14 *REPRODUCTIVE VALUE: LIFE TABLE APPROACH*

Objectives

- Perform standard life table calculations on a hypothetical data set.
- Compute the stable age distribution and reproductive values for individuals of age x from life table data.
- Evaluate how life history strategy affects reproductive values.

Suggested Preliminary Exercise: Life Tables and Survivorship Curves; Reproductive Value: Matrix Approach

INTRODUCTION

As we discussed in the previous exercise, the idea that different individuals have different "value" in terms of their contribution to future generations is called their *reproductive value* (Fisher 1930). As Caswell (2001) states, "The amount of future reproduction, the probability of surviving to realize it, and the time required for the offspring to be produced all enter into the **reproductive value** of an age-class."

The reproductive value of an individual of age x is designated at V_x, and is the number of offspring that an individual is expected to produce over its remaining life span (after adjusting for the growth rate of the population). Biologists are often interested in knowing the "value" of the different individuals from a practical standpoint because knowing something about the reproductive value can suggest which individuals should be harvested, killed, transplanted, etc. from a conservation or management perspective

The reproductive value of different ages is strongly tied to an organism's life history. Typically, reproductive value is low at birth, increases to a peak near the age of first reproduction, and then declines (Caswell 2001). In this exercise, you will calculate reproductive value of individuals of various ages from life table calculations. We will start with a brief review of the major calculations in the life table, and then move on to the calculations and explanations of reproductive value. We will then modify the life history schedule of organisms to compare how reproductive value changes under different life history scenarios.

Life Table Calculations

A typical life table is shown in Figure 1. If we were to build a cohort life table for a population born 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 **sur-**

vivorship schedule, or S_x. We would also record the **fecundity schedule**: the number of offspring born to members of each age class. The total number of offspring is usually divided by the number of individuals in the age class, giving the average number of offspring per individual, which is represented by b_x. The survivorship and fecundity schedules are the raw data of a life table. From these data, age-specific rates of survival, life expectancy, generation time, and net reproductive rate can be calculated.

You might recall that l_x is the proportion of original numbers surviving to the beginning of each interval, and is calculated as

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

We can also think of l_x as the probability that an individual survives from birth to the beginning of age-class x. Column E in Figure 1 is simply l_x multiplied by b_x, and Column F is simply l_x times b_x times x (the age class). The sum of Column E generates R_0, the net reproductive rate, which can be written mathematically as

$$R_0 = \sum_{x=0}^{k} l_x b_x$$
Equation 2

The net reproductive rate is the lifetime reproductive potential of the average female, adjusted for mortality. Assuming mortality 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 might recall from the life table exercise that R_0 measures population change in terms of generation time. To convert R_0 into an intrinsic rate of increase (r) or finite rate of increase (λ), we must first calculate generation time, and then adjust R_0 accordingly.

	A	B	C	D	E	F	G
1	Cohort Life Table: Fecundity Schedule and Population Growth						
2							
3	Age class (x)	S_x	b_x	l_x	$(l_x)(b_x)$	$(l_x)(b_x)(x)$	$(e^{-rx})(l_x)(b_x)$
4	0	3751	0.00	1.0000	0.0000	0.0000	0.0000
5	1	357	10.51	0.0952	1.0003	1.0003	1.0002
6	2	159	0.00	0.0424	0.0000	0.0000	0.0000
7	3	59	0.00	0.0157	0.0000	0.0000	0.0000
8	4	57	0.00	0.0152	0.0000	0.0000	0.0000
9	5	53	0.00	0.0141	0.0000	0.0000	0.0000
10	6	29	0.00	0.0077	0.0000	0.0000	0.0000
11	7	19	0.00	0.0051	0.0000	0.0000	0.0000
12	8	17	0.00	0.0045	0.0000	0.0000	0.0000
13	9	13	0.00	0.0035	0.0000	0.0000	0.0000
14	10	7	0.00	0.0019	0.0000	0.0000	0.0000
15	11	0		0.0000	0.0000	0.0000	0.0000
16				Total	1.0003	1.0003	1.0002
17	R_0	1.0003					
18	G	1.0000					
19	r est.	0.0003					
20	r Euler	0.0001					
21	Should be 1	1.0002					

Figure 1   A cohort of 3751 individuals tracked over time. The number alive at the beginning of each year is given in Column B, and the average number of offspring per female is given in Column C. Columns D through G are calculated from information in columns A through C.

