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Age-Specific Population Growth

The growth in time of a female population divided into age classes is investigated using the Leslie matrix model. The limiting age distribution and growth rate of the population are determined.

PREREQUISITES: Eigenvalues and eigenvectors
Diagonalization of a matrix
Intuitive understanding of limits

INTRODUCTION

One of the most common models of population growth used by demographers is the so-called "Leslie model", developed in the nineteen forties. This model describes the growth of the female portion of a human or animal population. In this model, the females are divided into age classes of equal duration. To be specific, suppose the maximum age attained by any female in the population is L years (or some other time unit) and we divide the population into n age classes. Then each class is L/n years in duration. We label the age classes according to the following table:

Age Class	Age Interval
1	$[0,\ L/n)$
2	$[L/n,\ 2L/n)$
3	$[2L/n,\ 3L/n)$
$\vdots$	$\vdots$
$n-1$	$[(n-2)L/n,\ (n-1)L/n)$
n	$[(n-1)L/n,\ L]$

Suppose we know the number of females in each of the n classes at time $t=0$. In particular, let there be $x_1^{(0)}$ females in the first class, $x_2^{(0)}$ females in the second class, and so forth. With these n numbers we form a column vector $\mathbf{x}^{(0)}$ as follows:

$$\mathbf{x}^{(0)} = \begin{bmatrix} x_1^{(0)} \\ x_2^{(0)} \\ \vdots \\ x_n^{(0)} \end{bmatrix}.$$

We call this vector the *initial age distribution vector*.

As time progresses, the number of females within each of the n classes changes because of three biological processes: birth, death, and aging. By describing these three processes quantitatively, we shall see how to project the initial age distribution vector into the future.

The easiest way to study the aging process is to observe the population at discrete times, say $t_0, t_1, t_2, \ldots, t_k, \ldots$. The Leslie model requires that the duration between any two successive observation times be the same as the duration of the age intervals. We therefore set

$$\begin{aligned} t_0 &= 0 \\ t_1 &= L/n \\ t_2 &= 2L/n \\ &\vdots \\ t_k &= kL/n \\ &\vdots \end{aligned}$$

With this assumption, all females in the $(i+1)$st class at time t_{k+1} were in the i-th class at time t_k.

The birth and death processes between two successive observation times may be described by means of the following demographic parameters:

a_i $i = 1, 2, \ldots, n$	The average number of daughters born to a single female during the time she is in the i-th age class.
b_i $i = 1, 2, \ldots, n-1$	The fraction of females in the i-th age class that can be expected to survive and pass into the $(i+1)$st age class.

By their definitions, we have that

(i) $a_i \geq 0$ for $i = 1, 2, \ldots, n$

(ii) $0 < b_i \leq 1$ for $i = 1, 2, \ldots, n-1$.

Notice that we do not allow any b_i to equal zero, since then no females will survive beyond the i-th age class. We also assume that at least one a_i is positive so that some births occur. Any age class for which the corresponding value of a_i is positive is called a *fertile age class.*

We next define the age distribution vector $\mathbf{x}^{(k)}$ at time t_k by

$$\mathbf{x}^{(k)} = \begin{bmatrix} x_1^{(k)} \\ x_2^{(k)} \\ \vdots \\ x_n^{(k)} \end{bmatrix}$$

where $x_i^{(k)}$ is the number of females in the i-th age class at time t_k. Now, at time t_k, the females in the first age class are just those daughters born between times t_{k-1} and t_k. Thus we can write

$$\begin{Bmatrix}\text{number of}\\ \text{females}\\ \text{in class 1}\\ \text{at time } t_k\end{Bmatrix} = \begin{Bmatrix}\text{number of}\\ \text{daughters}\\ \text{born to}\\ \text{females in}\\ \text{class 1}\\ \text{between times}\\ t_{k-1} \text{ and } t_k\end{Bmatrix} + \begin{Bmatrix}\text{number of}\\ \text{daughters}\\ \text{born to}\\ \text{females in}\\ \text{class 2}\\ \text{between times}\\ t_{k-1} \text{ and } t_k\end{Bmatrix} + \cdots + \begin{Bmatrix}\text{number of}\\ \text{daughters}\\ \text{born to}\\ \text{females in}\\ \text{class } n\\ \text{between times}\\ t_{k-1} \text{ and } t_k\end{Bmatrix}$$

or mathematically,

$$x_1^{(k)} = a_1x_1^{(k-1)} + a_2x_2^{(k-1)} + \cdots + a_nx_n^{(k-1)} . \qquad (13.1)$$

The number of females in the $(i+1)$st age class $(i = 1, 2, \ldots, n-1)$ at time t_k are those females in the i-th class at time t_{k-1} who are still alive at time t_k. Thus,

$$\begin{Bmatrix}\text{number of}\\ \text{females in}\\ \text{class } i+1\\ \text{at time } t_k\end{Bmatrix} = \begin{Bmatrix}\text{fraction of}\\ \text{females in}\\ \text{class } i\\ \text{who survive}\\ \text{and pass into}\\ \text{class } i+1\end{Bmatrix} \begin{Bmatrix}\text{number of}\\ \text{females in}\\ \text{class } i\\ \text{at time } t_{k-1}\end{Bmatrix}$$

or mathematically,

$$x_{i+1}^{(k)} = b_ix_i^{(k-1)} , \qquad i = 1, 2, \ldots, n-1 \quad (13.2)$$

Using matrix notation, Eqs. (13.1) and (13.2) can be written

$$\begin{bmatrix}x_1^{(k)}\\ x_2^{(k)}\\ x_3^{(k)}\\ \vdots\\ x_n^{(k)}\end{bmatrix} = \begin{bmatrix}a_1 & a_2 & a_3 & \cdots & a_{n-1} & a_n\\ b_1 & 0 & 0 & \cdots & 0 & 0\\ 0 & b_2 & 0 & \cdots & 0 & 0\\ \vdots & \vdots & \vdots & & \vdots & \vdots\\ 0 & 0 & 0 & \cdots & b_{n-1} & 0\end{bmatrix} \begin{bmatrix}x_1^{(k-1)}\\ x_2^{(k-1)}\\ x_3^{(k-1)}\\ \vdots\\ x_n^{(k-1)}\end{bmatrix},$$

