

9

CHAPTER

Leslie Matrix Models and Eigenvalues

The models presented and discussed in Chapters 6, 7, and 8 are limited by the assumption that nothing is created or destroyed. Each area on a landscape may change from one class to another, and each individual in a population changes only from one disease status to another. We did not consider the case of a population in which new individuals are born or individuals die. So in these models, each component (area or individuals) changes only in state. In the landscape succession examples, we never created or destroyed land, but each area on the landscape could change from one state to another. In the disease model, there were no births or deaths, but individuals could move between infected and susceptible states. Much of biology deals with systems in which the entities (cells and individuals) can be born and can die. In this chapter, we discuss models that take into account births and deaths and develop methods to see what happens to the structure of the biological system in this case.

Intuitively, unless we somehow can match up the number of births and deaths regularly, a population will either grow or decline. This should happen no matter how we structure the population, unless there are different birth rates and death rates for the different classes or groups in the population. You may have heard of zero-population growth as arising when births and deaths are exactly matched, but this is difficult to achieve for mammal populations in which there is age structure and the birth rates and death rates vary with age.

The matrix methods we develop in this chapter allow us to project the future changes in a population that is structured, typically by age but more generally by what we call their stage, and to account for the differences in births and mortality for different ages. This is the basis for demographic analysis in humans (and in wildlife populations) that provides an overall growth rate of the population and allows us to project the age structure of the population in a way similar to how we used eigenvalues previously to determine landscape structure. It provides a means to determine whether a wildlife population can be harvested without leading to major declines in the population and guidance as to the magnitude of allowable harvest.

9.1 Leslie Matrix Models

Suppose that we are studying a population of locusts and want to know how their population changes over time. Locusts have three stages in their life cycle: (1) egg, (2) nymph or hopper, and (3) adult. Not all locust eggs will survive to become adults. Some will die while they are still eggs. Others will die while they are hoppers. Locusts are able to reproduce (lay eggs) only during the adult stage of their life.

Suppose that in the particular population of locusts we are studying, each year 2% of the eggs survive to become hoppers, 5% of the hoppers survive to become adults, and the adults die soon after they reproduce (i.e., they do not survive to the next year). Additionally, the average female adult locust will produce 1000 eggs before she dies.

Since it is the females that reproduce, we model only the females of the population. Let $x_1(t)$ be the number of female eggs in the locust population at time step t (measured in years), let $x_2(t)$ be the number of female hoppers in the locust population at time step t , and let $x_3(t)$ be the number of female adults in the locust population at time step t . We can write a system of equations to represent how this population changes each year:

$$x_1(t+1) = 1000x_3(t). \quad (9.1)$$

$$x_2(t+1) = 0.02x_1(t). \quad (9.2)$$

$$x_3(t+1) = 0.05x_2(t). \quad (9.3)$$

Equation (9.1) shows that each adult at time step t , that is, $x_3(t)$, produces 1000 eggs, resulting in $1000x_3(t)$ eggs at time step $t+1$. Equation (9.2) shows that 2% of the eggs at time step t , that is, $x_1(t)$, move into the hopper class by time step $t+1$, and Equation (9.3) shows that 5% of the hoppers at time step t , that is, $x_2(t)$, move into the adult class by time step $t+1$.

Can we rewrite our system of Equations (9.1) to (9.3) as a matrix equation? If we rewrite the system of Equations (9.1) to (9.3) as

$$\begin{aligned} x_1(t+1) &= 0x_1(t) + 0x_2(t) + 1000x_3(t), \\ x_2(t+1) &= 0.02x_1(t) + 0x_2(t) + 0x_3(t), \text{ and} \\ x_3(t+1) &= 0x_1(t) + 0.05x_2(t) + 0x_3(t), \end{aligned}$$

it should become clear that, yes, we can write the system of equations as the matrix equation.

$$\begin{aligned} \begin{bmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \end{bmatrix} &= \begin{bmatrix} 0 & 0 & 1000 \\ 0.02 & 0 & 0 \\ 0 & 0.05 & 0 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \end{bmatrix} \\ \mathbf{x}(t+1) &= \begin{bmatrix} 0 & 0 & 1000 \\ 0.02 & 0 & 0 \\ 0 & 0.05 & 0 \end{bmatrix} \mathbf{x}(t). \end{aligned} \quad (9.4)$$

Now, as in the previous chapters, we are able to find how the population changes over time.

Example 9.1 (Six Years of Locusts)

How does the population of locusts change over the course of 6 years if

- (a) there are only 50 adults at the initial time (no eggs and no hoppers)?
- (b) there are 50 eggs, 100 hoppers, and 50 adults at the initial time?

Solution: Let

$$A = \begin{bmatrix} 0 & 0 & 1000 \\ 0.02 & 0 & 0 \\ 0 & 0.05 & 0 \end{bmatrix}.$$

In both cases, we will use the following to find the population structure for each of the 6 years:

$$\mathbf{x}(1) = A\mathbf{x}(0)$$

$$\mathbf{x}(2) = A^2\mathbf{x}(0)$$

$$\mathbf{x}(3) = A^3\mathbf{x}(0)$$

$$\mathbf{x}(4) = A^4\mathbf{x}(0)$$

$$\mathbf{x}(5) = A^5\mathbf{x}(0)$$

$$\mathbf{x}(6) = A^6\mathbf{x}(0).$$

- (a) If we start with

$$\mathbf{x}(0) = \begin{bmatrix} 0 \\ 0 \\ 50 \end{bmatrix},$$

then

t	Eggs	Hoppers	Adults
0	0	0	50
1	50,000	0	0
2	0	1000	0
3	0	0	50
4	50,000	0	0
5	0	1000	0
6	0	0	50

- (b) If we start with

$$\mathbf{x}(0) = \begin{bmatrix} 50 \\ 100 \\ 50 \end{bmatrix},$$

(Continued)

then

t	Eggs	Hoppers	Adults
0	50	100	50
1	50,000	1	5
2	5000	1000	0.05
3	50	100	50
4	50,000	1	5
5	5000	1000	0.05
6	50	100	50

We see that in both cases, the population cycles, but the initial condition determines the cycle.