Generation time is calculated as the sum of Column F divided by the sum of Column E, or

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

Equation 3

With G and R_0 calculated, we can estimate r, the intrinsic rate of increase, as

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

Equation 4

We need to know r in order to calculate the reproductive value of each age class. However, Equation 4 provides only an estimate of r. To obtain a more precise estimate of r, we need to solve for r in the following equation:

$$1 = \sum\limits_{x=0}^{k} e^{-rx} l_x b_x$$

Equation 5

This is called the **Euler equation**, named after the Swiss mathematician Leonhard Euler (Gotelli 2001). In the life table exercise, you solved the Euler equation by plugging numbers in until the equation was solved. In this exercise, you will use the Solver option in Excel to solve the Euler equation. You might remember that when $r = 0$, the population remains constant in numbers over time; when $r < 0$, the population declines exponentially, and when $r > 0$ the population increases exponentially. When a population has a **stable age structure**, it means that all age classes increase or decrease at a constant rate of r, even if the numbers of individuals in each age class differ.

With an estimate of r for our population, we are ready to calculate the **reproductive value** for individuals of age x (Fisher 1930), which can be calculated from a life table as

$$v_x = \frac{e^{rx}}{l_x} \sum\limits_{y=x+1}^{\Omega} e^{-ry} l_y b_y$$

Equation 6

where $y = x + 1$ is the first age class subsequent to age class x, and Ω is the final age class into the future. Equation 6 can be written out in full as

$$\begin{aligned} v_x = \frac{e^{rx}}{l_x} [e^{-r(x+1)} & l_{x+1} b_{x+1} \\ & + e^{-r(x+2)} l_{x+2} b_{x+2} \\ & + e^{-r(x+3)} l_{x+3} b_{x+3} \\ & + \ldots] \end{aligned}$$

This equation assumes that the next reproductive bout for individuals of age x will occur at age $x + 1$, i.e., individuals of age x have already reproduced as x year olds. In order for us to understand how Equation 6 was derived, its useful to recall that the reproductive value of an individual of age x is the expected number of offspring that this individual will produce over the rest of its life, adjusted by population growth. Let's start by computing the expected number of offspring that an individual of age x will produce over the rest of its life. If we let any age class beyond age x be denoted with the letter y, the total number of future offspring can be calculated as:

$$\sum\limits_{y=x+1}^{\Omega} \frac{l_y b_y}{l_x}$$

Expression 6.1

This term can be written out in full as

$$\frac{l_{x+1} b_{x+1}}{l_x} + \frac{l_{x+2} b_{x+2}}{l_x} + \frac{l_{x+3} b_{x+3}}{l_x} + \ldots$$

Thus, for each age class following age class x, compute the probability that an individual of age class x will survive to a given future class as $Pr = l_y/l_x$ and multiply by the corresponding birth rate, b_y. It should be fairly straightforward why l_y/l_x and b_x must be computed to calculate the expected number of offspring that an individual of age x will produce in the future: in order to produce future offspring in year $x + 3$ (for example), you must survive from age x to age $x + 3$ to realize the reproduction.

But this expected number of future offspring isn't quite the same thing as the "value" of those offspring. Ronald A. Fisher (1930) got the idea of treating offspring like money. If the economy is growing, a dollar received today is worth more to me than a dollar received next week, because that same dollar will be "diluted" by all the extra money around next week, and even more so in the following year. Similarly, if the population size is different when the future offspring are produced, their values depend on whether the population is increasing or decreasing: the value of each offspring produced by individuals in the future is "diluted" when the population is increasing, and the value of each offspring is "concentrated" when the population is decreasing.

