# 9

# Population Growth and Regulation

- *Case Study*: Human Population Growth
- Life Tables
- Age Structure
- Exponential Growth
- Effects Of Density
- Logistic Growth
- *Case Study Revisited*
- *Connections in Nature*: Your Ecological Footprint

# Case Study: Human Population Growth

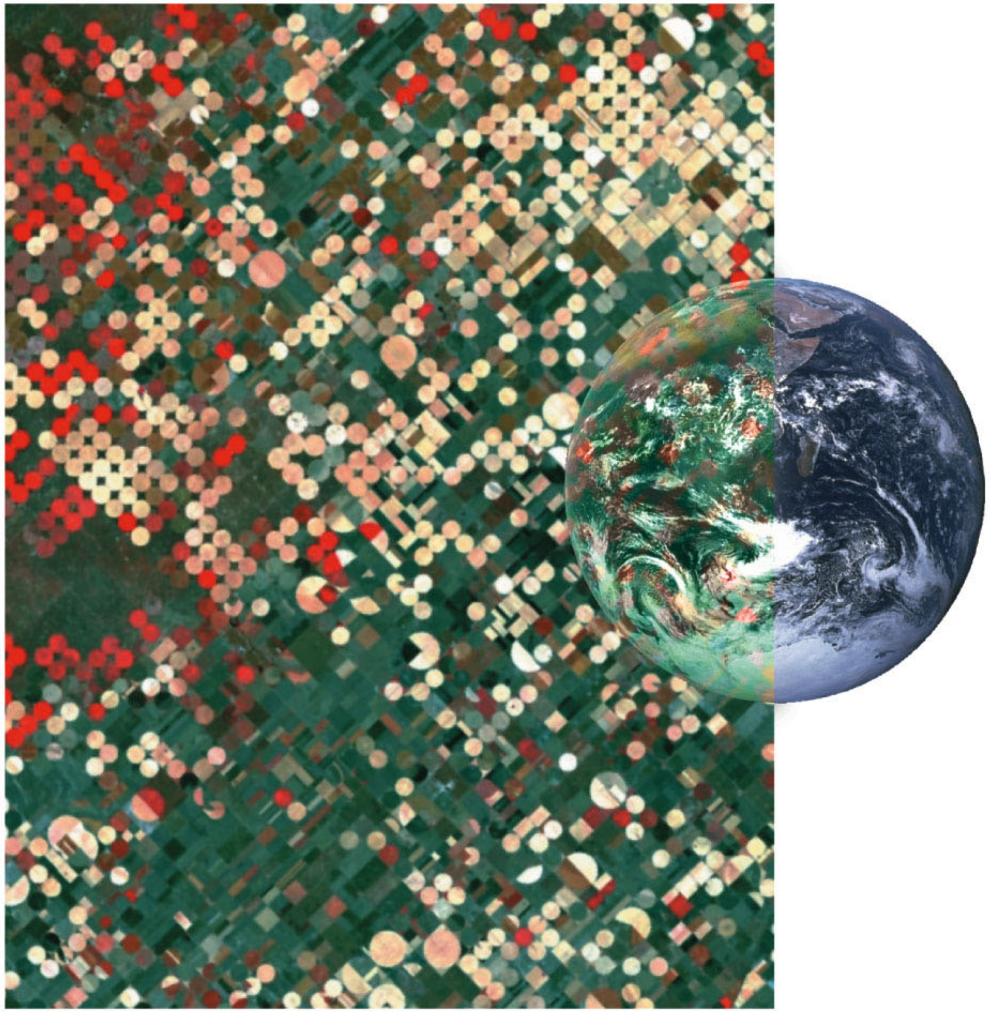


Figure 9.1 Transforming the Planet

Humans have a large impact on the global environment because our population has grown explosively, along with our use of energy and resources.

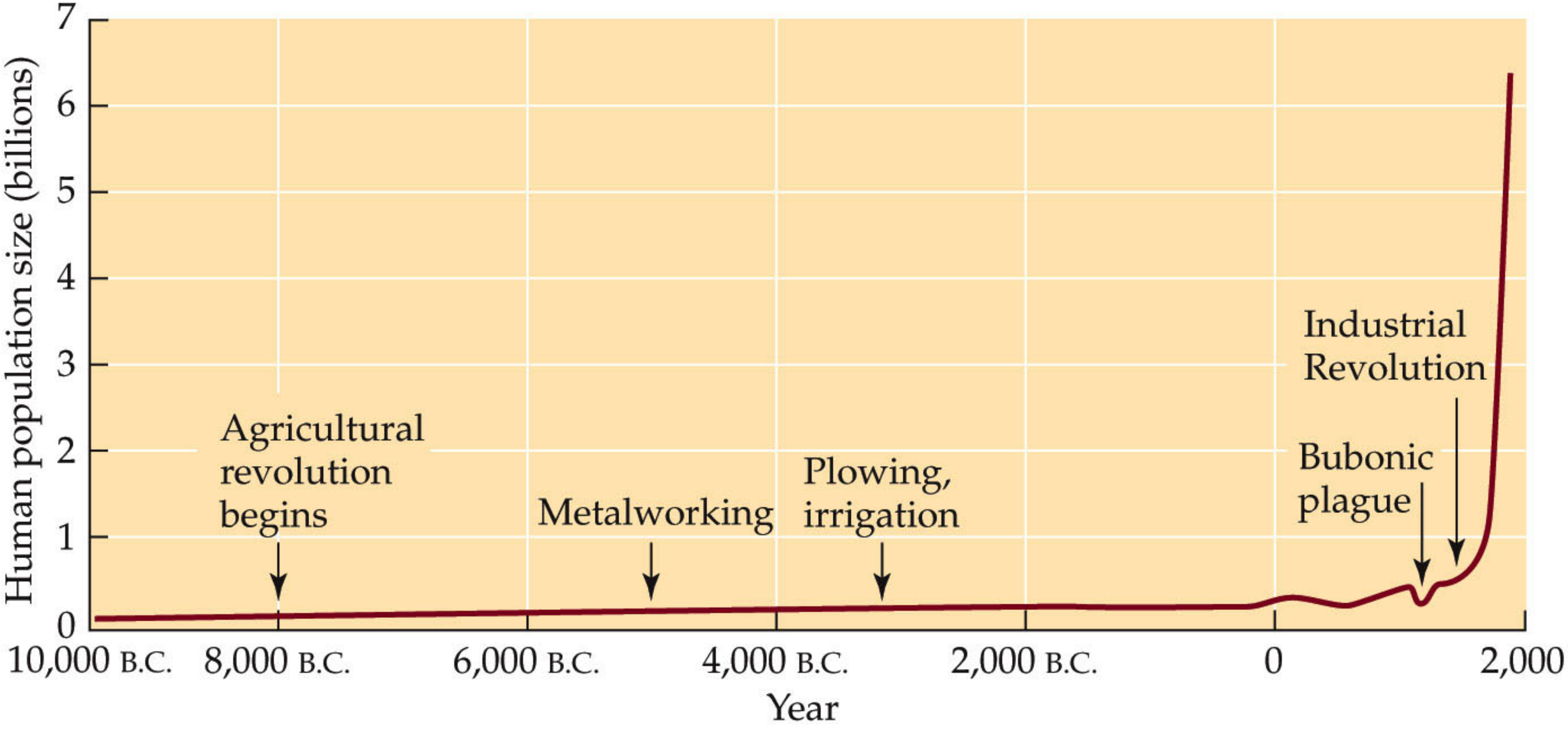
# Case Study: Human Population Growth

Human population reached 6.6 billion in 2007, more than double the number of people in 1960.

Our use of energy and resources has grown even more rapidly.

From 1860 to 1991 human population quadrupled in size, and energy consumption increased 93-fold.

# Figure 9.2 Explosive Growth of the Human Population




ECOLOGY, Figure 9.2

## Case Study: Human Population Growth

For thousands of years our population grew relatively slowly, reaching 1 billion for the first time in 1825.

Now we are adding 1 billion people every 13 years.

# Case Study: Human Population Growth

In 1975, the population was growing at an annual rate of nearly 2%.

At this rate, a population will double in size every 35 years.

If this growth rate were sustained, we would reach 32 billion by 2080.

## Case Study: Human Population Growth

But growth rate has slowed recently, to about 1.21% per year.

If this rate is maintained, there would be roughly 16 billion people on Earth in 2080.

Could Earth support 16 billion people?

One of the ecological maxims is *"No population can increase in size forever."*

The limits imposed by a finite planet restrict what otherwise appears to be a universal feature of all species: A capacity for rapid population growth.

Ecologists try to understand the factors that limit or promote population growth.

## Introduction

Population studies have shown that some methods of protecting endangered species work poorly.

Protection of loggerhead sea turtles initially focused on hatchlings, but other research has identified more effective ways to protect loggerheads.

# Figure 9.3 Dash to the Sea

# Life Tables

**Concept 9.1: Life tables show how survival and reproductive rates vary with age, size, or life cycle stage.**

Information about births and deaths is essential to predict trends or future population size.

Data for a life table for the grass *Poa annua* were collected by marking 843 naturally germinating seedlings and then following their fates over time.

## TABLE 9.1

### Life Table for the Grass *Poa annua*

| Age (in 3-month periods)[a] $x$ | Number alive[b] $N_x$ | Survival rate[c] $S_x$ | Survivorship[d] $l_x$ | Fecundity[e] $F_x$ |
|---|---|---|---|---|
| 0 | 843 | 0.856 | 1.000 | 0 |
| 1 | 722 | 0.730 | 0.856 | 300 |
| 2 | 527 | 0.600 | 0.625 | 620 |
| 3 | 316 | 0.456 | 0.375 | 430 |
| 4 | 144 | 0.375 | 0.171 | 210 |
| 5 | 54 | 0.278 | 0.064 | 60 |
| 6 | 15 | 0.200 | 0.018 | 30 |
| 7 | 3 | 0.000 | 0.004 | 10 |
| 8 | 0 | | 0.000 | |

*Source*: Data from Table 1.1 in Begon et al. 1996.

[a]Age ($x$) is measured in 3-month periods, so an individual of age $x = 5$, for example, is 15 months old.

[b]$N_x$ = number of individuals alive at age $x$.

[c]$S_x$ = proportion of individuals of age $x$ that survive to age $x + 1$; $S_x = N_{x+1}/N_x$.

[d]$l_x$ = proportion of individuals that survive from birth (age 0) to age $x$; $l_x = N_x/N_0$.

[e]$F_x$ = average number of offspring born to a female while she is of age $x$.

$S_x$ = age-specific **survival rate**—chance that an individual of age $x$ will survive to age $x + 1$.

$l_x$, = **survivorship**—proportion of individuals that survive from birth (age 0) to age $x$.

$F_x$, = **fecundity**—average number of offspring produced by a female while she is of age $x$.

# Life Tables

A **cohort life table** follows the fate of a group of individuals all born at the same time (a cohort).

For organisms that are highly mobile or have long life spans, it is hard to observe the fate of individuals from birth to death.

## Life Tables

In some cases, a **static life table** can be used—survival and reproduction of individuals of different ages during a single time period are recorded.

Requires estimating the age of individuals.

For some species, age is important because birth and death rates differ greatly between individuals of different ages.

In other species, age is not so important. For many plants, reproduction is more dependent on size (related to growth conditions) than age.

Life tables can also be based on size or life cycle stage.

# Life Tables

Life tables are constructed for humans for many applications.

Life insurance companies use census data to construct static life tables that provide a snapshot of current survival rates.

They use these data to determine premiums they charge customers of different ages.

## TABLE 9.2

### Survivorship, Fecundity, and Life Expectancy by Age for U.S. Females in 2001

| Age (in years) $x$ | Survivorship $l_x$ | Fecundity $F_x$ | Life expectancy (at age $x$) |
|---|---|---|---|
| 0–4 | 0.993 | 0.0 | 77.3 |
| 5–9 | 0.992 | 0.0 | 72.4 |
| 10–14 | 0.992 | 0.002 | 67.4 |
| 15–19 | 0.990 | 0.113 | 62.5 |
| 20–24 | 0.988 | 0.265 | 57.7 |
| 25–29 | 0.985 | 0.283 | 52.8 |
| 30–34 | 0.982 | 0.230 | 48.0 |
| 35–39 | 0.977 | 0.102 | 43.2 |
| 40–44 | 0.970 | 0.020 | 38.5 |
| 45–49 | 0.959 | 0.001 | 33.9 |
| 50–54 | 0.944 | 0.0 | 29.4 |
| 55–59 | 0.921 | 0.0 | 25.1 |
| 60–64 | 0.885 | 0.0 | 21.0 |
| 65–69 | 0.831 | 0.0 | 17.2 |
| 70–74 | 0.754 | 0.0 | 13.7 |
| 75–79 | 0.647 | 0.0 | 10.5 |
| 80–84 | 0.502 | 0.0 | 7.8 |
| 85–89 | 0.323 | 0.0 | 5.7 |
| 90–94 | 0.157 | 0.0 | 4.2 |
| 95–99 | 0.052 | 0.0 | 3.1 |
| ≥100 | 0.029 | 0.0 | 2.8 |

*Source*: Martin et al. (2003) and Arias (2004).

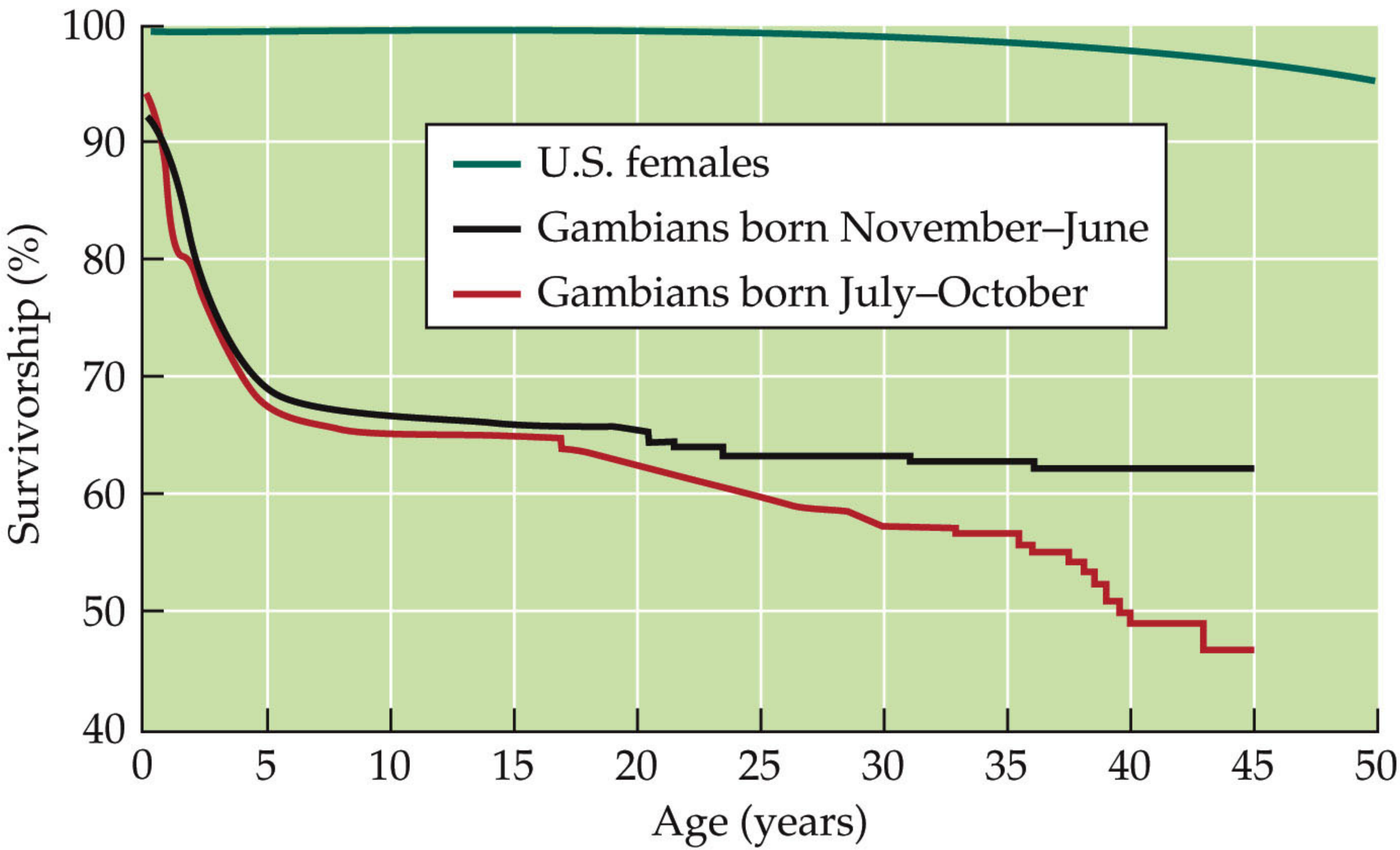
# Life Tables

Probability of survivorship for U.S. females remains high until age 70.

In contrast, only 47%–62% of Gambians survived to reach age 45.

Gambians born during the “hungry season” (when food stored from the previous year is in low supply) had lower survivorship than children born at other times of the year.

## Figure 9.4 Survivorship Varies among Human Populations



A **survivorship curve** is a plot of the number of individuals from a hypothetical cohort that will survive to reach different ages.