This type of matrix population model that takes into account births and the survival rates of each class to the next stage is known as a *Leslie matrix model*. In general, they have the form $\mathbf{x}(t + 1) = \mathbf{A}\mathbf{x}(t)$, where

$$\mathbf{A} = \begin{bmatrix} F_1 & F_2 & F_3 & \cdots & F_n \\ S_1 & 0 & 0 & \cdots & 0 \\ 0 & S_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & S_{n-1} & S_n \end{bmatrix},$$

where F_i is the average number of female offspring born to a female individual per time step in class i and S_i is the fraction of individuals in class i that survive to class $i + 1$ per time step, for $i < n$. For $i = n$, S_n is the proportion of individuals in class n that survive a subsequent time period (with the same proportion surviving for each future time period). The parameter F_i is known as the *fecundity rate*, and the parameter S_i is known as the *survival rate*. Note that the first row gives the equation corresponding to the first stage class x_1 (like eggs or newborns). In Leslie matrix models, we assume that we census the population after reproduction and that only the females are counted. After spending time in the last stage class, individuals die if $S_n = 0$, but if $S_n > 0$ then some fraction of individuals in the last class remain in that class for the next time step. The survival and fecundity rates are assumed to be constant over time. Those rates are independent of the total population. Leslie matrix models do not account for the effects of density-dependent parameters such as overcrowding, environmental disturbances such as natural disasters and weather, seasonal changes, or the harvesting of individuals from the population.

Before we continue on to look at the long-term dynamics of a population modeled by a Leslie matrix, let us consider one more example.

Example 9.2 (American Bison [16])

The Leslie matrix for the American bison is given by

$$\mathbf{A} = \begin{bmatrix} 0 & 0 & 0.42 \\ 0.60 & 0 & 0 \\ 0 & 0.75 & 0.95 \end{bmatrix}.$$

The population is divided into calves, yearlings, and adults (age 2 or more). Thus, 95% of the females that reach the age of 2 years survive an additional year and reproduce with the same regularity. If we start a herd with 100 adult females (and an appropriate number of adult males), what will the herd population structure look like for the subsequent 5 years?

Solution: If we start a herd with 100 adult females, then next year's herd structure is given by

$$\begin{bmatrix} 0 & 0 & 0.42 \\ 0.60 & 0 & 0 \\ 0 & 0.75 & 0.95 \end{bmatrix} \begin{bmatrix} 0 \\ 0 \\ 100 \end{bmatrix} = \begin{bmatrix} 42 \\ 0 \\ 95 \end{bmatrix}.$$

Multiplying the prior year's stage structure vector by \mathbf{A} will give population predictions for subsequent years, which we show in the table below.

Year	Calves	Yearlings	Adults	Total
0	0	0	100	100
1	42	0	95	137
2	40	25	90	155
3	38	24	104	166
4	44	23	117	184
5	49	26	128	203

Notice that the total female population size is growing each year.

9.2 Long-Term Growth Rate (Eigenvalues)

Given a Leslie matrix, we would like to find a stable stage distribution. By this is meant a distribution so that the population remains at that distribution once there. In the case of the locust population, this would mean that the fractions of the population that were eggs, hoppers, and adults would stay the same through time. We saw in Example 9.2 that a Leslie matrix could model a growing population; thus, we do not necessarily want to find vectors $\mathbf{x}(t)$ such that $\mathbf{x}(t + 1) = \mathbf{x}(t)$ as we did in Chapter 8. What we want to do is find a distribution among the stage classes so that the proportion in each class does not change from one time period to the next, though the overall “number” in each class could change. If the overall population increased by a factor of λ , then each class would have increased by a factor of λ if the population were at a stable stage structure. The population will have this property if it satisfies the equation

$$\mathbf{x}(t + 1) = \lambda \mathbf{x}(t), \tag{9.5}$$

where the value λ is known as an *eigenvalue*.

In Equation 9.5, it is important that this equation holds no matter what time t is used if the population distribution $\mathbf{x}(t)$ is at a stable stage distribution. If $\lambda > 1$, then the population is growing over time when it is at a stable stage distribution. If $\lambda < 1$, then the population is declining over time. If $\lambda = 1$, then the population is remaining constant over time (this is what occurred in the transfer matrices examples). Often, the λ is referred to as the *long-term growth rate*. This is also called the Malthusian growth rate, after Thomas Malthus, whose treatise, originally published in 1798, *An Essay on the Principle of Population*, pointed out clearly the capacity for populations to increase exponentially.

When population growth is discussed, just as when we talk about the growth of money in a bank account, it is common to state that a population is growing at a rate of 5%, for example. This means that each time step, the population is 5% larger than it was previously, which would correspond to $\lambda = 1 + 0.05 = 1.05$. This is identical to the case of having a bank account with a 5% annual interest rate compounded annually: you would have \$105 at the end of 1 year if you had \$100 in the account at the start of the year. As another example, if a population were declining by 8% per time step, the growth rate per time step would be $\lambda = 1 - 0.08 = 0.92$.

In general, the change in the growth (or decay) rate per time step is

$$\lambda - 1.$$

If $0 < \lambda < 1$, then the population is declining, and the change in the rate per time step is

$$\lambda - 1 < 0.$$

If $\lambda = 0.8$, then

$$\lambda - 1 = 0.8 - 1 = -0.2,$$

and we say that the population is declining by 20% per time step.

