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LIFE TABLES, SURVIVORSHIP CURVES, AND POPULATION GROWTH

Objectives

- Discover how patterns of survivorship relate to the classic three types of survivorship curves.
- Learn how patterns of survivorship relate to life expectancy.
- Explore how patterns of survivorship and fecundity affect rate of population growth.

Suggested Preliminary Exercise: Geometric and Exponential Population Models

INTRODUCTION

A **life table** is a record of survival and reproductive rates in a population, broken out by age, size, or developmental stage (e.g., egg, hatchling, juvenile, adult). Ecologists and demographers (scientists who study human population dynamics) have found life tables useful in understanding patterns and causes of mortality, predicting the future growth or decline of populations, and managing populations of endangered species.

Predicting the growth and decline of human populations is one very important application of life tables. As you might expect, whether the population of a country or region increases or decreases depends in part on how many children each person has and the age at which people die. But it may surprise you to learn that population growth or decline also depends on the age at which they have their children. A major part of this exercise will explore the effects of changing patterns of survival and reproduction on population dynamics.

Another use of life tables is in species conservation efforts, such as in the case of the loggerhead sea turtle of the southeastern United States (Crouse et al., 1987). We explore this case in greater depth in Exercise 12, “Stage-Structured Matrix Models,” but generally speaking, the loggerhead population is declining and mortality among loggerhead eggs and hatchlings is very high. These facts led conservation biologists to advocate the protection of nesting beaches. When these measures proved ineffective in halting the population decline, compiling and analyzing a life table for loggerheads indicated that reducing mortality of *older* turtles would have a greater probability of reversing the population decline. Therefore, management efforts shifted to persuading fishermen to install turtle exclusion devices on their nets to prevent older turtles from drowning.

Life tables come in two varieties: cohort and static. A **cohort life table** follows the survival and reproduction of all members of a cohort from birth to death. A cohort is the set of all individuals born, hatched, or recruited into a population during a defined time interval. Cohorts are frequently defined on an annual basis (e.g., all individuals born in 1978), but other time intervals can be used as well.

A **static life table** records the number of living individuals of each age in a population and their reproductive output. The two varieties have distinct advantages and disadvantages, some of which we discuss below.

Life tables (whether cohort or static) that classify individuals by age are called **age-based life tables**. Such life tables treat age the same way we normally do: that is, individuals that have lived less than one full year are assigned age zero; those that have lived one year or more but less than two years are assigned age one; and so on. Life tables represent age by the letter x , and use x as a subscript to refer to survivorship, fecundity, and so on, for each age.

Size-based and stage-based life tables classify individuals by size or developmental stage, rather than by age. Size-based and stage-based tables are often more useful or more practical for studying organisms that are difficult to classify by age, or whose ecological roles depend more on size or stage than on age. Such analyses are more complex, however, and we will leave them for a later exercise.

Cohort Life Tables

To build a cohort life table for, let's say, humans born in the United States during the year 1900, we would record how many individuals were born during the year 1900, and how many survived to the *beginning* of 1901, 1902, etc., until there were no more survivors. This record is called the **survivorship schedule**. Unfortunately, different textbooks use different notations for the number of survivors in each age; some write this as S_x , some a_x , and some n_x . We will use S_x here.

We must also record the **fecundity schedule**—the number of offspring born to individuals of each age. The total number of offspring is usually divided by the number of individuals in the age, giving the average number of offspring per individual, or per capita fecundity. Again, different texts use different notations for the fecundity schedule, including b_x (the symbol we will use) or m_x .¹

Many life tables count only females and their female offspring; for animals with two sexes and equal numbers of males and females of each age, the resulting numbers are the same as if males and females were both counted. For most plants, hermaphroditic animals, and many other organisms, distinctions between the sexes are nonexistent or more complex, and life table calculations may have to be adjusted.

Static Life Tables

A static life table is similar to a cohort life table but introduces a few complications. For many organisms, especially mobile animals with long life spans, it can be difficult or impossible to follow all the members of a cohort throughout their lives. In such cases, population biologists often count how many individuals of each age are alive *at a given time*. That is, they count how many members of the population are currently in the 0–1-year-old class, the 1–2-year-old class, etc.