or more compactly,

$$\mathbf{x}^{(k)} = L\mathbf{x}^{(k-1)}, \qquad k = 1, 2, \ldots \tag{13.3}$$

where L is the *Leslie matrix*

$$L = \begin{bmatrix} a_1 & a_2 & a_3 & \cdots & a_{n-1} & a_n \\ b_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & b_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & b_{n-1} & 0 \end{bmatrix}. \tag{13.4}$$

From Eq. (13.3) it follows that

$$\begin{aligned} \mathbf{x}^{(1)} &= L\mathbf{x}^{(0)} \\ \mathbf{x}^{(2)} &= L\mathbf{x}^{(1)} = L^2\mathbf{x}^{(0)} \\ \mathbf{x}^{(3)} &= L\mathbf{x}^{(2)} = L^3\mathbf{x}^{(0)} \\ &\vdots \\ \mathbf{x}^{(k)} &= L\mathbf{x}^{(k-1)} = L^k\mathbf{x}^{(0)}. \end{aligned} \tag{13.5}$$

Thus, if we know the initial age distribution $\mathbf{x}^{(0)}$ and the Leslie matrix L, we can determine the female age distribution at any later time.

EXAMPLE 13.1 Suppose the oldest age attained by the females in a certain animal population is 15 years, and we divide the population into three equal age classes of durations five years. Let the Leslie matrix for this population be

$$L = \begin{bmatrix} 0 & 4 & 3 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{4} & 0 \end{bmatrix}.$$

If there are initially 1,000 females in each of the three age classes, then from Eq. (13.3) we have

$$\mathbf{x}^{(0)} = \begin{bmatrix} 1{,}000 \\ 1{,}000 \\ 1{,}000 \end{bmatrix},$$

$$\mathbf{x}^{(1)} = L\mathbf{x}^{(0)} = \begin{bmatrix} 0 & 4 & 3 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{4} & 0 \end{bmatrix} \begin{bmatrix} 1{,}000 \\ 1{,}000 \\ 1{,}000 \end{bmatrix} = \begin{bmatrix} 7{,}000 \\ 500 \\ 250 \end{bmatrix},$$

$$\mathbf{x}^{(2)} = L\mathbf{x}^{(1)} = \begin{bmatrix} 0 & 4 & 3 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{4} & 0 \end{bmatrix} \begin{bmatrix} 7{,}000 \\ 500 \\ 250 \end{bmatrix} = \begin{bmatrix} 2{,}750 \\ 3{,}500 \\ 125 \end{bmatrix},$$

$$\mathbf{x}^{(3)} = L\mathbf{x}^{(2)} = \begin{bmatrix} 0 & 4 & 3 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{4} & 0 \end{bmatrix} \begin{bmatrix} 2{,}750 \\ 3{,}500 \\ 125 \end{bmatrix} = \begin{bmatrix} 14{,}375 \\ 1{,}375 \\ 875 \end{bmatrix}.$$

Thus, after 15 years there are 14,375 females between 0 and 5 years of age, 1,375 females between 5 and 10 years of age, and 875 females between 10 and 15 years of age.

Limiting Behavior

Although Eq. (13.5) gives the age distribution of the population at any time, it does not immediately give a general picture of the dynamics of the growth process. For this we need to investigate the eigenvalues and eigenvectors of the Leslie matrix. The eigenvalues of L are the roots of its characteristic polynomial. As we ask the reader to verify in Exercise 13.2, this characteristic polynomial is

$$p(\lambda) = |\lambda I - L|$$

$$= \lambda^n - a_1\lambda^{n-1} - a_2b_1\lambda^{n-2} - a_3b_1b_2\lambda^{n-3} - \cdots - a_nb_1b_2\cdots b_{n-1}.$$

To analyze the roots of this polynomial, it will be convenient to introduce the function

$$q(\lambda) = \frac{a_1}{\lambda} + \frac{a_2b_1}{\lambda^2} + \frac{a_3b_1b_2}{\lambda^3} + \cdots + \frac{a_nb_1b_2\cdots b_{n-1}}{\lambda^n}. \qquad (13.6)$$

Using this function, the characteristic equation $p(\lambda) = 0$ can be written (verify)

$$q(\lambda) = 1 \quad \text{for } \lambda \neq 0. \tag{13.7}$$

Since all of the a_i and b_i are nonnegative, we see that $q(\lambda)$ is monotonically decreasing for λ greater than zero. Furthermore, $q(\lambda)$ has a vertical asymptote at $\lambda = 0$ and approaches zero as $\lambda \to \infty$. Consequently, as Fig. 13.1 indicates, there is a unique λ, say λ_1, such that $q(\lambda) = 1$. That is, the matrix L has a unique positive eigenvalue. It may further be shown (see Exercise 13.3) that λ_1 is simple; i.e., λ_1 has multiplicity one. Although we shall omit the computational details, the reader can verify that an eigenvector corresponding to λ_1, that is, a nonzero vector solution of

$$L\mathbf{x}_1 = \lambda_1 \mathbf{x}_1 ,$$

is

$$\mathbf{x}_1 = \begin{bmatrix} 1 \\ b_1/\lambda_1 \\ b_1 b_2/\lambda_1^2 \\ b_1 b_2 b_3/\lambda_1^3 \\ \vdots \\ b_1 b_2 \cdots b_{n-1}/\lambda_1^{n-1} \end{bmatrix}. \tag{13.8}$$

