

Life Tables, Survivorship Curves, and Population Growth

Objectives:

- Discover how patterns of survivorship relate to the classic 3 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.
- Learn more about how to use the remarkable functionality of Excel 2010 to plot and analyze wildlife population data.

Life Tables

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). Wildlife population ecologists have found life tables useful in understanding patterns and causes of mortality, predicting the future growth or decline of populations, and managing populations of T&E species.

Predicting the growth and decline of a wildlife population is an important application of life table use. As you might expect, whether the population increases or decreases depends in part on reproductive rate (i.e., litter or clutch size) and longevity, especially how long the females produce young. But it may surprise you to learn that population growth or decline is also driven by the age at which the females begin to have their young. 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 loggerhead sea turtles (*Caretta caretta*), which occur off the coast of the southeastern United States. We will explore loggerhead sea turtle population dynamics in more detail in problem set 3, but generally speaking, loggerhead populations are declining in part because egg and hatchling mortality is high. This situation has 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 (TEDs) on their nets to prevent older turtles from drowning.

There are 2 types of life tables: 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 black bear (*Ursus americanus*) cubs born in the Ozarks in 2014 form a cohort), but other time intervals such as days, weeks, or months 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 2 varieties of life tables have distinct advantages and disadvantages, some of which are discussed below.

Life tables (cohort or static) that classify individuals by age are called **age-based life tables**. Such life tables treat age the way it's normally treated: that is, individuals that have lived <1 full year are assigned age 0; those that have lived ≥ 1 year but <2 years are assigned age 1; and so on. Life tables represent age by the letter x , and use x as a subscript to refer to age-specific survivorship (g_x) and age-specific life expectancy (e_x) 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. We will not deal with these kinds of life tables in this problem set.

Cohort Life Tables

To build a cohort life table for, let's say, black bears born in the Ozarks in 2010, we would record how many individuals were born during the year 2010, and how many survived to the *beginning* of 2011, 2012, 2013, etc., until there were no more survivors in that cohort. This record is called the **survivorship schedule**. Unfortunately, different ecology 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 . I will use S_x .

We must also record the **fecundity schedule**, the number of offspring born to females of each age class. The total number of offspring is usually divided by the number of individuals in the age class, giving the mean number of offspring produced per individual. Again, different texts use different notations for the fecundity schedule, including b_x (the symbol we will use) or m_x . Since fecundity schedules include the number of offspring born to females of each age class, most life tables deal with only females and their female offspring.

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 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 age class, the 1–2-year-old age 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 is assuming that age-specific survivorship and fertility rates have remained constant since the oldest members of the population were born. This is an important assumption. So keep it in mind. Age-specific survival and reproductive rates, however, are rarely constant through time, which can lead to some strange results, such as negative mortality rates. We can resolve some of these problems by averaging across several ages, or by making additional assumptions. We will avoid these complications in this problem set by focusing 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. The 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, here I present 2 applications of life tables. First, you will build life tables that illustrate the 3 classic **survivorship curves**. These curves are a powerful visual tool for understanding the patterns of survivorship and mortality in populations. Second, you will use a life table to predict the future growth or decline of a wildlife population.

Survivorship Curves

Ecology textbooks frequently present the 3 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).

