# 12

# STAGE-STRUCTURED MATRIX MODELS

## Objectives

- Set up a model of population growth with stage structure.
- Determine the stable stage distribution of the population.
- Estimate the finite rate of increase from Lefkovitch matrix calculations.
- Construct and interpret the stage distribution graphs.

*Suggested Preliminary Exercise: Geometric and Exponential Population Models; Life Tables and Survivorship Curves*

## INTRODUCTION

Recall from Exercise 7 that the geometric model describes a population growing in discrete time. That is, the model treats time as if it moved in steps rather than flowing continuously. This kind of model is realistic for many populations that have seasonal, synchronous reproduction. For example, insectivorous songbirds in North America typically breed during the spring and summer months, when their major food sources peak in abundance. The geometric growth model has the form

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

where $R$ is the per capita change in population size, or intrinsic (or geometric) rate of natural increase. You might recall that $R$ is equal to $b - d$ for discretely growing populations, or the difference in the per capita birth and death rates. We can factor $N_t$ out of the terms on the right-hand side, to get

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

The quantity $(1 + R)$ is called the finite rate of increase, $\lambda$, and so we can write

$$N_{t+1} = \lambda N_t \qquad \text{Equation 1}$$

where $N$ is the number of individuals present in the population, and $t$ is a time interval of interest. Equation 1 says that the size of a population at time $t + 1$ equals the size of the population at time $t$ multiplied by a constant, $\lambda$. When $\lambda = 1$, the population will remain constant in size over time. When $\lambda < 1$, the population declines geometrically, and when $\lambda > 1$, the population increases geometrically.

Equation 1 predicts change in numbers in a population over time, given the numbers of individuals currently in the population and λ. Simplistically speaking, the models assume that all individuals in the population make equal contributions to population change, regardless of their size, age, stage, genetic make-up, or sex. Many natural populations violate at least one of these assumptions because the populations are **structured**—they are composed of individuals whose birth and death rates *differ* depending on age, size, sex, stage, or genetic make-up. For example, small fish in a population differ in mortality rates from large fish, and larval insects differ in birth rates from adult insects.

Differences among individuals in a population are a cornerstone of ecology and evolutionary biology, and can greatly affect the population's finite rate of increase (λ). In this exercise, you will develop a **matrix model** to explore the growth of populations that have size or stage structure. This approach will enable you to estimate λ in Equation 1 for size- or stage-structured populations.

If you have completed the Life Tables exercise, you learned that *age structure* is often a critical variable in determining the size of a population over time. In fact, a primary goal of life table analysis and Leslie matrix modeling is to estimate the population's growth rate, λ, when the population has age structure. For many organisms, however, age is *not* an accurate predictor of birth or death rates. For example, a small sugar maple in a northeastern forest can be 50 years old and yet have low levels of reproduction. In this species, size is a better predictor of birth rate than age. In other species, birth and death rates are a function of the *stage in the life cycle* of an organism. For instance, death rates in some insect species may be higher in the larval stages than in the adult stage. Such organisms are best modeled with **size-** or **stage-structured** matrix models.

## Model Notation

We begin our exercise with some notation often used when modeling structured populations (Caswell 2001; Gotelli 2001). For modeling purposes, the first decision is whether to develop a stage-structured or a size-structured model for the organism of interest. This in turn depends on whether size or life-history stage is a better state variable.

The second step is to assign individuals in the population to either stage or size **classes**. It is fairly straightforward to categorize individuals with stage structure, such as insects—simply place them in the appropriate stage, such as larva, pupa, or adult. Size, however, is a *continuous variable* because is not an either/or situation, but can take on a range of values. In our sugar maple example, size classes might consist of seedlings, small-sized individuals, medium-sized individuals, and large-sized individuals. The number of size classes you select for your model would depend on how "different" groups are in terms of reproduction and survival. If medium- and large-sized individuals have the same reproductive and survival rates, we might choose to lump them into a single class.

Note that the projection interval (the amount of time that elapses between time *t* and time *t* + 1) and the stage durations can be different. For instance, the larval stage may typically last 4 months, and the pupa stage might typically last only 2 months, and the projection interval may also be different. This is quite different from the age-based matrix model, in which the interval of the different classes, as well as the projection interval from time step to time step, must be equal.

