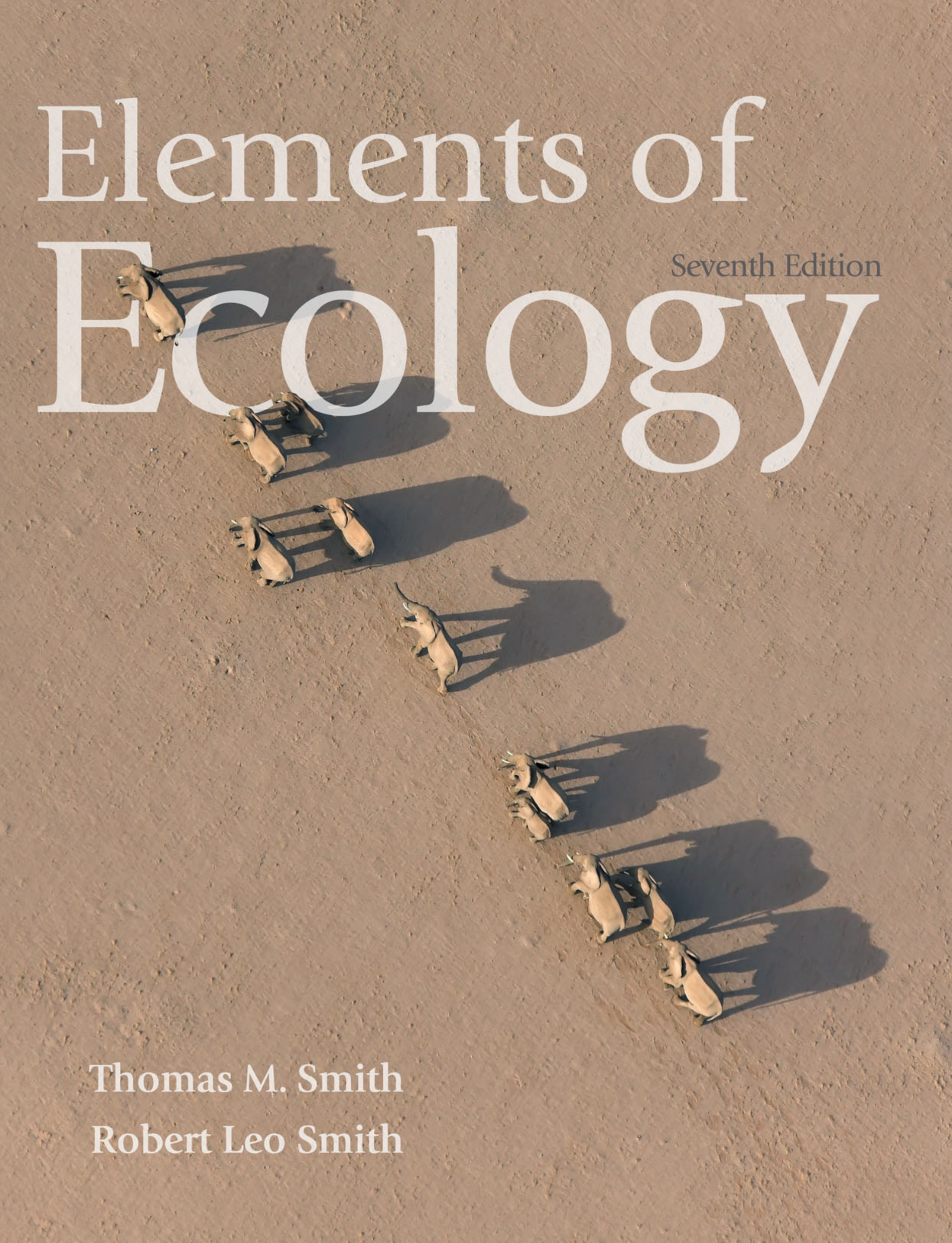


Chapter 9

Population Growth

Lecture prepared by
Aimee C. Wyrick

Chapter 10 Population Growth

- **Population growth** refers to how the number of individuals in a population increases or decreases with time
  - Individuals added via birth and **immigration**
  - Individuals removed via death and **emigration**
- Immigration and emigration occur in **open populations** but not in **closed populations**

10.1 Population Growth Reflects the Difference between Rates of Birth and Death

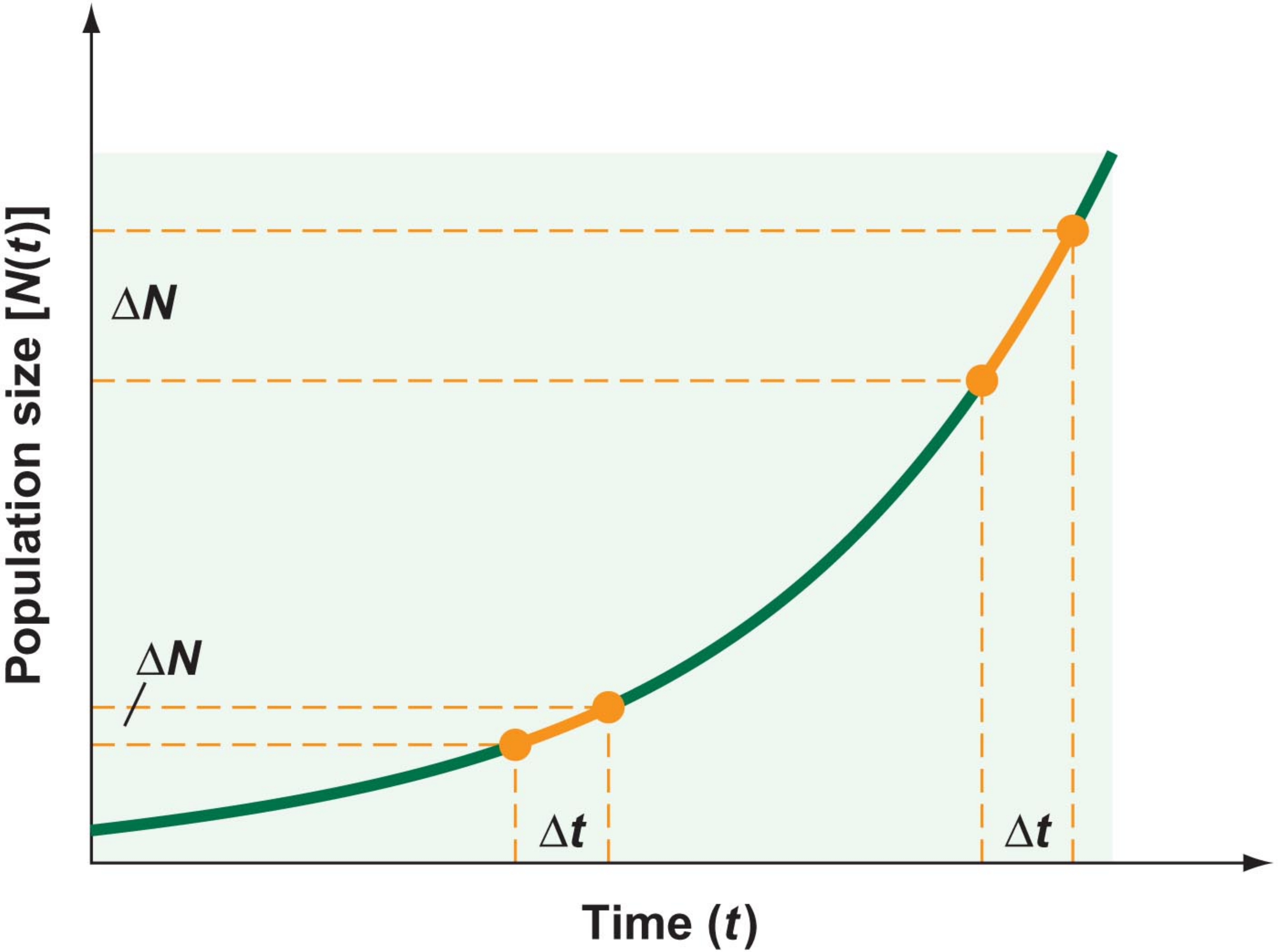
- A (closed) population of a freshwater hydra
  - Will increase as a result of new "births" (budding, a form of asexual reproduction)
  - Will decrease as a result of some hydra death
- Birth and death are continuous
  - ***b*** = the proportion of hydra producing a new individual per unit time
  - ***d*** = the proportion of hydra dying

10.1 Population Growth Reflects the Difference between Rates of Birth and Death

- Population size at a particular time = $N(t)$
- The number of hydra reproducing [$B(t)$] or dying [D(t)] over a particular time period ($\Delta\ t$) can be calculated
  - $B(t) = bN(t)\Delta\ t$
  - $D(t) = dN(t)\Delta\ t$
- The population size (N) at the next time period ($t + \Delta t$) would be
  - $N(t + \Delta\ t) = N(t) + B(t) + \Delta\ (t)$

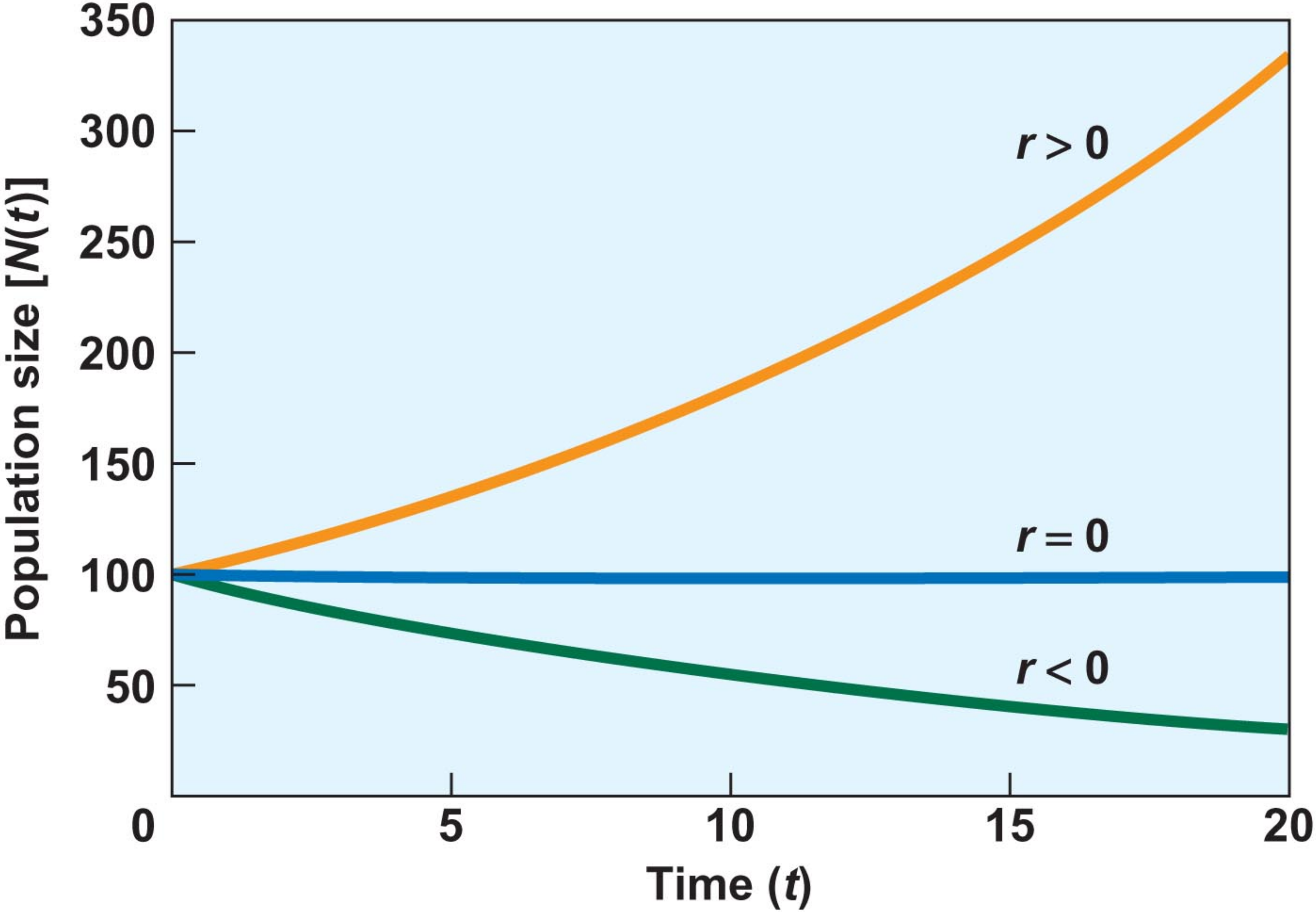
10.1 Population Growth Reflects the Difference between Rates of Birth and Death