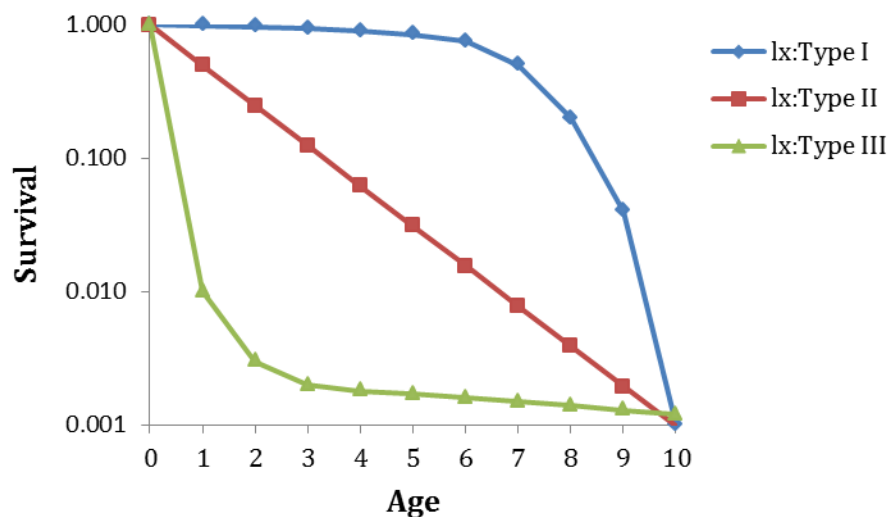


Figure 1. Hypothetical survivorship curves. Note that the y-axis has a logarithmic scale. Type 1 organisms have high survivorship throughout life until old age sets in, and then survivorship declines dramatically. Humans, for example, are type 1 organisms. Type III organisms, in contrast, have very low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

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 0, S_0 . 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

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

You 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 1 (i.e., S_0/S_0), and can only decrease with time. At the last age, k , $S_k = 0$.

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 $x + 1$? You can 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). 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 3 steps.

Step 1: 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,

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

Step 2: Sum all the L_x values from the age of interest (n) up to the oldest age, k :

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

(Read this equation as “The sum of L_x as x goes from n to k .”)

Step 3: 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 (e.g., years) remaining to members of a given age. The statistic most often quoted 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 wildlife 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 the net reproductive rate to estimate the intrinsic rate of increase (r).

Net Reproductive Rate (R_0). The net reproductive rate is the lifetime reproductive potential of the average female, adjusted for survival. We can calculate it by multiplying the standardized survivorship of each age (l_x) by its fecundity (b_x), and summing these products:

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

(Read this equation as “The sum of l_x times b_x as x goes from 0 to k .”)

Assuming survival and fertility schedules remain constant over time (an unreasonable assumption in most situations), 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 that $R_0 = r$. However, this is not quite correct: r measures population change in absolute units of time (e.g., years); R_0 measures population change in terms of generation time.

We can convert R_0 into r . First we must calculate generation time (G). Then we must 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 1 year, the numerator and denominator will be equal, and generation time will equal 1 year. For all longer-lived organisms, generation time will be >1 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 species that delays reproduction.

Intrinsic Rate of Increase. We can use our knowledge of exponential population growth and our value of R_0 to estimate r . 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 (2.72) and r is the intrinsic rate of increase. If we consider the growth of such a population from time 0 through 1 generation time, G , it is

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

Dividing both sides by N_0 gives us

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

(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 1 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 :

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

Equation 8

Finally, we can use our estimate of r 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. If we assume that all age groups are roughly equivalent in size, a similar analysis can be done for T&E 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

My purpose here is to show you how survivorship curves are generated and what they mean. In section A: Survivorship curves, we 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 section B: Population growth and decline, you will see how this information can be used to predict population rise and decline.

General directions followed by a step-by-step breakdown of these directions, as well as other explanatory comments, are given. If you are not familiar with an operation called for in these instructions, refer to “Spreadsheet Hints and Tips,” available on the Wildlife Ecology course website (http://www.afrc.uamont.edu/whited/wildlife_ecology_syllabus.htm.)

I hope that, with practice, you will gain enough skill in using spreadsheets that you will be able to modify my models, or create your own from scratch, to suit your own needs. By the way, as you enter data and formulas in this exercise, think about what you are doing and why you are doing it. You will use spreadsheets for years to come. Use this problem set as an opportunity to sharpen and improve your Excel skills. As always, save your work frequently.

Instructions

A. Survivorship curves

1. Open a new spreadsheet and set up titles and column headings in cells A1–J3 as shown in Figure 2. These are all called literals, so just select the appropriate cells and type them in.

- Set up a linear series from 0 to 11 in column A. In cell A4 enter the value 0. In cell A5 enter the formula =A4+1. Copy the formula in cell A5 into cells A6–A15.

