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ISSUES : DATA SET

Demographic vital rates and population growth: an introduction to projection matrices and elasticity analysis

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Loggerhead sea turtle at Archie Carr National Wildlife Refuge. Credit: Ryan Hagerty/ U.S. Fish and Wildlife Service

THE ECOLOGICAL QUESTION:
How do changes in demographic vital rates influence the rate of population growth?

ECOLOGICAL CONTENT:
Population ecology, demography, life history

WHAT STUDENTS DO:
Students learn how projection matrices and elasticity analysis can be applied to a case-study exploring loggerhead sea turtle (*Caretta caretta*) conservation and population dynamics. Students are first introduced to the concept of vital rates and population growth. Students use published data on vital rates of loggerhead sea turtles to identify various vital rate values, draw a life cycle graph, and construct a matrix of vital rates. Students use the vital rate values and population matrix to calculate population growth rate (λ) and graph population size over time. Students also determine the relative influence of vital rates on population growth rate (λ) by calculating elasticity values for each vital rate.

STUDENT-ACTIVE APPROACHES:
Guided inquiry, think-pair-share, write before discussion, cooperative learning

SKILLS:
Data analysis, graph preparation, use of spreadsheets, use of primary literature, natural history

ASSESSABLE OUTCOMES:
Calculations of population growth rate, graphs for population growth

SOURCES:
Crouse, D.T., L.B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68: 1412-1423.

Crowder, L.B., D.T. Crouse, S.S. Heppell, and T.H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. Ecological Applications 4: 437-445.

Frazer, N.B. 1983a. Survivorship of adult female loggerhead sea turtles (*Caretta caretta*), nesting on Little Cumberland Island, Georgia, U.S.A. Herpetologica 39:436-447.

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Frazer, N.B. 1983b. Demography and life history evolution of the Atlantic loggerhead sea turtle, *Caretta caretta*. Ph.D. Dissertation, University of Georgia, Athens.

OVERVIEW OF THE ECOLOGICAL BACKGROUND

Loggerhead sea turtles (*Caretta caretta*) are a species of conservation concern in the United States and are exposed to an array of threats due in part to extensive migratory movements that occurs during various life-stages. One of the major movement events in the life-cycle involves the movement of females from marine feeding grounds to nesting beaches (Schroeder et al. 2003). Upon reaching maturity, individual female loggerheads typically return to nest on these beaches every two to four years (Miller et al. 2003). On the nesting beach, females dig a nest in the sandy beaches and lay approximately 3-5 separate clutches of eggs at various sites periodically throughout the nesting season (Schroeder et al. 2003). Following hatching, the hatchlings emerge from the nest and quickly crawl towards the water where they begin a long-distance journey that culminates in the open ocean (Bolten 2003).

Estimates of loggerhead sea turtle survival and fecundity were reported by Frazer (1983a, 1983b). Estimates of adult survival and fecundity were based on a long-term study of nesting female loggerhead sea turtles on Little Cumberland Island, Georgia (Frazer 1983a). Part of this study included monitoring nesting beaches hourly from dusk to dawn during the nesting season in order to tag adult female loggerhead turtles, measure clutch size, and estimate the time interval between nesting attempts (Heppell et al. 2003). Demographic data from this study was compiled into a life-table for loggerhead turtles by Frazer (1983a) and this data was subsequently used to parameterize a population projection matrix with seven life-stages (Crouse et al. 1987). Further refinements to the model resulted in several of the life-stages being combined to construct a population model for loggerhead sea turtles that included five life-stages (eggs/hatchlings, small juveniles, large juveniles, subadults, and adults) (Crowder et al. 1994). This data was used by Crowder et al. (1994) to explore how various scenarios to regulate the use of turtle excluder devices (TED) might influence populations of loggerhead sea turtles in the Atlantic. This model from Crowder et al. (1994) based on data collected by Frazer (1983a) is used as part of the lab exercise to examine relationships between various demographic parameters and population growth rate for the loggerhead sea turtle.

References:

Bolten, A.B. 2003. Active swimmers – passive drifters: the oceanic juvenile stage of loggerheads in the Atlantic system. Pp. 63-78 *in* Loggerhead Sea Turtles. Bolten, A.B. and B.E. Witherington, eds. Smithsonian Books, Washington, D.C.

Crouse, D.T., L.B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68: 1412-1423.

Crowder, L.B., D.T. Crouse, S.S. Heppell, and T.H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. Ecological Applications 4: 437-445.

Frazer, N.B. 1983a. Survivorship of adult female loggerhead sea turtles (*Caretta caretta*), nesting on Little Cumberland Island, Georgia, U.S.A. Herpetologica 39:436-447.

Frazer, N.B. 1983b. Demography and life history evolution of the Atlantic loggerhead sea turtle, *Caretta caretta*. Ph.D. Dissertation, University of Georgia, Athens.

Heppell, S.S., L.B. Crowder, D.T. Crouse, S.P. Epperly, and N.B. Frazer. 2003. Pp 255-273 *in* Loggerhead Sea Turtles. Bolten, A.B. and B.E. Witherington, eds. Smithsonian Books, Washington, D.C.

Miller, J.D., C.J. Limpus, and Matthew H. Godfrey. 2003. Pp. 125-143 *in* Loggerhead Sea Turtles. Bolten, A.B. and B.E. Witherington, eds. Smithsonian Books, Washington, D.C.