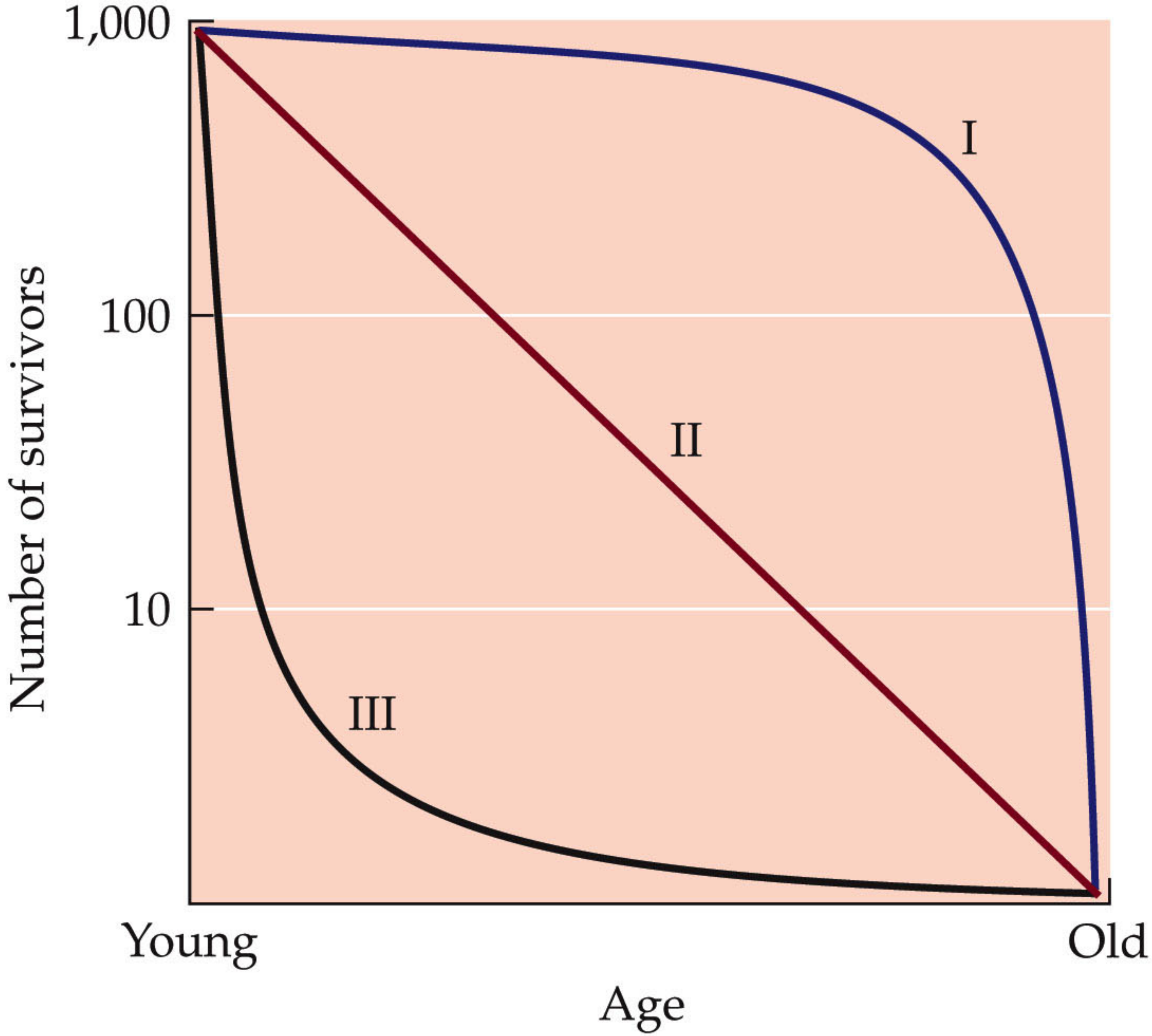
Survivorship curves can be classified into three general types.

**Type I**: Most individuals survive to old age (U.S. females, Dall sheep).

**Type II**: The chance of surviving remains constant throughout the lifetime (some birds, and others).

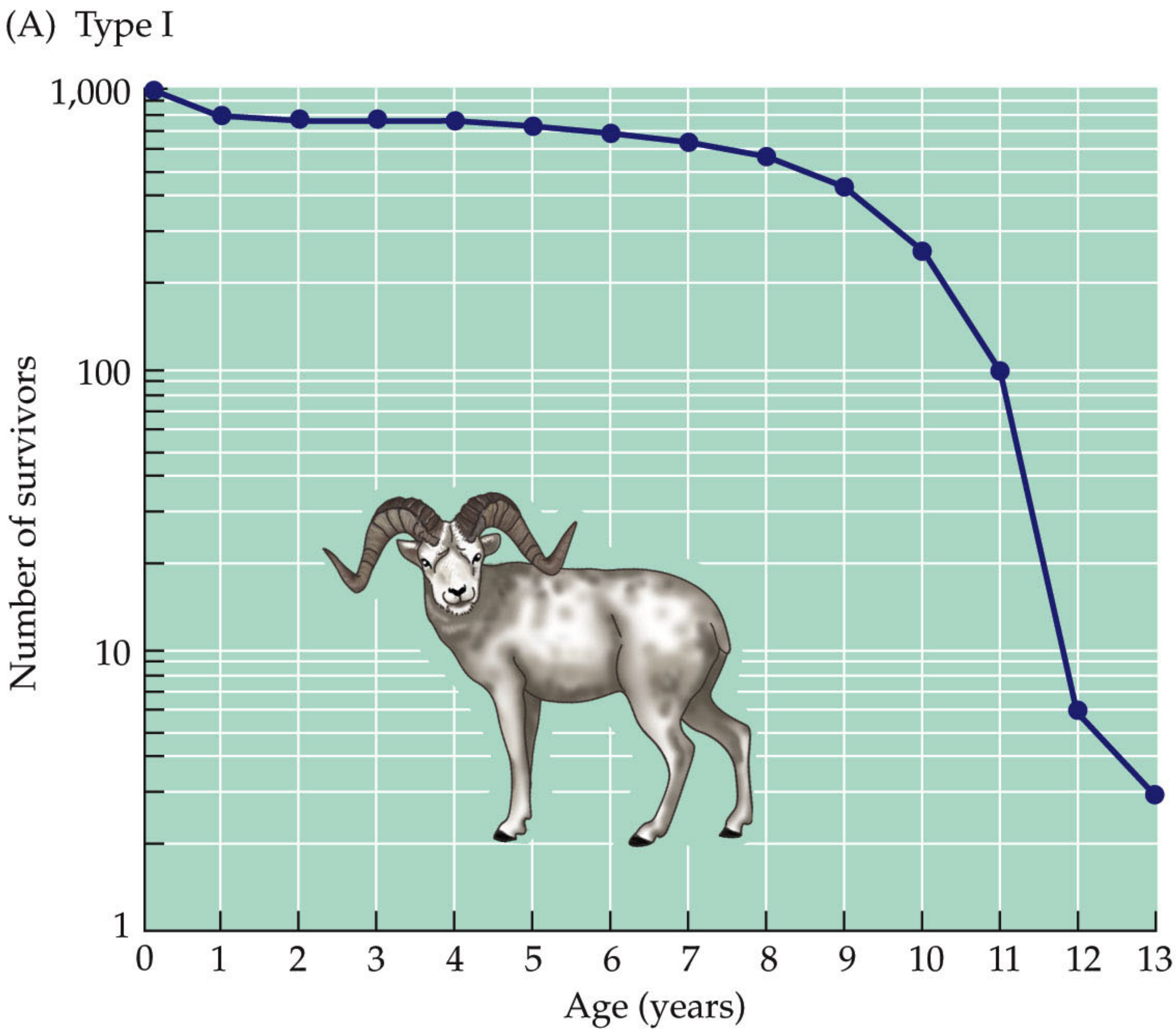
**Type III**: Individuals die at high rates when young, those that reach adulthood survive well (oysters, species that produce large numbers of offspring).

## Figure 9.5 Three Types of Survivorship Curves



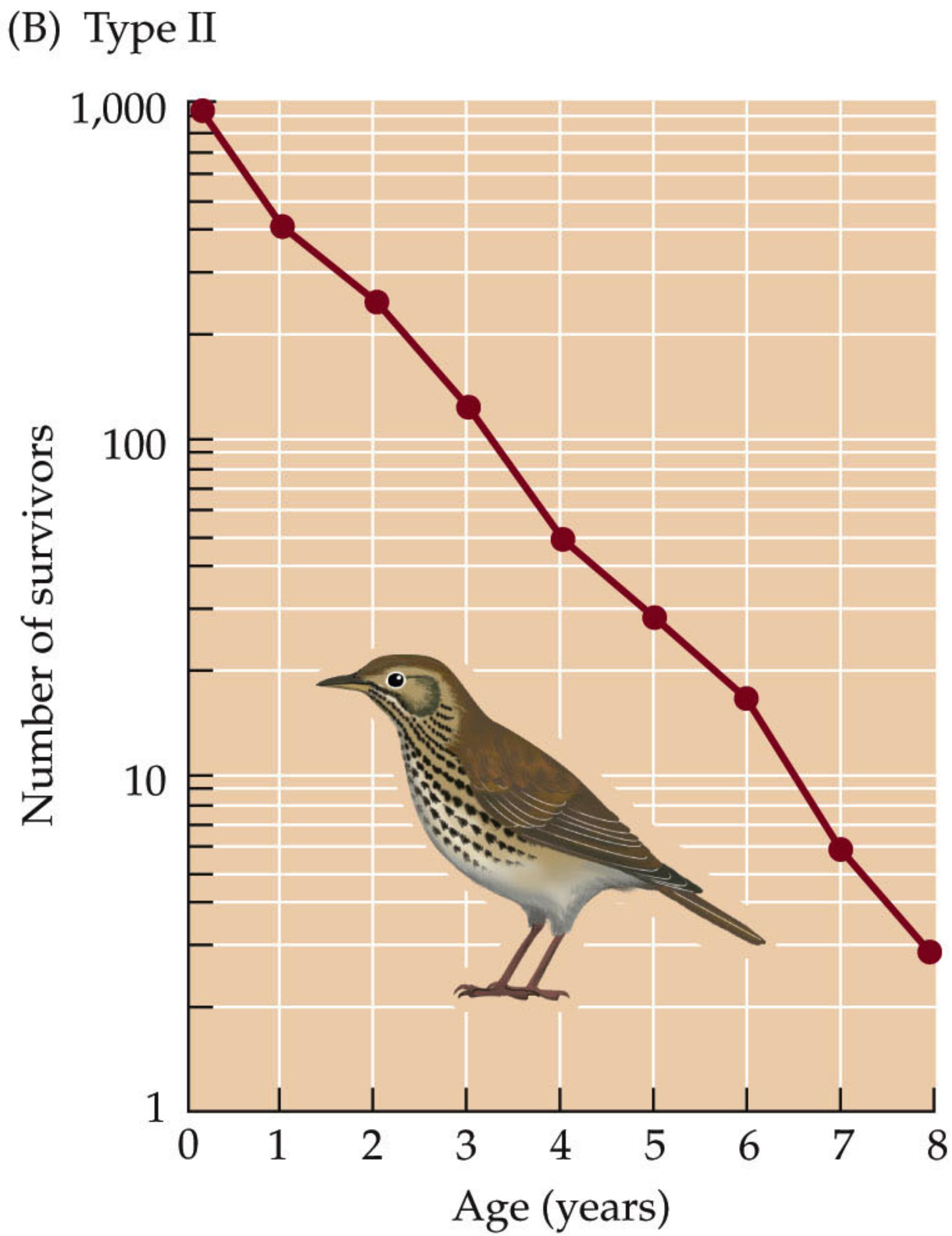

ECOLOGY, Figure 9.5

# Figure 9.6 Species with Type I, II, and III Survivorship Curves (Part 1)



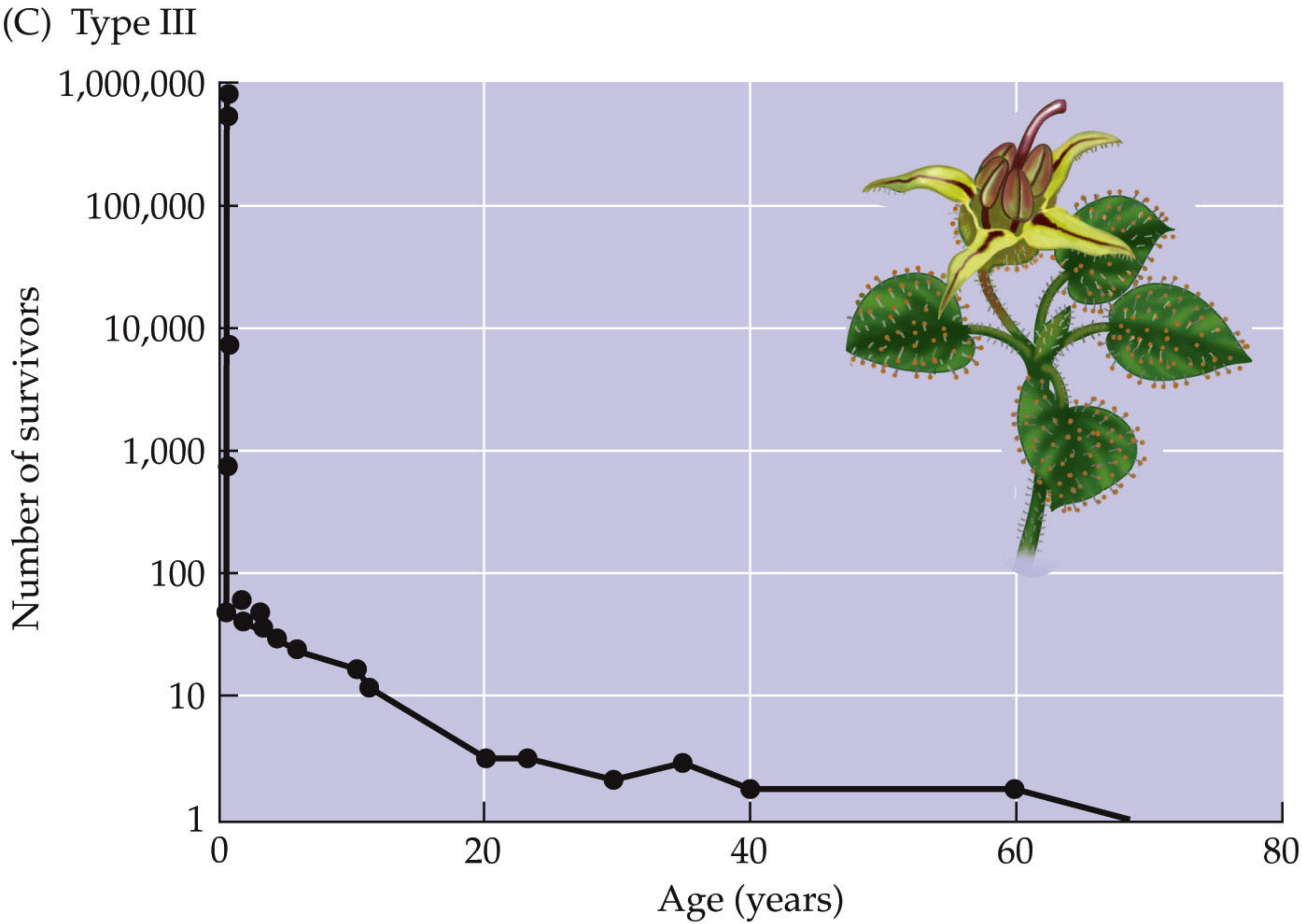

**ECOLOGY, Figure 9.6 (Part 1)**

## Figure 9.6 Species with Type I, II, and III Survivorship Curves (Part 2)




**ECOLOGY, Figure 9.6 (Part 2)**

# Figure 9.6 Species with Type I, II, and III Survivorship Curves (Part 3)




ECOLOGY, Figure 9.6 (Part 3)

# Life Tables

Survivorship curves can vary among populations of a species, between males and females, and among cohorts that experience different environmental conditions.

