TWELFTH EDITION

CAMPBELL BIOLOGY URRY · CAIN · WASSERMAN MINORSKY · ORR



Chapter 53

Population Ecology

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# What affects the size of a population and how it changes over time?

 Population ecology is the study of factors affecting the size of a population and how it changes over time



### What affects the size of a population and how it changes over time?



## CONCEPT 53.1: Biotic and abiotic factors affect 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 (number of individuals)
- Boundaries may be natural (a lake or island) or arbitrarily defined by an investigator (a county)

### **Density and Dispersion**

- Density is the number of individuals per unit area or volume
  - For example, the number of oak trees per square kilometer in the Minnesota county
- Dispersion is the pattern of spacing among individuals within the boundaries of the population

#### Density: A Dynamic Perspective

- In most cases, it is impractical or impossible to count all individuals in a population
- Various sampling techniques can be used to estimate densities and total population sizes
  - Count the number of individuals in randomly located plots, calculate density in plots, extend to entire area
  - Use an indicator of population size, such as the number of nests, burrows, tracks, or fecal droppings
  - Use the mark-recapture method

# Figure 53.2 Determining Population Size Using the Mark-Recapture Method

#### Determining Population Size Using the Mark-Recapture Method

- Capture, tag, and release a random sample of individuals (s) in a population
- Marked individuals are given time to mix back into the population
- Capture a second sample of individuals (n), and note how many of them are marked (x)

- The data collected is used to estimate population size (N) by applying the following formula:
  - $\frac{x}{n} = \frac{s}{N}$  or, solving for population size,  $N = \frac{sn}{x}$



- Density is a dynamic property; it increases and decreases as individuals are added or removed
  - Immigration, the influx of new individuals from other areas, and births increase population size
  - Emigration, the movement of individuals out of a population, and deaths decrease population size

# Animation: Techniques for Estimating Population Density and Size

Terranetees for Paralleling Provide Link Second by 2011 State



#### **Patterns of Dispersion**

- The pattern of dispersion is determined by the spacing among individuals within the boundaries of a population
- Differences in spacing can provide insight into the biotic and abiotic factors affecting individuals

- The most common pattern of dispersion is *clumped*, in which individuals aggregate in patches
- Individuals may aggregate in areas of high resource availability or favorable physical conditions
- Mating behavior and group predation or defense against predators can also influence clumped dispersions

### (a) Clumped



#### Video: Flapping Geese



#### **Video: Albatross Courtship Ritual**



- A *uniform* dispersion is one in which individuals are evenly spaced
- Some plants secrete chemicals that inhibit germination and growth of competing individuals
- Animals often exhibit territoriality, the defense of a bounded physical space against other individuals

## (b) Uniform



- In a random dispersion (unpredictable spacing), the position of each individual is independent of other individuals
- It occurs in the absence of strong attractions or repulsions among individuals or constant distribution of key physical or chemical factors across the habitat

### (c) Random



#### (a) Clumped



#### (b) Uniform



#### (c) Random



### Demographics

- Biotic and abiotic factors influence birth, death, and migration rates of populations
- Demography is the study of these vital statistics of a population and how they change over time

#### Life Tables

- A **life table** is an age-specific summary of the survival and reproductive rates within a population
- It is often made by following a cohort, a group of individuals of the same age, from birth to death

- Building a life table requires a method for determining the proportion of individuals surviving from one age-group to the next
- The number of offspring produced by females in each age-group is also needed
- Males are often ignored because only females produce offspring

#### Table 53.1 Life Table for Female Belding's Ground Squirrels (Tioga Pass, in the Sierra Nevada of California)

Age (years)	Number Alive at Start of Year	Proportion Alive at Start of Year*	Death Rate <sup>†</sup>	Average Number of Female Offspring per Female
0–1	653	1.000	0.614	0.00
1–2	252	0.386	0.496	1.07
2–3	127	0.197	0.472	1.87
3–4	67	0.106	0.478	2.21
4–5	35	0.054	0.457	2.59
5–6	19	0.029	0.526	2.08
6–7	9	0.014	0.444	1.70
7–8	5	0.008	0.200	1.93
8–9	4	0.006	0.750	1.93
9–10	1	0.002	1.00	1.58

Data from P. W. Sherman and M. L. Morton, Demography of Belding's ground squirrel, *Ecology* 65: 1617–1628 (1984).

\*Indicates the proportion of the original cohort of 653 individuals that are still alive at the start of a time interval.