Schroeder, B.A., A.M. Foley, and D.A. Bagley. 2003. Nesting patterns, reproductive migrations, and adult foraging areas of loggerhead turtles. Pp. 114-124 *in* Loggerhead Sea Turtles. Bolten, A.B. and B.E. Witherington, eds. Smithsonian Books, Washington, D.C.

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STUDENT INSTRUCTIONS

Before beginning

You will analyze much of the data in this lab using the POPTOOLS extension for Microsoft Excel. POPTOOLS is a freely available extension developed by Greg Hood that provides a variety of tools that can be used to analyze population projection matrices.

Use the following steps to install POPTOOLS

1. Open your internet browser and navigate to http://www.poptools.org/ to download the POPTOOLS extension for Microsoft Excel.

2. Click on the "Download" link and download the executable setup file. Save the file to a location on the computer. Go to the downloaded setup file and click on "run" to start the Poptools Setup Wizard. Follow the instructions in the setup wizard to install Poptools.

3. Start Microsoft Excel and POPTOOLS will be accessible as a drop-down menu in the "Add-Ins" toolbar.

Introduction

Loggerhead sea turtles (*Caretta caretta*) are a species of marine turtle that have a wide distribution with populations found in the Atlantic, Pacific, and Indian Oceans along with the Mediterranean Sea. Loggerhead sea turtles undertake long-distance movements during various phases of the life-cycle and one of the major movement events involves the return of females from the ocean to nesting beaches (Schroeder et al. 2003). Upon reaching maturity, female loggerheads typically nest on the same nesting beaches every two to four years (Miller et al. 2003). On a nesting beach, females dig a nest in the sand and lay approximately 3-5 separate clutches of eggs at various sites periodically throughout the nesting season (Schroeder et al. 2003). The average number of eggs that are laid in a single clutch is around 112 eggs / clutch (Van Buskirk and Crowder 1994). Loggerhead sea turtles from the Atlantic Ocean are known to lay eggs on beaches of the southeastern United States, Cuba, Mexico, and Brazil with major nesting areas located in southern Florida (Ehrhart et al. 2003). Following hatching, the hatchlings emerge from the nest and quickly crawl towards the water where they begin a long-distance journey that culminates in the open ocean (Bolten 2003). After maturing, these turtles will eventually return to natal nesting beaches to reproduce as adults.

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Loggerhead sea turtles (*Caretta caretta*) are a species of conservation concern in the United States and are currently listed as a federally threatened species. Loggerhead sea turtles are exposed to a diverse variety of threats due in part to the extensive migratory movements that occur during various life-stages. On nesting beaches, the presence of artificial lighting may reduce nesting attempts and cause hatchlings to become disoriented when attempting to move towards the ocean (Witherington 1992, Lutcavage et al. 1997). In the ocean, survival of loggerheads may be negatively impacted by ingestion of tar or plastics (Witherington 2003). While loggerhead sea turtles are not commercially harvested, turtles may be incidentally caught in lines or entangled in trawls of commercial fisheries. While regulations requiring the use of turtle excluder devices on trawl nets has probably reduced incidental mortality from trawling in the Atlantic and Gulf of Mexico (Lewison et al. 2003), longline fishing operations in the Pacific Ocean pose a serious threat to loggerhead populations as turtles may become entangled in fishing gear or take bait from numerous hooks present along the line (Lewison et al. 2004).

The population status of the loggerhead sea turtle is ultimately determined by rates of reproductive success and survival during various life-stages. Changes in the values of vital rates, such as survival and fecundity, will result in changes in the growth rate of the sea turtle population. Our objective is to construct a population matrix using vital rate values to determine the rate of population growth for loggerhead sea turtles and to determine how changes in vital rates influence population growth rate.

To construct a population matrix it is first necessary to conceptualize the life cycle of an organism as a series of separate classes each possessing a distinct set of vital rate values. Demographic vital rate values can be used to determine the probability of transitions between classes of the life-cycle for a specified time-interval. One way that the life cycle can be classified is into age-classes, such that an organism remains within an age class for a set length of time interval before transitioning to the next age class. However, vital rates for some species may be more dependent on body size, social status or life stage (i.e. juvenile vs. adult) than on the age of the organism. For these species, it is preferable to conceptualize the life cycle as a series of stage-classes or size-classes with distinct vital rate values. For loggerhead sea turtles, one way that the life cycle can be classified is as a series of stage-classes that include: eggs/hatchlings, small juveniles, large juveniles, subadults, and adults (Crowder et al. 1994).

Life cycle graphs – A life cycle graph can be used to depict the progression between classes that occur throughout the life cycle of an organism. When drawing a life cycle graph, each distinct class is represented by a circle (known

