maturation rate of immature females (s_{MI}) depends on the fraction of the population that is affected (u_I) as well as the reproductive value of the mature individuals that are produced by increasing the maturation rate of immature females (v_M). Performing the same calculation for s_{IC} yields $d\lambda_1/ds_{IC} = u_C v_I/(\vec{v}^T\vec{u})$. Thus, the relative value of the two options is $(d\lambda_1/ds_{MI})/(d\lambda_1/ds_{IC}) = (u_I v_M)/(u_C v_I)$. Here, we have obtained general insights without actually specifying the elements of the left and right eigenvectors.

We can proceed further numerically, using the reproductive values obtained earlier along with the stable class distribution, $\vec{u} = (0.04, 0.23, 0.61, 0.12)$. In this case,

$$\left(\frac{d\lambda_1/ds_{MI}}{d\lambda_1/ds_{IC}}\bigg|_{\substack{s_{MI}=0.08\\ s_{IC}=0.92}}\right) = \frac{(0.23)(1.5)}{(0.04)(1.1)} \approx 7.8.$$

Thus, increasing the maturation rate of immature females (s_{MI}) is nearly eight times more effective at increasing the long-term growth rate of the population than increasing the maturation rate of calves. This makes sense because the maturation rate is so low ($s_{MI} = 0.08$) that it represents a more severe bottleneck to the growth of the population.

10.6 Age-Structured Models—The Leslie Matrix

Age structure is a special type of class structure that is important enough to warrant a separate section of its own. Nearly all populations have some important component of age structure, and the transition matrices of all age-structured models have the same special form. This type of matrix is referred to as a Leslie matrix, after P. H. Leslie (see Caswell 2001 for a discussion), who was one of the first to analyze this form of class-structured model.

10.6.1 Construction of Age-Structured Models

Let us construct an age-structured model for the females of the three-spine stickleback, a freshwater fish. Sticklebacks are temperate fish with a distinctly seasonal reproductive pattern, and therefore it makes sense to measure age in this species in years. Female sticklebacks tend not to live more than four years, and therefore we will build a model that keeps track of the number of individuals that are 1, 2, 3, and 4 years old (i.e., $n_1(t)$, $n_2(t)$, $n_3(t)$, and $n_4(t)$). We will census the population at the beginning of the season, before reproduction occurs. (This is an arbitrary choice, and many demographic models census immediately after reproduction.)

The number of 1-year-old sticklebacks at the beginning of the next season is equal to the number of offspring produced by all individuals this year, multiplied by the probability that an offspring survives to reach age 1:

$$n_1(t+1) = n_1(t)\, m_1 + n_2(t)\, m_2 + n_3(t)\, m_3 + n_4(t)\, m_4, \tag{10.14a}$$

where m_i is the expected number of female offspring produced by an i-year-old female that survive to become 1-year-olds in the next season. Similarly, the number of 2-year-old sticklebacks at the beginning of next season is equal to the number of 1-year-olds this year, multiplied by the probability that an individual survives year 1 to become a 2-year-old, p_1:

$$n_2(t+1) = n_1(t)\, p_1. \tag{10.14b}$$

This same principle applies for 3- and 4-year old sticklebacks; i.e.,

$$n_3(t+1) = n_2(t)\, p_2, \tag{10.14c}$$
$$n_4(t+1) = n_3(t)\, p_3, \tag{10.14d}$$

where p_i is the probability that an individual survives age class i.

Equations (10.14a)–(10.14d) can be written in matrix form as

$$\begin{pmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \\ n_4(t+1) \end{pmatrix} = \mathbf{L} \begin{pmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ n_4(t) \end{pmatrix}, \tag{10.15}$$

where

$$\mathbf{L} = \begin{pmatrix} m_1 & m_2 & m_3 & m_4 \\ p_1 & 0 & 0 & 0 \\ 0 & p_2 & 0 & 0 \\ 0 & 0 & p_3 & 0 \end{pmatrix} \tag{10.16}$$

is the Leslie matrix. Figure 10.6 illustrates an example of the dynamics of the stickleback population.

> A *Leslie matrix* describes an age-structured population; surviving individuals always move to the next age class and can give birth to individuals in the first age class.

Leslie matrices always have the form of (10.16), where the top row of the matrix is the effective fecundity of individuals of each age class, and all other rows contain one element p_i. With age-structure, all individuals must pass through each class in succession, and assuming that time is measured in terms of the age classes, an individual must move on to the next class every time step. Thus, the survival probabilities p_i enter the matrix in the cells immediately below the diagonal. The elements of Leslie matrices are often referred to as the life-history parameters of the model.

10.6.2 Analysis of Age-Structured Models

The special form of Leslie matrices allows us to write its characteristic polynomial in a pleasingly simple form (Box 10.3):