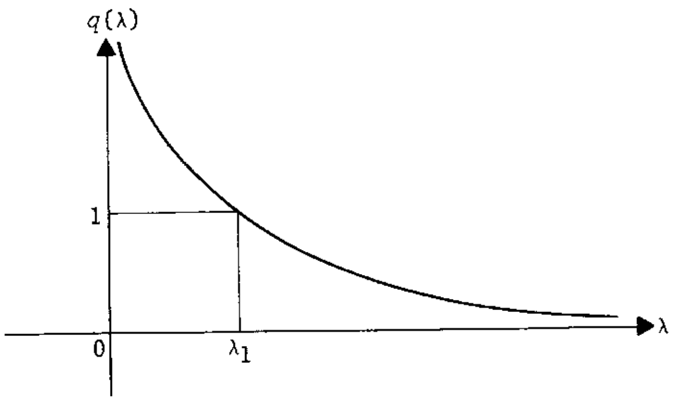

Figure 13.1

Since λ_1 is simple, its corresponding eigenspace has dimension one, and so any eigenvector corresponding to it is some multiple of $\mathbf{x}_1$. Let us summarize these results in the following theorem:

> **THEOREM 13.1** *A Leslie matrix L has a unique positive eigenvalue λ_1. This eigenvalue is simple and has an eigenvector $\mathbf{x}_1$ all of whose entries are positive.*

We shall now show that the long-term behavior of the age distribution of the population is determined by the positive eigenvalue λ_1 and its eigenvector $\mathbf{x}_1$.

In Exercise 13.9, we ask the reader to prove the following result:

> **THEOREM 13.2** *If λ_1 is the unique positive eigenvalue of a Leslie matrix L and λ_i is any other real or complex eigenvalue of L, then $|\lambda_i| \leq \lambda_1$.*

Because of Theorem 13.2, λ_1 is called a *dominant eigenvalue* of L. For our purposes we actually need more; namely, that $|\lambda_i| < \lambda_1$ for all other eigenvalues of L. In this case, we say that λ_1 is a *strictly dominant eigenvalue* of L. However, as the following example shows, not all Leslie matrices satisfy this condition.

EXAMPLE 13.2

Let

$$L = \begin{bmatrix} 0 & 0 & 6 \\ 1/2 & 0 & 0 \\ 0 & 1/3 & 0 \end{bmatrix}.$$

Then the characteristic polynomial of L is

$$p(\lambda) = |\lambda I - L| = \lambda^3 - 1\,.$$

The eigenvalues of L are thus the solutions of $\lambda^3 = 1$; namely,

$$\lambda = 1,\ -\frac{1}{2} + \frac{\sqrt{3}}{2}i,\ -\frac{1}{2} - \frac{\sqrt{3}}{2}i\ .$$

All three eigenvalues have absolute value one, and so the unique positive eigenvalue $\lambda_1 = 1$ is not strictly dominant. Note that this matrix has the property that $L^3 = I$. This means that for any choice of the initial age distribution $\mathbf{x}^{(0)}$, we have

$$\mathbf{x}^{(0)} = \mathbf{x}^{(3)} = \mathbf{x}^{(6)} = \cdots = \mathbf{x}^{(3k)} = \cdots .$$

The age distribution vector thus oscillates with a period of three time units. Such oscillations (or *population waves*, as they are called) could not occur if λ_1 were strictly dominant, as we shall see below.

It is beyond the scope of this book to discuss necessary and sufficient conditions for λ_1 to be a strictly dominant eigenvalue. However, we will state the following sufficient condition without proof:

> **THEOREM 13.3** *If two successive entries a_i and a_{i+1} in the first row of a Leslie matrix L are nonzero, then the positive eigenvalue of L is strictly dominant.*

Thus, if the female population has two successive fertile age classes, then its Leslie matrix has a strictly dominant eigenvalue. This is always the case for realistic populations if the duration of the age classes is sufficiently small. Notice that in Example 13.2 there is only one fertile age class (the third), and so the condition of Theorem 13.3 is not satisfied. In what follows, we shall always assume that the condition of Theorem 13.3 is satisfied.

Let us assume that L is diagonalizable. This is not really necessary for the conclusions we shall draw, but it does simplify the arguments. In this case, L has n eigenvalues, $\lambda_1, \lambda_2, \ldots, \lambda_n$, not necessarily distinct, and n linearly independent eigenvectors, $\mathbf{x}_1, \mathbf{x}_2, \ldots, \mathbf{x}_n$, corresponding to them. In this listing we place the strictly dominant eigenvalue λ_1 first. We construct a matrix P whose columns are the eigenvectors of L:

$$P = \left[\mathbf{x}_1 \mid \mathbf{x}_2 \mid \mathbf{x}_3 \mid \cdots \mid \mathbf{x}_n\right].$$

The diagonalization of L is then given by the equation

$$L = P \begin{bmatrix} \lambda_1 & 0 & 0 & \cdots & 0 \\ 0 & \lambda_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & & \vdots \\ 0 & 0 & 0 & \cdots & \lambda_n \end{bmatrix} P^{-1}.$$