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as a "node") and the transition between various nodes is represented by arrows (known as "arcs" or "fluxes") that depict transitions between classes of the life cycle over a given interval of time. For example, the following life cycle graph shows the life cycle of killer whales and transitions that occur between various stage-classes (Brault and Caswell 1993) (Fig. 1). In this figure, the life cycle depicts transitions from yearlings to juveniles to mature females to post-reproductive females (Fig. 1). The time-step interval for this model is one year in length. Since individuals may remain in the juvenile, mature, and post-reproductive stages for more than one year, it is possible that individuals stay in the same stage for more than one time-step. In the life cycle graph, arcs that point to the same node indicate the probability of surviving but remaining in the same stage (P). Other arcs in the life cycle graph represent the probability of surviving and moving to the next stage-class (G) and fecundity (F).
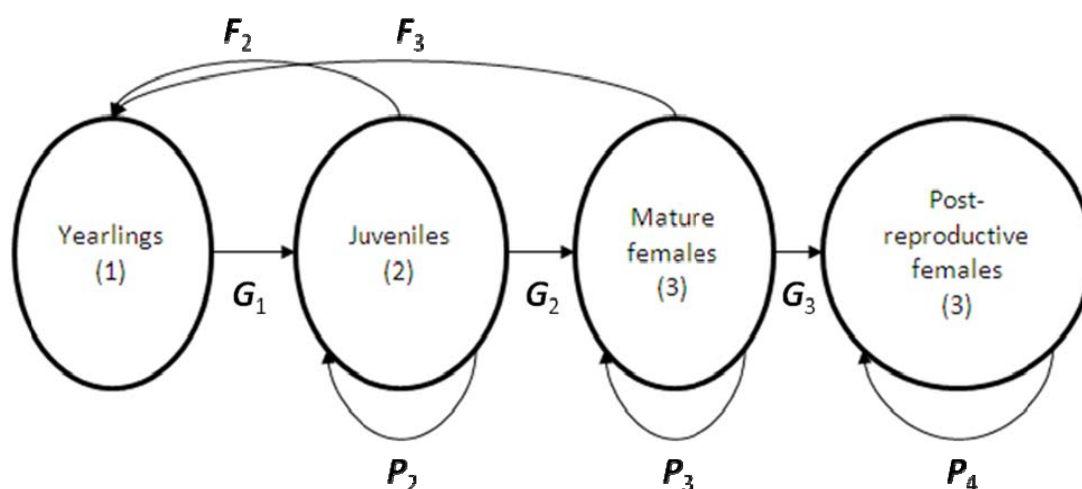

Fig. 1. Stage-structured killer whale life cycle graph (from Brault and Caswell 1993)

Projection matrices - The information contained within a life cycle graph can also be written in the form of a projection matrix. A projection matrix can be constructed based on the classes and transition pathways between classes depicted in the life-cycle graph. A matrix consists of an equal number of rows and columns and the number of rows or columns is the same as the total number of classes in the life cycle of the organism. For instance, the life cycle of the killer whale includes four distinct stage-classes (yearling, juveniles, mature females, and post-reproductive females). Therefore, the matrix summarizing the life cycle of the killer whale consists of four columns and four rows. This matrix includes

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the following elements: the probability of survival and staying in the same stage-class (P), the probability of survival and moving to the next stage-class (G), and fecundity (F) (Fig. 2). The numerical values for each element of the matrix can be calculated based on values of vital rates (survival and fecundity) in various classes.

<div align="center">

FROM STAGE-CLASS:

	1	2	3	4
1	0	F_2	F_3	0
2	G_1	P_2	0	0
3	0	G_2	P_3	0
4	0	0	G_3	P_4

TO STAGE-CLASS: (rows 1–4)

</div>

Fig. 2. Stage-classified population projection matrix (**A**) for a killer whale population (Brault and Caswell 1993). Stage-classes include: yearlings (1), juveniles (2), mature females (3), and post-reproductive females (4).

Note that each entry in the matrix can be thought of as corresponding to the transition <u>from</u> the stage-class in the given <u>column</u> <u>to</u> the stage-class in the given <u>row</u>. For instance, the vital rate F_2 describes the transition from the juvenile stage-class (column 2) to the yearling stage-class (row 1). If a matrix entry is "0" this indicates that a transition does not exist between the corresponding column and row life-stages. For example, since post-reproductive females do not give birth there is a "0" value for the transition from post-reproductive females to yearlings (column 4, row 1) (Fig. 2).

To perform calculations based on the matrix, numerical values for individual matrix elements must first be calculated based on actual values of survival probabilities, transitions probabilities, and reproductive output measured for each stage-class. For example, the matrix element P_4 describes the probability that a post-reproductive killer whale survives and remains in the same stage-class over a one-year time-step interval. In this case, the numerical value for this matrix element is simply based on the estimated annual survival probability for post-reproductive females (0.9804). Other matrix elements must be calculated to reflect not only the probability of surviving but also the probability of transitioning between stages or remaining in the same stage.

Once the numerical value for all individual matrix elements have been determined it is possible to use the matrix to project the future size of a

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population based on observed vital rates and the number of individuals present in each stage class. To project future population sizes the projection matrix can be multiplied by a population vector. The population vector simply consists of the number of individuals in each class at a given point in time. For species where reproduction occurs in a single annual 'pulse', this point in time is typically chosen to reflect the status of the population immediately prior to reproduction (pre-breeding census) or immediately following reproduction (post-breeding census). The population vector is expressed as a single column with values reflecting the number of individuals present within each class. The total population size is obtained by adding up all of the entries in the population vector. Multiplying the projection matrix by the population vector gives a new population vector at the next time step (Fig. 3).

$$
\begin{bmatrix}
0 & F_2 & F_3 & 0 \\
G_1 & P_2 & 0 & 0 \\
0 & G_2 & P_3 & 0 \\
0 & 0 & G_3 & P_4
\end{bmatrix}
\times
\begin{bmatrix}
n_{1,\,t} \\
n_{2,\,t} \\
n_{3,\,t} \\
n_{4,\,t}
\end{bmatrix}
=
\begin{bmatrix}
n_{1,\,t+1} \\
n_{2,\,t+1} \\
n_{3,\,t+1} \\
n_{4,\,t+1}
\end{bmatrix}
$$

Projection matrix (**A**)   Population vector (n_t)   Population vector (n_{t+1})

Fig. 3. Example of projecting population size based on multiplying a population matrix from the killer whale population example (Brault and Caswell 1993) by a population vector. The initial population vector includes a population size (n_i) for each stage-class at time t. Stage-classes for the population vector include: yearlings (1), juveniles (2), mature females (3), and post-reproductive females (4). Multiplying the projection matrix by the population vector at time t results in the population vector at time t+1.