	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

- Enter the values shown in Figure 2 for cells B4–D15. These are the raw data for the 3 survivorship schedules, 1 for each survivorship curve. Each number is the number of surviving individuals from a cohort at each age.
- Enter formulae to calculate the standardized survivorship, l_x , for each survivorship schedule. In cell E4 enter the formula =B4/\$B\$4. Copy this formula into cells E5–E15. This corresponds to Equation 1. 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.
- Enter formulae to calculate age-specific survivorship, g_x , for each survivorship schedule. 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 0 and thus generate an error. Copy cells H4–H14 into cells I4–J14. This corresponds to Equation 2. Note that all cell addresses are relative. At this point, your spreadsheet should look like Figure 3.
- Enter titles and column headings in cells A17–J18 as shown in Figure 4. These are all literals, so just select the appropriate cells and type the words and letters 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	1	1	1	0.99	0.5	0.01
5	1	990	1024	100	0.99	0.5	0.01	0.979798	0.5	0.3
6	2	970	512	30	0.97	0.25	0.003	0.969072	0.5	0.66666667
7	3	940	256	20	0.94	0.125	0.002	0.957447	0.5	0.9
8	4	900	128	18	0.9	0.0625	0.0018	0.944444	0.5	0.94444444
9	5	850	64	17	0.85	0.03125	0.0017	0.882353	0.5	0.94117647
10	6	750	32	16	0.75	0.015625	0.0016	0.666667	0.5	0.9375
11	7	500	16	15	0.5	0.007813	0.0015	0.4	0.5	0.93333333
12	8	200	8	14	0.2	0.003906	0.0014	0.2	0.5	0.92857143
13	9	40	4	13	0.04	0.001953	0.0013	0.025	0.5	0.92307692
14	10	1	2	12	0.001	0.000977	0.0012	0	0	0
15	11	0	0	0	0	0	0			

Figure 3

	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	1	1	1	0.99	0.5	0.01
5	1	990	1024	100	0.99	0.5	0.01	0.979798	0.5	0.3
6	2	970	512	30	0.97	0.25	0.003	0.969072	0.5	0.66666667
7	3	940	256	20	0.94	0.125	0.002	0.957447	0.5	0.9
8	4	900	128	18	0.9	0.0625	0.0018	0.944444	0.5	0.94444444
9	5	850	64	17	0.85	0.03125	0.0017	0.882353	0.5	0.94117647
10	6	750	32	16	0.75	0.015625	0.0016	0.666667	0.5	0.9375
11	7	500	16	15	0.5	0.007813	0.0015	0.4	0.5	0.93333333
12	8	200	8	14	0.2	0.003906	0.0014	0.2	0.5	0.92857143
13	9	40	4	13	0.04	0.001953	0.0013	0.025	0.5	0.92307692
14	10	1	2	12	0.001	0.000977	0.0012	0	0	0
15	11	0	0	0	0	0	0			
16										
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

Figure 4

7. Copy the values of age from cells A4–A15 into cells A19–A30. Select cells A4–A15. Copy. Select cell A19. Paste.
8. Echo the values of l_x from cells E4–G15 in cells B19–D30. To do that, in cell B19 enter the formula =E4. Copy this formula into cells C19 and D19. Copy cells B19–D19 down 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. Nifty!
9. Enter formulae to calculate the number of survivors at the midpoint of each age, L_x . In cell E19 enter the formula =(B19+B20)/2. Copy this

formula into cells F19 and G19. Copy cells E19–G19 down to E20–G30. This corresponds to Equation 3.

10. Enter formulae to calculate life expectancy, e_x , for each age. 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 of the formulae **SUM(E19:E\$30)** corresponds to Equation 4. The entire formula corresponds to Equation 5. Do not copy the formula into row 30, because l_x in age class 11 is 0, and so Equation 5 would be undefined.
11. Your spreadsheet is complete and should look like Figure 5.

