ESRM 350

Demography and Population Growth

Autumn 2016

“The amazing herds of buffaloes which resort thither, by their size and number, fill the traveller with amazement and terror”

- John Filson (author and historian of Kentucky), 1784

Wildlife Demography

- The study of wildlife populations
- Involves
  (1) Description of population characteristics (last time)
  (2) Exploration of determinants of population size
  (3) Use of mathematical techniques to predict (model) growth of populations
- First, **determinants of population size**…

Drivers of Population Size

Reproduction, births, natality (B)

↓

Immigration (I) → Population → Emigration (E)

↓

Mortality, death (D)

"BIDE"

Population Growth

- Populations increase in proportion to their size
- e.g., at a 10% annual rate if increase
  - a population of 100 adds 10 individuals in one year
  - A population of 1000 adds 100 individuals in one year
- Allowed to grow unchecked, populations growing at a constant rate will rapidly approach infinity
- Process known as…

Exponential Population Growth

- There are **two** kinds of exponential population growth
  - Correspond to differences in life history

(1) Continuous exponential growth
  - Individuals added to population without interruption

(2) Discrete exponential growth (aka “geometric growth”)
  - Individuals added to population in pulses (non-overlapping generations)

Exponential Growth

Building from first principles*

- Let N_t = size of a population at some time t
- Size of population at some future time t + 1, or N_{t+1} is a function of
  - number of new individuals **added** to population, births (B) + immigrants (I)
  - number of individuals **subtracted** from population, deaths (D) + emigrants (E)

$$N_{t+1} = N_t + B - D + I - E$$

*Gotelli, N.J. (1998) *A Primer of Ecology*

Exponential Growth

<u>In a closed population</u>

- i.e., no immigration and emigration

$$N_{t+1} = N_t + \mathrm{B} - \mathrm{D}$$

or…

$$\Delta N = \mathrm{B} - \mathrm{D}$$

Continuous Exponential Growth

When population growth is continuous…

- i.e., time step between t and $t + 1$ infinitely small (no pause in growth)
- Growth, ΔN, modeled as the change in population size (dN) that occurs over very small interval of time (dt)

$$dN/dt = B - D$$

*Continuous differential equation
expressing growth as an instantaneous **rate***

Continuous Exponential Growth

$$dN/dt = B - D$$

- Because this is a continuous differential equation (growth rate)…
- …B and D are now instantaneous values (rates) as well
- We calculate them as follows