Multiplication of the population vector by the matrix can be easily accomplished using matrix algebra. Begin by multiplying the value from the first row and first column of the matrix by the value from the first entry in the population vector. Next, multiply the value from the first row and second column of the matrix by the value from the second entry in the population vector. Continue by multiplying the next column from the first row of the matrix by the next entry in the population vector. Repeat this process until every value from the first row has been multiplied by a value from the population vector. Now sum up all of these values and the resulting number is the first entry in the new population vector. Repeat

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this process for each subsequent row in the matrix to generate the new population vector at time t+1.

An example of multiplying a population matrix by a population vector is given in Figure 4. Figure 4 simply uses the population matrix from the killer whale example (Brault and Caswell 1993) and multiplies this matrix by a population vector. In this case we have simply designated an arbitrary population size for each stage class (n_i) at time t ($n_{1,t}$ = 40, $n_{2,t}$ = 50, $n_{3,t}$ = 60, $n_{4,t}$ = 70) in the starting population vector (Figure 4).

Fig. 4. Procedure to multiply a population matrix by a population vector. The initial population vector includes the population size (n_i) for each stage-class at time t. From the killer whale example, stage-classes include: yearlings (1), juveniles (2), mature females (3), and post-reproductive females (4). Multiplying the projection matrix by the population vector at time t results in the population vector at time t+1.

The matrix can be multiplied by subsequent population vectors to project the future size of the population over multiple time-steps.

The rate of population growth (R) from one year (N_t) to the next (N_{t+1}) can be expressed as:

$$N_{(t+1)} / N_t$$

Following repeated multiplication of the projection matrix by subsequent population vectors, the proportion of individuals in each stage-class will

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eventually stabilize and population size will change at a constant rate over each time-step. At this point, the rate of growth (R) is approximately equivalent to the asymptotic rate of population growth (λ). A population matrix is useful because the asymptotic rate of population growth (λ) is the dominant eigenvalue of the matrix and can be derived directly from the matrix (Caswell 2000).

Perturbation analysis - A population projection matrix can be used to project the expected values for population size and growth rate based on current population size and vital rate values. The rate of population growth will change if values for vital rates change. Perturbation analysis is a type of prospective analysis that examines how changes in vital rates would influence the rate of population growth (λ).

To quantify how changes in vital rates influence λ, it is possible to measure the change in λ that would occur due to a small absolute change in a given matrix element. This is known as sensitivity analysis and sensitivity values (s_{ij}) can be calculated for any element of the matrix. For example, sensitivity values can even be calculated for life-cycle transitions that do not actually occur and are parameterized as a zero value in the matrix. This is possible because sensitivity measures the impact of what would happen to λ if a given matrix element was increased by a small absolute amount while all other elements were held constant. Thus, sensitivity may be useful for examining 'what-if' scenarios for a hypothetical transition in the life-cycle.

It is also possible to calculate an elasticity value (e_{ij}), which expresses the proportional change in λ that would occur as a result of a small proportional change in the numerical value for a given non-zero element of the matrix. For a given life cycle, the elasticity values for all transitions sums to 1.0 and thus can be interpreted as the relative influence that a given matrix element has on population growth rate. Therefore, proportional changes in vital rates with higher elasticity values are expected to have a greater influence on population growth rate than the same proportional change in a vital rate with a lower elasticity value. Elasticity analysis has been applied to conservation and management scenarios to help understand how changes in vital rate values could influence future rates of population growth.

Data has been collected on vital rates (survival and reproduction) for various phases of the life cycle of a loggerhead sea turtle population (Fraser et al. 1983a). Crowder et al. (1994) created a stage-based population projection matrix based on vital rates collected by Fraser et al. (1983a) for loggerhead sea turtles. We will use a dataset published by Crowder et al. (1994) to determine expected rates of population growth (λ) and the elasticity of λ to changes in individual vital rates.

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Dataset analysis:

1. **Constructing a life-cycle diagram -** Loggerhead sea turtle populations can be classified into five life stages including: eggs/hatchlings, small juveniles, large juveniles, subadults, and adults. Vital rate values for loggerhead sea turtles were used to generate parameters that can be used to characterize the life cycle of the loggerhead sea turtle. Parameters in the dataset include the probability of survival and staying in the same stage-class (*P*), the probability of survival and moving to the next stage-class (*G*), and fecundity (*F*). Based on parameter values from this dataset draw a life cycle diagram for the loggerhead sea turtle population. When constructing the life cycle diagram, recall that arrows between nodes indicate the probability of surviving and moving to the next stage. Arrows that point to the same node indicate the probability of an individual surviving and staying in the same stage (self-loops). Start by drawing a separate node for each of the five stages (eggs/hatchling, small juveniles, large juveniles, subadults, adults) and use the dataset to correctly draw arcs as part of the life cycle diagram.

2. **Constructing a population matrix -** After completing the life cycle diagram, use the values from the dataset to construct a parameterized population matrix (**A**) for the loggerhead sea turtle population. Remember that the number of nodes (circles) in the life cycle diagram should equal the number of rows or columns in the matrix. When constructing the matrix it may be useful to label each row and column with the corresponding stage from the life cycle.