	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	1	1	1	0.99	0.5	0.01
5	1	990	1024	100	0.99	0.5	0.01	0.979798	0.5	0.3
6	2	970	512	30	0.97	0.25	0.003	0.969072	0.5	0.66666667
7	3	940	256	20	0.94	0.125	0.002	0.957447	0.5	0.9
8	4	900	128	18	0.9	0.0625	0.0018	0.944444	0.5	0.94444444
9	5	850	64	17	0.85	0.03125	0.0017	0.882353	0.5	0.94117647
10	6	750	32	16	0.75	0.015625	0.0016	0.666667	0.5	0.9375
11	7	500	16	15	0.5	0.007813	0.0015	0.4	0.5	0.93333333
12	8	200	8	14	0.2	0.003906	0.0014	0.2	0.5	0.92857143
13	9	40	4	13	0.04	0.001953	0.0013	0.025	0.5	0.92307692
14	10	1	2	12	0.001	0.000977	0.0012	0	0	0
15	11	0	0	0	0	0	0			
16										
17	Age-specific life expectancy									
18	Age (x)	l_x : Type I	l_x : Type II	l_x : Type III	e_x : Type I	e_x : Type II	e_x : Type III	e_x : Type I	e_x : Type II	e_x : Type III
19	0	1	1	1	0.995	0.75	0.505	6.641	1.4991	0.5255
20	1	0.99	0.5	0.01	0.98	0.375	0.0065	5.70303	1.4982	2.05
21	2	0.97	0.25	0.003	0.955	0.1875	0.0025	4.810309	1.4964	4.66666667
22	3	0.94	0.125	0.002	0.92	0.09375	0.0019	3.947872	1.4928	5.75
23	4	0.9	0.0625	0.0018	0.875	0.0469	0.00175	3.101111	1.4856	5.33333333
24	5	0.85	0.0313	0.0017	0.8	0.02345	0.00165	2.254118	1.46805112	4.61764706
25	6	0.75	0.0156	0.0016	0.625	0.0117	0.00155	1.488	1.44230769	3.875
26	7	0.5	0.0078	0.0015	0.35	0.00585	0.00145	0.982	1.38461538	3.1
27	8	0.2	0.0039	0.0014	0.12	0.00295	0.00135	0.705	1.26923077	2.28571429
28	9	0.04	0.002	0.0013	0.0205	0.0015	0.00125	0.525	1	1.42307692
29	10	0.001	0.001	0.0012	0.0005	0.0005	0.0006	0.5	0.5	0.5
30	11	0	0	0	0	0	0			

Figure 5

12. Graph standardized survivorship, l_x , against age. Select cells A3–A15. Hold down the Ctrl button and select cells E3–G15. Create an XY graph by opening Insert | Charts | Other Charts | All Chart Types... | X Y (Scatter), and then select the scatter plot type with straight lines and

markers. Click OK. Your graph will appear. Click on the graph and Chart Tools will pop up. Edit your graph for readability using the Design, Layout, and Format tabs available with Chart Tools. Remove gridlines, add chart and axes titles, and give each function an easily distinguished line type and color. Change the maximum x-axis value to 10 by clicking on the horizontal axis. Within Chart Tools |Format | Axes | Primary Horizontal Axis | More Primary Horizontal Axis Options change the **Maximum** value to 10. While you are there change the **Major** unit to 1 so that every age class number (0-10) is displayed on the x-axis. Don't be afraid to play around manipulating your graph to make it look the way you want it to. It is important that you know how to create Excel graphs. Your graph should resemble Figure 6.