$$B = bN$$

  - where *b* is the instantaneous (per capita) birth rate

$$D = dN$$

  - where d is the instantaneous (per capita) death rate

Continuous Exponential Growth

- Thus…

$$dN/dt = bN - dN$$

or, rearranging terms,

$$dN/dt = (b - d)N$$

- $b - d = r$, or the instantaneous (per capita) rate of increase, so…

Continuous Exponential Growth

$$dN/dt = rN$$

Two implications of this equation

Population growth rate (dN/dt) proportional to r

- r (i.e., $b - d$) > 0 : increase
- r = 0 : no change
- r < 0 : decrease

Population growth rate (dN/dt) proportional to N

- Larger the population, faster the rate of change

Modeling Population Size

$$dN/dt = rN$$

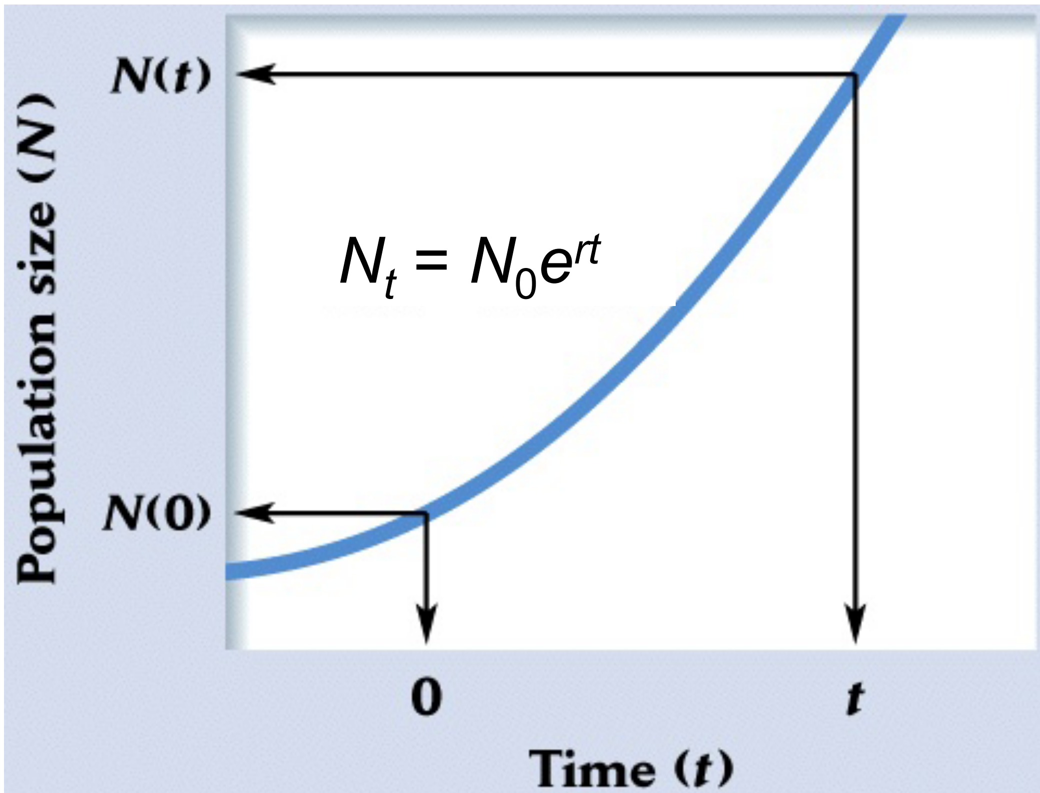
- So, if we know r and N, we can describe the growth rate of a population

  To predict its size at some point in the future, we use the equation

$$N_t = N_0 e^{rt}$$

  where
  - N_t = number of individuals after t time units
  - N_0 = initial population size
  - e = base of the natural logarithms (about 2.72)
  - r = per capita rate of increase

The Exponential Growth Curve



- A population exhibiting continuous exponential growth has a smooth curve of population increase as a function of time

Exponential Population Growth

- There are **two** kinds of exponential population growth
  - Correspond to differences in life history

(1) Continuous exponential growth
  - Individuals added to population without interruption

(2) Discrete exponential growth (aka "geometric growth")
  - Individuals added to population in pulses (non-overlapping generations)

Discrete Exponential Growth

When generations do not overlap…

- Population growth described by the discrete difference equation

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

where

- N_{t+1} = number of individuals after 1 time unit
- N_t = initial population size
- λ = finite (geometric) rate of increase (ratio of future to current population size; N_{t+1}/N_t)

Discrete Exponential Growth

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

Recursive equation

– "output" for one time interval becomes "input" for next time interval

General solution after t time intervals is

$$N_t = \lambda^t(N_0)$$

i.e., the original population size (N_0) is multiplied by the finite rate of increase (λ) for the appropriate number of time intervals, t

Discrete Exponential Growth

e.g., for a population growing at a finite rate of 50% per year ($\lambda = N_{t+1}/\mathrm{N}_t = 1.50$)

an initial population (N_0) of 100 individuals would grow to 5,767 after 10 years

i.e., $N_{10\ \mathrm{years}} = N_0\lambda^{10} = 100(1.5^{10}) = 5{,}767$

λ and *r*

The finite rate of increase (λ) is equivalent to the instantaneous rate of increase (r) when

- the time step between t and t+1 is infinitely small
- if we know one we can convert to the other

