

Chapter 5

Demography



Figure 5.1 Great Blue Heron, with nestlings.

INTRODUCTION

Simple models for calculating population growth assume that all individuals in a group contribute equally to survival and reproduction of the population. Is this a reasonable assumption? Let's consider the exponential growth equation, first introduced in Chapter 4, and apply it to a rookery (or colonial nesting area) of Great Blue Herons (Figure 5.1).

The exponential growth equation states that the number of herons next year (N_{t+1}) will equal the current population size (N_t), plus the new recruits to the population, calculated as $N_t(r)$. This last term contains a questionable assumption, because new recruits are calculated by multiplying the **intrinsic rate of increase** (r) by every individual in the population, regardless of age, sex, or breeding condition. If heron populations always had the same composition, this would be a reasonable approach, because r is calibrated to reflect the reproductive potential of the average individual. However, it is easy to imagine that the composition of a heron population could change from year to year or

Exponential Growth Equation (Discrete Form)

$$N_{t+1} = N_t + N_t(r)$$

N_{t+1} = population size at the next time interval

N_t = population size at the current time

r = intrinsic rate of population increase

from place to place. Would a 400-bird population composed of 55% females build the same number of nests as a 400-bird population composed of 45% females? Would a population of young adult birds nesting for the first time enjoy the same breeding success as a population of more experienced parents? Ecologists attempting to make more accurate assessments of growth and survival of populations, particularly for species with longer lives and more complex life histories, have developed more accurate ways to track population characteristics such as age composition and sex ratio. Many, in fact, were adapted from mathematical techniques previously developed by insurance and pension analysts. This approach to the study of populations is called **demography**.

Check your progress:

If you were asked to project the birth rate for a human population of 1500 people on a small Pacific island having an average family size of 2.4 children, what additional information would be most helpful in making an accurate estimate?

Answer: Sex ratio and age structure are among the most important factors.

Survivorship

If we census the number of herons in the rookery this year, and ask how many will return to breed next year, we need to know probabilities of survival for each bird in the population. Since a bird's age is an important consideration in this calculation, we can simplify the task by grouping the birds according to age. As a first step, we can ask, what is the age-dependent probability of survival, or **survivorship schedule** for these birds? A survivorship schedule calculates year-to-year probabilities of survival throughout the life cycle, from birth or hatching, to fledging, maturation, and senescence.

Suppose we could place leg bands on a sample of 1000 nestling herons, and follow up with careful observation throughout their lives. We could keep records on the number that died and the number that survived each year. This sample of 1000 herons is called a **cohort**, defined as a subset of the population all of the same age. Cohort data can be used to calculate mortality and survival rates as shown in the following table, which is based on heron life history information from R. W. Butler (1992).

AGE IN YEARS x	NUMBER OF HERONS ALIVE AT BEGINNING OF YEAR n_x	DEATHS DURING THIS YEAR d_x	SURVIVAL RATE = (NUMBER ALIVE AT BEGINNING OF YEAR) / 1000 L_x
0	1000	690	1.000
1	310	112	0.310
2	198	44	0.198
3	155	34	0.155
4	121	27	0.121
5	94	21	0.094
6	73	16	0.073
7	57	13	0.057
8	45	10	0.045
9	35	8	0.035
10	27	6	0.027
11	21	5	0.021
12	17	4	0.017
13	13	3	0.013
14	10	2	0.010
15	8	2	0.008
16	6	1	0.006
17	5	5	0.005
18	0		0.000

In this table, each row represents a year in the life of our cohort of herons. We use x to represent the herons' age. Since n is the symbol used for a census count, we can designate n_x as the size of our cohort population at age x . Each year, the number dying during that year is subtracted from the population size to calculate the number alive in the following year. In mathematical terms, $n_x - d_x = n_{x+1}$. The proportion of the population still living at age x , designated as L_x , is calculated by dividing the number still alive by the original cohort of 1000. In mathematical terms, $L_x = n_x / 1000$. In survivorship tables, L_x values always begin with 1.000, representing 100% alive at the cohort's beginning, and end with a value of 0 when the last member of the cohort dies.

Check your progress:

If a cohort that began with 1000 newborns had 650 living members at age 5, and declined to 530 at age 6, what are d_x and L_x for age 5?

Answer: $d_x = 120$, and $L_x = 0.650$

What life history information can we derive from the heron survivorship table? The riskiest time of life for a Great Blue Heron is its first year, with 69% of the hatchlings failing to survive to age 1. The death rate falls to 36% in the second year, and then settles down to a constant 22% per year after that. A constant death rate is fairly typical of adult birds, since most mortality is due to accidents independent of the bird's age, such as getting caught in a storm or encountering a predator. To illustrate the pattern of survivorship, we can plot age in years on the x-axis, and numbers left alive per 1000 on the y-axis (Figure 5.2).

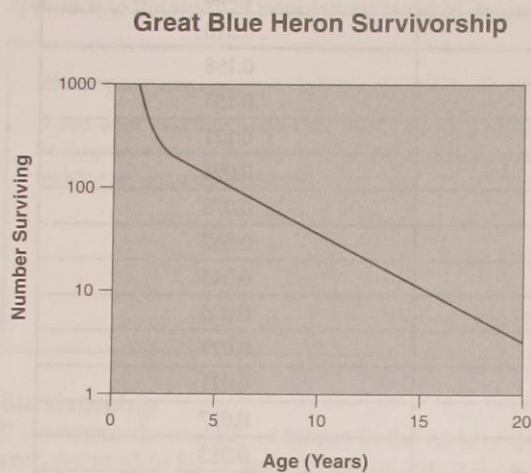


Figure 5.2 Survivorship curve for Great Blue Heron (based on data from Butler, 1992).

Following a system proposed by E. S. Deevey (1947), population ecologists classify organisms according to their patterns of survivorship (Figure 5.3). **Type I** organisms, such as humans, exhibit comparatively low juvenile and young adult mortality, with most deaths occurring at the end of the life span. This produces a convex survivorship curve, bowing up and to the right on the log plot. **Type II** organisms, including most birds, experience a constant risk of mortality throughout their lives. On a log scale, the constant risk of death generates a straight line for Type II species, descending from birth to the end of the life span. **Type III** organisms, such as trees, experience very high mortality of juveniles (seeds and seedlings), but an exceptionally low death rate once established as adults. Their survivorship curve is said to be concave, since it bows downward toward the origin of the graph.

Check your progress:

Which type of survivorship curve in the Deevey classification best describes the life history of the Great Blue Heron? If Deevey's model is not a perfect fit for heron survivorship, comment on reasons for any differences that you see.

Answer: Type II, except for juveniles

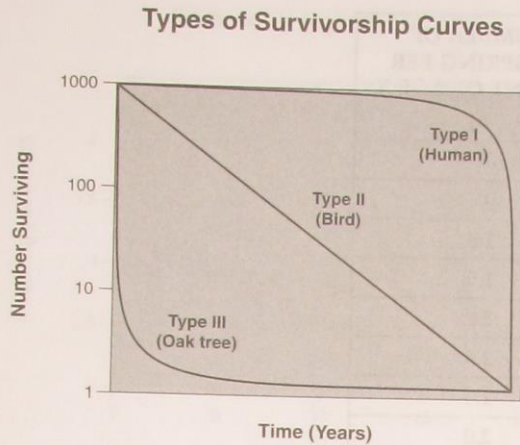


Figure 5.3 Three types of survivorship curves. Type I species, such as humans, have low mortality until the end of the life span. Type II species have constant mortality rates throughout the life span. Type III species have very high juvenile mortality, but high survival after establishment as adults. (Terminology from Deevey, 1947.)