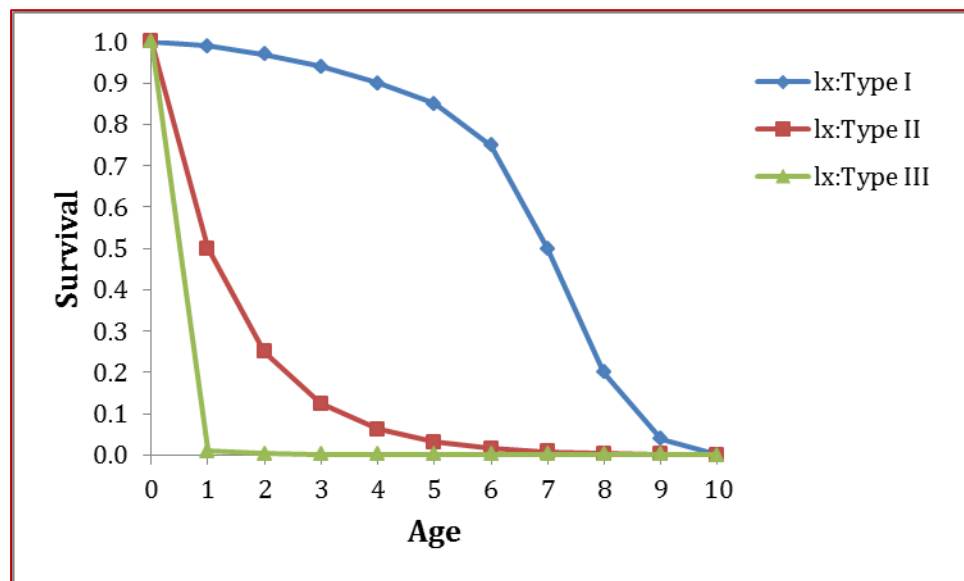


Figure 6

- Repeat step 12 and create another graph of standardized survivorship against age and manipulate it to make it look like Figure 6. Then change the y-axis to a logarithmic scale. Because negative or 0 values cannot be plotted correctly on a log graph, and only positive values can be interpreted on a log scale, you must change the value at which the horizontal axis crosses. Double click on the vertical axis to open a Format Axis dialog box (see Figure 7). Select the Axis Options tab. At the bottom of the window, make sure Axis Value is selected under the "Horizontal Axis Crosses" options (Figure 7). Then type in 0.001. At the top of the window, also change the Minimum Value to fixed and

type in 0.001 (Figure 7). Now select the Logarithmic Scale check box. Do not close the dialog box. Select the Number tab and set the number of decimal places to 3 in the y-axis. Your graph should resemble Figure 8.