- The pattern of population size is a function of time
- Rearranging the equation:
  - $N(t + \Delta t) - N(t) / \Delta t = \Delta N / \Delta t = (b - d) N(t)$
- The relationship (slope) between $N(t)$ and t is nonlinear (curve)


Population size [$N(t)$]
ΔN
ΔN
Δt
Δt
Time (t)

10.1 Population Growth Reflects the Difference between Rates of Birth and Death

- Rate of change is best described by the derivative of the equation = $dN/dt = (b - d)N$
  - This derivative expresses that as the Δt approaches zero and the rate of change is instantaneous
- $\boldsymbol{r} = (b - d)$ = **instantaneous** (per capita) rates of birth and death (growth)
- **Exponential population growth** = $dN/dt = rN$
  - Predicts the *rate* of population change through time

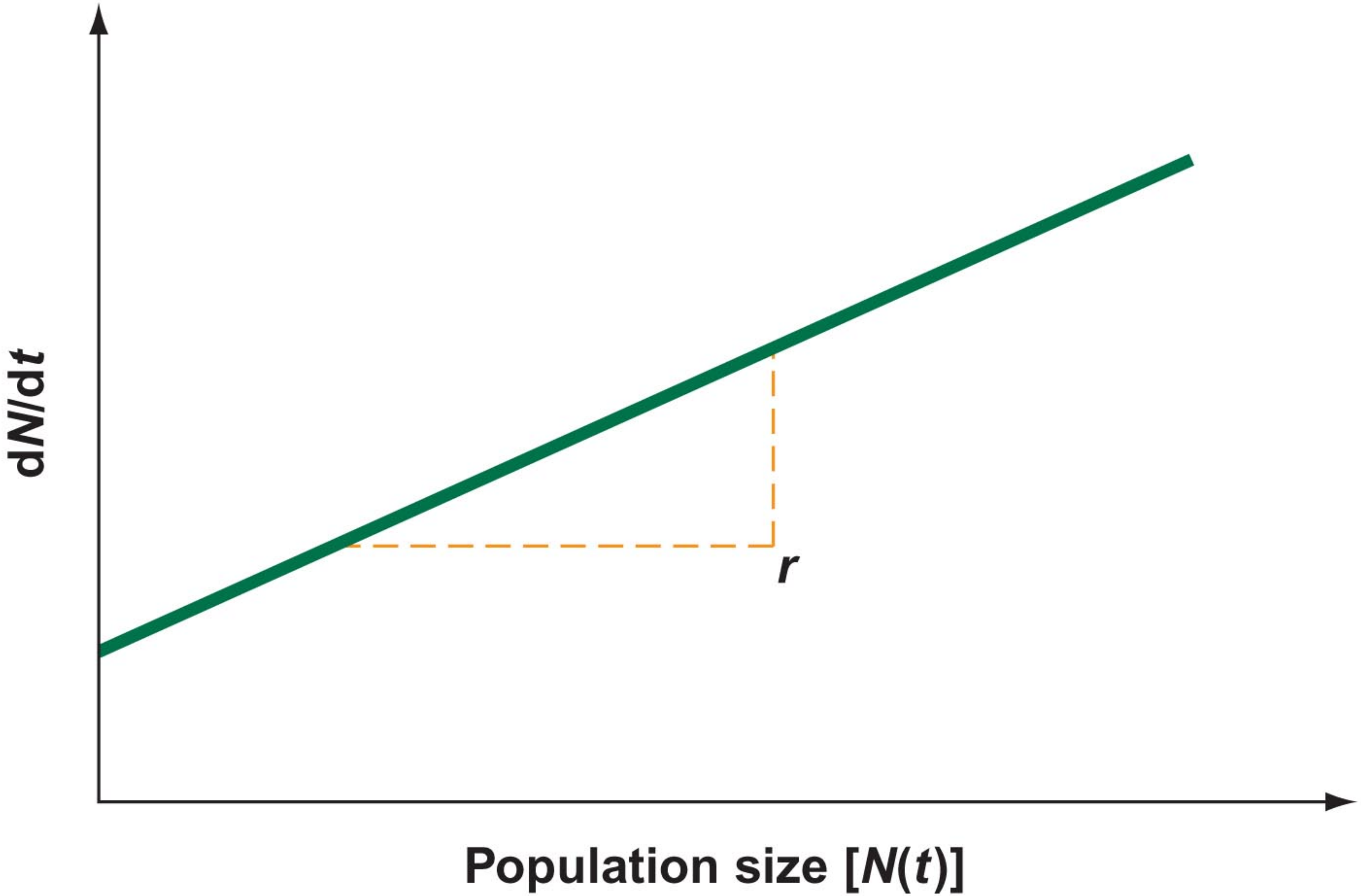

350
300
250
200
150
100
50
0
5
10
15
20
Population size [N(t)]
Time (t)
r > 0
r = 0
r < 0

10.1 Population Growth Reflects the Difference between Rates of Birth and Death

- An alternate differential equation allows us to predict population size $N(t)$ under conditions of exponential growth
  - $N(t) = N(0)e^{rt}$

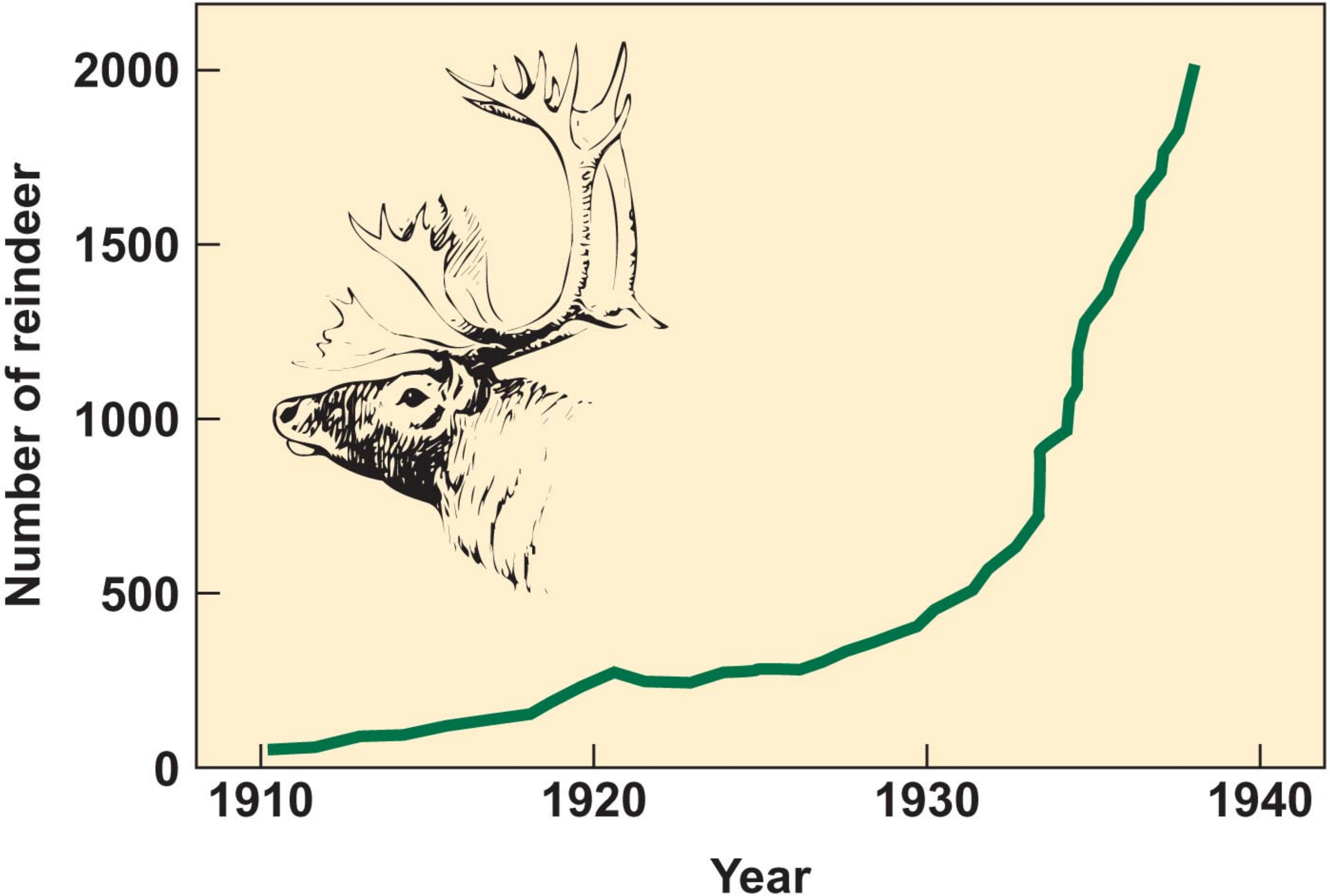
10.1 Population Growth Reflects the Difference between Rates of Birth and Death

- Exponential growth rate
  - When $r = 0$, there is no change in population size
  - When $r > 0$, the population increases exponentially
  - When $r < 0$, the population decreases exponentially
- Exponential growth results in a continuously accelerating (or decelerating) rate of population increase (or decrease)


dN/dt
r
Population size [N(t)]