These counts can be used as if they were counts of survivors in a cohort, and all the calculations described below for a cohort life table can be performed using them. In doing this, however, the researcher must bear in mind that she or he is assuming that age-specific survivorship and fertility rates have remained constant since the oldest members of the population were born. This is usually not the case and can lead to some

¹ Some demographers use the term fecundity to be the physiological maximum number of eggs produced per female per year, and the term fertility to be the number of *offspring* produced per female per year. In this book, we will assume that the two are equivalent unless noted otherwise.

strange results, such as negative mortality rates. These are often resolved by averaging across several ages, or by making additional assumptions. We will avoid these complications by focusing this exercise on cohort life tables.

Quantities in a Life Table

Survivorship and fecundity schedules are the raw data of any life table. From them we can calculate a variety of other quantities, including age-specific rates of survival, mortality, fecundity, survivorship curves, life expectancy, generation time, net reproductive rate, and intrinsic rate of increase. Which of these quantities you calculate will depend on your goals in constructing the life table. Rather than presenting all the quantities that may appear in a life table, we will present two applications of life tables, using the quantities needed in each case. First you will build life tables that illustrate the three classic **survivorship curves**. These curves are a powerful visual tool for understanding the patterns of survivorship and mortality in populations. Then you will use a life table to predict the future growth or decline of a population. This kind of analysis is frequently used in studies of human populations, in management of fish and game, and in attempts to rescue endangered species.

Survivorship Curves

Ecology textbooks frequently present the three classic survivorship curves, called type I, type II, and type III (Figure 1). To understand survivorship curves you can use survivorship schedules (S_x) to calculate and graph **standardized survivorship** (l_x), **age-specific survivorship** (g_x), and **life expectancy** (e_x).

Standardized Survival Schedule (l_x). Because we want to compare cohorts of different initial sizes, we standardize all cohorts to their initial size at time zero, S_0 . We do this by dividing each S_x by S_0 . This proportion of original numbers surviving to the beginning of each interval is denoted l_x , and calculated as

$$l_x = \frac{S_x}{S_0} \quad \text{Equation 1}$$

We can also think of l_x as the probability that an individual survives from birth to the beginning of age x . Because we begin with *all* the individuals born during the year (or other interval), l_x always begins at a value of one (i.e., S_0/S_0), and can only decrease with time. At the last age, k , S_k is zero.

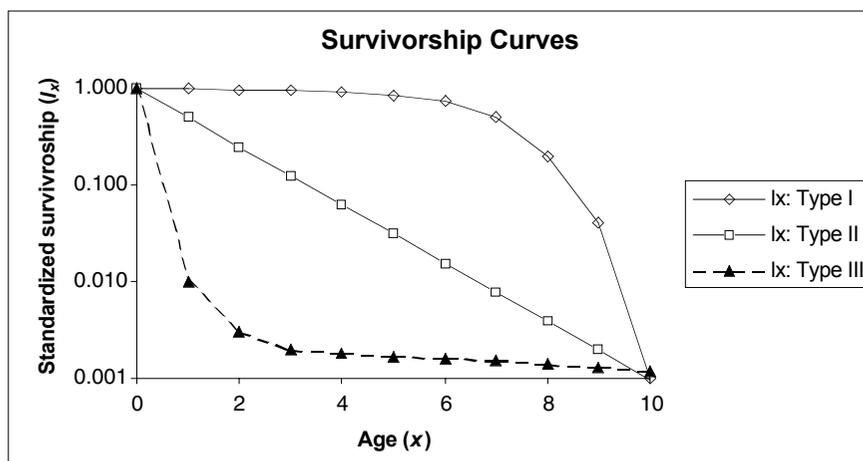


Figure 1 Hypothetical survivorship curves. Note that the y -axis has a logarithmic scale. Type 1 organisms have high survivorship throughout life until old age sets in, and then survivorship declines dramatically to 0. Humans are type 1 organisms. Type III organisms, in contrast, have very low survivorship early in life, and few individuals live to old age.