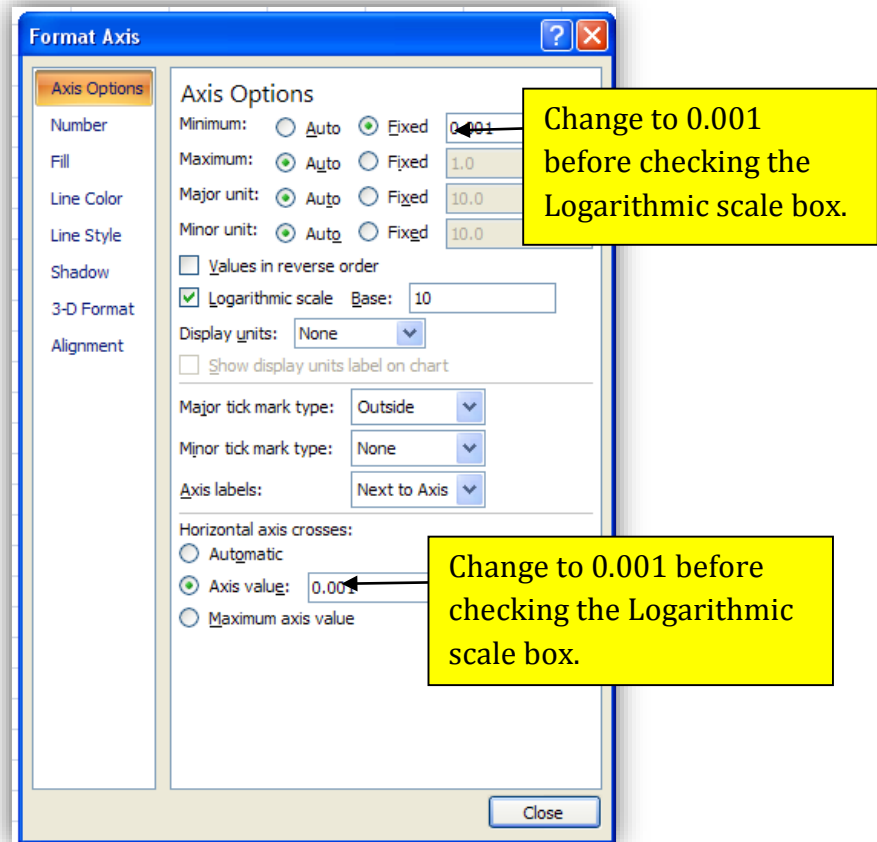


Figure 7

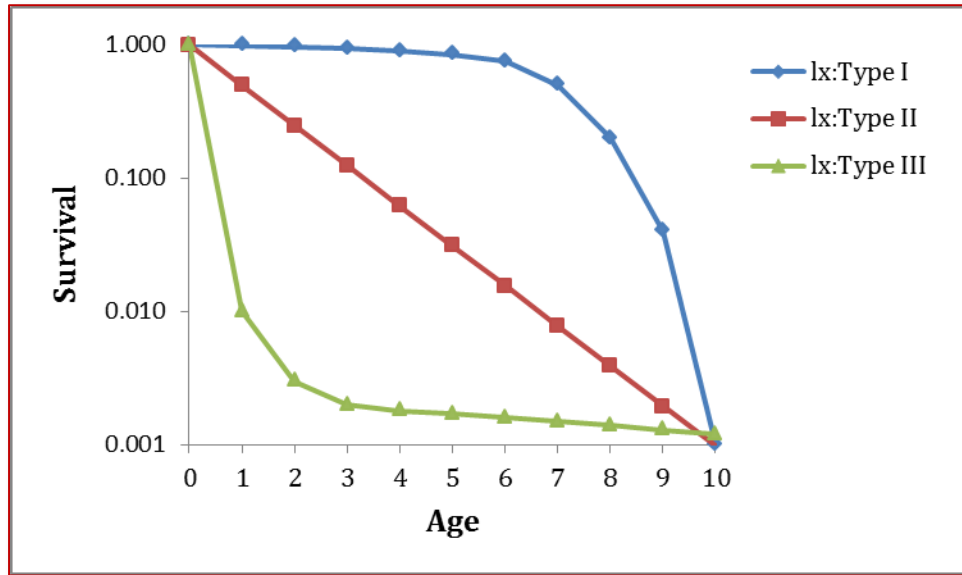


Figure 8

14. Graph age-specific survival g_x , against age. Select cells A3–A14 and cells H3–J14. Make an X-Y graph. Your graph should resemble Figure 9.

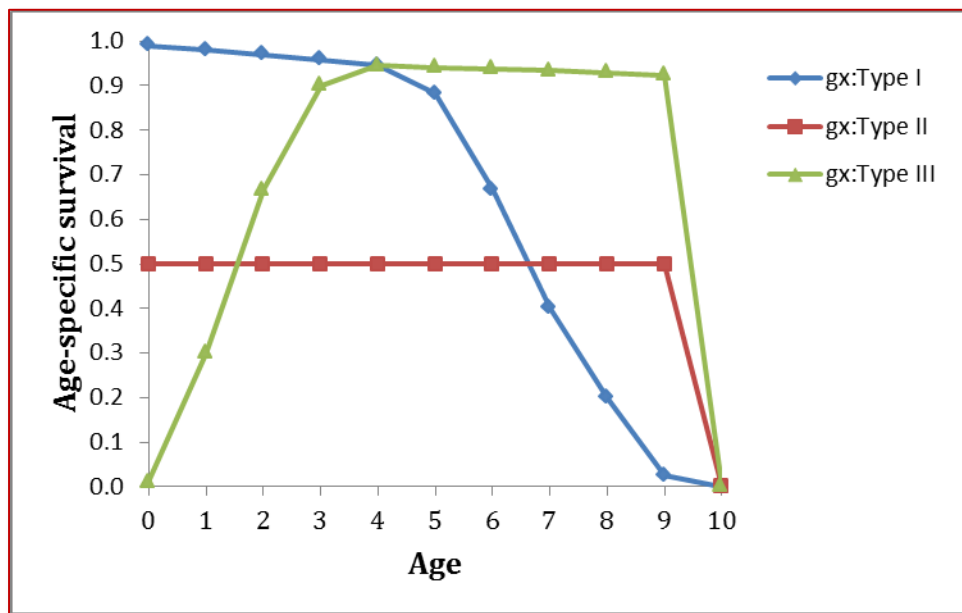


Figure 9

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 X-Y graph. Your graph should resemble Figure 10.