A typical life cycle model for a species with stage or size structure is shown in Figure 1. The horizontal arrows between each stage (circles) represent **survival probabilities**, or the probability that an individual in stage/size class *i* will survive and move into stage/size class *i* + 1, designated by the letter *P* followed by two different subscripts.*

The curved arrows at the bottoms of the diagrams in Figure 1 represent the proba-

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*Caswell 2001 calls these "graduation probabilities," designated by the letter *G*.
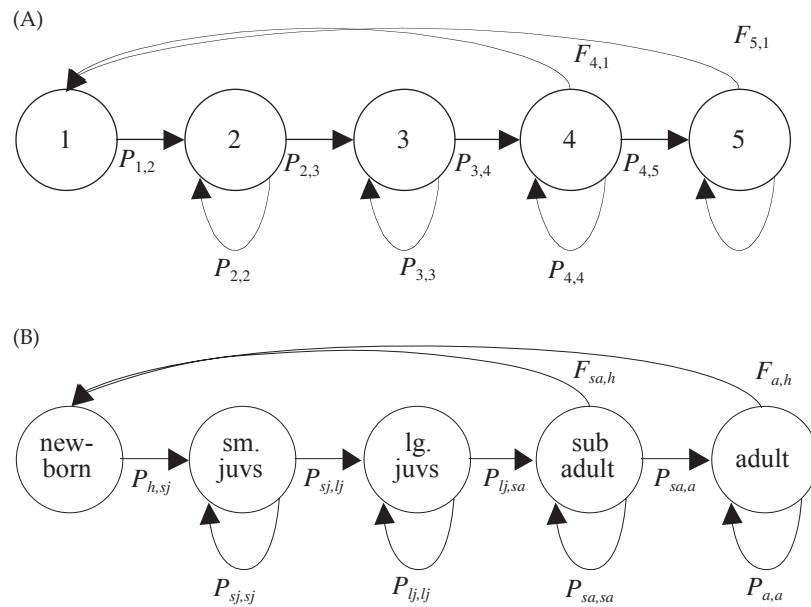
(A)



(B)

Figure 1    (A) A theoretical life history model for an organism with a stage- or size-structured life history. Classes are represented by circles. The arrows between the stages are called transitions, indicating the probability $P$ of transitioning from one class to the next (horizontal arrows) or of remaining in the same class (lower curved arrows). The curved arrows at the top, labeled $F$, represent births. (B) Model of an organism with five specific size/stage structures (in this case, a combination of the two), as labeled. Two classes (subadults and adults) are capable of reproduction, so arrows associated with birth emerge from both classes returning to newborns (hatchlings). If only adult individuals reproduced, there would be a single arrow from adult to newborn.

bility of individuals surviving and remaining in their class from time $t$ to time $t + 1$, designated by the letter $P$ followed by two identical subscripts. For instance, the loop at the bottom of the small juvenile class represents the probability that a small juvenile in time $t$ will be alive and counted as a small juvenile in time $t + 1$. The loop at the bottom of the adult class represents the probability that an adult counted in time $t$ will be alive and counted as an adult in time $t + 1$. These self-loops are absent from age-based matrix models because individuals *must* move from one class to the next (you can't have two twentieth birthdays).

The curved arrows at the top of the diagrams represent births, designated by the letter $F$ followed by two different subscripts. The arrows all lead to the first class because newborns, by definition, enter the first class upon birth.

Note that for both $P$ and $F$, the subscripts have a definite pattern: the first subscript is the class *from* which individuals move, and the second subscripts indicate the class *to* which individuals move (Gotelli 2001).

## *Matrix Models*

Now let's move on and discuss the computations of $P$, $F$, and $\lambda$ for a population with stage structure. The major goal of the matrix model is to compute $\lambda$, the finite rate of increase, for a population with stage structure (Equation 1). In our matrix model, we can compute the **time-specific growth rate**, $\lambda_t$, by rearranging terms in Equation 1:

$$\lambda_t = \frac{N_{t+1}}{N_t}$$

Equation 2

This time-specific growth rate is not necessarily the same λ in Equation 1, but in our spreadsheet model we will compute it in order to arrive at λ (no subscript) in Equation 1. (We will discuss this important point later).

To determine $N_t$ and $N_{t+1}$, we need to count individuals at some standardized time period over time. We'll assume for this exercise that our population censuses are completed immediately after individuals breed (a **postbreeding census**). The number of individuals in the population in a census at time $t + 1$ will depend on how many individuals of each size class were in the population at time $t$, as well as the movements of individuals into new classes (by birth or transition) or out of the system (by mortality). Thus, in size- or stage-structured models, an individual in any class may move to the next class (i.e., grow larger), remain in their current class, or exit the system (i.e., die).

The **survival probability**, $P_{i,i+1}$, is the probability that an individual in size class $i$ will survive and move into size class $i + 1$. In our example, let's assume that small juveniles survive and become large juveniles with a probability of $P_{sj,lj} = 0.3$. This means that 30% of the small juveniles in one time step will survive to be censused as large juveniles in the next time step. The remaining 70% of the individuals either die or remain small juveniles. $P_{i,i}$ is the probability that an individual in size class $i$ will survive to be counted in the next time step, but will remain in size class $i$. Thus, an individual in size class $i$ may survive and grow to size class $i + 1$ with probability $P_{i,i+1}$, or may survive and remain the size class $i$ with probability $P_{i,i}$ (Caswell 2001).