From this it follows that

$$L^k = P \begin{bmatrix} \lambda_1^k & 0 & 0 & \cdots & 0 \\ 0 & \lambda_2^k & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & & \vdots \\ 0 & 0 & 0 & \cdots & \lambda_n^k \end{bmatrix} P^{-1},$$

for $k = 1, 2, \ldots$. For any initial age distribution vector $\mathbf{x}^{(0)}$ we then have

$$L^k \mathbf{x}^{(0)} = P \begin{bmatrix} \lambda_1^k & 0 & 0 & \cdots & 0 \\ 0 & \lambda_2^k & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & & \vdots \\ 0 & 0 & 0 & \cdots & \lambda_n^k \end{bmatrix} P^{-1} \mathbf{x}^{(0)}$$

for $k = 1, 2, \ldots$. Dividing both sides of this equation by λ_1^k and using the fact that $\mathbf{x}^{(k)} = L^k \mathbf{x}^{(0)}$, we have

$$\frac{1}{\lambda_1^k}\mathbf{x}^{(k)} = P \begin{bmatrix} 1 & 0 & 0 & \cdots & 0 \\ 0 & (\lambda_2/\lambda_1)^k & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & & \vdots \\ 0 & 0 & 0 & \cdots & (\lambda_n/\lambda_1)^k \end{bmatrix} P^{-1} \mathbf{x}^{(0)}. \qquad (13.9)$$

Since λ_1 is the strictly dominant eigenvalue, $|\lambda_i/\lambda_1| < 1$ for $i = 2, 3, \ldots, n$. It follows that

$$(\lambda_i/\lambda_1)^k \to 0 \quad \text{as} \quad k \to \infty \quad \text{for} \quad i = 2, 3, \ldots, n.$$

Using this fact, we may take the limit of both sides of (13.9) to obtain

$$\lim_{k\to\infty}\left\{\frac{1}{\lambda_1^k}\mathbf{x}^{(k)}\right\} = P\begin{bmatrix}1 & 0 & 0 & \cdots & 0\\ 0 & 0 & 0 & \cdots & 0\\ \vdots & \vdots & \vdots & & \vdots\\ 0 & 0 & 0 & \cdots & 0\end{bmatrix}P^{-1}\mathbf{x}^{(0)}. \qquad (13.10)$$

Let us denote the first entry of the column vector $P^{-1}\mathbf{x}^{(0)}$ by the constant c. As we ask the reader to show in Exercise 13.4, the righthand side of (13.10 can be written as $c\mathbf{x}_1$, where c is a positive constant which depends only on the initial age distribution vector $\mathbf{x}^{(0)}$. Thus (13.10) becomes

$$\lim_{k\to\infty}\left\{\frac{1}{\lambda_1^k}\mathbf{x}^{(k)}\right\} = c\mathbf{x}_1. \qquad (13.11)$$

Equation (13.11) gives us the approximation

$$\mathbf{x}^{(k)} \simeq c\lambda_1^k\mathbf{x}_1 \qquad (13.12)$$

for large values of k. From (13.12) we also have

$$\mathbf{x}^{(k-1)} \simeq c\lambda_1^{k-1}\mathbf{x}_1. \qquad (13.13)$$

Comparing Eqs. (13.12) and (13.13), we see that

$$\mathbf{x}^{(k)} \simeq \lambda_1\mathbf{x}^{(k-1)} \qquad (13.14)$$

for large values of k. This means that for large values of time each age distribution vector is a scalar multiple of the preceding age distribution vector, the scalar being the positive eigenvalue of the Leslie matrix. Consequently, the *proportion* of females in each of the age classes becomes constant. As we shall see in the following example, these limiting proportions can be determined from the eigenvector $\mathbf{x}_1$.

EXAMPLE 13.1 (REVISITED) The Leslie matrix in Example 13.1 was

$$L = \begin{bmatrix} 0 & 4 & 3 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{4} & 0 \end{bmatrix}.$$

Its characteristic polynomial is $p(\lambda) = \lambda^3 - 2\lambda - 3/8$, and the reader can verify that the positive eigenvalue is $\lambda_1 = 3/2$. From (13.8) the corresponding eigenvector $\mathbf{x}_1$ is

$$\mathbf{x}_1 = \begin{bmatrix} 1 \\ b_1/\lambda_1 \\ b_1 b_2/\lambda_1^2 \end{bmatrix} = \begin{bmatrix} 1 \\ (1/2)\big/(3/2) \\ (1/2)(1/4)\big/(3/2)^2 \end{bmatrix} = \begin{bmatrix} 1 \\ 1/3 \\ 1/18 \end{bmatrix}.$$

From (13.14) we have

$$\mathbf{x}^{(k)} \simeq (3/2)\mathbf{x}^{(k-1)}$$

for large values of k. Hence, every five years the number of females in each of the three classes will increase by about 50%, as will the total number of females in the population.

From (13.12) we have

$$\mathbf{x}^{(k)} \simeq c(3/2)^k \begin{bmatrix} 1 \\ 1/3 \\ 1/18 \end{bmatrix}.$$

Consequently, eventually the females will be distributed among the three age classes in the ratios 1 : 1/3 : 1/18. This corresponds to a distribution of 72% of the females in the first age class, 24% of the females in the second age class, and 4% of the females in the third age class.

EXAMPLE 13.3 In this example we shall use birth and death parameters from the year 1965 for Canadian females. Since few women over 50 years of age bear children, we shall restrict ourselves to the portion of the female population between 0 and 50 years of age. The data are for 5-year age classes, so there are a total of ten age classes. Rather than write out the 10×10 Leslie matrix in full, we list the birth and death parameters as follows:

Age Interval	a_i	b_i
[0, 5)	0.00000	0.99651
[5, 10)	0.00024	0.99820
[10, 15)	0.05861	0.99802
[15, 20)	0.28608	0.99729
[20, 25)	0.44791	0.99694
[25, 30)	0.36399	0.99621
[30, 35)	0.22259	0.99460
[35, 40)	0.10457	0.99184
[40, 45)	0.02826	0.98700
[45, 50)	0.00240	—

Using numerical techniques, the positive eigenvalue and corresponding eigenvector turn out to be

$$\lambda_1 = 1.07622 \quad \text{and} \quad \mathbf{x}_1 = \begin{bmatrix} 1.00000 \\ 0.92594 \\ 0.85881 \\ 0.79641 \\ 0.73800 \\ 0.68364 \\ 0.63281 \\ 0.58482 \\ 0.53897 \\ 0.49429 \end{bmatrix}$$

Thus, if Canadian women continued to reproduce and die as they did in 1965, eventually every five years their numbers would increase by 7.622%. From the eigenvector $\mathbf{x}_1$, we see that, in the limit, for every 100,000 females between 0 and 5 years of age, there will be 92,594 females between 5 and 10 years of age, 85,881 females between 10 and 15 years of age, and so forth.