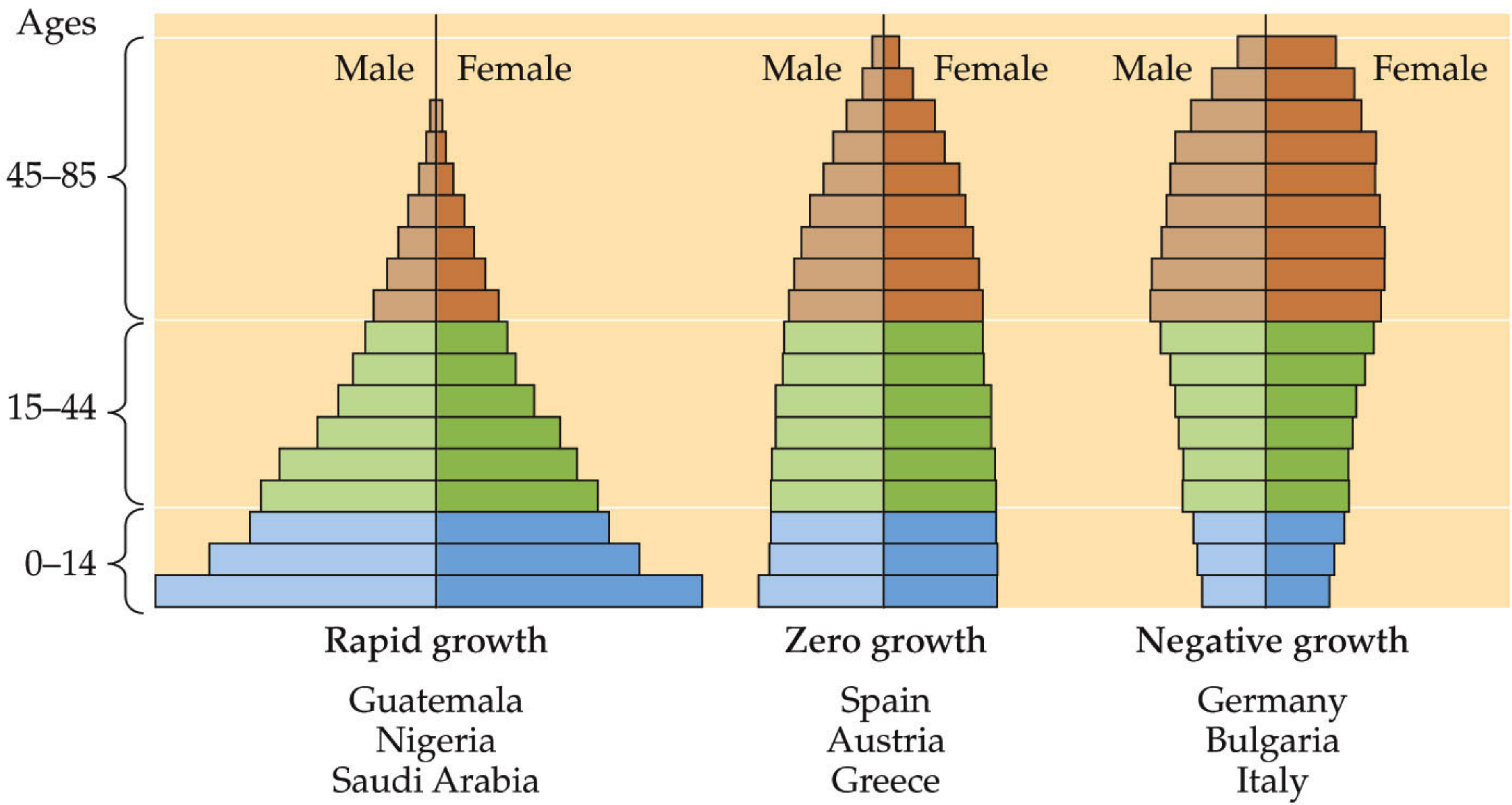
# Age Structure

**Concept 9.2: Life table data can be used to project the future age structure, size, and growth rate of a population.**

A population can be characterized by its **age structure**—the proportion of the population in each age class.

Age structure influences whether a population will increase or decrease in size.

# Figure 9.7 Age Structure Influences Growth Rate in Human Populations



# Age Structure

If a population has many people between ages 15 and 30, we would expect it to grow rapidly because it contains more individuals of reproductive age.

A population with many people older than 55 would grow more slowly.

Life table data can be used to predict age structure and population size.

**TABLE 9.3**

**Life Table for a Hypothetical Organism***

| Age $x$ | Survival rate $S_x$ | Survivorship $l_x$ | Fecundity $F_x$ |
|---|---|---|---|
| 0 | 0.3 | 1.00 | 0 |
| 1 | 0.8 | 0.30 | 2 |
| 2 | 0.0 | 0.24 | 4 |
| 3 | — | 0.0 | — |

*The organism reproduces in the spring and dies before it is 3 years old.

## Age Structure

Assume the population starts with 100 individuals:

Age class 0 ($n_0$) = 20 individuals

Age class 1 ($n_1$) = 30

Age class 2 ($n_2$) = 50

Assume that all mortality occurs over the winter, before spring breeding season, and that individuals are counted immediately after the breeding season

# Age Structure

To predict population size for the following year, two things must be calculated:

1. Number of individuals that will survive to the next time period.

2. Number of newborns those survivors will produce in the next time period.

## TABLE 9.4

**A Two-Step Method for Projecting the Size of the Hypothetical Population in Table 9.3**

| Age ($x$) | Current number of individuals of age $x$ | | STEP 1: COUNT SURVIVORS Number of surviving individuals of age $x$ in the next time period | STEP 2: ADD NEWBORNS Total number of individuals of age $x$ in the next time period |
|---|---|---|---|---|
| 0 | 20 | $S_0 = 0.3$ | | 108 |
| 1 | 30 | $S_1 = 0.8$ | 6 | 6 |
| 2 | 50 | $S_2 = 0.0$ | 24 | 24 |
| 3 | | | 0 | |
| **Total population size:** | **100** (current time period) | | | **138** (next time period) |

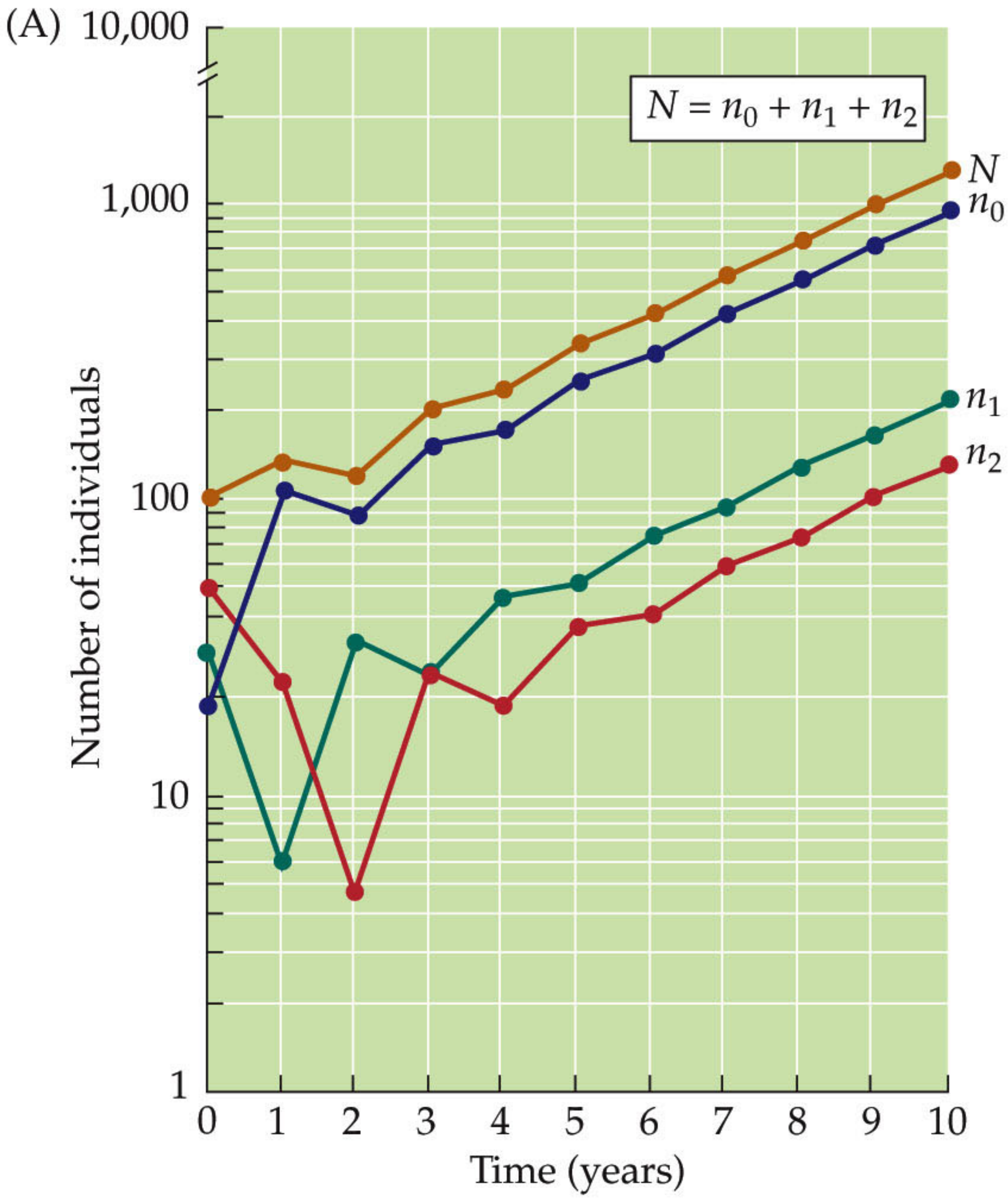
Calculations for one year can be extended to future years.

time $t$ = 0, population size was 100

time $t$ = 1, population size was 138

time $t$ = 2, population size can be calculated in the same way

# Figure 9.8 A  Growth of a Hypothetical Population

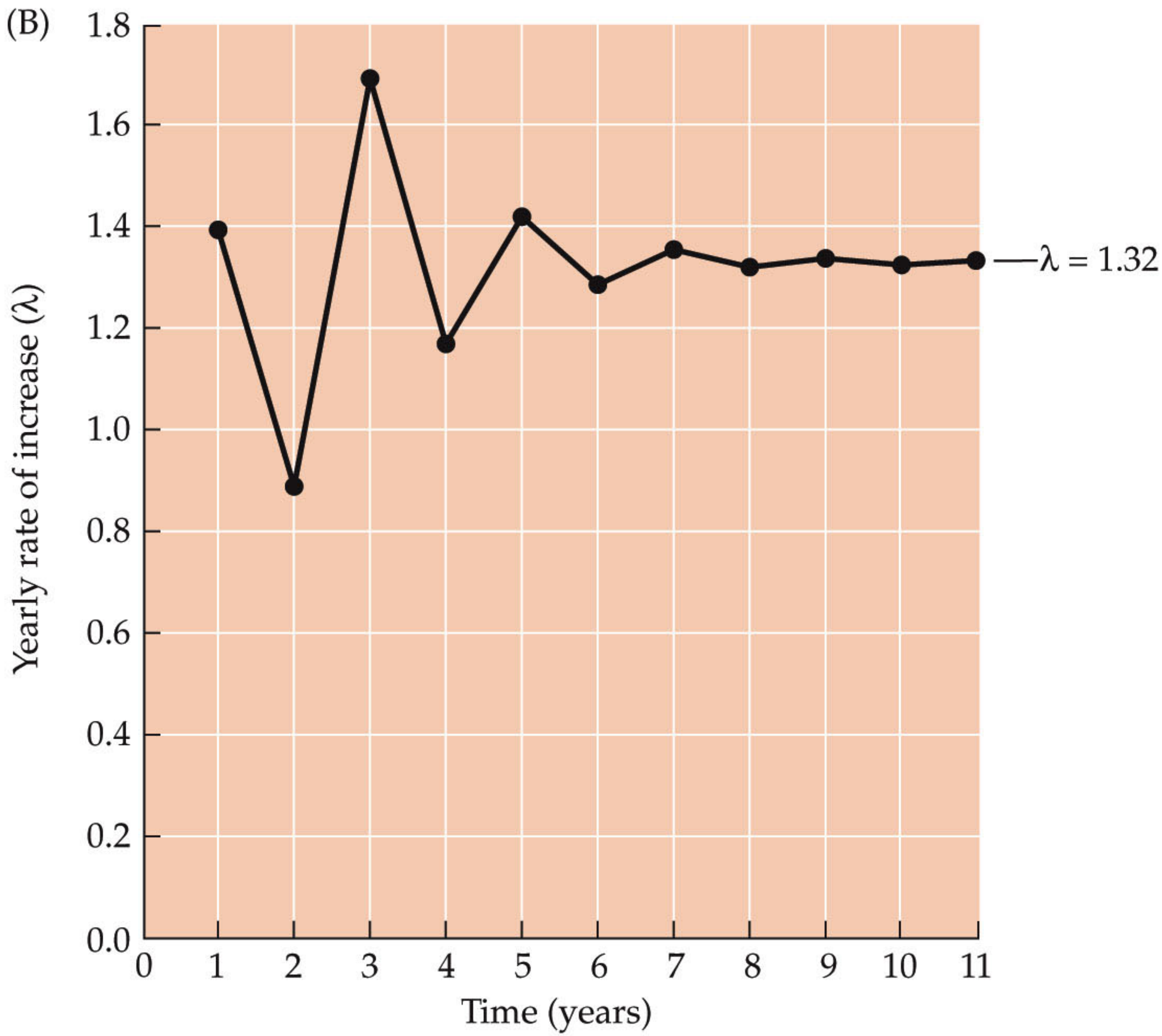



**_ECOLOGY,_ Figure 9.8 (Part 1)**

The growth rate ($\lambda$) can be calculated as the ratio of the population size in year $t + 1$ ($N_{t+1}$) to the population size in year $t$ ($N_t$).

$$\lambda = \frac{N_{t+1}}{N_t}$$

# Figure 9.8 B Growth of a Hypothetical Population




**ECOLOGY, Figure 9.8 (Part 2)**

## Age Structure

When age-specific survival and fecundity rates are constant over time, the population ultimately grows at a fixed rate.

The age structure does not change from one year to the next—it has a **stable age distribution**.

In the example, the stable age distribution is 0.73 in age class 0, 0.17 in age class 1, and 0.10 in age class 2.

If survival and fecundity rates change, we would obtain different values for the population growth rate and the stable age distribution.

For example, if $F_1$ changes from 2 to 5.07 (and other values remain equal), $\lambda$ increases to 2.0.

# Age Structure

Any factor that alters survival or fecundity of individuals can change the population growth rate.

Ecologists and managers try to identify age-specific birth and death rates that most strongly influence the population growth rate.

This can be used to develop management practices that decrease pest populations or increase an endangered population.

## Age Structure

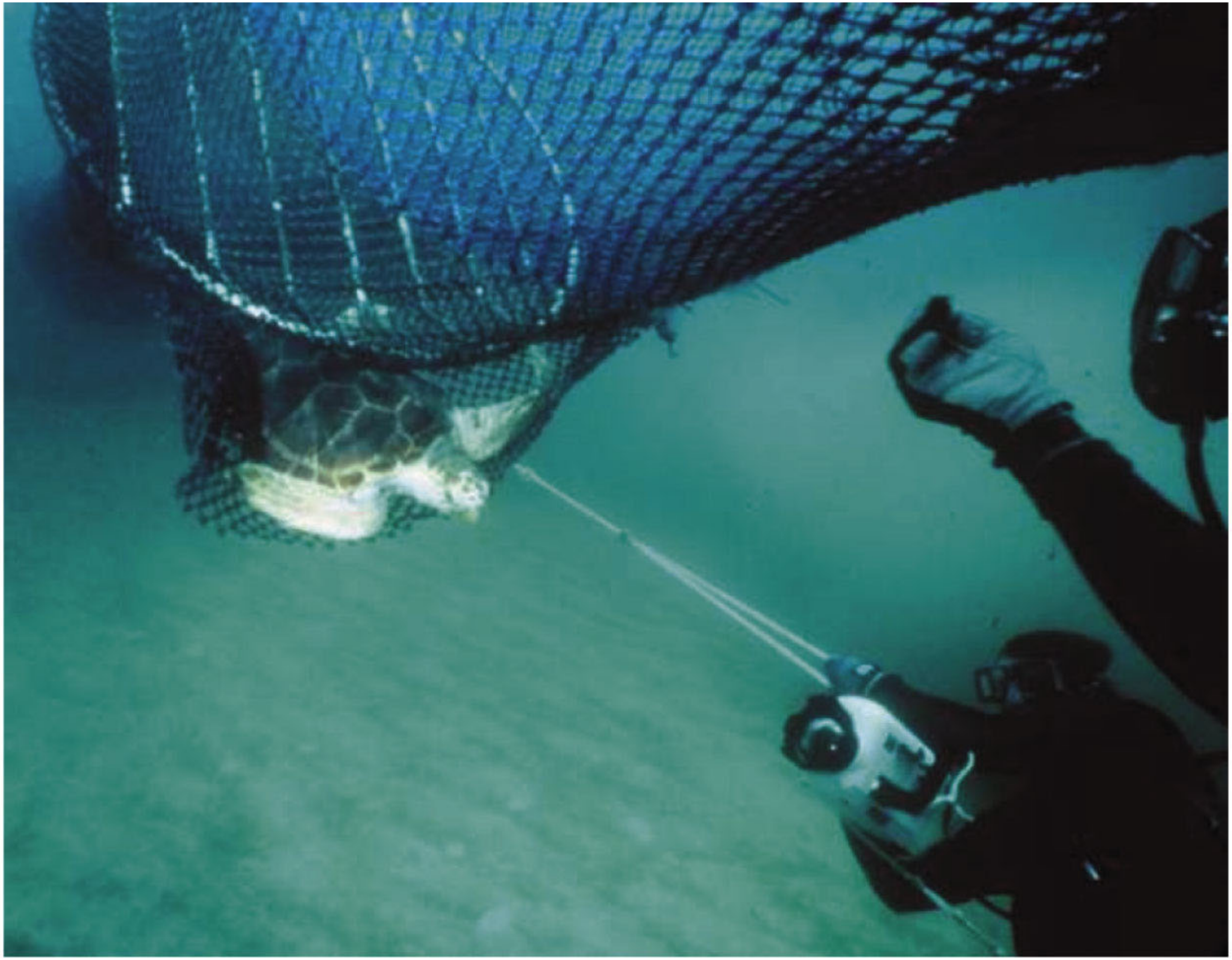
Example: Loggerhead sea turtles are threatened by development on nesting sites and commercial fishing nets.

