14.3 Time after Time: Age-Structured Models

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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 twelve 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. Likely it is a female Green Sea Turtle (*Chelonia mydas*) on her way to deposit her eggs. Although these turtles may feed normally in around other Hawaiian islands, they usually return to the beach where they hatched (natal beach) to nest. Ninety per cent of Green Turtle nests in Hawaii are found on these islets.

Nesting is an arduous process for this animal, and this may not be the only time she will make this journey this season. Though she may have several more clutches to lay, she will dig a hole with her front flippers to a depth of about two feet, deposit her 100± eggs, cover the eggs, and return to the water. She might return two weeks or so later to build another nest and deposit more eggs. Fortunately for her, she does this only every three years or so.

Undisturbed eggs deposited this night will incubate below the surface for about two months. After escaping from their leathery cases, one-ounce hatchlings will work together to emerge from their sandy womb. All of this will occur at night, when temperatures are lower and they 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. Adult 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 will swim out to sea, where they will feed on various floating plants and animals. As they become adults they will utilize large, shallower 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 twenty 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. Note in the photograph in Figure 14.3.1, taken by an International Space Station astronaut, the level of development on 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 the Space Station and 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. The International Space Station, with multiple missions, is a major project of NASA, in conjunction with space agencies of Europe, Japan, Russia and Canada. Additionally, NASA, with the CNES (Centre National d'Etudes Spatiales, the French space agency) and NOAA (the National

Oceanic and Atmospheric Administration), also established Argos, a satellite-based system that helps to collect, process, and disseminate environmental data various platforms. (Argos, 2009)

Figure 14.3.1 Photograph of St. Croix taken from the International Space Station (St. Croix, 2009)

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

On December 28, 1973 the Endangered Species Act became the law of 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 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 that 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. All of the populations are either threatened or endangered. Various interventions, primarily aimed at protecting the nests and hatchlings, have been attempted, but there is much about the biology and demography of these animals we do not know. Sea turtle life cycles are long and complex, and 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 don't understand how various management alternatives will 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 age of adult turtles is difficult to determine, some researchers have used the 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.

Resulting populations 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*) which projected the effects of the use of turtle exclusion devices (TED's) in trawl fisheries. These devices allow young turtles to escape the trawls that trap shrimp, and the model predicted that the required use of TED's for offshore trawling would allow a gradual increase in Loggerheads by an order of magnitude in about seventy 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)

An Age-Structured Model

We can classify many animals by discrete ages to determine reproduction and mortality. 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 of the intrinsic rate of growth of the population and the proportion of each age group in a stable age distribution.

For example, suppose a certain bird has a maximum life span of three years. During the first year, the animal does not breed. On the average, a typical female of this hypothetical species lays ten eggs during the second year but only eight 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 only consider the females in the population; and in this example, we assume that half the offspring are female.

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 years old, at the start of breeding season 5. Some of these survive to time $t + 1 = 6$ years and progress to the next class, those females in their third year of life. At that time (at time 6 years 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 five (5) female offspring and a Year 3 (ages 2-to-3 years old) mother has four (4) female offspring, the number of Year 1 (ages 0-to-1 years old) female eggs/chicks at time $t + 1$ is as follows:

$$5x_2(t) + 4x_3(t) = x_1(t + 1) \qquad (1)$$

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

$$0.15x_1(t) = x_2(t + 1) \qquad (2)$$

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

$$0.50x_2(t) = x_3(t + 1) \qquad (3)$$

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

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

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

$$\boldsymbol{Lx}(\boldsymbol{t}) = \boldsymbol{x}(\boldsymbol{t}+\mathbf{1}),$$

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

Suppose an initial population distribution has 3000 eggs/chicks, 440 Year 2, and 350 Year 3 birds, so that $\boldsymbol{x}(\mathbf{0}) = \begin{bmatrix} 3000 \\ 440 \\ 350 \end{bmatrix}$ 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 population at time $t = 1$ year:

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

Thus, at $t = 1$ year, there are more eggs/chicks but fewer Year 3 adults than initially present.