$$1 = \sum_{i=1}^{n} \frac{l_i m_i}{\lambda^i}, \tag{10.17}$$

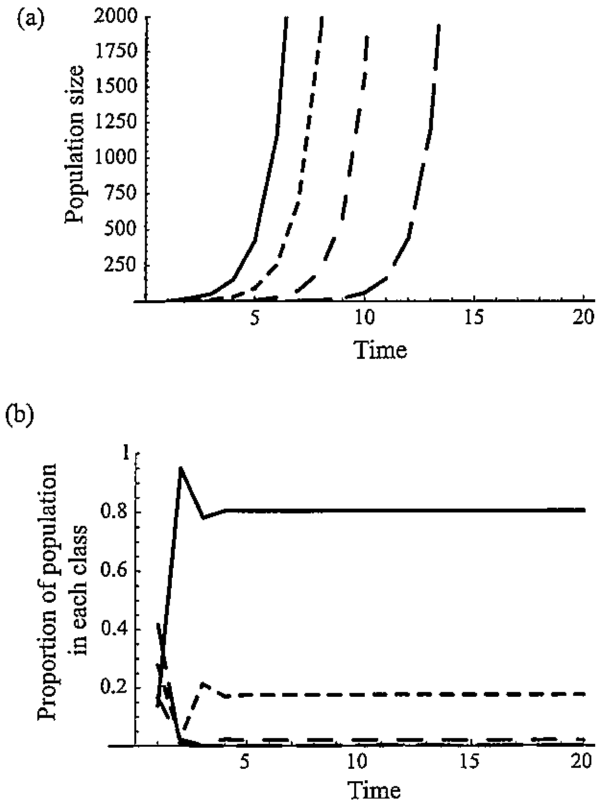

Figure 10.6: Growth of each age class of sticklebacks. Model (10.16) is iterated for a stickleback population. The 1-year old class is depicted by the solid line, and 2-, 3-, and 4-year old classes are depicted by lines with increasingly long dashes. (a) Population size of each age class. (b) Proportion of the population in each age class (the 4-year-old class is too rare to appear in the figure). Parameter values: $m_1 = 2$, $m_2 = 3$, $m_3 = 4$, $m_4 = 4$, $p_1 = 0.6$, $p_2 = 0.3$, and $p_3 = 0.1$.

where n is the number of age classes, $l_i = p_1 p_2 \ldots p_{i-1}$ is the probability that an individual survives until age class i, and $l_1 = 1$ because we defined the fecundities m_i as the number of offspring that survive to age 1. Regardless of the number of age classes, the n eigenvalues λ of a Leslie matrix are the n roots of equation (10.17).

Equation (10.17) is sometimes referred to as the Euler-Lotka equation. It features prominently in life-history theory, which is devoted to understanding the evolution of age-specific patterns of fecundity and survival (Roff 1992; Stearns 1992; Charlesworth 1994). The Euler-Lotka equation also provides an alternative way of calculating the long-term growth of a population, by solving (10.17) for the largest root λ_1. If the population were not growing in size ($\lambda_1 = 1$), then the expected lifetime reproductive success of a newborn individual, $\Sigma_{i=1}^{n} l_i m_i$, would be one—that is, each individual would exactly replace itself. The Euler-Lotka equation shows us how to generalize this statement for populations that are growing or shrinking in size. Now, the expected lifetime reproductive success of a newborn individual, discounted by the amount the population has grown from when it was born until it reaches age i, $\Sigma_{i=1}^{n} l_i m_i / \lambda_1^i$, will equal one.

For our model of sticklebacks, equation (10.17) can be written out as

$$1 = \lambda^{-1} l_1 m_1 + \lambda^{-2} l_2 m_2 + \lambda^{-3} l_3 m_3 + \lambda^{-4} l_4 m_4, \tag{10.18a}$$

or

$$1 = \lambda^{-1} m_1 + \lambda^{-2} p_1 m_2 + \lambda^{-3} p_1 p_2 m_3 + \lambda^{-4} p_1 p_2 p_3 m_4. \tag{10.18b}$$

Box 10.3. The Characteristic Polynomial of Leslie Matrices

Suppose we have a Leslie matrix with n age classes:

$$\mathbf{L} = \begin{pmatrix} m_1 & m_2 & m_3 & \cdots & m_n \\ p_1 & 0 & 0 & \cdots & 0 \\ 0 & p_2 & 0 & \cdots & 0 \\ \vdots & & \ddots & \ddots & 0 \\ 0 & 0 & 0 & p_{n-1} & 0 \end{pmatrix}. \tag{10.3.1}$$

From Definition (P2.7) of Primer 2, any eigenvalue λ of the matrix $\mathbf{L}$ must satisfy

$$\mathrm{Det}(\mathbf{L} - \mathbf{I}\lambda) = 0. \tag{10.3.2}$$

Because of the relatively simple form of Leslie matrices we can explicitly calculate (10.3.2) using the general definition for determinants (P2.18) in Primer 1. We get

$$(-1)^0(m_1-\lambda)(-\lambda)^{n-1} + (-1)^1 m_2 p_1(-\lambda)^{n-2} + (-1)^2 m_3 p_1 p_2(-\lambda)^{n-3} + \cdots$$
$$+ (-1)^{n-1} m_n p_1 p_2 \dots p_{n-1}(-\lambda)^0 = 0. \tag{10.3.3a}$$

We can define the probability of surviving from birth to age class i as $l_i = p_1 p_2 \dots p_{i-1}$, with $l_1 = 1$, allowing us to write equation (10.3.3) as

$$(-\lambda)^n + m_1(-\lambda)^{n-1} + (-1)^1 m_2 l_2(-\lambda)^{n-2} + (-1)^2 m_3 l_3(-\lambda)^{n-3} + \cdots + (-1)^{n-1} m_n l_n = 0. \tag{10.3.3b}$$

Factoring out $(-\lambda)^n$ then gives

$$1 - m_1\lambda^{-1} - m_2 l_2 \lambda^{-2} - m_3 l_3 \lambda^{-3} - \cdots - m_n l_n \lambda^{-n} = 0, \tag{10.3.3c}$$

or

$$1 = \sum_{i=1}^{n} \frac{l_i m_i}{\lambda^i}. \tag{10.3.3d}$$

In some demographic models, individuals survive in the last age class for multiple censuses, which adds an entry p_n to the last row and column of the Leslie matrix:

$$\mathbf{L} = \begin{pmatrix} m_1 & m_2 & m_3 & \cdots & m_n \\ p_1 & 0 & 0 & \cdots & 0 \\ 0 & p_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & 0 \\ 0 & 0 & 0 & p_{n-1} & p_n \end{pmatrix}. \tag{10.3.4}$$

(continued)

Box 10.3 (continued)

Revising the calculations in (10.3.3), the eigenvalues now solve

$$1 = \left(\sum_{i=1}^{n-1} \frac{l_i m_i}{\lambda^i}\right) + \left(\frac{l_n m_n}{\lambda^n}\right)\left(\frac{\lambda}{\lambda - p_n}\right). \quad (10.3.5)$$

If the last age class has zero fecundity ($m_n = 0$), then the long-term growth rate is unaffected by individuals in the oldest age class, and equation (10.3.5) reduces to (10.3.3d).