Early efforts focused on egg and hatchling stages.

This approach was tested using life table data.

# Box 9.1, Figure A  Loggerhead Sea Turtle

# Box 9.1, Figure B  Turtle Excluder Device (TED)



## Age Structure

Even if hatchling survival were increased to 100%, loggerhead populations would continue to decline.

Instead, population growth rate was most responsive to decreasing mortality of older juveniles and adults.

Because of these studies, Turtle Excluder Devices (TEDs) were required to be installed in shrimp nets.

The number of turtles killed in nets declined by about 44% after TED regulations were implemented.

It will be decades before we know whether TED regulations help turtle populations to increase in size.

# Exponential Growth

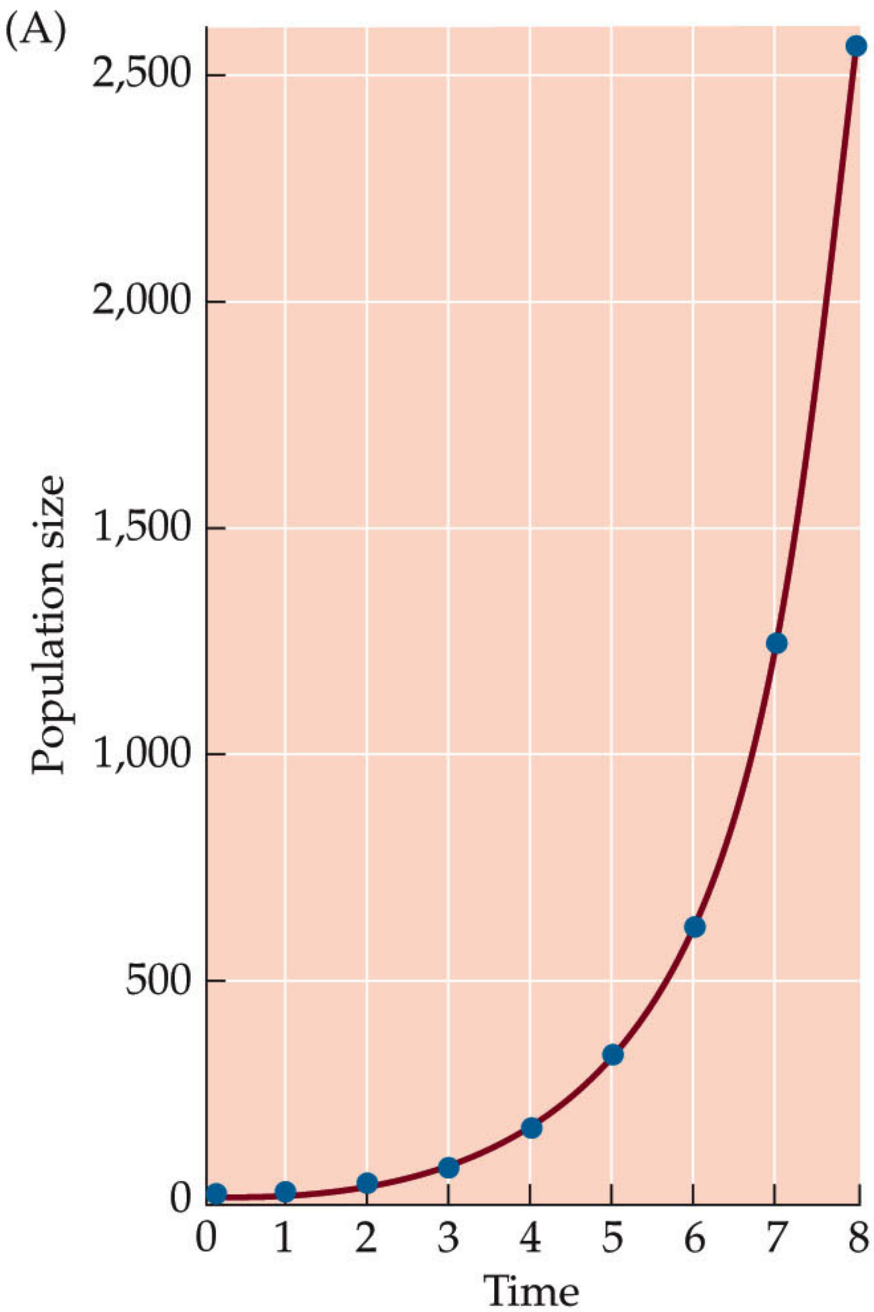
**Concept 9.3: Populations can grow exponentially when conditions are favorable, but exponential growth cannot continue indefinitely.**

In general, populations can grow rapidly whenever individuals leave an average of more than one offspring over substantial periods of time.

If a population reproduces in synchrony at regular time intervals (*discrete time periods*), and growth rate remains the same, **geometric growth** occurs.

The population increases by a constant proportion, so the number of individuals added to the population becomes larger with each time period.

Figure 9.9 A  Geometric and Exponential Growth



Geometric growth:

$$N_{t+1} = \lambda N_t$$

$\lambda$ = **geometric growth rate**; also known as the (per capita) **finite rate of increase**.

## Exponential Growth

Geometric growth can also be represented by

$$N_t = \lambda^t N_0$$

This predicts the size of the population after any number of discrete time periods.

# Exponential Growth

In many species, individuals do not reproduce in synchrony at discrete time periods, they reproduce *continuously*, and generations can overlap.

When these populations increase by a constant proportion, the growth is **exponential growth**.

Exponential growth is described by

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

$\frac{dN}{dt}$ = the rate of change in population size at each instant in time.

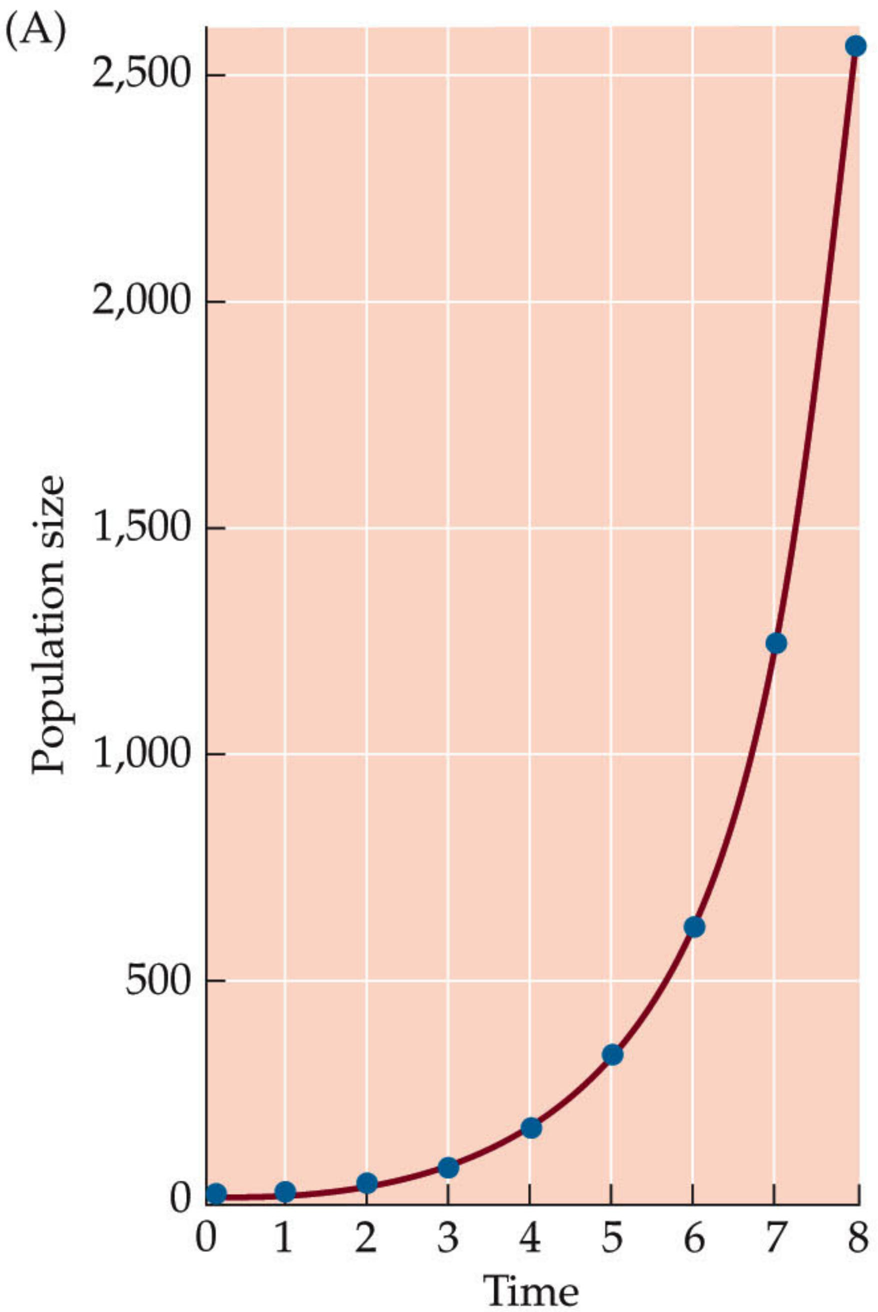
*r* is the **exponential population growth rate** or the (per capita) **intrinsic rate of increase**.

Exponential growth can also be described by

$$N(t) = N(0)\mathrm{e}^{rt}$$

This predicts the size of an exponentially growing population at any time *t*, if we have an estimate for *r* and know N(0), the initial population size.

Figure 9.9 A  Geometric and Exponential Growth



# Exponential Growth

Geometric and exponential growth curves overlap because the equations are similar in form, except that $\lambda$ is replaced by $e^{r}$.

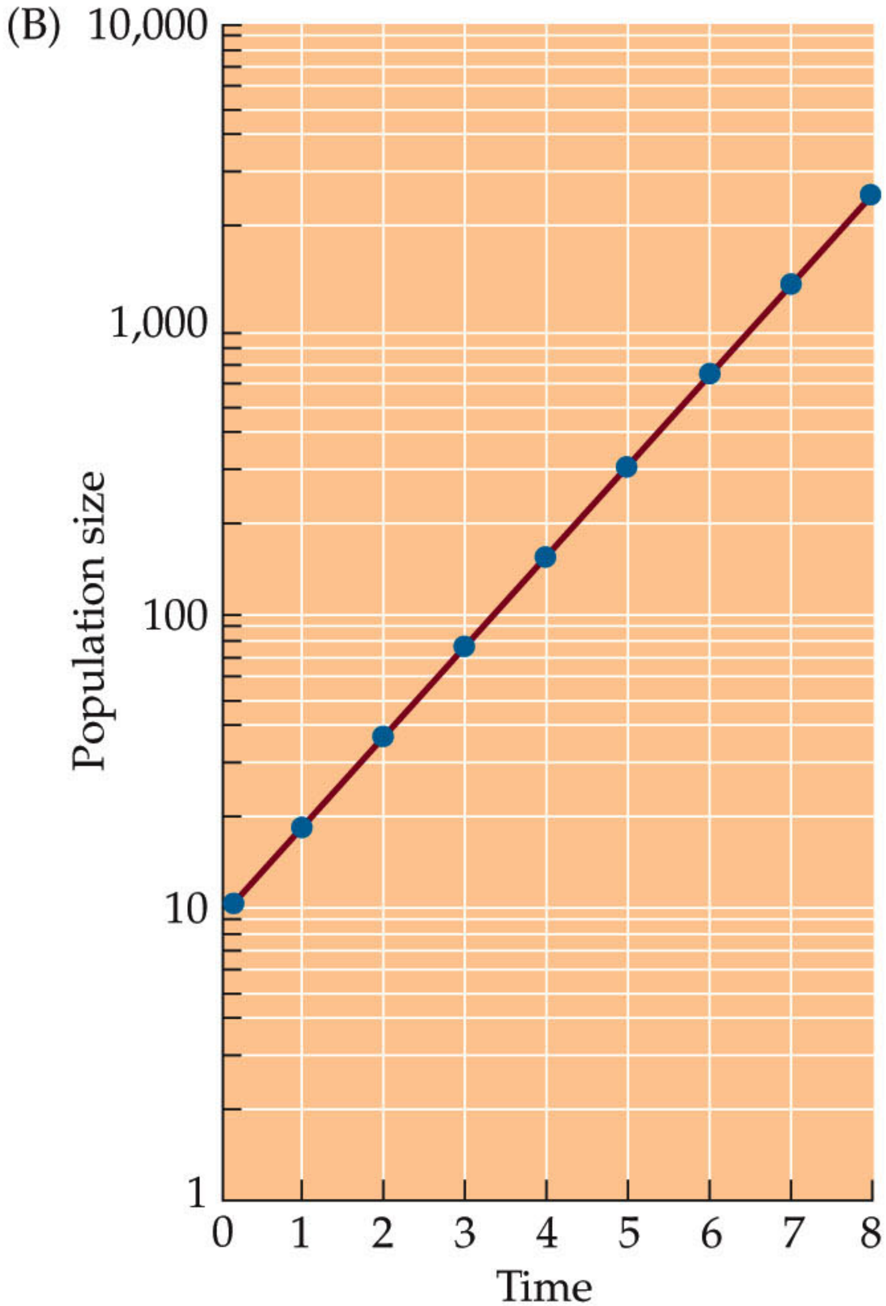
$$\lambda = e^{r}$$

$$r = \ln(\lambda)$$

## Exponential Growth

If a population is growing geometrically or exponentially, a plot of the natural logarithm of population size versus time will result in a straight line.

# Figure 9.9 B  Geometric and Exponential Growth



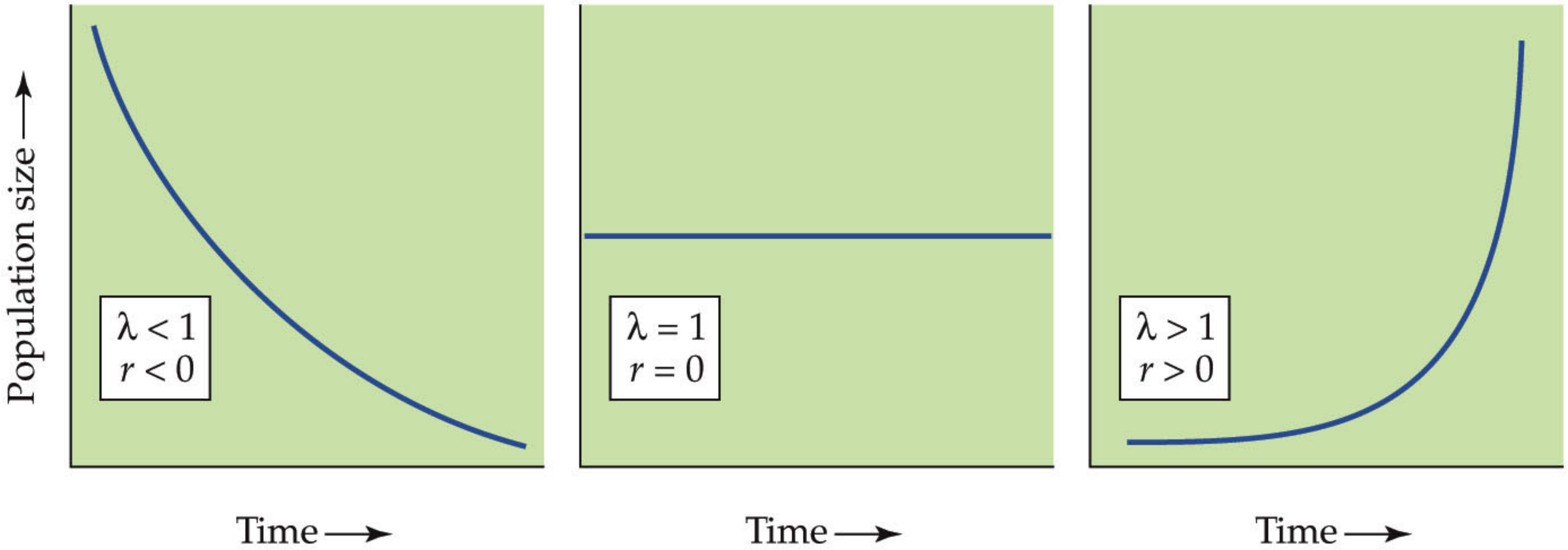
## Exponential Growth

When $\lambda = 1$ or $r = 0$, the population stays the same size.

When $\lambda < 1$ or $r < 0$, the population size will decrease.

When $\lambda > 1$ or $r > 0$, the population grows geometrically or exponentially.

# Figure 9.10 How Population Growth Rates Affect Population Size



Growth rate (*r* or $\lambda$) can be estimated in several ways.

Life table data can be used to predict future population size, plot the predicted population size versus time, and estimate growth rate ($\lambda$) from the graph.