If $\lambda > 1$, then the population is increasing, and the change in the growth rate per time step is

$$\lambda - 1.$$

If $\lambda = 1.3$, then

$$\lambda - 1 = 1.3 - 1 = 0.3,$$

and we say that the population is growing by 30% per time step.

All of this discussion of the long-term growth rate applies only when the population is at a stable stage distribution. It may take a number of years or time steps for a population to get close to the stable stage distribution; during this period, the population will typically not be changing by a factor of λ . How long it takes a population to reach a stable stage distribution and its long-term growth rate is one of many questions that mathematical models such as the Leslie matrix model address in the field of demography, which is the study of how a population stage distribution changes (and, in the case of many mammals, such as humans, the important stage distribution is based on age).

If we combine Equation (9.5) with $\mathbf{x}(t+1) = \mathbf{A}\mathbf{x}(t)$, where \mathbf{A} is our Leslie matrix, then we get

$$\mathbf{A}\hat{\mathbf{x}} = \lambda\hat{\mathbf{x}}, \tag{9.6}$$

where $\hat{\mathbf{x}}$ is the population vector after some period of time. If we can solve Equation (9.6) for λ , then we can determine how our population is growing or declining. This is rather simple for a

2×2 Leslie matrix. We seek to solve Equation (9.6) for λ and the corresponding nonzero vector

$$\hat{\mathbf{x}} = \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}$$

with either or both of x_1 and x_2 not being zero.

Suppose that our Leslie matrix is

$$\mathbf{A} = \begin{bmatrix} a & b \\ c & d \end{bmatrix}.$$

Equation (9.6) can be rewritten as $(\mathbf{A} - \lambda\mathbf{I})\hat{\mathbf{x}} = \mathbf{0}$, or

$$\begin{bmatrix} a - \lambda & b \\ c & d - \lambda \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}.$$

We can rewrite this matrix equation as a system of equations:

$$(a - \lambda)x_1 + bx_2 = 0. \tag{9.7}$$

$$cx_1 + (d - \lambda)x_2 = 0. \tag{9.8}$$

Multiply Equation (9.7) by c and Equation (9.8) by $a - \lambda$ to get

$$c(a - \lambda)x_1 + cbx_2 = 0. \tag{9.9}$$

$$c(a - \lambda)x_1 + (a - \lambda)(d - \lambda)x_2 = 0. \tag{9.10}$$

Subtract Equation (9.9) from Equation (9.10) to obtain

$$[(a - \lambda)(d - \lambda) - bc]x_2 = 0,$$

which implies that

$$x_2 = 0 \quad \text{or} \quad (a - \lambda)(d - \lambda) - bc = 0. \tag{9.11}$$

If $x_2 = 0$, then we know that $x_1 \neq 0$, and Equations (9.7) and (9.8) give

$$(a - \lambda)x_1 = cx_1 = 0,$$

and thus

$$\lambda = a \quad \text{and} \quad c = 0.$$

If $x_2 \neq 0$, then by Equation (9.11),

$$(a - \lambda)(d - \lambda) - bc = 0$$

$$\lambda^2 - (a + d)\lambda + (ad - bc) = 0. \tag{9.12}$$

Equation (9.12) is known as the *characteristic equation* of the 2×2 matrix \mathbf{A} . Solving (9.12) via the quadratic formula yields two solutions:

$$\lambda_1 = \frac{(a + d) + \sqrt{(a + d)^2 - 4(ad - bc)}}{2}, \quad \text{and}$$

$$\lambda_2 = \frac{(a + d) - \sqrt{(a + d)^2 - 4(ad - bc)}}{2}.$$

For any matrix, the eigenvalue with the largest absolute value is known as the *dominant eigenvalue*. For our matrix models, the dominant eigenvalue corresponds to the long-term growth rates of the systems we are modeling. A Leslie matrix has a unique positive eigenvalue, and its corresponding eigenvector has all positive entries. For a Leslie matrix, this positive eigenvalue is the dominant eigenvalue [12].

Example 9.3 (Finding an Eigenvalue)

Consider the 2×2 Leslie matrix

$$\mathbf{A} = \begin{bmatrix} 1 & 4 \\ 0.5 & 0 \end{bmatrix}.$$

Find the long-term growth rate of the population that this Leslie matrix is modeling.

Solution: To find the long-term growth rate of this population, we find the dominant eigenvalue. First, from the characteristic equation of \mathbf{A} , we have

$$\begin{aligned} \lambda^2 - (1 + 0)\lambda + (1 \cdot 0 - 0.5 \cdot 4) &= 0 \\ \lambda^2 - \lambda - 2 &= 0 \\ (\lambda - 2)(\lambda + 1) &= 0 \\ \lambda = 2, \quad \lambda = -1. \end{aligned}$$

The eigenvalue with the largest absolute value is $\lambda = 2$. The long-term growth rate is 2. This means for large times, our population is doubling every time step, that is eventually, $\mathbf{x}(t+1) = 2\mathbf{x}(t)$. If at time $t = 100$, our population has reached its long-term growth with a population size of 1000 individuals, then at time $t = 101$, we will have a total of 2000 individuals. The change in the growth rate per time step of our population (after a long time) is $\lambda - 1 = 2 - 1 = 1$. This population is growing per time step by 100%.