In order to keep track of how many individuals are present in a given class at a given time, we must consider both kinds of survival probabilities to account for those individuals that graduated into the class, plus those individuals that remained in the class (i.e., did not graduate). For example, we can compute the number of individuals in the large juvenile size class at time $t + 1$ as the number of small juveniles at time $t$ multiplied by $P_{sj,lj}$ (this gives the number of small juveniles in year $t$ that graduated to become large juveniles in year $t + 1$), plus the number of large juveniles at time $t$ multiplied by $P_{lj,lj}$ (this gives the number of large juveniles in year $t$ that remained in the large juvenile class in year $t + 1$). More generally speaking, the number of individuals in class $i$ in year $t + 1$ will be

$$n_i(t + 1) = [P_{i,i} n_i(t)] + [P_{i-1,i} n_{i-1}(t)] \qquad \text{Equation 3}$$

Equation 3 works for calculating the number of individuals at time $t + 1$ for each size class in the population except for the first, because individuals in the first stage class at time $t + 1$ will include those individuals in class 1 that remain in class 1 in the next time step, plus any new individuals that arise through birth. Accordingly, let's now consider birth rates.

There are many ways to describe the births in a population. Here we will assume a simple **birth-pulse model**, in which individuals give birth as soon as they enter a new stage class. On this day, not only do births occur, but transitions from one size class to another also occur. When populations are structured, the birth rate is often called the **fecundity**, or the average number of offspring born per unit time to an individual female of a particular age (Gotelli 2001). If you have completed the exercise on life tables, you might recall that fecundity is labeled as $b(x)$, where $b$ is for birth. Individuals that are of pre- or postreproductive age have fecundities of 0. Individuals of reproductive age typically have fecundities greater than 0.

To illustrate the concept of birth pulse and postbreeding census, consider a hypothetical diagram for a sea turtle (*Caretta caretta*) population with five stage classes that are censused at three time periods: $t – 1$, $t$, and $t + 1$ as shown in Figure 2. Since all individuals are born during the birth pulse, they have the same birthday. The birthday is also the "graduation day" for those individuals that move from one size class to the next. With a postbreeding census, the diagram shows that the number of individuals in the first size class (hatchlings, $h$) at time $t$ depends on the number of subadults and adults in the previous time step, $t – 1$.

If we knew how many breeders were producing those hatchlings, we could compute fecundity as the number of offspring produced per individual per year (Gotelli 2001).
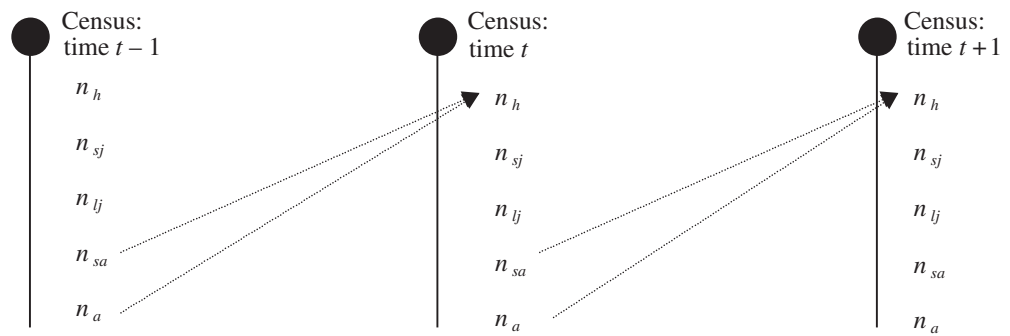
**Figure 2**    In this population, subadults (*sa*) and adults (*a*) can reproduce, represented by the dashed arrows that lead to the first class in the next time step. Births occur in a birth pulse (indicated by the filled circle and vertical line) and individuals are censused postbreeding (i.e., immediately after the young are born). (After Akçakaya et al. 1997.)

However, the number of breeders is not simply $N_{sa}$ and $N_a$ counted in time step $t − 1$; these individuals must survive a long period of time (almost a full year) until the birth pulse in time step $t − 1$ occurs. In other words, not all of the subadults and adults counted in year $t − 1$ will survive to the birth pulse and produce offspring that will be counted as hatchlings in year $t$. Thus, we need to discount the fecundity, $b(i)$, by the probability that an individual will actually survive from the time they were censused to the time they breed (Gotelli 2001). These adjusted estimates are used in matrix models and are commonly called **fertilities** (often defined as realized reproduction), designated by the letter $F$. (Be aware that various authors use the terms fertility and fecundity in different ways.) The adjustment is necessary to account for "lags" between the census and the timing of births.