The **doubling time** ($t_d$) of a population is the number of years it will take the population to double in size.

$$t_d = \ln(2)/r$$

**Net reproductive rate** ($R_0$) is the mean number of offspring produced by an individual during its lifetime.

$$R_0 = \sum_{x_{first}}^{x_{last}} l_x F_x$$

$x_{\text{first}}$ = age of first reproduction
$x_{\text{last}}$ = age of last reproduction

## Exponential Growth

Whenever $R_0 > 1$, $\lambda$ will be greater than 1 (and $r > 0$).

Under these conditions, populations have the potential to increase greatly in size.

Even a growth rate that appears to be small can cause a population to increase rapidly.

## Exponential Growth

For the human population, current annual growth rate is 1.21%, which implies that $r = 0.0121$.

If 2007 is time $t = 0$, and N(0) = 6.6 billion, population size 1 year later should be $N(1) = 6.6 \times e^{0.0121}$, or 6.68 billion.

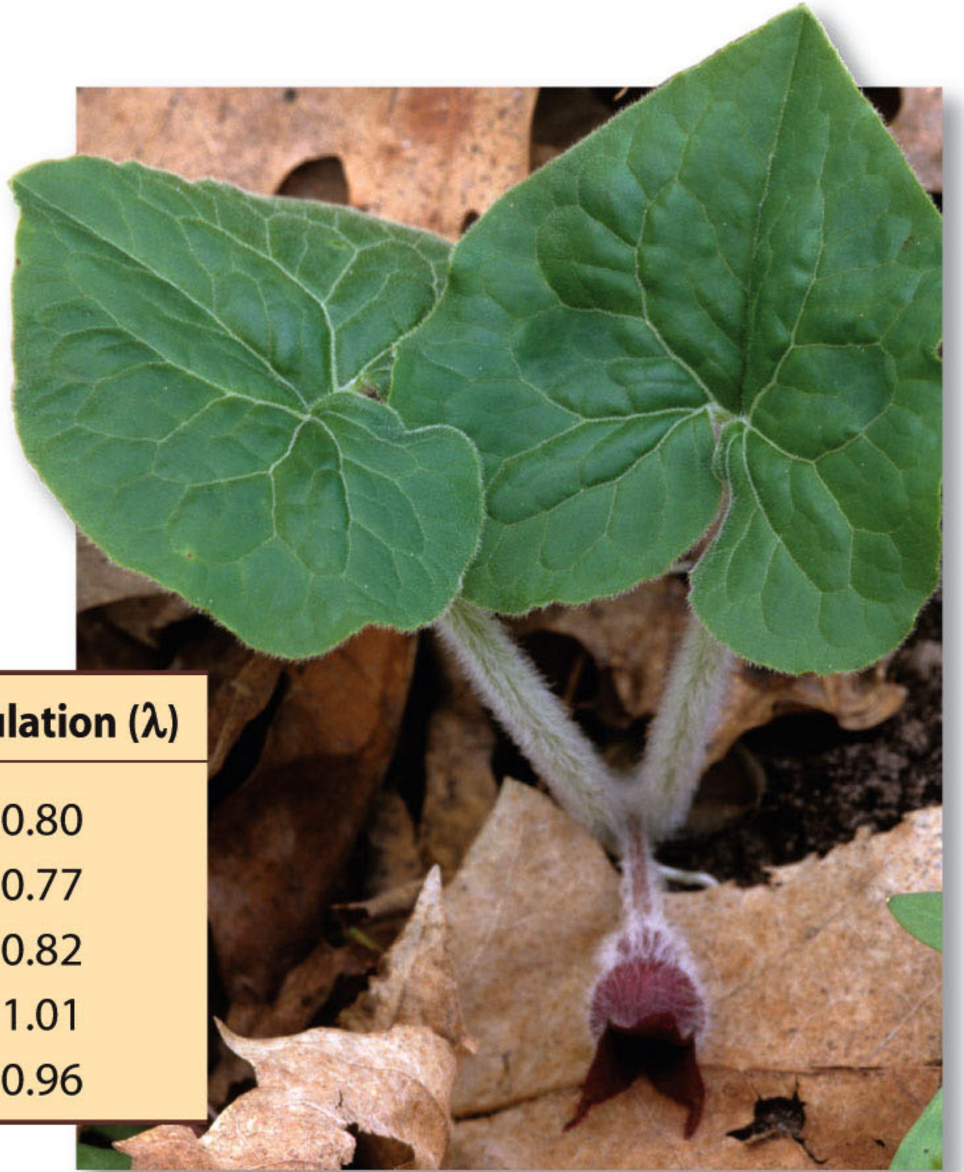
If $r$ remained constant, population would be over 80 billion in 210 years.

Populations of some species have observed $\lambda$ values close to 1.

25 reindeer were introduced to Saint Paul Island off the coast of Alaska in 1911. After 27 years, the population had increased to 2,046 individuals.

$\lambda$ = 1.18 for this population.

# Figure 9.11 Some Populations Have Slow Growth Rates



| Year | Population (λ) |
|---|---|
| 1990–1991 | 0.80 |
| 1991–1992 | 0.77 |
| 1992–1993 | 0.82 |
| 1993–1994 | 1.01 |
| 1994–1995 | 0.96 |

## Exponential Growth

Considerably higher annual population growth rates have been observed in many species, including western grey kangaroos ($\lambda = 1.9$), field voles ($\lambda = 24$), and rice weevils ($\lambda = 10^{17}$).

# Exponential Growth

In natural populations, favorable conditions result in exponential growth of populations, but can favorable conditions last for long?

Exponential growth cannot continue indefinitely. There are limits to population growth.

**Concept 9.4: Population size can be determined by density-dependent and density-independent factors.**

Under ideal conditions, $\lambda > 1$ for all populations.

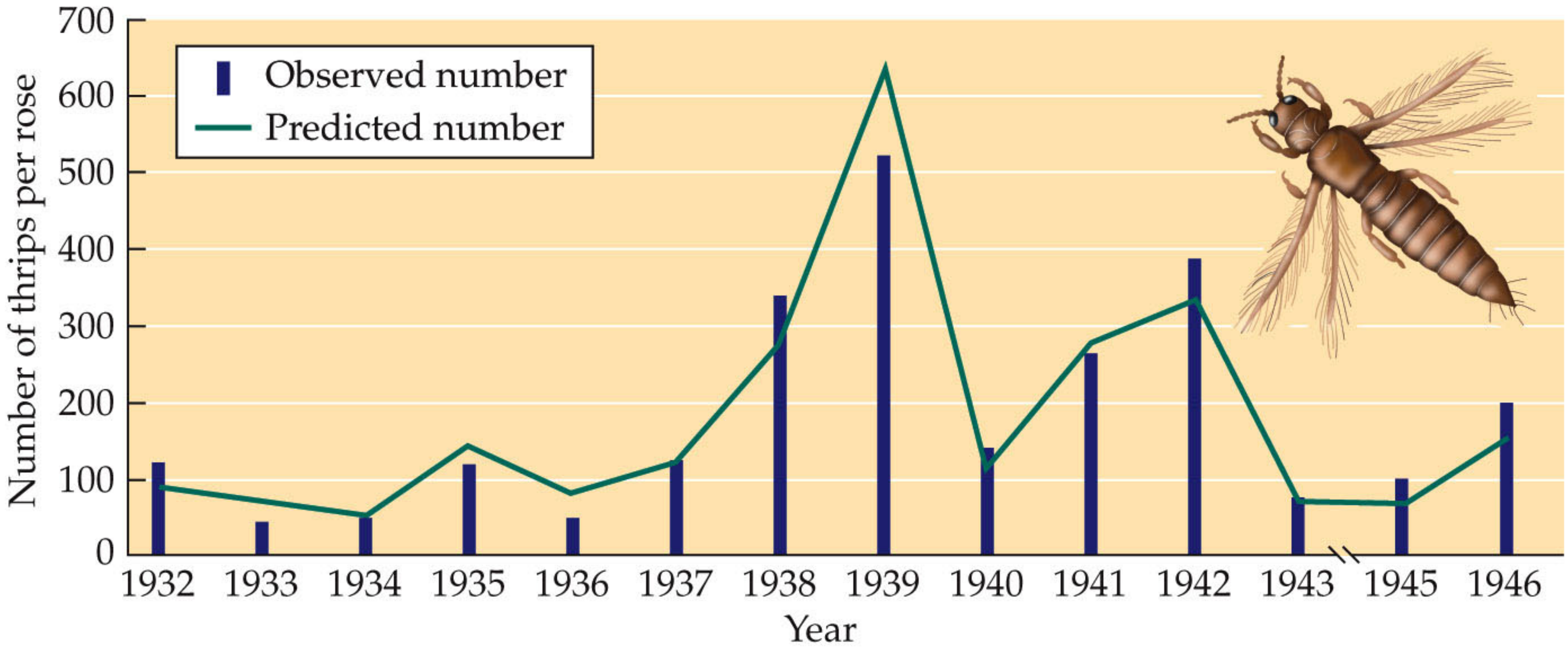
But conditions rarely remain ideal. What factors cause $\lambda$ to fluctuate over time?

Some factors are a function of population density, other are not dependent on density—**density-independent factors**.

Factors such as temperature and precipitation, and catastrophes such as floods or hurricanes.

In the insect *Thrips imaginis*, population size fluctuation is correlated with temperature and rainfall (Davidson and Andrewartha 1948).

# Figure 9.12 Weather Can Influence Population Size

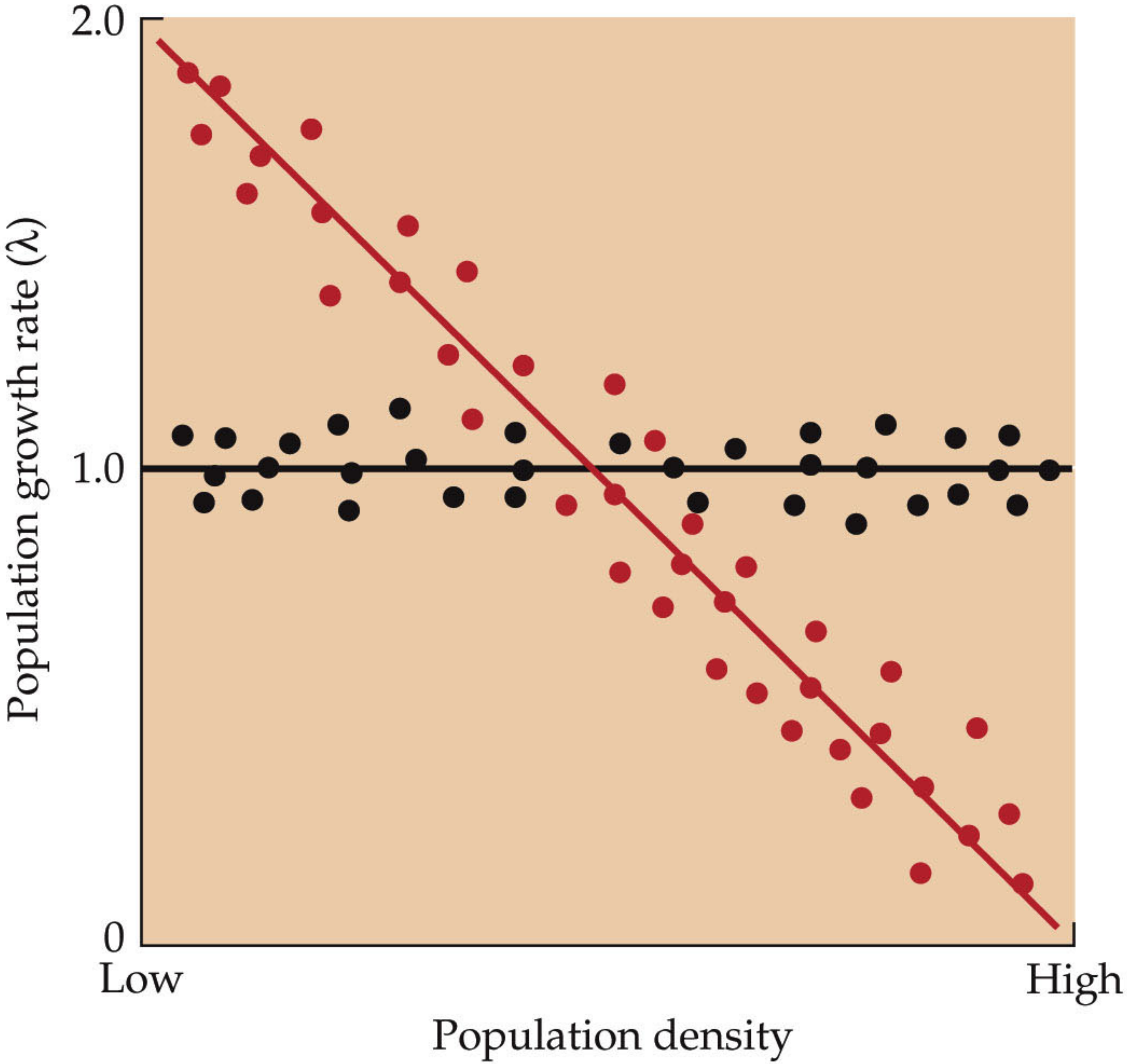


# Effects Of Density

**Density-dependent factors**: Cause birth rates, death rates, and dispersal rates to change as the density of the population changes.

As densities increase birth rates often decrease, death rates increase, and dispersal from the population (emigration) increases, all of which tend to decrease population size.

## Figure 9.13 Comparing Density Dependence and Density Independence




ECOLOGY, Figure 9.13

# Effects Of Density

**Population regulation** occurs when density-dependent factors cause population to increase when density is low and decrease when density is high.

Ultimately, food, space, or other essential resources are in short supply and population size decreases.

## Effects Of Density

Regulation refers to the effects of factors that tend to increase $\lambda$ or $r$ when the population size is small and decrease $\lambda$ or $r$ when the population size is large.

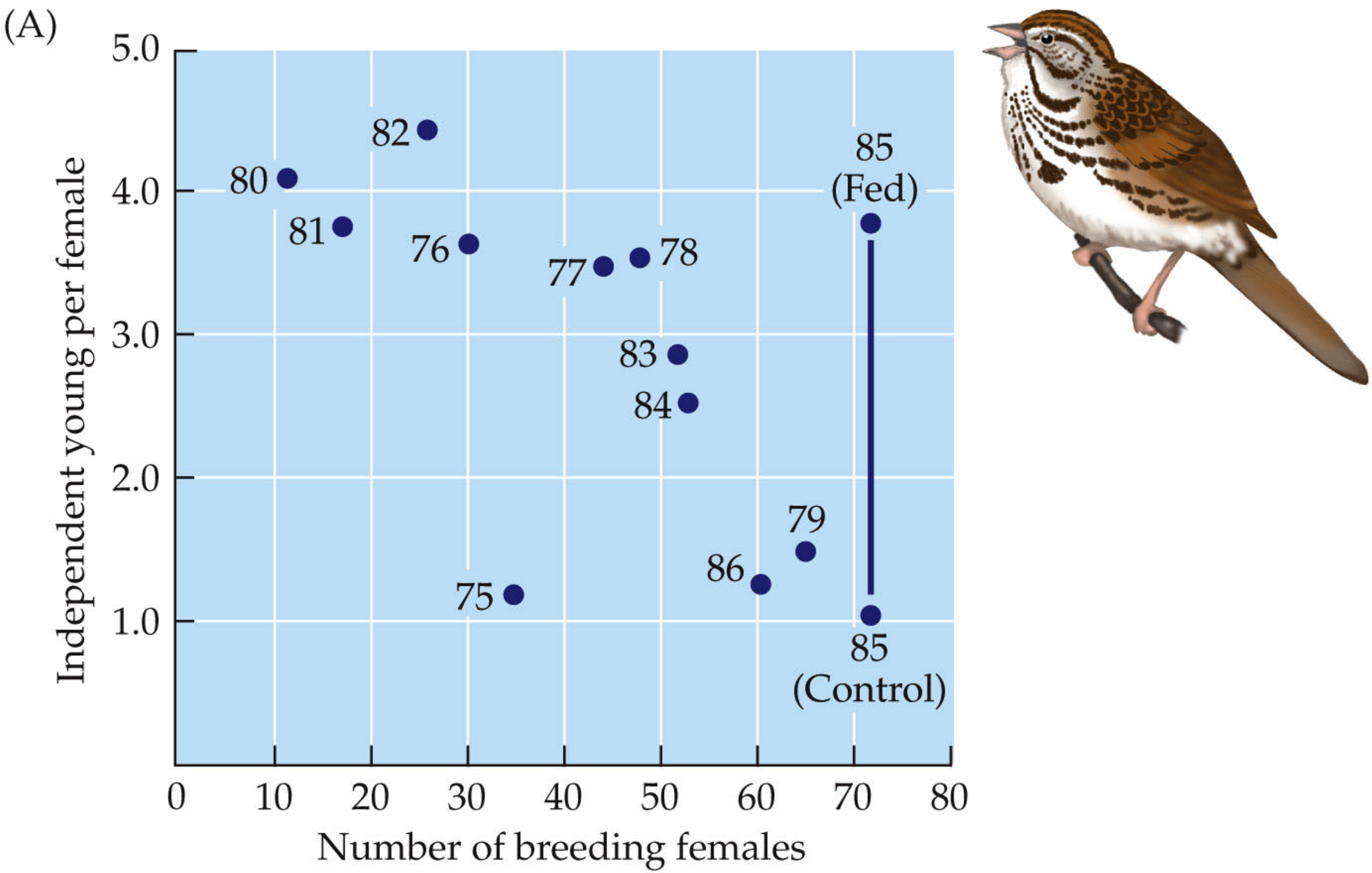
Density-independent factors can have large effects on population size, but they do not regulate population size.