Age-Specific Survivorship (g_x). Standardized survivorship, l_x , gives us the probability of an individual surviving from birth to the beginning of age x . But what if we want to know the probability that an individual who has already survived to age x will survive to age $x + 1$? We calculate this age-specific survivorship as $g_x = l_{x+1}/l_x$ or equivalently,

$$g_x = \frac{S_{x+1}}{S_x} \quad \text{Equation 2}$$

Life Expectancy (e_x). You may have heard another demographic statistic, life expectancy, mentioned in discussions of human populations. Life expectancy is how much longer an individual of a given age can be expected to live beyond its present age. Life expectancy is calculated in three steps. First, we compute the proportion of survivors at the mid-point of each time interval (L_x —note the capital L here) by averaging l_x and l_{x+1} ; that is,

$$L_x = \frac{l_x + l_{x+1}}{2} \quad \text{Equation 3}$$

Second, we sum all the L_x values from the age of interest (n) up to the oldest age, k :

$$T_x = \sum_{x=n}^k L_x \quad \text{Equation 4}$$

Finally, we calculate life expectancy as

$$e_x = \frac{T_x}{l_x} \quad \text{Equation 5}$$

(note the lowercase l_x).

Life expectancy is age-specific—it is the expected number of time-intervals remaining to members of a given age. The statistic most often quoted (usually without qualification) is the life expectancy at birth (e_0). As you will see, the implications of e_0 depend greatly on the survivorship schedule.

Population Growth or Decline

We frequently want to know whether a population can be expected to grow, shrink, or remain stable, given its current age-specific rates of survival and fecundity. We can determine this by computing the **net reproductive rate** (R_0). To predict long-term changes in population size, we must use this net reproductive rate to estimate the intrinsic rate of increase (r).

Net Reproductive Rate (R_0) We calculate net reproductive rate (R_0) by multiplying the standardized survivorship of each age (l_x) by its fecundity (b_x), and summing these products:

$$R_0 = \sum_{x=0}^k l_x b_x \quad \text{Equation 6}$$

The net reproductive rate is the lifetime reproductive potential of the average female, adjusted for survival. Assuming survival and fertility schedules remain constant over time, if $R_0 > 1$, then the population will grow exponentially. If $R_0 < 1$, the population will shrink exponentially, and if $R_0 = 1$, the population size will not change over time. You may be tempted to conclude the $R_0 = r$, the intrinsic rate of increase of the exponential model. However, this is not quite correct, because r measures population change in absolute units of time (e.g., years) whereas R_0 measures population change in terms of generation time. To convert R_0 into r , we must first calculate generation time (G), and then adjust R_0 .

Generation Time. Generation time is calculated as

$$G = \frac{\sum_{x=0}^k l_x b_x x}{\sum_{x=0}^k l_x b_x} \quad \text{Equation 7}$$

For organisms that live only one year, the numerator and denominator will be equal, and generation time will equal one year. For all longer-lived organisms, generation time will be greater than one year, but exactly how much greater will depend on the survival and fertility schedules. A long-lived species that reproduces at an early age may have a shorter generation time than a shorter-lived one that delays reproduction.

Intrinsic Rate of Increase. We can use our knowledge of exponential population growth and our value of R_0 to estimate the intrinsic rate of increase (r) (Gotelli 2001). Recall from Exercise 7, "Geometric and Exponential Population Models," that the size of an exponentially growing population at some arbitrary time t is $N_t = N_0 e^{rt}$, where e is the base of the natural logarithms and r is the intrinsic rate of increase. If we consider the growth of such a population from time zero through one generation time, G , it is

$$N_G = N_0 e^{rG}$$

Dividing both sides by N_0 gives us

$$\frac{N_G}{N_0} = e^{rG}$$

We can think of N_G/N_0 as roughly equivalent to R_0 ; both are estimates of the rate of population growth over the period of one generation.