These adjustments are a bit trickier for stage-based than for age-based models because both kinds of survival probabilities ($P_{i,i+1}$ and $P_{i,i}$) come into play. For example, suppose we want to compute the fertility rate of subadults, $F_{sa}$ that were censused in year $t$. We need to ask, "How many offspring are produced, on average, per subadult censused in year $t$?" To answer this question, we need to know how many subadults were counted during the census for year $t$, how many of those individuals survived to the birth pulse in the same time step, and the total number of young produced by those individuals. Keeping in mind that the graduation day is the same day as the birth pulse, the young produced by the breeding individuals comes from two sources: (1) those subadults that survived to the birth pulse and reproduced at the rate of subadults ($b_i \times P_{i,i}$), and (2) those subadults that survived to the birth pulse and graduated to adulthood and reproduced as adults ($b_{i+1} \times P_{i,i+1}$). Accordingly, we can compute the fertility rate as

$$F_i = (b_i \times P_{i,i}) + (b_{i+i} \times P_{i,i+1})$$    Equation 4

Thus, $F_i$ indicates the number of young that are produced per female of stage $i$ in year $t$, given the appropriate adjustments (Caswell 2001). The total number of individuals counted in stage 1 (newborns or hatchlings) in year $t + 1$ is simply the fertility rate of each age class, multiplied by the number of individuals in that size class at time $t$, plus any individuals that remained in the first size class from one time step to the next. Generally speaking,

$$n_1(t+1) = P_{1,1}n_1(t) + \sum_{i=1}^{k} F_i n_i(t)$$    Equation 5

Once we know the fertility and survivorship coefficients for each age class, we can calculate the number of individuals in each age at time $t + 1$, given the number of individuals in each class at time $t$ (Gotelli 2001):

$$n_h(t+1) = P_{h,h}n_h(t) + F_{sj,h}n_{sj}(t) + F_{lj,h}n_{lj}(t) + F_{sa,h}n_{sa}(t) + F_{a,h}n_a(t)$$

$$n_{sj}(t+1) = P_{sj,sj}n_{sj}(t) + P_{h,sj}n_h(t)$$

$$n_{lj}(t+1) = P_{lj,lj}n_{lj}(t) + P_{sj,lj}n_{sj}(t) \qquad \text{Equation 6}$$

$$n_{sa}(t+1) = P_{sa,sa}n_{sa}(t) + P_{lj,sa}n_{lj}(t)$$

$$n_a(t+1) = P_{a,a}n_a(t) + P_{sa,a}n_{sa}(t)$$

Equation 6 can be converted into a matrix form. A **matrix** is a rectangular array of numbers and symbols, designated by a bold-faced letter. Matrices that describe populations with stage or size structure are often called Lefkovitch matrices, after biologist L. P. Lefkovitch (1965).

$$\mathbf{L} = \begin{bmatrix} P_{h,h} & F_{sj} & F_{lj} & F_{sa} & F_a \\ P_{h,sj} & P_{sj,sj} & 0 & 0 & 0 \\ 0 & P_{sj,lj} & P_{lj,lj} & 0 & 0 \\ 0 & 0 & P_{lj,sa} & P_{sa,sa} & 0 \\ 0 & 0 & 0 & P_{sa,a} & P_{a,a} \end{bmatrix}$$

Since our population has only five classes, the matrix, denoted by the letter **L**, is a five-row × five-column matrix. The fertility rates are given in the top row. The survival probabilities, $P_{i,i+1}$, are given in the subdiagonal, which represent the survival from one class to the next. For example, $P_{sj,lj}$ is the probability of small juveniles will become large juveniles in year $t+1$. The survival probabilities, $P_{i,i}$, are given in the diagonal, which represent the probability that an individual in a given class will survive, but will remain in the same class in year $t+1$. The upper left entry in the **L** matrix gives the probability that a hatchling will remain a hatchling. If hatchlings could reproduce, we would add $F_{h,h}$ to $P_{h,h}$ for this matrix entry. Note that the $P_{i,i} + P_{i,i+1,}$gives the total rate of survival for individuals in a particular stage.

### *Vectors and Matrix Multiplication*
The composition of our population can be expressed as a column **vector**, $\mathbf{n}(t)$, which is a matrix that consists of a single column. Our column vector will consist of the number of individuals in the newborn, small juvenile, large juvenile, subadult, and adult classes. When the Leftkovitch matrix, **L**, is multiplied by the population vector, $\mathbf{n}(t)$, the result is another population vector (which also consists of 1 column); this vector is called the **resultant vector** and provides information on how many individuals are in each size class in year $t+1$.