Quick Review Question 1 Suppose an insect has maximum life expectancy of two 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 at time $t = 1$ month expressed to two decimal places.

e. Determine the number of females at time $t = 2$ months.

Leslie Matrices

L above is an example of a **Leslie Matrix**, which is a particular type of **projection 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, $x_0(t)$ is the number of females born between time t - 1 and time t. The model has the following system of equations:

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

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-by-n Leslie matrix is as follows:

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

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

Definitions 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 $\boldsymbol{x(t)}$ being the population distribution vector at time t, $(x_1(t), x_2(t), \ldots, x_n(t))$, and $\boldsymbol{x(t + 1)}$ being the 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):

$$\boldsymbol{Lx(t) = x(t+1)}$$

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 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 $\boldsymbol{x(1) = Lx(0)} = \begin{bmatrix} 3600 \\ 450 \\ 220 \end{bmatrix}$. Repeating the process, we have the following results at time $t = 2$ years:

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

Summing the elements of the result gives us a total population at that time of 3895. The percentage of birds 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 $\boldsymbol{x}(\mathbf{2}) = L\boldsymbol{x}(\mathbf{1}) = L(L\boldsymbol{x}(\mathbf{0})) = L^2\boldsymbol{x}(\mathbf{0})$. Similarly, $\boldsymbol{x}(\mathbf{3}) = L\boldsymbol{x}(\mathbf{2}) = L(L^2\boldsymbol{x}(\mathbf{0})) = L^3\boldsymbol{x}(\mathbf{0})$. In general, $\boldsymbol{x}(\boldsymbol{n}) = L^n\boldsymbol{x}(\mathbf{0})$.

For several values of n, Table 14.3.1 indicates the population change in the three classes by presenting the distributions, $\boldsymbol{x}(\boldsymbol{n}) = L^n\boldsymbol{x}(\mathbf{0})$, and the percentage of 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 $\boldsymbol{v} = \begin{bmatrix} 0.8206 \\ 0.1205 \\ 0.0590 \end{bmatrix} = \begin{bmatrix} 82.06\% \\ 12.05\% \\ 5.90\% \end{bmatrix}$.

From time $n = 20$ 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 a characteristic of such age-structured models.

Table 14.3.1 Population distributions and class percentages of the total population

Time, n	**Distribution** $\boldsymbol{x}(\boldsymbol{n}) = L^n\boldsymbol{x}(\mathbf{0})$	**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	$\begin{bmatrix} 3600 \\ 469.5 \\ 270 \end{bmatrix}$	$\begin{bmatrix} 82.96\% \\ 10.82\% \\ 6.22\% \end{bmatrix}$
$\vdots$	$\vdots$	$\vdots$
9	$\begin{bmatrix} 3913.31 \\ 574.45 \\ 281.813 \end{bmatrix}$	$\begin{bmatrix} 82.04\% \\ 12.04\% \\ 5.91\% \end{bmatrix}$
10	$\begin{bmatrix} 3999.5 \\ 586.997 \\ 287.225 \end{bmatrix}$	$\begin{bmatrix} 82.06\% \\ 12.04\% \\ 5.89\% \end{bmatrix}$
$\vdots$	$\vdots$	$\vdots$
20	$\begin{bmatrix} 4950.87 \\ 726.933 \\ 355.783 \end{bmatrix}$	$\begin{bmatrix} 82.06\% \\ 12.05\% \\ 5.90\% \end{bmatrix}$
21	$\begin{bmatrix} 5057.8 \\ 742.631 \\ 363.467 \end{bmatrix}$	$\begin{bmatrix} 82.06\% \\ 12.05\% \\ 5.90\% \end{bmatrix}$
$\vdots$	$\vdots$	$\vdots$
100	$\begin{bmatrix} 27353.5 \\ 4016.29 \\ 1965.7 \end{bmatrix}$	$\begin{bmatrix} 82.06\% \\ 12.05\% \\ 5.90\% \end{bmatrix}$
101	$\begin{bmatrix} 27944.3 \\ 4103.03 \\ 2008.15 \end{bmatrix}$	$\begin{bmatrix} 82.06\% \\ 12.05\% \\ 5.90\% \end{bmatrix}$

