MODULE 13.3

Time after Time—Age- and Stage-Structured Models

Prerequisites: Module 13.1, "Computational Toolbox—Tools of the Trade: Tutorial 7" or "Alternative Tutorial 7" (through section on "Eigenvalues and Eigenvectors") and Module 13.2, "Matrices for Population Studies—Linked for Life." Additional high-performance computing materials related to this module are available on the text's website.

Downloads

The text's website has the file *AgeStructured*, containing the models in this module, available for download for various computational tools.

Introduction

> The worst thing that can happen—will happen—is not energy depletion, economic collapse, limited nuclear war, or conquest by a totalitarian government. As terrible as these catastrophes will be for us, they can be repaired within a few generations. The one process ongoing. . .that will take millions of years to correct, is the loss of genetic and species diversity by the destruction of natural habitats. This is the folly our descendants are least likely to forgive us.
>
> –E. O. Wilson (Bean 2005)

If you were sitting on a beach on one of the 12 islets of French Frigate Shoals in northwestern Hawaii admiring the April moon, you might be surprised to see a rather large body crawling deliberately up the sand. It is likely a female green sea turtle (*Chelonia mydas*) on her way to deposit her eggs. Although these turtles may normally feed around other Hawaiian islands, they usually return to the beach where they hatched (natal beach) to nest. Ninety percent of green turtle nests in Hawaii are found on these islets.

Nesting is an arduous process for this animal, and she may make the journey more than once this season. Though she may have several more clutches to lay, she digs a hole with her front flippers to a depth of about 2 ft, deposits her 100± eggs, covers the eggs, and returns to the water. She might return 2 weeks or so later to build another nest and deposit more eggs. Fortunately for her, she does this only every 3 years or so.

Undisturbed eggs deposited this night incubate below the surface for about 2 months. After escaping from their leathery cases, 1-oz hatchlings work together to emerge from their sandy womb. All this occurs at night, when temperatures are lower and the turtles are less conspicuous. Once out of the nest, they sprint toward the bouncing glints of light on the ocean surface. Many do not make it, intercepted by birds, crabs, or other predators, which have learned that these hatching events provide tasty meals. Even if they make it to the water, no matter how fiercely they swim, carnivorous fish may eat them. Then, as adults, turtles have two main predators—sharks and human beings, the latter being more of a threat.

Those that survive the beach dash and shallow waters swim out to sea, where they feed on various floating plants and animals. As they become adults they utilize large, shallow sea grass beds for much of their diet. Such a diet results in the development of body fat that is green, which gives this animal its name. Long lived, this animal may not become sexually mature for 20 years or more. Few from that original clutch of eggs, however, will make it to return to this beach for breeding and nesting.

Marine predators are not the only obstacles to survival and breeding success. Turtles and their eggs are still consumed in many places in the world. Coastal development and subsequent habitat destruction also devastate breeding and nesting. For example, in St. Croix various species of sea turtles nest primarily in the Jack, East End and Isaac Bays, and Buck Island, where there is no development and the beaches are relatively undisturbed. Information from satellites has proved invaluable in collecting a wide variety of environmental data that help in protecting important, unique habitats, understanding environmental changes, and ensuring the survival of endangered species. NASA with the CNES (Centre National d'Etudes Spatiales, the French space agency) and NOAA (the National Oceanic and Atmospheric Administration) established Argos, a satellite-based system that helps to collect, process, and disseminate environmental data for various platforms (ARGOS 2013).

Pollution of various sorts may not only cause turtle mortality directly but also induce an ever-increasing incidence of fibropapilloma. This disease results in the development of large tumors that interfere with normal life activities of the animals, resulting in death.

On December 28, 1973, the Endangered Species Act became law in the United States. This act provides programs that promote the conservation of threatened and endangered plant and animal species and the habitats where they are found. **Endangered** organisms are species that are in danger of extinction throughout all or over a sizeable portion of their range. **Threatened** species are those likely to become endangered in the foreseeable future. Currently, there are almost 2000 threatened and endangered species worldwide found on the list maintained and published by the

Fish and Wildlife Service of the U.S. Department of Interior. Of the approximately 1200 animals on the list are six of the seven species of sea turtles. Green sea turtles were added to the list in 1978.

Many studies have been attempted to ascertain the status of green sea turtle populations worldwide. Various interventions, primarily aimed at protecting the nests and hatchlings, have been attempted. However, there is much we do not know about the biology and demography of these animals that need to be understood to make appropriate conservation efforts. Sea turtle life cycles are long and complex; because growth stops at sexual maturity, it has been difficult to determine the age of turtles. Also, it has been virtually impossible to mark hatchlings so that we can identify them as adults. Detailed information regarding the population demography of turtles is vital if we are to establish the status of wild populations and to implement effective management procedures. Decisions and conservation efforts we make today may be crucial to preventing their extinction. But, how can we make effective decisions if we do not understand how various management alternatives affect turtle populations?

One approach to studying sea turtle populations is the use of mathematical models, specifically Leslie and Lefkovitch matrix population projections. The Leslie matrix projection, developed by P. H. Leslie in 1945, uses mortality and fecundity rates to develop population distributions. These distributions are founded on initial population distribution of age groups. Because the age of adult turtles is difficult to determine, some researchers have used a Lefkovitch matrix, which divides the populations into stage classes. Some of the life stages are easily recognizable (eggs, hatchlings, nesting adults), but the juvenile stages are long lasting, and age is difficult to determine. So, size (length of carapace or shell) is used to define stages.

Resulting population projections have indicated that we may need to increase protective measures to juveniles and adults if we really want to increase the numbers of sea turtles. Crowder et al. (1994) published a stage-based population model for the loggerhead turtle (*Caretta caretta*) that projected the effects of the use of turtle-exclusion devices (TEDs) in trawl fisheries. These devices allow young turtles to escape the trawls that trap shrimp, and the model predicted that the required use of TEDs for offshore trawling would allow a gradual increase in Loggerheads by an order of magnitude in about 70 years. Such regulations may save thousands of turtles each year and help to save sea turtle species from extinction (Bjorndal et al. 2000; Crouse et al. 1987; Crowder et al. 1994; Earthtrust 2009; Forbes 1992; Zug 2002).

The Problem

We can classify many animals by discrete ages to determine reproduction and mortality. For example, suppose a certain bird has a maximum life span of 3 years. During the first year, the animal does not breed. On the average, a typical female of this hypothetical species lays 10 eggs during the second year but only 8 during the third. Suppose 15% of the young birds live to the second year of life, while 50% of the birds from age 1 to 2 years live to their third year of life, age 2 to 3 years. Usually, we consider only the females in the population; and in this example, we assume that half the offspring are female.

For such a situation, we are interested in the answers to several questions:

- Can we determine the projected population growth rate?
- In the case of declining populations, what is the predicted time of extinction?
- As time progresses, does the population reach a stable distribution?
- If so, what is the proportion of each age group in such a stable age distribution?
- How sensitive is the long-term population growth rate or predicted time of extinction to small changes in parameters?

Age-Structured Model

Figure 13.3.1 presents a state diagram for the problem with the states denoting ages (year 1, 2, or 3) of the bird. The information indicates that an **age-structured model** might be appropriate. In age-structured models we ignore the impact of other factors, such as population density and environmental conditions. We can use such models to answer questions about the rate of growth of the population and the proportion of each age group in a stable age distribution.

For the example in the previous section, three clear age classes emerge, one for each year. Thus, in formulating this deterministic model, we employ the following variables: x_i = number of females of such a bird at the beginning of the breeding season in year i (age $i - 1$ to i) of life, where $i = 1, 2,$ or 3. Thus, x_1 is the number of eggs and young birds in their first year of life.

Time, t, of the study is measured in years immediately before breeding season, and we use the notation $x_i(t)$ to indicate the number of year i females at time t. For example, $x_2(5)$ represents the number of females during their second year, ages 1 to 2 yr old, at the start of breeding season 5. Some of these survive to time $t + 1 = 6$ yr and progress to the next class, those females in their third year of life. At that time (at time 6 yr of the study), the notation for number of year 3 females is $x_3(6)$.