So Fisher discounted the value of the offspring produced at later ages by the amount by which the population will have grown by the time they are produced. Since the population is growing at the rate r, by the time our x-year-old individual reaches age y, the population will have grown by a factor

$$e^{r(y-x)}$$

Thus, to compute the value of future offspring, we need to "adjust" the number of future offspring by dividing by the factor by which the population will have grown. We can compute the "adjusted" number of expected future offspring for an individual of age x as

$$\frac{\sum_{y=x+1}^{\Omega} \frac{l_y b_y}{l_x}}{e^{r(y-x)}}$$

Expression 6.2

Expression 6.2 can be written out in full as

$$\frac{\frac{l_{x+1}b_{x+1}}{l_x}}{e^{r(x+1-x)}} + \frac{\frac{l_{x+2}b_{x+2}}{l_x}}{e^{r(x+2-x)}} + \frac{\frac{l_{x+3}b_{x+3}}{l_x}}{e^{r(x+3-x)}} + ...$$

If we graph $e^{r(y-x)}$ for various levels of r, we can visualize the denominator of Expression 6.2 and see how the adjustment works. This is shown in Figure 2.
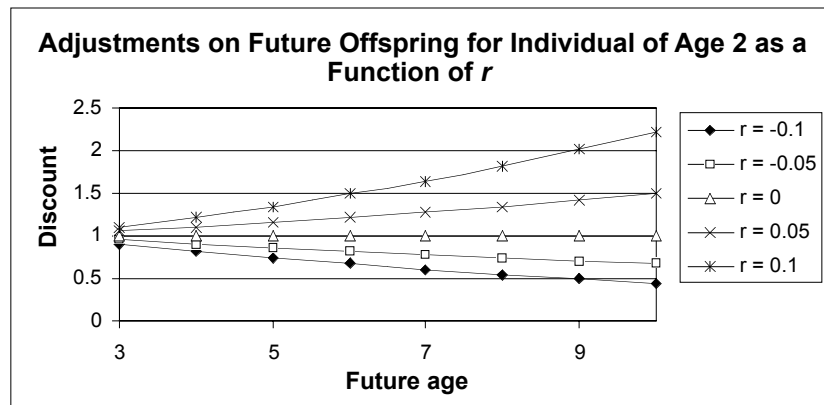

Figure 2   For an individual of age 2, the graph shows how offspring produced in the future are adjusted under various levels of r. When $r > 1$, the adjustment, $e^{r(y-x)}$, is positive and increases as ever more distant age classes are considered. This makes the denominator of Expression 6.2 large, which *decreases* the value of future offspring. When $r < 0$, the population is decreasing and the adjustment is below 1. This makes the denominator of Expression 6.2 small, which *increases* the value of future offspring. When $r = 0$, no adjustment is made.

We have now arrived at the number of future offspring expected to be produced by an individual of age x, adjusted by population growth (i.e., the reproductive value for an individual of age x). From here, we can arrive back at Fisher's computation of reproductive value (Equation 6) with a few simple mathematical steps. It might be helpful to recall certain mathematical principles before we proceed:

- If n is a positive integer, then a^{-n} is $1/a^n$.
- For any number a, and any integers m and n, $a^m \times a^n = a^{m+n}$.
- Any term expressed as $\dfrac{\frac{a}{b}}{\frac{c}{d}}$ can be written as $\dfrac{ad}{bc}$

Now let's proceed with Expression 6.2 and work our way towards Fisher's formula for computing reproductive value (Equation 6). With the mathematical principles in mind, we can rewrite Expression 6.2 as

$$\sum_{y=x+1}^{\Omega} \frac{l_y b_y}{l_x e^{ry} e^{-rx}} \qquad \text{Expression 6.3}$$

which can be written out in full as

$$\frac{l_{x+1} b_{x+1}}{l_x e^{r(x+1)} e^{-rx}} + \frac{l_{x+2} b_{x+2}}{l_x e^{r(x+2)} e^{-rx}} + \frac{l_{x+3} b_{x+3}}{l_x e^{r(x+3)} e^{-rx}} + \dots$$