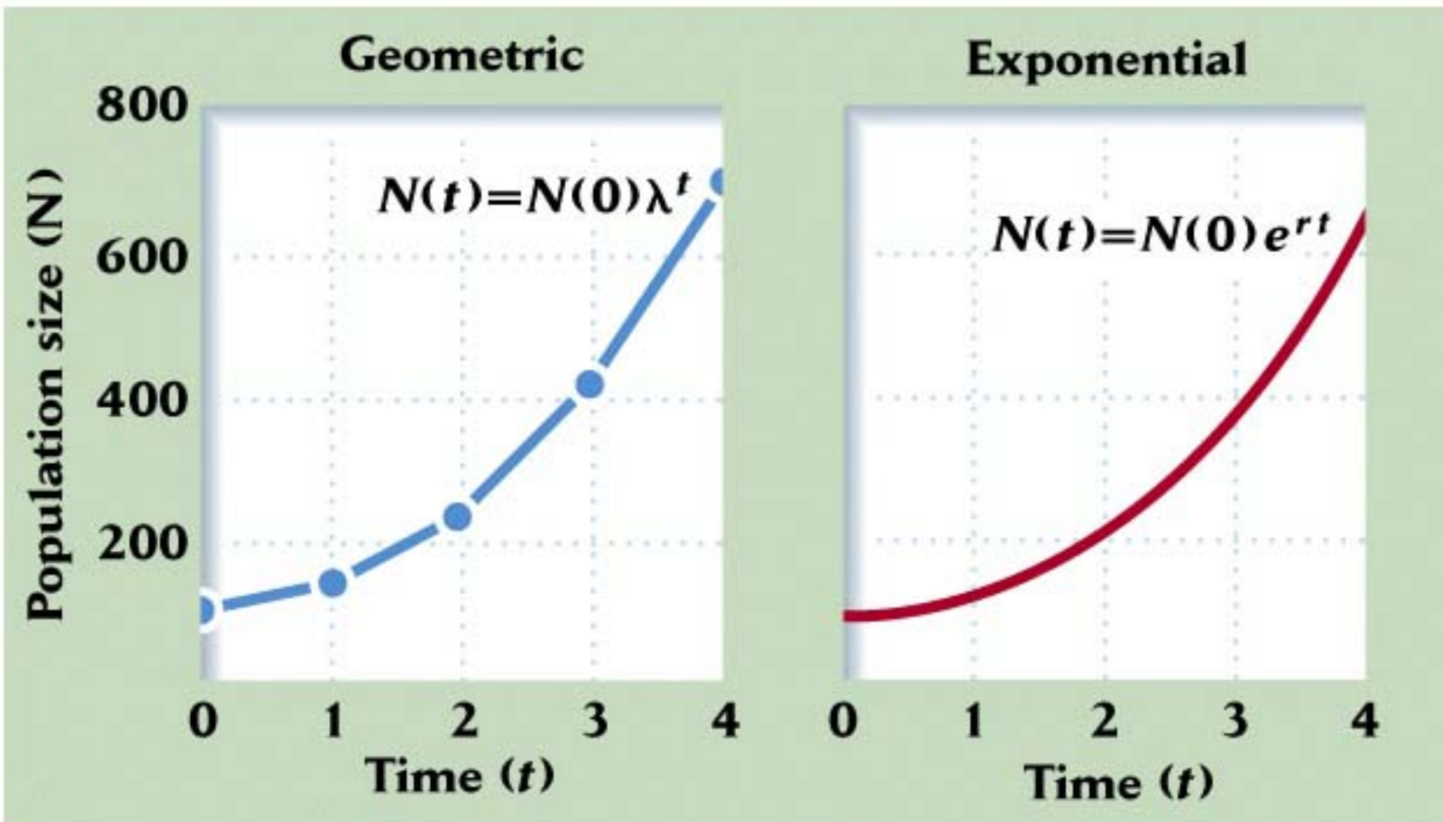
$$\lambda = e^r$$

or

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

λ and *r*

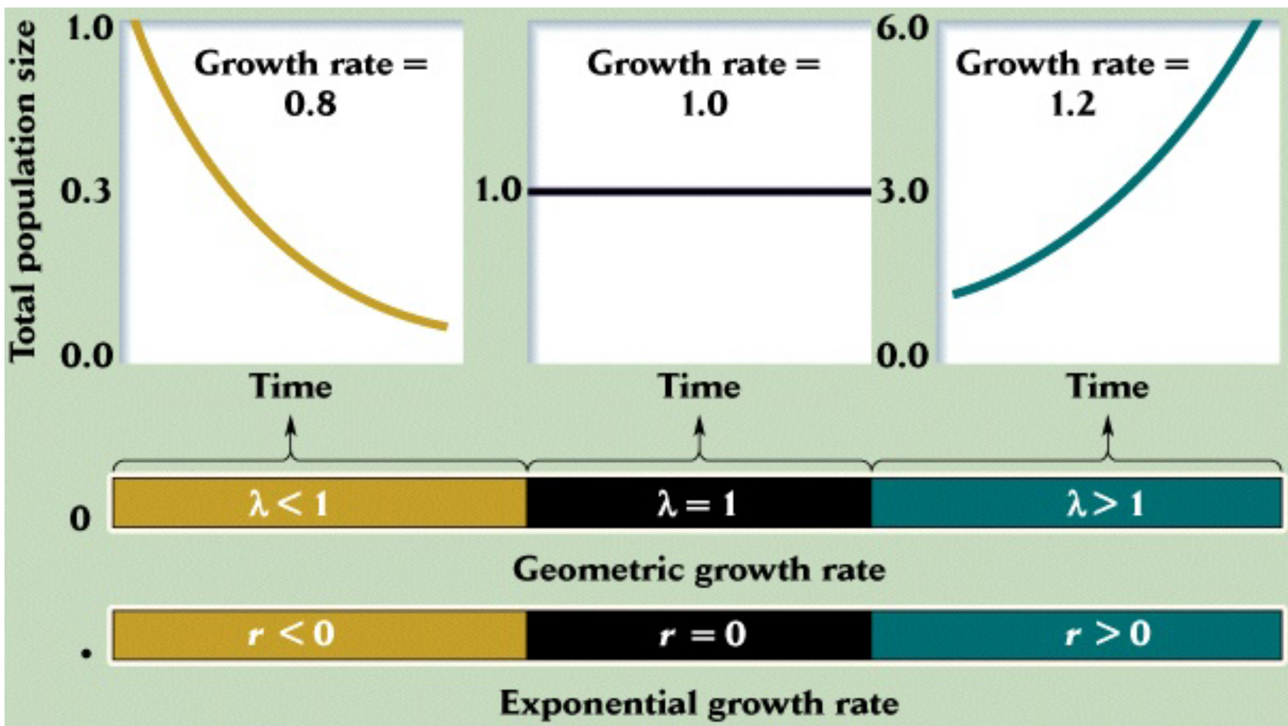
$\lambda = 1.6$ $\quad$ $r = \ln(\lambda) = 0.47$



λ and *r*

A population is

- growing when $\lambda > 1$ or $r > 0$
- constant when $\lambda = 1$ or $r = 0$
- declining when $\lambda < 1$ (but > 0) or $r < 0$



Exponential Growth Model: a Cornerstone of Population Biology

- All populations have *potential* for exponential growth
  - Exponential models valuable because they recognize the multiplicative nature of population growth (positive feedback yields accelerating growth)

- Realistically describes growth of many populations in the short term
  - i.e., resources are often *temporarily* unlimited (pest outbreaks, weed invasions, humans)

Two Key Assumptions

- No size or age structure
  - no differences in *b* and *d* among individuals due to age or body size (next)
- Constant *b* and *d* over time
  - Unlimited space, food, other resources required (a bit later)

Age-Structured Population Growth

- For most animals, birth and death rates a function of age
  - e.g., elephant takes decade to reach sexual maturity
  - old individuals more susceptible to predation, parasitism, disease
- Thus, age structure affects population growth
  - cannot assume same *r* for populations with different age structures
  - e.g., populations dominated by juveniles will growth less rapidly than population dominated by reproductively mature adults
- How do we model the growth of age-structured populations?