It turns out there is another method for solving $(\mathbf{P} - \lambda\mathbf{I})\hat{\mathbf{x}} = \mathbf{0}$, where \mathbf{P} is a general 2×2 matrix, but we need a new mathematical concept called the *determinant*. The determinant of the 2×2 matrix

$$\mathbf{P} = \begin{bmatrix} a & b \\ c & d \end{bmatrix}$$

is

$$\det(\mathbf{P}) = \begin{vmatrix} a & b \\ c & d \end{vmatrix} = ad - cb.$$

Thus, we could also derive the characteristic equation of the 2×2 matrix \mathbf{P} by solving $(\mathbf{P} - \lambda\mathbf{I}) = \mathbf{0}$ for λ :

$$\begin{aligned} \det(\mathbf{P} - \lambda\mathbf{I}) &= 0 \\ \begin{vmatrix} a - \lambda & b \\ c & d - \lambda \end{vmatrix} &= 0 \\ (a - \lambda)(d - \lambda) - bc &= 0 \\ ad - a\lambda - d\lambda + \lambda^2 - bc &= 0 \\ \lambda^2 - (a + d)\lambda + (ad - bc) &= 0. \end{aligned}$$

The straight vertical lines around the matrix elements above are the notation for the determinant of the matrix. The reason we introduce this second method is that it is easily expandable to larger matrices. For square matrices larger than 2×2 , we use a method known as “expansion by minors.” For this method, we pick a row along which we will expand. Here, we will use the example of expanding along the first row of a 3×3 matrix

$$\mathbf{A} = \begin{bmatrix} a & b & c \\ d & e & f \\ g & h & i \end{bmatrix}.$$

First, we take the first entry in the first row and multiply it by the determinant of the matrix that remains, called a minor, when we cross out the first row and the first column. Next, multiply -1 by the second entry in the first row by the determinant of the matrix that remains when we cross out the first row and the second column. Now, multiply the third entry in the first row by the determinant of the matrix that remains when we cross out the first row and third column. Finally, to get the determinant of the matrix \mathbf{A} , we sum each of the products together. Thus,

$$\det(\mathbf{A}) = a \begin{vmatrix} e & f \\ h & i \end{vmatrix} - b \begin{vmatrix} d & f \\ g & i \end{vmatrix} + c \begin{vmatrix} d & e \\ g & h \end{vmatrix}.$$

Notice that the definition of the determinant of a 3×3 matrix depends on the determinants of three 2×2 matrices. Likewise, the definition of the determinant of a 4×4 matrix is similarly defined and depends on the determinants of four 3×3 matrices.

Example 9.4 (Eigenvalue of a Transfer Matrix)

Verify that the dominant eigenvalue of the transfer matrix \mathbf{A} is 1, where

$$\mathbf{A} = \begin{bmatrix} 0.95 & 0 & 0 \\ 0.05 & 0.88 & 0 \\ 0 & 0.12 & 1 \end{bmatrix}.$$

Solution: To find the eigenvalues, we need to solve $\det(\mathbf{A} - \lambda\mathbf{I}) = 0$ for λ . Since \mathbf{A} is a 3×3 matrix, we will use the expansion of minors technique:

$$\begin{aligned} 0 &= \det(\mathbf{A} - \lambda\mathbf{I}) \\ 0 &= \begin{vmatrix} 0.95 - \lambda & 0 & 0 \\ 0.05 & 0.88 - \lambda & 0 \\ 0 & 0.12 & 1 - \lambda \end{vmatrix} \\ 0 &= (0.95 - \lambda) \begin{vmatrix} 0.88 - \lambda & 0 \\ 0.12 & 1 - \lambda \end{vmatrix} - 0 \begin{vmatrix} 0.05 & 0 \\ 0 & 1 - \lambda \end{vmatrix} + 0 \begin{vmatrix} 0.05 & 0.88 - \lambda \\ 0 & 0.12 \end{vmatrix} \\ 0 &= (0.95 - \lambda) [(0.88 - \lambda)(1 - \lambda) - 0] - 0 + 0 \\ 0 &= (0.95 - \lambda)(0.88 - \lambda)(1 - \lambda) \\ \lambda &= \{0.95, 0.88, 1\}. \end{aligned}$$

The eigenvalue of the largest absolute value is $\lambda = 1$. Thus, the dominant eigenvalue of the transfer matrix \mathbf{A} is 1.

Example 9.5 (Eigenvalues of a Leslie Matrix)

Find the long-term growth rate of the Leslie matrix

$$A = \begin{bmatrix} 0 & 4 & 3 \\ 0.5 & 0 & 0 \\ 0 & 0.25 & 0 \end{bmatrix}.$$

Solution: To find the eigenvalues, we need to solve $\det(\mathbf{A} - \lambda\mathbf{I}) = 0$ for λ . Since \mathbf{A} is a 3×3 matrix, we will use the expansion of minors technique:

$$\begin{aligned} 0 &= \det(\mathbf{A} - \lambda\mathbf{I}) \\ 0 &= \begin{vmatrix} -\lambda & 4 & 3 \\ 0.5 & -\lambda & 0 \\ 0 & 0.25 & -\lambda \end{vmatrix} \\ 0 &= -\lambda \begin{vmatrix} -\lambda & 0 \\ 0.25 & -\lambda \end{vmatrix} - 4 \begin{vmatrix} 0.5 & 0 \\ 0 & -\lambda \end{vmatrix} + 3 \begin{vmatrix} 0.5 & -\lambda \\ 0 & 0.25 \end{vmatrix} \\ 0 &= -\lambda(\lambda^2 - 0) - 4(-0.5\lambda - 0) + 3((0.5)(0.25) - 0) \\ 0 &= -\lambda^3 + 2\lambda + \frac{3}{8} \\ 0 &= \lambda^3 - 2\lambda - \frac{3}{8} \\ 0 &= \left(\lambda - \frac{3}{2}\right) \left(\lambda^2 + \frac{3}{2}\lambda + \frac{1}{4}\right) \\ 0 &= \left(\lambda - \frac{3}{2}\right) \left(\lambda - \frac{3 - \sqrt{5}}{4}\right) \left(\lambda - \frac{3 + \sqrt{5}}{4}\right) \\ \lambda &= \left\{ \frac{3}{2}, \frac{-3 + \sqrt{5}}{4}, \frac{-3 - \sqrt{5}}{4} \right\}. \end{aligned}$$

The eigenvalue with the largest absolute value is $\lambda = \frac{3}{2}$. The long-term growth rate is $\frac{3}{2}$. Thus, for large times, $\mathbf{x}(t + 1) = \frac{3}{2}\mathbf{x}(t)$. The change in the growth rate per time step of the population (after a long time) is $\lambda - 1 = \frac{3}{2} - 1 = \frac{1}{2}$; that is, the population is growing by 50% per time step.