Projected Population Growth Rate, λ

Interestingly, if we divide corresponding elements of the population distribution at time $n + 1$, $\mathbf{x}(n + 1)$, by the members of the distribution at time n, $\mathbf{x}(n)$, we have convergence of the quotients to the same number. Table 14.3.2 shows several of these quotients, which converge in this example to $\lambda = 1.0216$. Thus, eventually each age group changes by a factor of $\lambda = 1.0216 = 102.16\%$ from one year to the next. For instance, in going from time $n = 100$ years to $n + 1 = 101$ years, Table 14.3.1 shows that the number of Year 1 females changes by a factor of 102.16%, from 27353.5 to 1.0216(27353.5) = 27944.3. Similarly, the number of Year 2 females changes from 4016.29 to 1.0216(4016.29) = 4103.03, and the Year 3 females also goes up by the same factor, from 1965.7 to 1.0216(1965.7) = 2008.15. Thus, with each age group ultimately changing by a factor of 1.0216 = 102.16% annually, eventually the population will increase by 2.16% per year.

Table 14.3.2 $\mathbf{x}(n + 1)/\mathbf{x}(n)$

Time, n	$\mathbf{x}(n + 1)/\mathbf{x}(n)$
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	$\begin{bmatrix} 27944.3/27353.5 \\ 4103.03/4016.29 \\ 2008.15/1965.7 \end{bmatrix} = \begin{bmatrix} 1.0216 \\ 1.0216 \\ 1.0216 \end{bmatrix}$

With a value greater than 1, the projected population growth rate (λ) indicates that this bird population will increase with time. Had this intrinsic population growth rate been less than 1, the birds would eventually 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 reproduce successfully.

Even more striking is the fact that $L\boldsymbol{v} = \lambda\boldsymbol{v}$, as the following calculations indicate:

$$L\boldsymbol{v} = \begin{bmatrix} 0 & 5 & 4 \\ 0.15 & 0 & 0 \\ 0 & 0.50 & 0 \end{bmatrix} \begin{bmatrix} 0.8206 \\ 0.1205 \\ 0.0590 \end{bmatrix} = \begin{bmatrix} 0.83 \\ 0.12 \\ 0.06 \end{bmatrix} =$$

$$\lambda\boldsymbol{v} = 1.0216 \begin{bmatrix} 0.8206 \\ 0.1205 \\ 0.0590 \end{bmatrix} = \begin{bmatrix} 0.83 \\ 0.12 \\ 0.06 \end{bmatrix}$$

Multiplying both sides of the equation by a constant, c, maintains the equality, $cL\boldsymbol{v} = c\lambda\boldsymbol{v}$ or $L(c\boldsymbol{v}) = \lambda(c\boldsymbol{v})$. The formula holds for any multiple, c, of $\boldsymbol{v}$, 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 the product of the Leslie matrix by the distribution vector. λ is an **eigenvalue** for the matrix L, and $\boldsymbol{v}$ 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 $\boldsymbol{x}(\mathbf{0}) = \begin{bmatrix} 2 \\ 1 \end{bmatrix}$.

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 $\boldsymbol{v}$ that satisfies $L\boldsymbol{v} = \lambda\boldsymbol{v}$.