We can then pull two common terms out of the denominator, l_x and e^{-rx} and re-write Expression 6.3 as

$$\frac{1}{l_x e^{-rx}} \sum_{y=x+1}^{\Omega} \frac{l_y b_y}{e^{ry}} \qquad \text{Expression 6.4}$$

which is the same thing as:

$$\frac{e^{rx}}{l_x} \sum_{y=x+1}^{\Omega} \frac{l_y b_y}{e^{ry}} \qquad \text{Expression 6.5}$$

Expression 6.5 can be written out in full as:

$$\frac{e^{rx}}{l_x} \left[\frac{l_{x+1} b_{x+1}}{e^{r(x+1)}} + \frac{l_{x+2} b_{x+2}}{e^{r(x+2)}} + \frac{l_{x+3} b_{x+3}}{e^{r(x+3)}} + \dots \right]$$

Finally, we can move the term e^{ry} from the denominator to the numerator (in Expression 6.5) and arrive at Fisher's equation (Equation 6):

$$v_x = \frac{e^{rx}}{l_x} \sum_{y=x+1}^{\Omega} e^{-ry} l_y b_y \qquad \text{Equation 6}$$

Hopefully, Equation 6 will now make some sense to you. Equation 6 is specifically for populations in which there is a birth pulse and in which individuals are censused immediately after the breeding season (individuals of age x have already given birth). If individuals of age x have not yet given birth, the summation would begin with $y = x$ in Equation 6, rather than $y = x + 1$. In this case, reproductive value can be partitioned into current (imminent) reproduction, as well as future reproduction (Williams 1966). Although the equation might look a bit cumbersome, we'll walk you step by step through the calculations so that you can see exactly how the values are computed. Reproductive value can also be computed with a matrix approach (see the previous exercise). The critical pieces of information from a life table are r, the intrinsic rate of growth, l_x, or the survivorship schedule, and b_x, the fecundity schedule. If we know

these values for each age (with ages denoted by x), we can identify the reproductive value for each age.

In addition to reproductive value, we will also calculate the stable age distribution of the population. The stable age distribution gives the proportion of the population that consists of 0, 1, 2, 3, and 4 year olds, given that the population has reached an equilibrium growth rate. In other words, no matter what r is for the population, each age group will increase or decrease by a constant amount. For example, if the stable population is made up of 55% 0-year olds, 22% 1-year olds, 33% 2-year olds, and 0% 3-year olds, the stable age distribution is 0.55, 0.22, 0.33, and 0, respectively. These proportions are calculated from the following equation (Mertz 1970):

$$c_x = \frac{e^{-rx}l_x}{\sum\limits_{x=0}^{k} e^{-rx}l_x}$$ Equation 7

where c_x is the proportion of the population that consists of individuals of age class x when the population has stabilized.

PROCEDURES

In this exercise, you'll learn how to calculate reproductive value for individuals in a population, as well as the stable age distribution. In setting up this model, we have followed the life table computations Gotelli (2001) used to compute reproductive value. As a result, some steps in the computation have not been explained in the introductory material here, but the final results do indeed reflect the reproductive values from Equation 6.

After the model is completed, you will be able to change the life history schedule of the population to evaluate how life history schedules affect reproductive value. As always, save your work frequently to disk.