# Effects Of Density

Density dependence has been documented in natural populations.

In song sparrows, the number of eggs laid per female decreased with density, as did the number of young that survived (Arcese and Smith 1988).

# Figure 9.14 A  Examples of Density Dependence in Natural Populations



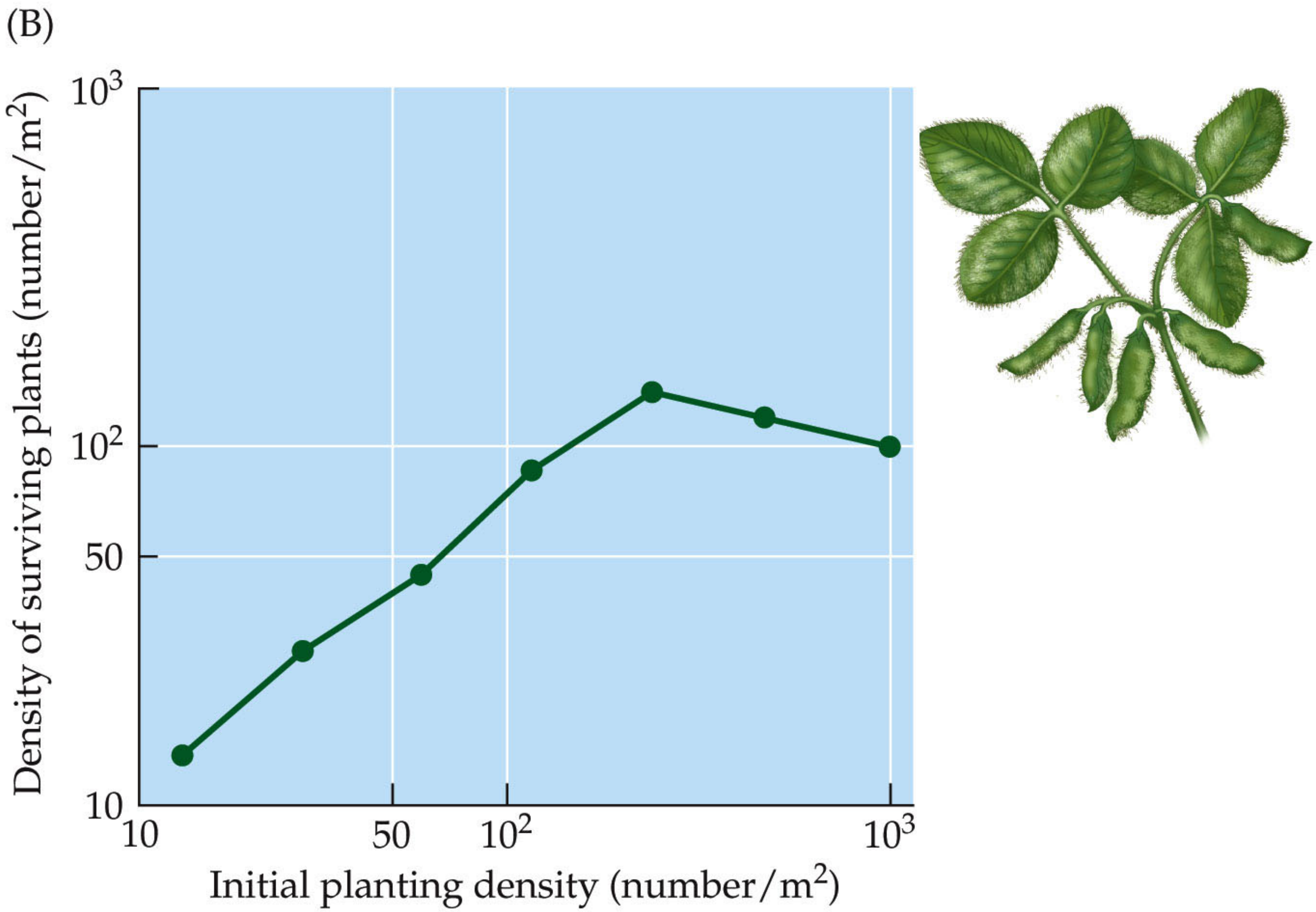

**_ECOLOGY_, Figure 9.14 (Part 1)**

# Effects Of Density

Density-dependent mortality has been observed in many populations.

Yoda et al. (1963) planted soybeans at various densities and found that at the highest planting densities, many of the seedlings had died by 93 days of age.

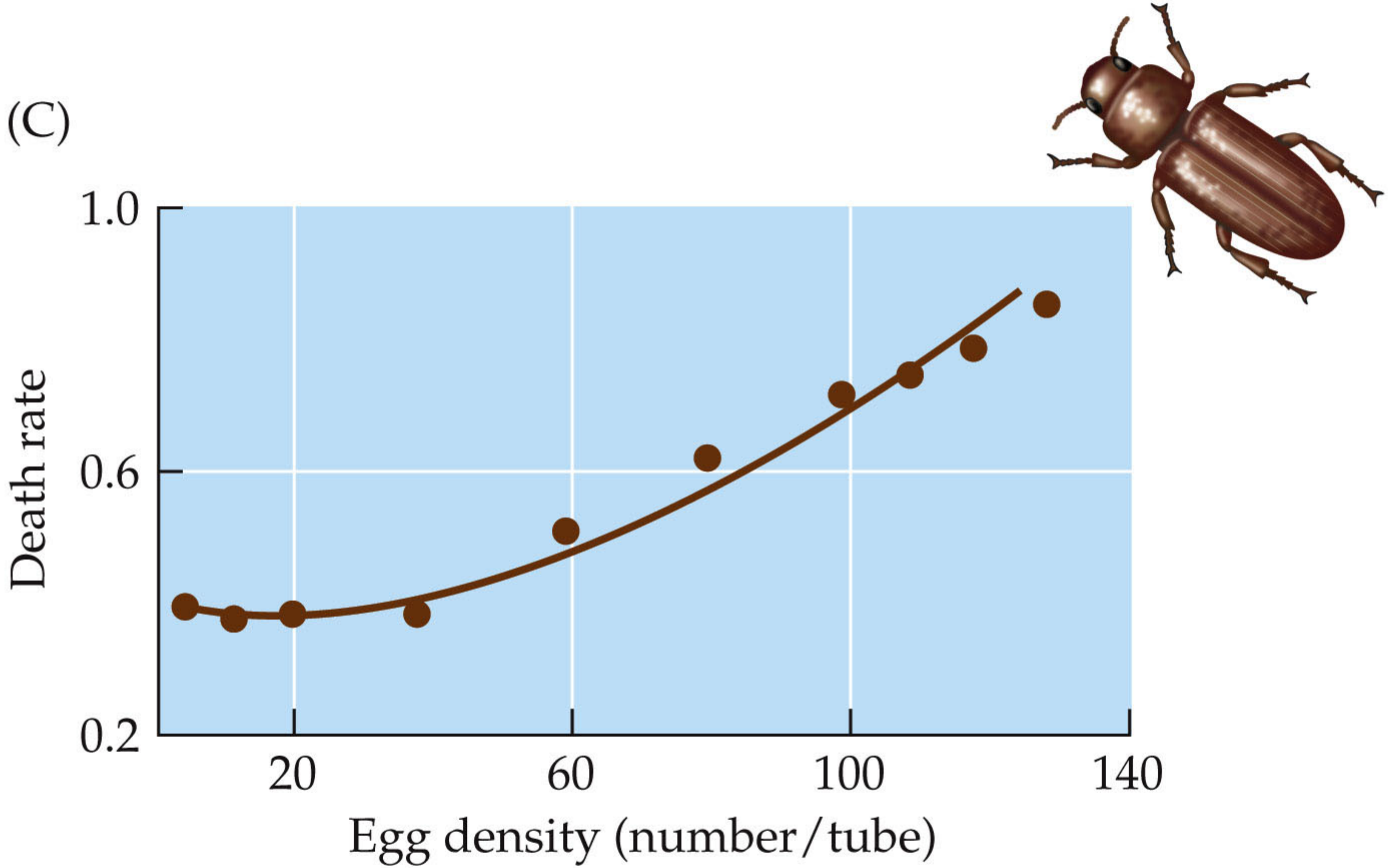
# Figure 9.14 B  Examples of Density Dependence in Natural Populations



# Effects Of Density

In an experiment where eggs of the flour beetle *Tribolium confusum* were placed in glass tubes, death rates increased as the density of eggs increased.

# Figure 9.14 C Examples of Density Dependence in Natural Populations



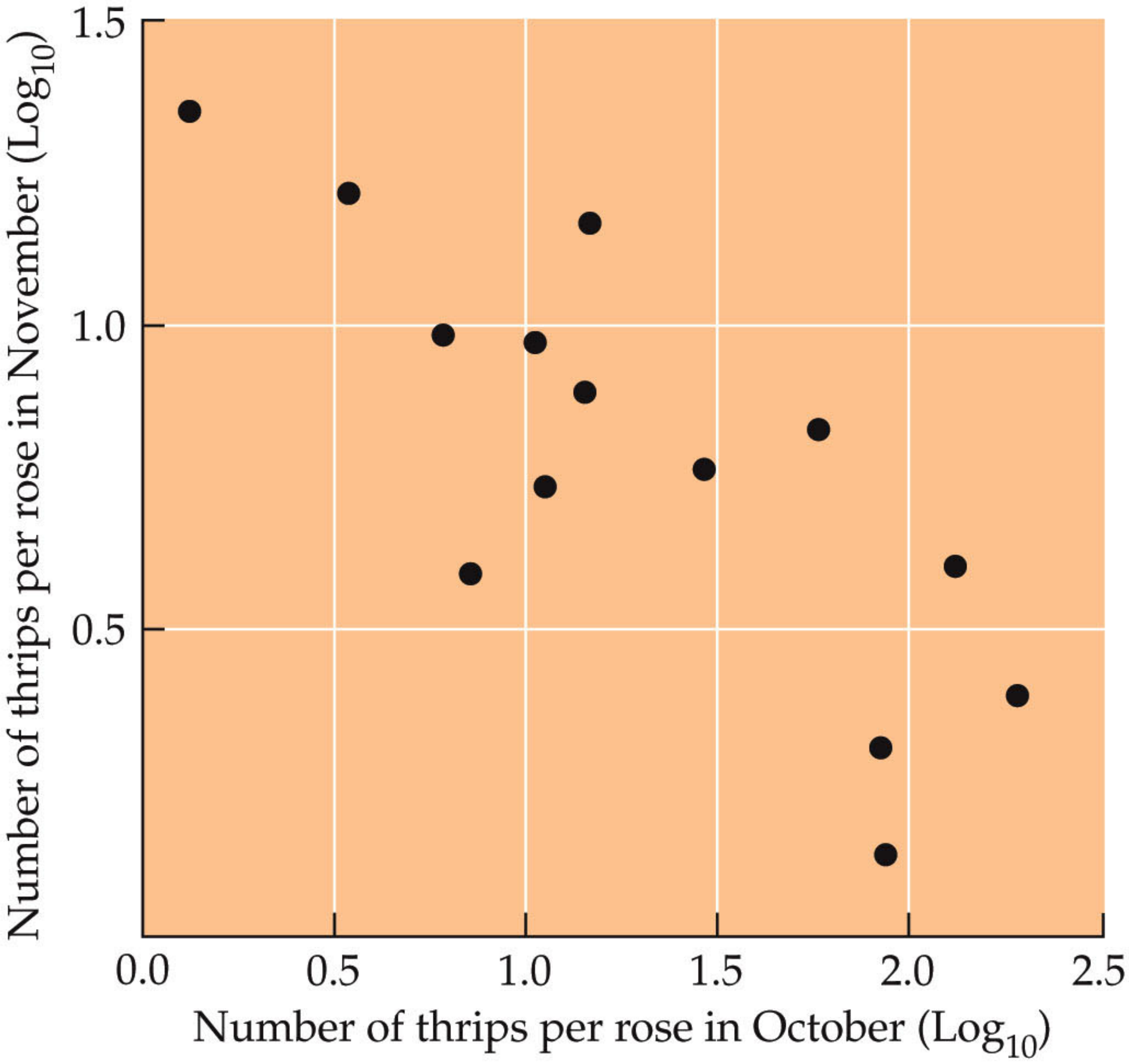

**ECOLOGY, Figure 9.14 (Part 3)**

# Effects Of Density

Density dependence can be detected even in populations whose abundance is largely controlled by density-independent factors.

Smith (1961) replotted Davidson and Andrewartha's data (1948): Change in population size from one time period to the next versus size of the population at the start of the time period.

## Figure 9.15 Density Dependence in *Thrips imaginis*



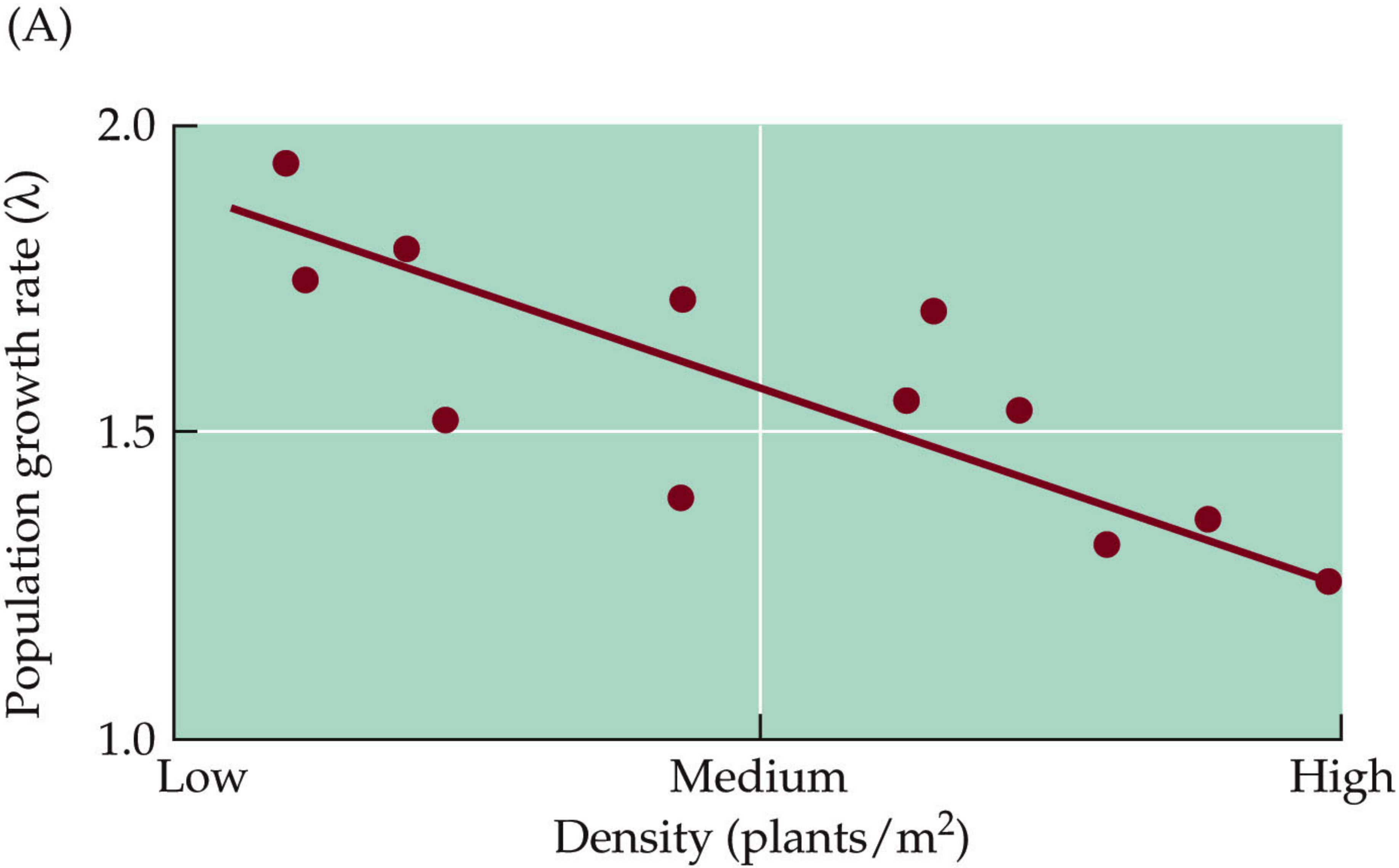

**ECOLOGY, Figure 9.15**

## Effects Of Density

When birth, death, or dispersal rates show strong density dependence, population growth rates may decline as densities increase.