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

Sensitivity Analysis

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 bird example above, we wish to examine the sensitivity of the long-term population growth rate to small changes in survivability of Year 1 birds. Adjusting P_1 and P_2 individually by ±10% and ±20%, Table 1 shows the corresponding new values of λ and the change in projected population growth rate, $\lambda_{new} - \lambda$, as calculated using a computational tool. For relative sensitivity, we divide the changes in projected population growth rate by the corresponding changes in P_1. For example, $P_1 = 0.15$ and $P_1 + 0.10P_1 = 1.10P_1 = 0.15 + 0.015 = 0.165$. The original eigenvalue $\lambda = 1.0216$, the new eigenvalue $\lambda_{new} = 1.06526$, and $\lambda_{new} - \lambda = 1.06526 - 1.0216 = 0.04366$. The relative sensitivity = $(\lambda_{new} - \lambda)/0.10P_1$ =

0.04366/0.015 = 2.9067. From these calculations we see that λ is most sensitive to changes in survivability of Year 1 birds. This analysis indicates that conservationists might concentrate their efforts on helping eggs and nestlings.

Table 1 Sensitivity and relative sensitivity of λ (originally 1.0216) to changes in survivability

	Survivability Parameter	**Percent Change**	λ_{new}	**Sensitivity** $\lambda_{new} - \lambda$	**Relative Sensitivity**
	P_1	+10%	1.0653	0.0437	0.2911
	P_1	+20%	1.1069	0.0853	0.5687
	P_1	-10%	0.9756	-0.0460	-0.3068
	P_1	-20%	0.9268	-0.0948	-0.6320
	P_2	+10%	1.0340	0.0124	0.0248
	P_2	+20%	1.0460	0.0244	0.0489
	P_2	-10%	1.0088	-0.0128	-0.0256
	P_2	-20%	0.9955	-0.0261	-0.0521

Applicability of Leslie Matrices

Leslie matrices are appropriate to use when we can classify individuals in a species by age. The dynamics of the populations are only based on the females, and an adequate number of males for fertilization are assumed. The model in this module only accommodates 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 model 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-structured module can allow us to use matrix operations to determine the projected population growth rate and the stable-age distribution. (Horne, 2008)

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 value to which its percentage of the total population converges as time progresses.

2. Suppose certain animal has a maximum life span of three years. This example predicts populations in each age category: Year 1 (0-1 yr), Year 2 (1-2 yr), and Year 3 (2-3 yr). We only consider females. A Year 1 female animal has no offspring; a Year 2 female has 3 daughters on the average; and a Year 3 female has an average of 2 daughters. A Year 1 animal has a 0.3 probability of living to Year 2. A Year 2 animal has a 0.4 probability of living to Year 3. Suppose at one instance, the number of Year 1, 2, and 3 females are 2030, 652, and 287, respectively.

a. Determine the corresponding Leslie matrix, L.

b. Give the initial population distribution vector $\boldsymbol{x}(\mathbf{0})$.

c. Calculate the population distribution at time $t = 1$, vector $\boldsymbol{x}(\mathbf{1})$.

d. Calculate the class percentages of the total population at time $t = 1$.

e. Give the vector for class the percentages of the total population, $\boldsymbol{v}$, expressed to two decimal places, to which $\boldsymbol{x}(\boldsymbol{n})/T(n)$ converges, where $T(n)$ is the total population at time n.

e. Find the number λ, expressed to two decimal places, to which $\boldsymbol{x}(\boldsymbol{n}+\mathbf{1})/\boldsymbol{x}(\boldsymbol{n})$ converges.

f. Using answers from Parts a, d, and e, verify that $L\boldsymbol{v} = \lambda\boldsymbol{v}$.

Projects

1. Scientists performed a four-year study of "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. They considered five age groups: < 1 year (juvenile), 1 year, 2 years, 3 years, > 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 post breeding time (post-birth pulse sampling), they calculated fecundity for Class *i* as the number of female nestlings born to mothers of age *i* + 1 years (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 $P_4x_4(t) + P_{4+}x_{4+}(t)$. Table 1 presents data for newly banded birds (NB) and for newly banded birds and unbanded 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.