3. *Projecting population size -* Once the numerical value for all individual matrix elements have been determined it is possible to use the matrix to project the future size of a population based on matrix values. To project future population sizes the projection matrix must be multiplied by a population vector. The population vector simply consists of the number of individuals in each class at a given point in time. Multiplication of the matrix by the population vector at time t will result in a population vector at time t+1. Matrix multiplication can be done by hand to generate the population vector at time t+1. For this example, use the following arbitrary population sizes in each stage-class: hatchlings = 40, small juveniles = 20, large juveniles = 20, subadults = 10, adults = 10. Remember that the population vector should consist of a single column with each entry corresponding to the population size in a given stage-class.

   Multiply the population matrix by the initial population vector and address the following questions.

What is the population size at time t?

What is the population size at time t+1?

Is the population growing or declining over this time period?

How many individuals are in each stage at time t+1?

4. **Graphing projected population sizes:** It is also possible to use computer software to perform calculations that involve multiplying a population matrix by a population vector to project future population sizes. One such software program that can be for this purpose is the POPTTOOLS extension for Microsoft Excel. To project future population sizes from the matrix using POPTOOLS you must first input your matrix into an Excel spreadsheet. Enter each value of the matrix into a separate cell in the Excel spreadsheet. The entered data should have the same number of rows and columns as the original matrix. Each cell value entered in the spreadsheet should correspond to an individual element of the matrix. See the example below for how to enter the values for the killer whale example (Fig. 5).

0	0.0043	0.1132	0
0.9775	0.9111	0	0
0	0.0736	0.9534	0
0	0	0.0452	0.9804

Fig. 5. Example illustrating how to enter the killer whale matrix into an Excel spreadsheet.

When your matrix is entered you must designate a starting population vector. The population vector consists of the starting number of individuals that are present in each stage-class of the life-cycle. To accurately project population size, the population vector must be based on actual population sizes estimated for each stage class. However, if the actual number of individuals in each stage-class is not known, it is possible to start with an arbitrarily determined number of individuals in each stage-class.

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Construct a population vector using numbers that you determine for each stage-class. Enter this population vector within a single column in your Excel spreadsheet with each entry representing the population size for a given stage-class. Make sure that you enter the population vector in the same Excel worksheet that contains your population matrix. Now choose the "Matrix Tools" submenu from the POPTOOLS dropdown menu and select "Matrix Projection". Click once on the box labeled Matrix, and highlight all of the cells within your matrix. Next, click on the box labeled State Vector and highlight the cells in your population vector. The number of iterations determines how many times that the matrix will be multiplied by subsequent population vectors. To project 100 time-steps into the future, enter 100 into the iterations box. Now click on the area for "Output", and select a different cell in the spreadsheet that will be the location of the output values. Click on "GO" and the resulting output provides the number of individuals present in each stage class at each time-step.

Based on the output, use Excel to prepare a line-graph of total population size vs. time. Make sure and label each axis appropriately.

> *Based on your graph, does the population appear to be changing at the same rate each year?*

> *Does the population appear to be increasing or decreasing?*

Recall that after repeated multiplication of the projection matrix by subsequent population vectors, the proportion of individuals in each stage-class will eventually stabilize and population size will change at a constant rate over each time-step. Use Excel to calculate $N_{(t+1)} / N_t$ at each time-step in your output.

> *How many time-steps does it take before the population size changes at a constant rate for each subsequent time-step?*

Recall that at this point, the rate of population change ($N_{(t+1)} / N_t$) approximates the asymptotic rate of population growth (λ). The fluctuations in population growth that occur prior to reaching equilibrium can be thought of as transient dynamics. In many populations, understanding these transient dynamics may be beneficial for developing short-term conservation and management strategies.

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5. **Calculating population growth rate (λ) directly from the matrix –** It is also possible to calculate λ based solely on the matrix, since the value for λ is the dominant eigenvalue of the projection matrix (see Caswell 2000 for further details). To do this using POPTOOLS, choose the "Matrix Tools" submenu from the POPTOOLS drop-down menu and click on "Finite Rate of Increase".

   This will produce a pop-up box with areas that allow you to specify your input matrix, and the location of your output. Click once on the box for Matrix, and highlight all of your cells within your matrix. Now click on the area for "Output", and select a different cell in the spreadsheet that will be the location of the output values. Click on "GO" and the resulting output value is the rate of population growth (λ). This value is the expected rate of population growth with the given vital rate values.

   Record the value of lambda (λ) for the loggerhead sea turtle population.

   Based on this value for λ is the population declining, stable, or increasing?

6. **Comparing transient vs. equilibrium dynamics –** In this section you will create a graph to compare the expected rate of population change at equilibrium (based on the calculated value of λ) vs. the transient dynamics of the matrix based on calculations from multiplying the matrix by the population vector.

   You have already created a graph of projected population size based on multiplying a population vector by the population matrix. Now, start with the same initial population size that you used for the population vector (from **4. Graphing project population sizes**) and multiply this by the value that you determined for λ. This gives the expected population size at time t+1 <u>if</u> the population is at a stable age distribution. Continue projecting population size by multiplying subsequent population sizes by λ for 100 time-steps. Use these values to create a graph in Excel and compare it to the graph that you created earlier based on multiplying the matrix by the population vector.

   What differences are present between your two graphs?