INSTRUCTIONS	ANNOTATION

A. Set up the life table spreadsheet.

1. Open a new spreadsheet and set up column headings as shown in Figure 3.

	A	B	C	D	E	F	G
1	*Reproductive Value: Life Table Approach*						
2				**Cohort life table**			
3	*x* (age)	S_x	b_x	l_x	g_x	l_x*b_x	l_x*b_x*x
4	0	500	0				
5	1	400	2				
6	2	200	3				
7	3	50	1				
8	4	0	0				
9					$R_0 =$		
10							
11		**Outputs**					
12		$R_0 =$					
13		$G =$					
14		r (estimate) =					
15		Euler equation =					
16		Euler r (adj) =					
17		$\lambda =$					

Figure 3

2. Enter the values shown in cells B4–C8 as shown.

We will start with 500 newborns (cell B4) and follow their numbers over time. S_x gives the number of individuals that are counted at the beginning of each age class. The fecundity schedule, b_x, gives the average number of female offspring per female per year for each age class.

3. Enter formulae in cells D4–G4 to compute the standard life table data, and copy your formulae down to row 8.

Refer back to the "Life Tables and Survivorship Curves" exercise if you cannot remember the formulae. We used the following formulae:

- D4 **=B4/$B$4**
- E4 **=D5/D4**
- F4 **=D4*C4**
- G4 **=F4*A4**

4. Graph the survivorship curve.

Select cells A3–B8. Use the scattergraph option and label your axes fully. Your graph should resemble Figure 4.
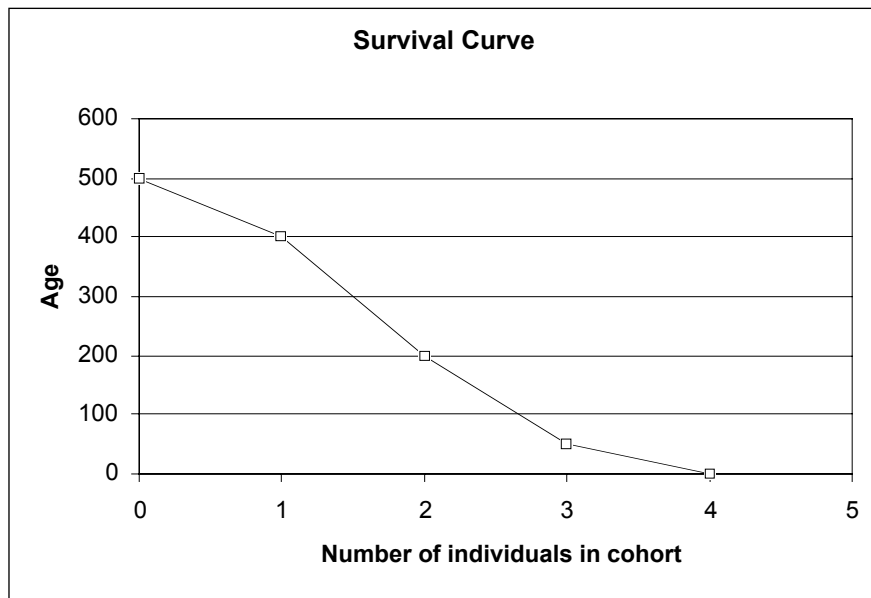

Survival Curve

Figure 4

5. Save your work.

B. Compute life table outputs.

1. Enter a formula in cell F9 and C12 to compute R_0.

Enter the formula **=SUM(F4:F8)** in cells F9 and C12.
R_0 is the **net reproductive rate**. It reveals the mean number of offspring produced per female over her lifetime (Gotelli 2001). R_0 can be calculated by multiplying $l_x \times b_x$ for each age class, and then summing up the values over age classes; this corresponds to **Equation 2**.

2. In cell C13, enter a formula to compute G.

Enter the formula **=SUM(G4:G8)/C12** in cell C13.
G is the generation time. It reveals the average age of the parents of all the offspring produced by a single cohort (Caughley 1977). G can be calculated by multiplying $l_x \times b_x \times x$ for each age class, and then summing up the values over age classes. This sum is then divided by (or adjusted for) R_0. This correspondes to **Equation 3**.