It is not possible to obtain any meaningful, explicit expression for the population growth rate by solving equation (10.18) for λ, but we can easily evaluate it for certain parameter values. For example, suppose that 1-year-olds produce an average of two female offspring that survive to the next year, 2-year-olds produce three such offspring, and 3- and 4-year-olds both produce four surviving female offspring (i.e., $m_1 = 2$, $m_2 = 3$, $m_3 = 4$, and $m_4 = 4$). Further, suppose that the age-specific survival probabilities are $p_1 = 0.6$, $p_2 = 0.3$, and $p_3 = 0.1$. Equation (10.18b) is then

$$1 = 2\lambda^{-1} + 1.8\lambda^{-2} + 0.72\lambda^{-3} + 0.072\lambda^{-4}. \quad (10.18c)$$

All eigenvalues of the Leslie matrix must satisfy (10.18c). *Mathematica* is readily able to solve (10.18c), giving the four eigenvalues $\lambda_1 = 2.75$, $\lambda_2 = -0.3 + 0.3i$, $\lambda_3 = -3 - 0.3i$, and $\lambda_4 = -0.14$. The long-term growth rate of this stickleback population is therefore $\lambda_1 = 2.75$.

The special form of Leslie matrices results in the dominant right and left eigenvectors (which represent the stable age distribution and the age-specific reproductive values respectively) having a very specific form as well, regardless of the number of age classes. Box 10.4 shows that the proportion of the population in each of the age classes at the stable age distribution (i.e., the elements of the dominant right eigenvector) is

$$u_x = \frac{l_x \lambda_1^{-(x-1)}}{\sum_{i=1}^{n} l_i \lambda_1^{-(i-1)}}. \quad (10.19)$$

For our stickleback population, equation (10.19) predicts 80.4% 1-year olds, 17.5% 2-year olds, 2% 3-year-olds, and 0.06% 4-year-olds over the long term, using the leading eigenvalue $\lambda = 2.75$ and the above parameter values. These values agree perfectly with simulation results (Figure 10.6b). The approach of Box 10.4 can also be used (see Problem 10.4) to show that the reproductive value of each age class (i.e., the elements of the dominant left eigenvector) measured relative to the reproductive value of newborns (ν_1) satisfies

$$\frac{\nu_x}{\nu_1} = \frac{\lambda_1^{x-1}}{l_x} \sum_{i=x}^{n} \frac{l_i m_i}{\lambda_1^i}. \quad (10.20)$$

Box 10.4: The Right Eigenvector Associated with the Leading Eigenvalue of a Leslie Matrix

Multiplying the n-dimensional Leslie matrix (10.3.1) in Box 10.3 on the right by the right eigenvector $\tilde{\vec{u}}$ gives $L\,\tilde{\vec{u}} = \lambda\,\tilde{\vec{u}}$ (the reason for labeling the eigenvector as $\tilde{\vec{u}}$ instead of $\vec{u}$ will become apparent shortly). This describes a system of n equations, and except for the first equation, these equations have the form:

$$\tilde{u}_{x-1}\,p_{x-1} = \lambda\tilde{u}_x. \tag{10.4.1}$$

Solving (10.4.1) for $\tilde{u}_x$ gives

$$\tilde{u}_x = \frac{\tilde{u}_{x-1}\,p_{x-1}}{\lambda}. \tag{10.4.2}$$

We can also use (10.4.2) to define $\tilde{u}_{x-1}$ in terms of $\tilde{u}_{x-2}$, which we can plug into (10.4.2) to write $\tilde{u}_x$ in terms of $\tilde{u}_{x-2}$. Continuing to work recursively backward, we can write a general formula for $\tilde{u}_x$ in terms of $\tilde{u}_1$:

$$\tilde{u}_x = \tilde{u}_1 l_x \lambda^{-(x-1)}. \tag{10.4.3}$$

Expression (10.4.3) gives all the elements of the stable age distribution, relative to age 1. We usually prefer to have the elements of the right eigenvector represent the proportion of the population in age class x, and we can obtain this scaled version of (10.4.3) by dividing (10.4.3) by the sum of all the elements. Using u to denote this scaled version of (10.4.3), we obtain

$$u_x = \frac{l_x \lambda^{-(x-1)}}{\sum_{i=1}^{n} l_i \lambda^{-(i-1)}}. \tag{10.4.4}$$

If individuals survive in the last age class for multiple censuses according to the Leslie matrix (10.3.4), then the last in the system of equations must be revised to:

$$\tilde{u}_{n-1}p_{n-1} + \tilde{u}_n p_n = \lambda\tilde{u}_n, \tag{10.4.5}$$

whose solution is

$$\tilde{u}_n = \frac{\tilde{u}_{n-1}p_{n-1}}{\lambda - p_n}. \tag{10.4.6}$$

Plugging in (10.4.3) and dividing by the sum of the $\tilde{u}_x$ gives the right eigenvector in terms of the proportion in each age class:

$$u_x = \frac{l_x \lambda^{-(x-1)}}{\left(\sum_{i=1}^{n-1} l_i \lambda^{-(i-1)}\right) + l_n \lambda^{-(n-2)}(\lambda - p_n)^{-1}} \quad \text{for } x < n \tag{10.4.7}$$

(continued)

Box 10.4 (continued)

and

$$u_n = \frac{l_n \lambda^{-(n-2)}(\lambda - p_n)^{-1}}{\left(\sum_{i=1}^{n-1} l_i \lambda^{-(i-1)}\right) + l_n \lambda^{-(n-2)}(\lambda - p_n)^{-1}}$$

For our stickleback population, equation (10.20) predicts reproductive values of $v_1=1$, $v_2=1.25$, $v_3=1.5$, and $v_4=1.45$. From these numbers we can see that a 3-year-old stickleback contributes more to the growth of the population than a stickleback of any other age. It makes sense that 3-year-olds have a higher reproductive value than 1- or 2-year-olds, because 3-year-olds have survived to the age of highest fecundity. It also makes sense that 3-year-olds have a higher reproductive value than 4-year-olds, because 3-year-olds have some chance of surviving to age 4 and reproducing again, whereas all 4-year-olds are assumed to die over the following year.