To establish equations, we use these data to project the number of female birds in each category for the following year. The number of eggs/chicks depends on the number of adult females, x_2 and x_3. Because on the average a year 2 (ages 1 to 2 years old) mother has 5 female offspring and a year 3 (ages 2 to 3 years old) mother has 4 female offspring, the number of year 1 (ages 0 to 1 year old) female eggs/chicks at time $t + 1$ is as follows:

$$5x_2(t) + 4x_3(t) = x_1(t + 1) \tag{1}$$

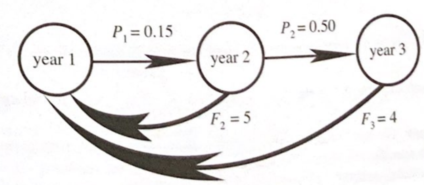

Figure 13.3.1 State diagram for problem

However, at time $t + 1$, the number of year 2 (ages 1 to 2 years old) females, $x_2(t + 1)$, depends only on the number of year 1 (ages 0 to 1 year old) females this year, $x_1(t)$, that live. The latter survives with a probability of $P_1 = 15\% = 0.15$, so that we estimate next year's number of year 2 females to be as follows:

$$0.15x_1(t) = x_2(t + 1) \tag{2}$$

Similarly, to estimate the number of year 3 (ages 2 to 3 years old) females next year, we need to know only the number of year 2 (ages 1 to 2 years old) females, $x_2(t)$, and their survival rate (here, $P_2 = 50\% = 0.50$). Thus, the number of year 2 females next year will be approximately the following:

$$0.50x_2(t) = x_3(t + 1) \tag{3}$$

Placing Equations 1, 2, and 3 together, we have the following system:

$$\begin{cases} \quad 5x_2(t) + 4x_3(t) = x_1(t+1) \\ 0.15x_1(t) \qquad\qquad\quad\; = x_2(t+1) \\ \qquad\quad 0.50x_2(t) \qquad\;\; = x_3(t+1) \end{cases}$$

This system of equations translates into the following matrix-vector form:

$$\begin{bmatrix} 0 & 5 & 4 \\ 0.15 & 0 & 0 \\ 0 & 0.50 & 0 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \end{bmatrix} = \begin{bmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \end{bmatrix}$$

or

$$L\mathbf{x}(t) = \mathbf{x}(t + 1), \text{ where}$$

$$L = \begin{bmatrix} 0 & 5 & 4 \\ 0.15 & 0 & 0 \\ 0 & 0.50 & 0 \end{bmatrix}, \mathbf{x}(t) = \begin{bmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \end{bmatrix}, \text{ and } \mathbf{x}(t+1)$$

$$= \begin{bmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \end{bmatrix}.$$

Suppose an initial population distribution has 3000 female eggs/chicks, 440 year 2, and 350 year 3 female birds, so that $\mathbf{x}(0) = \begin{bmatrix} 3000 \\ 440 \\ 350 \end{bmatrix}$ is the **initial age-distribution vector**. The next year, because of births, aging, and deaths, the number of females in each age class changes. The following vector gives the calculation for the estimated population at time $t = 1$ year:

$$\mathbf{x}(1) = L\mathbf{x}(0) = \begin{bmatrix} 0 & 5 & 4 \\ 0.15 & 0 & 0 \\ 0 & 0.50 & 0 \end{bmatrix} \begin{bmatrix} 3000 \\ 440 \\ 350 \end{bmatrix} = \begin{bmatrix} 3600 \\ 450 \\ 220 \end{bmatrix}$$

Thus, at $t = 1$ year, we project a population of more eggs/chicks but fewer year 3 female adults than initially present.

Quick Review Question 1

Suppose an insect has maximum life expectancy of 2 months. On the average, this animal has 10 offspring in the first month and 300 in the second. The survival rate from the first to the second month of life is only 1%. Assume half the offspring are female. Suppose initially a region has 2 females in their first month of life and 1 in her second.

a. Define the variables of the model.
b. Construct a system of equations for the model.
c. Give the matrix representation for the model.
d. Using matrix multiplication, determine the number of females for each age at time $t = 1$ month expressed to two decimal places.
e. Determine the number of females for each age at time $t = 2$ months.

Leslie Matrices

L is an example of a **Leslie matrix**, which is a particular type of **projection matrix**, or **transition matrix**. Such a square matrix has a row for each of a finite number (n) of equal-length age classes. Suppose F_i is the average **reproduction**, or **fecundity, rate** of class i; and P_i is the **survival rate** of those from class i to class $(i + 1)$. With $x_i(t)$ being the number of females in class i at time t, $x_1(t)$ is the number of females born between time $t - 1$ and time t and living at time t. The model has the following system of equations:

$$\begin{cases} F_1x_1(t) + F_2x_2(t) + \cdots + F_{n-1}x_{n-1}(t) + F_nx_n(t) = x_1(t+1) \\ P_1x_1(t) = x_2(t+1) \\ P_2x_2(t) = x_3(t+1) \\ \vdots \\ P_{n-1}x_{n-1}(t) = x_n(t+1) \end{cases} \tag{4}$$

where

F_i is the average reproduction rate (fecundity rate) of class i,
P_i is the survival rate of from class i to class $(i + 1)$, and
$x_i(t)$ is the number of females in class i at time t.

Therefore, the corresponding $n \times n$ Leslie matrix is as follows:

$$L = \begin{bmatrix} F_1 & F_2 & F_3 & \cdots & F_{n-1} & F_n \\ P_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & P_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & P_{n-1} & 0 \end{bmatrix}$$

F_i and P_i are nonnegative numbers, which appear along the first row and the **subdiagonal**, respectively; all other entries are zero.

Definition In an $n \times n$ square matrix B, the **subdiagonal** is the set of elements

$$\{b_{21}, b_{32}, \ldots, b_{n(n-1)}\}.$$

With $\mathbf{x}(t)$ being the population female distribution vector at time t, $(x_1(t), x_2(t), \ldots, x_n(t))$, and $\mathbf{x}(t + 1)$ being the female distribution vector at time $t + 1$, $(x_1(t + 1), x_2(t + 1), \ldots, x_n(t + 1))$, both expressed as column vectors, we have the following matrix equivalent of the system of Equations 4: $L\mathbf{x}(t) = \mathbf{x}(t + 1)$

Definition A **Leslie matrix** is a matrix of the following form, where all entries F_i and P_i are nonnegative:

$$\begin{bmatrix} F_1 & F_2 & F_3 & \cdots & F_{n-1} & F_n \\ P_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & P_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & P_{n-1} & 0 \end{bmatrix}$$

Quick Review Question 2

Give the Leslie matrix for a system with four classes, where the (female) reproduction rates are 0.2, 1.2, 1.4, and 0.7 for classes 1 to 4, respectively, and the survival rates are 0.3, 0.8, and 0.5 for classes 1 to 3, respectively.

Age Distribution over Time

Let us now consider the population distribution as time progresses. In the section "An Age-Structured Model," we considered the initial female age distribution of a hypothetical bird species to be $\begin{bmatrix} 3000 \\ 440 \\ 350 \end{bmatrix}$ and calculated the distribution at time $t = 1$ to be $\mathbf{x}(1) = L\mathbf{x}(0) = \begin{bmatrix} 3600 \\ 450 \\ 220 \end{bmatrix}$. Repeating the process, we have the following results at time $t = 2$ years:

$$\mathbf{x}(2) = L\mathbf{x}(1) = \begin{bmatrix} 0 & 5 & 4 \\ 0.15 & 0 & 0 \\ 0 & 0.50 & 0 \end{bmatrix} \begin{bmatrix} 3600 \\ 450 \\ 220 \end{bmatrix} = \begin{bmatrix} 3130 \\ 540 \\ 225 \end{bmatrix}$$

Summing the elements of the result gives us a total female population at that time of 3895. The percentage of females in each category is as follows:

$$\begin{bmatrix} 3130/3895 \\ 540/3895 \\ 225/3895 \end{bmatrix} = \begin{bmatrix} 0.803594 \\ 0.138639 \\ 0.0577664 \end{bmatrix} = \begin{bmatrix} 80.36\% \\ 13.86\% \\ 5.78\% \end{bmatrix}$$

We note that the calculation $\mathbf{x}(2) = L\mathbf{x}(1) = L(L\mathbf{x}(0)) = L^2\mathbf{x}(0)$. Similarly, $\mathbf{x}(3) = L\mathbf{x}(2) = L(L^2\mathbf{x}(0)) = L^3\mathbf{x}(0)$. In general, $\mathbf{x}(t) = L^t\mathbf{x}(0)$.

For several values of t, Table 13.3.1 indicates the population change in the three classes by presenting the distributions, $\mathbf{x}(t) = L^t\mathbf{x}(0)$, and the percentage of female animals in each class. As time goes on, although the numbers of birds in each class changes, the vector of percentages of animals in each category converges to $\mathbf{v} = \begin{bmatrix} 0.8206 \\ 0.1205 \\ 0.0590 \end{bmatrix} = \begin{bmatrix} 82.06\% \\ 12.05\% \\ 5.90\% \end{bmatrix}$. From time $t = 20$ years on, the percentages expressed to two decimal places do not change from one year to the next. Over time, the percentage of eggs/chicks stabilizes to 82.06% of the total population, while year 2 birds comprise 12.05% and year 3 birds are 5.90% of the population. This convergence to fixed percentages is characteristic of such age-structured models. Because we are assuming the number of females (or males) to be a fixed proportion (half) the population, the convergence of category percentages for females (or males) is the same as the convergence of category percentages for the entire population (females and males).