Substituting R_0 into the equation gives us

$$R_0 \approx e^{rG}$$

Taking the natural logarithm of both sides gives us

$$\ln(R_0) \approx rG$$

and dividing through by G gives us an estimate of r :

$$r \approx \frac{\ln(R_0)}{G} \quad \text{Equation 8}$$

Euler's Correction to r . The value of r as estimated above is usually a good approximation (within 10%), and it will suffice for most purposes. Some applications, however, may require a more precise value. To improve this estimate, you must solve the Euler equation:

$$1 = \sum_{x=0}^k e^{-rx} l_x b_x \quad \text{Equation 9}$$

The only way to solve this equation is by trial and error. We already know the values of $l_x b_x$ and e (it is the base of the natural logarithms, $e \approx 2.7183$), so we can plug in various guesses for r until Equation 9 comes up 1.0. That will tell us the corrected value of r . Fortunately, a spreadsheet is an ideal medium for such trial and error solution-hunting.

Finally, we can use our estimate of r (uncorrected or corrected) to predict the size of the population in the future. In this exercise, you will adjust survivorship and fecundity schedules and observe the effects on population growth or decline. This kind of analysis is done for human populations to predict the effects of changes in medical care and birth control programs. If we assume that all age groups are roughly equivalent in size, a similar analysis can be done for endangered species to determine what intervention may be most effective in promoting population growth. The same analysis can be applied to pest species to determine what intervention may be most effective in reducing population size.

PROCEDURES

Our purpose here is to show how survivorship curves are generated and what they mean. You will use survivorship schedules to calculate and graph l_x , g_x , and e_x , resulting in survivorship curves of type I, II, or III. In the final section of the exercise you will see how this information can be used to predict population rise and decline.
As always, save your work frequently to disk.

INSTRUCTIONS

A. Generate survivorship curves.

1. Open a new spreadsheet and set up titles and column headings as shown in Figure 2.

2. Set up a linear series from 0 to 11 in column A.

3. Enter the values shown in Figure 2 for cells B4–D15.

4. Enter formulae to calculate the standardized survivorship, l_x , for each survivorship schedule.

5. Enter formulae to calculate age-specific survivorship, g_x , for each survivorship schedule.

ANNOTATION

These are all literals, so just select the appropriate cells and type them in.

	A	B	C	D	E	F	G	H	I	J
1	Life Tables and Survivorship Curves									
2	Survivorship curves									
3	Age (x)	S _x : Type I	S _x : Type II	S _x : Type III	l _x : Type I	l _x : Type II	l _x : Type III	g _x : Type I	g _x : Type II	g _x : Type III
4	0	1000	2048	10000						
5	1	990	1024	100						
6	2	970	512	30						
7	3	940	256	20						
8	4	900	128	18						
9	5	850	64	17						
10	6	750	32	16						
11	7	500	16	15						
12	8	200	8	14						
13	9	40	4	13						
14	10	1	2	12						
15	11	0	0	0						

Figure 2

In cell A4 enter the value zero.

In cell A5 enter the formula =A4+1. Copy the formula in cell A5 into cells A6–A15.

These are the raw data of three survivorship schedules—one for each survivorship curve. Each number is the number of surviving individuals from a cohort at each age.

In cell E4 enter the formula =B4/\$B\$4. Copy this formula into cells E5–E15.

This corresponds to Equation 1:

$$l_x = \frac{S_x}{S_0}$$

Note the use of a relative cell address in the numerator and an absolute cell address in the denominator. The formula in cell F4 should be =C4/\$C\$4, and the formula in cell G4 should be =D4/\$D\$4. Copy cells F4–G4 down to F15–G15.

In cell H4 enter the formula =B5/B4. Copy this formula into cells H5–H14. Do not copy it into cell H15, because the formula would attempt to divide by zero and thus generate an error. Copy cells H4–H14 into cells I4–J14.

This corresponds to Equation 2:

$$g_x = \frac{S_{x+1}}{S_x}$$

Note that all cell addresses are relative.

These are all literals, so just select the appropriate cells and type them in.

