **survivorship curve** is a graphic way of representing the data in a life table
- The survivorship curve for Belding's ground squirrels shows a relatively constant death rate

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Figure 53.5



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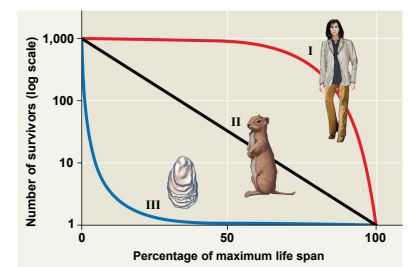
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- Survivorship curves can be classified into three general types
 - Type I: Low death rates during early and middle life and an increase in death rates among older age groups
 - Type II: A constant death rate over the organism's life span
 - Type III: High death rates for the young and a lower death rate for survivors
- Many species are intermediate to these curves

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Figure 53.6

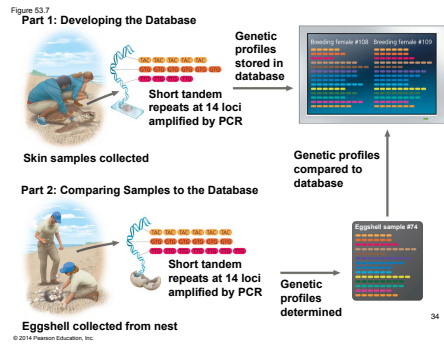


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Reproductive Rates

- For species with sexual reproduction, demographers often concentrate on females in a population
- Ecologists use many approaches to estimate the number of breeding females
 - For example, DNA profiling was used to determine the number of female loggerhead turtles laying eggs in a season



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Concept 53.2: The exponential model describes population growth in an idealized, unlimited environment

- It is useful to study population growth in an idealized situation
- Idealized situations help us understand the capacity of species to increase and the conditions that may facilitate this growth

Per Capita Rate of Increase

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

- If immigration and emigration are ignored, a population's growth rate (per capita increase) equals birth rate minus death rate

- A **reproductive table**, or fertility schedule, is an age-specific summary of the reproductive rates in a population
- It describes the reproductive patterns of a population

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

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

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

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- The population growth equation can be revised

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

- The per capita rate of increase (r) is given by

$$r = b - m$$

- Zero population growth (ZPG)** occurs when the birth rate equals the death rate ($r = 0$)

- Change in population size can now be written as

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

- Instantaneous growth rate can be expressed as

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

- where r_{inst} is the instantaneous per capita rate of increase

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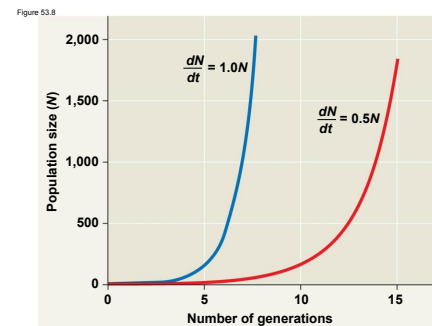
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Exponential Growth

- Exponential population growth** is population increase under idealized conditions
- Under these conditions, the rate of increase is at its maximum, denoted as r_{max}
- The equation of exponential population growth is

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

- Exponential population growth results in a J-shaped curve
- The rate of increase is constant, but the population accumulates more new individuals per unit time when it is large than when it is small



- The J-shaped curve of exponential growth characterizes some rebounding populations
 - For example, the elephant population in Kruger National Park, South Africa, grew exponentially after hunting was banned

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Figure 53.9

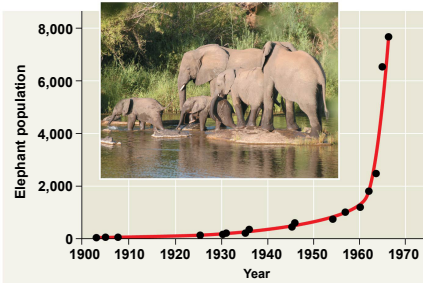


Figure 53.9a



Concept 53.3: The logistic model describes how a population grows more slowly as it nears its carrying capacity

- Exponential growth cannot be sustained for long in any population
- A more realistic population model limits growth by incorporating carrying capacity
- Carrying capacity (K)** is the maximum population size the environment can support
- Carrying capacity varies with the abundance of limiting resources