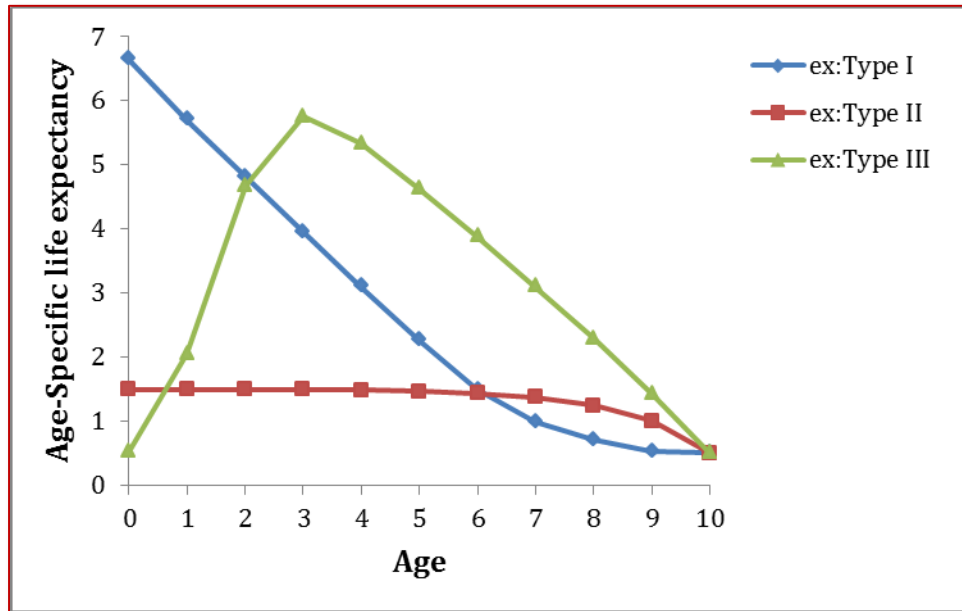


Figure 10

B. Population growth and decline

- Open a new spreadsheet and set up titles and column headings as shown in Figure 11. 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					
5	1	900					
6	2	250					
7	3	10					
8	4	0					

Figure 11

2. Enter a formula to calculate standardized survival, l_x . In cell C4 enter the formula **=B4/\$B\$4**. 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.
3. Enter the values shown for age-specific fertility, b_x . Enter the value 0.00 into cells D4, D5, D7, and D8. Enter the value 4.00 into cell D6.
4. Enter a formula to calculate the product of standardized survival times age-specific fertility, $l_x b_x$. In cell E4 enter the formula **=C4*D4**. Copy this formula into cells E5–E8.
5. Enter a formula to calculate net reproductive rate, R_0 . In cell E9 enter the formula **=SUM(E4:E8)**. This corresponds to Equation 6.
6. Echo the value of R_0 in cell B10. 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.
7. Enter a formula to calculate the product $l_x b_x x$. 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.
8. Enter a formula to calculate the sum of the products $l_x b_x x$. In cell F9 enter the formula **=SUM(F4:F8)**. This is another intermediate step in calculating generation time, G .
9. Enter a formula to calculate 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 . In cell B12 enter the formula **=LN(B10)/B11**. This corresponds to Equation 8.
11. Your spreadsheet is complete. At this point, your spreadsheet should look like Figure 12.