Fecundity

To forecast the future of our heron rookery, we need to know more than the survivorship schedule. Reproductive rates, also influenced by age, are equally important. In Great Blue Herons, we know that breeding begins at age two, and continues throughout the birds' lives. Adults returning to the rookery choose a new mate each year, and breeding pairs cooperate in the feeding of young. Nests are built of sticks and vegetation high in the tops of trees to avoid mammalian predators. The number of nestlings produced by each breeding pair varies from three to seven, depending on available resources, with four being typical during favorable conditions (Butler, 1992).

In demography studies, the number of offspring produced by a parent, called **fecundity**, is measured as a function of age. We will let b_x stand for the mean number of offspring produced by a parent of age x . In making this calculation, it is important to remember that two parents are involved in each nest, so numbers of fledglings in a nest reared by a *pair* of herons would have to be divided by 2 to calculate the number of offspring per parent.

For our hypothetical heron population, we will let $b_x = 0$ for age 0 and age 1, since herons do not begin nesting until they are two years of age. We will further assume young breeding adults are somewhat less successful than older birds, so $b_x = 1.5$ for ages 2 and 3. This would reflect a pair of young herons successfully rearing three nestlings in those years. After age 3, we will assume more experienced birds rear an average of four fledglings per nest, so $b_x = 2.0$ for herons age 4 and above. We will terminate the table at age 17, which is the maximum life span of the bird. From these assumptions, we construct a fecundity schedule as follows:

AGE IN YEARS x	NUMBER OF OFFSPRING PER PARENT OF AGE x b_x
0	0
1	0
2	1.5
3	1.5
4	2.0
5	2.0
6	2.0
7	2.0
8	2.0
9	2.0
10	2.0
11	2.0
12	2.0
13	2.0
14	2.0
15	2.0
16	2.0
17	2.0

Like the survivorship schedule, age-specific fecundity rates for our heron population can be represented on a graph (Figure 5.4).

Check your progress:

In a human population, if the birth rate for women between ages of 25–30 is 0.16 per year, what is b_x for this age group?

Answer: $b_x = 0.08$, assuming females make up half of the population

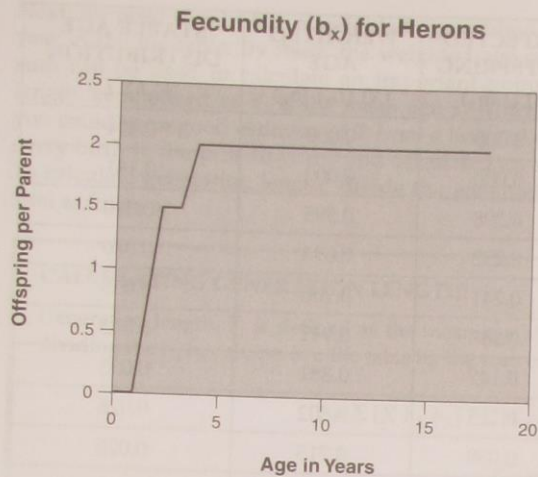


Figure 5.4 Fecundity schedule for Great Blue Heron population, showing numbers of offspring per parent as a function of parental ages.

Life Table

A life table combines survivorship and fecundity information to generate a comprehensive demographic model. In addition to survivorship and fecundity columns from earlier tables in this chapter, notice that the final three columns are made by multiplying values from the preceding columns. Column sums are shown at the bottom.

After the familiar survivorship and fecundity columns, find the column labeled “expected offspring.” Each figure in this column represents the number of offspring that a newly hatched heron can be expected to produce at the indicated age. To calculate this number, two questions must be asked: 1) what is the likelihood that the heron will survive to this age? and 2) if it attains this age, how many offspring is it expected to produce? Multiplying the L_x and b_x numbers together yields the joint probability of living x years and then producing the number of offspring typical of x -aged herons. The sum of the $L_x b_x$ column represents the expected number of young a typical heron is expected to produce, summed over its entire lifetime. Demographers call this total the **net reproductive rate**, represented by the symbol R_0 .

CALCULATING NET REPRODUCTIVE RATE:

Net reproductive rate, R_0 , is defined as the lifetime production of offspring per parent. It is calculated by summing the $L_x b_x$ column in a life table.

$$R_0 = \sum [L_x b_x]$$

The symbol

R_0 = net reproductive rate

Σ means the bracketed numbers are summed over all ages.

$L_x b_x$ = survivorship at age x times fecundity at age x

AGE IN YEARS X	SURVIVORSHIP L_x	FECUNDITY b_x	EXPECTED OFFSPRING $(L_x)(b_x)$	WEIGHTED AGE $(X)(L_x)(b_x)$	STABLE AGE DISTRIBUTION $L_x / \Sigma L_x$
0	1.000	0	0.000	0.000	0.454
1	0.310	0	0.000	0.000	0.141
2	0.198	1.5	0.298	0.595	0.090
3	0.155	1.5	0.232	0.696	0.070
4	0.121	2.0	0.241	0.966	0.055
5	0.094	2.0	0.188	0.942	0.043
6	0.073	2.0	0.147	0.881	0.033
7	0.057	2.0	0.115	0.802	0.026
8	0.045	2.0	0.089	0.715	0.020
9	0.035	2.0	0.070	0.627	0.016
10	0.027	2.0	0.054	0.544	0.012
11	0.021	2.0	0.042	0.466	0.010
12	0.017	2.0	0.033	0.397	0.008
13	0.013	2.0	0.026	0.335	0.006
14	0.010	2.0	0.020	0.282	0.005
15	0.008	2.0	0.016	0.235	0.004
16	0.006	2.0	0.012	0.196	0.003
17	0.005	2.0	0.010	0.162	0.002
18	0.000	0	0.000	0.000	0.000
TOTALS:	2.204		1.611	9.177	1.000

In our example, R_0 is equal to 1.611, which means that the average heron produces 1.611 offspring over its lifetime. Remember that a pair of herons would produce double this number of offspring on average, which would be 3.222 baby herons.

Check your progress:

Which makes the most significant contribution to family size in Great Blue Herons, offspring produced by herons younger than eight years of age, or offspring produced by herons older than eight? Why is reproduction in the first half of the life span more important than in the second half?

Hint: Compare values in the $L_x b_x$ column of the life table.

Next, we need to calculate a **weighted age** column by multiplying x , L_x , and b_x values together for each year in the life table. By itself, the weighted age column does not have much intuitive meaning, but its sum can be used to calculate an important population parameter: the **generation length**. Generation length, symbolized as T , is the mean age at which parents produce offspring. For a human population, you could get a good estimate of T from a hospital's birth records if you wrote down the mother's age for every birth in the past 10 years, and calculated an average age for all the mothers who delivered a child. To calculate generation length, divide the weighted age column total by the expected offspring column total as follows:

CALCULATING GENERATION LENGTH:

Generation length, T , is defined as the mean age at which parents produce offspring. It is calculated by dividing the $L_x b_x$ column in a life table by the sum of the weighted age column in the life table.

$$T = \sum [X L_x b_x] / \sum [L_x b_x]$$

T = generation length

$\sum [X L_x b_x]$ = sum of the weighted age column

$\sum [L_x b_x]$ = sum of the expected offspring column

In our example, the weighted age total for Great Blue Herons is 9.177, and the expected offspring total is 1.611, so the generation length is $9.177/1.611 = 5.7$ years.