6. Enter titles and column headings in cells A17–J18 as shown in Figure 3.

	A	B	C	D	E	F	G	H	I	J
17	Age-specific life expectancy									
18	Age (x)	l_x : Type I	l_x : Type II	l_x : Type III	l_x : Type I	l_x : Type II	l_x : Type III	e_x : Type I	e_x : Type II	e_x : Type III
19	0	1.0000	1.0000	1.0000						
20	1	0.9900	0.5000	0.0100						
21	2	0.9700	0.2500	0.0030						
22	3	0.9400	0.1250	0.0020						
23	4	0.9000	0.0625	0.0018						
24	5	0.8500	0.0313	0.0017						
25	6	0.7500	0.0156	0.0016						
26	7	0.5000	0.0078	0.0015						
27	8	0.2000	0.0039	0.0014						
28	9	0.0400	0.0020	0.0013						
29	10	0.0010	0.0010	0.0012						
30	11	0.0000	0.0000	0.0000						

Figure 3

7. Copy the values of age from cells A4–A15 into cells A19–A30.

8. Echo the values of l_x from cells E4–G15 in cells B19–D30.

9. Enter formulae to calculate the number of survivors at the midpoint of each age, L_x .

10. Enter formulae to calculate life expectancy, e_x , for each age.

Select cells A4–A15. Copy. Select cell A19. Paste.

In cell B19 enter the formula =E4. Copy this formula into cells C19 and D19. Copy cells B19–D19 into cells B20–D30.

Doing it this way, rather than copying and pasting the values, will automatically update this part of the spreadsheet if you change any of the S_x values in cells B4–D15.

In cell E19 enter the formula =(B19+B20)/2. Copy this formula into cells F19 and G19. Copy cells E19–G19 into cells E30–G30.

This corresponds to Equation 3:

$$L_x = \frac{l_x + l_{x+1}}{2}$$

In cell H19 enter the formula =SUM(E19:E\$30)/B19. Copy the formula from cell H19 into cells I19 and J19.

Copy cells H19–J19 into cells H20–J29.

The portion SUM(E19:E\$30) corresponds to Equation 4:

$$T_x = \sum_{x=n}^k L_x$$

The entire formula corresponds to Equation 5:

$$e_x = \frac{T_x}{l_x}$$

11. Your spreadsheet is complete. Save your work.

12. Graph standardized survivorship, l_x , against age.

Do not copy the formula into row 30, because l_x there is zero, and so Equation 5 would be undefined.

Select cells A3–A15. Select cells E3–G15 and create an XY graph. Edit your graph for readability. It should resemble Figure 4.

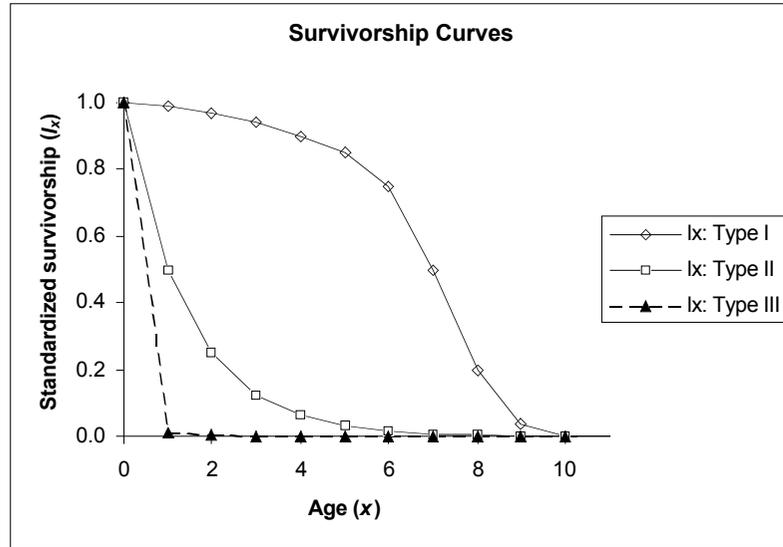


Figure 4

13. Change the y -axis to a logarithmic scale.

Double-click on the y -axis and choose the Number tab in the resulting dialog box. Set the number of decimal places to 3. Choose the Scale tab. Check the box for Logarithmic Scale. Set the Major unit to 10, and set Value (X) axis Crosses at to 0.0001. Your graph should resemble Figure 5.