From Example 9.5, we can see that solving the cubic equations resulting from the expansion of minors technique for the determinant of a 3×3 matrix is a bit more involved than solving the quadratic equation resulting from the determinant of a 2×2 matrix. In general, we will use Matlab to find eigenvalues of square matrices larger than 2×2 (see the “Matlab Skills” section at the end of this chapter for details).

In Examples (9.3), (9.4), and (9.5), all the roots of the polynomials derived from $\det(\mathbf{A} - \lambda\mathbf{I}) = 0$ were real numbers. However, it is possible to have complex roots to these polynomials. When there are complex roots, the resulting population structure will exhibit oscillations. Consider Example 9.1, where we saw a locust population oscillating every 3 years.

Example 9.6 (Eigenvalues of an Oscillating Population)

Recall the Leslie matrix of a locust population presented in Example 9.1:

$$A = \begin{bmatrix} 0 & 0 & 1000 \\ 0.02 & 0 & 0 \\ 0 & 0.05 & 0 \end{bmatrix}.$$

Find the eigenvalues for this Leslie matrix.

Solution: To find the eigenvalues, we need to solve the equation $\det(\mathbf{A} - \lambda\mathbf{I}) = 0$ for λ . Since \mathbf{A} is a 3×3 matrix, we will use the expansion of minors technique:

$$\begin{aligned} 0 &= \det(\mathbf{A} - \lambda\mathbf{I}) \\ 0 &= \begin{vmatrix} -\lambda & 0 & 1000 \\ 0.02 & -\lambda & 0 \\ 0 & 0.05 & -\lambda \end{vmatrix} \\ 0 &= -\lambda \begin{vmatrix} -\lambda & 0 \\ 0.05 & -\lambda \end{vmatrix} - 0 \begin{vmatrix} 0.02 & 0 \\ 0 & -\lambda \end{vmatrix} + 1000 \begin{vmatrix} 0.02 & -\lambda \\ 0 & 0.05 \end{vmatrix} \\ 0 &= -\lambda(\lambda^2 - 0) - 0 + 1000(0.001 - 0) \\ 0 &= -\lambda^3 + 1 \\ 0 &= \lambda^3 - 1 \\ 0 &= (\lambda - 1)(\lambda^2 + \lambda + 1) \\ \lambda &= \left\{ 1, \frac{-1 + i\sqrt{3}}{2}, \frac{-1 - i\sqrt{3}}{2} \right\}. \end{aligned}$$

Which eigenvalue is dominant? Let $\lambda_1 = 1$, $\lambda_2 = \frac{-1 + i\sqrt{3}}{2} = -\frac{1}{2} + i\frac{\sqrt{3}}{2}$, and $\lambda_3 = \frac{-1 - i\sqrt{3}}{2} = -\frac{1}{2} - i\frac{\sqrt{3}}{2}$. Then

$$|\lambda_1| = 1$$

$$|\lambda_2| = \sqrt{\left(-\frac{1}{2}\right)^2 + \left(\frac{\sqrt{3}}{2}\right)^2} = \sqrt{\frac{1}{4} + \frac{3}{4}} = 1$$

$$|\lambda_3| = \sqrt{\left(-\frac{1}{2}\right)^2 + \left(\frac{\sqrt{3}}{2}\right)^2} = \sqrt{\frac{1}{4} + \frac{3}{4}} = 1$$

(Continued)

In this case, where all the eigenvalues have the same absolute value, the dominant eigenvalue is the positive real eigenvalue, $\lambda = 1$. However, because the complex eigenvalues have the same absolute value as the dominant eigenvalue, the population structure never attains an equilibrium proportion structure. Instead, the population will oscillate, as we saw in Example 9.1.

9.3 Long-Term Population Structure (Corresponding Eigenvectors)

Now that we have determined how to calculate the long-term growth rate of a population modeled by a Leslie matrix, we would like to determine the long-term population structure, that is, the proportion of the population that is in each class. We do this by finding the eigenvector that corresponds with the dominant eigenvalue of the matrix.

Again, we return to Equation (9.6):

$$\mathbf{A}\hat{\mathbf{x}} = \lambda\hat{\mathbf{x}}.$$

Once we know the value of the dominant eigenvalue, we plug that in for λ and solve the system of equations corresponding to the equation $\mathbf{A}\hat{\mathbf{x}} = \lambda\hat{\mathbf{x}}$. Remember that for our eigenvector to represent the proportions of the population, we normalize it so that the sum of its components is 1.

Example 9.7 (Finding an Eigenvector)

Recall the Leslie matrix from Example 9.3:

$$\mathbf{A} = \begin{bmatrix} 1 & 4 \\ 0.5 & 0 \end{bmatrix}.$$

Find the long-term population structure for this population represented by the Leslie matrix \mathbf{A} .

Solution: In Example 9.3, we found that the dominant eigenvalue of \mathbf{A} is 2. To find the long-term population structure, we must find the eigenvector associated with the dominant eigenvalue. We do this by solving

$$\mathbf{A}\hat{\mathbf{x}} = 2\hat{\mathbf{x}}.$$

The corresponding system of equations is

$$1x_1 + 4x_2 = 2x_1. \quad (9.13)$$

$$0.5x_1 + 0x_2 = 2x_2. \quad (9.14)$$

(Continued)

We can solve either Equation (9.13) or Equation (9.14) for x_1 in terms of x_2 to get the relationship

$$x_1 = 4x_2.$$

Let us choose $x_2 = 1$; then $x_1 = 4$. Thus, an eigenvector is

$$\begin{bmatrix} 4 \\ 1 \end{bmatrix}.$$

We normalize this eigenvector to get the long-term population structure:

$$\begin{bmatrix} 4/5 \\ 1/5 \end{bmatrix}.$$

Thus, for large times, we can expect to find 80% of the population in the first class and 20% of the population in the second class.