Multiplying each element in first row of the **L** matrix by the corresponding element in the **n** vector, and then repeating the process for the remaining elements in the first row and summing the products together generate the first entry in the resultant vector. In other words, the first entry in the first row of the **L** matrix is multiplied by the first entry in **n** vector, plus the second entry in the first row of the **L** matrix by the second entry in the **n** vector, and so on. In the example below, a $4 \times 4$ matrix on the left is multiplied by column vector (center). The resultant vector is on the right-hand side of the equation (note that summing the components would compress this vector to a single column).

$$\begin{bmatrix} a & b & c & d \\ e & f & g & h \\ i & j & k & l \\ m & n & o & p \end{bmatrix} \times \begin{bmatrix} w \\ x \\ y \\ z \end{bmatrix} = \begin{bmatrix} aw + bx + cy + dz \\ ew + fx + gy + hz \\ iw + jx + ky + lz \\ mw + nx + oy + pz \end{bmatrix} \qquad \text{Equation 7}$$

Rearranging the matrices so that the resultant vector is on the left, we can compute the population size at time $t + 1$ by multiplying the Leftkovitch matrix by the population vector at time $t$:

$$
\begin{bmatrix} n_h(t+1) \\ n_{sj}(t+1) \\ n_{lj}(t+1) \\ n_{sa}(t+1) \\ n_a(t+1) \end{bmatrix} = \begin{bmatrix} P_{h,h} & F_{sj} & F_{lj} & F_{sa} & F_a \\ P_{h,sj} & P_{sj,sj} & 0 & 0 & 0 \\ 0 & P_{sj,lj} & P_{lj,lj} & 0 & 0 \\ 0 & 0 & P_{lj,sa} & P_{sa,sa} & 0 \\ 0 & 0 & 0 & P_{sa,a} & P_{a,a} \end{bmatrix} \times \begin{bmatrix} n_h(t) \\ n_{sj}(t) \\ n_{lj}(t) \\ n_{sa}(t) \\ n_a(t) \end{bmatrix}
$$
Equation 8

For example, assume that you have been following a population that consists of 45 newborns, 18 small juveniles, 56 large juveniles, 10 subadults, and 8 adults. The initial vector of abundances is written

$$
\begin{bmatrix} 45 \\ 18 \\ 56 \\ 4 \\ 1 \end{bmatrix}
$$

Assume that the Leftkovitch matrix for this population is

$$
\mathbf{L} = \begin{bmatrix} 0 & 0 & 0 & 4.6 & 61.8 \\ .6 & .7 & 0 & 0 & 0 \\ 0 & .05 & .66 & 0 & 0 \\ 0 & 0 & .02 & .68 & 0 \\ 0 & 0 & 0 & .02 & .8 \end{bmatrix}
$$

The number of newborns, small juveniles, large juveniles, subadults, and adults in year $t + 1$ (rounded) would be computed as

$$
\begin{bmatrix} 0 & 0 & 0 & 4.6 & 61.8 \\ .6 & .7 & 0 & 0 & 0 \\ 0 & .05 & .66 & 0 & 0 \\ 0 & 0 & .02 & .68 & 0 \\ 0 & 0 & 0 & .02 & .8 \end{bmatrix} \times \begin{bmatrix} 45 \\ 18 \\ 56 \\ 4 \\ 1 \end{bmatrix} = \begin{bmatrix} 0\times45+0\times18+0\times56+4.6\times4+61.8\times1 \\ .6\times45+.7\times18+0\times56+0\times4+0\times1 \\ 0\times45+.05\times18+.66\times56+0\times4+0\times1 \\ 0\times45+0\times18+.02\times56+.68\times4+0\times1 \\ 0\times45+0\times18+0\times56+.02\times4+.8\times1 \end{bmatrix} = \begin{bmatrix} 80 \\ 40 \\ 38 \\ 4 \\ 1 \end{bmatrix}
$$

Upon inspection, you will see that the Lefkovitch matrix computes population numbers in year t + 1 in the manner of Equation 6. For this population, the time-specific growth rate is

$$
\lambda_t = \frac{N_{t+1}}{N_t} = \frac{80+40+38+4+1}{45+18+56+4+1} = \frac{163}{124} = 1.31
$$

The Lefkovitch matrix not only allows you to calculate $\lambda_t$ (by summing the total number of individuals in the population at time $t + 1$ and dividing this number by the total individuals in the population at time $t$), but also lets you evaluate how the composition of the population changes from one time step to the next. If you continued projecting the population dynamics into the future, you would be able to ascertain how the population "behaves" if the present conditions ($P$'s and $F$'s) were to be maintained indefinitely (Caswell 2001). Continued multiplication of a vector of abundance by the Lefkovitch matrix eventually produces a population with a **stable size** or **stable stage**

**distribution**, where the proportion of individuals in each stage remains constant over time, and there is a stable (unchanging) finite rate of increase, $\lambda_t$. When the $\lambda_t$'s converge to a constant value, this constant is an estimate of $\lambda$ in Equation 1, and is called the **asymptotic growth rate.** At this point, if the population is growing or declining, all stage classes grow or decline at the same rate, even if the numbers of individuals in each class are different. You will see how this happens as you work through the exercise.