10.1 Population Growth Reflects the Difference between Rates of Birth and Death

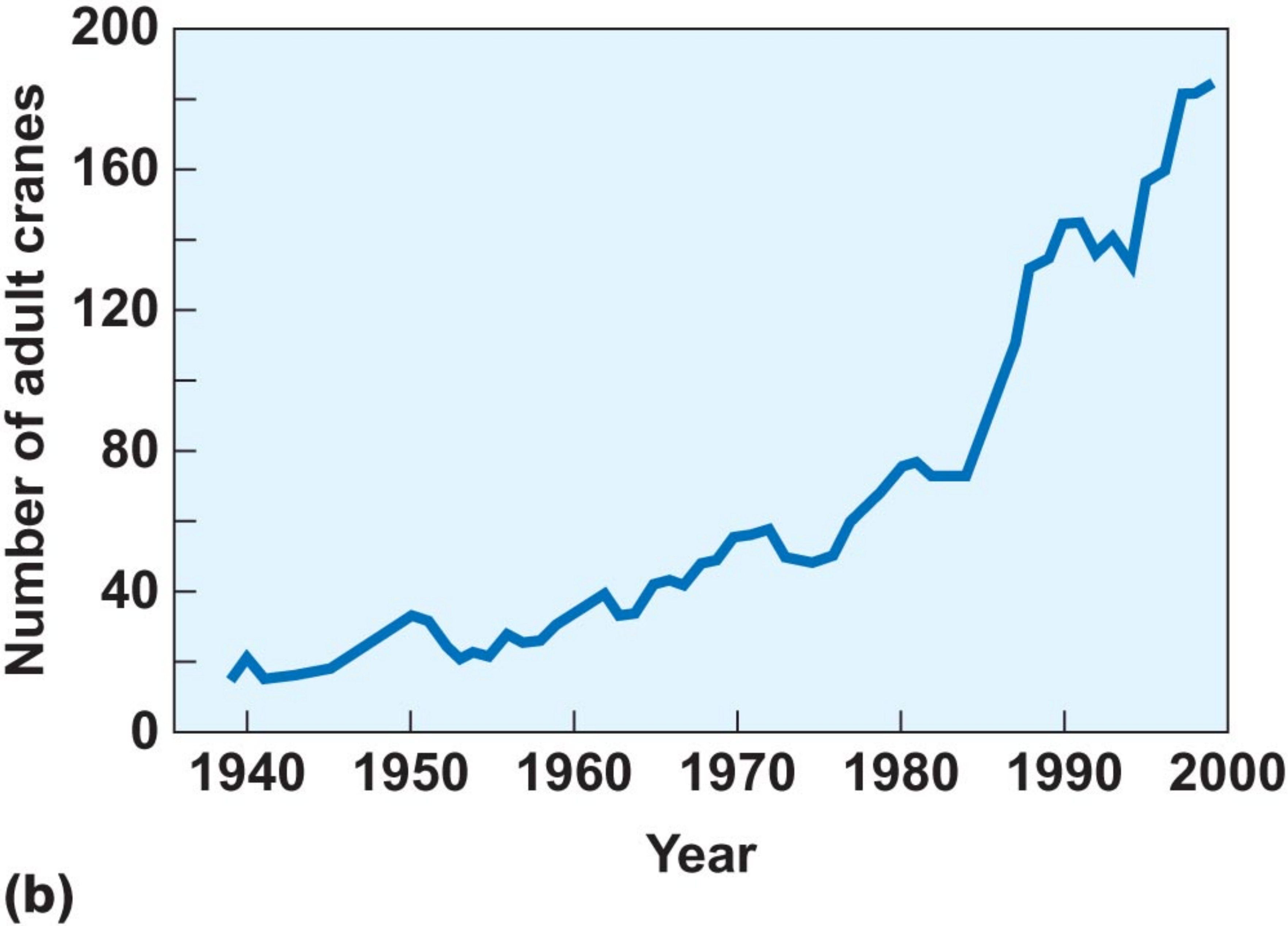
- Exponential growth rate is characteristic of populations that inhabit favorable conditions at low population densities (e.g., conditions of colonization)



Number of reindeer
2000
1500
1000
500
0
1910
1920
1930
1940
Year

(a)

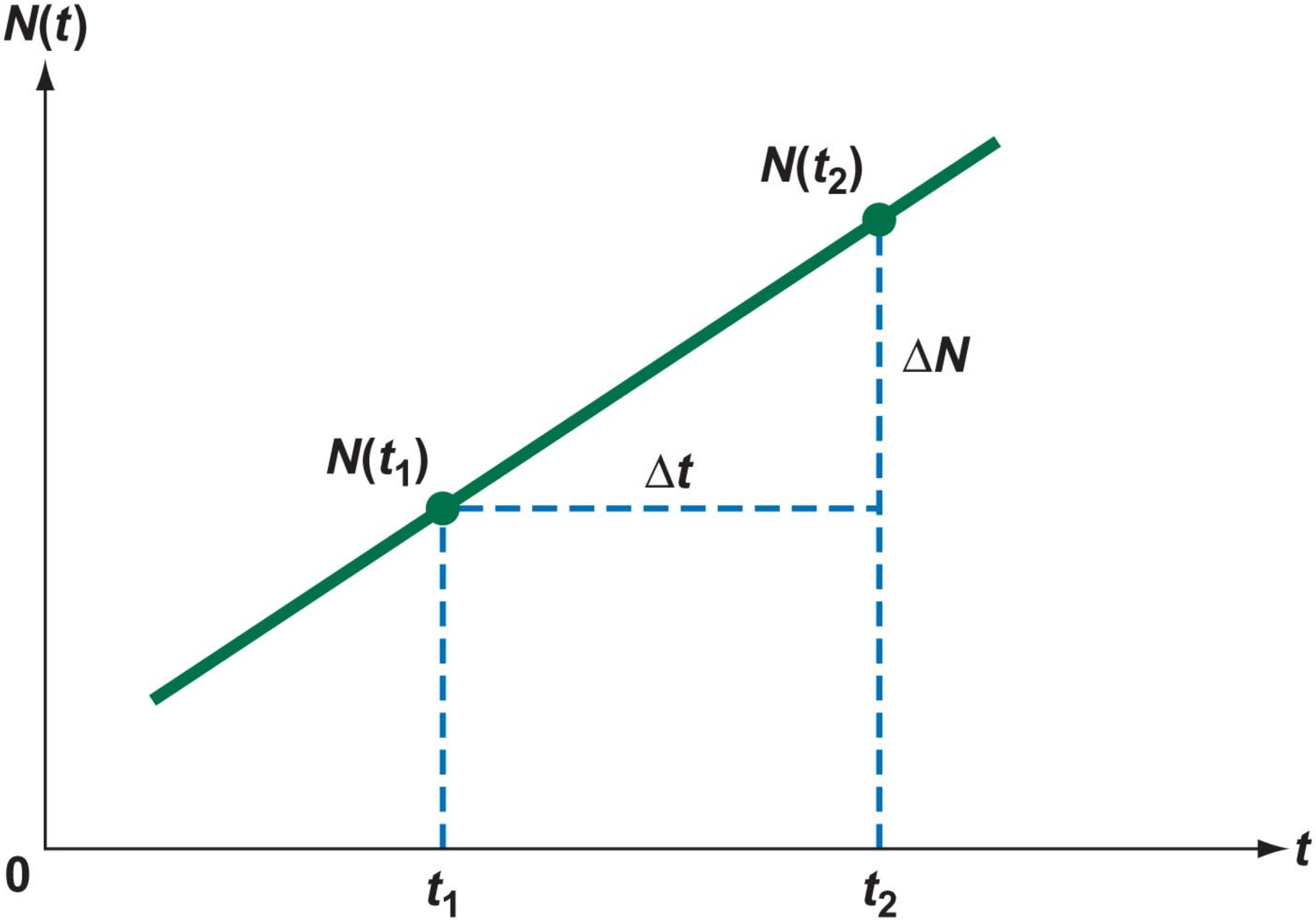
Cranes



200
160
120
80
40
0
Number of adult cranes
1940
1950
1960
1970
1980
1990
2000
Year
(b)

Quantifying Ecology 10.1 Derivatives and Differential Equations

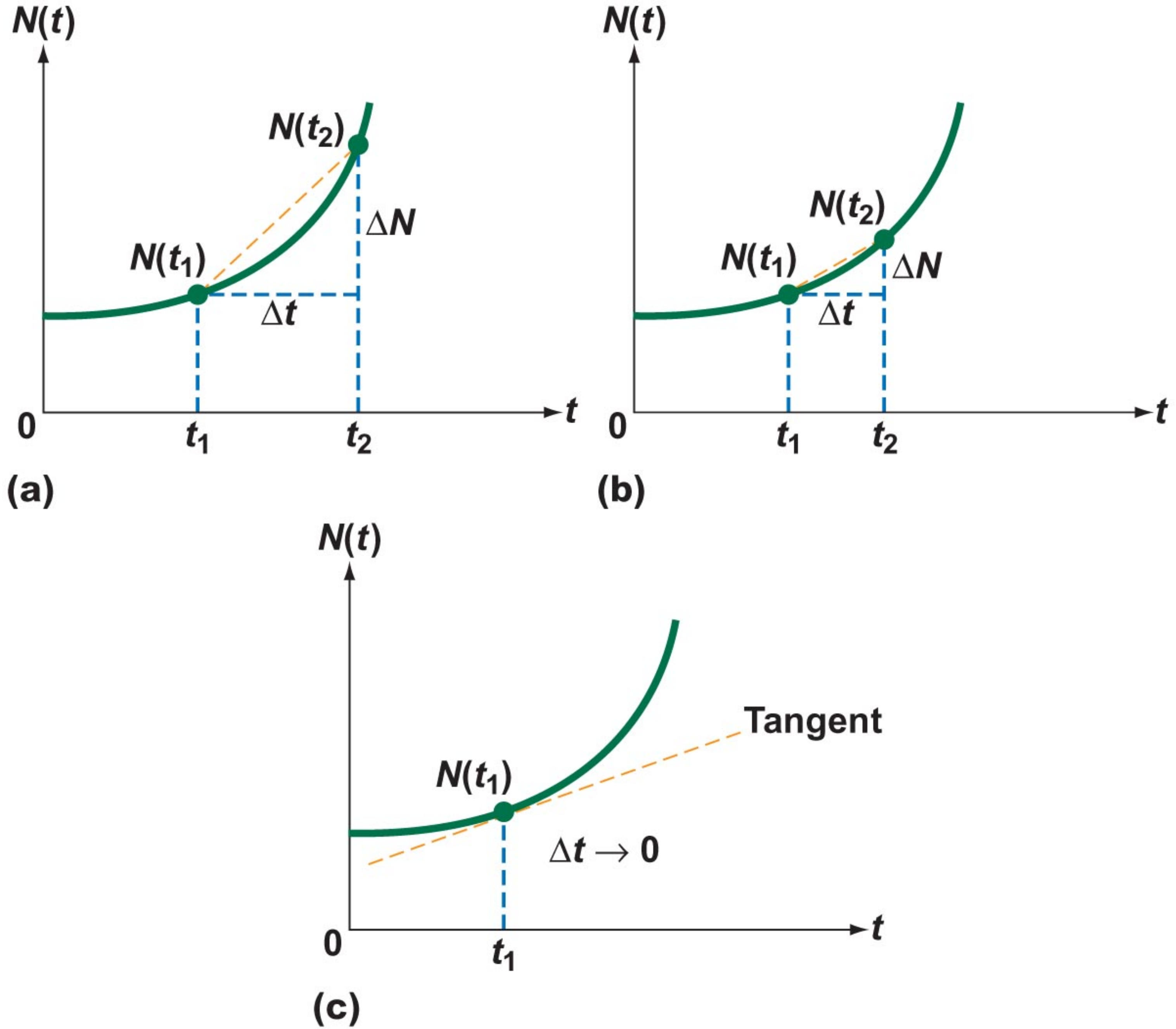
- If $N(t)$ is a linear function of t then the resulting graph will be a straight line
- The rate of population change is given by the slope = s = $\Delta N/\Delta t = N(t_2) - N(t_1)/t_2 - t_1$
  - The slope of a linear function does not depend on the value of t



N(t)
N(t2)
ΔN
N(t1)
Δt
0
t1
t2
t

Quantifying Ecology 10.1 Derivatives and Differential Equations

- The slope of a nonlinear function (curve) *does* depend on the value of t
  - As t_2 moves closer to t_1, the slopes vary by smaller and smaller amounts and will eventually approach a constant "limiting value"
- The slope of the function $N(t)$ at t_1 is known as the derivative of $N(t)$ written as $dN(t)/dt$



N(t)
N(t2)
ΔN
N(t1)
Δt
0
t1
t2
t
(a)
N(t)
N(t2)
N(t1)
ΔN
Δt
0
t1
t2
t
(b)
N(t)
Tangent
N(t1)
Δt → 0
0
t1
t
(c)