Projected Population-Growth Rate

Interestingly, if we divide corresponding elements of the population distribution at time $t + 1$, $\mathbf{x}(t + 1)$, by the members of the distribution at time t, $\mathbf{x}(t)$, we have convergence of the quotients to the same number. Table 13.3.2 shows several of these quotients, which converge in this example to 1.0216, which we call λ. Thus, eventually each age group changes by a factor of $\lambda = 1.0216$ (102.16%) from one year to

Table 13.3.1
Population Distributions and Class Percentages of the Total Population

Time, t	*Distribution* $x(t) = L^n x(0)$	*Class Percentages*
0	$\begin{bmatrix} 3000 \\ 440 \\ 350 \end{bmatrix}$	$\begin{bmatrix} 79.16\% \\ 11.61\% \\ 9.23\% \end{bmatrix}$
1	$\begin{bmatrix} 3600 \\ 450 \\ 220 \end{bmatrix}$	$\begin{bmatrix} 84.31\% \\ 10.54\% \\ 5.15\% \end{bmatrix}$
2	$\begin{bmatrix} 3130 \\ 540 \\ 225 \end{bmatrix}$	$\begin{bmatrix} 80.36\% \\ 13.86\% \\ 5.78\% \end{bmatrix}$
3	$\begin{bmatrix} 3600 \\ 469.5 \\ 270 \end{bmatrix}$	$\begin{bmatrix} 82.96\% \\ 10.82\% \\ 6.22\% \end{bmatrix}$
⋮	⋮	⋮
9	$\begin{bmatrix} 3913.31 \\ 574.45 \\ 281.813 \end{bmatrix}$	$\begin{bmatrix} 82.04\% \\ 12.04\% \\ 5.91\% \end{bmatrix}$
10	$\begin{bmatrix} 3999.5 \\ 586.997 \\ 287.225 \end{bmatrix}$	$\begin{bmatrix} 82.06\% \\ 12.04\% \\ 5.89\% \end{bmatrix}$
⋮	⋮	⋮
20	$\begin{bmatrix} 4950.87 \\ 726.933 \\ 355.783 \end{bmatrix}$	$\begin{bmatrix} 82.06\% \\ 12.05\% \\ 5.90\% \end{bmatrix}$
21	$\begin{bmatrix} 5057.8 \\ 742.631 \\ 363.467 \end{bmatrix}$	$\begin{bmatrix} 82.06\% \\ 12.05\% \\ 5.90\% \end{bmatrix}$
⋮	⋮	⋮
100	$\begin{bmatrix} 27353.5 \\ 4016.29 \\ 1965.7 \end{bmatrix}$	$\begin{bmatrix} 82.06\% \\ 12.05\% \\ 5.90\% \end{bmatrix}$
101	$\begin{bmatrix} 27944.3 \\ 4103.03 \\ 2008.15 \end{bmatrix}$	$\begin{bmatrix} 82.06\% \\ 12.05\% \\ 5.90\% \end{bmatrix}$

Table 13.3.2
$x(t+1)/x(t)$ for Table 13.3.1

Time, t	$x(t+1)/x(t)$
0	$\begin{bmatrix} 3600/3000 \\ 450/440 \\ 220/350 \end{bmatrix} = \begin{bmatrix} 1.2 \\ 1.02273 \\ 0.628571 \end{bmatrix}$
1	$\begin{bmatrix} 3130/3600 \\ 540/450 \\ 225/220 \end{bmatrix} = \begin{bmatrix} 0.869444 \\ 1.2 \\ 1.02273 \end{bmatrix}$
2	$\begin{bmatrix} 3600/3130 \\ 469.5/540 \\ 270/225 \end{bmatrix} = \begin{bmatrix} 1.15016 \\ 0.869444 \\ 1.2 \end{bmatrix}$
⋮	⋮
9	$\begin{bmatrix} 3999.5/3913.31 \\ 586.997/574.45 \\ 287.225/281.813 \end{bmatrix} = \begin{bmatrix} 1.02202 \\ 1.02184 \\ 1.01921 \end{bmatrix}$
⋮	⋮
20	$\begin{bmatrix} 5057.8/4950.87 \\ 742.631/726.933 \\ 363.467/355.783 \end{bmatrix} = \begin{bmatrix} 1.0216 \\ 1.02159 \\ 1.0216 \end{bmatrix}$
⋮	⋮
100	$\begin{bmatrix} 27944.3/27353.5 \\ 4103.03/4016.29 \\ 2008.15/1965.7 \end{bmatrix} = \begin{bmatrix} 1.0216 \\ 1.0216 \\ 1.0216 \end{bmatrix}$

the next. For instance, in going from time $t = 100$ years to $t + 1 = 101$ years, Table 13.3.1 shows that the number of year 1 females increases 2.16%, from 27,353.5 to 1.0216(27,353.5) = 27,944.3. Similarly, the number of year 2 females changes from 4,016.29 to 1.0216(4,016.29) = 4,103.03, and the year 3 females also goes up by the same factor, from 1,965.7 to 1.0216(1,965.7) = 2,008.15. Thus, with each age group ultimately changing by a factor of 1.0216 = 102.16% annually, eventually we estimate the population will increase by 2.16% per year. Thus, for an initial total population of P_0, the estimated population at time t is $P = P_0(1.0216)^t$.

With an annual increase in population of 2.16% per year and, correspondingly, $\lambda = 1.0216 > 1$, we expect that this bird population will increase with time. Had the population been projected to decline each year with $0 < \lambda < 1$, we would expect the birds eventually to become extinct. A value of $\lambda = 1$ would signal a stable population in which, on the average, an adult female produces one female offspring that will live to adulthood. Thus, λ is an important concept related to the stability of a population.

Interestingly, multiplying the constant λ by the vector of percentages to which the category distributions converge, **v**, has the same effect as multiplying the Leslie matrix L by **v**, or $L\mathbf{v} = \lambda\mathbf{v}$, as the following calculations indicate:

$$L\mathbf{v} = \begin{bmatrix} 0 & 5 & 4 \\ 0.15 & 0 & 0 \\ 0 & 0.50 & 0 \end{bmatrix} \begin{bmatrix} 0.8206 \\ 0.1205 \\ 0.0590 \end{bmatrix} = \begin{bmatrix} 0.84 \\ 0.12 \\ 0.06 \end{bmatrix}$$

$$\lambda\mathbf{v} = 1.0216 \begin{bmatrix} 0.8206 \\ 0.1205 \\ 0.0590 \end{bmatrix} = \begin{bmatrix} 0.84 \\ 0.12 \\ 0.06 \end{bmatrix}$$

Multiplying both sides of the equation by a constant, c, maintains the equality, $cL\mathbf{v} = c\lambda\mathbf{v}$ or $L(c\mathbf{v}) = \lambda(c\mathbf{v})$. The formula holds for any constant, c, and, consequently, for any population distribution where the percentages of the total for the three classes are 82.06%, 12.05%, and 5.90%, respectively. Thus, multiplication of the population distribution vector by the constant 1.0216 is identical to the product of the Leslie matrix by the distribution vector. λ is an **eigenvalue** for the matrix L, and **v** is a corresponding **eigenvector** for L.

Quick Review Question 3

Consider the Leslie matrix $L = \begin{bmatrix} 5 & 150 \\ 0.01 & 0 \end{bmatrix}$ from Quick Review Question 1c with the initial population distribution vector $\mathbf{x}(0) = \begin{bmatrix} 2 \\ 1 \end{bmatrix}$.

a. Using a computational tool, for each age class give the value to which its percentage of the total population converges as time progresses. Express your answer to six significant figures.

b. Using a computational tool, give the number, λ, to which the quotient of each class population at time t over the class population at time $t - 1$ converges as time progresses. Express your answer to six significant figures.

c. Using the values from Parts a and b, give a vector **v** that satisfies $L\mathbf{v} = \lambda\mathbf{v}$.

d. Give another vector **v** that satisfies the equation from Part c, where a million times more insects are in their first month of life.

Using mathematics, which we do not show here, or a computational tool, we can obtain three eigenvalues and three corresponding eigenvectors for the 3 × 3 matrix L (Table 13.3.3). Two of the three eigenvalues are imaginary numbers, and the corresponding two eigenvectors contain imaginary numbers. The eigenvalue with the largest magnitude (for real numbers, the largest absolute value), 1.0216, is the **dominant eigenvalue** and is the projected annual growth rate associated with the Leslie matrix. Leslie matrices always have such a unique positive eigenvalue. The sum of

Table 13.3.3
Eigenvalues and Vectors for **L**

Eigenvalue	*Eigenvector*
1.0216	(–0.9869, –0.144906, –0.0709212)
–0.510798 + 0.180952 *i*	(0.935827, –0.244171 – 0.0864985 *i*, 0.185709 + 0.150458 *i*)
0.510798 – 0.180952 *i*	(0.935827, –0.244171 + 0.0864985 *i*, 0.185709 – 0.150458 *i*)

the components of the corresponding eigenvector, (–0.9869, –0.144906, –0.0709212), is –1.20273. Dividing this sum into each element, we obtain another eigenvector, (0.8206, 0.1205, 0.0590), which is the preceding vector of projected proportions for the three classes.

Definition For square matrix M, the constant λ is an **eigenvalue** and **v** is an **eigenvector** if multiplication of the constant by the vector accomplishes the same results as multiplying the matrix by the vector; that is, the following equality holds:

$$M\mathbf{v} = \lambda\mathbf{v}$$

The **dominant eigenvalue** for a matrix is the largest eigenvalue for that matrix.

Stage-Structured Model

An age-structured model, where we distinguish life stages by age, is a special case of a **stage-structured model**, where we divide the life of an organism into stages. Frequently, it is convenient or necessary to consider the life of a species in stages instead of equally spaced time intervals, such as years. Perhaps the animal, such as a loggerhead sea turtle, typically lives for a number of years, and we cannot accurately determine the age of an adult. Conceivably the stages differ greatly in lengths of time. Also, rates may be strongly associated with developmental stages or animal size.