The Logistic Growth Model

- In the **logistic population growth** model, the per capita rate of increase declines as carrying capacity is reached
- The logistic model starts with the exponential model and adds an expression that reduces per capita rate of increase as *N* approaches *K*

$$\frac{dN}{dt} = r_{inst} N \left(\frac{K - N}{K} \right)$$

- When *N* is small compared to *K*, the term $(K - N)/K$ is close to 1 and the per capita rate of increase approaches the maximum
- When *N* is large compared to *K*, the term $(K - N)/K$ is close to 0 and the per capita rate of increase is small
- When *N* equals *K*, the population stops growing

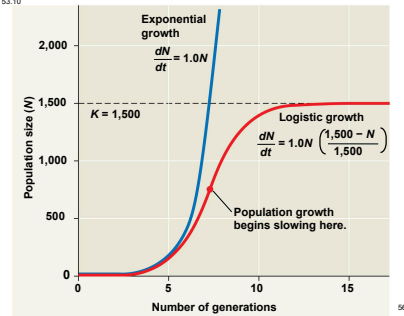
Table 53.3 Logistic Growth of a Hypothetical Population (*K* = 1,500)

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

*Rounded to the nearest whole number.

- The logistic model of population growth produces a sigmoid (S-shaped) curve
- New individuals are added to the population most rapidly at intermediate population sizes
- The population growth rate decreases as *N* approaches *K*

Figure 53.10



The Logistic Model and Real Populations

- The growth of laboratory populations of paramecia fits an S-shaped curve
- These organisms are grown in a constant environment lacking predators and competitors

Figure 53.11

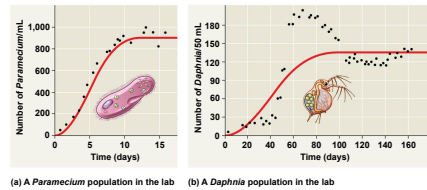


Figure 53.11a

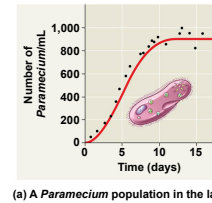
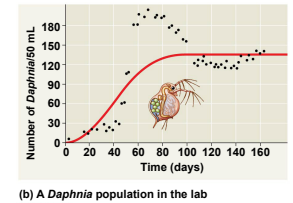


Figure 53.11b



- Some populations overshoot *K* before settling down to a relatively stable density

- Some populations fluctuate greatly and make it difficult to define *K*
- Some populations show an Allee effect, in which individuals have a more difficult time surviving or reproducing if the population size is too small

- The logistic model fits few real populations but is useful for estimating possible growth
- Conservation biologists can use the model to estimate the critical size below which populations may become extinct

Figure 53.12



Concept 53.4: Life history traits are products of natural selection

- An organism's **life history** comprises the traits that affect its schedule of reproduction and survival
- Life history traits are evolutionary outcomes reflected in the development, physiology, and behavior of an organism

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Figure 53.13a



(a) Semelparity, one-time reproducer

69

Figure 53.14a



73

Figure 53.15b



(b) Brazil nut tree seeds in pod

77

Evolution and Life History Diversity

- A life history entails three main variables
 - The age at which reproduction begins
 - How often the organism reproduces
 - How many offspring are produced per reproductive episode

66

Figure 53.13b



(b) Iteroparity, repeat reproducer

70

- Some plants produce a large number of small seeds, ensuring that at least some of them will grow and eventually reproduce

74

Figure 53.15c



(b) Brazil nut tree

78

- Species that exhibit **semelparity**, or big-bang reproduction, reproduce once and die
- Species that exhibit **iteroparity**, or repeated reproduction, produce offspring repeatedly
- Highly variable or unpredictable environments likely favor semelparity, while dependable environments may favor iteroparity

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"Trade-offs" and Life Histories

- Organisms have finite resources, which may lead to trade-offs between survival and reproduction
 - For example, there is a trade-off between survival and paternal care in European kestrels

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Figure 53.13



(a) Semelparity, one-time reproducer



(b) Iteroparity, repeat reproducer

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Figure 53.14

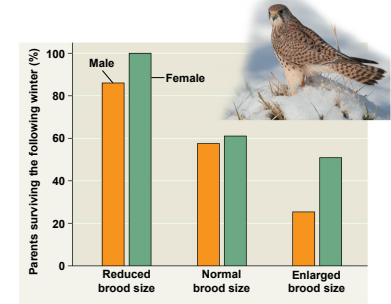


Figure 53.14

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Figure 53.15



(a) Dandelion



(b) Brazil nut tree (right) and seeds in pod (above)

