Chapter 2
Linear Discrete Dynamical Systems

Aims and Objectives

- To introduce recurrence relations for first- and second-order difference equations
- To introduce the theory of the Leslie model
- To apply the theory to modeling the population of a single species

On completion of this chapter, the reader should be able to

- solve first- and second-order homogeneous linear difference equations;
- find eigenvalues and eigenvectors of matrices;
- model a single population with different age classes;
- predict the long-term rate of growth/decline of the population;
- investigate how harvesting and culling policies affect the model.

This chapter deals with linear discrete dynamical systems, where time is measured by the number of iterations carried out and the dynamics are not continuous. In applications this would imply that the solutions are observed at discrete time intervals.

Recurrence relations can be used to construct mathematical models of discrete systems. They are also used extensively to solve many differential equations which do not have an analytic solution; the differential equations are represented by recurrence relations (or difference equations) that can be solved numerically on a computer. Of course one has to be careful when considering the accuracy of the numerical solutions. Ordinary differential equations are used to model continuous dynamical systems later in the book.

The bulk of this chapter is concerned with a linear discrete dynamical system that can be used to model the population of a single species. As with continuous systems, in applications to the real world, linear models generally produce good results over only a limited range of time. The Leslie model introduced here is useful when establishing harvesting and culling policies. Nonlinear discrete dynamical systems will be discussed in the next chapter.

The Poincaré maps introduced in Chap. 15, for example, illustrates how discrete systems can be used to help in the understanding of how continuous systems behave.

2.1   Recurrence Relations

This section is intended to give the reader a brief introduction to *difference equations* and illustrate the theory with some simple models.

First-Order Difference Equations

A *recurrence relation* can be defined by a difference equation of the form

$$x_{n+1} = f(x_n), \tag{2.1}$$

where x_{n+1} is derived from x_n and $n = 0, 1, 2, 3, \ldots$. If one starts with an initial value, say, x_0, then *iteration* of (2.1) leads to a sequence of the form

$$\{x_i : i = 0 \text{ to } \infty\} = \{x_0, x_1, x_2, \ldots, x_n, x_{n+1}, \ldots\}.$$

In applications, one would like to know how this sequence can be interpreted in physical terms. Equations of the form (2.1) are called *first-order difference equations* because the suffices differ by one. Consider the following simple example.

Example 1. The difference equation used to model the interest in a bank account compounded once per year is given by

$$x_{n+1} = \left(1 + \frac{3}{100}\right) x_n, \quad n = 0, 1, 2, 3, \ldots.$$

Find a general solution and determine the balance in the account after 5 years given that the initial deposit is 10,000 dollars and the interest is compounded annually.

Solution.   Using the recurrence relation

$$x_1 = \left(1 + \frac{3}{100}\right) \times 10,000,$$

$$x_2 = \left(1 + \frac{3}{100}\right) \times x_1 = \left(1 + \frac{3}{100}\right)^2 \times 10,000,$$

and, in general,

$$x_n = \left(1 + \frac{3}{100}\right)^n \times 10,000,$$

where $n = 0, 1, 2, 3, \ldots$. Given that $x_0 = 10,000$ and $n = 5$, the balance after 5 years will be $x_5 = 11,592.74$ dollars.

Theorem 1. *The general solution of the first-order linear difference equation*

$$x_{n+1} = mx_n + c, \quad n = 0, 1, 2, 3, \ldots,$$ (2.2)

is given by

$$x_n = m^n x_0 + \begin{cases} \frac{m^n - 1}{m - 1} c & \text{if } m \neq 1 \\ nc & \text{if } m = 1. \end{cases}$$

Proof. Applying the recurrence relation given in (2.2)

$$x_1 = mx_0 + c,$$

$$x_2 = mx_1 + c = m^2 x_0 + mc + c,$$

$$x_3 = mx_2 + c = m^3 x_0 + m^2 c + mc + c,$$

and the pattern in general is

$$x_n = m^n x_0 + (m^{n-1} + m^{n-2} + \ldots + m + 1)c.$$

Using geometric series, $m^{n-1} + m^{n-2} + \ldots + m + 1 = \frac{m^n - 1}{m - 1}$, provided that $m \neq 1$. If $m = 1$, then the sum of the geometric sequence is n. This concludes the proof of Theorem 1. Note that if $|m| < 1$, then $x_n \to \frac{c}{1-m}$ as $n \to \infty$.   □

Second-Order Linear Difference Equations

Recurrence relations involving terms whose suffices differ by two are known as *second-order linear difference equations*. The general form of these equations with constant coefficients is

$$ax_{n+2} = bx_{n+1} + cx_n.$$ (2.3)

Theorem 2. *The general solution of the second-order recurrence relation (2.3) is*

$$x_n = k_1 \lambda_1^n + k_2 \lambda_2^n,$$

where k_1, k_2 are constants and $\lambda_1 \neq \lambda_2$ are the roots of the quadratic equation $a\lambda^2 - b\lambda - c = 0$. If $\lambda_1 = \lambda_2$, then the general solution is of the form

$$x_n = (k_3 + nk_4)\lambda_1^n.$$

Note that when λ_1 and λ_2 are complex, the general solution can be expressed as

$$x_n = k_1 \lambda_1^n + k_2 \lambda_2^n = k_1 (re^{i\theta})^n + k_2 (re^{-i\theta})^n = r^n \left(A \cos(n\theta) + B \sin(n\theta)\right),$$

where A and B are constants. When the eigenvalues are complex, the solution oscillates and is real.