Morris, Shertzer, and Rice generated a stage-structured model of the Indo-Pacific lionfish *Pterois volitans* to explore control of this invasive and destructive species to reef habitats (Morris et al. 2011). Such consideration is very important because in a Caribbean region study, Albins and Hixon found lionfish reduced recruitment of native fishes (addition of new native fishes) by an average of 79% over a 5-week period (Albins and Hixon 2008). A lionfish goes through three life stages: larva (L, about 1 month), juvenile (J, about 1 year), and adult (A). With 1 month being the basic time step, the probability that a larva survives and grows to the next stage is $G_L = 0.00003$, while the probability that a juvenile survives and remains a juvenile in a 1-month period is $P_J = 0.777$. In 1 month, $G_J = 0.071$ of the juveniles mature to the adult stage, while $P_A = 0.949$ of the adults survive in a month. Only adults give birth, and the number of female larvae she produces per month is $R_A = 35{,}315$. Figure 13.3.2 presents a state diagram for these circumstances.

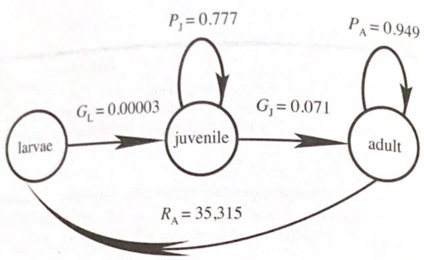

Figure 13.3.2 State diagram for lionfish (Morris et al. 2011)

Thus, if $x_L(t)$, $x_J(t)$, and $x_A(t)$ represent the number of female larvae, juveniles, and adults at time t, respectively, we have the following system of equations for the distribution at time $t + 1$:

$$\begin{cases} 35315x_A(t) = x_L(t+1) \\ 0.00003x_L(t) + 0.777x_J(t) = x_J(t+1) \\ 0.071x_J(t) + 0.949x_A(t) = x_A(t+1) \end{cases}$$

Thus, we have the following transition matrix, called a **Lefkovitch matrix**:

$$\begin{bmatrix} 0 & 0 & 35315 \\ 0.00003 & 0.777 & 0 \\ 0 & 0.071 & 0.949 \end{bmatrix}$$

Using these values, the lionfish monthly growth rate (λ) is about 1.13. Because adult lionfish reproduce monthly over the entire year, adult survivorship has a great impact on the population's growth rate. With all else being the same, not until the probability of an adult surviving in a 1-month period is reduced approximately 30%, from $P_A = 0.949$ to $P_A = 0.66$ or less, could a negative population growth be achieved. Harvesting 30% of the adult lionfish each month is quite a challenge. However, simultaneous reductions of 17% for the probabilities of juvenile and adult survivorship could also produce a declining population. Thus, "results indicate that an eradication program targeting juveniles and adults jointly would be far more effective than one targeting either life stage in isolation" (Morris et al. 2011).

Algorithms

For an age-structured or a stage-structured problem, we form the appropriate matrix, L, and the vector representing initial female population distribution, $\mathbf{x}$, and determine the distribution at time t by calculating $L^t\mathbf{x}$.

For the projected population growth rate, we calculate the eigenvalue, λ, which is available through a command with many computational tools. When it is not available, to estimate the projected population growth rate to within m decimal places, we keep calculating the ratio of age distributions, $\mathbf{x}(t + 1)/\mathbf{x}(t)$, until two subsequent ratios differ by no more than 10^{-m}. For the preceding example with birds, to estimate population growth to within four decimal places, we consider any one of the components, say the first, of $\mathbf{x}(t + 1)/\mathbf{x}(t) = L^{t+1}\mathbf{x} / L^t\mathbf{x}$. After repeated calculation, we discover with $\mathbf{x}(15)/\mathbf{x}(14) = L^{15}\mathbf{x}/L^{14}\mathbf{x} = (1.02153, 1.02173, 1.02136)$ and $\mathbf{x}(16)/\mathbf{x}(15) = L^{16}\mathbf{x}/L^{15}\mathbf{x} = (1.02162, 1.02153, 1.02173)$ that the first components are sufficiently close to each other:

$$|\,1.02153 - 1.02162\,| = 0.00009 < 10^{-4} = 0.0001$$

These first elements, 1.02153 and 1.02162, differ by no more than 10^{-4}, so our projected population growth rate is 1.0216. Similarly, we can determine the category percentages of the total to within m decimal places by finding when each of the corresponding elements of $\mathbf{x}(t)$/(total population) and $\mathbf{x}(t + 1)$/(total population) differ by no more than 10^{-m}.

Sensitivity Analysis for the Age-Structured Example

We can use **sensitivity analysis** to examine how sensitive values, such as long-term population growth rate (dominant eigenvalue λ) or predicted time of extinction, are to small changes in parameters, such as survivability and fecundity. Suppose in the preceding bird example, we wish to examine the sensitivity of the long-term population growth rate to small changes in survivability of year 1 and year 2 birds, P_1 and P_2, respectively. Adjusting P_1 and P_2 individually by ±10% and ±20%, Table 13.3.4 shows the corresponding new values of λ and the change in projected population growth rate, $\lambda_{new} - \lambda$, as calculated using a computational tool. **Relative sensitivity** or **sensitivity of λ with respect to P_i** measures the numeric impact on λ of a change in P_i, or the instantaneous rate of change of λ with respect to P_i (the partial derivative of λ with respect to P_i, $\partial\lambda/\partial P_i$). Thus, to approximate this relative sensitivity, we divide the change in projected population growth rate by the corresponding small change in P_i:

$$\textbf{sensitivity of } \lambda \textbf{ to } P_i = \frac{\partial\lambda}{\partial P_i} \approx \frac{\lambda_{new} - \lambda}{P_{i,new} - P_i},$$

where $P_{i,new}$ is the new value of P_i and λ_{new} is the resulting new value of λ. For example, $P_1 = 0.15$, and $P_1 + (10\% \text{ of } P_1) = P_1 + 0.10P_1 = 1.10P_1 = 0.15 + 0.015 = 0.165$. With $P_1 = 0.15$, the original dominant eigenvalue λ is 1.0216. Replacing the chance of a year 1 bird surviving with $P_{1,new} = 1.10P_1 = 0.165$, the new dominant eigenvalue λ_{new} is 1.06526, and $\lambda_{new} - \lambda = 1.06526 - 1.0216 = 0.04366$. Thus, the relative sensitivity of P_1 using +10% is approximately $(\lambda_{new} - \lambda)/(P_{1,new} - P_1) = (\lambda_{new} - \lambda)/(0.10P_1) = 0.04366/0.015 = 2.9067$. Similarly for −10% of P_1, the sensitivity is 3.0677. However, the relative sensitivity of λ to small changes in P_2 (+10% and −10%) is much smaller (0.2480 and 0.2562, respectively). From these calculations in

Table 13.3.4
Sensitivity of λ (Originally 1.0216) to Changes in Survivability

Survivability Parameter	Percent Change	$P_{i,new}$	λ_{new}	$\lambda_{new} - \lambda$	$P_{i,new} - P_i$	$\frac{\lambda_{new} - \lambda}{P_{i,new} - P_i}$
$P_1 = 0.15$	+10%	0.165	1.0653	0.0437	0.015	2.9111
$P_1 = 0.15$	+20%	0.180	1.1069	0.0853	0.030	2.8435
$P_1 = 0.15$	−10%	0.135	0.9756	−0.0460	−0.015	3.0677
$P_1 = 0.15$	−20%	0.120	0.9268	−0.0948	−0.030	3.1599
$P_2 = 0.50$	+10%	0.550	1.0340	0.0124	0.050	0.2480
$P_2 = 0.50$	+20%	0.600	1.0460	0.0244	0.100	0.2443
$P_2 = 0.50$	−10%	0.450	1.0088	−0.0128	−0.050	0.2562
$P_2 = 0.50$	−20%	0.400	0.9955	−0.0261	−0.100	0.2607

Table 13.3.4, we see that λ is most sensitive to changes in survivability of year 1 birds, P_1. This analysis indicates that conservationists might concentrate their efforts on helping eggs and nestlings survive.

Definition The **relative sensitivity**, or **sensitivity**, of λ to parameter P in a transition matrix is the partial derivative of the dominant eigenvalue of the matrix (λ) with respect to P, $\partial\lambda/\partial P$, or the instantaneous rate of change of λ with respect to P. Thus, this relative sensitivity of λ with respect to P is approximately the change in λ divided by the corresponding small change in P:

$$\textbf{sensitivity of } \lambda \textbf{ to } P = \frac{\partial\lambda}{\partial P} \approx \frac{\lambda_{new} - \lambda}{P_{new} - P},$$

where P_{new} is the new value of P close to P and λ_{new} is the resulting new value of λ.

Sensitivity Analysis for the Stage-Structured Example

Using sensitivity analysis, Morris et al. (2011) determined that lionfish population growth λ is very sensitive to lower-level mortality parameters of larval, juvenile, and adult mortality and is "most sensitive to the lower-level parameter of larval mortality." However, the larvae have venomous spines, probably making them less appealing prey than many of the native reef fish. A project explores a lionfish sensitivity analysis and the model of Morris et al. model more closely.