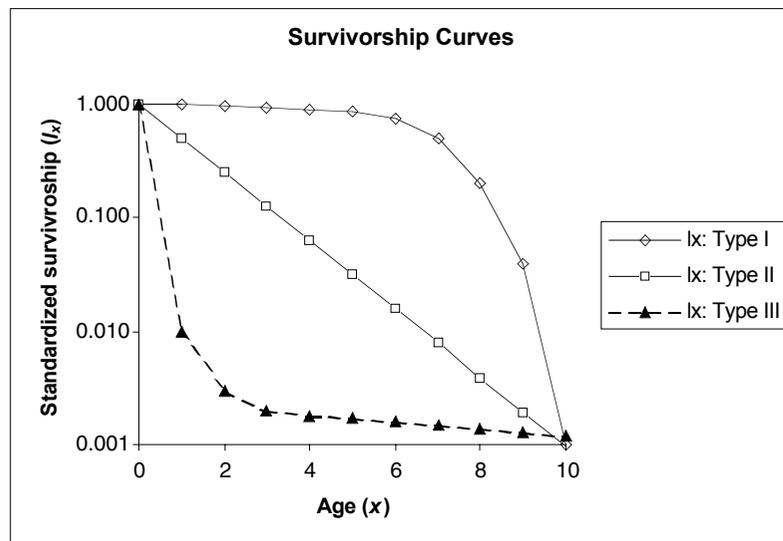


Figure 5 Survivorship curves are always plotted with a logarithmic y -axis. Can you see why?

14. Graph age-specific survival g_x against age.

Select cells A3–A14 and cells H3–J14. Make an XY graph. Your graph should resemble Figure 6.

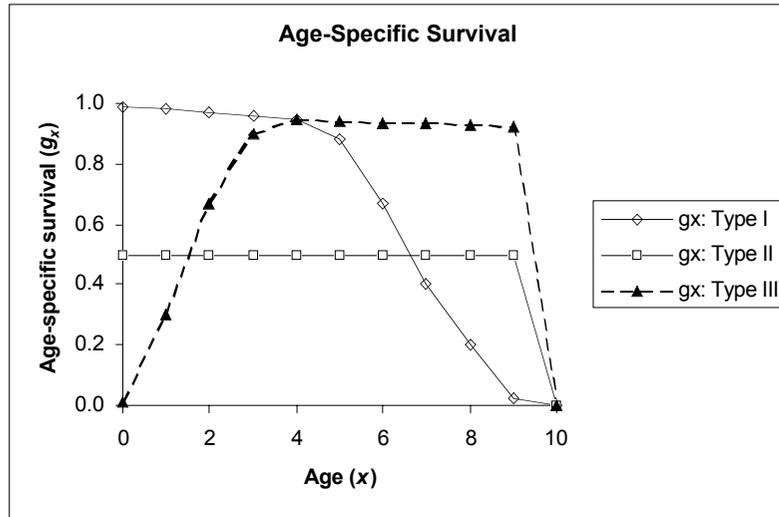


Figure 6

15. Graph life expectancy, e_x , against age.

Select cells A18–A29 and cells H18–J29. Do not include row 30 in either block. Make an XY graph. Your graph should resemble Figure 7.