7. **How changes in matrix elements impact λ-** Extensive efforts have been put in place to increase loggerhead reproductive success and egg

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survival. Efforts are also being made to increase juvenile, subadult and adult survival by enforcing regulations requiring turtle excluder devices (TED's) on trawl nets. These devices allow turtles captured in trawl nets to escape safely. It may be possible to increase the effectiveness of conservation strategies by focusing efforts on vital rates that have the greatest impact on population growth. Therefore, it is important to consider whether increasing fecundity or survival will have a greater impact on population growth.

> *Which of these do you believe might have the greatest impact on population growth rates?*

Now test your initial idea by increasing one of the individual matrix elements by a given percentage (i.e. 5%) while holding all other matrix elements constant. Remember that matrix elements related to survival must always remain < 1.0. Use POPTOOLS to calculate the new value for λ following the increase in this vital rate. Now sequentially increase individual matrix elements by the same chosen percentage while holding all other matrix elements constant at the original value. Calculate the changes in lambda that result after increasing each individual matrix element in turn while holding other matrix elements constant.

> *Changing which matrix element resulted in the greatest increase in lambda?*

> *Does it appear that survival or fecundity will have the greatest impact on population growth?*

8. **Elasticity analysis from the matrix:**

For the final step, we will determine which matrix elements have the greatest influence on λ by calculating elasticity values for each element in the matrix.

To calculate elasticities, again select the "Matrix tools" submenu from the POPTOOLS drop-down menu, and click on "Matrix elasticity". This will produce a pop-up window where you can input your matrix range (simply click on the input area and highlight your matrix cells).

Click on the output area, select an output cell, and click "GO". This outputs a matrix of elasticity values. Each cell value in the output is the elasticity for the corresponding element of the original projection matrix.

Which vital rate value has the highest elasticity?

Which vital rate value has the lowest elasticity?

The questions and calculations that you have completed in this section will be used as the basis for further discussion and critical thinking questions.

Questions for Further Thought and Discussion:

1. Begin by reading Crouse et al. (1987) and Crowder et al. (1994). Crowder et al. (1994) used five different stage-classes to describe the loggerhead sea turtle life cycle. However, other studies of loggerhead sea turtles (Crouse et al. 1987) classify the life cycle into seven distinct stage-classes. After reading both Crowder et al. (1994) and Crouse et al. (1987), why do you think that there are differences between how each of these authors defines the number of stage-classes for loggerhead sea turtles? How do you think that ecologists determine an appropriate number of stage-classes? Which number of stage-classes do you think is the most appropriate to use for modeling loggerhead sea turtle populations? Explain your answer.

2. Looking at the matrix for the killer whale population (Fig. 2), what impact do you think that a change in the vital rate value for matrix element P_4 would have on the growth rate of the population? Explain your answer.

3. Based on the matrix and the life cycle diagram for the loggerhead sea turtle population, what two life stages are reproductively active? Which of these stages has the highest fecundity? Why might there be differences in fecundity between these two life stages? How do you think that reproductive output might change over the life-stages of an organism?

4. What differences did you observe between elasticity values for vital rates related to survival and growth compared to those of fecundity? If you were in charge of conserving sea turtle populations, which type of vital rate would you try to increase? Why?

5. Do you think that there would be any relationship between the variation of a vital rate occurring over time (or in response to environmental change) and the elasticity of a vital rate? In other words, would you expect a vital rate with high elasticity to exhibit more or less temporal variation than a vital rate with low variability? Consult papers by Pfister et al. (1998) and Morris and Doak (2004) to help with your answer.

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6. Compare the graph that you created of population size vs. time for the "**4. Graphing Projected Population Size**" part of the dataset analysis to graphs created by other lab groups. Are these graphs of projected population size similar for different groups? Why might these graphs vary? Do think that there are situations in which it might be more important to know expected patterns of short-term change in population size (transient dynamics) rather than just the value for (λ)?

References and Links:

Bolten, A.B. 2003. Active swimmers – passive drifters: the oceanic juvenile stage of loggerheads in the Atlantic system. Pp. 63-78 *in* Loggerhead Sea Turtles. Bolten, A.B. and B.E. Witherington, eds. Smithsonian Books, Washington, D.C.

Brault, S., and H. Caswell. 1993. Pod-specific demography of killer whales (*Orcinus orca*). Ecology 74: 1444-1454.

Caswell, H. 2000. Matrix population models. 2nd edition. Sinauer, Sunderland, Massachusetts.

Crouse, D.T., L.B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68: 1412-1423.

Crowder, L.B., D.T. Crouse, S.S. Heppell, and T.H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. Ecological Applications 4: 437-445.

Ehrhart, L.M., D.A. Bagley, and W.E. Redfoot. 2003. Pp. 157-176 *in* Loggerhead Sea Turtles. Bolten, A.B. and B.E. Witherington, eds. Smithsonian Books, Washington, D.C.

Frazer, N.B. 1983a. Survivorship of adult female loggerhead sea turtles (*Caretta caretta*), nesting on Little Cumberland Island, Georgia, U.S.A. Herpetologica 39:436-447.

Frazer, N.B. 1983b. Demography and life history evolution of the Atlantic loggerhead sea turtle, *Caretta caretta*. Ph.D. Dissertation, University of Georgia, Athens.

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Teaching Issues and Experiments in Ecology - Volume 7, May 2011

Heppell, S.S., L.B. Crowder, D.T. Crouse, S.P. Epperly, and N.B. Frazer. 2003. Pp 255-273 *in* Loggerhead Sea Turtles. Bolten, A.B. and B.E. Witherington, eds. Smithsonian Books, Washington, D.C.