Once we have calculated the net reproductive rate R_0 and generation length T , we can calculate a fair approximation of the **intrinsic rate of population increase**, represented by r in the population growth equations. To find r , first realize that after a generation of population growth, the number of new individuals is equal to the population size in the previous generation, multiplied by the net reproductive rate. If we let N_0 designate the original population size, and N_T be the population size after one generation,

$$N_T = N_0 R_0$$

Now from the continuous equation for population growth (see Chapter 4), we know that:

$$N_T = N_0 e^{rT}$$

By substitution, we can equate the two expressions for N_T as follows:

$$N_0 R_0 = N_0 e^{rT}$$

Check your progress:

If you cancel units of measurement in the numerator and denominator of the equation for T , what units are you left with? Does this make sense as a measure of generation length?

Answer: Units for L_x and b_x cancel, leaving x (in years) for generation length.

ESTIMATING THE INTRINSIC RATE OF INCREASE (r) FROM LIFE TABLE DATA:

$$r \equiv (\ln R_0) / T$$

r = intrinsic rate of population increase
 R_0 = net reproductive rate
 T = generation length

Dividing both sides of the equation by N_0 we get:

$$R_0 = e^{rT}$$

Then we can take the natural log of both sides:

$$\ln R_0 = rT$$

And finally rearranging for r ,

$$r = (\ln R_0) / T$$

This method is simple to calculate, and is very accurate in short-lived organisms that reproduce only once, such as annual plants and many insects. If generations overlap as we see in the Great Blue Heron, this method gives only an approximation of r because the new generation does not completely replace the old at time T . A more accurate calculation of r can be derived from a more complex equality, called the **Euler equation**. An explanation of this method can be found in population biology texts (e.g., Ebert, 1999). For this laboratory exercise, we will use the simpler approximation.

For our example, family size in Great Blue Herons is 1.611, and the generation length is 5.7 years. Therefore, a good estimate of r for these birds is:

$$r \equiv \ln(1.611) / 5.7 = .084$$

Check your progress:

Organizations concerned with global human overpopulation often discuss ways to reduce family size. From the equation for r above, can you see a second way to reduce the intrinsic rate of increase? What social factors are involved in this approach to the problem?

Hint: Since T is in the denominator, increasing T reduces r .

Finally, we can use the column at the extreme right of the life table to project the **stable age distribution** of the population. This column forecasts what portion of our herons will be newborns, one-year-olds, two-year-olds, three-year-olds, etc., after the population reaches equilibrium. This column is calculated by dividing this year's survivorship by the total for all years:

$$L_x / \sum L_x$$

We can think of this fraction as the portion of the total life span that a typical heron lives in year x . If we extrapolate from our cohort of 1000 herons to the whole population, this same fraction approximates the proportion of the population expected to be x years old. Of course, a population might start out with a different age distribution, but if the survivorship and fecundity schedules remain constant as written in the life table, the population will achieve a stable age distribution within a few generations. Interestingly, a stable age distribution is achieved whether the population is growing or not; stable population size and stable age distribution are distinct properties of the population.

To demonstrate from our example, the $L_x/\Sigma L_x$ value for three-year-old herons is 0.070, which means that 7% of the heron population will be members of the three-year-old age class. We can use all the entries in this column to generate proportional representation for the whole array of age classes. The $L_x/\Sigma L_x$ column always sums to 1.000, since its column total represents 100% of the age classes.

Demographic Patterns

A population's history of survival and reproduction is reflected in its age structure. Trees provide good examples for demographic analysis, since individuals can be aged by the rings of xylem laid down in the wood with each year's growth (Figure 5.5). It is not necessary to cut down the tree to see the rings. A core sample taken from the trunk can be used to determine age without harming the tree (Figure 5.6). If you used core samples to age trees in a stand of pines, and found all the trees were 32 years old, you could guess the area had been logged 32 years ago. Recruitment of new seedlings after logging resulted in a population dominated by a single cohort. From the logger's perspective, this age structure has advantages. All the trees in this forest will mature at the same time, so the trees can be clear-cut again at some point in the future. From the resource management perspective, this is not generally accepted as good forestry practice, since even-aged stands of trees provide a less diverse habitat for forest species, and clear-cutting leaves the soil exposed to erosion and nutrient loss. A more balanced use of woodlands for wildlife management, soil conservation, watershed protection, and forestry can be achieved by selectively cutting mature trees from mixed-aged stands. Even this practice removes the hyper-mature trees needed by some woodland species. For example, the red-cockaded woodpecker nests only in the hollow cavities of old pines, and became endangered as mature trees were cut out of forests throughout the Southeastern U.S. A tree population protected from logging typically develops a broad range of age classes, reflecting constant recruitment of seedlings over time, and providing habitat for a diverse forest community (Figure 5.7).

Check your progress:

After the population reaches a stable age distribution, what percentage of this heron rookery will be composed of one-year-old birds?

Answer: 14.1%



Figure 5.5 Growth rings in a tree trunk's cross section indicate age of the tree.



Figure 5.6 Ecologist removing a core sample to analyze tree ring data.

In many plant species, the size of the organism is a better predictor of survival and fecundity than the individual's age. Demographers working with these species use size classes or life stages rather than age in their models. Stage-specific survivorship and fecundity can be analyzed to make population projections, just as we have done with ages in this chapter.

Demographic analysis has proven quite useful in understanding human populations. Figure 5.8 illustrates demographic patterns for the United States population, based on year 2000 census data. In this kind of graph, each horizontal bar represents an age class, with males shown on the left side and females on the right. Age classes are arrayed from babies (age 0–4) at the bottom to the oldest members of the population (age 85+) at the top. Notice that the U.S. population graph is roughly rectangular, with some tapering at the top due to age-related mortality. The asymmetry at the top of the graph is caused by a longer life expectancy for females than for males. You will notice a bulge in the middle of the graph, caused by the “baby boom” post-WWII generation, who were primarily between age 35 and 49 during the 2000 census. The demographic “echo” of the baby boomers’ children, ages 5–19, is not quite as large as the baby boom cohort, but still creates a significant “bulge” in the age structure. Although it has some cohorts larger than others, the general shape of the U.S. age distribution is called “rectangular.” This shape is characteristic of stable populations maintaining a fairly constant population size from one generation to the next.



Figure 5.7 A maple forest exhibits a broad range of tree ages.

Now examine the age distribution for India (Figure 5.9). For many years, family size in India has been large, so each generation has more people than the last. This creates a pyramid-shaped age distribution dominated by a very large base of young people at the bottom. Note that Indian society has taken some steps to curb population growth prior to the 2000 census, so the rate of expansion in the 0–4 age class is beginning to show signs of slower growth. Because of the demographic structure, however, the population of India is projected to continue growing as the large number of children in that country mature into their childbearing years.

Compare the structure of India with the age structure of Italy, which has a contracting population. The bottom of the age structure is smaller than the middle, because family size averages fewer than two children per couple. If this trend continues, Italian society will be dominated by older people, with fewer demands on schools but greater demand for health care and retirement benefits as the population ages. Clearly, a view of the age structure of a population, whether herons, trees, or humans, tells us a lot about a population's past, and helps us predict its future as well.

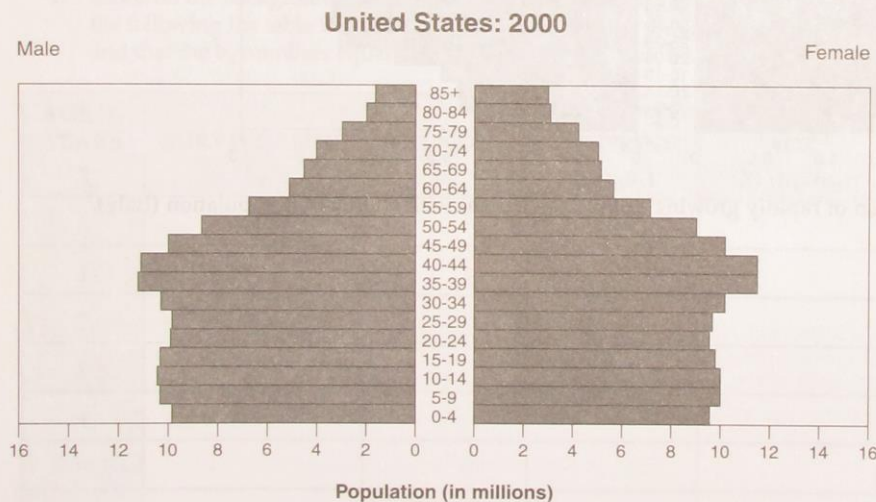


Figure 5.8 Demographic profile of U.S. population, from the 2000 census.