Applicability of Leslie and Lefkovitch Matrices

Leslie or Lefkovitch matrices are appropriate to use when we can classify individuals in a species by age or stage, respectively. The dynamics of the populations are based only on the females, and an adequate number of males for fertilization is assumed. The models in this module accommodate only population growths that do not depend on the densities of the populations so that the fecundity and survival rates remain constant. However, we can extend the models to incorporate density dependence by dampening values in the matrix. Unfortunately, estimations of fecundity and survival rates can be difficult. If appropriate, however, an age- or a stage-structured model can allow us to use matrix operations to determine the projected population growth rate and the stable-age distribution (Horne 2008).

Need for High-Performance Computing

Typically, a Leslie matrix is small enough so that high-performance computing (HPC) is unnecessary to model the long-term situation for one type of animal. However, one species might be a small part of a much bigger network of other species of animals and plants and their environment. Execution of models of such larger problems involves extensive computation that can benefit from HPC.

For example, PALFISH is a parallel, age-structured population model for freshwater small planktivorous fish and large piscivorous fish, structured by size, in south Florida. The model contains 111,000 landscape cells, with each cell corresponding to a 500-m by 500-m area and containing an array of floating-point numbers representing individual fish density of various age classes. Researchers reported a significant improvement in runtime of PALFISH over the corresponding sequential version of the program. The mean simulation time of the sequential model was about 35 h, while the parallel version with 14 processors and dynamic load balancing was less than 3 h (Wang et al. 2006).

Another use of HPC can be in **parameter sweeping**, or executing a model for each element in a set (often a large set) of parameters or of collections of parameters. The results can help the modeler obtain a better overall picture of the model's behavior, determine the relationships among the variables, find variables to which the model is most sensitive, find ranges where small variations in parameters cause large output changes, locate particular parameter values that satisfy certain criteria, and ascertain variables that might be eliminated to reduce model complexity (Luke et al. 2007).

Definition **Parameter sweeping** is the execution of a model for each element in a set of parameters or of collections of parameters to observe the resulting change in model behavior.

For example, suppose in our simple example of the bird, which has a maximum life span of 3 years, we are interested in determining the impact on the projected growth rate (positive eigenvalue) of changing the probabilities of the animal living from year 1 to 2 and from year 2 to 3. Such a problem is embarrassingly parallel on a high-performance system; we can divide computation into many completely independent experiments with virtually no communication. Thus, we could have multiple nodes on a cluster running the same program with different probability pairs and with their own output files. After completion, we can compare the results, perhaps using these to predict the impact of various interventions to improve the one, the other, or both probabilities. For more computationally intensive programs that require significant runtime, HPC can be particularly useful for such parameter sweeping.

For example, researchers are modeling biological metabolism at a kinetic level for a green alga, *Chlamydomonas reinhardtii* (Chang et al. 2008). However, limited knowledge exists of parameters for enzymes with known kinetic responses. Consequently, the researchers have developed the High-Performance Systems Biology Toolkit, HiPer SBTK, to perform sensitivity analysis and fitting of differential equations to the data. One problem involves 64 parameters and approximately 450,000 calculations for a full sensitivity matrix. Chang et al. (2008) wrote, "In moving from desktop-scale simulations of a small set of biochemical reactions to genome-scale simulations in the high-performance computing (HPC) arena, a paradigm shift must occur in the way we think of biological models. A complete representation of metabolism for a single organism implies model networks with thousands of nodes and edges." Because parallelism of the calculations is extremely well balanced, where each process has approximately the same amount of work as any other process, the scientists are optimistic that the code will scale to thousands of processors. Thus, ultimately, they plan to develop an *in silico* cell model of metabolism that contains all reliable experimental data for *C. reinhardtii* with problem sizes perhaps thousands of times larger than the current problem.

Exercises

1. a. Suppose a Leslie matrix associated with an age-structured population model has an eigenvalue of 0.984. Is the equilibrium population growing or shrinking?
   b. By how much?
   c. Suppose a corresponding eigenvector is (–2.35, –1.04, –0.87, –0.69). For each age class, give the estimated percentage of the total population to which the class converges as time progresses.
2. Suppose certain animal has a maximum life span of 3 years. A year 1 (0–1-year) female has no offspring; a year 2 (1–2-years) female has 3 daughters on the average; and a year 3 (2–3-years) female has a mean of 2 daughters. Thirty percent of year 1 animals live to year 2, and 40% of year 2 animals live to year 3. Suppose the numbers of year 1, 2, and 3 females are 2030, 652, and 287, respectively.
   a. Determine the corresponding Leslie matrix, L.
   b. Give the initial female population distribution vector $\mathbf{x}(\mathbf{0})$.
   c. Calculate the population distribution at time $t = 1$, vector $\mathbf{x}(\mathbf{1})$.
   d. Calculate the class percentages of the total population at time $t = 1$.
   e. Give the vector for class percentages of the total population, $\mathbf{v}$, expressed to two decimal places, to which $\mathbf{x}(t)/T(t)$ converges, where $T(t)$ is the total population at time t.

   f. Find the number λ, expressed to two decimal places, to which $\mathbf{x}(t+1)/\mathbf{x}(t)$ converges.
   g. Using answers from Parts a, d, and f, verify that $L\mathbf{v} = \lambda\mathbf{v}$.
3. Consider the following Leslie matrix representing a population, where the basic unit of time is 1 year:

$$\begin{bmatrix} 0 & 0.2 & 1.3 & 3.5 \\ 0.1 & 0 & 0 & 0 \\ 0 & 0.2 & 0 & 0 \\ 0 & 0 & 0.4 & 0 \end{bmatrix}$$

   a. Give the animal's maximum life span, and describe the meaning of each positive number in the matrix.
   b. Determine the dominant eigenvalue and the annual growth rate. Do you expect the animal's numbers to grow or decline?
   c. Draw a state diagram for the animal.
   d. Using –10% of the parameter, determine the sensitivity of λ to the second row, first column parameter (0.1).
   e. Determine the sensitivity of λ to the third row, second column parameter.
   f. Determine the sensitivity of λ to the fourth row, third column parameter.
   g. Based on your answers to Parts d–f, where should conservation efforts focus?
4. Crouse et al. (1987) considered the following seven stages in the life of loggerhead sea turtles (*Caretta caretta*): (1) eggs and hatchlings (< 1 year); (2) small juveniles (1–7 years); (3) large juveniles (8–15 years); (4) subadults (16–21 years); (5) novice breeders (22 years); (6) first-year emigrants (23 years); (7) mature breeders (> 23 years). Only the last three stages reproduce with female fecundities of 127, 4, and 80 per year, respectively. Table 13.3.5 gives the probabilities per year of a stage *From* turtle surviving and remaining at or advancing to stage *To*.

Table 13.3.5
The Probabilities per Year of a Stage *From* Loggerhead Sea Turtle Surviving to Stage *To*

From *Stage*	To *Stage*	*Probability per Year*
1	2	0.6747
2	2	0.7370
2	3	0.0486
3	3	0.6611
3	4	0.0147
4	4	0.6907
4	5	0.0518
5	6	0.8091
6	7	0.8091
7	7	0.8089

a. Give the Lefkovitch matrix for this model.
b. Determine the dominant eigenvalue and the annual growth rate. Do you expect the animal's numbers to grow or decline?
c. Give the annual mortality rate for stage 1 animals.
d. Give the annual mortality rate for stage 2 animals.
e. Give the annual mortality rate for stage 3 animals.
f. Give the annual mortality rate for stage 4 animals.
g. Give the annual mortality rate for stage 5 animals.
h. Give the annual mortality rate for stage 6 animals.
i. Give the annual mortality rate for stage 7 animals.
j. Draw a state diagram for the animal.
k. Determine the sensitivity of λ to each parameter indicated in Table 13.3.5.

5. Consider the following Lefkovitch matrix representing a population, where the basic unit of time is 1 year:

$$\begin{bmatrix} 0 & 0 & 3.4 & 7.5 \\ 0.1 & 0.2 & 0 & 0 \\ 0 & 0.3 & 0 & 0 \\ 0 & 0 & 0.4 & 0.5 \end{bmatrix}$$

a. Describe the meaning of each positive number in the matrix.
b. If possible, give the animal's maximum life span. Give the length of time for any stage that you can determine.
c. Determine the dominant eigenvalue and the annual growth rate. Do you expect the animal's numbers to grow or decline?
d. Draw a state diagram for the animal.
e. Determine the sensitivity of λ to the second-row, first-column parameter (0.1).
f. Determine the sensitivity of λ to the second-row, second-column parameter.
g. Determine the sensitivity of λ to the third-row, second-column parameter.
h. Determine the sensitivity of λ to the fourth-row, third-column parameter.
i. Determine the sensitivity of λ to the fourth-row, fourth-column parameter.
j. Based on your answers to Parts e–j, where should conservation efforts focus?