Rule 10.2: Long-Term Growth of an Age-Structured Population

An age-structured population with n age classes is described by a Leslie matrix:

$$\mathbf{L} = \begin{pmatrix} m_1 & m_2 & m_3 & \cdots & m_n \\ p_1 & 0 & 0 & \cdots & 0 \\ 0 & p_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & 0 \\ 0 & 0 & 0 & p_{n-1} & 0 \end{pmatrix}.$$

- The leading eigenvalue of a Leslie matrix is the largest root of $1 = \Sigma_{i=1}^{n} l_i m_i / \lambda^i$, which describes the long-term growth of the population.
- In the long term, the proportion of individuals in age class x is

$$u_x = \frac{l_x \lambda_1^{-(x-1)}}{\sum_{i=1}^{n} l_i \lambda_1^{-(i-1)}}$$

(the elements of the dominant right eigenvector), which describes the stable age distribution.

(continued)

Rule 10.2 *(continued)*

- In the long term, the reproductive value of individuals in age class x relative to the youngest age class is

$$\frac{v_x}{v_1} = \frac{\lambda_1^{x-1}}{l_x}\sum_{i=x}^{n}\frac{l_i m_i}{\lambda_1^i}$$

(the elements of the dominant left eigenvector).

10.6.3 The Effect of Life-History Parameters on Population Growth in Age-Structured Models

Now suppose that we want to know how a change in some life-history parameter in the Leslie matrix affects the population growth rate. We examined this sort of question in section 10.5, where we found that equation (10.13) describes the effect of changing a parameter, z, on the long-term growth rate. Because of the very special form of Leslie matrices, equation (10.13) can be greatly simplified. In fact, there are only two kinds of life-history parameters in age-structured models: age-specific survival probabilities and age-specific fecundities. Here we simplify equation (10.13) for each.

Suppose first that the parameter of interest is the age-specific survival probability p_i. The matrix of derivatives in (10.13) contains zeros everywhere except for a 1 in column i of row $i+1$. Carrying out the matrix multiplication in (10.13) gives

$$\frac{d\lambda}{dp_i} = \frac{u_i v_{i+1}}{E[v_k]}, \tag{10.21}$$

where $E[v_k] = \vec{v}^T\vec{u} = u_1v_1 + u_2v_2 + \cdots + u_nv_n$ is the frequency of each age class at the stable age distribution (u_i) times its reproductive value (v_i), which is just the long-term average reproductive value of the population. Equation (10.21) has a simple interpretation. A proportion u_i of the population is in age class, i, and increasing their survival probability creates more age $i+1$ individuals, each of which has reproductive value v_{i+1}. The total effect on the growth rate is therefore the product of the two, standardized by the average reproductive value of the population.

Suppose next that the parameter of interest is the age-specific fecundity m_i. The matrix of derivatives in (10.13) now contains zeros everywhere except for a one in column i of row 1. Carrying out the matrix multiplication in (10.13) then gives

$$\frac{d\lambda}{dm_i} = \frac{u_i v_1}{E[v_k]}. \tag{10.22}$$

TABLE 10.1
The effect of life history parameters on stickleback population growth. $d\lambda/dx$ describes the sensitivity of the eigenvalue to the parameter x. If the parameter x is increased by a small amount, Δx, the long-term growth rate is altered by $\Delta x\,(d\lambda/dx)$.

$$\frac{d\lambda}{dp_1} = 0.18, \quad \frac{d\lambda}{dp_2} = 0.27, \quad \frac{d\lambda}{dp_3} = 0.31$$

$$\frac{d\lambda}{dm_1} = 0.14, \quad \frac{d\lambda}{dm_2} = 0.18, \quad \frac{d\lambda}{dm_3} = 0.22, \quad \frac{d\lambda}{dm_4} = 0.21$$

Equation (10.22) has an analogous interpretation to (10.21). A proportion u_i of the population is in age class i, and increasing their fecundity will create more age 1 individuals, each of which has reproductive value v_1. The total effect on the growth rate is again the product of the two, standardized by the average reproductive value of the population.

With equations (10.21) and (10.22), we can now return to our sticklebacks and use the right and left eigenvectors that we obtained earlier to examine the effect of all life history parameters on the growth rate of the population. Table 10.1 presents these results, illustrating that an increase in the survival probability from age 3 to age 4 (i.e., p_3) has the greatest impact on the population growth rate. Even so, increasing p_3 by 1% is expected to lead to only a 0.31% increase in the growth rate of the population. This result suggests that it would be difficult to substantially improve the growth rate of the population by targeting conservation efforts on the survival of only one age class.

Before considering another example, it is worth mentioning that equations (10.21) and (10.22) feature prominently in life-history theory. Life-history theory has been developed to explain how natural selection has shaped the way individuals invest their resources in fecundity and survival at different ages. The underlying assumption is that an individual has limited resources at its disposal, and therefore it must trade off fecundity and/or survival at each age with fecundity and/or survival at other ages. We might expect that natural selection would favor the best balance in this tradeoff. Much of life-history theory has assumed that the "best" balance is the one that maximizes the long-term population growth rate λ_1 (we'll have more to say on this in Chapter 12). To predict the best balance, equations (10.21) and (10.22) are used to evaluate the effect of investing in age-specific survival versus reproduction. These equations are often written in a more explicit form, using equations (10.19) and (10.20) for the elements of the right and left eigenvectors:

$$\frac{d\lambda_1}{dp_i} = \frac{\sum_{j=i+1}^{n} \lambda_1^{-(j-1)} l_j m_j}{p_i T} \tag{10.23}$$

and

$$\frac{d\lambda_1}{dm_i} = \frac{\lambda_1^{-(i-1)} l_i}{T}, \tag{10.24}$$

where $T = \sum_{x=1}^{n} \sum_{j=x}^{n} l_j m_j \lambda_1^{-j} = \sum_{x=1}^{n} x\, l_x m_x \lambda_1^{-x}$.