Proof. The solution of system (2.2) gives us a clue where to start. Assume that $x_n = \lambda^n k$ is a solution, where λ and k are to be found. Substituting, (2.3) becomes

$$a\lambda^{n+2}k = b\lambda^{n+1}k + c\lambda^n k$$

or

$$\lambda^n k(a\lambda^2 - b\lambda - c) = 0.$$

Assuming that $\lambda^n k \neq 0$, this equation has solutions if

$$a\lambda^2 - b\lambda - c = 0. \tag{2.4}$$

Equation (2.4) is called the *characteristic equation*. The difference equation (2.3) has two solutions, and because the equation is linear, a solution is given by

$$x_n = k_1 \lambda_1^n + k_2 \lambda_2^n,$$

where $\lambda_1 \neq \lambda_2$ are the roots of the characteristic equation.

If $\lambda_1 = \lambda_2$, then the characteristic equation can be written as

$$a\lambda^2 - b\lambda - c = a(\lambda - \lambda_1)^2 = a\lambda^2 - 2a\lambda_1\lambda + a\lambda_1^2.$$

Therefore, $b = 2a\lambda_1$ and $c = -a\lambda_1^2$. Now assume that another solution is of the form $kn\lambda^n$. Substituting, (2.3) becomes

$$ax_{n+2} - bx_{n+1} - cx_n = a(n+2)k\lambda_1^{n+2} - b(n+1)k\lambda_1^{n+1} - cnk\lambda_1^n,$$

therefore

$$ax_{n+2} - bx_{n+1} - cx_n = kn\lambda_1^n(a\lambda_1^2 - b\lambda_1 - c) + k\lambda_1(2a\lambda_1 - b),$$

which equates to zero from the above. This confirms that $kn\lambda_n$ is a solution to (2.3). Since the system is linear, the general solution is thus of the form

$$x_n = (k_3 + nk_4)\lambda_1^n.$$

$\square$

The values of k_j can be determined if x_0 and x_1 are given. Consider the following simple examples.

Example 2. Solve the following second-order linear difference equations:

(i) $x_{n+2} = x_{n+1} + 6x_n, n = 0, 1, 2, 3, \ldots$, given that $x_0 = 1$ and $x_1 = 2$;
(ii) $x_{n+2} = 4x_{n+1} - 4x_n, n = 0, 1, 2, 3, \ldots$, given that $x_0 = 1$ and $x_1 = 3$;
(iii) $x_{n+2} = x_{n+1} - x_n, n = 0, 1, 2, 3, \ldots$, given that $x_0 = 1$ and $x_1 = 2$.

Solution.   (i) The characteristic equation is

$$\lambda^2 - \lambda - 6 = 0,$$

which has roots at $\lambda_1 = 3$ and $\lambda_2 = -2$. The general solution is therefore

$$x_n = k_1 3^n + k_2(-2)^n, \quad n = 0, 1, 2, 3, \ldots.$$

The constants k_1 and k_2 can be found by setting $n = 0$ and $n = 1$. The final solution is

$$x_n = \frac{4}{5} 3^n + \frac{1}{5}(-2)^n, \quad n = 0, 1, 2, 3, \ldots.$$

(ii) The characteristic equation is

$$\lambda^2 - 4\lambda + 4 = 0,$$

which has a repeated root at $\lambda_1 = 2$. The general solution is

$$x_n = (k_3 + k_4 n)2^n, \quad n = 0, 1, 2, 3, \ldots.$$

Substituting for x_0 and x_1, gives the solution

$$x_n = \left(1 + \frac{n}{2}\right)2^n, \quad n = 0, 1, 2, 3, \ldots.$$

(iii) The characteristic equation is

$$\lambda^2 - \lambda + 1 = 0,$$

which has complex roots $\lambda_1 = \frac{1}{2} + i\frac{\sqrt{3}}{2} = e^{\frac{i\pi}{3}}$ and $\lambda_2 = \frac{1}{2} - i\frac{\sqrt{3}}{2} = e^{\frac{-i\pi}{3}}$. The general solution is

$$x_n = k_1 \lambda_1^n + k_2 \lambda_2^n, \quad n = 0, 1, 2, 3, \ldots.$$

Substituting for λ_1 and λ_2 the general solution becomes

$$x_n = (k_1 + k_2)\cos\left(\frac{n\pi}{3}\right) + i(k_1 - k_2)\sin\left(\frac{n\pi}{3}\right), \quad n = 0, 1, 2, 3, \ldots.$$