Projects

1. In the 1960s and 1970s, scientists did an experimental reduction in population density of Uinta ground squirrels in three types of habitats in Utah: lawn, nonlawn, and edge (Oli et al. 2001). For 4 years, they collected life table data; then for 2 years, they reduced the population by about 60%, keeping the same sex and age composition. Subsequently, they collected new life-table data. Data was collected postbreeding, after the birth pulse. Table 13.3.6 presents their data for the nonlawn habitat in three categories: Young (< 1 year), Yearling (1–2 years), and Adult (> 2 years).

Table 13.3.6
Pre- and Postreduction Survival and Fertility data for Nonlawn Uinta Ground Squirrels (Oli et al. 2001)

	Prereduction		*Postreduction*	
Category	*Survival*	*Fertility*	*Survival*	*Fertility*
Young	0.375	0.353	0.474	0.792
Yearling	0.419	0.741	0.481	0.981
Adult	0.500	0.885	0.588	1.200

a. Use a **partial life cycle model** to analyze the effect of the population reduction. Consider five age groups with year 1 being young, year 2 being yearling, and years 3, 4, and 5 being adults. Do not consider any of these animals after age 5 years. Determine the projected population growth rate (λ) pre- and postreduction.
b. By changing each survival rate in the prereduction data one at a time by ±10% and ±20%, determine to which parameter λ is most sensitive. Discuss the results.

2. People in Europe and Asia enjoy eating skates, which are closely related to sharks. Consequently, the animal has declined since the 1970s. Frisk, Miller, and Fogarty did a study of little skates, winter skates, and barndoor skates to determine sustainable harvest levels and strategies (Frisk et al. 2002). For the little skate (*Leucoraja erinacea*), the scientists used an age-structured model incorporating 1-year age categories with 8-year longevity. Data from a previous study indicated age of 50% maturity to be 4 with annual female fecundity of 15 for mature females. They assumed this level to be constant for mature females. For age-specific survival (P_i), they adopted an exponential decay based on natural mortality (M_i) and fishing mortality (H_i): $P_i = e^{-(M_i + H_i)}$, $i = 1, 2, \ldots, 8$. The original analysis considered skates to be large enough for fishing by age 2, at which time the fishing mortality became 0.35. The probability of death by natural causes was assumed be 0.45 for these fish and 0.70 for year 1 skates.
a. Develop a Leslie matrix for the little skate and determine the long-term annual population growth rate, λ. The intrinsic rate of population increase, r, is the natural logarithm of λ, which the researchers calculated as 0.21 for little skates. Do you get the same value? What is the meaning of r? Interpret λ and r for the long-term forecast of little skates.
b. The researches also performed a stochastic analysis to test the sensitivity of their model to parameter estimation. For little skate, they drew adult fecundity, first-year survival, and adult survival from normal distributions with means and standard deviations as indicated in Table 13.3.7. Develop a stochastic version of the model. Run the simulation 1000 times for at least 200 years on each simulation. Determine average values for λ and r.
c. Researchers did a similar study for winter skate using an adult female fecundity mean of 17.5 and standard deviation of 5. Due to a lack of adequate information about adult mortality, they held M_1 and M constant (Frisk et al. 2002). Repeat Part a using this information.

Table 13.3.7
Means and Standard Deviations for Adult Fecundity, First-Year Survival, and Adult Survival of Little Skate Used for Stochastic Analysis (Frisk et al. 2002)

	Mean	*Standard Deviation*
little skate		
adult fecundity (female)	15	2.5
first-year survival (M_1)	1.21	0.4
adult-year survival (M)	0.45	0.05

3. Scientists conducted a 4-year study, "Population Viability Analysis for Red-Cockaded Woodpeckers in the Georgia Piedmont," to evaluate the risk of extinction for this endangered species and to recommend management to minimize this danger (Maguire et al. 1995). They considered five age groups: < 1 year (juvenile; class 1), 1 year (class 2), 2 years (class 3), 3 years (class 4), and > 3 years (class 4+). From observed data, they modeled the population and performed various simulations. For the survival rate of class i (P_i), they calculated the observed number of class i females surviving to class $i + 1$ divided by the number of females in class i. To consider the situation at postbreeding time (postbirth pulse sampling), they calculated fecundity for class i as the average number of female nestlings born to mothers of class $i + 1$ (m_{i+1}) multiplied by the proportion of females entering class i that will survive to class $i + 1$ (P_i). Because the study placed all female red-cockaded woodpeckers from age 4 years on into the same class, class 4+, they calculated the number in that group at time $t + 1$, $x_{4+}(t + 1)$, as $P_4 x_4(t) + P_{4+} x_{4+}(t)$. Table 13.3.8 presents data for newly banded birds (NB) and for newly banded birds and nonbanded birds (NBU). The researchers found an initial distribution of (20, 10, 9, 9, 6) for the five classes. In their simulations, they considered extinction to be the time at which the total population was less than or equal to 1.
   a. Develop a deterministic model for each set of birds, NB and NBU, using a stage-structured 5 × 5 Leslie matrix. What happens to the population over a period of time? Assuming extinction when a population is less than 1, when does extinction occur? How might you explain the difference between the outcomes of NB and NBU populations?
   b. By changing each survival rate, P_i, one at a time by ±10% and ±20%, determine which parameter poses the greatest sensitivity to extinction risk. Use NB data. By determining the parameter that has the greatest impact, ecologists can focus their efforts on improving that group's survival.
   c. Researchers determined that in 1987–88, the area contained 41 potential nesting sites. Develop a **habitat saturation model** by limiting the number of breeding woodpeckers each year to 41. Give nesting preference to older birds. Thus, with n_{Bi} being the number of class i breeding females, n_i being the number of class i females, and min being the minimum function, we have $n_{B4+} = min(n_{4+}P_{4+}, 41)$. That is, the number of potential class 4+ breeders is $n_{4+}P_{4+}$, but at most 41 can breed. If $n_{4+}P_{4+}$ is greater than 41, no nesting sites remain for birds in other classes. If $n_{4+}P_{4+}$ is less than 41, the model allows $n_{B4} = min(n_4P_4, 41 - n_{B4+})$ woodpeckers in class 4 to breed in the remaining number of sites. Similarly, $n_{B3} = min(n_3P_3, 41 - n_{B4+} - n_{B4})$, and so on.
   d. Table 13.3.9 gives the researchers' calculations for P_1 along with the corresponding probability for each of the 4 years of the study. Starting with an initial population distribution of (20, 10, 9, 9 6), which was their 1988 estimate, develop a stochastic version of the model for NB or NBU birds. To do so, at each year with the given probabilities, randomly select the juvenile (class 1) survival rate from the estimations in the table. That is, at each time step, generate a uniformly distributed random number, r, between 0 and 1. For the NB data, if r is less than the first probability, 0.295, use the first value, 0.3708, for P_1; else if r is less than 0.295 + 0.310 = 0.605, use $P_1 = 0.4131$; and so on. Run the simulation 1000 times for at least 200 years on each simulation. Determine the range of extinction, the average extinction, and the probability of extinction within 100 years. Discuss the results.

   These simulations correspond to **environmental stochasticity**, or variation in parameters caused by random environmental changes. The researchers simplified the model to use variations in P_1 to reflect this environmental stochasticity. Why might they make such an assumption?

Table 13.3.8
Data on Red-Cockaded Woodpeckers in the Georgia Piedmont, 1983–1988, for Newly Banded Birds (NB) and for Newly Banded Birds and Nonbanded Birds (NBU), Where P_i is the Proportion of Females Entering Class i That Will Survive to Class $i + 1$ and m_i Is the Average Number of Female Offspring per Female of Class i (Maguire et al. 1995)

Class	NB		NBU	
	P_i	m_i	P_i	m_i
1	0.380	0.000	0.401	0.000
2	0.653	0.133	0.734	0.126
3	0.850	1.082	0.961	1.023
4	0.400	1.194	0.456	1.129
4+	0.589	1.590	0.667	1.504

Table 13.3.9
Yearly Estimates of Juvenile Survival Rates (P_1) and Corresponding Probabilities for Red-Cockaded Woodpeckers in the Georgia Piedmont, 1983–1988, for Newly Banded Birds (NB) and for Newly Banded Birds and Nonbanded Birds (NBU) (Maguire 1995).

Year	*NB*		*NBU*	
	P_1	*Probability*	P_1	*Probability*
1984	0.3708	0.295	0.3793	0.285
1985	0.4131	0.310	0.4220	0.318
1986	0.2176	0.135	0.2353	0.095
1987	0.4354	0.260	0.4508	0.302

Table 13.3.10
Values from (Morris et al. 2011) Assuming 30 Days/Month

Symbol	Meaning	Value
M_E	Egg mortality	9.3/month
M_L	Larval mortality	10.5/month
M_J	Juvenile mortality	0.165/month
M_A	Adult mortality	0.052/month
D_E	Egg duration	0.1 month
D_L	Larval duration	1 month
ρ	Proportion female	46%
f	Fecundity	194,577 eggs/month/female

e. Repeat Part c at each time step selecting randomly a juvenile survival rate in an appropriate range as discussed in Part d.

f. For NB or NBU, perform a sensitivity analysis to determine the parameters P_i to which the growth rate λ is most sensitive. Using these results, make recommendations about where to concentrate conservation efforts.