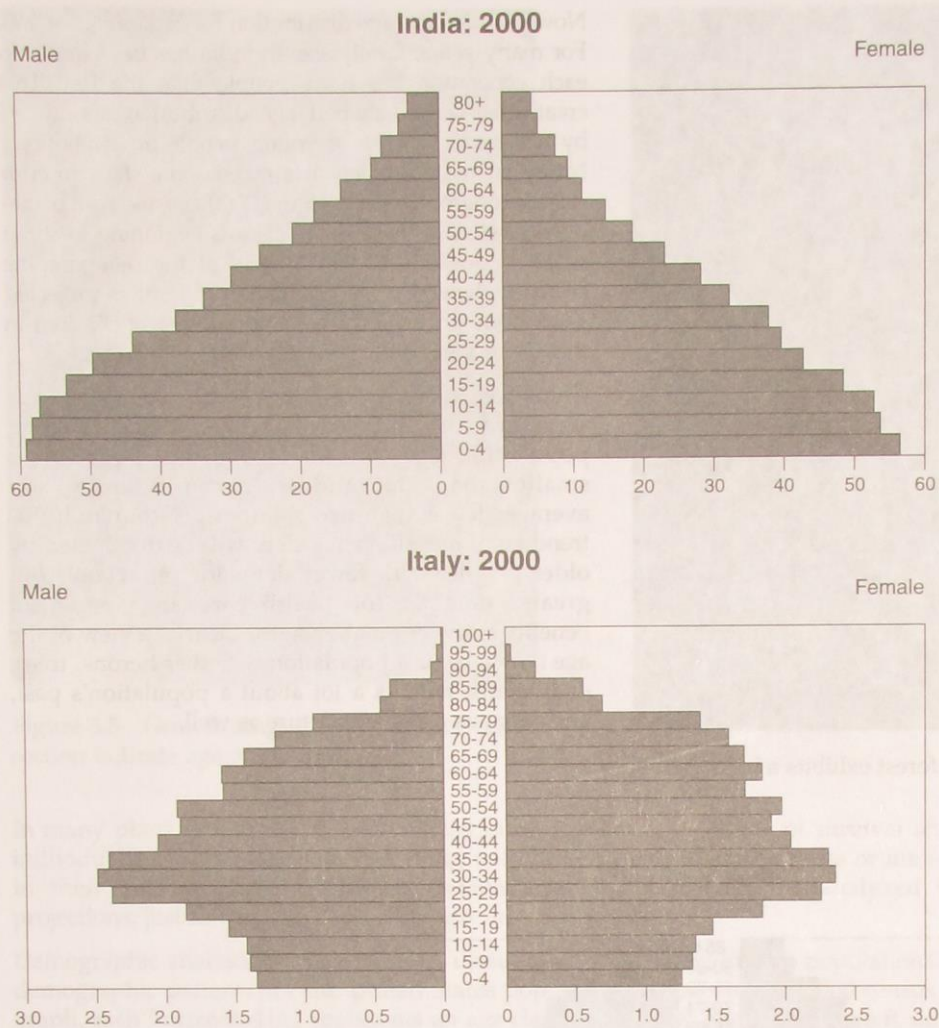


Figure 5.9 Comparison of rapidly growing population (India) with contracting population (Italy).

METHOD A: DEMOGRAPHY SIMULATION

[Computer activity]

Research Question

How do populations achieve a stable age distribution?

Preparation

Because demographic concepts are built on ideas about population growth, it is highly recommended that students complete readings and exercises from Chapter 4 before attempting exercises in this chapter. Instructions for this simulation are appropriate for Microsoft Excel software. If you use other spreadsheet software, instructions for writing cell formulas given in this procedure may require modification.

Materials (per laboratory team)

A computer station, with spreadsheet software

Background

This exercise simulates age-specific survivorship and reproduction for an imaginary population of medium-sized burrowing mammals; let's call them marmunks. Female marmunks begin breeding at age 1, and produce one viable offspring in their first year. In their second year, they produce three viable offspring. In their third and subsequent years, they produce five offspring per year. Newborn marmunks experience 65% mortality before age 1, but annual mortality rates are only 35% per year after that. The maximum life span is six years. Our task is to develop a model that shows age distributions for a marmunk population year by year as the population grows.

Procedure

1. Based on the background information, and following the heron illustration in this chapter, complete the following life table for marmunks. Don't forget that the L_x column begins with 1.000 alive at age 0, and that the b_x numbers equal half the family sizes for each age group.

AGE IN YEARS X	SURVIVORSHIP L_x	FECUNDITY b_x	EXPECTED OFFSPRING $(L_x)(b_x)$	WEIGHTED AGE $(X)(L_x)(b_x)$	STABLE AGE DISTRIBUTION $L_x / \Sigma L_x$
0					
1					
2					
3					
4					
5					
6					

If you have completed the life table correctly, it will predict some of the results of the simulation to follow.

2. Set up a computer spreadsheet with the following column headings. Numbers in the first column indicate the year in our simulation, so each row will show the state of the population in another year as we go down the page. Numbers in columns 2 through 8 represent the number of marmunks in the population that are newborns, one-year-old, two-year-old, etc. The column on the right is a sum of all the marmunks in the population.

	A	B	C	D	E	F	G	H	I
1	YEAR	AGE 0	AGE 1	AGE 2	AGE 3	AGE 4	AGE 5	AGE 6	TOTAL POPULATION
2									

3. The first entry in cell A2, under "year" should be 0, the starting point of our simulation. Go down this column, numbering years 1, 2, 3, 4, etc. If you do not want to type all those numbers in, just enter 0 in cell A2, and then in cell A3 type the formula = A2+1. If you copy and paste this formula down the column to the thirty-second row, you will get a series of numbered years from 0 through 30. Format all the cells below the first row to display numerical values, with no decimal places. The top of your spreadsheet should now look like this:

	A	B	C	D	E	F	G	H	I
1	YEAR	AGE 0	AGE 1	AGE 2	AGE 3	AGE 4	AGE 5	AGE 6	TOTAL POPULATION
2	0								
3	1								
4	2								
5	3								
6	4								

4. To begin our population, let's release 100 juvenile marmunks, just weaned and ready to start life on their own. To do this, enter the number 100 in cell B2, and zeroes in cells C2 through H2. In cell G2, enter the formula = SUM(B2:H2). Copy and paste this formula down all the cells in column G, to the 30th row. This will give you the population size each year of your simulation. Your spreadsheet should now look like this:

	A	B	C	D	E	F	G	H	I
1	YEAR	AGE 0	AGE 1	AGE 2	AGE 3	AGE 4	AGE 5	AGE 6	TOTAL POPULATION
2	0	100	0	0	0	0	0	0	100
3	1								0
4	2								0
5	3								0
6	4								0

5. Next we need to model survival of newborns through their first year. The 100 newborns in year 0 will become one-year-olds in year 1. Thus, the survivors from our 100 released marmunks will be in cell C3 as one-year-olds. To calculate how many marmunks survive, recall that the death rate for newborns is 65%. This means that 0.35 of the newborns will be one-year-olds the following year. We can calculate this number by entering the formula $=B2 * 0.35$ in cell C3. Copy and paste this formula all the way down column C so that your spreadsheet will calculate the number of one-year-olds each year. Your spreadsheet should now look like this:

	A	B	C	D	E	F	G	H	I
1	YEAR	AGE 0	AGE 1	AGE 2	AGE 3	AGE 4	AGE 5	AGE 6	TOTAL POPULATION
2	0	100	0	0	0	0	0	0	100
3	1		35						35
4	2		0						0
5	3		0						0
6	4		0						0

6. To calculate survival of all the other age classes, recall that survivorship is 65% for older marmunks. In cell D3, enter the formula $=C2*0.65$. Copy and paste the formula into all the cells in columns D, E, F, G, and H from rows 3 through 32. The top of your spreadsheet should now look like this:

	A	B	C	D	E	F	G	H	I
1	YEAR	AGE 0	AGE 1	AGE 2	AGE 3	AGE 4	AGE 5	AGE 6	TOTAL POPULATION
2	0	100	0	0	0	0	0	0	100
3	1		35	0	0	0	0	0	35
4	2		0	23	0	0	0	0	23
5	3		0	0	15	0	0	0	15
6	4		0	0	0	10	0	0	10

As you follow the diagonal from your 100 young marmunks down and to the right, you are following the fate of the cohort as it ages through years 1, 2, 3, 4, 5, and 6.

5. To complete the life history, we need to model reproduction. In cell B3, enter the following formula:

$$=C3*0.5 + D3*1.5 + \text{SUM}(E3:H3)*2.5$$

This equation states that the number of newborn marmunks this year equals $\frac{1}{2}$ times the number of one-year-old parents, plus $1\frac{1}{2}$ times the number of two-year-old parents, plus $2\frac{1}{2}$ times the number of parents over two years of age. The offspring produced *per parent* correspond to family sizes of one, three, or five per pair, depending on parental ages, as described in the background section. Copy and paste this formula all the way down column B. Your spreadsheet now reflects both survival and reproduction, and should look like this:

	A	B	C	D	E	F	G	H	I
1	YEAR	AGE 0	AGE 1	AGE 2	AGE 3	AGE 4	AGE 5	AGE 6	TOTAL POPULATION
2	0	100	0	0	0	0	0	0	100
3	1	18	35	0	0	0	0	0	53
4	2	37	6	23	0	0	0	0	66
5	3	49	13	4	15	0	0	0	81
6	4	52	17	8	3	10	0	0	90

6. Finally, create a row at the very bottom of the spreadsheet to calculate the age distribution at year 30. In cell A34, put the label "Age Distribution." Change the format in row 34 to show numbers in three decimal places. Then, in cell B34, enter the formula: `=B32/$I$32`. Copy and past this formula into cells C34 through H34. This formula takes the numbers of marmunks of each age in the 32nd row (30th year) and converts numbers to proportions. In theory, this row will give you the stable age distribution predicted by the $L_x/\Sigma L_x$ column in your marmunk life table.

Questions (Method A)

1. From your life table, calculate the net reproductive rate $R_0 = \sum [L_x b_x]$. Does your answer make sense, given what you know about family sizes and survivorship in marmunks? Does this net reproductive rate allow each marmunk to replace itself to ensure continuity of the population?

2. From your life table, calculate the generation length $T = \sum [x L_x b_x] / \sum [L_x b_x]$. Comment on the meaning of this answer, noting that marmunks begin to reproduce at age 1 and continue bearing offspring until age 6.

3. Use the values of R_0 and T calculated above to compute the intrinsic rate of increase for marmunks, using $r \equiv (\ln R_0) / T$.

4. How accurate is your estimate of r ? To find out, use the exponential growth equation, solved for r . To ensure that the population has reached a stable age structure and is growing in a smooth exponential curve, let's look at the final 10 years of population growth. Using N_{20} as a starting point, and measuring population growth over the 10 years to N_{30} , we can use:

$$N_{30} = N_{20} e^{r(10)}$$

Taking the $\log_e$ of both sides and rearranging, we get:

$$r = (\ln N_{30} - \ln N_{20}) / 10$$

Plug in values from your simulation to calculate the rate of increase, using natural logs of the population sizes at N_{20} and N_{30} to calculate marmunk population growth over the final decade of your simulation. Now you have calculated r in two ways. The first is a theoretical value estimated from the life table, and the second is an empirical determination from the simulation results. How do the two r values compare? Comment on reasons for any discrepancies in your two calculations of r .

5. Compare the final age distribution of marmunks in year 30 with the stable age distribution projected from the $L_x/\Sigma L_x$ column in your marmunk life table. How do the two compare? Did it take 30 years for the population to reach a stable age distribution? Check frequencies across the row in earlier years to find out.

METHOD B: DEVELOPING A LIFE TABLE FROM THE ALUMNI NEWSLETTER

[Laboratory activity]

Research Question

What are the demographic characteristics of the alumni population of your school?

Preparation

Because alumni are not a population in the biological sense, this exercise should be viewed as a demonstration of demographic principles. Alumni newsletters vary significantly in the amount and kinds of information they present. The best source for this study would list obituaries and birth announcements for a representative sample of alums—not just the more successful or famous ones. This exercise also works best if your institution is over 70 years old, to ensure that alumni from all portions of the life span are represented. Obituaries that list age at death and all surviving children are best, but ages can be estimated from the graduating class year if necessary. This entails several assumptions which introduce error, such as age at matriculation during the historical period included in your study. Since many alumni magazines are available in an on-line format, students may find it easier to search back issues posted on web sites rather than paper copies. If your alumni magazine does not carry birth and death announcements, a city newspaper might provide an alternative source of data.

Materials (per laboratory team)

Access to back issues of the alumni newsletter, with at least 50 birth announcements and 50 obituaries available to each laboratory team

Background

This exercise demonstrates how to build a life table from information supplied by your alumni newsletter. Because access to this information may be limited to alums and students at your school, be sure to respect the confidentiality of the families involved, and do not identify individual names in any reports you produce.

Be aware that an alumni newsletter reports data from a biased sample of the human population as a whole. Since one must be a college student before becoming an alum, deaths occurring before the age of 18 will not be represented in your data set. If your university or college has many nontraditional students, a significant number of children born before their parents matriculate will be excluded from the sample. Finally, college-educated persons typically exhibit different demographic characteristics from the population at large.

The purpose of the exercise is not to estimate demographic parameters for the population as a whole, but to demonstrate in general how birth and death records can be used to construct a life table for a particular group of interest.

Procedure

1. *From obituary notices*, complete the longevity and fecundity tables on the calculation pages for Method B. Assign each obituary that you read a unique record number to preserve the anonymity of the people included in the study. Longevity can be estimated in any of three ways: first, the year of birth may be listed in the notice. If so, subtract the year of birth from the year of death to determine longevity. Second, the class year may be listed. If so, you can subtract 22 from the graduation class year as an estimate of the date of birth, assuming a typical college student is 22 years old at the time of graduation. Then subtract estimated year of birth from the year of death. Third, if the age at death is reported, skip the year of birth and year of death columns, and enter age at death under the "Longevity" heading.

Enter the gender of the deceased under the column titled "sex." Finally, under the heading "No. Offspring," enter the number of children listed as survivors. This number may not include all children, but provides a reasonable estimate of family size in most cases. Sample records are illustrated in the following abbreviated table:

Record Number	Year of Birth	Year of Death	Longevity	Sex	Number of Offspring
100	1943	2004	61	F	3
101	1930	2005	75	M	2

- For the next step, go down the table you have just created line by line, reading only the records for female alums. In the table titled "Grouped Longevity Data for Females," place tally marks in the appropriate boxes to count the number of females who died in each of the 10-year age classes: 0–9, 10–19, 20–29, etc. Sample entries are shown in the abbreviated table below. If you like, you can pool data from the entire class at this step for a larger sample size and greater accuracy. After you have gone through all the obituary records, add up the tally marks and enter a total number of females who died in each age class as shown. Then sum the column of numbers to find the grand total of females of all ages in your obituary sample.