Recall from Chapter 8 how we found the normalized eigenvector of the transfer matrix

$$\mathbf{T} = \begin{bmatrix} 0.9 & 0.2 \\ 0.1 & 0.8 \end{bmatrix},$$

which described the spread of a nonfatal disease. We solved the system of equations that came from $\hat{\mathbf{x}} = \mathbf{T}\hat{\mathbf{x}}$. If we calculate the eigenvalues of \mathbf{T} ,

$$0 = \lambda^2 - (0.9 + 0.8)\lambda + (0.9 \cdot 0.8 - 0.2 \cdot 0.1)$$

$$0 = \lambda^2 - 1.7\lambda + 0.7$$

$$0 = (\lambda - 1)(\lambda - 0.7)$$

$$\lambda = \{1, 0.7\},$$

we find that the dominant eigenvalue for \mathbf{T} is $\lambda = 1$. In fact, for all transfer matrices (matrices in which the values in any column sum to 1), the dominant eigenvalue is 1. Thus, when we were calculating the normalized eigenvector, we were actually using the equation $\lambda\hat{\mathbf{x}} = \mathbf{T}\hat{\mathbf{x}}$, where λ is the dominant eigenvalue.

Note that we are only introducing the ideas of eigenvalues and eigenvectors, which can be explored with careful mathematical analysis for more general matrices. Matrix models giving oscillations in the populations have been mentioned only briefly. The properties of matrices with negative eigenvalues and corresponding eigenvectors have not been explored here. The eigenvectors for the dominant eigenvalues for the population models in this unit have positive components. Note that an eigenvector corresponding to the eigenvalue $\lambda = -1$ in Example 9.3 is

$$\begin{bmatrix} -0.5 \\ 1 \end{bmatrix}.$$

9.4 Matlab Skills

In Matlab, the `eig` function calculates both the eigenvalues and their associated eigenvectors. If we have defined a matrix `A`, then the command

```
eig(A)
```

will produce a column vector of eigenvalues. If `A` is a 3×3 matrix, then the column vector will be 3×1 . To calculate the eigenvectors as well, we need to tell Matlab that we need the second output from the `eig` function. The command

```
[v,lambda] = eig(A)
```

will output two matrices: the second, named `lambda`, contains the eigenvalues along the diagonal and the first, named `v`, contains the eigenvectors that correspond to each of the eigenvalues. The first column of `v` contains the eigenvector that corresponds with the eigenvalue shown in `lambda(1,1)`. The second column of `v` contains the eigenvector that corresponds with the eigenvalue shown in `lambda(2,2)` and so on with the other columns of `v`.

Thus, if we wanted to find the eigenvalues and corresponding eigenvectors of

$$A = \begin{bmatrix} 1 & 4 \\ 0.5 & 0 \end{bmatrix},$$

we could use the following commands in the command window:

```

Command Window
>> A = [1 4; 0.5 0]
A =
    1.0000    4.0000
    0.5000     0

>> eig(A)
ans =
     2
    -1

>> [v,lambda] = eig(A)
v =
    0.9701   -0.8944
    0.2425    0.4472

lambda =
     2     0
     0    -1

```

We see that the eigenvalues are $\lambda = \{2, -1\}$, matching what we found in Example 9.3. The dominant eigenvalue is $\lambda = 2$, which is shown in `lambda(1,1)`. Note that Matlab always displays the dominant eigenvalue in the first row, first column. We look to the first column of `v` to get the eigenvector corresponding to the dominant eigenvalue. Matlab tells us that this is

$$\begin{bmatrix} 0.9701 \\ 0.2425 \end{bmatrix}.$$

You might notice that this eigenvector does not match the one we found in Example 9.7. However, recall that eigenvectors are not unique; rather, only the normalized eigenvector is unique. Let us normalize the eigenvector corresponding to the dominant eigenvalue. To do this in Matlab, we divide the eigenvector by the sum of the entries in the eigenvector, which we can obtain by using the function `sum`:

```

Command Window
>> v(:,1)/sum(v(:,1))
ans =
    0.8000
    0.2000

```

Now, this normalized eigenvector matches the normalized eigenvector for the dominant eigenvalue we found in Example 9.7.

Now that we know how to find eigenvalues and normalized eigenvectors, we would like to see how eigenvectors change when we modify values in the transfer or Leslie matrices. For this, we will make use of loops.

Suppose that we know that the Leslie matrix

$$A = \begin{bmatrix} 0 & 2 & 3 \\ 0.5 & 0 & 0 \\ 0 & 0.25 & 0 \end{bmatrix}$$

models a population that contains three age classes: hatchlings, juveniles, and adults. Suppose that we wanted to explore how changing the juvenile fecundity changes the long-term population structure (i.e., the eigenvector associated with the dominant eigenvalue). We can construct a *for* loop, to loop through the juvenile fecundity values we want to evaluate and then display the results in a table or graph. Let us look at the following set of juvenile fecundity values:

$$a_{1,2} = \{0.1, 0.2, 0.5, 1.5, 2, 2.5, 3, 4\}.$$

Below is an m-file that finds the dominant eigenvalue and corresponding normalized eigenvector for **A** given each juvenile fecundity value. The m-file constructs a table of results and plots the long-term population structure against the juvenile fecundity:

```

LeslieFecundity.m
1  % Filename: LeslieFecundity.m
2  % M-file to
3  %     - Find the dominant eigenvalue and corresponding
4  %     - eigenvector for an array of juvenile fecundities
5  %     - Print out a table of the results
6  %     - Print out results graphically
7
8  % Print out the header for the table
9  fprintf('Juvenile   Dominant   Proportion Structure   \n')
10 fprintf('Fecundity Eigenvalue Hatchlings Juveniles Adults\n')
11 fprintf('-----\n')
12
13 % Array of juvenile fecundity values
14 f = [0.1 0.2 0.5 1.5 2 2.5 3 4];
15
16 % Start the loop
17 for i = 1:length(f) % loop thru length of f vector
18