10.2 Life Tables Provide a Schedule of Age-Specific Mortality and Survival

- Change in population abundance through time is a function of the birth and death rates (r = per capita growth rate)
- A **life table** is an age-specific account of mortality
- A **cohort** is a group of individuals born in the same period of time

10.2 Life Tables Provide a Schedule of Age-Specific Mortality and Survival

- Life table of gray squirrels (*Sciurus carolinensis*)
  - $\boldsymbol{x}$ = age classes
  - $\boldsymbol{n_x}$ = the number of individuals from the original cohorts that are alive at the specified age (x)

x	n_x
0	530
1	159
2	80
3	48
4	21
5	5

10.2 Life Tables Provide a Schedule of Age-Specific Mortality and Survival

- Life table of grey squirrels (*Sciurus carolinensis*)
  - l_x = the probability at birth of surviving to any given age (x)

x	n_x	l_x
0	530	1.00
1	159	0.30
2	80	0.15
3	48	0.09
4	21	0.04
5	5	0.01

$n_0 / n_0 = 530 / 530$

$n_1 / n_0 = 159 / 530$

$n_2 / n_0 = 80 / 530$

10.2 Life Tables Provide a Schedule of Age-Specific Mortality and Survival

- Life table of gray squirrels (*Sciurus carolinensis*)
  - $\boldsymbol{d_x}$ = age-specific mortality = the difference between the number of individuals alive for any age class (n_x) and the next older age class (n_{x+1})

x	n_x	d_x
0	530	371
1	159	79
2	80	32
3	48	27
4	21	16
5	5	5

$n_0 - n_1 = 530 - 159$

$n_1 - n_2 = 159 - 80$

10.2 Life Tables Provide a Schedule of Age-Specific Mortality and Survival

- Life table of gray squirrels (*Sciurus carolinensis*)
  - q_x = age-specific mortality rate = the number of individuals that died in a given time interval (d_x) divided by the number alive at the beginning of that interval (n_x)

x	n_x	d_x	q_x
0	530	371	0.70
1	159	79	0.50
2	80	32	0.40
3	48	27	0.55
4	21	16	0.75
5	5	5	1.00

$d_0 / n_0 = 371 / 530$

$d_1 / n_1 = 79 / 159$

Table 10.1 | Gray Squirrel Life Table

x	n_x	l_x	d_x	q_x
0	530	1.0	371	0.7
1	159	0.3	79	0.5
2	80	0.15	32	0.4
3	48	0.09	27	0.55
4	21	0.04	16	0.75
5	5	0.01	5	1.0

Quantifying Ecology 10.3 Life Expectancy

- Life expectancy (e) refers to the average number of years an individual is expected to live from the time of its birth
- Using the life table for the gray squirrel
- $\boldsymbol{e_x}$ = age-specific life expectancy = the average number of years that an individual of a given age (n_x) is expected to live into the future
  - Several initial calculations are necessary to determine e_x

Quantifying Ecology 10.3 Life Expectancy

- ***Lx*** = the average number of individuals alive during the age interval x to $x + 1$.
  - Assumes mortality is evenly spread over the year

x	n_x	L_x
0	530	344.5
1	159	119.5
2	80	64.0
3	48	34.5
4	21	13.0
5	5	2.5

$= (n_0 + n_1) / 2 = (530 + 159) / 2 = 344.5$

$= (n_2 + n_3) / 2 = (80 + 48) / 2 = 64$

$= (n_5 + n_6) / 2 = (5 + 0) / 2 = 2.5$

Quantifying Ecology 10.3 Life Expectancy

- ***Tx*** = the total years lived into the future by individuals of age class *x* in the population

x	L_x	T_x
0	344.5	578.0
1	119.5	233.5
2	64.0	114.0
3	34.5	50.0
4	13.0	15.5
5	2.5	2.5

$$= L_0 + L_1 + L_2 + L_3 + L_4 + L_5$$
$$= 344.5 + 119.5 + 64 + 34.5 + 13 + 2.5 = 578$$

$$= L_4 + L_5 = 13 + 2.5 = 15.5$$

$$= L_5 = 2.5$$

Quantifying Ecology 10.3 Life Expectancy

- $\boldsymbol{e_x}$ = age-specific life expectancy = the average number of years that an individual of a given age (n_x) is expected to live into the future

x	n_x	T_x	e_x
0	530	578.0	1.09
1	159	233.5	1.47
2	80	114.0	1.43
3	48	50.0	1.06
4	21	15.5	0.75
5	5	2.5	0.50

$= T_0 \,/\, n_0 = 578 \,/\, 530 = 1.09$

$= T_2 \,/\, n_2 = 114 \,/\, 80 = 1.43$

10.3 Different Types of Life Tables Reflect Different Approaches to Defining Cohorts and Age Structure

- A **cohort** or **dynamic life table** is used to track the fate of a group of individuals born at a given time
  - These individuals are followed from birth to death
- A **dynamic composite life table** constructs a cohort from individuals born over several time periods

10.3 Different Types of Life Tables Reflect Different Approaches to Defining Cohorts and Age Structure

- A **time-specific life table** is a distribution of age classes during a single time period
- Several assumptions are made in this approach
  - Each age class was sampled in proportion to its numbers in the population
  - Age-specific mortality rates (and birthrates) are constant over time

10.3 Different Types of Life Tables Reflect Different Approaches to Defining Cohorts and Age Structure

- Many animals (e.g., insects) live only one breeding season. Because generations do not overlap, all individuals belong to the same age class
  - n_x is measured by estimating the population size several times over its annual season

Sparse Gypsy moth

http://en.wikipedia.org/wiki/Lymantria_dispar_dispar

Table 10.2 | Life Table of a Sparse Gypsy Moth Population in Northeastern Connecticut

x	n_x	l_x	d_x	q_x
Eggs	450	1.000	135	0.300
Instars I–III	315	0.700	258	0.819
Instars IV–VII	57	0.127	33	0.582
Prepupae	24	0.053	1	0.038
Pupae	23	0.051	7	0.029
Adults	16	0.036	0	1.000

Source: Data from R. W. Campbell 1969.

10.3 Different Types of Life Tables Reflect Different Approaches to Defining Cohorts and Age Structure

- The life table is useful for studying several areas of plant demography
  - Seedling mortality and survival
  - Population dynamics of perennial plants marked as seedlings
  - Life cycles of annual plants

Sedum smallii H. E. Ahles

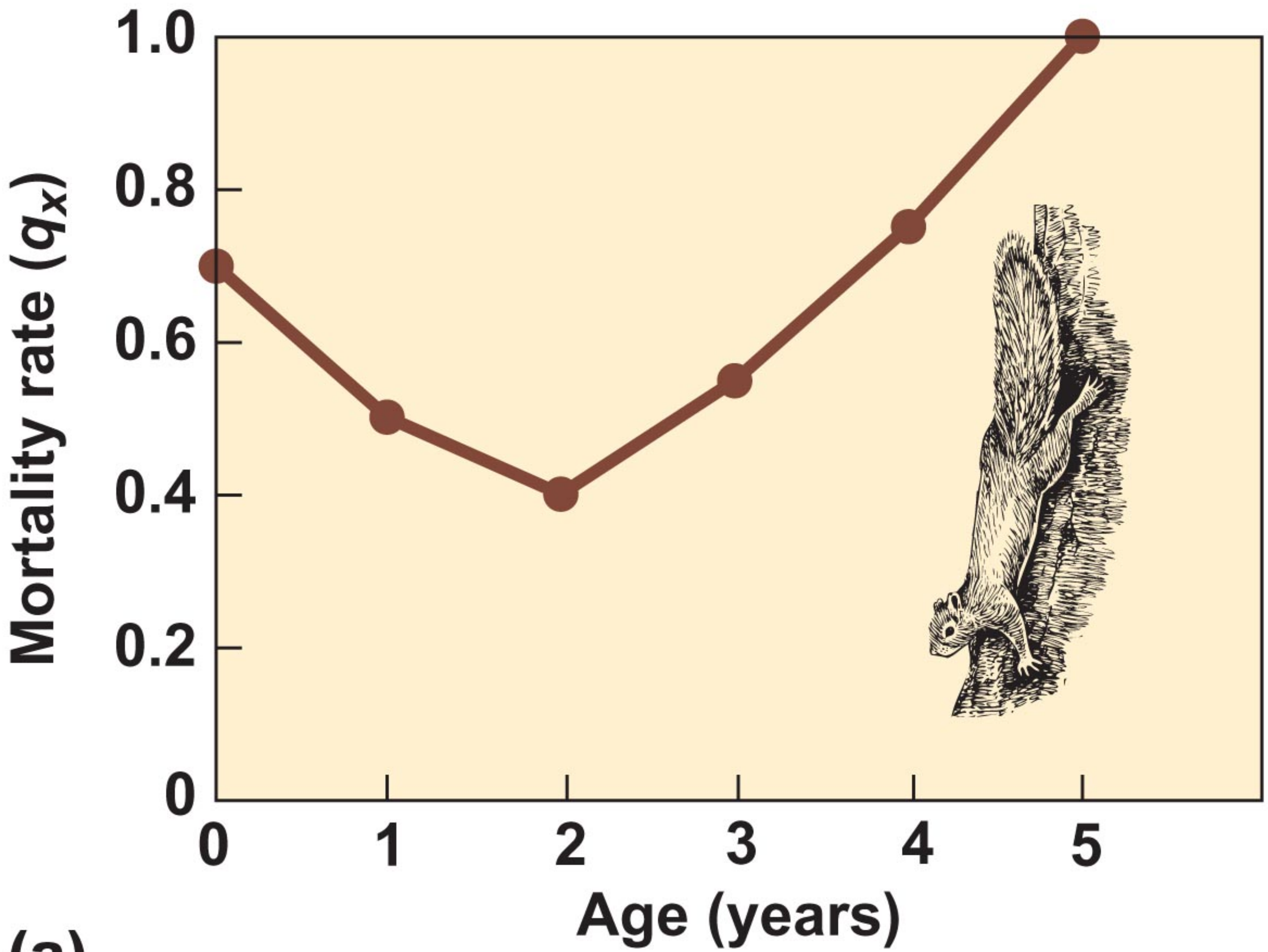
Table 10.3 | Life Table for a Natural Population of *Sedum smallii*

x	l_x	d_x	q_x
Seed produced	1.000	0.16	0.160
Available	0.840	0.630	0.750
Germinated	0.210	0.177	0.843
Established	0.033	0.009	0.273
Rosettes	0.024	0.010	0.417
Mature plants	0.014	0.014	1.000