3. In cell C14, enter a formula to estimate r.

Enter the formula **=LN(C12)/C13** in cell C14.
This corresponds to **Equation 4**.

4. **Manually** enter the estimated value of r in cell C16.

Enter 0.72 in cell C16.
You might remember that r can be more precisely estimated by using the Euler equation (Gotelli 2001). The exact solution for r can be found by solving for r in the Euler equation:

$$1 = \sum_{x=0}^{k} e^{-rx} l_x b_x \qquad \text{Equation 5}$$

You should have reached $r = 0.72$ as an estimate. Knowing that r is approximately 0.72, you can plug various values of r (a bit higher or lower) until the equation is solved (as you did in the "Life Tables" exercise), or you can use the Solver spreadsheet tool to solve the problem for you. For now, you've entered 0.72 into cell C16. The Solver will change this value to the precise estimate in the next couple of steps.

5. Enter a formula in cell C15 to calculate the right-hand side of the Euler equation, using the r value in cell C16.

Enter the formula **=SUM(EXP(-C16*A4)*F4,EXP(-C16*A5)*F5,EXP(-C16*A6)*F6,EXP(-C16*A7)*F7,EXP(-C16*A8)*F8)** in cell C15.
In Excel, the **EXP** function is used to raise e to a given power. You'll see that your Euler equation does not add up to 1 as it should (it adds up to 1.07), which means r needs a bit of adjusting.

Your spreadsheet should now look like Figure 5.

	A	B	C	D	E	F	G
1	*Reproductive Value: Life Table Approach*						
2			**Horizontal (cohort) life table**				
3	*x* (age)	S_x	b_x	l_x	g_x	l_x*b_x	l_x*b_x*x
4	0	500	0	1	0.8	0	0
5	1	400	2	0.8	0.5	1.6	1.6
6	2	200	3	0.4	0.25	1.2	2.4
7	3	50	1	0.1	0	0.1	0.3
8	4	0	0	0		0	0
9					$R_0 =$	2.9	4.3
10							
11		**Outputs**					
12		$R_0 =$	2.9				
13		$G =$	1.4827586				
14		r (estimate) =	0.7180607				
15		Euler equation =	1.0746494				
16		Euler r (adj) =	0.72				
17		$\lambda =$					

Figure 5

C. Use the Solver function to adjust the value of r.

1. Access Solver.

Go to Tools | Solver and select Solver. If Solver does not appear in the menu, go to Tools | Add-ins and select the Solver add-in. (Your computing administrator may need to help you with the installation.) The dialog box in Figure 6 will appear.
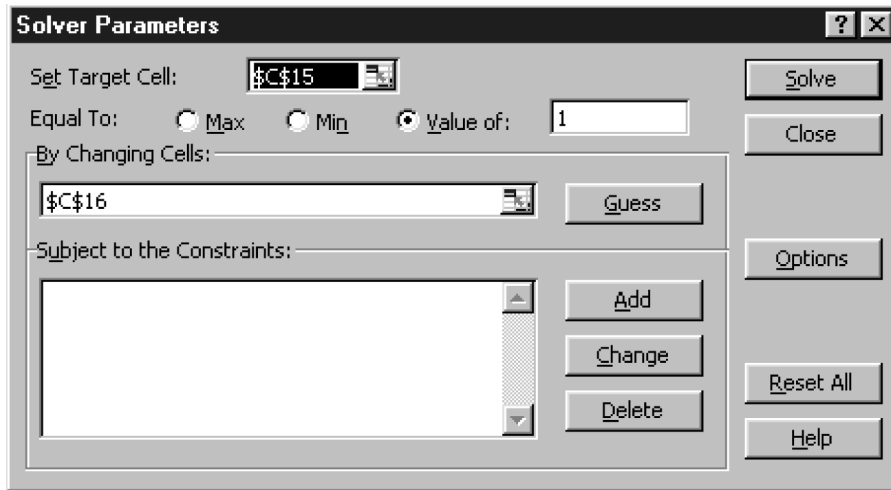
Figure 6

2. Use the Solver function to set cell C15 (the Euler equation) to 1 by changing cell C16.

Enter **$C$15** in the Set Target Cell box
Set the target cell equal to a Value of 1.
Enter **$C$16** in the By Changing Cells box.