```

```

19 % Construct Leslie matrix with appropriate juvenile fecundity
20 A = [ 0 f(i) 3 ;
21       0.5 0 0 ;
22       0 0.25 0 ];
23
24 % Get eigenvalues and eigenvectors
25 [v,lambda] = eig(A);
26
27 % Find dominant eigenvalue in lambda
28 % and make note of position in lambda matrix
29 lambdavector = max(lambda); % array of eigenvalues
30 for j = 1:length(lamdavector)
31     if max(abs(lambda)) == abs(lamdavector(j))
32         loc = j; % position of dom eig in lambda matrix
33         deig = lambda(j,j); % dominant eigenvalue
34     end
35 end
36
37 % Normalize eigenvector associated with dominant eigenvalue
38 normv(:,i) = v(:,loc)/sum(v(:,loc));
39 % This creates a matrix called normv in which the
40 % ith column corresponds to the dominant eigenvector
41 % associated with the ith juvenile fecundity value
42
43 % Print these values
44 fprintf(' %3.1f ',f(i)) % juvenile fecundity value
45 fprintf(' %5.3f ',deig) % dominant eigenvalue
46 fprintf(' %5.3f ',normv(1,i)) % hatchling propotion at eq
47 fprintf(' %5.3f ',normv(2,i)) % juvenile propotion at eq
48 fprintf(' %5.3f ',normv(3,i)) % adult propotion at eq
49 fprintf('\n') % new line
50 end
51
52 % Generate graph
53 h = normv(1,:); % vector of hatchling proportions at eq
54 j = normv(2,:); % vector of juvenile proportions at eq
55 a = normv(3,:); % vector of adult proportions at eq
56 plot(f,h,'r.-',f,j,'g.-',f,a,'b.-')
57 legend('hatchlings','juveniles','adults')
58 xlabel('Juvenile Fecundity')
59 ylabel('Equilibrium Structure')

```

When this m-file is run in the command window, the output looks like the following:

Command Window				
>> LeslieFecundity				
Juvenile Fecundity	Dominant Eigenvalue	Equilibrium Structure Hatchlings	Juveniles	Adults
0.1	0.744	0.527	0.354	0.119
0.2	0.767	0.536	0.350	0.114
0.5	0.836	0.563	0.337	0.101
1.5	1.052	0.630	0.299	0.071
2.0	1.151	0.654	0.284	0.062
2.5	1.245	0.675	0.271	0.054
3.0	1.335	0.692	0.259	0.049
4.0	1.500	0.720	0.240	0.040

The graphical output of this m-file is shown in Figure 9.1.

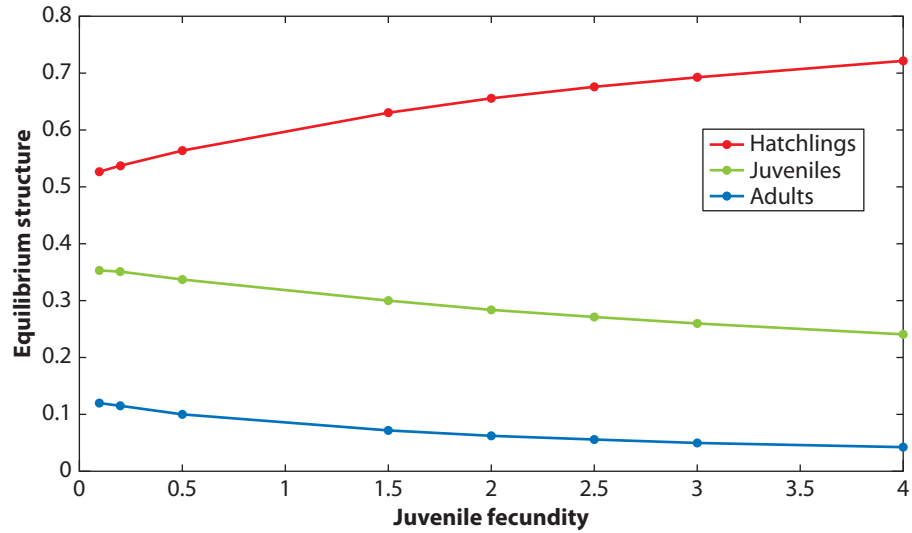


Figure 9.1 Plot generated from the m-file LeslieFecundity.m.

9.5 Exercises

For the Leslie matrices in Exercises 9.1 to 9.6,

- find the dominant eigenvalue,
- find the normalized eigenvector corresponding to the dominant eigenvalue, and
- interpret the values found in (a) and (b) biologically.