Example: Demography of the Canadian Population

Let us now see how Leslie matrices can be used to understand more complex age-structured populations by modeling the demographic trends in the human population of Canada (data are from Statistics Canada, catalogues 84–210, 84–211, 91–213-XPB, and from the U.S. Census Bureau). Figure 10.7 presents census data for the total population size of Canada at five-year intervals, from 1950 to 2005. The population has more than doubled in size over this period, from 14.0 million in 1950 to 32.8 million in 2005. If we use the discrete-time equation $n(2005) = n(1950)\,\lambda^{55}$ as a model of population growth, where λ is the growth rate per year, then we can estimate the annual growth rate as $\lambda = 1.0156$ (i.e., the population has grown by approximately 1.56% per year).

The above estimate for the population growth rate can be used to predict the total population size at different times in the future. This approach, however, ignores the pronounced differences in age structure of the population over the last half of the twentieth century (Figure 10.8). 1951 was near the beginning of the "baby boom" (1946–1964), and more individuals were in the (0–5)-year-old age class than in any other class. In contrast, the most common age class in 1991 was the (30–35)-year-old class. Therefore, it would be much more accurate to have a model that predicts the future age distribution, in addition to the total population size. Leslie matrix models are perfect for this task.

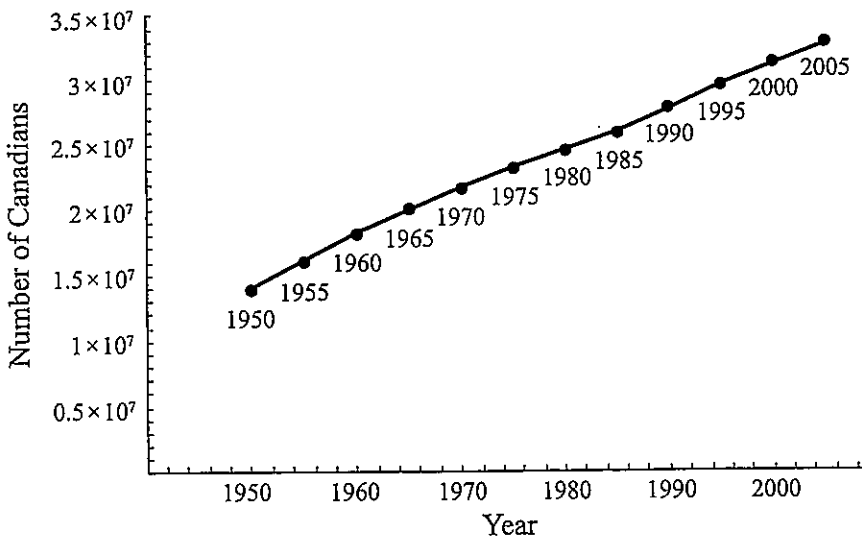

Figure 10.7: The total population size of Canada over time. Based on Table 001 in U.S. Census Bureau, Total Midyear Population, International Data Base (IDB), (http://www. census.gov/ipc/www/idbprint.html release; date April 26, 2005).

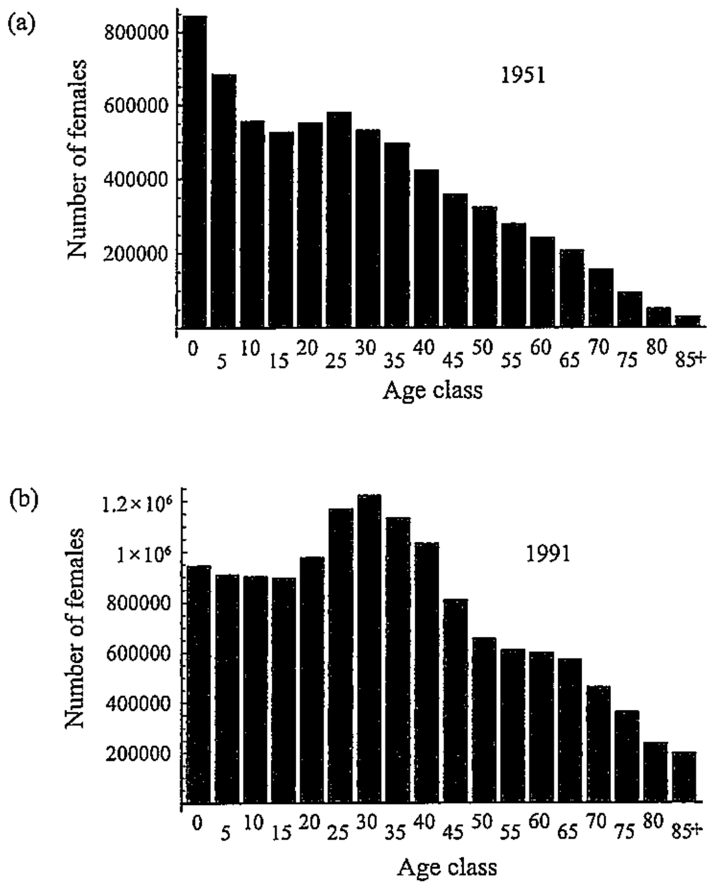

Figure 10.8: The number of females in Canada by age class. (a) 1951 (from Table 004 in U.S. Census Bureau, Enumerated and Adjusted Census Data, International Data Base (IDB), http://www.census.gov/ipc/www/idbprint.html, release date: April 26, 2005). (b) 1991 (see Table 10.2b). Age classes are grouped into five-year intervals.

We will break down the age classes of the Canadian population into five-year intervals. We chose five-year intervals because the census takes place every five years. Choosing age categories whose lengths match the time between censuses ensures that all individuals either die or move to the next age class between censuses. This causes the transition matrix to have the form of a Leslie matrix (10.3.1).