+The death rate is the proportion of individuals alive at the start of a time interval that die during that time interval.



#### Table 53.1



#### Researchers working with a Belding's ground squirrel

#### Survivorship Curves (1 of 5)

- A survivorship curve, a plot of the proportion or numbers in a cohort still alive at each age, shows the pattern of survivorship for a population
  - For example, the approximately straight line of the survivorship curve for Belding's ground squirrels indicates a relatively constant rate of death

1,000 Number of survivors (log scale) Age (years)

- Survivorship curves can be classified into three general types
  - Type I : Low death rates during early and middle life and a sharp increase in death rates later in life
  - Found in large mammals (for example, humans and elephants) that produce few offspring but provide them with good care

- Type II: Constant death rate over the life span
- Found in some rodents, invertebrates, lizards, and annual plants

- Type III: High death rates for the young; death rate steeply declines for survivors of early period die-off
- Found in organisms that produce very large numbers of offspring but provide little or no care (for example, long-lived plants, many fishes, and most marine invertebrates)



#### Animation: Investigating the Survivorship Curve of Oysters



- Many species are intermediate to these curves or show more complex patterns
  - For example, in birds, mortality is often high early in life (Type III) but fairly constant among adults (Type III)
- Survivorship curves can also differ among populations within a single species
#### **Reproductive Rates**

- The reproductive pattern of a population is described by identifying how reproductive output varies with the number of breeding females and their ages
- Direct counts, mark-recapture, and molecular tools, such as DNA profiling, can be used to estimate the number of breeding females





Eggshell collected from nest

- Reproductive output for sexual organisms is measured as the average number of female offspring produced by the females in an age group
- Age-specific reproductive rates vary considerably by species
  - For example, squirrels have one litter of two to six young per year for less than a decade, whereas oak trees drop thousands of acorns per year for tens or hundreds of years

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

- Populations of all species have the potential to expand greatly when resources are abundant
- In nature, unlimited growth is unsustainable because resources are depleted as the population gets larger
- Studying population growth under ideal conditions reveals how fast and under what conditions rapid growth can occur

# **Changes in Population Size**

 Change in population size during a fixed time interval can be defined by the following verbal equation:

Change in				Immigrants				Emigrants
population	=	Births	+	entering	—	Deaths	—	leaving
size				population				population

 If immigration and emigration are ignored, the change in population size equals births minus deaths  The population growth rate can be expressed mathematically as:

$$\frac{\Delta N}{\Delta t} = B - D$$

where  $\Delta N$  is the change in population size,  $\Delta t$  is the time interval, *B* is the number of births, and *D* is the number of deaths during the time interval

The population growth equation can be revised to

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

where R represents the difference between the number of births (B) and the number of deaths (D) that occur in the time interval

- Per capita (per individual) change in population size  $(r_{\Delta t})$  is the average contribution each individual makes to the population size during the time interval
  - For example, for a population of 1,000 individuals that increases by 16 individuals per year,

$$r_{\Delta t} = 16/1,000 = 0.016$$

- The formula  $R = r_{\Delta t}N$  is used to calculate how many individuals will be added to a population each year
  - For example, if  $r_{\Delta t} = 0.016$  and the population size is 500,

$$R = r_{\Delta t} N = 0.016 \times 500 = 8$$
 per year

• Change in population size can now be written as:

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

 Population growth can also be expressed as a rate of change at each instant in time:

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

where *r* represents the per capita change in population size at each instant in time

*dN/dt* represents very small changes in population size over short (instantaneous) time intervals

#### **Exponential Growth**

- Exponential population growth occurs under ideal conditions; all individuals have access to abundant food and reproduce at physiological capacity
- Under such conditions, populations may increase in size by a constant proportion at each instant

• The equation of exponential population growth is:

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

where *r* is the **intrinsic rate of increase**, the per capita rate at which an exponentially growing population increases in size at each instant in time

- Exponential population growth results in a Jshaped curve when population size is plotted over time
- The per capita rate of increase is constant, but more new individuals are added per unit time when the population is large than when it is small

Figure 53.7



#### **BioFlix® Animation: Exponential Growth**



- Exponential growth is characteristic of populations that are introduced to a new environment
- It also represents populations that are rebounding after drastic reduction by a catastrophic event
  - For example, the elephant population in Kruger National Park, South Africa, grew exponentially after hunting was banned