4. This project considers the lionfish example in the section "Stage-Structured Model." With data from the literature on average mortalities of eggs and lionfish in the various stages, durations of eggs and larvae, fecundity, and proportion female as in Table 13.3.10, Morris et al. (2011) calculated various probabilities using the following exponentially decreasing models:

$$G_L = e^{-M_L D_L},\ G_J = e^{-M_J}/12,\ P_J = 11e^{-M_J}/12,\ P_A = e^{-M_A},\ R_A = \rho f e^{-M_E D_E}$$

a. With these models and the values in Table 13.3.10, recalculate G_L, G_J, P_J, P_A, and R_A and use these calculations for a Lefkovitch matrix. Revise the last paragraph in the section "Stage-Structured Model" for this matrix. That is, update the growth rate λ, the percentage that reduces probability of an adult surviving to produce negative population growth, and the percentages of simultaneous reductions of probabilities of juvenile and adult survivorship to produce a declining population.

b. Perform a sensitivity analysis to determine the higher-level parameters—G_L, G_J, P_J, P_A, and R_A—to which the monthly growth rate λ is most sensitive. Using these results, make recommendations for controlling this menace.

c. Perform a sensitivity analysis to determine the lower-level parameters from Table 13.3.10 to which the monthly growth rate λ is most sensitive. Using these results, make recommendations for controlling this menace.

d. Adult mortality, M_A, is dependent upon fishing intensity. Draw 1000 values of adult mortality from a normal distribution with mean 0.052/month and standard deviation 5% of this mean, excluding numbers beyond two standard deviations from the mean. Generate 1000 Lefkovitch matrices and calculate the resulting growth rates λ for these matrices. (Morris et al. 2011) used similar calculations to "illustrate sensitivity to misspecification of parameter values." Discuss your results.

5. Typically, spawning (breeding) Pacific salmon travel up the same river where they were born, breed, lay their eggs, and then die. The eggs hatch; the young salmon develop for 1 or 2 years in the streams; the juvenile salmon travel downstream to the ocean; then, as smolts they enter the ocean, where they may remain for several years, continuing to grow.

Between 1961 and 1975, four dams were constructed on the lower Snake River. Unfortunately, the dams inhibited the usual migration of spring/summer chinook salmon, so officials made various dam passage improvements, including transportation of spawning salmon upstream and of juvenile salmon downstream. Kareiva, Marvier, and McClure studied the situation using age-structured models (Kareiva et al. 2000). They tested the effectiveness of various implemented management interventions and examined whether improving the survival of any of the life stages could stop population declines. The study assumed a 5-year life expectancy, equal proportion of male and female salmon, and breeding at year 3 or later. Table 13.3.11 contains the study's parameters. As we will see, parameters s_2 (probability of surviving from year 1 to year 2) and μ (probability of surviving upstream migration) are calculated from the parameters indented immediately below them.

Researchers are continuing to gather data, to further develop population models, and to publish their results (Zabel et al. 2006; Interior Columbia

Table 13.3.11
Parameters from Tables 1 and 2 (Kareiva et al. 2000)

Symbol	Meaning	Value
s_1	Probability of surviving from year 0 to year 1	0.022
s_2	Probability of surviving from year 1 to year 2	
z	Proportion of fish transported	0.729
s_z	Probability of surviving transportation	0.98
s_d	Probability of surviving in-river migration (no transportation)	0.202
s_e	Probability of surviving in estuary and during ocean entry	0.017
s_3	Probability of surviving from year 2 to year 3	0.8
s_4	Probability of surviving from year 3 to year 4	0.8
s_5	Probability of surviving from year 4 to year 5	0.8
b_3	Probability of a year 3 female to breed	0.013
b_4	Probability of a year 4 female to breed	0.159
b_5	Probability of a year 5 female to breed	1.0
μ	Probability of surviving upstream migration	
h_{ms}	Harvest rate in main stem of columbia river	0.020
s_{ms}	Probability of survival of unharvested spawner from bonneville dam to spawning basin	0.794
h_{sb}	Harvest rate in subbasin	0
s_{sb}	Probability of survival of unharvested adult in subbasin before spawning	0.9
m_3	Number of eggs per year 3 female spawner	3257
m_4	Number of eggs per year 4 female spawner	4095
m_5	Number of eggs per year 5 female spawner	5149

Technical Recovery Team 2007). Moreover, these results are playing a part in salmon recovery planning (NOAA 2011).

a. To survive to year 2, a year 1 fish must travel downstream past the dam and survive in one of the following two ways:
1. have transportation over the dam and survive;
2. migrate on its own past the dam and survive.

In either case, the fish must then survive journeys in the estuary and into the ocean. With z being the proportion of fish transported, give the formula for the proportion of fish that migrate in-river past the dam without transportation. Using z, s_z, s_d, and s_e from Table 13.3.11, develop a model for s_2, the probability of a salmon surviving from year 1 to year 2. Using the indicated parameter values from Table 13.3.11, evaluate s_2.

b. With h_{ms} being the harvest rate in main stem of Columbia River, give the formula for the proportion not harvested in the river. Similarly, with h_{sb} being the harvest rate in the subbasin, give the formula for the proportion not harvested in the subbasin. To survive upstream migration, a fish must survive in the river and the subbasin. Thus, it must survive the danger of harvest and travel in both locations. Using h_{ms}, s_{ms}, h_{sb}, and s_{sb} from Table 13.3.11, develop a model for μ, the probability of survival of an unharvested spawner from Bonneville Dam to spawning basin. Using the indicated parameter values from Table 13.3.11, evaluate μ.

c. With b_3 being the probability of a year 3 female to breed, give the formula for the proportion of year 3 females that do not breed. Using this formula and s_4, the probability of surviving from year 3 to year 4, determine the proportion of females that survive to year 4, that is, the probability that a female does not breed and survives to year 4. Using the indicated parameter values, evaluate the proportion of females that survive to year 4. Why do we not include the proportion that spawn? Using the indicated parameter values from Table 13.3.11, evaluate the proportion of females that survive to year 4.

d. Similarly to Part c, determine the proportion of females that survive to year 5.

e. Determine a formula for the fecundity of year 3 salmon; that is, the average number of female young from a year 3 mother. For your formula consider the probability that a year 3 salmon breeds, the probability that the salmon then survives the upstream journey, the average number of eggs for a 3-year-old, the proportion of those that are female offspring, and the probability that the egg hatches and the offspring survives the first year. Using the indicated parameter values from Table 13.3.11, calculate the fecundity of year 3 salmon.

f. Similarly to Part e, determine the fecundity of year 4 salmon.

g. Similarly to Part e, determine the fecundity of year 5 salmon.

h. Using the previous parts, determine the Leslie matrix. After calculating its dominant eigenvalue, discuss the long-term prospects for the chinook salmon on the Snake River if the situation does not change.

i. Kareiva et al. (2000) examined the impact on long-term population growth had authorities not taken the following actions: (i) "reductions of harvest rates, from approximately 50% in the 1960s to less than 10% in the 1990s"; (ii) "engineering improvements that increased juvenile downstream migration survival rates from approximately 10% just after the last turbines were installed to 40 to 60% in most recent years"; (iii) "the transportation of approximately 70% of juvenile fish from the uppermost dams to below Bonneville Dam, the lowest dam on the Columbia River." Based on calculations, they concluded, "If such improvements had not been made, the rates of decline would likely have been 50 to 60% annually. . .." Discuss which parameters would need to be adjusted for their calculations.

j. Many conservation efforts have been focused on transportation through the dams. If such efforts were completely successful (an impossible goal), determine the long-term growth. Would such actions be enough to reverse the population declines? Based on these results, should conservation efforts focus solely on transportation?

k. Justify the following statement (Kareiva et al. 2000): "management actions that reduce mortality during the first year by 6% or reduce ocean/estuarine mortality by 5% would be sufficient" to reverse the population declines.

l. Justify the statement (Kareiva et al. 2000) that "a 3% reduction in first-year mortality and a 1% reduction in estuarine mortality" would be sufficient to reverse the population declines.

m. Perform a sensitivity analysis to determine the s_i parameters (Table 13.3.11) to which the monthly growth rate λ is most sensitive. Using these results, make recommendations on where to focus conservation efforts.

6. Furbish's lousewort, *Pedicularis furbishiae*, is an endangered herbaceous plant that grows along a 140-mi stretch of the St. John River in northern Maine and New Brunswick, Canada. This perennial does well in areas having little cover from woody plants and little riverbank disturbance. Wetter conditions promote growth and colonization, but moist soil is more likely to slide into the river. River ice flows scrape the banks, advantageously removing woody vegetation but also disturbing *P. furbishiae*. If disturbances occur too frequently (more frequently than every 6 to 10 years), the lousewort does not have adequate time to reestablish itself. Thus, success of the plant appears to depend on a delicate balance of conditions.

To examine the long-term prospects of the species' survival, Eric Menges performed a 3-year (1983–1986), spring-to-spring study of *P. furbishiae*, recording plant and environmental data. Then, he used stage-based modeling with the following six stages: seedling; juvenile, which is below minimum flowering size; vegetative, which is not flowering but is above minimum flower size; small repro.—flowering plant with one **scape**, or leafless flower stalk; medium repro.—flowering plant with two to four scapes; and large repro.—flowering plants with more than four scapes. Table 13.3.12 gives probabilities of transitioning from one stage to another based on the data from 1984–1985. The plants reproduce only sexually, so fecundity as presented in Table 13.3.13 was determined using an estimate of the number of seedlings produced (Menges 1990).

a. Draw a state diagram for the model.