Let us look again at Eq. (13.12) which gives the age distribution vector of the population for large times:

$$\mathbf{x}^{(k)} \simeq c\lambda_1^k \mathbf{x}_1 . \tag{13.15}$$

Three cases arise according to the value of the positive eigenvalue λ_1:

(i) The population is eventually increasing if $\lambda_1 > 1$.

(ii) The population is eventually decreasing if $\lambda_1 < 1$.

(iii) The population stabilizes if $\lambda_1 = 1$.

The case $\lambda_1 = 1$ is particularly interesting since it determines a population which has *zero population growth*. For any initial age distribution, the population approaches a limiting age distribution which is some multiple of the eigenvector $\mathbf{x}_1$. From Eqs. (13.6) and (13.7), we see that $\lambda_1 = 1$ is an eigenvalue if and only if

$$a_1 + a_2 b_1 + a_3 b_1 b_2 + \cdots + a_n b_1 b_2 \cdots b_{n-1} = 1. \tag{13.16}$$

The expression

$$R = a_1 + a_2 b_1 + a_3 b_1 b_2 + \cdots + a_n b_1 b_2 \cdots b_{n-1} \tag{13.17}$$

is called the *net reproduction rate* of the population. (See Exercise 13.5 for a demographic interpretation of R.) Thus we can say that a population has zero population growth if and only if its net reproduction rate is one.

Exercises

13.1 Suppose a certain animal population is divided into two age classes and has a Leslie matrix

$$L = \begin{bmatrix} 1 & 3/2 \\ 1/2 & 0 \end{bmatrix}.$$

(a) Calculate the positive eigenvalue λ_1 of L and the corresponding eigenvector $\mathbf{x}_1$.

(b) Beginning with the initial age distribution vector

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

calculate $\mathbf{x}^{(1)}$, $\mathbf{x}^{(2)}$, $\mathbf{x}^{(3)}$, $\mathbf{x}^{(4)}$, and $\mathbf{x}^{(5)}$, rounding off to the nearest integer when necessary.

(c) Calculate $\mathbf{x}^{(6)}$ using the exact formula $\mathbf{x}^{(6)} = L\mathbf{x}^{(5)}$ and the approximate formula $\mathbf{x}^{(6)} \simeq \lambda_1 \mathbf{x}^{(5)}$.

13.2 Find the characteristic polynomial of a general Leslie matrix given by Eq. (13.4).

13.3 Show that the positive eigenvalue λ_1 of a Leslie matrix is always simple. Recall that a root λ_0 of a polynomial $q(\lambda)$ is simple if and only if $q'(\lambda_0) \neq 0$.

13.4 Show that the righthand side of Eq. (13.10) is $c\mathbf{x}_1$ where c is the first entry of the column vector $P^{-1}\mathbf{x}^{(0)}$.

13.5 Show that the net reproduction rate R, defined by (13.17), can be interpreted as the average number of daughters born to a single female during her expected lifetime.

13.6 Show that a population is eventually decreasing if and only if its net reproduction rate is less than one. Similarly, show that a population is eventually increasing if and only if its net reproduction rate is greater than one.

13.7 Calculate the net reproduction rate of the animal population in Example 13.1.

13.8 (For readers with a hand calculator) Calculate the net reproduction rate of the Canadian female population in Example 13.3.

13.9 (For readers who have had a course in Complex Variables) Prove Theorem 9.2. Hint: write $\lambda_i = re^{i\theta}$, substitute into (13.7), take the real parts of both sides, and show that $r \leq \lambda_1$.

14

Harvesting of Animal Populations

The Leslie matrix model of population growth is used to model the sustainable harvesting of an animal population. The effect of harvesting different fractions of different age groups is investigated.

PREREQUISITES: Chapter 13: Age-Specific Population Growth

INTRODUCTION

In Chapter 13, the Leslie matrix model for the growth of a female population divided into discrete age classes was described. In this chapter, we shall investigate the effects of harvesting an animal population growing according to such a model. By *harvesting* we mean the removal of animals from the population. The word "harvesting" is not necessarily a euphemism for "slaughtering"; the animals may be removed from the population for other purposes.

We shall restrict ourselves to what are called *sustainable harvesting policies*. By this we mean the following:

Sustainable Harvesting Policy

A harvesting policy in which an animal population is periodically harvested is said to be sustainable if the yield of each harvest is the same and the age distribution of the population remaining after each harvest is the same.

Thus, the animal population is not depleted by a sustainable harvesting policy; only the excess growth is exploited.

As in Chapter 13, we shall only discuss the females of the population. If the number of males in each age class is equal to the number of females — a reasonable assumption for many populations — then our harvesting policies will also apply to the male portion of the population.

The Harvesting Model

Figure 14.1 illustrates the basic idea of the model. We begin with a population having a particular age distribution. It undergoes a growth period which will be described by the Leslie matrix. At the end of the growth period, a certain fraction of each age class is harvested. The duration of the harvest is to be short in comparison with the growth period so that any growth or change in the population during the harvest period may be neglected. Finally, the population left unharvested is to have the same age distribution as the original population. This cycle repeats after each harvest, so that the yield is sustainable.

To describe this harvesting model mathematically, let

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

be the age distribution vector of the population at the beginning of the growth period. Thus x_i is the number of females in the i-th class left unharvested. As in Chapter 13, we require that the duration of each age class be identical with the duration of the growth period. For example, if the population is harvested once a year, then the population is to be divided into one-year age classes.