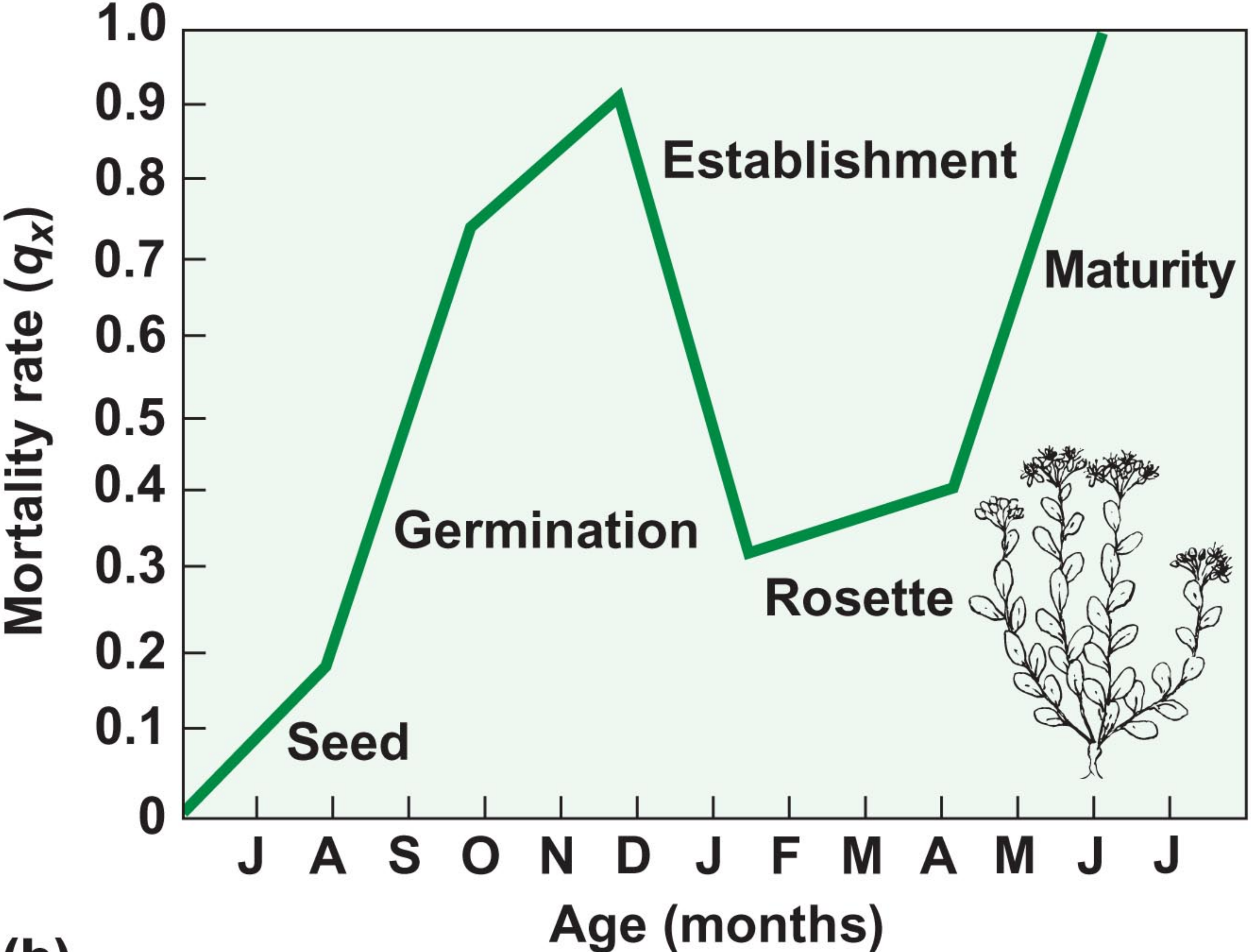
Source: Data from Sharitz and McCormick 1973.

10.4 Life Tables Provide Data for Mortality and Survivorship Curves

- Life table data are generally presented as:
  - A **mortality curve** that plots the q_x column against age (x)
  - A **survivorship curve** that plots the l_x column against age (x)
- Life tables and curves are based on data from one population at a specific time and under certain environmental conditions

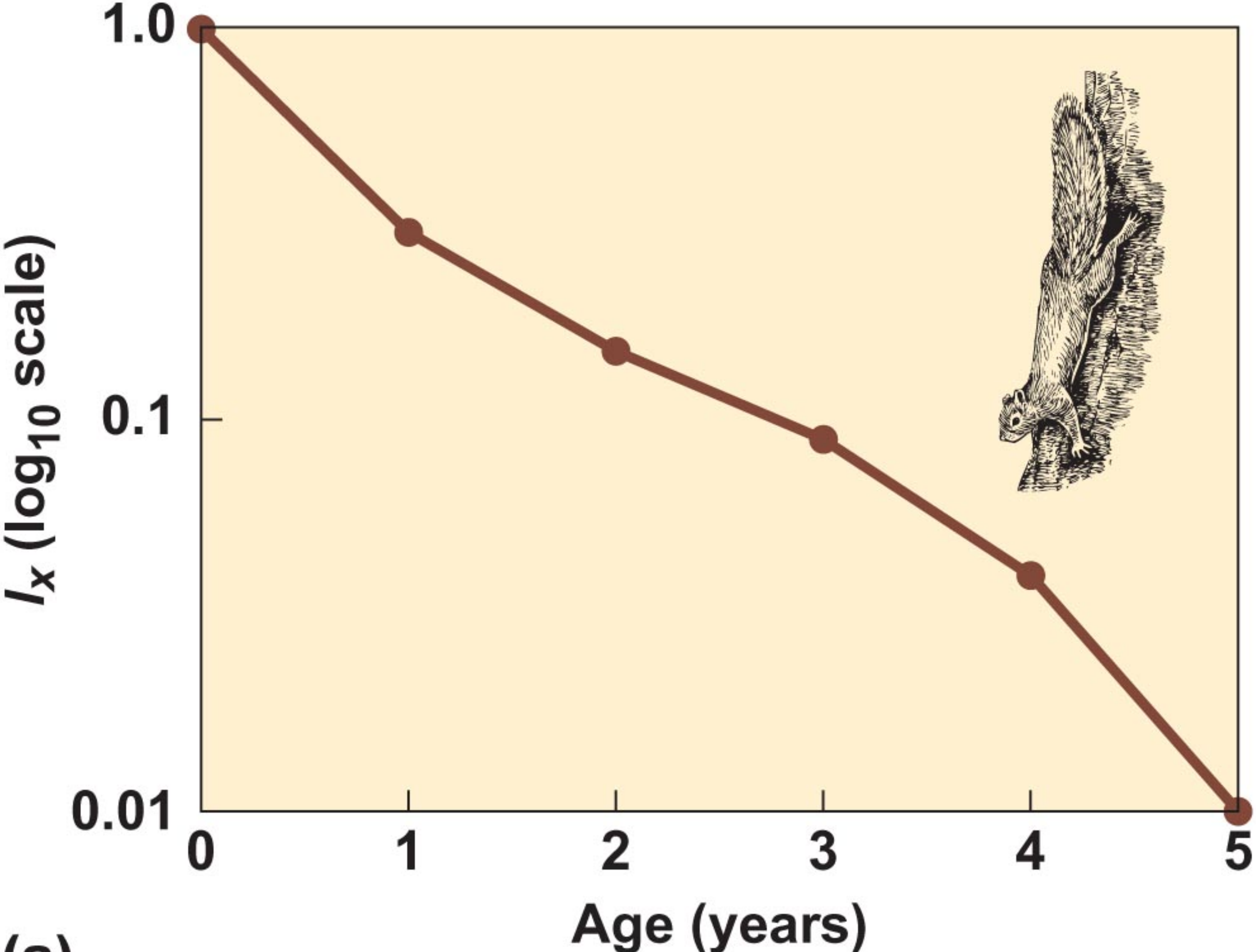


(a)

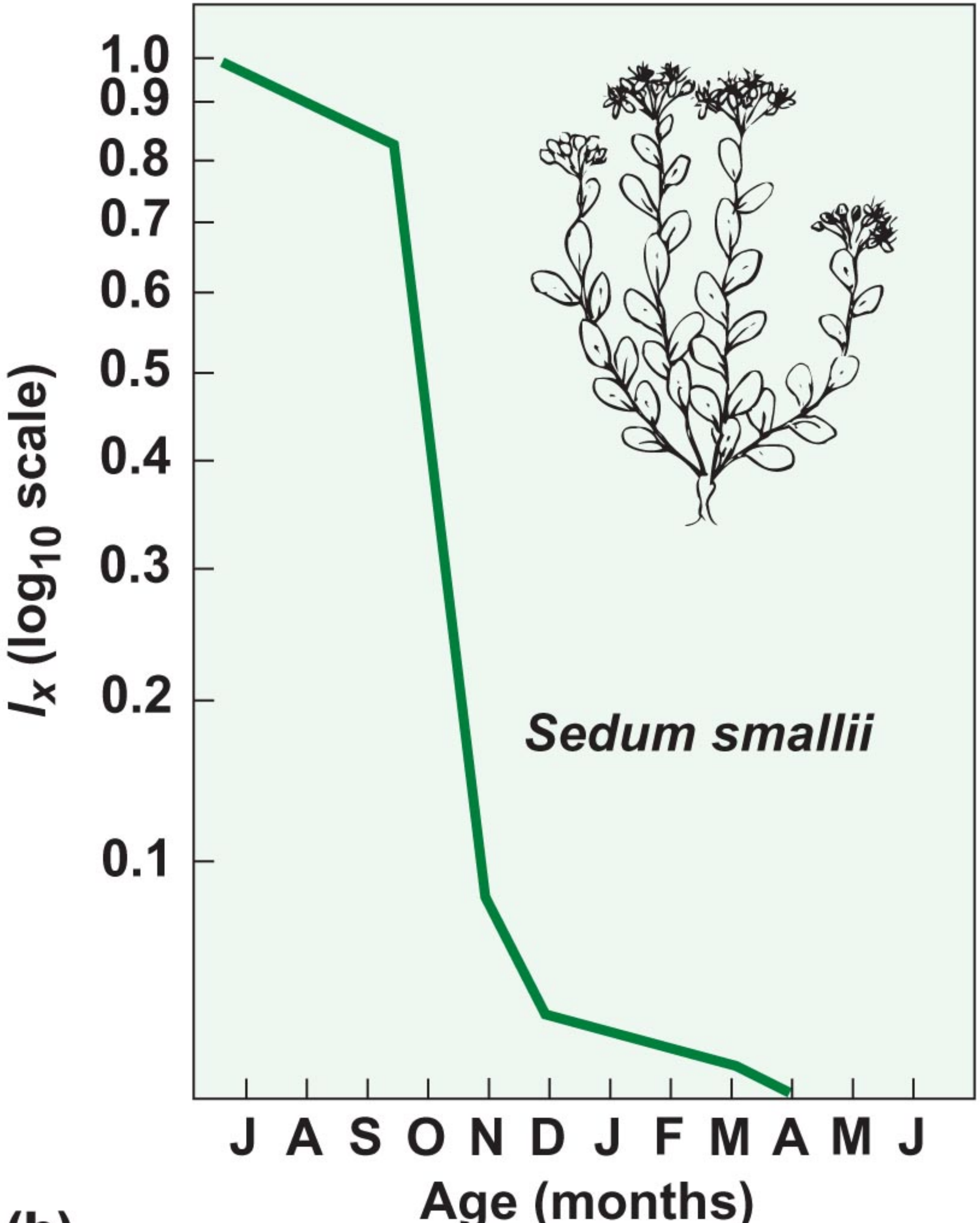


1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Mortality rate (q_x)
Establishment
Maturity
Germination
Rosette
Seed
J A S O N D J F M A M J J
Age (months)