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

- The exponential growth model assumes resources will remain abundant as population size increases
- In nature, each individual has access to fewer resources as population size increases
- Realistic models of population growth incorporate carrying capacity (K), the maximum population size that a particular environment can sustain

- Carrying capacity varies over space and time with the abundance of limiting resources
- Energy, shelter, refuge from predators, nutrient availability, water, and suitable nesting sites are all limiting factors

- Crowding and resource limitation will affect the per capita birth and death rates, causing the per capita rate of population growth (r) to drop
  - Per capita birth rates decline when individuals cannot obtain sufficient resources to reproduce
  - Per capita death rates increase if starvation or disease increases with density

#### **The Logistic Growth Model**

- In the **logistic population growth** model, the per capita rate of population growth approaches zero as the population size nears carrying capacity (*K*)
- The logistic model starts with the exponential model and adds an expression that reduces per capita rate of population growth as population size (N) increases

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

- When N is small compared to K, the term (K N)/K is close to 1, and the per capita rate of population growth will be close to r
- When N is large and resources are limiting, the term (K – N)/K is close to 0, and the per capita rate of population growth is small
- When *N* equals *K*, the population stops growing

# Table 53.2Logistic Growth of a Hypothetical Population(K= 1,500)

Population Size ( <i>N</i> )	Intrinsic Rate of Increase (r)	<u>K – N</u> K	Per Capita Population Growth Rate, $r \frac{(K - N)}{K}$	Population Growth Rate,* <i>rN</i> (K - N) K
25	1.0	0.983	0.983	+25
100	1.0	0.933	0.933	+93
250	1.0	0.833	0.833	+208
500	1.0	0.667	0.667	+333
750	1.0	0.500	0.500	+375
1,000	1.0	0.333	0.333	+333
1,500	1.0	0.000	0.000	0

\*Rounded to the nearest whole number.

- The logistic model produces a sigmoid (S-shaped) curve when population size (*N*) is plotted over time
- New individuals are added most rapidly at intermediate population size, when the the breeding population is substantial and resources are abundant
- The population growth rate (*dN/dt*) decrease as *N* approaches *K*



#### **BioFlix® Animation: Logistic Growth**



# The Logistic Model and Real Populations

- Growth of laboratory populations of some small animals and microorganisms fit an S-shaped curve if resources are limited
- These populations are grown in a constant environment lacking predators and competitors



- Some populations overshoot K before settling down to a relatively stable density
  - For example, if food becomes limiting, females may use energy reserves to continue reproducing; birth rates will decline when reserves are depleted
- Other populations fluctuate greatly and make it difficult to define K



(b) A Daphnia population in the lab

- Conservation biologists use the logistic growth model for several applications
  - Predicting rate of recovery for small populations
  - Estimating sustainable harvest rates for wildlife
  - Estimating the critical size below which populations become at risk for extinction



#### **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

# **Diversity of Life Histories**

- An organism's life history entails three key components
  - The age at first reproduction (maturity)
  - How often the organism reproduces
  - How many offspring are produced per reproductive episode

- The age at first reproduction varies considerably across species
  - For example, loggerhead turtles typically begin reproducing when they are about 30 years old, whereas coho salmon first reproduce when they are only three or four years old

- Organisms also vary in how often they reproduce
  - Semelparity refers to the case where individuals undergo a "one-shot" pattern of big-bang reproduction
  - Iteroparity refers to the case where individuals undergo repeated reproductive events throughout their lifetime


(a) Semelparity: one-time reproduction

(b) Iteroparity: repeat reproduction

- Organisms vary widely in the number of offspring they produce per reproduction
  - For example, white rhinoceros produce only one calf per reproduction, while most insects and many plants produce large numbers
- Species that produce one or few offspring may provision them better than those that produce many

# "Trade-offs" and Life Histories

- Trade-offs occur because organisms do not have access to unlimited resources
- The use of resources for one function (such as reproduction) can reduce the resources available for another function (such as survival)
  - For example, caring for a larger number of young reduced survival rates of parents in Eurasian kestrels



- Selective pressures influence trade-offs between the number and size of offspring
- Species whose young have a low chance of survival often produce many small offspring
  - For example, plants that colonize disturbed environments, such as dandelions, usually produce many small seeds



# (a) Dandelion

- In some species, parents produce relatively few offspring and invest more energy in each offspring to increase the probability of survival for each
  - For example, Brazil nut trees produce large seeds packed with nutrients that help seedlings become established

Figure 53.14b



(b) Seed in pod



### (b) Brazil nut tree

- Variation in life history traits can be related to the logistic growth model
  - *K-selection* refers to selection for life history traits that are advantageous when density is high (near *K*), resources are low, and competition is strong
  - *r-selection* refers to selection for life history traits that maximize reproductive success when density is low and there is little competition for resources
- These concepts represent two extremes in a range of actual life histories

# CONCEPT 53.5: Density-dependent factors regulate population growth

- Answers to the following questions are important in practical applications:
  - What environmental factors stop a population from growing indefinitely?
  - Why are some populations fairly stable in size, while others are not?