## PROCEDURES

In this exercise, you will develop a stage-based model for sea turtles (*Caretta caretta*). In this population, the size stages are hatchlings (*h*), small juveniles (*sj*), large juveniles (*lj*), subadults (*sa*), adults (*a*). Turtles are counted every year in a postbreeding census, where the numbers of individuals in each stage class are tallied.

   As always, save your work frequently to disk.

| INSTRUCTIONS | ANNOTATION |
|---|---|

*A. Set up the model population.*

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

| | A | B | C | D | E | F | G | H |
|---|---|---|---|---|---|---|---|---|
| 1 | *Stage-Structured Matrix Models* | | | | | | | **Initial** |
| 2 | *Five-stage matrix model of the loggerhead sea turtle* | | | | | | | **population** |
| 3 | | *F(h)* | *F(sj)* | *F(lj)* | *F(sa)* | *F(a)* | | **vector** |
| 4 | | 0 | 0 | 0 | 4.665 | 61.896 | | 2000 |
| 5 | | 0.675 | 0.703 | 0 | 0 | 0 | | 500 |
| 6 | | 0 | 0.047 | 0.657 | 0 | 0 | | 300 |
| 7 | | 0 | 0 | 0.019 | 0.682 | 0 | | 300 |
| 8 | | 0 | 0 | 0 | 0.061 | 0.8091 | | 1 |

**Figure 3**

2. Enter the values shown in cells B4–F8. Write your interpretation of what each cell value means in the chart.

These are the matrix values derived by Crowder et al.1994. For example, the value in cell B5 is the probability that a hatchling in year *t* will become a small juvenile in year *t* + 1.

| B4: |
|---|
| C4: |
| D4: |
| E4: |
| F4: |
| B5: |
| C5: |
| C6: |
| D6: |
| D7: |
| E7: |
| E8: |
| F8: |

3. Enter the values shown in cells H4–H8.

These values make up the initial population vector, or how many individuals of each stage are currently in the population.

4. Set up new column headings as shown in Figure 4 and set up a linear series in column A that will track abundances of individuals for 100 years.

|    | A | B | C | D | E | F | G | H |
|----|------|------------|---------|---------|----------|--------|-------|-------------|
| 10 | Year | Hatchlings | S. juvs | L. juvs | Subadults | Adults | Total | $\lambda_t$ |
| 11 | 0 | | | | | | | |
| 12 | 1 | | | | | | | |

**Figure 4**

Enter 0 in cell A11.
Enter the formula **=A11+1** in cell A12. Copy this formula down to cell A111 to simulate 100 years of population growth.
(You can generate the $\lambda$ symbol by typing in the letter l, then select this letter in the formula bar and change its font to Symbol.)

5. Link the initial vector abundances to the appropriate cells in B11–F11.

Enter the formula **=H4** in cell B11 to indicate that at year 0, the population consists of 2000 hatchlings. Enter a similar formula in cells C11–F11 to link the initial population vector with the proper stages.
  • Cell C11 **=H5**
  • Cell D11 **=H6**
  • Cell E11 **=H7**
  • Cell F11 **=H8**

6. In cell G11, use the **SUM** function to obtain the total population size for year 0.

Enter the formula **=SUM(B11:F11)** in cell G11.

7. In cell H11, enter a formula to compute $\lambda_t$.

Enter the formula **= G12/G11** in cell H11.
Remember that $\lambda_t$ can be computed as $N_{t+1}/N_t$. Your result will not make sense until you compute the total population size for year 1.

8. Save your work.

***B. Project the population sizes over time.***

We will use matrix multiplication to project the population size and structure at year 1. Multiply your matrix of fecundities and survival values by your initial vector of abundances (given in year 0, row 11). The result will be the number of individuals in the next generation that are hatchlings, small juveniles, large juveniles, subadults, and adults. Recall how matrices are multiplied: The **L** matrix is located on the left, and is multiplied by the initial vector of abundances (**v**). The result is a new vector of abundances for the year $t + 1$. Refer to Equations 7 and 8. (Equation 7 is a $4 \times 4$ matrix; you will carry out the multiplication for a $5 \times 5$ matrix.)

1. Enter a formula in cell B12 to obtain the number of hatchlings in year 1.

Enter the formula **=$B$4*B11+$C$4*C11+$D$4*D11+$E$4*E11+$F$4*F11** in cell B12. Make sure you refer to the initial abundances listed in row 11 in your formula, rather than the initial abundances listed in column H.