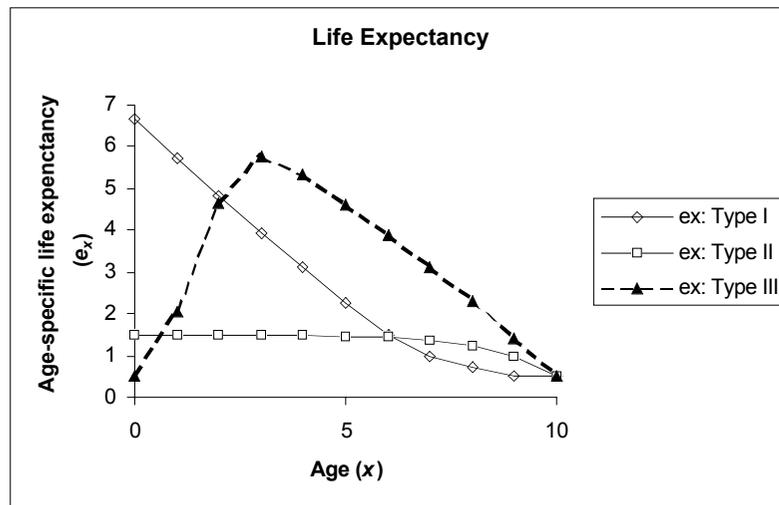


Figure 7

B. Population growth and decline.

1. Open a new spreadsheet and set up titles and column headings as shown in Figure 8. Set up a linear series of ages from 0 to 4 in column A. Enter the values shown for S_x .

We will use fewer ages here to simplify the manipulations that you will do later.

	A	B	C	D	E	F	G
1	Cohort Life Table: Fertility, Survival, and Population Growth						
2							
3	Age (x)	S_x	l_x	b_x	$(l_x)(b_x)$	$(x)(l_x)(b_x)$	$(e^{-rx})(l_x)(b_x)$
4	0	1000	1.0000	0.00000	0.0000	0.0000	0.0000
5	1	900	0.9000	0.00000	0.0000	0.0000	0.0000
6	2	250	0.2500	4.00000	1.0000	2.0000	1.0000
7	3	10	0.0100	0.00000	0.0000	0.0000	0.0000
8	4	0	0.0000	0.00000	0.0000	0.0000	0.0000
9				Total	1.0000	2.0000	1.0000
10	R_0	1.00000					
11	G	2.00000					
12	r est.	0.00000					
13	r adj.	0.00000					
14	Should be 1	1.00000					

Figure 8

2. Enter a formula to calculate standardized survival, l_x .

3. Enter the values shown for age-specific fertility, b_x .

4. Enter a formula to calculate the product of standardized survival times age-specific fertility, $l_x b_x$.

5. Enter a formula to calculate net reproductive rate, R_0 .

6. Echo the value of R_0 in cell B10.

7. Enter a formula to calculate the product $l_x b_x x$.

8. Enter a formula to calculate the sum of the products $l_x b_x x$.

9. Enter a formula to calculate generation time, G .

In cell C4 enter the formula `=B4/B4`. Copy this formula into cells C5–C8. Do not copy into cell C9.

Again, this corresponds to Equation 1. Note the use of a relative cell address in the numerator, and an absolute cell address in the denominator.

Enter the value 0.00 into cells D4, D5, D7, and D8, Enter the value 4.00 into cell D6.

In cell E4 enter the formula `=C4*D4`. Copy this formula into cells E5–E8.

In cell E9 enter the formula `=SUM(E4:E8)`.

This corresponds to Equation 6:

$$R_0 = \sum_{x=0}^k l_x b_x$$

In cell B10 enter the formula `=E9`.

We do this because you will soon change the values of S_x and b_x , and this layout will make it easier to compare the effects of different survival and fertility schedules on population growth or decline.

In cell F4 enter the formula `=E4*A4`.

This is an intermediate step in calculating generation time, G . Copy the formula from cell F4 into cells F5–F8.

In cell F9 enter the formula `=SUM(F4:F8)`.

This is another intermediate step in calculating generation time, G .

In cell B11 enter the formula `=F9/E9`.

This corresponds to Equation 7:

10. Enter a formula to estimate the intrinsic rate of increase, r .

11. Your spreadsheet is complete. Save your work.

12. Create a survivorship curve from your S_x values.

$$G = \frac{\sum_{x=0}^k l_x b_x x}{\sum_{x=0}^k l_x b_x}$$

In cell B12 enter the formula =LN(B10)/B11.
This corresponds to Equation 8:

$$r \approx \frac{\ln(R_0)}{G}$$

Follow the procedures in Steps 12 and 13 of Section A. Your graph should resemble Figure 9.