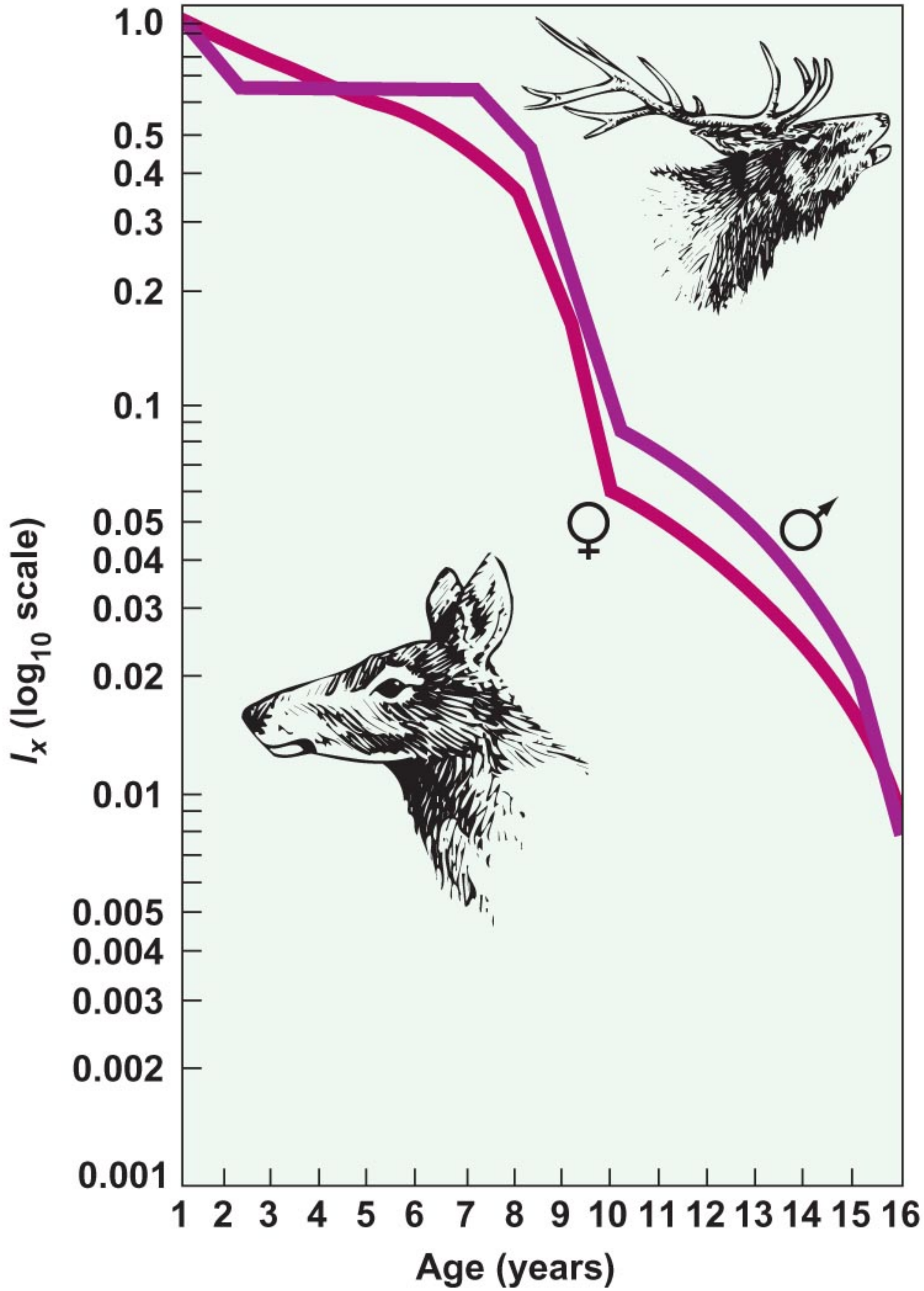
(b)



(a)


1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
l_x ($\log_{10}$ scale)
Sedum smallii
J A S O N D J F M A M J
Age (months)

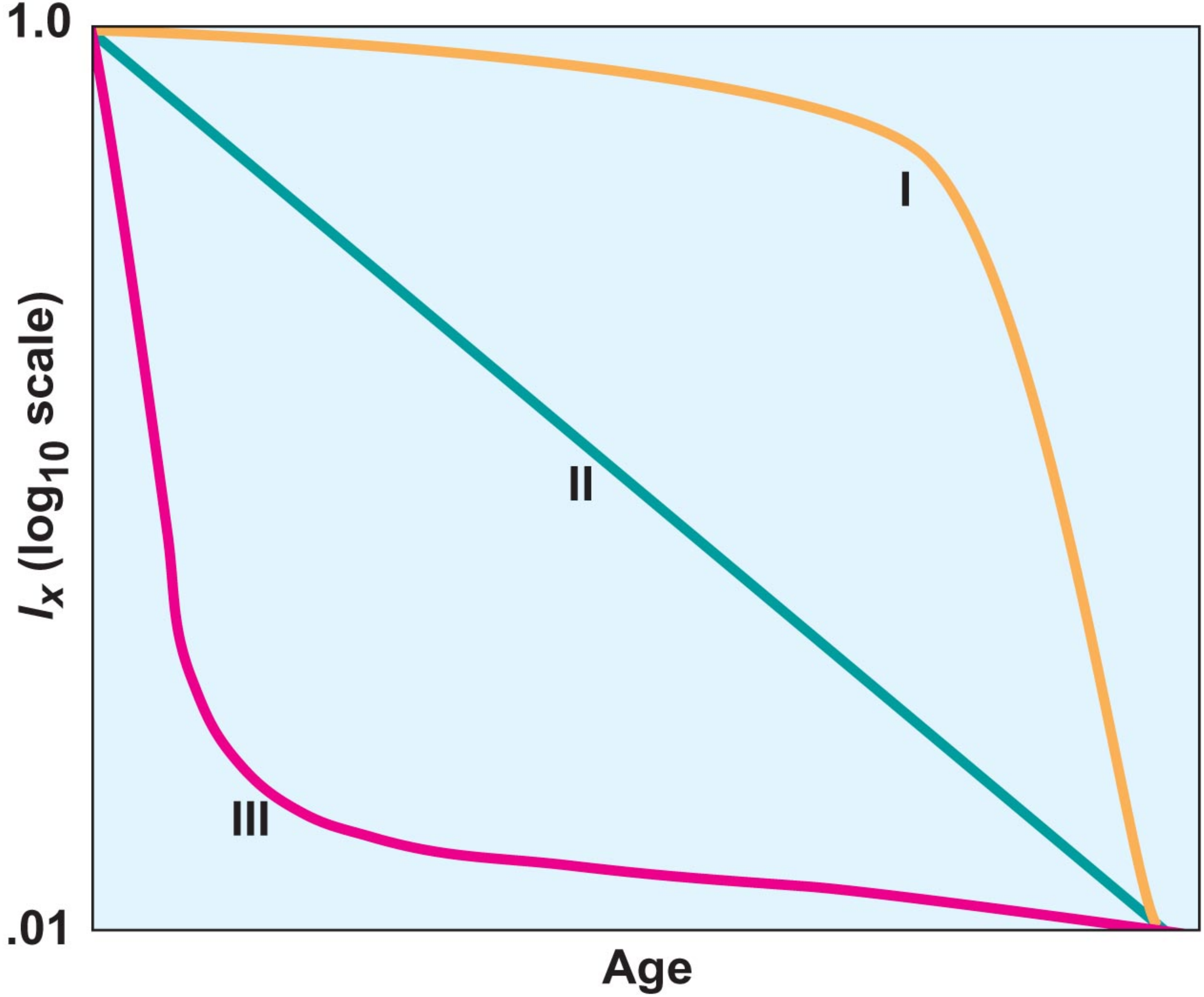
(b)



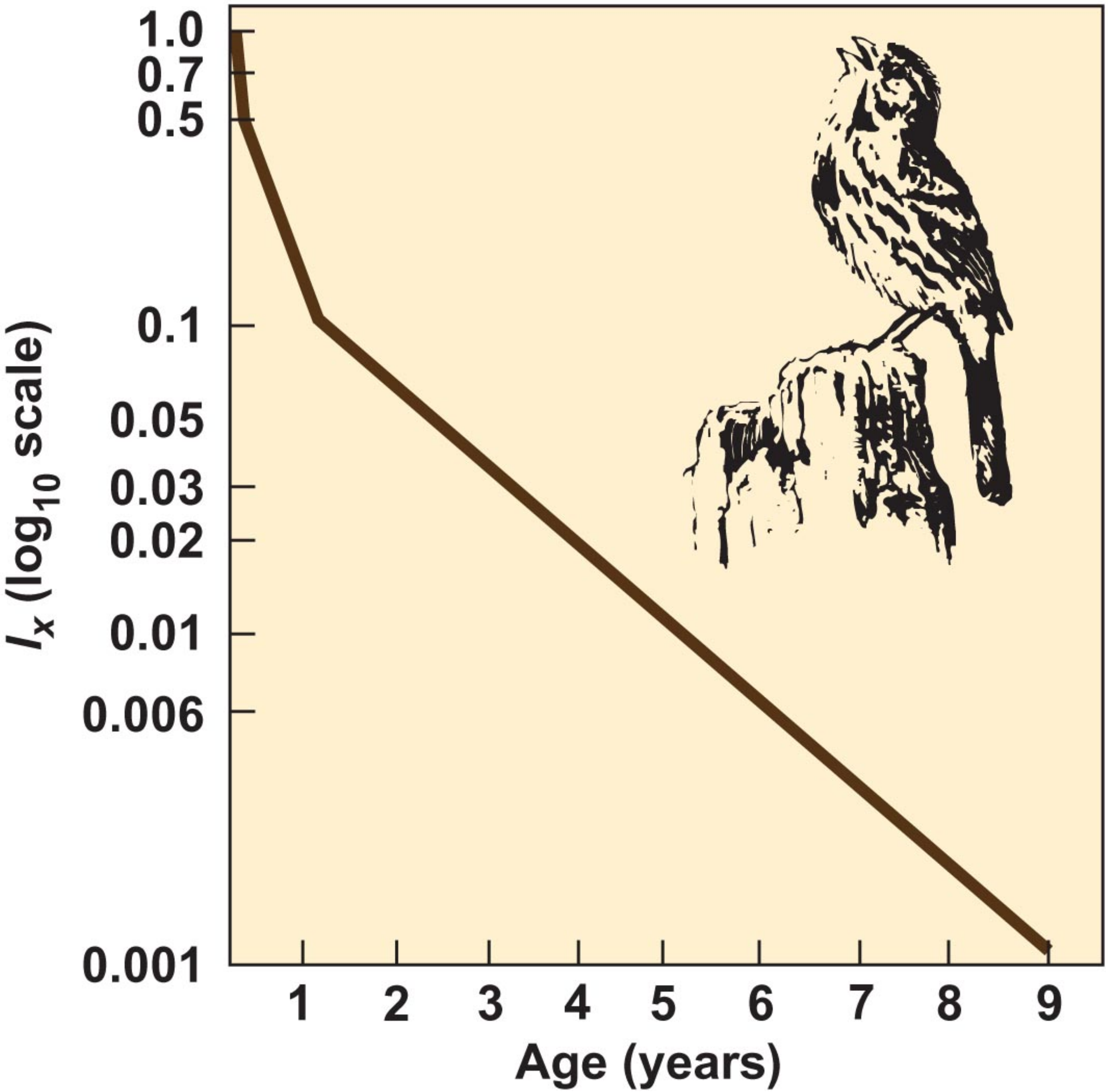
1.0
0.5
0.4
0.3
0.2
0.1
0.05
0.04
0.03
0.02
0.01
0.005
0.004
0.003
0.002
0.001
l_x ($\log_{10}$ scale)
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
Age (years)
♀
♂

10.4 Life Tables Provide Data for Mortality and Survivorship Curves

- There are three *idealized* types of survivorship curves
  - **Type I**: typical of populations in which individuals have long life spans, survival rate is high throughout the life span with heavy mortality at the end
    - Humans, other mammals, some plants
  - **Type II**: survival rates do not vary with age
    - Adult birds, rodents, reptiles, perennial plants
  - **Type III**: mortality rates are extremely high in early life
    - Fish, many invertebrates, and plants