2. Enter formulae in cells C12–F12 to obtain the number of small juveniles, large juveniles, subadults, and adults in year 1.

We used the following formulae:
  • Cell C12 **=$B$5*B11+$C$5*C11+$D$5*D11+$E$5*E11+$F$5*F11**
  • Cell D12 **=$B$6*B11+$C$6*C11+$D$6*D11+$E$6*E11+$F$6*F11**
  • Cell E12 **=$B$7*B11+$C$7*C11+$D$7*D11+$E$7*E11+$F$7*F11**
  • Cell F12 **=$B$8*B11+$C$8*C11+$D$8*D11+$E$8*E11+$F$8*F11**

3. In cell G12, use the **SUM** function to sum the individuals in the different stages.

Enter the formula **=SUM(B12:F12)** in cell G12.

4. In cell H12, calculate the time-specific growth rate, $\lambda_t$.

Copy cell H11 into H12. When $\lambda_t = 1$, the population remained constant in size. When $\lambda_t < 1$, the population declined, and when $\lambda_t > 1$, the population increased in numbers.

5. Select cells B12–H12, and copy the formulae down to cells B111–H111.

This will complete a 100-year simulation of stage-structured population growth. Click on a few random cells and make sure you can interpret the formulae and how they work.

6. Save your work.

*C. Create graphs.*

1. Graph your population abundances for all stages over time.

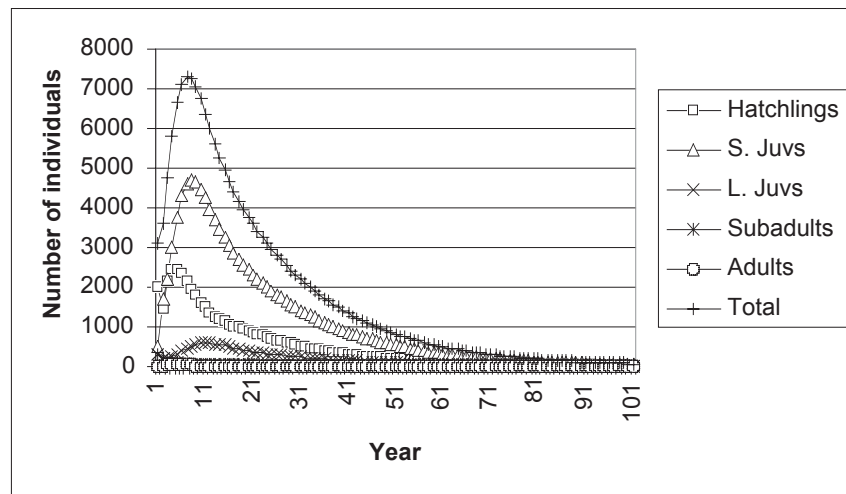Use the line graph option and label your axes fully. Your graph should resemble Figure 5.



**Figure 5**

2. Copy the graph in Figure 5. Change the *y*-axis to a log scale.

To adjust the scale of the *y*-axis, double click on the values in the *y*-axis. You'll see the dialog box in Figure 6 on the facing page. Click on the Logarithmic scale box in the lower part of the dialog box. Your scale will be automatically adjusted.
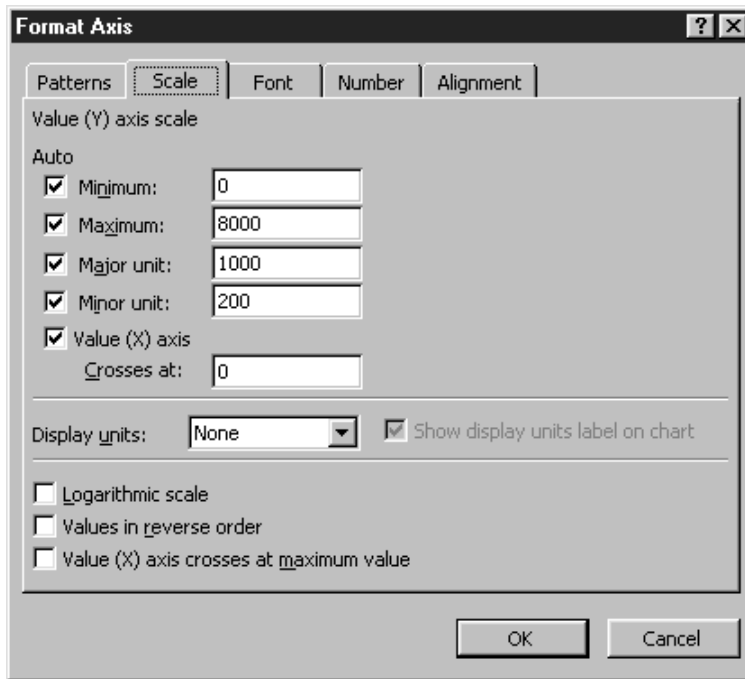
**Figure 6**