# **Population Change and Population Density**

- Assuming immigration and emigration offset each other, a population will
  - grow when the birth rate exceeds the death rate
  - decline when the death rate exceeds the birth rate
- A birth rate or death rate that does not change with population density is **density independent**

- If a death rate increases or a birth rate decreases with increasing density, it is **density dependent**
- A population is regulated when one or more density-dependent factors cause it to decrease when large (or increase when small)
- Density-independent factors cannot regulate population size



Population density —

### **BioFlix®** Animation: Density Dependence



# Mechanisms of Density-Dependent Population Regulation

- Density-dependent birth and death rates are an example of negative feedback that regulates population growth
  - For example, in a study of kelp perch populations, the death rate increased as hiding spaces from predators became scarce at high densities



# Figure 53.17 Exploring Mechanisms of Density-Dependent Regulation

- In addition to predation, several other mechanisms can cause density-dependent regulation:
  - Competition for resources
  - Disease
  - Intrinsic factors
  - Territoriality
  - Toxic wastes



#### **Competition for Resources**



Territoriality







Disease

**Intrinsic Factors** 

### **Competition for Resources**

- In crowded populations, increasing population density intensifies competition for resources and reduces birth rates
  - For example, farmers reduce competition by applying fertilizers to reduce nutrient limitations on crop yield



### **Competition for Resources**

### Disease

- A disease can regulate population density if its transmission rate increases as the population becomes more crowded
  - For example, influenza (flu) and tuberculosis affect a greater percentage of people in densely populated cities than in rural areas

#### Figure 53.17b



### Disease

## Territoriality

- Territoriality can limit population density when space becomes the resource for which individuals compete
  - For example, cheetahs use chemical markers in urine to warn other cheetahs of their territorial boundaries



# Territoriality

### **Intrinsic Factors**

- For some populations, intrinsic (physiological) factors appear to regulate population size
  - For example, hormonal changes in white-footed mice delay sexual maturation and depress the immune system at high density
  - Birth rates drop even when food and shelter are abundant

#### Figure 53.17d



### **Intrinsic Factors**

### **Toxic Wastes**

- Accumulation of toxic wastes at high population density can contribute to density-dependent regulation of population size
  - For example, the concentration of ethanol produced by brewer's yeast becomes toxic at high population density



# **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

- Populations of large mammals were once thought to be relatively stable, but long-term studies show that they can fluctuate substantially
  - For example, there have been two major population increases and collapses in the moose population on Isle Royale during the last 50 years
  - The first collapse coincided with a peak in the wolf population, the second with harsh winter conditions



# Population Cycles: Scientific Inquiry

- While many populations fluctuate at unpredictable intervals, others undergo regular boom-and-bust cycles
  - For example, snowshoe hares and lynx both follow roughly 10-year population cycles in the forests of northern Canada and Alaska

Figure 53.19





- Lynx might be expected to increase and decrease in response to the availability of their prey species, but it is unclear why the hare population cycles
- Two main hypotheses have been proposed to explain the hare's population cycle
  - It follows a cycle of winter food supply
  - It is caused by predator-prey interactions

- If the hare's population cycle follows a cycle of winter food supply, then the cycles should stop if the food supply is increased
- Populations experimentally provided with additional food increased in size, but continued to cycle
- Food supplies alone do not cause the population cycle in snowshoe hares

- Ecologists used radio collars to track individual hares and determine causes of death
- Predation by several species killed 95% of the hares in these studies; none died of starvation
- When predators were excluded from certain areas, the collapse in hare survival was nearly eliminated
- Overexploitation by predators is an essential factor affecting snowshoe hare cycles
#### Immigration, Emigration, and Metapopulations

- In addition to births and deaths, immigration and emigration also influence populations
- When a population becomes crowded and resource competition increases, emigration often increases

- Metapopulations are groups of local populations linked by immigration and emigration
- Local populations in a metapopulation occupy discrete patches of suitable habitat surrounded by unsuitable habitat