Lewison, R.L., L.B. Crowder, and D.J. Shaver. 2003. The impacts of turtle excluder devices and fisheries closures on loggerhead and Kemp's Ridley strandings in the western Gulf of Mexico. Conservation Biology 17:1089-1097.

Lewison, R.L., S.A. Freeman, and L.B. Crowder. 2004. Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. Ecology Letters 7: 221-231.

Lutcavage, M.E., P.Plotkin, B. Witherington, and P.L. Lutz. 1997. Human impacts on sea turtle survival. Pp. 387-410 *in* P.L. Lutz and J.A. Musick. Eds. The Biology of Sea Turtles. CRC Press, Boca Raton, Florida.

Miller, J.D., C.J. Limpus, and Matthew H. Godfrey. 2003. Pp. 125-143 *in* Loggerhead Sea Turtles. Bolten, A.B. and B.E. Witherington, eds. Smithsonian Books, Washington, D.C.

Mills, L.S., D.F. Doak, and M.J. Wisdom. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. Conservation Biology 13: 815-829.

Morris, W.F., and D.F. Doak. 2004. Buffering of life histories against environmental stochasticity: accounting for a spurious correlation between the variabilities of vital rates and their contributions to fitness. American Naturalist 163: 579-590.

Pfister, C.A. 1998. Patterns of variance in stage-structured populations: evolutionary predications and ecological implications. Proceedings of the National Academy of Science 95: 213-218.

Schroeder, B.A., A.M. Foley, and D.A. Bagley. 2003. Nesting patterns, reproductive migrations, and adult foraging areas of loggerhead turtles. Pp. 114-124 *in* Loggerhead Sea Turtles. Bolten, A.B. and B.E. Witherington, eds. Smithsonian Books, Washington, D.C.

Van Buskirk, J., and L.B. Crowder. 1994 Life-history variation in marine turtles. Copeia 1994: 66-81.

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Teaching Issues and Experiments in Ecology - Volume 7, May 2011

Witherington, B.E. 1992. Behavioral responses of nesting sea turtles to artificial lighting. Herpetologica 48: 31-39.

Witherington, B.E. 2003. Biological conservation of loggerheads: challenges and opportunities. Pp. 295-312 *in* Loggerhead Sea Turtles. Bolten, A.B. and B.E. Witherington, eds. Smithsonian Books, Washington, D.C.

Web Site Links:

ARKive: Images of Life on Earth: http://www.arkive.org/loggerhead-turtle/caretta-caretta/video-15.html

NOAA Fisheries: Marine Turtles: http://www.nmfs.noaa.gov/pr/species/turtles/

NOTES TO FACULTY

Description of Excel Files:
- Student Dataset: This file contains data from Crowder et al. (1994) needed to construct a population matrix for loggerhead sea turtles. [xlsx]
- Faculty Dataset: This file contains data from Crowder et al. (1994) needed to construct a population matrix for loggerhead sea turtles. Also included are worksheets with examples of projecting population size, calculating lambda, and determining elasticity values. [xlsx]

Challenges to Anticipate and Solve:

1. Students in the class may have different backgrounds and familiarity in working with spreadsheet programs such as Microsoft Excel. If students do not have strong computer skills the process of downloading and installing the POPTOOLS software can be time-consuming and even distract from the intended learning objectives.

Solution: If you are aware that some of your students have limited computer skills, it may be beneficial to download and install POPTOOLS onto computers that students will be using for class so that the POPTOOLS add-in is already installed when students begin the experiment. This solution works well if you are using a computer lab, but may be more difficult if students are working on personal laptops. Another good solution is to work through the download and installation process as part of the experiment with the students (on your own

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computer attached to a projector). This way students can actually see what they are supposed to be doing at each step in the process of installing the software and starting the experiment.

2. It may be difficult to stimulate class discussion on some of the questions if students have not had adequate time to think out thoughtful responses to the questions.

Solution: It could be possible to have students use a "write before discussing" approach or "think-pair-share" approach to answering these questions. This allows students to formulate thoughts on the questions and could enhance discussion responses in a class or small-group setting.

3. Students may have a variety of math backgrounds and may not be familiar with matrix algebra.

Solution: It may be necessary to explain and work through several other examples of matrix multiplication so that students grasp this concept before applying it to the lab exercise.

Comments on the Experiment:

Comments on Introducing the Experiment to Your Students: This experiment is introduced within the context of a lecture section of the course that is focused on population biology. Students need an understanding of basic principles of population growth before doing this experiment. For introducing this particular experiment, I generally give some life-history background on loggerhead sea turtles and show pictures or videos of each life-stage to increase interest and draw students into the scenario. There are short videos of several key stages in the logger head life-cycle available through these links: egg laying, hatchling emergence, and hatchlings entering the ocean.

This lab can also be introduced as an applied ecological question related to sea turtle conservation and challenging students to think about how various methods used to influence vital rate values might or might not be effective in changing the rate of population growth.

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Comments on the Data Analysis Methods Used in the Experiment: It is helpful for faculty to be familiar with Excel and the POPTOOLS extension before performing the experiment. This should help with any "trouble-shooting" questions that arise when students are working on calculations.

Comments on Data Analysis:

Perturbation analysis: Make sure that students only change a single vital rate at a time while holding all other vital rates constant. If they do this correctly, they should see that matrix elements related to survival should have a greater impact on lambda than matrix elements related to fecundity.