Life Tables

- **Life Tables:** age-specific schedules of survival and fecundity that enable us to project a population's size and age structure into the future

Table 14.1 Life table for a hypothetical population of 100 individuals

Age (x)	Survival (s_x)	Fecundity (b_x)	Number of individuals (n_x)
0 (newborns)	0.5	0	20
1	0.8	1	10
2	0.5	3	40
3	0.0	2	30

Life Table Calculations (1 Gen)

Table 14.2 Steps in the projection of a population through one time period of survival and reproduction. Each age class becomes one time unit older from one breeding season to the next.

Age	(1) Census of population just after reproduction ($t = 0$)	(2) Survival rate of individuals (s_x) (Table 14.1)	(3) Number surviving to next breeding season (1) × (2)	(4) Number of offspring per adult (b_x) (Table 14.1)	(5) Total number of offspring produced (3) × (4)	(6) Census of population just after reproduction ($t = 1$) (3) and sum of (5)
0	20	0.5		0		74
1	10	0.8	10	1	10	10
2	40	0.5	8	3	24	8
3	30	0.0	20	2	40	20
4	0		0			0
Total	100		38		74	112

Life Table Calculations (Many Generations)

Table 14.3 Projection of age distribution and total size through time for the hypothetical population described in Table 14.1

	Time Interval									
	0	1	2	3	4	5	6	7	8	Percent
n_0	20	74	69	132	175	274	399	599	889	63.4
n_1	10	10	37	34	61	87	137	199	299	21.3
n_2	40	8	8	30	28	53	70	110	160	11.4
n_3	30	20	4	4	15	14	26	35	55	3.9
N	100	112	118	200	279	428	632	943	1,403	100
λ^*	1.12	1.05	1.69	1.40	1.53	1.48	1.49	1.49		

Note: *The population was projected by multiplying the number of individuals in each age class by the survival to obtain the number in the next older age class in the next time period:* $n_x(t) = n_{x-1}(t-1)s_x$. *Then the number of individuals in each age class was multiplied by its fecundity to obtain the number of newborns:* $n_0(t) = \Sigma n_x(t)b_x$.

Stable Age Distribution

- Proportion of each age class in population does not change (thus the “stable” part)
- Occurs when a population grows with constant schedules of survival and fecundity
- Under a stable age distribution:
  - all age classes grow or decline at the same rate, λ
  - the population also grows or declines at this constant rate, λ

Life Table Breakdown

- Summarize demographic information (typically for females) in a convenient format, including:
  - age (x)

Table 14.4 Life table of the grass *Poa annua*

Age (x)*	Number alive	Survivorship (l_x)	Mortality rate (m_x)	Survival rate (s_x)	Fecundity (b_x)
0	843	1.000	0.143	0.857	0
1	722	0.857	0.271	0.729	300
2	527	0.625	0.400	0.600	620
3	316	0.375	0.544	0.456	430
4	144	0.171	0.626	0.374	210
5	54	0.064	0.722	0.278	60
6	15	0.018	0.800	0.200	30
7	3	0.004	1.000	0.000	31
8	0	0.000			

*Number of 3-month periods; in other words, 3 = 9 months.

Source: *M. Begon and M. Mortimer,* Population Ecology, *2d ed., Blackwell Scientific Publications, Oxford (1986). After data of R. Law.*

Summary of life-table variables

l_x Survival of newborn individuals to age x	m_x Proportion of individuals of age x dying by age $x + 1$
b_x Fecundity at age x	s_x Proportion of individuals of age x surviving to age $x + 1$

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- Summarize demographic information (typically for females) in a convenient format, including:
  - age (x)
  - number alive
  - survivorship (l_x): $l_x = s_0 s_1 s_2 s_3 \ldots s_{x-1}$ (multiply survival probabilities at each age); this is the probability of surviving from birth to age x

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Life Table Breakdown

- Summarize demographic information (typically for females) in a convenient format, including:
  - age (x)
  - number alive
  - survivorship
  - mortality rate (m_x) probability an individual dies before reaching age $x + 1$