75

Figure 53.15

- Other types of plants produce a moderate number of large seeds that provide a large store of energy that will help seedlings become established

79

Figure 53.15a



(a) Dandelion

76

Figure 53.15a

- **K-selection**, or density-dependent selection, selects for life history traits that are sensitive to population density
- **r-selection**, or density-independent selection, selects for life history traits that maximize reproduction

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Figure 53.15a

- The concepts of *K*-selection and *r*-selection are oversimplifications but have stimulated alternative hypotheses of life history evolution

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Mechanisms of Density-Dependent Population Regulation

- Density-dependent birth and death rates are an example of negative feedback that regulates population growth
- Density-dependent birth and death rates are affected by many factors, such as competition for resources, territoriality, disease, predation, toxic wastes, and intrinsic factors

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Concept 53.5: Many factors that regulate population growth are density dependent

- There are two general questions about regulation of population growth
 - What environmental factors stop a population from growing indefinitely?
 - Why do some populations show radical fluctuations in size over time, while others remain stable?

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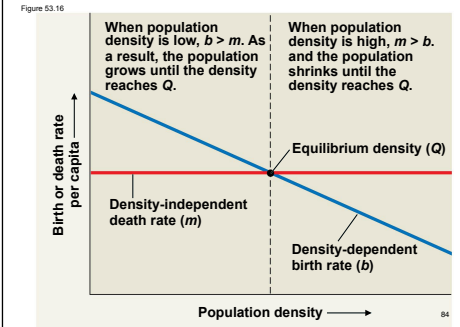
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Population Change and Population Density

- In **density-independent** populations, birth rate and death rate do not change with population density
- In **density-dependent** populations, birth rates fall and death rates rise with population density

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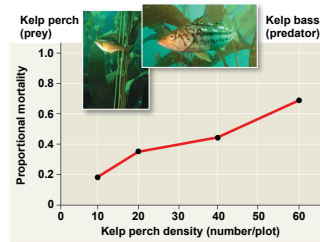
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Figure 53.17



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Figure 53.17a



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Figure 53.17b



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Competition for Resources

- In crowded populations, increasing population density intensifies competition for resources and results in a lower birth rate

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Figure 53.18



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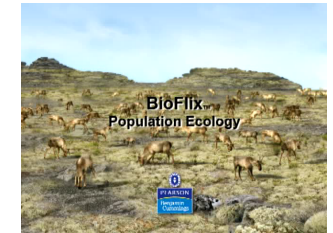
Figure 53.18a



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BioFlix: Population Ecology



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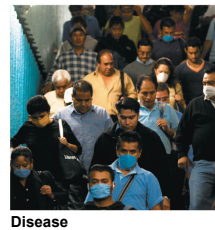
Disease

- Population density can influence the health and survival of organisms
- In dense populations, pathogens can spread more rapidly

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Figure 53.18b



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Predation

- As a prey population builds up, predators may feed preferentially on that species

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Figure 53.18c



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Territoriality

- In many vertebrates and some invertebrates, competition for territory may limit density

Figure 53.18d



Territoriality

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Intrinsic Factors

- For some populations, intrinsic (physiological) factors appear to regulate population size

Figure 53.18e



Intrinsic factors

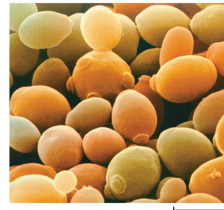
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Toxic Wastes

- Accumulation of toxic wastes can contribute to density-dependent regulation of population size

Figure 53.18f



Toxic wastes 5 μm

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Population Dynamics

- The study of **population dynamics** focuses on the complex interactions between biotic and abiotic factors that cause variation in population size