3. Press Solve to return the precise estimate of r in cell C16.

You should get a value of $r = 0.776$, and you'll see that cell C15 is very close to 1.

4. Calculate λ, the finite rate of increase, in cell C17.

Enter the formula **=EXP(C16)** in cell C17.
Lambda is the finite rate of increase. It can be calculated from r as $\lambda = e^r$.

5. Save your work.

D. Calculate the stable age distribution.

The stable age distribution gives the proportion of the population that consists of 0, 1, 2, 3, and 4 year olds, given that the population has reached an equilibrium growth rate. For example, if the stable population is made up of 50% 0-year olds, 22% 1-year olds, 33% 2-year olds, and 0% 3-year olds, the stable age distribution is 0.50, 0.22, 0.33, and 0, respectively. These proportions are calculated from **Equation 7**, the Mertz equation:

$$c_x = \frac{e^{-rx}l_x}{\displaystyle\sum_{x=0}^{k} e^{-rx}l_x}$$

Equation 7

1. Set up new spreadsheet headings as shown in Figure 7.

	H	I	J	K	L	M
2	**Stable age distribution**		**Reproductive value distribution**			
3	$l_x e^{-rx}$	c_x	e^{rx}/l_x	$e^{-rx}l_x b_x$	$\Sigma e^{-ry}l_y b_y$	v_x
4						
5						
6						
7						
8						
9						

Figure 7

2. In cells H4–H8, enter a formula in cell H4 to calculate the numerator of the Mertz equation for each age class.

Enter the formula =**D4*EXP(-$C$16*A4)** in cell H4 to calculate the numerator of the Mertz equation for age class 0. Copy this formula down to cell H8 to obtain this value for the remaining age classes.

3. In cell H9, sum cells H4–H8 to obtain the denominator of the Mertz equation.

Enter the formula **=SUM(H4:H8)** in cell H9.

4. Calculate c_x for age class 0 in cell I4. Copy this formula down for the remaining ages.

Enter the formula **=H4/$H$9** in cell I4 and copy down the column.
The results of this formula give, for each age class, the proportionate makeup of the population when the population has reached a stable distribution.

5. Sum the c_x values in cell I9.

Enter the formula **=SUM(I4:I8)** in cell I9.
This is to double-check your results. The values should sum to 1.

6. Save your work.

Your spreadsheet should now resemble Figure 8.

	A	B	C	D	E	F	G	H	I
2				Horizontal (cohort) life table				Stable age distribution	
3	x (age)	S_x	b_x	l_x	g_x	l_x*b_x	l_x*b_x*x	$l_x e^{-rx}$	c_x
4	0	500	0	1	0.8	0	0	1.000	0.684
5	1	400	2	0.8	0.5	1.6	1.6	0.368	0.252
6	2	200	3	0.4	0.25	1.2	2.4	0.085	0.058
7	3	50	1	0.1	0	0.1	0.3	0.010	0.007
8	4	0	0	0		0	0	0.000	0.000
9					$R_0 =$	2.9	4.3	1.463	1.000

Figure 8

7. Graph the stable age distribution for the population.

Use the column graph option, and label your axes fully. Your graph should resemble Figure 9.

Figure 9

8. Save your work. Review your results and computations and make sure you understand the spreadsheet thus far.

E. Calculate the reproductive value distribution.

Remember that reproductive value can be computed by Fisher's equation (**Equation 6**):

$$v_x = \frac{e^{rx}}{l_x} \sum_{y=x+1}^{\Omega} e^{-ry} l_y b_y$$

Equation 6

1. In cells J4–J8, enter a formula to compute the left-hand side of Fisher's equation (e^{rx}/l_x).

Enter the formula **=EXP($C$16*A4)/D4** in cell J4. Copy your formula down to cell J8.