AGE CLASS	FEMALE LONGEVITY		PROPORTION DYING IN THIS AGE CLASS d_x	AGE-SPECIFIC SURVIVORSHIP L_x
	Tally marks for females dying within this age class.	Total		
0–9		0	0	1.000
10–19	/	1	.020	1.000
20–29	///	3	.060	.980
30–39	////	4	.080	.920

Next, compute d_x values by dividing the number who died in each age class by the total number of females in the sample. (Note that we are expressing d_x as a proportion and not as a whole number here.) For example, if our sample had a total of 50 females, the three women who died between the ages of 20 and 29 would comprise $3/50 = 0.060$ of the total population. Finally, calculate L_x values by subtracting d_x from the L_x value in one line to get the L_{x+1} value for the next line, as shown in the table. For example, in the line representing age class 20–29, the subtraction gives us $0.980 - 0.060 = 0.920$, which is the L_x value for the next age class. Complete these calculations all the way through the table. If calculated correctly, entries in the L_x column should decline toward 0 in the 100+ age class.

- Repeat step 2 for the records on males in your obituary data. Complete the table titled "Grouped Longevity Data for Males" in the calculation pages.
- Calculate net reproductive rate R_0 by summing all the numbers of surviving children in the "Number of Offspring" column in the obituary data, and dividing by 2 times the total number of people in your obituary sample. The 2 in the denominator accounts for two parents in each family, so the result represents the number of offspring per parent. Enter these calculations in the small table entitled "Estimating Net Reproductive Rate."

5. Draw survivorship curves on the graph following the grouped longevity data tables. Plot the survivorship L_x as a function of age class separately for males and females. Connect male points with a dotted line, and female points with a solid line. Compare your results.
6. From birth notices, determine the mother's birth year, and whether the baby is male or female. You will need to estimate the mother's birth year by subtracting 22 from the graduation year. Enter the year of birth of the child. Subtract the mother's birth year from the baby's birth year to determine the age of the mother. Finally, record the sex of the child as female (F), male (M), or not stated (NS). If it is reasonable to use first names to infer the sex of the child, do so, with an awareness that some error will be introduced by wrong guesses. In cases of twins, fill out a separate line for each of the two children. A sample record is included below for illustration.

Record Number	Mother's graduation year	Mother's birth year	Baby's birth year	Mother's age at time of birth	Sex of child (F) (M) (NS)
1	2000	1978	2005	27	M

7. In the table titled "Grouped Fecundity Data," place tally marks in the appropriate boxes to count the number of females who gave birth in each of the 10-year age classes: 0-9, 10-19, 20-29, etc. Sample entries are shown in the abbreviated table below.

AGE CLASS	FECUNDITY		PROPORTION OF BIRTHS OCCURRING IN THIS AGE CLASS	EXPECTED OFFSPRING $L_x b_x$
	Tally marks for females giving birth within this age class.	Total		
0-9		0	0	0
10-19	//	2	.040	0.072
20-29	//////////	26	.520	0.936
30-39	//////////	18	.360	0.648

Divide each of the age-specific birth counts by the total births in the entire sample to calculate the proportion of births occurring in each age class. For example, if the whole sample included 50 births, the proportion born to mothers in the 20-29 age class would be $26/50 = 0.520$, as shown in the sample table. After you have calculated all the proportions, multiply each of these fractions by R_0 to convert expected proportions to expected offspring. For example, if R_0 were 1.8, then the number of expected offspring per 20-29-year-old in the population would be $(0.520)(1.8) = 0.936$ children per parent.

8. In the table titled "Calculation of Sex Ratios," enter numbers of records you found for males and females in the obituary data in the top row, and from birth announcements in the second row. Divide numbers of each sex by total sample size to calculate a sex ratio for deceased alumni and a sex ratio for alumni children as indicated in the table.
9. Use your data to complete a "Life Table for Alumni" at the end of the calculation pages for Method B. You have L_x values from the obituary data, and $L_x b_x$ values from the birth announcements. If you like, you can divide each $L_x b_x$ value by L_x to get a b_x value for that age class. At the bottom of the table are questions about the generation length, net reproductive rate, intrinsic rate of reproduction, and stable age distribution for the alumni population. Refer to the Introduction if you have forgotten how to make these calculations from a life table. Answer the questions that conclude this demography exercise.

Data From Obituary Notices (Page 1)

Record Number	Year of Birth	Year of Death	Longevity	Sex	No. Offspring
1					
2					
3					
4					
5					
6					
7					
8					
9					
10					
11					
12					
13					
14					
15					
16					
17					
18					
19					
20					
21					
22					
23					
24					
25					

Data From Obituary Notices (Page 2)

Record Number	Year of Birth	Year of Death	Longevity	Sex	No. Offspring
26					
27					
28					
29					
30					
31					
32					
33					
34					
35					
36					
37					
38					
39					
40					
41					
42					
43					
44					
45					
46					
47					
48					
49					
50					

Grouped Longevity Data For Females

AGE CLASS	FEMALE LONGEVITY		PROPORTION DYING IN THIS AGE CLASS d_x	AGE- SPECIFIC SURVIVOR- SHIP L_x
	Tally marks for females dying within this age class.	Total		
0-9				1.000
10-19				
20-29				
30-39				
40-49				
50-59				
60-69				
70-79				
80-89				
90-99				
100+				

Total Females =

Grouped Longevity Data For Males

AGE CLASS	MALE LONGEVITY		PROPORTION DYING IN THIS AGE CLASS d_x	AGE- SPECIFIC SURVIVOR- SHIP L_x
	Tally marks for males dying within this age class.	Total		
0-9				1.000
10-19				
20-29				
30-39				
40-49				
50-59				
60-69				
70-79				
80-89				
90-99				
100+				