	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	1.00000	0.00000	0.00000	0.00000	0.00000
5	1	900	0.90000	0.00000	0.00000	0.00000	0.00000
6	2	250	0.25000	4.00000	1.00000	2.00000	2.00000
7	3	10	0.01000	0.00000	0.00000	0.00000	0.00000
8	4	0	0.00000	0.00000	0.00000	0.00000	0.00000
9				TOTAL	1.00000	2.00000	
10	R_0	1.00000					
11	G	2.00000					
12	r est.	0.00000					
13	r adj.	0.00000					

Figure 12

12. Create a survivorship curve from your l_x values. Follow the procedures in Steps 12 and 13 of Section A, except make sure the Axis Value is 0.01 under the "Horizontal Axis Crosses:" options. Similarly, change the Minimum Value to fixed and type in 0.01. Now select the Logarithmic Scale check box. Your graph should resemble Figure 13.

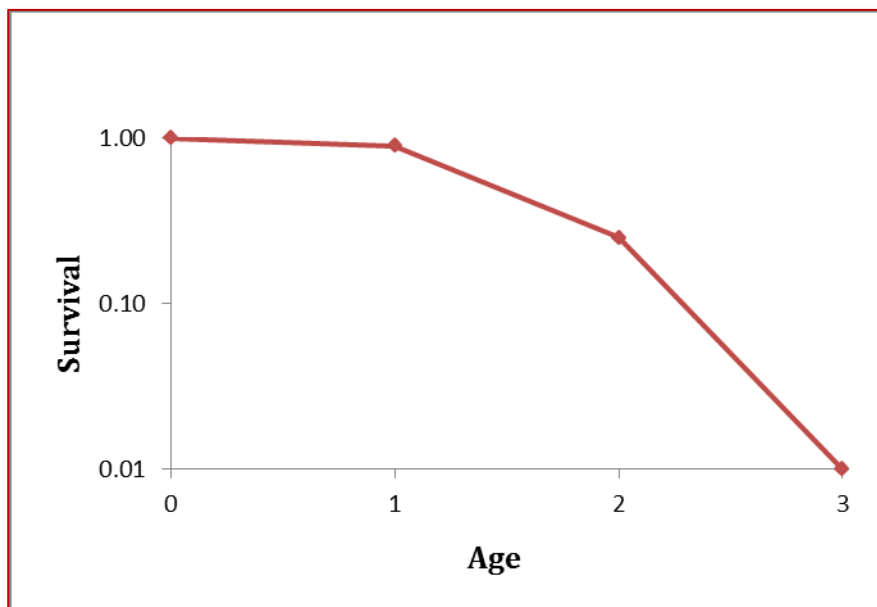


Figure 13

Discussion Questions

1. What can be gained by plotting survivorship curves on a semi-log graph?
2. What do the shapes of the survivorship curves (Figures 6, 8, and 9) tell you about patterns of survival and mortality?
3. What does the graph of life expectancies (Figure 10) tell you about a population?
4. According to the life table you constructed in part B of this problem set, is the population increasing, decreasing, or static?
5. According to the life table you constructed in part B of this problem set, what age classes are contributing young to the population?
6. According to the life table you constructed in part B of this problem set, what percentage of newborns survive to be 3 years old? What percentage of 1-year-olds survive to their second year?
7. What effect does changing the survival schedule (S_x) in your life table have on R_0 , G , and r ? Increase the number of surviving animals in the 2-year age class from 250 to 500. In reality this could be done by reducing the harvest of this age class by 50%. After increasing the survival of the 2-year olds what do you expect the population do: increase, decrease, or stay the same?
8. What effect does changing the fecundity schedule (b_x) have on R_0 , G , and r ? Decrease the mean number of young produced per female in the 2-year age class by half. In reality this might occur during a drought year. Note the changes in R_0 , G , and r .

Acknowledgement

This problem set was adapted from Exercise 12: Life tables, survivorship curves, and population growth, pages 164-175 in Donovan, T. M. and C. Welden. 2002. Spreadsheet exercises in ecology and evolution. Sinauer Associates, Inc. Sunderland, MA, USA. This publication is available at <http://www.uvm.edu/rsenr/vtcfwru/spreadsheets/?Page=ecologyevolution/EE12.htm>.

Your write-up should include the following: (1) an introductory paragraph explaining the objectives of this problem set, and (2) your answers to the 8 discussion questions above. Email me (whited@uamont.edu) your spreadsheet.