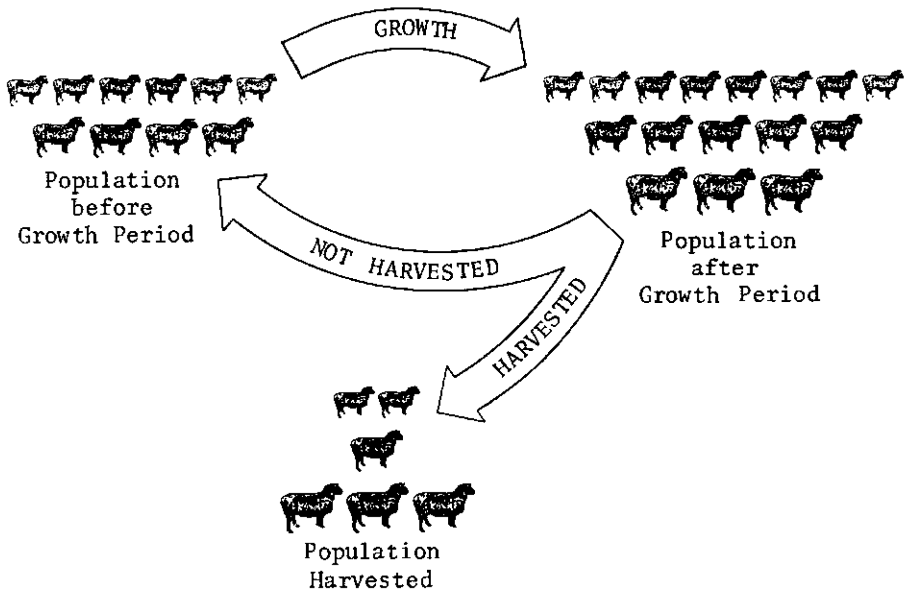

Figure 14.1

If L is the Leslie matrix describing the growth of the population, then the vector $L\mathbf{x}$ is the age distribution vector of the population at the end of the growth period, immediately before the periodic harvest. Let h_i, for $i = 1, 2, \ldots, n$, be the fraction of females from the i-th class which is harvested. We use these n numbers to form an $n \times n$ diagonal matrix

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$$H = \begin{bmatrix} h_1 & 0 & 0 & \cdots & 0 \\ 0 & h_2 & 0 & \cdots & 0 \\ 0 & 0 & h_3 & \cdots & 0 \\ \vdots & \vdots & \vdots & & \vdots \\ 0 & 0 & 0 & \cdots & h_n \end{bmatrix}$$

which we shall call the *harvesting matrix*. By definition, we have

$$0 \leq h_i \leq 1 \qquad \text{for } i = 1, 2, \ldots, n.$$

That is, we may harvest none ($h_i = 0$), all ($h_i = 1$), or some proper fraction ($0 < h_i < 1$) of each of the n classes. Since the number of females in the i-th class immediately before each harvest is the i-th entry $(L\mathbf{x})_i$ of the vector $L\mathbf{x}$, it can be seen that the i-th entry of the column vector

$$HL\mathbf{x} = \begin{bmatrix} h_1(L\mathbf{x})_1 \\ h_2(L\mathbf{x})_2 \\ \vdots \\ h_n(L\mathbf{x})_n \end{bmatrix}$$

is the number of females harvested from the i-th class.

From the definition of a sustainable harvesting policy, we have

$$\begin{pmatrix}\text{age distribution}\\ \text{at end of}\\ \text{growth period}\end{pmatrix} - \begin{pmatrix}\text{harvest}\end{pmatrix} = \begin{pmatrix}\text{age distribution}\\ \text{at beginning of}\\ \text{growth period}\end{pmatrix}$$

or mathematically,

$$L\mathbf{x} - HL\mathbf{x} = \mathbf{x}. \tag{14.1}$$

If we write Eq. (10.1) in the form

$$(I - H)L\mathbf{x} = \mathbf{x} \tag{14.2}$$

we see that $\mathbf{x}$ must be an eigenvector of the matrix $(I - H)L$ corresponding to the eigenvalue one. As we shall now describe, this places certain restrictions on the values of h_i and $\mathbf{x}$.

Suppose the Leslie matrix of the population is

$$L = \begin{bmatrix} a_1 & a_2 & a_3 & \cdots & a_{n-1} & a_n \\ b_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & b_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & b_{n-1} & 0 \end{bmatrix}.$$

Then the matrix $(I - H)L$ is easily computed:

$$(I - H)L = \begin{bmatrix} (1-h_1)a_1 & (1-h_1)a_2 & (1-h_1)a_3 & \cdots & (1-h_1)a_{n-1} & (1-h_1)a_n \\ (1-h_2)b_1 & 0 & 0 & & 0 & 0 \\ 0 & (1-h_3)b_2 & 0 & & 0 & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & (1-h_n)b_{n-1} & 0 \end{bmatrix}.$$

We thus see that $(I - H)L$ is a matrix which has the same mathematical form as a Leslie matrix. In Chapter 13, we showed that a necessary and sufficient condition for a Leslie matrix to have one as an eigenvalue is that its net reproduction rate also be one. (See Eq. (13.16) on page 178.) Calculating the net reproduction rate of $(I - H)L$ and setting it equal to one, we obtain (verify):

$$(1-h_1)[a_1 + a_2b_1(1-h_2) + a_3b_1b_2(1-h_2)(1-h_3) + \cdots$$
$$+ a_nb_1b_2\cdots b_{n-1}(1-h_2)(1-h_3)\cdots(1-h_n)] = 1. \qquad (14.4)$$

This equation places a restriction on the allowable harvesting fractions. Only those values of $h_1, h_2, \ldots, h_n$ which satisfy Eq. (14.4) and which lie in the interval [0, 1] can produce a sustainable yield.