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  - number alive
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  - mortality rate (m_x)
  - survival rate (s_x) probability of surviving from x to $x+1$

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  - age (x)
  - number alive
  - survivorship (l_x)
  - mortality rate (m_x)
  - survival rate (s_x)
  - Fecundity (b_x)
    - *in a life table, this is the number of **female offspring** per **female (why?)***

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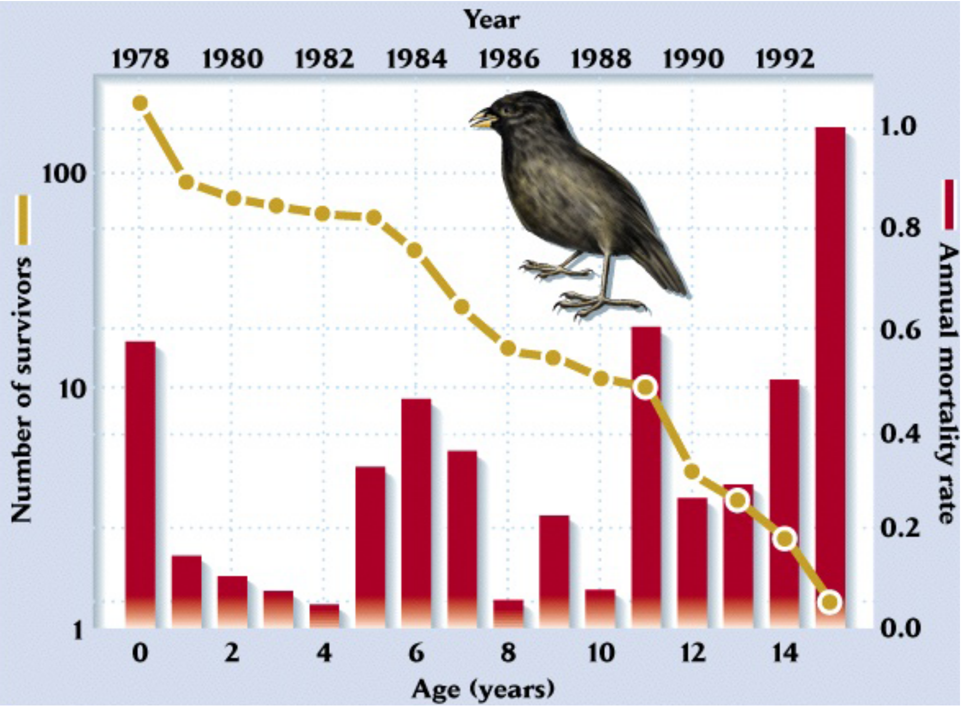
Building Life Tables

- **Cohort life tables** are based on data collected from a group of individuals born at the same time and followed throughout their lives
  - difficult to apply to mobile and/or long-lived animals (another pitfall?)



Building Life Tables

- **Static life tables** consider survival of individuals of known age during a single time interval
  - Remove confounds of yearly variation in the environment (assumes year is representative)
  - require some means of determining ages of individuals
  - e.g., Murie (1944) Dall sheep, determined age by horn growth
  - survivorship determined through carcasses

Table 14.5 **Life table for Dall mountain sheep constructed from the age at death of 608 sheep in Denali National Park**

Age interval (years)	Number dying during age interval	Number surviving at beginning of age interval	Number surviving as a fraction of newborns (l_x)
0–1	121	608	1.000
1–2	7	487	0.801
2–3	8	480	0.789
3–4	7	472	0.776
4–5	18	465	0.764
5–6	28	447	0.734
6–7	29	419	0.688
7–8	42	390	0.640
8–9	80	348	0.571
9–10	114	268	0.439
10–11	95	154	0.252
11–12	55	59	0.096
12–13	2	4	0.006
13–14	2	2	0.003
14–15	0	0	0.000

Source: *Based on data of O. Murie,* The Wolves of Mt. McKinley, *U.S. Department of the Interior, National Park Service, Fauna Series No. 5, Washington, D.C. (1944); quoted by E. S. Deevey, Jr.,* Quarterly Review of Biology *22:283–314 (1947).*