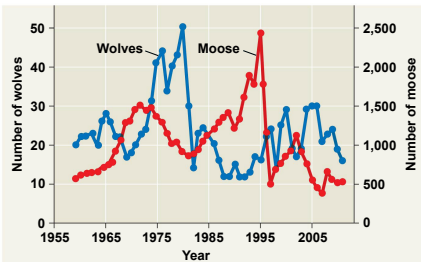
Stability and Fluctuation

- Long-term population studies have challenged the hypothesis that populations of large mammals are relatively stable over time
- Both weather and predator population can affect population size over time
 - For example, the moose population on Isle Royale collapsed during a harsh winter, and when wolf numbers peaked

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Figure 53.19



Population Cycles: Scientific Inquiry

- Some populations undergo regular boom-and-bust cycles
- Lynx populations follow the 10-year boom-and-bust cycle of hare populations
- Two main hypotheses have been proposed to explain the hare's 10-year interval

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Figure 53.20

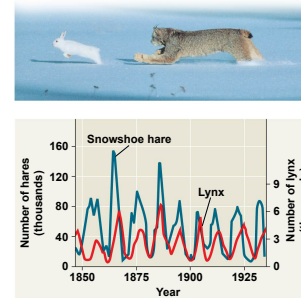
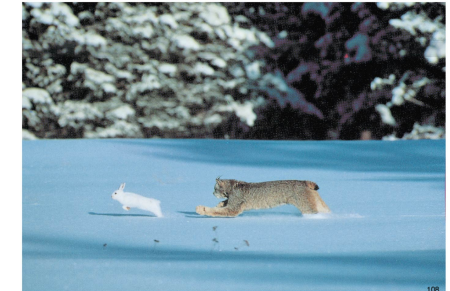


Figure 53.20a



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- Hypothesis: The hare's population cycle follows a cycle of winter food supply
- If this hypothesis is correct, then the cycles should stop if the food supply is increased
- Additional food was provided experimentally to a hare population, and the whole population increased in size but continued to cycle
- These data do not support the first hypothesis

- Hypothesis: The hare's population cycle is driven by pressure from other predators
- In a study conducted by field ecologists, 95% of the hares were killed by predators, including lynx, coyotes, hawks, and owls
- These data support the second hypothesis

- The availability of prey is a major factor influencing predator population dynamics
- When prey become scarce, predator species begin to prey on one another, accelerating the collapse of predator populations

Immigration, Emigration, and Metapopulations

- When a population becomes crowded and resource competition increases, emigration often increases

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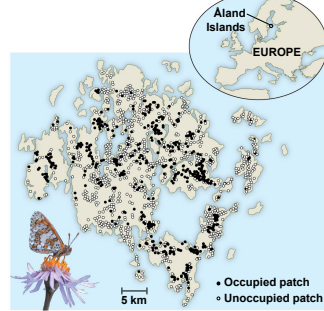
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- **Metapopulations** are groups of populations linked by immigration and emigration
- Local populations in a metapopulation occupy patches of suitable habitat surrounded by unsuitable habitat
- Local populations lost through extinctions can be recolonized by immigration from other patches

Figure 53.21



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Figure 53.21a



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- An individual's ability to move between populations depends on a number of factors, including its genetic makeup
- For example, Glanville fritillary butterflies that are heterozygous at the *Pgi* gene fly further at low temperatures than homozygous individuals

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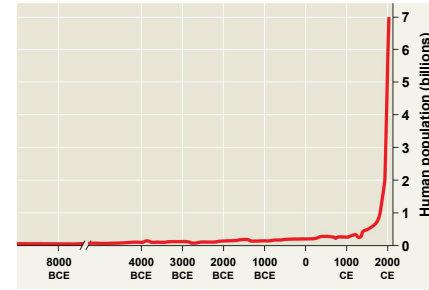
Concept 53.6: The human population is no longer growing exponentially but is still increasing rapidly

- No population can grow indefinitely, and humans are no exception

The Global Human Population

- The human population increased relatively slowly until about 1650 and then began to grow exponentially

Figure 53.22



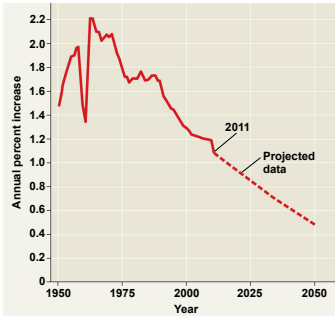
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- The global population is now more than 7 billion people
- Though the global population is still growing, the rate of growth began to slow during the 1960s

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Figure 53.23



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Regional Patterns of Population Change