1.0
.01
l_x (log$_{10}$ scale)
Age
I
II
III



1.0
0.7
0.5
0.1
0.05
0.03
0.02
0.01
0.006
0.001
l_x ($\log_{10}$ scale)
1
2
3
4
5
6
7
8
9
Age (years)

10.5 Birthrate is Age-Specific

- The **crude birthrate** is expressed as births per 1000 population per unit time
  - Only females give birth
  - Birthrate of females generally varies with age
- Birthrate is better expressed as the number of births per female of age x

10.5 Birthrate is Age-Specific

- b_x = mean number of females born to a female in each age group
  - Continuing with the gray squirrel example
- Σ = **gross reproductive rate** = the average number of female offspring born to a female over her lifetime

x	b_x
0	0
1	2
2	3
3	3
4	2
5	0
Σ	10

10.6 Birthrate and Survivorship Determine Net Reproductive Rate

- A **fecundity table** combines the survivorship (l_x) with the age-specific birthrates (b_x)
- $\boldsymbol{l_x b_x}$ = mean number of females born in each age group, adjusted for survivorship

10.6 Birthrate and Survivorship Determine Net Reproductive Rate

- ***R_0*** = **net reproductive rate** = the average number of females that will be produced during a lifetime by a newborn female

Table 10.4 | Gray Squirrel Fecundity Table

x	l_x	b_x	$l_x b_x$
0	1.0	0.0	0.00
1	0.3	2.0	0.60
2	0.15	3.0	0.45
3	0.09	3.0	0.27
4	0.04	2.0	0.08
5	0.01	0.0	0.00
Σ		10.0	1.40

10.6 Birthrate and Survivorship Determine Net Reproductive Rate

- $R_0 = 1$; on average, females will replace themselves in the population
- $R_0 < 1$; females are not replacing themselves in the population
- $R_0 > 1$; females are more than replacing themselves in the population

10.7 Age-Specific Mortality and Birthrates Can Be Used to Project Population Growth

- For simplicity, age-specific mortality (q_x) is converted to **age-specific survival** ($\boldsymbol{s_x}$)
  - $s_x = 1 - q_x$
- A **population projection table** can be constructed using s_x and b_x

Table 10.5 | Age-Specific Survival and Birthrates for Squirrel Population

x	l_x	q_x	s_x	b_x
0	1.0	0.7	0.3	0.0
1	0.3	0.5	0.5	2.0
2	0.15	0.4	0.6	3.0
3	0.09	0.55	0.45	3.0
4	0.04	0.75	0.25	2.0
5	0.01	1.0	0.0	0.0

10.7 Age-Specific Mortality and Birthrates Can Be Used to Project Population Growth

- We will use the life and fecundity table values of the gray squirrel to illustrate a hypothetical population of squirrels introduced into an unoccupied forest
- Females are only used to construct the **population projection table**

10.7 Age-Specific Mortality and Birthrates Can Be Used to Project Population Growth

- Initial population size
  - x_0 = 20 individuals of age 0
  - x_1 = 10 adults of age 1

Number of individuals in each age class (x) at year 0

x	b_x	s_x
0	0.0	0.30
1	2.0	0.50
2	3.0	0.60
3	3.0	0.45
4	2.0	0.25
5	0.0	0.00

	Year 0	Year 1
	20	27
	10	6
		5
Total	30	38

$$= (b_1 \times 6) + (b_2 \times 5)$$
$$= (2.0 \times 6) + (3.0 \times 5)$$
$$= 12 + 15 = 27$$

$$= 20 \times s_0 = 20 \times 0.3 = 6$$

$$= 10 \times s_1 = 10 \times 0.5 = 5$$

10.7 Age-Specific Mortality and Birthrates Can Be Used to Project Population Growth

- Survivorship and fecundity are determined in a similar manner for each succeeding year

Table 10.6 | Population Projection Table, Squirrel Population

	Year (t)										
Age	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
0	20	27	34.1	40.71	48.21	58.37	70.31	84.8	101.86	122.88	148.06
1	10	6	8.1	10.23	12.05	14.46	17.51	21.0	25.44	30.56	36.86
2	0	5	3.0	4.05	5.1	6.03	7.23	8.7	10.50	12.72	15.28
3	0	0	3.0	1.8	2.43	3.06	3.62	4.4	5.22	6.30	7.63
4	0	0	0	1.35	0.81	1.09	1.38	1.6	1.94	2.35	2.83
5	0	0	0	0	0.33	0.20	0.27	0.35	0.40	0.49	0.59
Total $N(t)$	30	38	48.2	58.14	68.93	83.21	100.32	120.85	145.36	175.30	211.25
Lambda	λ	1.27	1.27	1.21	1.19	1.21	1.20	1.20	1.20	1.20	1.20

10.7 Age-Specific Mortality and Birthrates Can Be Used to Project Population Growth

- An **age distribution** for each successive year can be calculated from a population projection table
  - Age distribution is the proportion of individuals in the various age classes for any one year
- A **stable age distribution** is attained when the proportions of each age group in the population remain the same year after year (even though $N(t)$ increases)

Table 10.7 | Approximation of Stable Age Distribution, Squirrel Population

Age	Proportion in Each Age Class for Year										
	0	1	2	3	4	5	6	7	8	9	10
0	.67	.71	.71	.71	.69	.70	.70	.70	.70	.70	.70
1	.33	.16	.17	.17	.20	.17	.17	.18	.18	.18	.18
2		.13	.06	.07	.06	.07	.07	.07	.07	.07	.07
3			.06	.03	.03	.04	.04	.03	.03	.03	.03
4				.02	.01	.01	.01	.01	.01	.01	.01
5					.01	.01	.01	.01	.01	.01	.01

10.7 Age-Specific Mortality and Birthrates Can Be Used to Project Population Growth

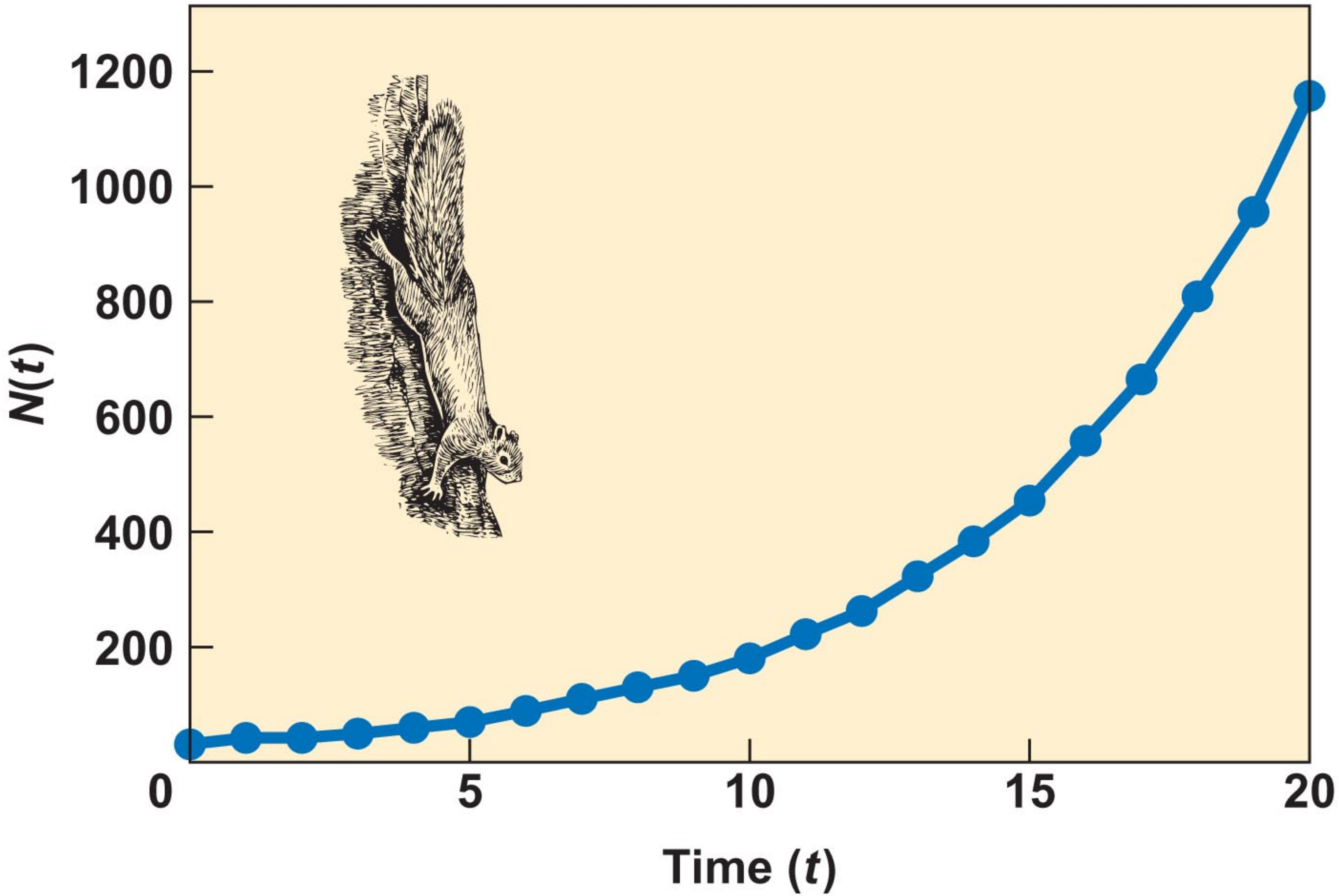
- An estimate of population growth can be derived from a population projection table
- λ = **finite multiplication rate** = $N(t + 1)/N(t)$
  - Once the population reaches a stable age distribution, the value of λ remains constant
- λ **>** 1.0 indicates a population that is growing
- λ **<** 1.0 indicates a population in decline
- λ **=** 1.0 indicates a stable population size through time

10.7 Age-Specific Mortality and Birthrates Can Be Used to Project Population Growth

- The population projection table demonstrates two concepts of population growth
  - λ (estimated population growth rate) is a function of s_x and b_x
  - The constant rate of population increase from year to year and the stable age distribution are results of s_x and b_x that are constant through time

10.7 Age-Specific Mortality and Birthrates Can Be Used to Project Population Growth

- If λ does *not* vary (under conditions of stable age distribution), population size in the future can be projected
  - $N(t) = N(0)\,\lambda t$
    - Describes a pattern of population growth similar to the exponential growth model


N(t)
1200
1000
800
600
400
200
0
5
10
15
20
Time (t)

10.7 Age-Specific Mortality and Birthrates Can Be Used to Project Population Growth

- **Geometric population growth =** $N(t) = N(0)\lambda^{t}$
  - Finite
- **Exponential population growth** = $N(t)$ **=** $N(0)e^{rt}$
  - Continuous
- $\lambda = e^{r}$ **or** $r = \ln\lambda$

10.8 Stochastic Processes Can Influence Population Dynamics

- Population dynamics represent the combined outcome of many individual probabilities
  - Age-specific survival rates (s_x) represent the **probability** that a female of that age will survive to the next age class
- This reality has led ecologists to develop probabilistic or stochastic models of population growth to account for these variations