- Habitat patches vary in size, quality, and isolation from other patches
- Local populations lost through extinctions can be recolonized by immigration from other patches
  - For example, migration of the Glanville fritillary (butterfly) among habitat patches constantly shifts the location of occupied and unoccupied patches



- In the Glanville fritillary, migration ability depends on a number of factors, including genetic makeup
- Ecologists used radar and transponders to track individuals with different genotypes at the Pgi gene, which codes for an enzyme involved in glycolysis
- Individuals that are heterozygous for this gene can fly farther at low temperatures and are more likely to colonize new locations compared to homozygotes



#### **BioFlix® Animation: Population Ecology**



# CONCEPT 53.6: The human population is no longer growing exponentially but is still increasing extremely rapidly

- In the last few centuries, the human population has grown at an unprecedented rate
- No population can grow indefinitely, and humans are no exception

## **The Global Human Population**

- The human population has grown explosively over the last four centuries
- The time required for the population to double in size decreased from 200 years in 1650 to just 45 years in 1975
- This is faster than exponential growth, which has a constant rate of increase and a constant doubling time



- The global population is now more than 7.6 billion people and is increasing by 80 million per year, or more than 200,000 people per day
- It is predicted to reach 9.8 billion by the year 2050

- Though the global population is still growing, the rate of growth began to slow during the 1960s
- The annual rate of increase peaked at 2.2% in 1962, but was only 1.1% in 2018
- Current models project a growth rate of 0.5% by 2050, adding 49 million more people per year if the population reaches the projected 9.8 billion



#### **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
- Populations are near or below the replacement level of 2.1 children per female in industrialized nations
- Most of the current global population growth is concentrated in less industrialized countries

- The ability to control family sizes through planning and voluntary contraception is unique to humans
- In many cultures, women are helping to decrease population growth by choosing to delay reproduction
- The amount of support that should be provided for global family planning efforts is a point of contention

## Age Structure

- One important factor affecting population growth is a country's age structure
- Age structure is the relative number of individuals of each age in a population

- Age-structure diagrams (pyramids) can help predict a population's growth trends
  - For example, the pyramid for Zambia is skewed toward young individuals who could sustain explosive population growth through their future reproduction



- Age-structure diagrams can also illuminate social conditions and help us plan for the future
  - For example, we can predict that employment and education opportunities will continue to be a problem for Zambia in the foreseeable future
  - In the United States and Italy, a decreasing population of younger working-age people will be supporting an increasing population of retired "boomers"

# Infant Mortality and Life Expectancy

- Infant mortality and life expectancy at birth vary widely in different countries and can influence reproductive choices by parents
- Global life expectancy been increasing since 1950
- Social upheaval, decaying infrastructure, and disease have reduced life expectancy in some countries

# **Global Carrying Capacity**

- Population ecologists predict a global population of 9.8 billion people in 2050
- How many humans can the biosphere support?

# **Estimates of Carrying Capacity**

- The carrying capacity of Earth for humans is uncertain; estimates have varied from less than 1 billion to more than 1,000 billion (1 trillion)
- Scientists have based estimates on logistic growth models, area of habitable land, and food availability

### Limits on Human Population Size

- Humans require food, water, fuel, building materials, and other resources such as clothing and transport
- The ecological footprint concept summarizes the aggregate land and water area needed to sustain a person, city, or nation

- One way to estimate the footprint is to add up all productive land and divide by the number of people
- This allots 1.7 global hectares (gha) per person; any more is unsustainable
- Countries vary greatly in footprint size; the average per person is 8 gha in the United States and 2.7 gha globally
- This overshoots sustainable use by more than 50%



#### Per capita ecological footprint in global hectares (gha)

0–3 🗾 3–6 🔜 >6 📰 Insufficient data

- Ecological footprints can also be calculated using energy use
- Average energy use differs greatly across different regions of the world
  - For example, a typical person in the United States, Canada, or Norway consumes about 30 times the energy of a person in central Africa



- Fossil fuels are the source of 80% or more of the energy used in most developed nations
- Reliance on fossil fuels is changing Earth's climate and increasing the amount of waste humans produce

- Our carrying capacity may also be limited by food, space, nonrenewable resources, or waste production
- Humans could choose to regulate population growth through social change
- Otherwise, it will happen through increased mortality due to resource limitation, plagues, war, and environmental degradation



# Daphnia



#### **Patterns of dispersion**



Number of generations



Number of generations