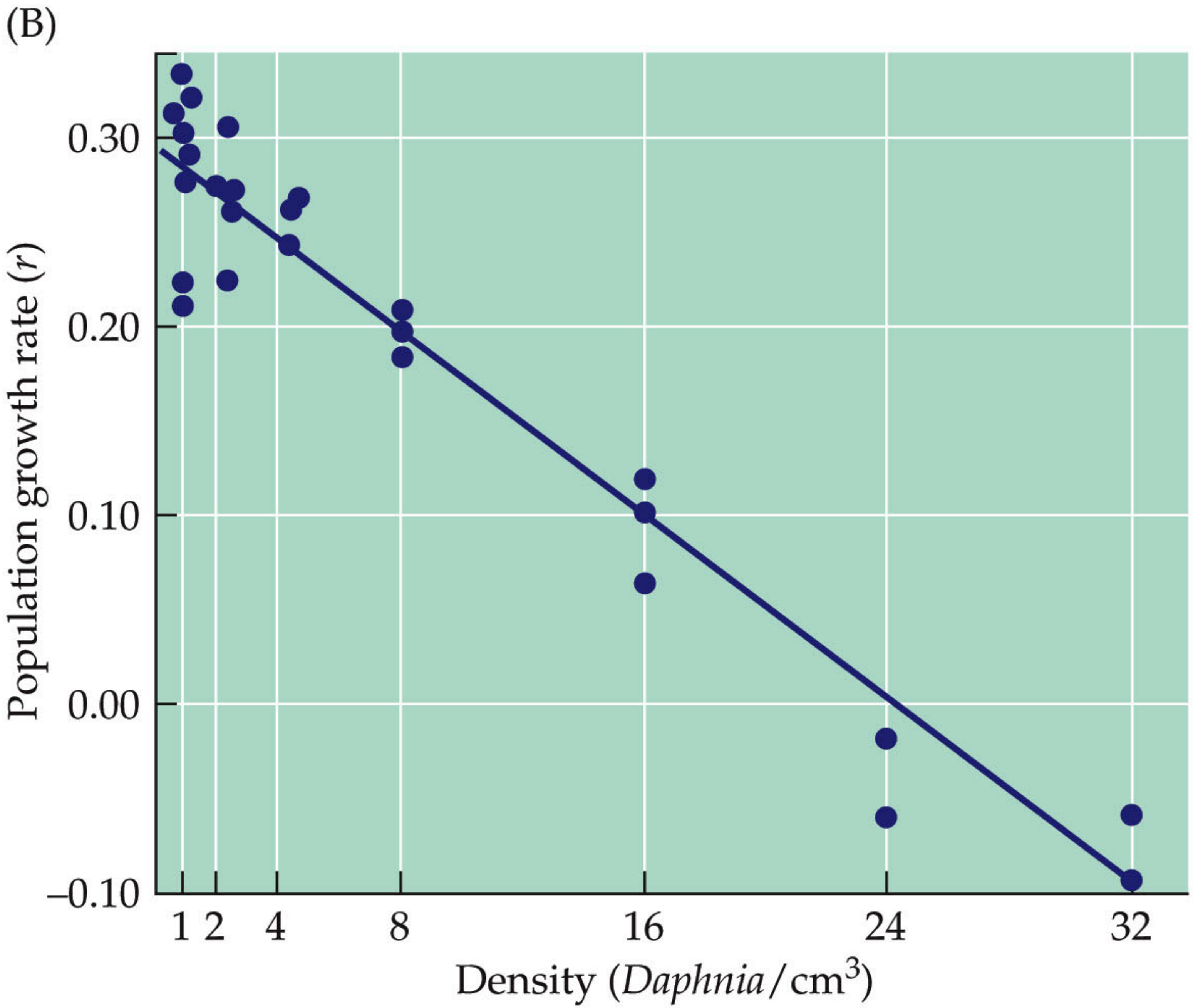
If densities become high enough to cause $\lambda = 1$ (or $r = 0$), the population decreases in size.

## Figure 9.16 Population Growth Rates May Decline at High Densities (Part 1)




ECOLOGY, Figure 9.16 (Part 1)

Figure 9.16 Population Growth Rates May Decline at High Densities (Part 2)



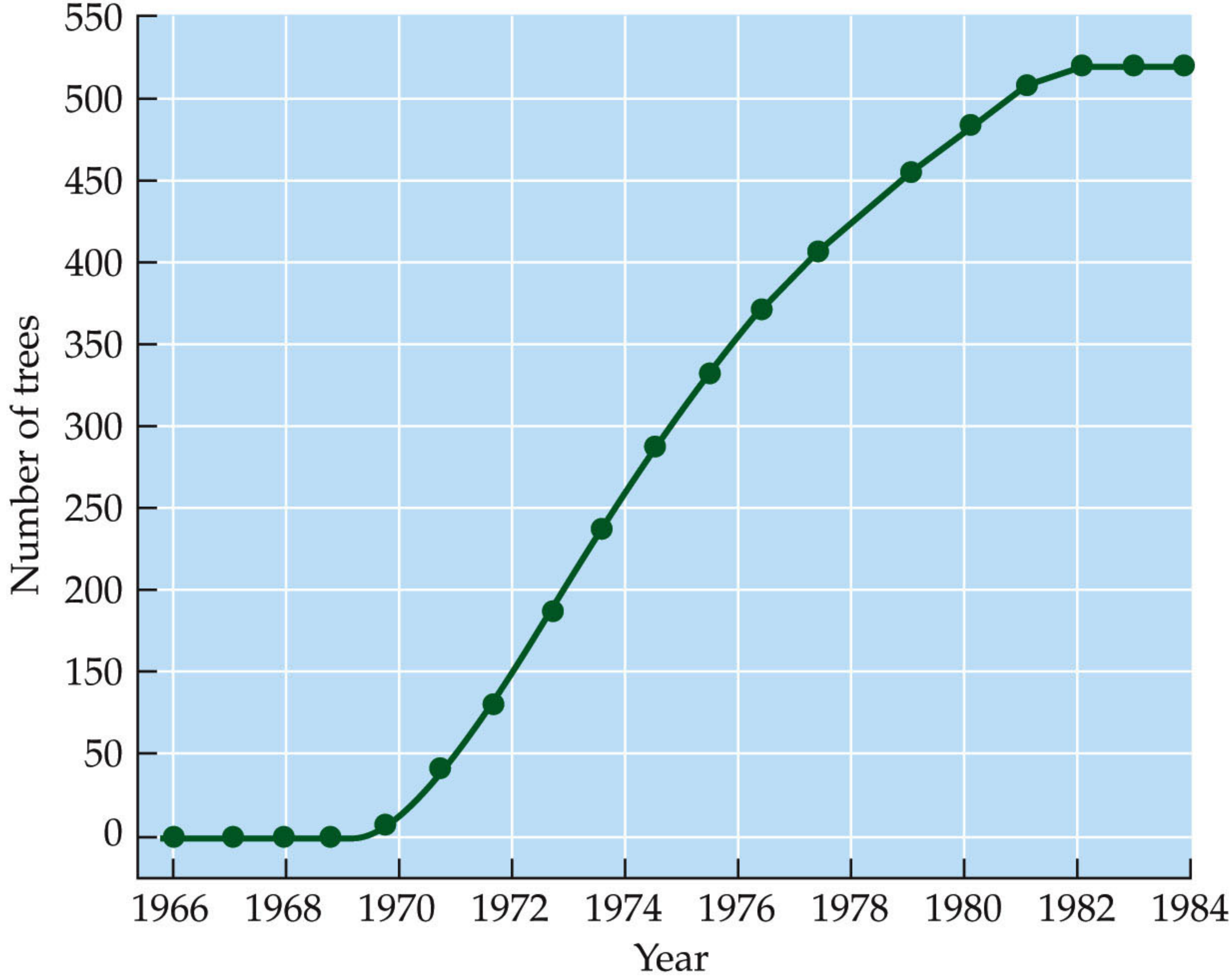

**ECOLOGY, Figure 9.16 (Part 2)**

# Logistic Growth

**Concept 9.5: The logistic equation incorporates limits to growth and shows how a population may stabilize at a maximum size, the carrying capacity.**

**Logistic growth:** Population increases rapidly at first, then stabilizes at the **carrying capacity** (maximum population size that can be supported indefinitely by the environment).

# Figure 9.17 An S-shaped Growth Curve in a Natural Population




**_ECOLOGY,_ Figure 9.17**

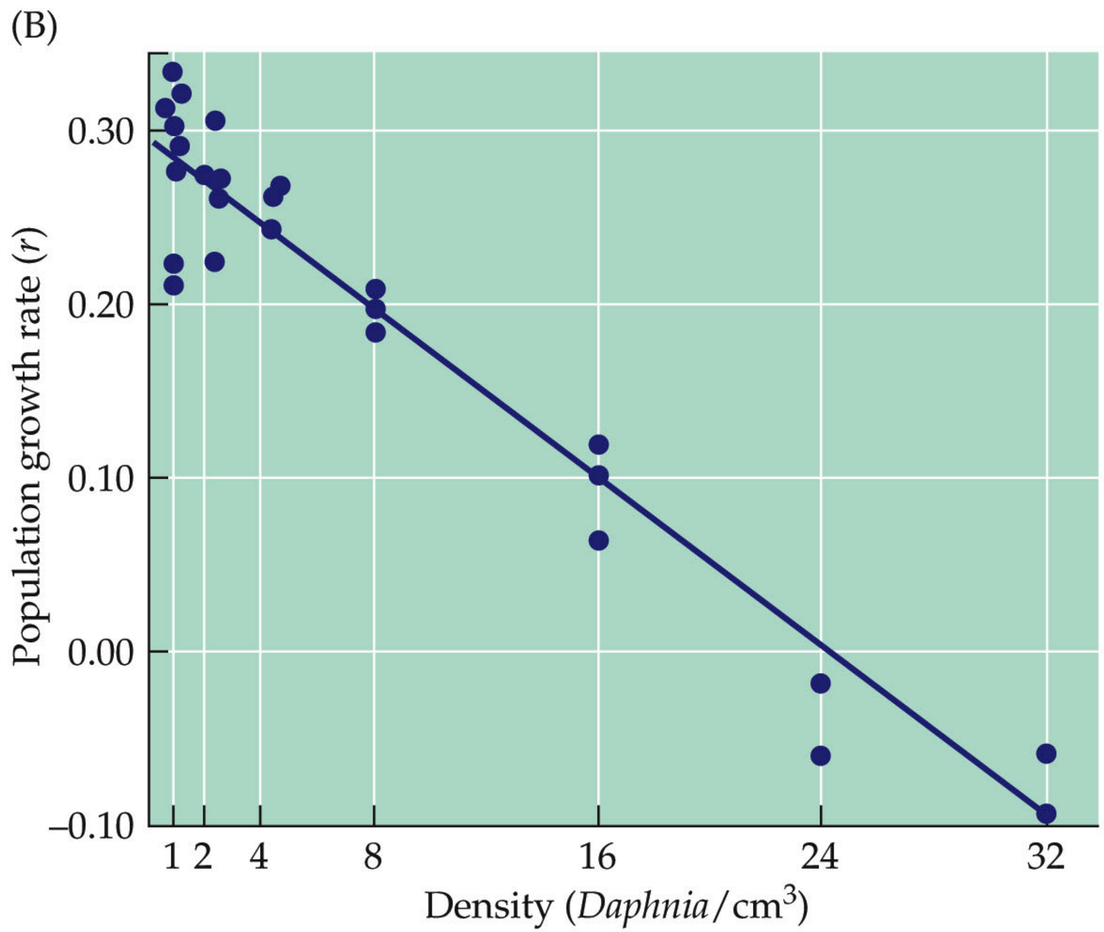
## Logistic Growth

The growth rate decreases as the population size nears carrying capacity because resources such as food, water, or space begin to run short.

At carrying capacity, the growth rate is zero, so population size does not change.

In the exponential growth equation ($dN/dt = rN$), $r$ is assumed to be constant.

To make it more realistic, we assume that $r$ declines in a straight line as density ($N$) increases.



This results in the *logistic equation*:

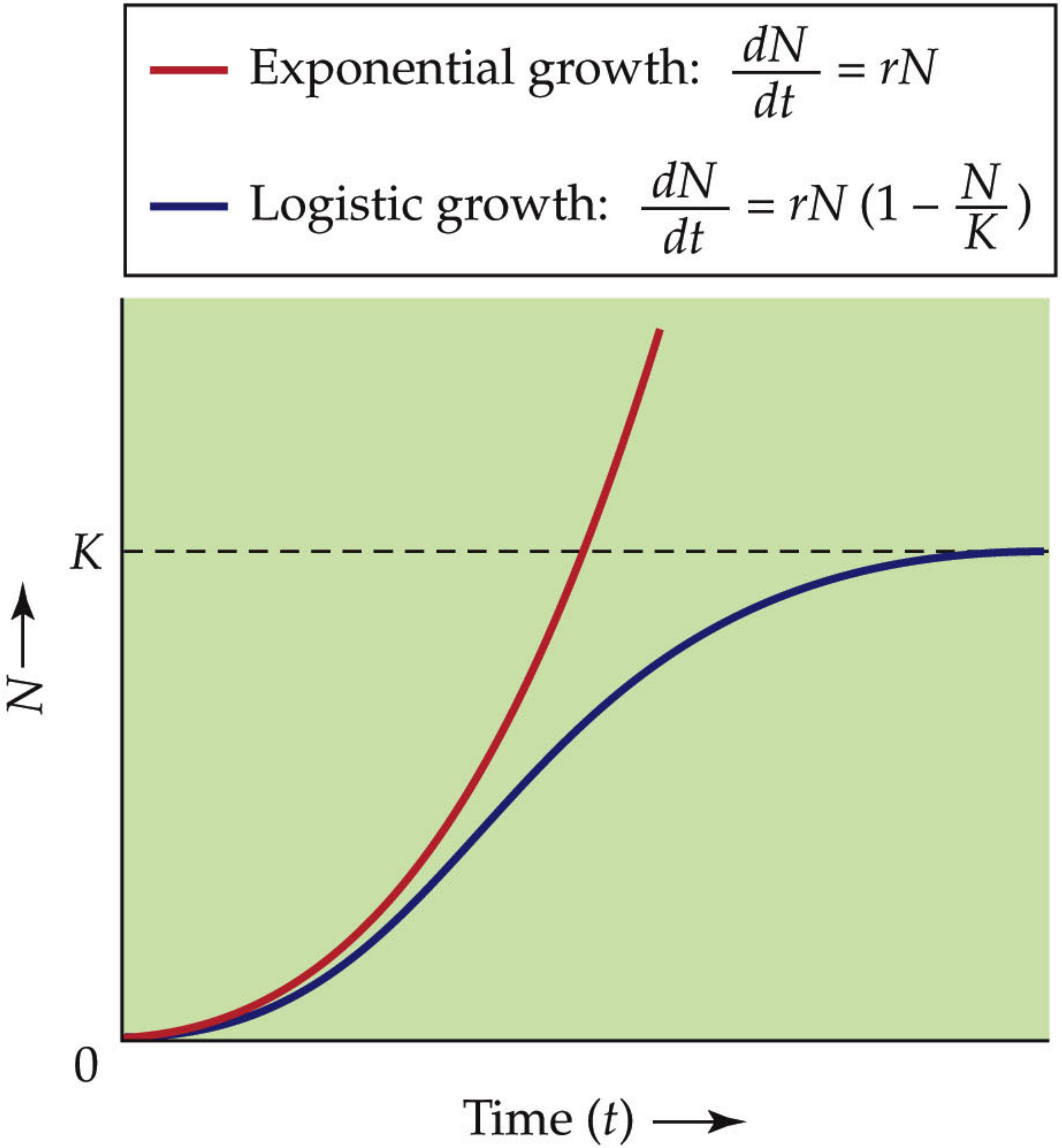
$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

*N* = population density

*r* = per capita growth rate

*K* = carrying capacity

## Figure 9.18  Logistic and Exponential Growth Compared




**ECOLOGY, Figure 9.18**

# Logistic Growth

When densities are low, logistic growth is similar to exponential growth.