10.8 Stochastic Processes Can Influence Population Dynamics

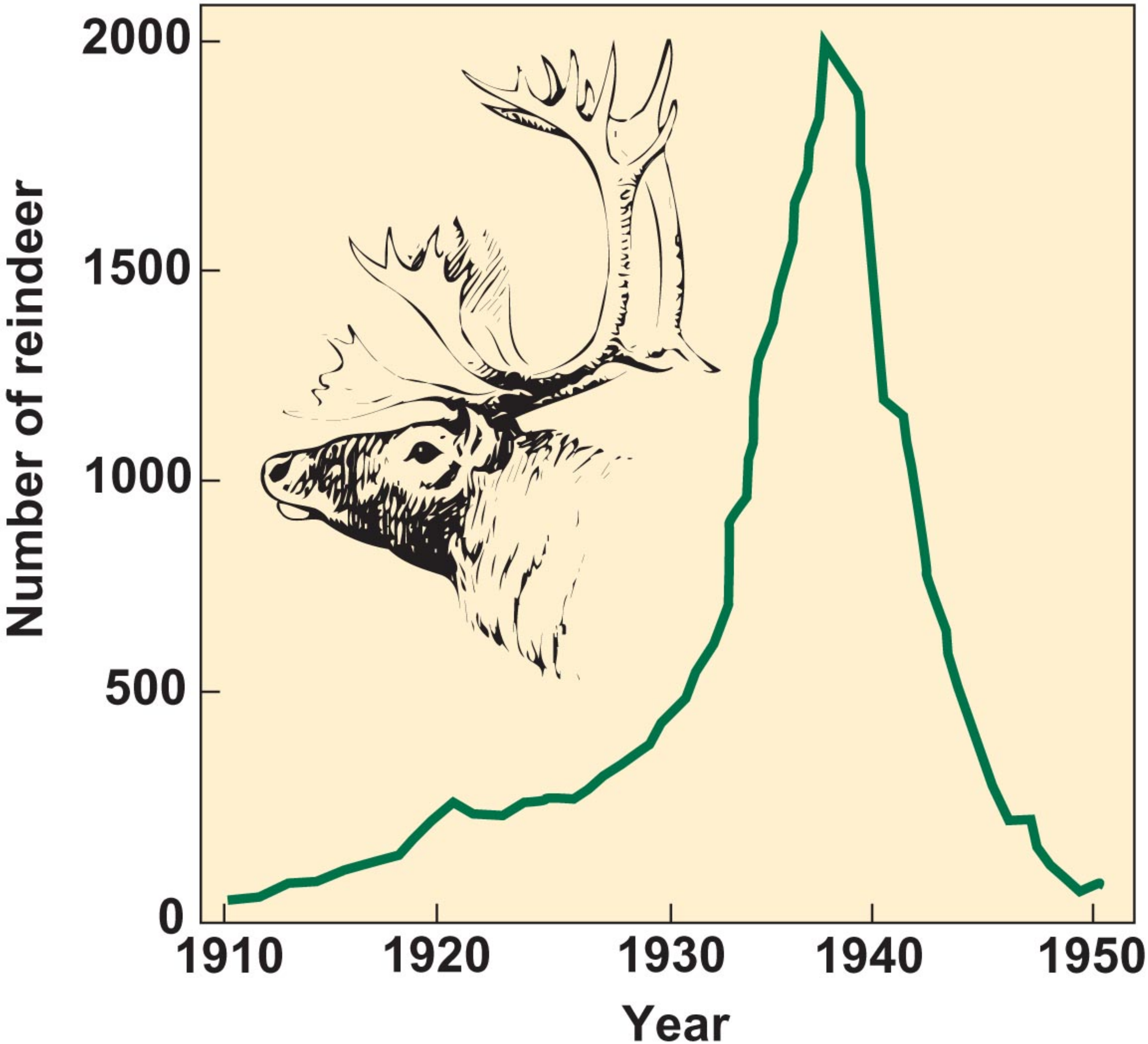
- **Demographic stochasticity** is the random (stochastic) variations in birth and death rates from year to year
  - The variations in *d* and *b* cause populations to deviate from the predictions based on deterministic models
- **Environmental stochasticity** is the random variations in the environment or the occurrence of natural disasters
  - These events directly influence *d* and *b*

10.9 A Variety of Factors Can Lead to Population Extinction

- Under the following conditions, a population can become so small that it declines toward extinction:
  - When deaths exceed births, populations decline
  - R_0 becomes less than 1.0
  - r becomes negative

10.9 A Variety of Factors Can Lead to Population Extinction

- Under the following conditions, a population can become so small that it declines toward extinction:
  - Extreme environmental events
  - Severe shortage of resources


2000
1500
1000
500
0
Number of reindeer
1910
1920
1930
1940
1950
Year

10.9 A Variety of Factors Can Lead to Population Extinction

- Under the following conditions, a population can become so small that it declines toward extinction:
  - Introduction of a novel predator, competitor, or parasite (disease)
  - Habitat loss (due to human activities)
  - Small population size

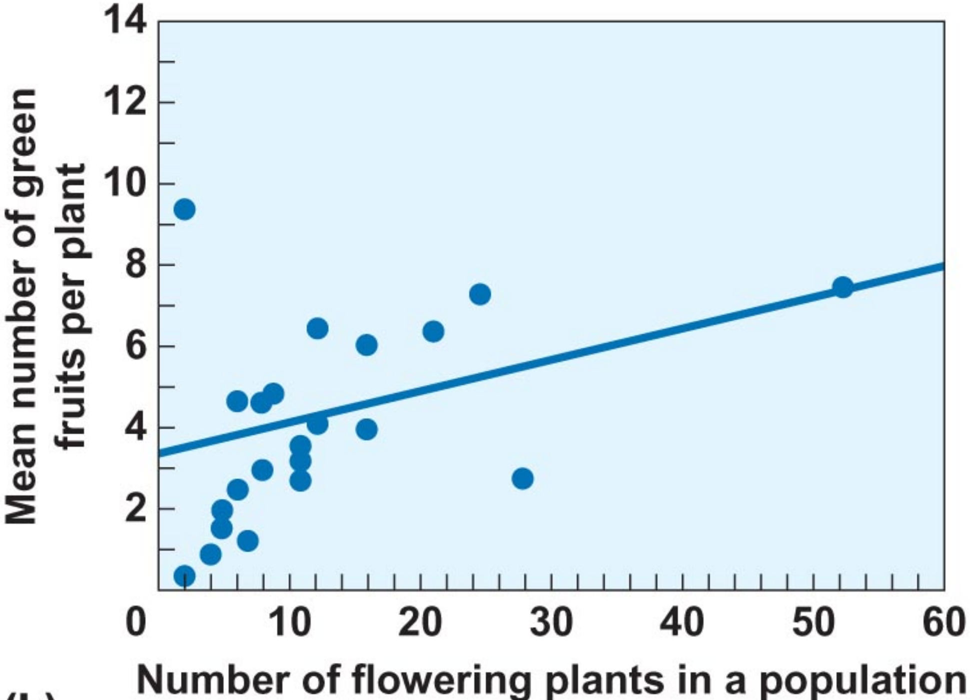
10.10 Small Populations Are Susceptible to Extinction

- Small populations are more susceptible to both demographic and environmental stochasticity
- When only a few individuals make up a population, the fate of each individual can be crucial to population survival
  - Over large territories, it can be impossible to find a mate (large cats)
  - Chemical signals will not be intercepted (insects)
  - Pollination is unlikely (plants)

10.10 Small Populations Are Susceptible to Extinction

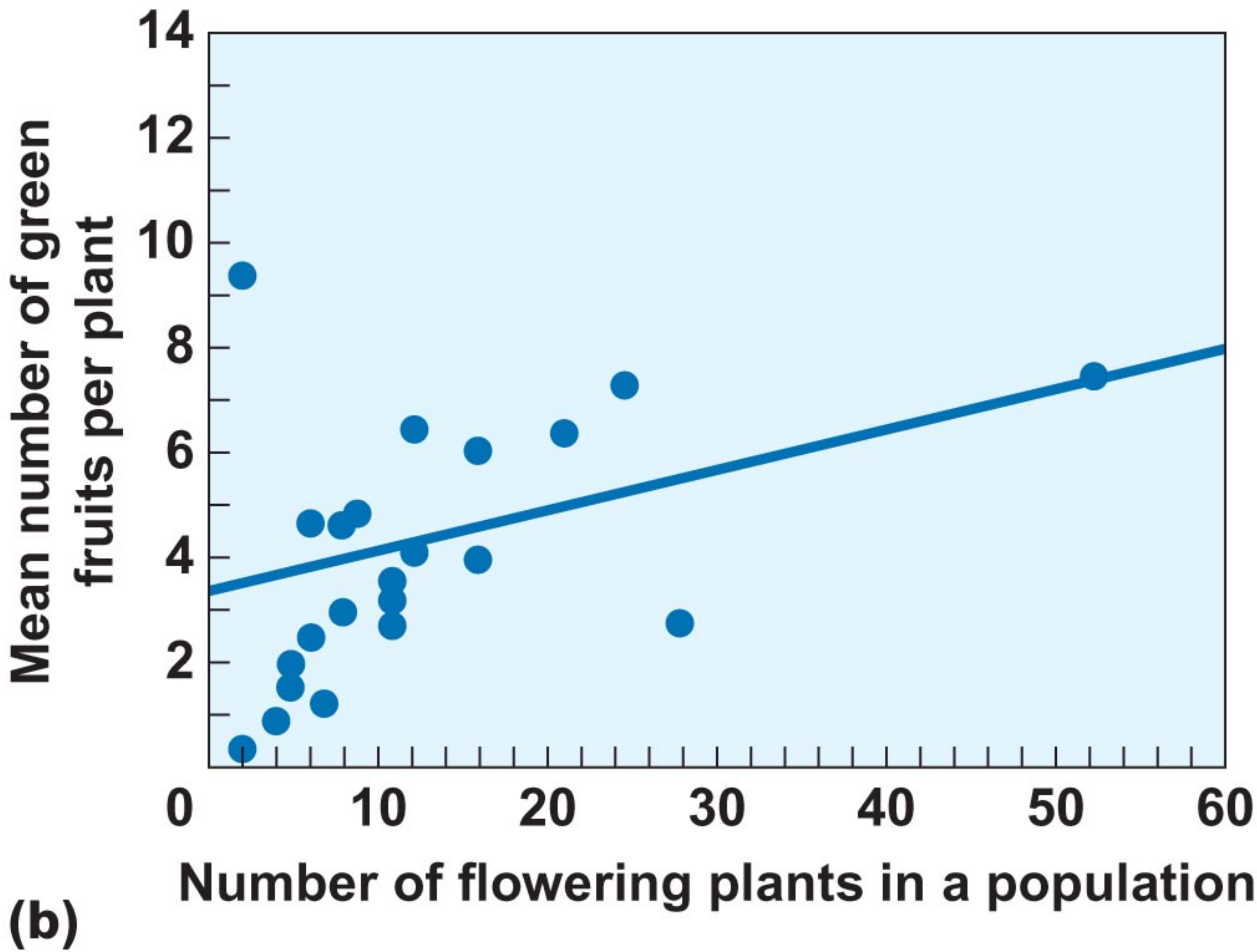
- Hackney and McGraw (West Virginia University) examined the reproductive limitations by small population size on American ginseng (*Panax quinquefolius*)
  - Fruit production per plant declined with decreasing population size due to reduced visitation by pollination

(a)


Mean number of green fruits per plant
0
2
4
6
8
10
12
14
10
20
30
40
50
60
Number of flowering plants in a population

(b)

(a)


14
12
10
8
6
4
2
0
10
20
30
40
50
60
Mean number of green fruits per plant
Number of flowering plants in a population
(b)

10.10 Small Populations Are Susceptible to Extinction

- Small population size may result in the breakdown of social structures that are integral to successful cooperative behaviors (mating, foraging, defense)
- The **Allee effect** is the decline in reproduction or survival under conditions of low population density
- There is less genetic variation in a small population and this may affect the population's ability to adapt to environmental change