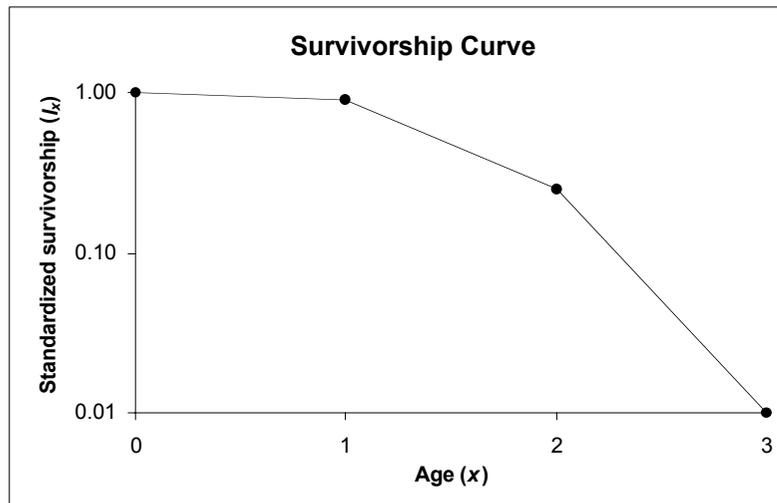


Figure 9

C. Euler's correction (Optional)

1. (*Optional) Enter a guess for the correct value of r into cell B13.

2. Enter a formula to calculate $e^{-rx}l_x b_x$.

3. Enter a formula to compute Euler's equation.

4. In cell B14, echo the result of the formula in cell G9.

Start by entering the estimated value of r from cell B12. You will see how to use this guess below.

In cell G4 enter the formula =EXP(-\$B\$13*A4)*E4.
This is an intermediate step in applying Euler's correction to the estimate of r calculated in Step 11 of Section B. Note that the formula uses your guess for the value of r .

In cell G9 enter the formula =SUM(G4:G8).
This corresponds to the right side of Equation 9:

$$\sum_{x=0}^k e^{-rx} l_x b_x$$

If your guess for r is correct, this formula will yield a value of 1.0.

In cell B14 enter the formula =G9.
Again, this is simply a convenient layout for comparing the effects of changing S_x and b_x .

QUESTIONS

1. Why do we plot survivorship curves on a semi-log graph?
2. What do the shapes of the survivorship curves tell us about patterns of survival and mortality? Compare each curve to the corresponding graph of age-specific survivorship.
3. How can we interpret the graph of life expectancies?
4. Use the S_x values for real populations provided in the Appendix at the end of this exercise to compare survivorship curves between animal species. You may also wish to visit the U.S. Census Bureau's web site (<http://www.census.gov/>), from which you can download survivorship data for human populations in most of the countries of the world.
5. What effect does changing the fecundity schedule have on R_0 , G , and r ?
6. What effect does changing the survival schedule have on R_0 , G , and r ?

LITERATURE CITED

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Appendix: SAMPLE SURVIVORSHIP SCHEDULES FROM NATURAL POPULATIONS OF ANIMALS

In all cases, assume S_x for the next age after the oldest in the table is 0.

Table A. Survivorship schedule for Dall Mountain Sheep (*Ovis dalli dalli*).

Age (years)	S_x	Age (years)	S_x
0	1000	7	640
1	801	8	571
2	789	9	439
3	776	10	252
4	764	11	96
5	734	12	6
6	688	13	3

Data from Deevey (1947). Numbers have been standardized to $S_0 = 1000$.

Table B. Survivorship schedule for the Song Thrush.

Age (years)	S_x	Age (years)	S_x
0	1000	5	30
1	444	6	17
2	259	7	6
3	123	8	3
4	51		

Data from Deevey (1947). Numbers have been standardized to $S_0 = 1000$.

Table C. Survivorship and fertility schedules for the barnacle *Balanus glandula*.

Age (years)	S_x	Age (years)	S_x
0	1000	7	640
1	801	8	571
2	789	9	439
3	776	10	252
4	764	11	96
5	734	12	6
6	688	13	3

Data are from Connell (1970). Values of S_4 and S_6 have been interpolated and rounded to the next integer.