Comments on Questions for Further Thought:

1. *Begin by reading Crouse et al. (1987) and Crowder et al. (1994). Crowder et al. (1994) used five different stage-classes to describe the loggerhead sea turtle life cycle. However, other studies of loggerhead sea turtles (Crouse et al. 1987) classify the life cycle into seven distinct stage-classes. After reading both Crowder et al. (1994) and Crouse et al. (1987), why do you think that there are differences between how each of these authors defines the number of stage-classes for loggerhead sea turtles? How do you think that ecologists determine an appropriate number of stage-classes?   Which number of stage-classes do you think is the most appropriate to use for modeling loggerhead sea turtle populations? Explain your answer.*

This question provides an opportunity to introduce students to the idea that various life-stages of an organism have distinct survival and reproductive rates. This could be an opportunity to talk about senescence or sexual maturation within the context of the life-history of an organism. It's also an opportunity to have students think about how life-stages may be easily distinguished for some species, or may only have subtle differences for other organisms. Students may also realize that creating a life cycle graph also involves expert opinion about which life-stages are truly distinct when determining the structure and number of unique stages to include in the life cycle.

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2. *Looking at the matrix for the killer whale population (Fig. 2), what impact do you think that a change in the vital rate value for matrix element P_4 would have on the growth rate of the population? Explain your answer.*

   This question should allow students to think about what exactly contributes to population growth and that survival rates of some non-reproductive stages may not influence population growth. However, students should be able to recognize that survival and growth rates of other non-reproductive stages (yearlings in the killer whale example) could have an impact on population growth. If students are familiar with the biology of killer whales, they might also recognize that a post-reproductive female may function as the matriarch of a killer whale pod. In this matriarchal system, the fate of post-reproductive matriarchs may influence the survival and reproductive success of other whales in the pod and thus survival or post-reproductive females could potentially have an indirect impact on overall rates of population growth.

3. *Based on the matrix and the life cycle diagram for the loggerhead sea turtle population, what two life stages are reproductively active? Which of these stages has the highest fecundity? Why might there be differences in fecundity between these two life stages? How do you think that reproductive output might change over the life-stages of an organism?*

   These questions provide students an opportunity to think about how reproductive output may change with the age of an organism. Examples could be incorporated of how reproductive output may not be as high for novice breeders of some species and also reproductive output may decline with age in some species. It's also another way to think about how changes in reproductive output at different life-stages may have different impacts on population growth rate.

4. *What differences did you observe between elasticity values for vital rates related to survival and growth compared to those of fecundity? If you were in charge of conserving sea turtle populations, which type of vital rate would you try to increase? Why?*

   This is a good opportunity to discuss the role of elasticity analysis as a tool for conservation planning. This is also a chance to discuss some of the caveats related to applying elasticity analysis to make conservation decisions (see Mills et al. 1999). For example, just because a vital rate has a high elasticity value does not mean that it will be easily possible to effectively manipulate this vital rate.

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5. *Do you think that there would be any relationship between the variation of a vital rate occurring over time (or in response to environmental change) and the elasticity of a vital rate? In other words, would you expect a vital rate with high elasticity to exhibit more or less temporal variation than a vital rate with low variability? Consult papers by Pfister et al. (1998) and Morris and Doak (2004) to help with your answer.*

    The relationship between the elasticity and temporal variability of a vital rate may not be intuitively obvious for students. However, this question should make them think more deeply about the relationship between the temporal variability and elasticity of vital rates and the underlying reasons for this relationship. This question serves as an opportunity to introduce students to the negative relationship between the elasticity and variability of vital rates, in that vital rates with high elasticity values may also be relatively invariant (Pfister et al. 1999). This is an opportunity to discuss that vital rates with high elasticity values may be relatively invariant in response to environmental changes and may also be more difficult to influence through management actions. This question also gives students a good chance to use ecological literature as the basis for gaining further insight into this question.

6. *Compare the graph that you created of population size vs. time for the "4. Graphing Projected Population Size" part of the dataset analysis to graphs created by other lab groups. Are these graphs of projected population size similar for different groups? Why might these graphs vary? Do think that there are situations in which it might be more important to know expected patterns of short-term change in population size (transient dynamics) rather than just the value for (λ)?*

    Graphs of projected population size should differ between groups based on the number of initial individuals that they chose to include in each stage-class when they created the initial population vector. Some groups may actually observe an increase in population size over the short-term until proportions in each stage-class stabilize and the population begins to decrease at the same rate each year. This may be a good opportunity to note that age structure can have a substantial impact on short-term population trends. The differences between groups should also illustrate that transient dynamics may exhibit great variation and that it may be just as interesting to understand how the population might change in the short-term as to understand asymptotic rates of population change (λ**).**

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Comments on the Assessment of Student Learning Outcomes:

Assessing answers to discussion questions may be a challenging part of the assessment process. It may be useful to have students prepare written responses to these questions to make assessment of student learning easier.

Comments on Formative Evaluation of this Experiment:

Formative evaluation for the experiment can be conducted based in part on the level of student understanding as shown in discussion questions. The experiment and supporting literature should enable students to provide answers to these questions that demonstrate an understanding of key learning objectives. Students should not only be able to go through the process of calculating elasticities and λ but also be able to describe the purpose or interpretation of these calculations. Simply asking students to define and explain the terms that are being calculated is one way to begin to determine if the process has been effective in increasing student understanding of these topics.

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