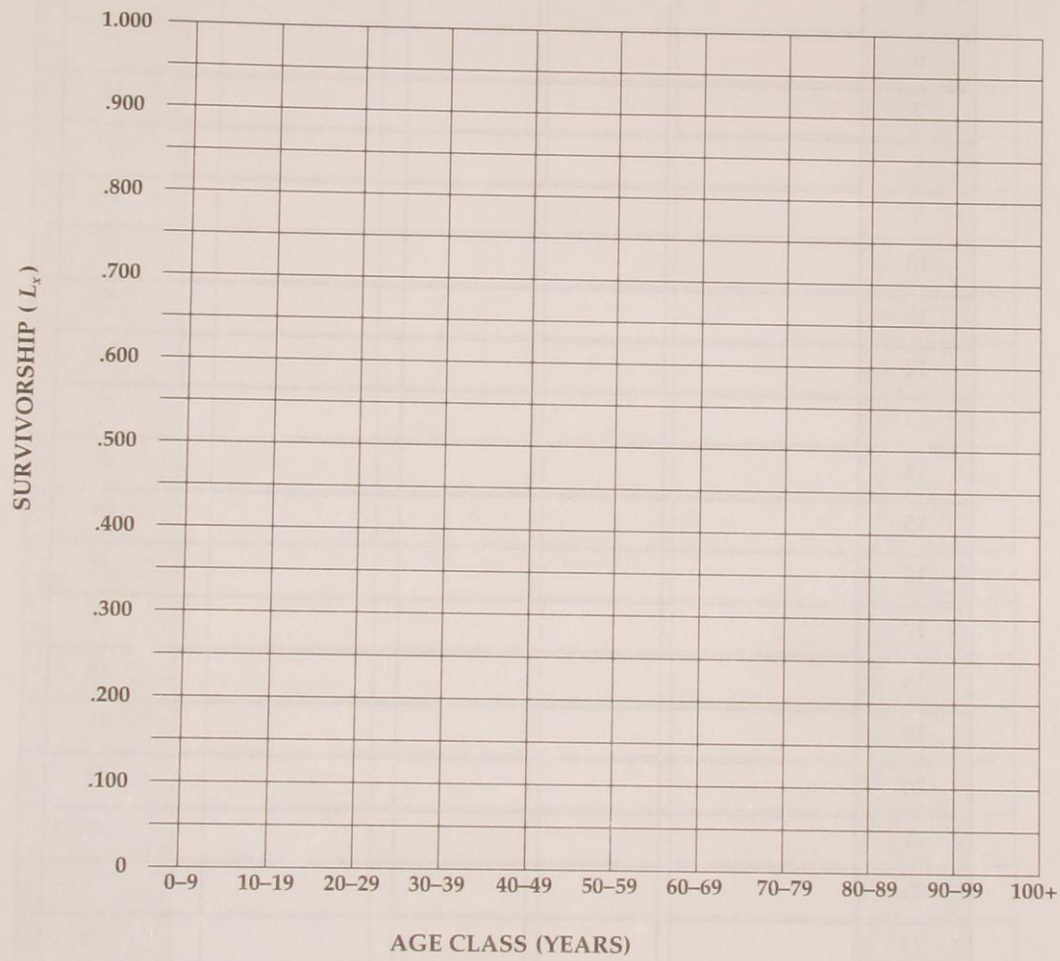
Total Males =

Estimating Net Reproductive Rate

TOTAL NUMBER OF RECORDS FROM OBITUARY DATA = n	TOTAL NUMBER OF SURVIVORS LISTED = s	$R_0 = s / (2 n)$

Survivorship Curves for Alumni

----- Males ————— Females



Data From Birth Announcements (Page 1)

Record Number	Mother's graduation year	Mother's birth year	Baby's birth year	Mother's age at time of birth	Sex of child (F) (M) (NS)
1					
2					
3					
4					
5					
6					
7					
8					
9					
10					
11					
12					
13					
14					
15					
16					
17					
18					
19					
20					
21					
22					
23					
24					
25					

Data From Birth Announcements (Page 2)

Record Number	Mother's graduation year	Mother's birth year	Baby's birth year	Mother's age at time of birth	Sex of child (F) (M) (NS)
26					
27					
28					
29					
30					
31					
32					
33					
34					
35					
36					
37					
38					
39					
40					
41					
42					
43					
44					
45					
46					
47					
48					
49					
50					

Grouped Fecundity Data

AGE CLASS	FECUNDITY		PROPORTION OF BIRTHS OCCURRING IN THIS AGE CLASS	EXPECTED OFFSPRING $L_x b_x$
	Tally marks for females giving birth within this age class.	Total		
0-9				
10-19				
20-29				
30-39				
40-49				
50-59				
60-69				
70-79				
80-89				
90-99				
100+				

Total Births =

Calculation of Sex Ratios

DATA SOURCE	TOTAL SAMPLE SIZE	MALES		FEMALES	
		NUMBER	%	NUMBER	%
OBITUARY DATA (SEX OF DECEASED)					
BIRTH ANNOUNCEMENT DATA (SEX OF CHILDREN)					

Life Table for Alumni

AGE CLASS X	SURVIVORSHIP L_X	FECUNDITY b_X	EXPECTED OFFSPRING $(L_X) (b_X)$	WEIGHTED AGE $(X) (L_X) (b_X)$	STABLE AGE DISTRIBUTION $L_X / \Sigma L_X$
0-9					
10-19					
20-29					
30-39					
40-49					
50-59					
60-69					
70-79					
80-89					
90-99					
100+					
TOTALS:					

1. Net Reproductive Rate =

2. Generation Length =

3. Estimate of intrinsic rate of population growth =

4. Stable age distribution =

Questions (Method B)

1. Compare the survivorship curves for male and female alums. If they differ, comment on biological and sociological explanations. Do you expect survivorship curves for your own cohort to resemble these, or do you expect changes due to diet, lifestyle, medical advances, or environmental factors? Explain your reasoning.

2. How did your method of data collection potentially affect the shape of the survivorship curves? How might missing data be collected?

3. Comment on the sex ratio for alums vs. the sex ratio for infants born to alums. Are they the same? What social factors or reporting bias might be responsible for these differences?

4. To develop an accurate life table from past birth and death records, rather than from cohort data, one must assume the population is in a stable age distribution, and not changing rapidly in overall size. Is this true of the alumni population of your institution? If not, what kinds of error did you introduce in your life table? For example, how would your age-specific fecundity data be affected if the number of female graduates has been increasing every year over the past two decades?

5. How might demographic analysis of a human population help state and national leaders develop plans for education, health care, economic development, or retirement benefits? Give one or two specific examples, based on information gathered in this exercise.

METHOD C: DEMOGRAPHY OF CAMPUS TREES

[Outdoor activity, any season]

Research Question

What size-class structure do shade trees exhibit on campus?

Preparation

This outdoor exercise treats shade trees on your campus as a population of carefully managed organisms of varying ages. Size classes are used rather than ages, so you will not have to take core samples of your trees. To get sufficient data, there should be at least 30 individuals of the same tree species for a lab group to measure. Ideally, trees of different ages should be included in your sample, with some of the largest ones nearing the maximum life span. If more than one species is abundant on your campus, assign different species to different laboratory groups.

Materials (per laboratory team)

Metric measuring tape, 3 meters or longer

Background

Consider the life history of a shade tree on your campus. New trees typically enter the population as transplanted saplings. If recruits survive transplanting, they have a high survival rate in comparison to forest trees, because they are spaced far enough apart to avoid serious competition. However, at the end of the life span, campus trees probably die more quickly than they would in a forest, because hyper-mature specimens with dead limbs or hollow trunks are generally removed before they can fall on someone.

Although campus trees do not include the very beginning or the very end of a wild tree's life history, we can examine their demographic characteristics between those extremes. Because trees add xylem to their trunks at a fairly constant rate in annual growth rings, the diameter of a tree trunk is positively correlated with the tree's age. We will use trunk diameter to place trees in size classes, and develop a size-class structure diagram, similar to the age-structure diagrams shown for human populations in the Introduction. Both the history and the future of this tree population can be examined through your demographic analysis.

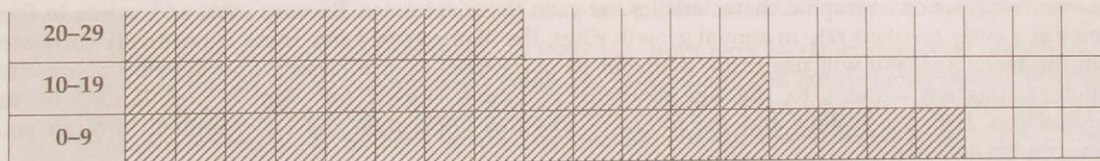
Procedure

1. Select a tree species abundant on your campus. You will need 30–50 individuals to generate a size-class structure diagram. If you cannot include all of these trees in your study, develop a sampling plan to generate data representative of the whole population, without bias toward larger or smaller individuals.
2. For each tree in your sample, use a metric tape to measure the circumference of the trunk at chest height to the nearest cm. In the column labeled "Observations," note any dead limbs, peeling bark, or other indications of the tree's health. If you find a plaque or marker indicating the year the tree was planted, be sure to record that information as well.
3. Return to the lab or classroom to analyze your data. Because the circumference of a circle is π times its diameter, you can divide the circumference by 3.14 to calculate a tree's diameter, as shown in the data table. Round off your calculation to the nearest cm.