In our model, we keep track of females only. The number of females in each age class is expected to change according to the matrix recursion

$$\begin{pmatrix} n_{0-4}(t+5) \\ n_{5-9}(t+5) \\ n_{10-14}(t+5) \\ \vdots \\ n_{85+}(t+5) \end{pmatrix} = \mathbf{L} \begin{pmatrix} n_{0-4}(t) \\ n_{5-9}(t) \\ n_{10-14}(t) \\ \vdots \\ n_{85+}(t) \end{pmatrix}, \tag{10.25a}$$

where

$$\mathbf{L} = \begin{pmatrix} m_{0-4} & m_{5-9} & m_{10-14} & \cdots & m_{85+} \\ p_{0-4} & 0 & 0 & \cdots & 0 \\ 0 & p_{5-9} & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & 0 & p_{80-84} & p_{85+} \end{pmatrix} \tag{10.25b}$$

The elements of the Leslie matrix (10.25b) are the survival probabilities and fecundities over five-year intervals.

The structure of (10.25b) is slightly different from that of (10.3.1) in that it has an additional element in the bottom right corner. This stems from the fact that the Canadian census groups all individuals over 85 into one class, and such individuals can continue to live through more than one census. This element causes only a slight adjustment to the methods, as discussed in Boxes 10.3 and 10.4.

We now need to obtain estimates for the values of all these elements. We do so using data from the 1991 census and treat the parameters in matrix (10.25b) as constants. In reality, the rates of reproduction and probabilities of survival will change over time as social mores, disease prevalence, health care, and economic conditions change.

First consider the survival probabilities. Table 10.2a gives the number of females that died in each age class in the year 1991. From this data we need to

TABLE 10.2:
Canadian mortality records. (a) The total number of female deaths by age class in 1991 (from Table 3 in Statistics Canada, *Deaths, 1991*, Catalogue 84-211). (b) The total number of females in 1991 (p. 41 in Statistics Canada, *Deaths, 1991*, Catalogue 84-211). (c) The mortality rate of females per census; column (c) was estimated from columns (a) and (b) as $1 - p_i = 1 - (1 - (a)/(b))^5$. (d) Probability of surviving from birth to age class i, $l = p_1 p_2 \ldots p_{i-1}$.

Age class	(a) Number deaths (per year)	(b) Total number of females	(c) Mortality rate (per census)	(d) Survival to age i
0–4	1344	945400	0.00709	1
5–9	155	909700	0.000852	0.993
10–14	152	901500	0.000843	0.992
15–19	345	895900	0.00192	0.991
20–24	361	976800	0.00185	0.989
25–29	556	1168800	0.00238	0.987
30–34	681	1221800	0.00278	0.985
35–39	939	1133000	0.00414	0.982
40–44	1337	1031500	0.00646	0.978
45–49	1659	807500	0.0102	0.972
50–54	2142	656600	0.0162	0.962
55–59	3275	610100	0.0266	0.946
60–64	5032	599400	0.0413	0.921
65–69	7763	571800	0.0661	0.883
70–74	9757	461700	0.101	0.825
75–79	12949	362600	0.166	0.741
80–84	14261	237900	0.266	0.618
85+	27415	197100	0.527	0.454

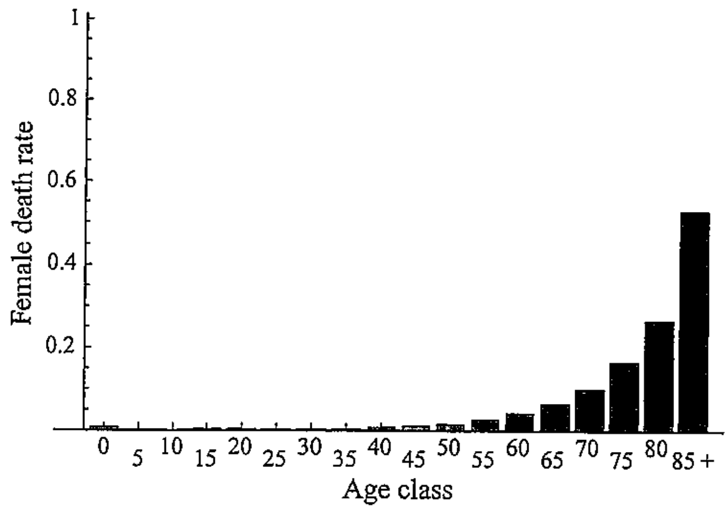

Figure 10.9: The death rate per female per five-year census period. See Table 10.2c.

calculate the probability of an individual surviving through each five-year age class. This is done by calculating the annual probability of surviving, which equals one minus the number that died divided by the number of individuals in each age class (using the columns in Table 10.2, this is 1 – (a)/(b)). The probability of surviving over a census, p_i, is given by this survival probability raised to the power five (the length of the census). The age-specific probability of dying, $1 - p_i$, over the five-year interval between censuses is illustrated in Figure 10.9 (see also Table 10.2c).

Now consider fecundity. Table 10.3 gives the total number of babies produced by Canadian females in the various age classes in 1991. From these data we need to calculate the age-specific expected number of daughters per female, over the five-year census period. This is done by first multiplying the annual number of births in Table 10.3a by the fraction of daughters and by five to obtain the total number of daughters over the census period. We then divide by the number of females in each age class to convert this into a fecundity per female. This gives the results of Table 10.3b and Figure 10.10.

Our model is now completely parameterized. The leading eigenvalue of the Leslie matrix (10.25b) can be calculated using the standard methods of Primer 2 or, more directly, by solving (10.3.5). Either way, the leading eigenvalue is $\lambda = 0.977$. Similarly, the right eigenvector can be solved using standard methods or by plugging the parameters into (10.4.7), giving $\vec{u}^T$ = (0.0495, 0.0503, 0.0515, 0.0526, 0.0537, 0.0549, 0.0560, 0.0572, 0.0583, 0.0592, 0.0600, 0.0604, 0.0602, 0.0590, 0.0564, 0.0519, 0.0443, 0.0645).