If $h_1, h_2, \ldots, h_n$ do satisfy (14.4), then the matrix $(I - H)L$ has the desired eigenvalue $\lambda_1 = 1$; and, furthermore this eigenvalue has multiplicity one since the positive eigenvalue of a Leslie matrix always has multiplicity one (Theorem 13.1, page 172). This means that there is only one linearly independent eigenvector $\mathbf{x}$ satisfying Eq. (14.2). As in Chapter 13 (Eq. 13.8, page 171), we pick the following normalized eigenvector:

$$\mathbf{x}_1 = \begin{bmatrix} 1 \\ b_1(1-h_2) \\ b_1b_2(1-h_2)(1-h_3) \\ b_1b_2b_3(1-h_2)(1-h_3)(1-h_4) \\ \vdots \\ b_1b_2b_3\cdots b_{n-1}(1-h_2)(1-h_3)\cdots(1-h_n) \end{bmatrix}. \qquad (14.5)$$

Any other solution $\mathbf{x}$ of (14.2) is a multiple of $\mathbf{x}_1$. The vector $\mathbf{x}_1$ thus determines the proportion of females within each of the n classes after a harvest under a sustainable harvesting policy. But there is an ambiguity in the total number of females in the population after each harvest. This can be determined by some auxilliary condition, such as an ecological or economic constraint. For example, for a population economically supported by the harvester, the largest population the harvester can afford to raise between harvests would determine the particular constant $\mathbf{x}_1$ is multiplied by to produce the appropriate vector $\mathbf{x}$ in (10.2). For a wild population — deer, whales, bears, etc. — the natural habitat of the population would determine how large the total population may be between harvests.

Summarizing our results so far, we see that there is a wide choice in the values of $h_1, h_2, \ldots, h_n$ which will produce a sustainable yield. But once these values are selected, the proportional age distribution of the population after each harvest is uniquely determined by the normalized eigenvector $\mathbf{x}_1$ defined by Eq. (10.5). Let us now consider a few particular harvesting strategies of this type.

Uniform Harvesting

With many populations it is difficult to distinguish or catch animals of specific ages. If animals are caught at random, we may reasonably assume the same fraction of each age class is harvested. Let us therefore set

$$h = h_1 = h_2 = \cdots = h_n.$$

Equation (10.2) then reduces to (verify):

$$L\mathbf{x} = \left(\frac{1}{1-h}\right)\mathbf{x}.$$

Hence, $1/(1-h)$ must be the unique positive eigenvalue λ_1 of the Leslie growth matrix L. That is,

$$\lambda_1 = \frac{1}{1-h}.$$

Solving for the harvesting fraction h, we obtain

$$h = 1 - 1/\lambda_1. \tag{14.6}$$

The vector $\mathbf{x}_1$, in this case, is the same as the eigenvector of L corresponding to the eigenvalue λ_1. From Chapter 13 (Eq. (13.8), page 115), this is

$$\mathbf{x}_1 = \begin{bmatrix} 1 \\ b_1/\lambda_1 \\ b_1b_2/\lambda_1^2 \\ b_1b_2b_3/\lambda_1^3 \\ \vdots \\ b_1b_2\cdots b_{n-1}/\lambda_1^{n-1} \end{bmatrix}. \tag{14.7}$$

From Eq. (14.6), we can see that the larger λ_1 is, the larger is the fraction of animals we can harvest without depleting the population. We also notice that we need $\lambda_1 > 1$ in order that the harvesting fraction h lie in the interval $(0, 1]$. This is to be expected since $\lambda_1 > 1$ is the condition that the population be increasing.

EXAMPLE 14.1 For a certain species of domestic sheep in New Zealand with a growth period of one year, the following Leslie matrix was found (G. Caughley, "Parameters for Seasonally Breeding Populations," *Ecology*, Vol. 48, 1967, pages 834 - 839):

$$L = \begin{bmatrix} .000 & .045 & .391 & .472 & .484 & .546 & .543 & .502 & .468 & .459 & .433 & .421 \\ .845 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & .975 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & .965 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & .950 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & .926 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & .895 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & .850 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & .786 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & .691 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & .561 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & .370 & 0 \end{bmatrix}$$

The sheep have a lifespan of 12 years so that they are divided into 12 age classes of duration one year each. By the use of numerical techniques, the unique positive eigenvalue of L can be found to be

$$\lambda_1 = 1.221$$

From Eq. (10.6), the harvesting fraction h is

$$h = 1 - 1/\lambda_1 = 1 - 1/1.221 = 0.181 \ .$$

Thus, the uniform harvesting policy is one in which 18.1% of the sheep from each of the 12 age classes is harvested every year. From Eq. (14.7), the age distribution vector of the sheep after each harvest is proportional to

$$\mathbf{x}_1 = \begin{bmatrix} 1.000 \\ 0.692 \\ 0.552 \\ 0.436 \\ 0.339 \\ 0.257 \\ 0.189 \\ 0.131 \\ 0.084 \\ 0.048 \\ 0.022 \\ 0.007 \end{bmatrix}. \qquad (14.8)$$

From (14.8) we see that for every 1000 sheep between 0 and 1 years of age which are not harvested, there are 692 sheep between 1 and 2 years of age, 552 sheep between 2 and 3 years of age, and so forth.