Table 2 Data on Red-Cockaded Woodpeckers in the Georgia Piedmont, 1983-1988, for newly banded birds (NB) and for newly banded birds and unbanded 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 number of female offspring per female of age *i* years

		NB			**NBU**	
	Age (years)	P_i	m_i		P_i	m_i
	0	0.380	0.000		0.401	0.000
	1	0.653	0.133		0.734	0.126
	2	0.850	1.082		0.961	1.023

	3	0.400	1.194		0.456	1.129
	4	0.589	1.590		0.667	1.504
	5	0.589	1.590		0.667	1.504
	6	0.589	1.590		0.667	1.504
	…	…	…		…	…

a. Develop a deterministic model for each set of birds, NB and NBU. What happens to the population over a period of time? 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. Repeat Part b determining the impact on the finite rate of population change, λ, the dominant (largest real) eigenvalue.

d. 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 at each time step 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, $n_{B3} = min(n_3P_3, 41 - n_{B4+} - n_{B4})$, etc.

e. Table 2 gives the researchers' calculations for P_1 along with the corresponding probability for each of the four years of the study. Develop a stochastic version of the model for NB or NBU birds, where at each time step the juvenile (Class 1) survival rate is randomly selected with the given probabilities from the estimations in the table. Run the simulation 1000 times for at least 200 years on each simulation. Determine the range of extinction and the average extinction. This simulation corresponds 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?

f. Repeat Part e at each time step selecting randomly a juvenile survival rate in an appropriate range.

Table 3 Yearly estimates of juvenile survival rates (P_i) and corresponding probabilities for Red-Cockaded Woodpeckers in the Georgia Piedmont, 1983-1988, for newly banded birds (NB) and for newly banded birds and unbanded birds (NBU)

	NB			NBU	
Year	**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

(Maguire, 1995)

2. 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. For four years, they collected life table data; then for two 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 post-breeding, after the birth pulse. Table 3 presents their data the nonlawn habitat in three categories, Young (< 1 year), Yearling (1-2 years), and Adult (> 2 years).

Table 4 Pre- and post-reduction survival and fertility data for nonlawn Uinta Ground Squirrels

		Pre-reduction			Post-reduction	
	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

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 post-reduction. By changing each survival rate in the pre-reduction data one at a time by ±10% and ±20%, determine to which parameter λ is most sensitive. Discuss the results. (Oli, 2001)

3. People in Europe and Asia enjoy eating skate, which are similar to shark. Thus, the animal has declined since the 1970s. Frisk, Miller, and Fogarty did a study of little skate, winter skate, and barndoor skate to determine sustainable harvest levels and strategies. For the little skate (*Leucoraja erinacea*), the scientists used an age-structured model incorporating one-year age categories with eight-year longevity. Data from a previous study indicated age of 50% maturity to be 4 with annual 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 two 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.

Develop a Leslie model for the little skate and determine the long-term 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 skate. Do you get the same value? What is the meaning of *r*? Interpret λ and *r* for the long-term forecast for little skates. (Frisk, 2002)

Answers to Quick Review Questions

1. **a.** $x_i(t)$ = number of this insect in the *i*-th 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 insects and 0.02 month-2 insects because $L\mathbf{x}(\mathbf{0}) = \begin{bmatrix} 5 & 150 \\ 0.01 & 0 \end{bmatrix}\begin{bmatrix} 2 \\ 1 \end{bmatrix}$

$= \begin{bmatrix} 160.00 \\ 0.02 \end{bmatrix}$

e. 803 month-1 insects and 1.6 month-2 insects

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.** 99.9998%, 0.189254%

b. 5.28388

c. $\begin{bmatrix} 0.999998 \\ 0.00189254 \end{bmatrix}$

d. $\begin{bmatrix} 999998 \\ 1892.54 \end{bmatrix}$

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