- To maintain population stability, a regional human population can exist in one of two configurations
 - Zero population growth = High birth rate - High death rate
 - Zero population growth = Low birth rate - Low death rate
- The **demographic transition** is the move from the first state to the second state

- The demographic transition is associated with an increase in the quality of health care and improved access to education, especially for women
- Most of the current global population growth is concentrated in developing countries

Age Structure

- One important demographic factor in present and future growth trends is a country's **age structure**
- Age structure is the relative number of individuals at each age

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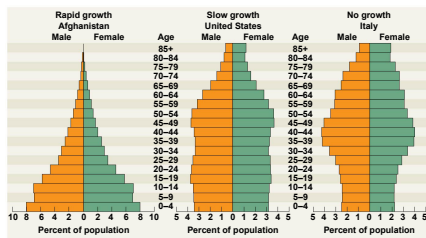
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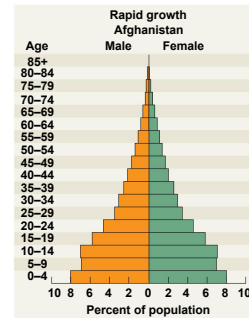
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Figure 53.24



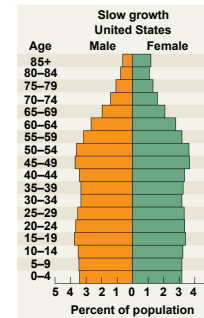
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Figure 53.24a



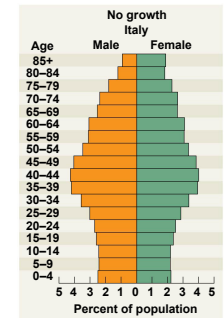
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Figure 53.24b



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Figure 53.24c



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- Age structure diagrams can predict a population's growth trends
- They can illuminate social conditions and help us plan for the future

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Limits on Human Population Size

- The **ecological footprint** concept summarizes the aggregate land and water area needed to sustain the people of a nation
- It is one measure of how close we are to the carrying capacity of Earth
- Countries vary greatly in footprint size and available ecological capacity

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Infant Mortality and Life Expectancy

- Infant mortality and life expectancy at birth vary greatly among developed and developing countries but do not capture the wide range of the human condition

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Global Carrying Capacity

- How many humans can the biosphere support?
- Population ecologists predict a global population of 8.1–10.6 billion people in 2050

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Estimates of Carrying Capacity

- The carrying capacity of Earth for humans is uncertain
- Scientists have based estimates on logistic growth models, area of habitable land, and food availability

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Figure 53.25

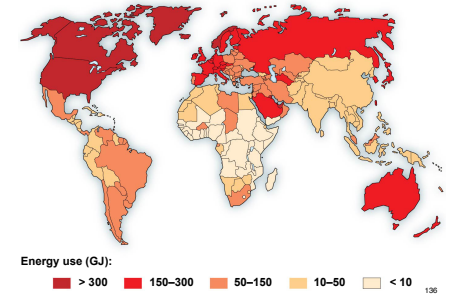


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- Ecological footprints can also be calculated using energy use
- Average per capita energy use differs greatly between developed and developing nations

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Figure 53.26



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- Our carrying capacity could potentially be limited by food, space, nonrenewable resources, or buildup of wastes
- Unlike other organisms, we can regulate our population growth through social changes

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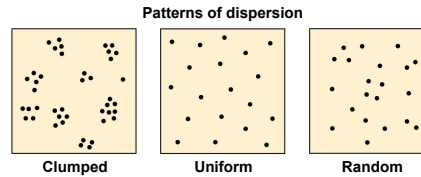
Figure 53.UN01



Daphnia

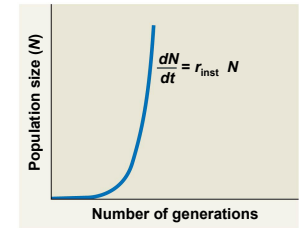
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Figure 53.UN02



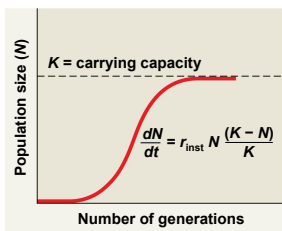
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Figure 53.UN03



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Figure 53.UN04



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Figure 53.UN05



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