4. To group your tree diameter records into size classes, place a tally mark in the appropriate size-class box for each tree in your sample as shown in the following table fragment. Count the tally marks and record the number in the "Totals" column. Divide this number by the sample size (50 in this example) to get a frequency. Multiply by 100% to convert the frequency to a percentage. The percentage expresses what portion of the whole population resides in this size class. Complete the table with data for all size classes you observed on the campus.

SIZE CLASS (cm)	NUMBER OF TREES		FREQUENCY (Percentage) $\frac{(\text{number})}{(\text{sample size})} \times 100\%$
	Tally marks for trees with diameters falling within this size class.	Totals	
0-9	//////////	17	34%
10-19	////////	13	26%
20-29	////	8	16%

5. Finally, color in squares in the graph labeled "Size Class Diagram for Campus Trees" to show the results of this demography study. If you have fewer than 20% of the whole sample in any given size class, let each square in the graph stand for 1%, and color in squares from left to right to show proportions in each size class. If you have more than 20% in a single class as shown in the illustration above, let each square represent 2%. Your graph will not be symmetrical like the human "population pyramids" illustrated in the Introduction, because we are not keeping separate records for male and female trees. (Some plant species, including Ginkgo and holly trees, do have separate sexes, but many do not.) A sample result for the bottom three rows of the graph is shown here. Interpret your graph and answer the questions at the end of the chapter.



Data from Tree Demography Study (Page 1)

Record Number	Circumference at chest height (cm)		Diameter (cm)	Observations
1		+3.14 =		
2		+3.14 =		
3		+3.14 =		
4		+3.14 =		
5		+3.14 =		
6		+3.14 =		
7		+3.14 =		
8		+3.14 =		
9		+3.14 =		
10		+3.14 =		
11		+3.14 =		
12		+3.14 =		
13		+3.14 =		
14		+3.14 =		
15		+3.14 =		
16		+3.14 =		
17		+3.14 =		
18		+3.14 =		
19		+3.14 =		
20		+3.14 =		
21		+3.14 =		
22		+3.14 =		
23		+3.14 =		
24		+3.14 =		
25		+3.14 =		

Data from Tree Demography Study (Page 2)

Record Number	Circumference at chest height (cm)		Diameter (cm)	Observations
26		+3.14 =		
27		+3.14 =		
28		+3.14 =		
29		+3.14 =		
30		+3.14 =		
31		+3.14 =		
32		+3.14 =		
33		+3.14 =		
34		+3.14 =		
35		+3.14 =		
36		+3.14 =		
37		+3.14 =		
38		+3.14 =		
39		+3.14 =		
40		+3.14 =		
41		+3.14 =		
42		+3.14 =		
43		+3.14 =		
44		+3.14 =		
45		+3.14 =		
46		+3.14 =		
47		+3.14 =		
48		+3.14 =		
49		+3.14 =		
50		+3.14 =		

Grouped Tree Demography Data

Tree species sampled: _____

Grouped Tree Demography Data

Tree species sampled: _____

SIZE CLASS (cm)	NUMBER OF TREES		FREQUENCY (number) (sample size)
	Tally marks for trees with diameters falling within this size class.	Totals	
0-9			
10-19			
20-29			
30-39			
40-49			
50-59			
60-69			
70-79			
80-89			
90-99			
100+			

	Total Sample Size =	
--	---------------------	--

[illegible]

Questions (Method C)

1. Do you think you have measured any trees near the end of their life span in this study? Do the largest trees show any signs of decay, peeling bark, or dead limbs?

2. From the shape of the size-class distribution, what can you guess about the history of tree planting on your campus? Does the size-class distribution show that trees have been continuously planted, or are there large cohorts indicating periods of intense tree planting, followed by years of no new additions to the population?

3. From the shape of the size-class distribution, what can you guess about the future of the shade tree population on your campus? When existing large trees finally die, are there younger trees growing into the larger size classes so that the campus will keep some shade?

4. In our study of size classes, we assume all trees grow at a similar rate so that a larger diameter indicates an older tree. However, growth rates in trees depend on soil quality, access to water, shading, severe pruning, and many other factors. Do you think differences in growth rate could compromise the accuracy of your study? If so, how could you document the actual ages of these trees?

5. Since forest trees compete for light, moisture, and nutrients, juvenile mortality is quite high in a natural environment. How would you expect a size-class distribution for a forest population to differ from the size-class distribution you documented on campus?

FOR FURTHER INVESTIGATION

1. Rerun the simulation in Method A by typing different initial numbers into the "Year 0" row at the top of your spreadsheet. Does the population get a faster start if you introduce adults as well as newborn marmunks to begin the simulation? Does the initial age structure have any effect on the ultimate stable age distribution?
2. Try different combinations of survivorship and age-specific fecundity schedules to achieve a stable population size in the marmunk simulation (Method A). As you change the formulae for survival or for calculating births, remember to copy and paste them in the appropriate areas of the spreadsheet. Compare the relative importance of survivorship and fecundity in determining the value of r .
3. Look up the Euler method for calculating the intrinsic rate of increase from life table data. (See Ebert, T. A. 1999, p. 15.) Use this approach to develop a more accurate calculation of r , and check it against your simulation results. Does this method yield a significantly improved estimate?
4. On the web site for the U.S. Census Bureau (<http://www.census.gov>), look up demographic parameters such as intrinsic rate of increase, longevity, and family size for the population at large. Develop a life table for the U.S. population, and compare it with the life table you developed in this exercise. In what ways are alumni atypical of the population at large?
5. If you have records that go back far enough, try compiling a life table based on only one graduating class, using Method B calculations. You should choose a graduating class from about 60 years ago to ensure that you have data through the entire life span. This amounts to a cohort study, and provides more accurate demographic data than assessments based on a mixture of cohorts. Do you see any significant changes when you compare newer or older cohorts?
6. Compare demographic information found in alumni newsletters published on-line from other universities across the country and around the world. Does a demographic analysis yield meaningful information about the history and mission of a university?
7. Look at memorial plaques, old photographs, or university records to find out when some of the trees in your sample were planted. Then you can divide the diameter of the tree by its age in years to determine the growth rate, expressed in cm per year. If you can age more than one tree of the same species, calculate an average growth rate for the species in this environment. Then divide each tree diameter by the mean growth rate to convert all sizes in your data set to equivalent ages. Use the converted numbers to construct an age-structure diagram for the population.
8. Consult with your physical facilities director, landscaping committees, and ecology or botany faculty to find out if there is a long-range plan for planting trees on your campus. If not, contribute ideas for tree planting and get involved in making landscaping improvements as a class project. A collection of tree species, called an **arboretum**, is a significant asset for a campus. If possible, think about adding species native to your region. They tend to require less maintenance, and provide a valuable and convenient resource for botany instruction.

FOR FURTHER READING

- Butler, R. W. 1992. Great Blue Heron (*Ardea herodias*). In: *The birds of North America*, No. 25 (A. Poole, P. Stettenheim, and F. Gill, eds.) Philadelphia: The Academy of Natural Sciences, Washington, D.C.: The American Ornithologists' Union.
- Deevey, E. S., 1947. Life tables for natural populations of animals. *Quarterly Review of Biology* 22: 283–314.
- Ebert, T. A. 1999. *Plant and animal populations: methods in demography*. Academic Press, San Diego.
- Preston, Richard J. 1989. *North American Trees*. Iowa State University Press, Ames.
- United States Census Bureau. <http://www.census.gov>