Your graph should resemble Figure 7. It is sometimes easier to interpret your population projections with a log scale.
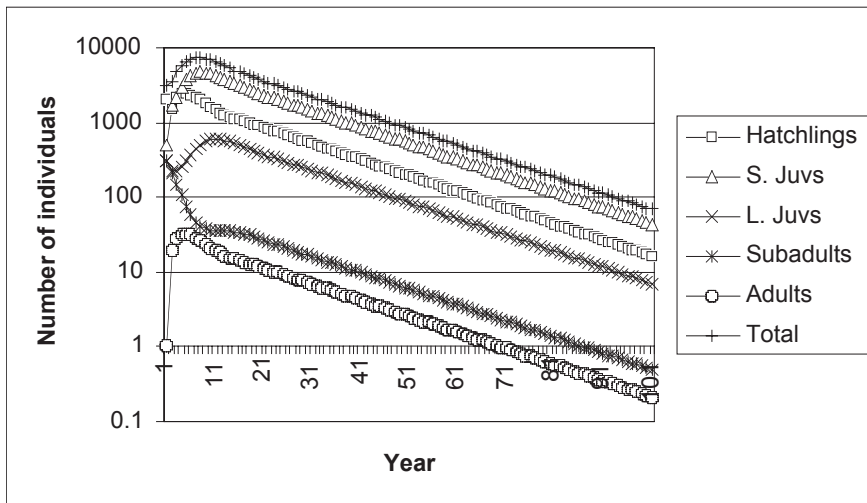


3. Save your work.

**Figure 7**

## QUESTIONS

1. What are the assumptions of the model you have built?

2. At what point in the 100-year simulation does $\lambda_t$ not change (or change very little) from year to year? This constant is an estimate of the asymptotic growth rate, $\lambda$, from Equation 1. What value is $\lambda$?  Given this value of $\lambda$, how would you describe population growth of the sea turtle population?

3. What is the composition of the population (proportion of individuals that are hatchlings, small juveniles, large juveniles, subadults, and adults) when the population has reached a stable distribution? Set up the headings shown below. In the cell below the Hatchlings cell (cell I11) enter a formula to calculate the proportion of the total population in year 100 that consists of hatchlings (assuming $\lambda_t$ has stabilized by year 100). Enter formulae to compute the proportions of the remaining stage classes in cells below the other stage-class headings. The five proportions calculated should sum to 1, and give the stable stage distribution.

| | I | J | K | L | M |
|---|---|---|---|---|---|
| 9 | **Proportion of individuals in class** | | | | |
| 10 | **Hatchlings** | **Small juvs** | **Large juvs** | **Subadults** | **Adults** |

4. How does the initial population vector affect $\lambda$ and the stable age distribution? How does it affect $\lambda_t$ and the stage distribution prior to stabilization? Change the initial vector of abundances so that the population consists of 75 hatchlings, and 1 individual in each of the remaining stage classes. Graph and interpret your results. Do your results have any management implications?

5. One of the threats to the loggerhead sea turtle is accidental capture and drowning in shrimp trawls. One way to prevent this occurrence is to install escape hatches in shrimp trawl nets. These "turtle exclusion devices" (TEDS) can drastically reduce the mortality of larger turtles. The following matrix shows what might happen to the stage matrix if TEDS were widely installed in existing trawl nets:

$$
\begin{bmatrix}
0 & 0 & 0 & 5.448 & 69.39 \\
.675 & .703 & 0 & 0 & 0 \\
0 & .047 & .767 & 0 & 0 \\
0 & 0 & .022 & .765 & 0 \\
0 & 0 & 0 & 0.068 & .876
\end{bmatrix}
$$

If the initial abundance is 100,000 turtles, distributed among stages at 30,000 hatchlings, 50,000 small juveniles, 18,000 large juveniles, and 2,000 subadults, and 1 adult, how does the use of TEDS influence population dynamics? Provide a graph and discuss your answer in terms of population size, structure, and growth. Discuss how the use of TEDS affects the *F* and *P* parameters in the Lefkovitch matrix.

6. Another important source of mortality for most marine turtles occurs in the very beginning of their lives, between the time the eggs are laid in a nest in the beach, and the time they hatch and are able to reach a safe distance into the sea. Most turtle conservation efforts in the past have concentrated on enhancing egg survival by protecting nests on beaches or removing eggs to protected hatch-

eries. If TEDS are not used, how much must fertilities increase in order to produce the population dynamics that would have been achieved with TEDS?

*7. (Advanced) Add stochasticity to the model by letting the $P_i$'s, and $F_i$'s vary stochastically with each time step.

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