Table 13.3.12
Probabilities with Standard Errors of *P. furbishiae* Changing from One Stage to Another Based on Data from Spring 1984 to Spring 1985 (Menges 1990)

From	*To*	*Probability*
Seedling	Juvenile	0.39
Seedling	Vegetative	0.01
Juvenile	Juvenile	0.47
Juvenile	Vegetative	0.21
Juvenile	Small repro.	0.11
Juvenile	Medium repro.	0.00
Vegetative	Juvenile	0.14
Vegetative	Vegetative	0.24
Vegetative	Small repro.	0.45
Vegetative	Medium repro.	0.11
Small repro.	Juvenile	0.09
Small repro.	Vegetative	0.24
Small repro.	Small repro.	0.36
Small repro.	Medium repro.	0.21
Small repro.	Large repro.	0.01
Medium repro.	Juvenile	0.04
Medium repro.	Vegetative	0.16
Medium repro.	Small repro.	0.26
Medium repro.	Medium repro.	0.42
Medium repro.	Large repro.	0.10
Large repro.	Vegetative	0.01
Large repro.	Medium repro.	0.28
Large repro.	Large repro.	0.61

Table 13.3.13
Fecundities of *P. furbishiae* Based on Data from Spring 1984 to Spring 1985 (Menges 1990)

Stage	*Fecundity*
Small repro.	2.45
Medium repro.	7.48
Large repro.	29.93

b. Develop a Lefkovitch matrix model, *L84to85*, using data from Tables 13.3.12 and 13.3.13 and determine the finite rate of population change, λ. If the plant could maintain such annual population growth, would you anticipate the population of *P. furbishiae* to increase or decrease over time?

c. The growing season in 1984–85 was advantageous for *P. furbishiae*. However, disturbance from ice scour and riverbank slumping in 1983–84 were challenging and resulted in a transition matrix *L83to84* with dominant eigenvalue $\lambda = 0.77$. In 1985–86, the environmental conditions resulted in a transition matrix *L85to86* with $\lambda = 1.02$. Using these values and your result from Part b, discuss the wisdom of using data from one year to make long-term predictions.

d. Because environmental conditions can vary greatly from year to year, using one year's data can be misleading for making long-term predictions. To account for such environmental stochasticity, Menges (1990) performed 100 simulations following the population for 100 simulated years, where each year he used a Lefkovitch matrix selected at random from the observed matrices for 1983–84, 1984–85, and 1985–86. Perform these simulations; for each simulation multiply the matrices together and calculate the finite rate of population change for the resulting final matrix. Assuming an initial population distribution of (156, 158, 82, 55, 44, 5) for 500 individuals, calculate the final population distribution and total population for each simulation. Discuss your results.

Menges (1990) did not give all the data for 1983-84 and 1985-86. For crude estimates of the Lefkovitch matrices (say, *L83to84* and *L85to86*) for these years, multiply matrix *L84to85* from Part b by appropriate constants; in each case, multiply by the desired dominant eigenvalue (0.77 and 1.02, respectively) and divide by the dominant eigenvalue, $\lambda = 1.27$, for *L84to85*.

7. During the early part of the twentieth century, sugar cane growers in Puerto Rico were desperately seeking something to control beetle grubs (larvae) that were destroying the roots of their crops. In response, the U.S. Department of Agriculture imported some rather large toads, *Bufo marinus*, from Barbados. Within 10 years, the beetle grubs numbers were reduced to the level of a mere nuisance. This was a relatively rare example of a positive outcome from introducing species to new geography. The toad, commonly called the cane toad, was introduced to cane-growing areas in other countries, including Australia; but in Australia they have become a major pest. Dispersing widely through several Australian states, these voracious predators and nimble competitors are threatening native species and disrupting biological communities (Markula et al. 2010).

One method that has been successful in controlling certain insect pests, particularly for initial invasions into an area, is the release of sterile males. With the release of a large number of such males relative to the number of fertile males, the hope is that many nonproductive matings will occur, resulting in a population reduction. However, usually the female insect causes most of the damage, whereas the male cane toad is as destructive as the female. Moreover, typically insects have very short life spans, but a large influx of sterile male toads that live for several years can increase the population size significantly and cause extensive environmental damage.

Stage-based models in McCallum (2006) with data from Lampo and De Leo (1998) demonstrate the impracticality of using sterile males to control the cane toad population in Australia. Table 13.3.14 summarizes the model probability parameters for the following stages: egg, tadpole, juvenile, and adult. With data indicating a range of from 7500 to 20,000 eggs in a clutch, the models use a clutch size of 15,000 eggs, half of which are assumed to be female.

a. Draw a state diagram for the model.

b. Develop a Lefkovitch matrix model, L, using the mean probabilities from Table 13.3.14 with a fecundity of 7500 female eggs, and determine the

Table 13.3.14
Australian Cane Toad Data (Lampo and De Leo 1998)

From	*To*	*Mean Probability*	*Probability Range*
Egg	Tadpole	0.718	0.688–0.738
Tadpole	Juvenile	0.05	0.012–0.176
Juvenile	Adult	0.05	0.03–0.07
Adult	Adult	0.50	0.3–0.7

finite rate of population change, λ. If the animal could maintain such annual population growth, would you anticipate the cane toad population to increase or decrease over time?

c. Repeat Part b for the lower and upper extremes of the probability and fecundity ranges. Discuss the results.

d. Determine an eigenvector associated with the dominant eigenvalue, λ, for the matrix of Part b. Scale the vector so that the number of adult cane toad females is 100. Plot the number of adult females versus time over a 15-year period. Because of the exponential growth involved, create another plot of the common logarithm (logarithm to the base 10) of the number of adult females versus time. Plot the log of the number of adults versus time.

e. Suppose a control effort releases 5000 sterile males into the population each year. Develop a program to estimate the number of adult females per year for 15 years. Each simulation year, adjust the Lefkovitch matrix of Part b so that the female fecundity is the probability that a male is fertile multiplied by the mean female clutch size of 7500. Thus, each year, calculate the number of sterile males in the population; besides an additional release of 5000 sterile males, the data indicate that on the average an adult has a 0.50 chance of surviving from one year to the next. Also, calculate the total number of males (fertile and sterile) in the population each year. Assume that the number of fertile males equals the number of females in the population. Plot the common log of the number of adult females versus time on the same graph as the corresponding plot for Part d. Plot the common log of the number of adults versus time on the same graph as the corresponding plot for Part d. Does the model predict that such a control effort would be successful?

f. Repeat Part e for a sterile male release of 10,000 per year. Discuss the results and the practicality of such a control effort.

g. Repeat Part e where 10,000 sterile males are released each year until the number of females falls below 50, half the original number of females. Discuss the results.

h. Perform a sensitivity analysis to determine the parameters to which the annual growth rate λ is most sensitive. Using these results, make recommendations on where to focus conservation efforts.

8. For several constants in Table 11.4.2 of the agent-based Module 11.4, "Introducing the Cane Toad—Able Invader," perform a sensitivity analysis to determine how sensitive the death percentage is to each of the constants with value less than 1.

Answers to Quick Review Questions

1. a. $x_i(t)$ = number of this female insect in the ith month of life alive in the area at time t, where $i = 1$ or 2

b. Assuming that an insect gives birth to half females, 5 and 150 in the first or second month of life, respectively, we have the following system of equations:

$$5x_1(t) + 150x_2(t) = x_1(t+1)$$
$$0.01x_1(t) \qquad = x_2(t+1)$$

c. $L = \begin{bmatrix} 5 & 150 \\ 0.01 & 0 \end{bmatrix}$

d. 160 month 1 female insects and 0.02 month 2 female insects because

$$\mathbf{x(1)} = L\mathbf{x(0)} = \begin{bmatrix} 5 & 150 \\ 0.01 & 0 \end{bmatrix}\begin{bmatrix} 2 \\ 1 \end{bmatrix} = \begin{bmatrix} 160.00 \\ 0.02 \end{bmatrix}$$

e. 803 month 1 female insects and 1.6 month 2 female insects because

$$\mathbf{x(2)} = L\mathbf{x(1)} = \begin{bmatrix} 5 & 150 \\ 0.01 & 0 \end{bmatrix}\begin{bmatrix} 160.00 \\ 0.02 \end{bmatrix} = \begin{bmatrix} 803.00 \\ 1.6 \end{bmatrix}$$

2. $\begin{bmatrix} 0.2 & 1.2 & 1.4 & 0.7 \\ 0.3 & 0 & 0 & 0 \\ 0 & 0.8 & 0 & 0 \\ 0 & 0 & 0.5 & 0 \end{bmatrix}$

3. a. 99.811103%, 0.188897%

b. 5.28388

c. $\begin{bmatrix} 0.99811103 \\ 0.00188897 \end{bmatrix}$

d. $\begin{bmatrix} 998111.03 \\ 1888.97 \end{bmatrix}$

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