These results are very informative. Over the long term, the Canadian population is predicted to decrease in size by a factor of 0.977 every five-year period. This amounts to a 2.3% decline every census (in the absence of immigration), rather than the increase that we predicted by extrapolating from past growth (Figure 10.7). Furthermore, at the stable age distribution, the fraction of the population over age 60 is expected to equal 0.0602 + 0.0590 + 0.0564 + 0.0519 + 0.0443 + 0.0645, or 33.6%. Similarly, 21.7% are expected to be over the age of

TABLE 10.3
Canadian birth records. (a) The total number of births by age class in 1991 (from Table 11 in Statistics Canada, *Births, 1991*, Catalogue 84-210). (b) The birth rate of daughters per census, obtained by multiplying (a) by the sex ratio (48.67% daughters; from Table 1 in Statistics Canada, *Births, 1991*, Catalogue 84-210), times the census period (×5), divided by the number of females (column b in Table 10.2).

Age class	(a) Total births (per year)	(b) Female birth rate (per census)
0–4	0	0
5–9	0	0
10–14	265	0.000715
15–19	24180	0.0657
20–24	80723	0.201
25–29	150024	0.312
30–34	107560	0.214
35–39	33107	0.0711
40–44	4124	0.00973
45–49	138	0.000416
50–54	0	0
55–59	0	0
60–64	0	0
65–69	0	0
70–74	0	0
75–79	0	0
80–84	0	0
85+	0	0

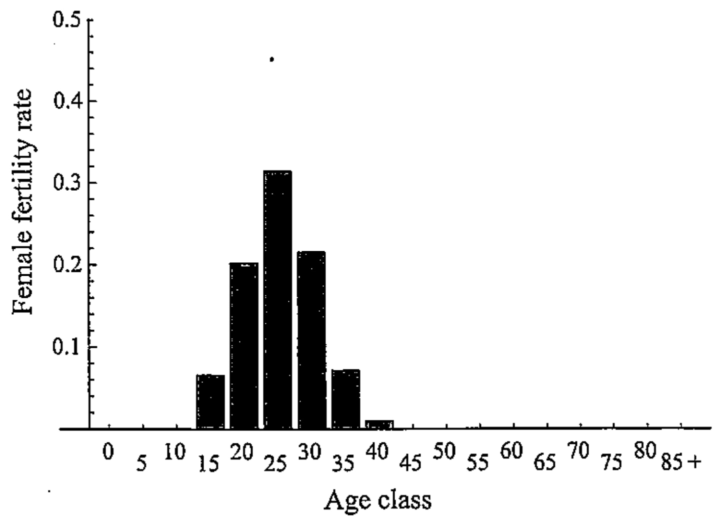

Figure 10.10: The number of daughters born per female per five-year census period. See Table 10.3b.

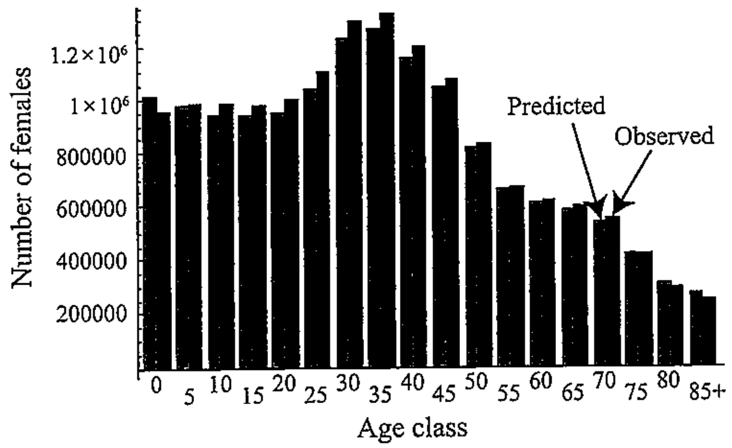

Figure 10.11: Observed and predicted age distribution. The observed age distribution of females in Canada in 1996 (black bars, from Table 1.4 in Statistics Canada, *Annual Demographic Statistics, 1996*, Catalogue 91-213-XPB) is compared with that predicted by multiplying the Leslie matrix (10.25b) with the 1991 data from Table 10.2b (gray bars).

70. If we compare these statistics with the 1991 proportions of 17.76% and 9.20%, respectively, we expect roughly twice the fraction of senior citizens at the stable age distribution. Such predictions have led to a call for the reallocation of government resources, in preparation for the medical and social infrastructure required by these age classes.

We can also iterate the Leslie matrix in *Mathematica*, starting with the number of females in each age class in the 1991 census data (Figure 10.8b). From this we can see that the Leslie matrix does reasonably well at predicting the 1996 census data, but it slightly underestimates the number in most age classes (Figure 10.11). Moreover, the predicted age distribution does differ slightly from that observed. These discrepancies are due to three main factors: (1) immigration and emigration, (2) changing values in the Leslie matrix, and (3) overly coarse age categories. In fact, the net migration rate into Canada over this time period was nearly 500,000 females (Chart 1 in Statistics Canada, *Annual Demographic Statistics, 1996*, Catalogue 91–213-XPB). Furthermore, the birth rate has continued to drop over this period, especially for women under 30.

Sometimes governmental programs aim to increase or decrease the future population size. If such a program were to focus on a particular age group in the Canadian population, which age group would be most effective to target? Interestingly, equation (10.22) reveals that it is best to focus on the most abundant age class, because all u_i are weighted by the same factor $v_1/E[v_k]$. (We can continue to apply equation (10.22) even for this Leslie matrix where p_{85+} is not zero, because the oldest age class does not reproduce; see Box 10.3.) The dominant right eigenvector shows that, in the long term, the most abundant age class will be the (55–59)-year-old age group. This result is disturbing, because females over the age of 55 are typically not physiologically capable of producing offspring. Indeed, Table 10.3b reveals that no such females reproduced in 1991. What has gone wrong? The sensitivity of the leading eigenvalue (10.22) tells us the effect on the long-term growth rate of an *absolute* change in fecundity. But fecundity cannot be changed by the same absolute amount for all age classes. More likely, family planning programs might affect fecundity in a *proportional* manner, by a factor $1 + f$ (that is, $m_i \to m_i(1+f)$). In this case, targeting individuals of age class i would increase the leading eigenvalue by $\Delta m_i \, d\lambda/dm_i = f m_i \, d\lambda/dm_i = f m_i \, u_i v_i / E[v_k]$. As a result, the most effective program would target the age class with the highest product of fecundity and abundance, $m_i \, u_i$, which is the (25–29)-year-old class.