Calculating r From Life Tables

- The **intrinsic rate of increase** (r) can be approximated from a life table under assumption of a stable age distribution
- This process requires that we first compute R_0, the **net reproductive rate**, (sum of $l_x b_x$)
  - average # of female offspring produced per female per lifetime

Table 14.6 Estimation of the exponential rate of increase for the hypothetical population described in Table 14.1

x	s_x	l_x	b_x	$l_x b_x$	$x l_x b_x$
0	0.5	1.0	0	0.0	0.0
1	0.8	0.5	1	0.5	0.5
2	0.5	0.4	3	1.2	2.4
3	0.0	0.2	2	0.4	1.2
Net reproductive rate (R_0)				2.1	

Note: *The sums of the $l_x b_x$ column (net reproductive rate) and the $x l_x b_x$ column are used to estimate r_a according to the equation given in the text. In this case, we calculate r_a to be 0.38; this is equivalent to λ = 1.46, close to the observed value of about 1.49 after the population achieved a stable age distribution.*

Net Reproductive Rate (R_0)

- the expected total number of offspring of an individual over the course of her life span (remember we only count females)
  - $R_0 = 1$ represents the replacement rate
  - $R_0 < 1$ represents a declining population
  - $R_0 > 1$ represents an increasing population

Generation Time T

- The **generation time** (T) is the average age at which females produce offspring

$$T = \frac{\Sigma x l_x b_x}{\Sigma l_x b_x} = 4.1 / 2.1 = 1.95$$

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2	0.5	0.4	3	1.2	2.4
3	0.0	0.2	2	0.4	1.2
Net reproductive rate (R_0)				2.1	
Expected number of births weighted by age					4.1

Note: *The sums of the $l_x b_x$ column (net reproductive rate) and the $x l_x b_x$ column are used to estimate r_a according to the equation given in the text. In this case, we calculate r_a to be 0.38; this is equivalent to $\lambda = 1.46$, close to the observed value of about 1.49 after the population achieved a stable age distribution.*

Intrinsic Rate of Increase (*r*)

- Computation of r is based on R_0 and T as follows:

$$r = \log_e R_0 / T$$

The intrinsic rate of natural increase depends on both the net reproductive rate and the generation time such that:

  - large values of R_0 (high per capita female productivity) and small values of T (short time to reproductive readiness) lead to the most rapid population growth

Growth Potential of Wildlife Populations is High

- e.g., population growth of the ring-necked pheasant (*Phasianus colchicus*)
  - 8 individuals introduced to Protection Island, Washington, in 1937, increased to 1,325 adults in 5 years:
    - 166-fold increase
    - $r = 1.02$, $\lambda = 2.78$

And Yet…

- Despite potential for exponential increase, most populations remain at relatively stable levels
  - for population growth to be checked, a decrease in the birth rate or an increase in the death rate (or both) must occur as overall population size gets large
  - What causes these changes in birth and death rates?

Crowding

- As populations grow, crowding…
- Reduces access to food (other resources) for individuals and their offspring
- Aggravates social strife
- Promotes the spread of disease
- Attracts the attention of predators
- As a result, population growth slows and eventually halts
- Process known as **DENSITY DEPENDENCE**
  - decreasing growth with increasing pop size

The Logistic Growth Model

- Populations with density dependence (decreasing growth rate with increasing population size) modeled using the logistic growth equation
- Logistic model incorporates idea that populations tend to level off at **carrying capacity (K)**
- **K**: size at which no more individuals can be supported over long time periods

The Logistic Growth Equation

- The logistic equation takes the form

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

As N approaches K, growth rate approaches zero

- Where

  K is the carrying capacity

  r is the exponential growth rate

Logistic Growth Curve

- Graph of *N* versus time (*t*) for logistic growth features S-shaped curve (**sigmoid growth**)
  - Populations below *K* increase
  - Populations above *K* decrease
  - Populations at *K* remain constant
- Inflection point at *K*/2 separates **accelerating** and **decelerating** phases of growth