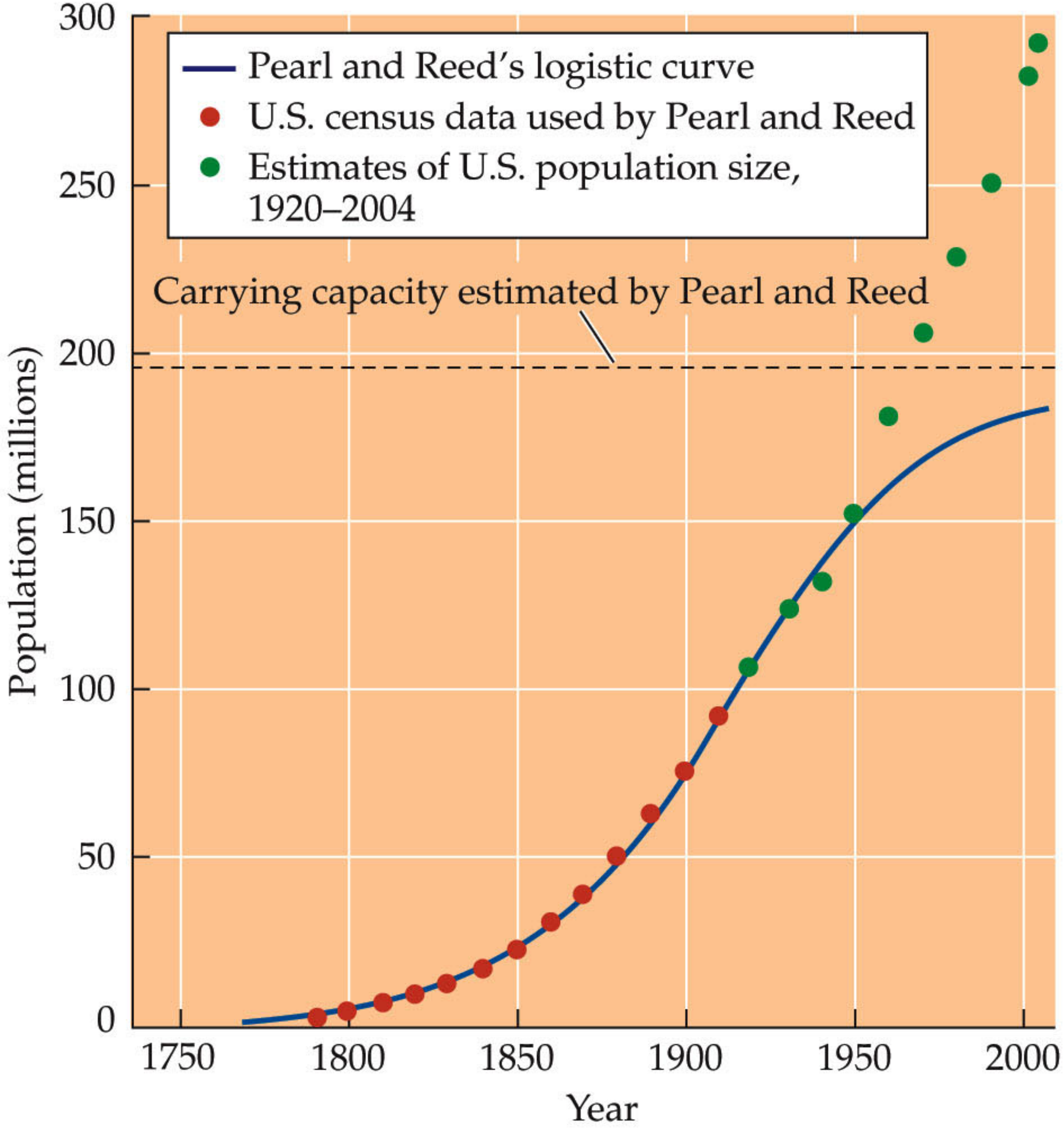
When $N$ is small, $(1 – N/K)$ is close to 1, and a population with logistic growth increases at a rate close to $r$.

As density increases, growth rate approaches zero.

Pearl and Reed (1920) derived the logistic equation and used it to predict a carrying capacity for the U.S. population, using census data.

The logistic curve fit the U.S. data well, through 1950. After that, however, the actual population size differed considerably from the predicted curve.

# Figure 9.19 Fitting a Logistic Curve to the U.S. Population Size




**ECOLOGY, Figure 9.19**

Pearl and Reed recognized that if conditions changed—for example, if agricultural productivity increased—the population could increase beyond the predicted carrying capacity.

Some ecologists have shifted to the concept of the ecological footprint: The total area required to support a human population.

## Case Study Revisited: Human Population Growth

If a population is growing exponentially, plotting the natural log of population size versus time will result in a straight line.

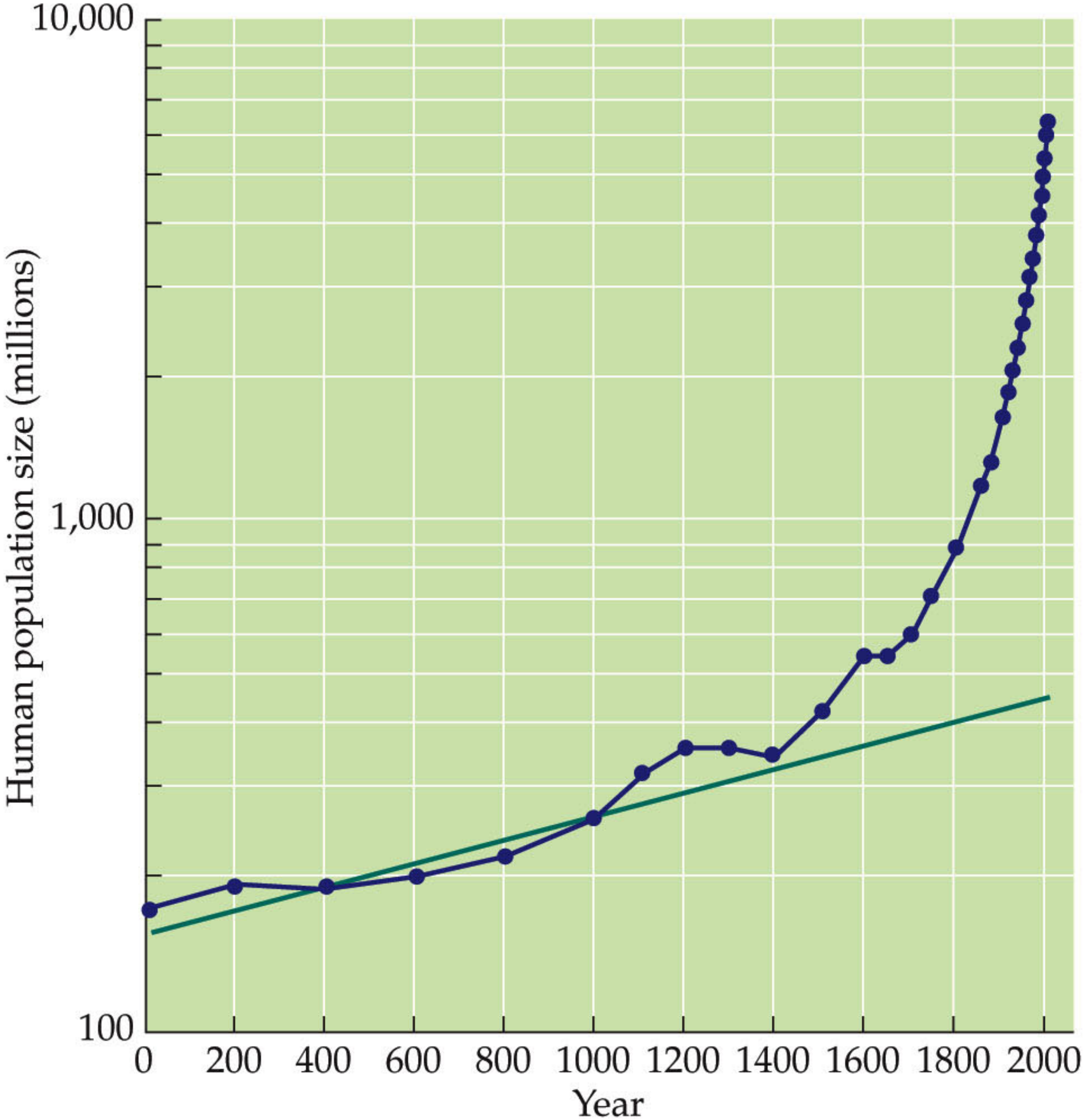
When the natural log of human population size is plotted, the line deviates considerably.

Human population has increased faster than exponential growth.

| Year | Population size | Doubling time ($t_d$) |
|---|---|---|
| 5000 B.C. | 5 million | 1400 years |
| 1550 | 500 million | 275 years |
| 1825 | 1 billion | 105 years |
| 1930 | 2 billion | 45 years |
| 1960 | 3 billion | 35 years* |
| 1999 | 6 billion | 51 years* |
| 2007 | 6.6 billion | 57 years* |

*Doubling times calculated from the relation to $t_d = \frac{\ln(2)}{r}$

## Figure 9.20  Faster than Exponential (Part 2)




**_ECOLOGY_, Figure 9.20 (Part 2)**

## Case Study Revisited: Human Population Growth

In a population that grows exponentially, the doubling time remains constant.

Our population's doubling time dropped from roughly 1,400 years in 5000 B.C. to a mere 45 years in 1930, which also shows that it is growing more rapidly than exponential growth.

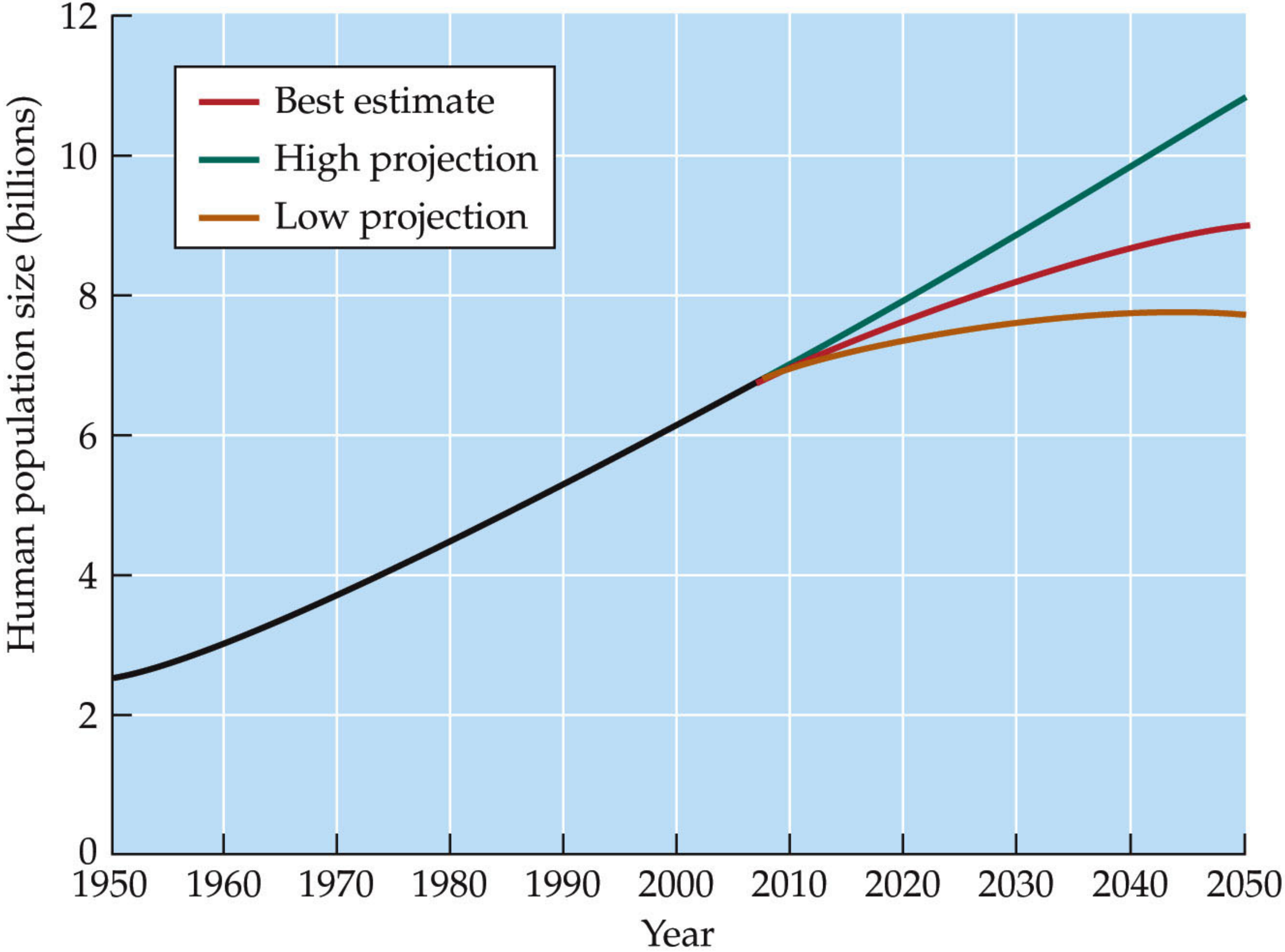
## Case Study Revisited : Human Population Growth

United Nations projections indicate that population growth rates are likely to continue to fall, leading to a predicted population size of 8.9 billion in 2050.

Extending that curve to 2080 suggests that there will be roughly 9–10 billion.

Is 10 billion above the carrying capacity of the human population?

## Figure 9.21 United Nations Projections of Human Population Size



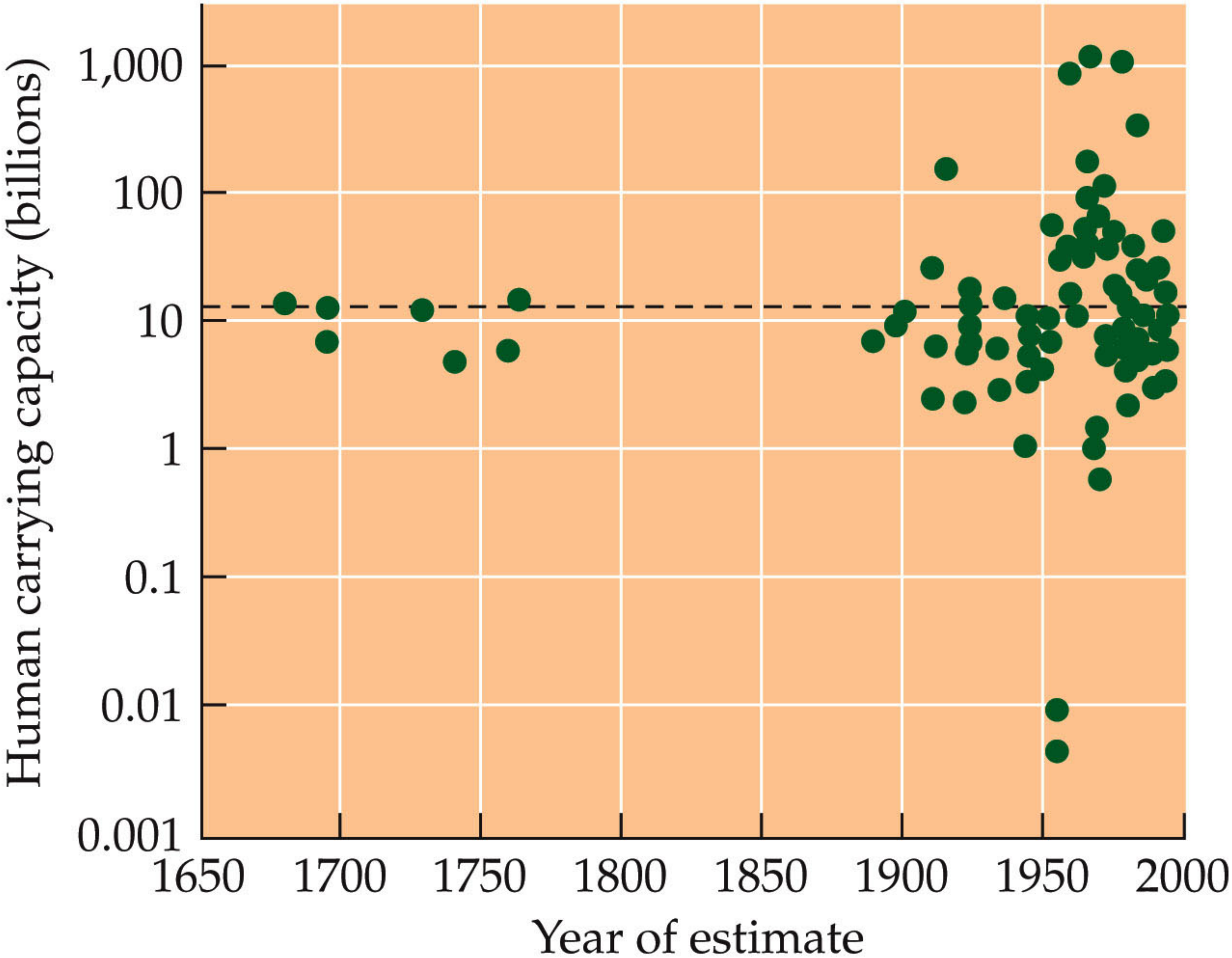

ECOLOGY, Figure 9.21

Many people have tried to estimate human carrying capacity.

The researchers must make assumptions about how people would live and how technology would influence our future.

Estimates range from fewer than 1 billion to more than 1,000 billion.

Figure 9.22 The Human Carrying Capacity




ECOLOGY, Figure 9.22

## Case Study Revisited : Human Population Growth

Using the ecological footprint approach, we see that the carrying capacity depends on the amount of resources used by each person.

## Case Study Revisited : Human Population Growth

If everyone used the amount of resources used by people in the U.S. in 1999, the world could support only 1.2 billion people.

If everyone used the amount of resources used by people in India in 1999, the world could support over 14 billion people.

## Connection in Nature: Your Ecological Footprint

The environmental impact of a population is called its **ecological footprint**.

Ultimately, every aspect of our economy depends on the ecosystems of Earth.

# Connection in Nature: Your Ecological Footprint

Ecological footprints are calculated from national statistics on agricultural productivity, production of goods, resource use, population size, and pollution.

The area required to support these activities is then estimated.

# Connection in Nature: Your Ecological Footprint

In the U.S. the average ecological footprint was 9.7 hectares per person in 1999 and there were 1,800 million hectares of productive land available.

This suggests that the carrying capacity of the U.S. in 1999 was 186 million; the actual population was 279 million, a 50% overshoot.

# Connection in Nature: Your Ecological Footprint

The ecological footprint approach highlights the fact that all of our actions depend on and affect the natural world.