We can also use our general results to explore the likely effects of improvements in medical care on the growth rate of the population. As the medical facilities in a country are enhanced, the population growth rate will increase. Some of the medical improvements result in a greater survival rate of young children, while others result in a greater survival rate of adults. We can use equation (10.21) to determine the different effects that these sorts of medical improvements will have on the population growth rate. To evaluate this equation, we first need to calculate the dominant left eigenvector (i.e., the reproductive value of an individual in each age class), giving $\vec{v}^T = (1, 0.984, 0.963, 0.941, 0.855, 0.634, 0.306, 0.084, 0.010, 0.00043, 0, 0, 0, 0, 0, 0, 0, 0)$. The zeroes in the last several elements reveal that females above the age 50 contribute nothing to population growth. You can then evaluate equation (10.21) for all possible i using this eigenvector. Doing so reveals that medical improvements that enhance the survival rate of newborns (i.e., (0–4)-year-olds) cause the greatest increase in the population growth rate.

Example: Calculating the Risk of Infection with HIV Using an Age-Structured Model

Age-structured models are essential in cases where we know that the parameters are likely to change dramatically with age. Although the models of HIV that we considered in previous chapters assumed that all age classes are equivalent, sexual behavior and risk factors depend strongly on age. Thus, accurate predictions of the dynamics of sexually transmitted diseases also require an age-structured model. In Supplementary Materials 10.2, we explore the age-structured model mentioned in Chapter 1 that was used by Williams et al. (2001) to estimate the age-specific risk of contracting HIV in South Africa.

10.7 Concluding Message

In this chapter we have developed techniques for constructing and analyzing a very wide variety of linear models for which the population of interest is class structured. Often, the focus is on the long-term dynamics, and in such cases, the long-term growth rate is given by the leading eigenvalue of the transition matrix. The long-term proportion in each class (the stable class distribution) is given by the right eigenvector. The long-term reproductive value of each class is given by the left eigenvector. We have also described techniques that can be used to assess how the long-term growth rate of a population is affected by a change in the number of individuals or a change in a parameter of the model (the sensitivity of the eigenvalues). Such techniques have been used, for example, to assess the efficacy of programs aimed at conserving a species.

A special form of class structure is age structure. With age structure, individuals move from one age class up to the next age class in subsequent censuses.

Age-structured models are described by a special transition matrix, called the Leslie matrix. The form of the Leslie matrix allows us to develop specific formulas for the characteristic polynomial, the eigenvectors, and the sensitivity of the eigenvalues to changes in parameters.

The range of applications of the techniques for class-structured population models is enormous. Caswell (2001) provides an excellent survey of biological examples, along with more advanced material related to such matrix models. The techniques of this chapter also prove to be invaluable when constructing evolutionary models for populations that are class structured (Charlesworth 1994; Chapter 12).

Problems

Problem 10.1: Figure 10.12 illustrates a model with three patches of plants, arranged from west to east.

Each generation, b seeds are produced, of which a fraction d disperse and $1-d$ remain on the parental patch. Of the dispersing seeds, a fraction f disperse west and $1-f$ disperse east. The parents then die and all seeds that have landed on a patch grow into plants. This model can be described by the following transition matrix:

$$\mathbf{M} = \begin{pmatrix} b\,(1-d) & b\,d\,(1-f) & 0 \\ b\,d\,f & b\,(1-d) & b\,d\,(1-f) \\ 0 & b\,d\,f & b\,(1-d) \end{pmatrix}$$

The eigenvalues and associated eigenvectors of this transition matrix are

$$\begin{array}{lll} (1) & \lambda = b\,(1-d), & \vec{u} = (1-f,\ \ 0,\ \ -f), \\ (2) & \lambda = b\,(1-d) - b\,d\sqrt{2f(1-f)}, & \vec{u} = (1-f,\ \ -\sqrt{2f(1-f)},\ \ f), \\ (3) & \lambda = b\,(1-d) + b\,d\sqrt{2f(1-f)}, & \vec{u} = (1-f,\ \ \sqrt{2f(1-f)},\ \ f), \end{array}$$

(a) At what rate will the population eventually grow? (b) In the long term, what fraction of plants inhabits each patch? (c) Explain why f affects the growth rate of the population.

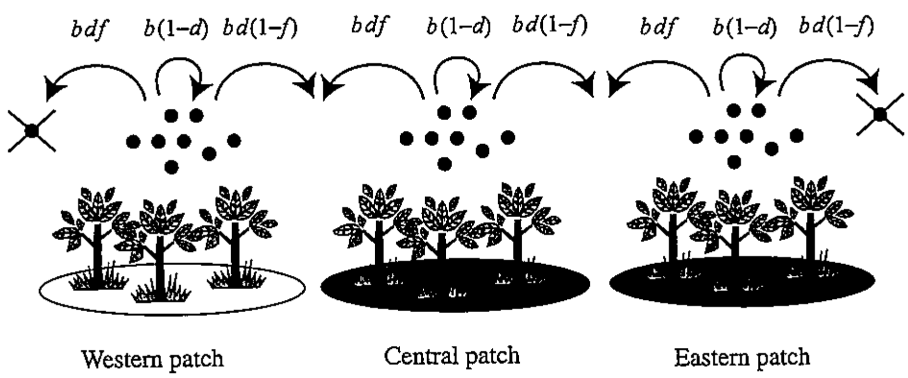

Figure 10.12: A schematic of a three-patch plant population.