9.1 $\begin{bmatrix} 0.7 & 0.9 \\ 0.6 & 0 \end{bmatrix}$

9.2 $\begin{bmatrix} 0.5 & 0.9 \\ 0.4 & 0 \end{bmatrix}$

9.3 $\begin{bmatrix} 2 & 4 \\ 0.1 & 0.2 \end{bmatrix}$

9.4 $\begin{bmatrix} 0.2 & 0.7 \\ 0.7 & 0.2 \end{bmatrix}$

9.5 $\begin{bmatrix} 0.7 & 0.2 \\ 0.2 & 0.4 \end{bmatrix}$

9.6 $\begin{bmatrix} 0.1 & 1.2 \\ 0.4 & 0.3 \end{bmatrix}$

9.7 The Leslie matrix for an insect population is

$$\mathbf{A} = \begin{bmatrix} 0 & 20 & 0 \\ 0.1 & 0 & 0 \\ 0 & 0.2 & 0 \end{bmatrix}.$$

The age classes are 0 to 1 weeks, 2 to 3 weeks, and 4 to 5 weeks, and only insects 2 to 3 weeks old can reproduce. Notice that the time step here is 2 weeks.

(a) If

$$\mathbf{x}(0) = \begin{bmatrix} 0 \\ 100 \\ 0 \end{bmatrix}$$

specifies the initial age structure, project the population forward 2 months (or 4 time periods). Complete these calculations by hand.

(b) Show that $\mathbf{A}^3 = 2\mathbf{A}$ and that $\mathbf{A}^4 = 2\mathbf{A}^2$. Conclude that the population in each age class doubles every month.

(c) Find the long-term growth rate of the population. Is the population growing or declining?

9.8 Cattle on a large ranch are divided into calves, yearlings, and adults. Data indicate that 70% of the calves survive the first year to become yearlings, while 80% of the yearlings mature into adults. In addition, 90% of adults survive a given year, and an adult female produces a single calf each year. Construct the Leslie matrix, assuming that we census the population after reproduction and count only females.

9.9 A population of insects is divided into two stage categories. The females in the first category or stage produce on average 2 female offspring and have a survival rate of 25% to stage 2. The females in stage 2 produce on average 5 female offspring and die after one time period in stage 2.

(a) If the population were to exist for a long time with the above-mentioned conditions staying the same, what would the long-term growth rate of the population be per time period? If at time 150 the population of insects had reached the long-term growth rate with 1 million females present, approximately how many females would be present at time 151?

(b) the population were to exist for a long time with the above-mentioned conditions staying the same, approximately what fraction of the population would be in each of the two stages?

9.10 A population fits the Leslie matrix model with three life stages. The dominant eigenvalue is computed to be 0.3, and a corresponding eigenvector is

$$\begin{bmatrix} 3 \\ 7 \\ 2 \end{bmatrix}.$$

If at time step 400 the population has reached the long-term growth rate with 1200 individuals, how many individuals will be in each class at time step 401?

9.11 A population fits the Leslie matrix model with four life stages. The dominant eigenvalue is computed to be 1.2, and a corresponding eigenvector is

$$\begin{bmatrix} 3 \\ 7 \\ 10 \\ 2 \end{bmatrix}.$$

If at time step 500 the population has reached the long-term growth rate with 6400 individuals, how many individuals will be in each class at time step 501?

- 9.12 (From [29]) Suppose that the female animals in a population live 3 years. The first year, they are immature and do not reproduce. The second year, they are adolescent and reproduce at a rate of 0.8 female offspring per female individual. The last year, they are adults and produce 3.5 female offspring per female individual. Further suppose that 80% of the first-year females survive to become second-year females and that 90% of second-year females survive to become third-year females. All third-year females die. We are interested in modeling only the female portion of this population.
- Construct the Leslie matrix.
 - Find the long-term growth rate for the population. Is the population growing or declining?
 - Suppose that a population of 100 first-year females are released into a study area along with a sufficient number of males for reproductive needs. Track the female population over 10 years. Construct a table to display the population structure over the 10 years.
 - Find the long-term structure of the population.
- 9.13 (From [29]) In an attempt to save the endangered northern spotted owl, the U.S. Fish and Wildlife Service imposed strict guidelines for the use of 12 million acres of Pacific Northwest forest. This decision led to a national debate between the logging industry and environmentalists. Mathematical ecologists have created a mathematical model to analyze population dynamics of the northern spotted owl by dividing the female owl population into three categories: juvenile (up to 1 year old), subadult (1 to 2 years old), and adult (over 2 years old). The female owl population can be modeled by the Leslie matrix model:

$$\begin{bmatrix} j(t+1) \\ s(t+1) \\ a(t+1) \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0.33 \\ 0.18 & 0 & 0 \\ 0 & 0.71 & 0.94 \end{bmatrix} \begin{bmatrix} j(t) \\ s(t) \\ a(t) \end{bmatrix}.$$

- If there are currently 4000 female northern spotted owls made up of 900 juveniles, 500 subadults, and 2600 adults, use Matlab to determine the total number of female owls for each of the next 5 years. Round each answer to the nearest whole number.
 - Using Matlab, determine the long-term growth rate of the population. What can we conclude about the long-term survival of the northern spotted owl?
 - Notice that only 18% of the juveniles become subadults. Assuming that, through better habitat management, this number could be increased to 40%, rework part (b). What can we conclude about the long-term survival of the northern spotted owl if the habitat is improved enough to increase juvenial survival?
- 9.14 (From [47]) Showing that a model is correct can be difficult. Often it is much easier to show that a model is incorrect. Consider the following model that has been proposed [8] to describe the growth of redwoods (*Sequoia sempervirens*). Redwoods frequently live 1000 years or more. The model classifies redwoods into three stages: 0 to 200 years (young), 200 to 800 years (mature), and older than 800 years (old). A current census in a particular stand finds that currently there are 1696 young redwoods, 485 mature redwoods, and 82 old redwoods. The transition between stages over a 50-year period is given by the matrix

$$\begin{bmatrix} 12 & 26 & 6 \\ 0.30 & 0.92 & 0 \\ 0 & 0.18 & 0.67 \end{bmatrix}.$$

Trace this stand of trees through five time steps (five 50-year periods for a total of 250 years) and explain how we know that this model cannot possibly be correct.