Harvesting Only the Youngest Age Class

In some populations, only the youngest females are of any economic value, and so the harvester seeks to harvest only the females from the youngest age class. Accordingly, let us set

$$h_1 = h,$$
$$h_2 = h_3 = \cdots = h_n = 0.$$

Equation (14.4) then reduces to

$$(1 - h)(a_1 + a_2b_1 + a_3b_1b_2 + \cdots + a_nb_1b_2\cdots b_{n-1}) = 1,$$

or

$$(1 - h)R = 1$$

where R is the net reproduction rate of the population. (See Eq. (13.17), page 122.) Solving for h, we obtain

$$h = 1 - 1/R. \qquad (14.9)$$

We notice from this equation that only if $R > 1$ is a sustainable harvesting policy possible. This is reasonable since only if $R > 1$ is the population increasing. From Eq. (14.5), the age distribution vector after each harvest is proportional to the vector

$$\mathbf{x}_1 = \begin{bmatrix} 1 \\ b_1 \\ b_1b_2 \\ b_1b_2b_3 \\ \vdots \\ b_1b_2b_3\cdots b_{n-1} \end{bmatrix}. \qquad (14.10)$$

Example 14.2 Let us apply this type of sustainable harvesting policy to the sheep population in Example 14.1. For the net reproduction rate of the population, we find:

$$R = a_1 + a_2 b_1 + a_3 b_1 b_2 + \cdots + a_n b_1 b_2 \cdots b_{n-1}$$

$$= (.000) + (.045)(.845) + \cdots + (.421)(.845)(.975) \cdots (.370)$$

$$= 2.513.$$

From Eq. (14.9), the fraction of the first age class harvested is

$$h = 1 - 1/R = 1 - 1/2.513 = .602 \; .$$

From Eq. (14.10), the age distribution of the sheep population after the harvest is proportional to the vector

$$\mathbf{x}_1 = \begin{bmatrix} 1.000 \\ 0.845 \\ (.845)(.975) \\ (.845)(.975)(.965) \\ \\ \\ \vdots \\ \\ \\ \\ \\ (.845)(.975)\cdots(.370) \end{bmatrix} = \begin{bmatrix} 1.000 \\ 0.845 \\ 0.824 \\ 0.795 \\ 0.755 \\ 0.699 \\ 0.626 \\ 0.532 \\ 0.418 \\ 0.289 \\ 0.162 \\ 0.060 \end{bmatrix} . \qquad (14.11)$$

A direct calculation gives us the following (see also Exercise (14.3):

$$L\mathbf{x}_1 = \begin{bmatrix} 2.513 \\ 0.845 \\ 0.824 \\ 0.795 \\ 0.755 \\ 0.699 \\ 0.626 \\ 0.532 \\ 0.418 \\ 0.289 \\ 0.162 \\ 0.060 \end{bmatrix} . \qquad (14.12)$$

The vector Lx_1 is the age distribution vector immediately before the harvest. The total of all entries in Lx_1 is 8.518, so that the first entry 2.513 is 29.5% of the total. This means that immediately before each harvest, 29.5% of the population is in the youngest age class. Since 60.2% of this class is harvested, it follows that 17.8% (= 60.2% of 29.5%) of the entire sheep population is harvested each year. This can be compared with the uniform harvesting policy of Example 14.1, in which 18.1% of the sheep population is harvested each year.

Optimal Sustainable Yield

We saw in Example 14.1 that a sustainable harvesting policy in which the same fraction of each age class is harvested produces a yield of 18.1% of the sheep population. In Example 14.2, we saw that if only the youngest age class is harvested, the resulting yield is 17.8% of the population. There are many other possible sustainable harvesting policies, and each will provide a generally different yield. It would be of interest to find a sustainable harvesting policy which produces the largest possible yield. Such a policy is called an *optimal sustainable harvesting policy* and the resulting yield is called the *optimal sustainable yield*. However, the determination of the optimal sustainable yield requires Linear Programming theory, and we cannot discuss it in detail in this chapter. (See Chapter 17 for an introduction to Linear Programming theory.) We shall, though, state the following result for reference (J. R. Beddington and D. B. Taylor, "Optimum Age Specific Harvesting of a Population," *Biometrics*, Vol. 29, 1973, pages 801-809):

Optimal Sustainable Yield

An optimal sustainable harvesting policy is one in which either one or two age classes are harvested. If two age classes are harvested, then the older age class is completely harvested.

As an illustration, it can be shown using Linear Programming that the optimal sustainable yield of the sheep population is attained when

$$h_1 = 0.522 \qquad (14.13)$$
$$h_9 = 1.000$$

and all other values of h_i are zero. Thus, 52.2% of the sheep between 0 and 1 years of age and all of the sheep between 8 and 9 years of age are harvested. As we ask the reader to show in Exercise 14.2, the resulting optimal sustainable yield is 19.9% of the population.

EXERCISES

14.1 Let a certain animal population be divided into three one-year age classes and have as its Leslie matrix

$$L = \begin{bmatrix} 0 & 4 & 3 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{4} & 0 \end{bmatrix}.$$

(a) Find the yield and the age distribution vector after each harvest if the same fraction of each of the three age classes is harvested every year.

(b) Find the yield and the age distribution vector after each harvest if only the youngest age class is harvested every year. Also, find the fraction of the youngest age class which is harvested.

14.2 For the optimal sustainable harvesting policy described by Eqs. (14.13), find the vector $\mathbf{x}_1$ which specifies the age distribution of the population after each harvest. Also, calculate the vector $L\mathbf{x}_1$ and verify that the optimal sustainable yield is 19.9% of the population.

14.3 If only the first age class of an animal population is harvested, use Eq. (14.10) to show that

$$L\mathbf{x}_1 - \mathbf{x}_1 = \begin{bmatrix} R-1 \\ 0 \\ 0 \\ \vdots \\ 0 \end{bmatrix}$$

where R is the net reproduction rate of the population.

14.4 If only the I-th class of an animal population is to be periodically harvested ($I = 1, 2, \ldots, n$), find the corresponding harvesting fraction h_I.

14.5 Suppose all of the J-th class and a certain fraction h_I of the I-th class of an animal population is to be periodically harvested ($1 \leq I < J \leq n$). Calculate h_I.