2. In cells K4–K8 enter an equation to calculate $e^{-rx}l_x b_x$.

Enter the formula **=EXP(-$C$16*A4)*F4** in cell K4. Copy your formula down to cell K8. This calculation is an intermediate step that will be helpful for future calculations

3. In cells L4–L7, enter a formula in cell L4 to calculate the right-hand side of the reproductive value equation,

$$\sum_{x}^{\Omega} e^{-ry} l_y b_y$$

Enter the formula **=SUM(K4:$K$7)** in cell L4. Copy this formula down to cell L7. Now that we have $e^{-rx}l_x b_x$ for each age class, we are able to sum these values over age classes into the future. Note that we include the individual of age x as well as individuals of any age class in the future (denoted by the letter y) in the computations. We have added this step to facilitate the computations in the next step.

4. In cells M4–M7, enter a formula to calculate v_x.

Enter the formula **=J4*L5** in cell M4. Copy your formula down to cell M7.
Finally, we can compute v_x, the reproductive value, for each age class. The formula **=J4*L5** offsets the formula by one row, so that the reproductive value is computed as e^{rx}/l_x times the sum of $e^{-ry}l_y b_y$ for any age classes into the future. The result gives the expected number of offspring to be produced by an individual of age x over its remaining life span, adjusted by the population growth rate, r.

5. Save your work.

Your spreadsheet should now resemble Figure 10.

	H	I	J	K	L	M
2	**Stable age distribution**		**Reproductive value distribution**			
3	$l_x e^{-rx}$	c_x	e^{rx}/l_x	$e^{-rx}l_x b_x$	$\Sigma e^{-ry}l_y b$	v_x
4	1.000	0.684	1.000	0.000	1.000	1.000
5	0.368	0.252	2.717	0.736	1.000	0.717
6	0.085	0.058	11.808	0.254	0.264	0.115
7	0.010	0.007	102.653	0.010	0.010	0.000
8	0.000	0.000				
9	1.463	1.000	1.000			

Figure 10

QUESTIONS

1. Interpret your model results fully. Which age class has the highest reproductive value, which age class has the lowest reproductive value? Interpret your results in terms of r, and the birth and survivorship data from the life table.

2. Interpret the reproductive values from your models from the standpoint of conservation of a game species whose populations are harvested and maintained at a high level, versus a pest species whose populations you would like to control, versus a threatened species that is being reintroduced to an area. Based on your knowledge of reproductive value, does your decision also depend on the proportion of the population that occurs in the various age classes? Why or why not?

3. The model currently computes reproductive value for a population that is increasing. Adjust the birth rates values in cells C5–C7 in various ways to generate different values of r, (keep the S_x column the same). For each of your model runs, interpret how the birth schedule, and r, affect reproductive values. For each run, remember to use the Solver again to generate a correct r.

4. Change the life history parameters in the life table (cells B4–C8) to generate a different life history schedule (a Type III survival curve). Set up new life table entries as follows:

	A	B	C
3	x (age)	S_x	b_x
4	0	500	0
5	1	200	0
6	2	100	0
7	3	50	8
8	4	0	0

This life history schedule represents a Type III survival curve in which reproduction occurs once and then organisms die (semelparous or annual). For such a life history, which individuals have the highest reproductive value? You will need to use the Solver again to obtain a correct r in cell C16 so that your reproductive value calculations are correct.

5. Compare this life history with a species with a Type I survival curve, in which reproduction is delayed but occurs over different age classes. Set up new life table entries as follows:

	A	B	C
3	x (age)	S_x	b_x
4	0	500	0
5	1	499	0
6	2	400	2
7	3	300	2.1
8	4	0	0

For such a life history, which individuals have the highest reproductive value? You will need to use the Solver again to obtain a correct r in cell C16 so that your reproductive value calculations are correct.

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