Substituting for x_0 and x_1 gives $k_1 = \frac{1}{2} - \frac{i}{2\sqrt{3}}$ and $k_2 = \frac{1}{2} + \frac{i}{2\sqrt{3}}$, and so

$$x_n = \cos\left(\frac{n\pi}{3}\right) + \sqrt{3}\sin\left(\frac{n\pi}{3}\right), \quad n = 0, 1, 2, 3, \ldots.$$

Example 3. Suppose that the national income of a small country in year n is given by $I_n = S_n + P_n + G_n$, where S_n, P_n, and G_n represent national spending by the populous, private investment, and government spending, respectively. If the national income increases from 1 year to the next, then assume that consumers will spend more the following year; in this case, suppose that consumers spend $\frac{1}{6}$ of the previous year's income, then $S_{n+1} = \frac{1}{6}I_n$. An increase in consumer spending should also lead to increased investment the following year; assume that $P_{n+1} = S_{n+1} - S_n$. Substitution for S_n then gives $P_{n+1} = \frac{1}{6}(I_n - I_{n-1})$. Finally, assume that the government spending is kept constant. Simple manipulation then leads to the following economic model

$$I_{n+2} = \frac{5}{6}I_{n+1} - \frac{1}{6}I_n + G, \qquad (2.5)$$

where I_n is the national income in year n and G is a constant. If the initial national income is G dollars and 1 year later is $\frac{3}{2}G$ dollars, determine

  (i) a general solution to this model;
 (ii) the national income after 5 years; and
(iii) the long-term state of the economy.

Solution.   (i) The characteristic equation is given by

$$\lambda^2 - \frac{5}{6}\lambda + \frac{1}{6} = 0,$$

which has solutions $\lambda_1 = \frac{1}{2}$ and $\lambda_2 = \frac{1}{3}$. Equation (2.5) also has a constant term G. Assume that the solution involves a constant term also; try $I_n = k_3 G$, then from (2.5)

$$k_3 G = \frac{5}{6}k_3 G - \frac{1}{6}k_3 G + G,$$

and so $k_3 = \frac{1}{1 - \frac{5}{6} + \frac{1}{6}} = 3$. Therefore, a general solution is of the form

$$I_n = k_1 \lambda_1^n + k_2 \lambda_2^n + 3G.$$

 (ii) Given that $I_0 = G$ and $I_1 = \frac{3}{2}G$, simple algebra gives $k_1 = -5$ and $k_2 = 3$. When $n = 5$, $I_5 = 2.856G$, to three decimal places.
(iii) As $n \to \infty$, $I_n \to 3G$, since $|\lambda_1| < 1$ and $|\lambda_2| < 1$. Therefore, the economy stabilizes in the long term to a constant value of $3G$. This is obviously a very crude model.

  A general n-dimensional linear discrete population model is discussed in the following sections using matrix algebra.

2.2   The Leslie Model

The Leslie model was developed around 1940 to describe the population dynamics of the female portion of a species. For most species the number of females is equal to the number of males, and this assumption is made here. The model can be applied to human populations, insect populations, and animal and fish populations. The model is an example of a discrete dynamical system. As explained throughout the text, we live in a nonlinear world and universe; since this model is linear, one would expect the results to be inaccurate in the long term. However, the model can give some interesting results, and it incorporates some features not discussed in later chapters. The following characteristics are ignored—diseases, environmental effects, and seasonal effects. The book [8] provides an extension of the Leslie model, investigated in this chapter and most of the [1–7] cited here, where individuals exhibit migration characteristics. A nonlinear Leslie matrix model for predicting the dynamics of biological populations in polluted environments is discussed in [7].

Assumptions: The females are divided into n age classes; thus, if N is the theoretical maximum age attainable by a female of the species, then each age class will span a period of $\frac{N}{n}$ equally spaced, days, weeks, months, years, etc. The population is observed at regular discrete time intervals which are each equal to the length of one age class. Thus, the kth time period will be given by $t_k = \frac{kN}{n}$. Define $x_i^{(k)}$ to be the number of females in the ith age class after the kth time period. Let b_i denote the number of female offspring born to one female during the ith age class, and let c_i be the proportion of females which continue to survive from the ith to the $(i + 1)$st age class.

In order for this to be a realistic model the following conditions must be satisfied:

$$(i) \quad b_i \geq 0, \quad 1 \leq i \leq n;$$
$$(ii)\ 0 < c_i \leq 1,\ 1 \leq i < n.$$

Obviously, some b_i have to be positive in order to ensure that some births do occur and no c_i are zero; otherwise, there would be no females in the $(i + 1)$st age class.

Working with the female population as a whole, the following sets of linear equations can be derived. The number of females in the first age class after the kth time period is equal to the number of females born to females in all n age classes between the time t_{k-1} and t_k; thus,

$$x_1^{(k)} = b_1 x_1^{(k-1)} + b_2 x_2^{(k-1)} + \ldots + b_n x_n^{(k-1)}.$$

The number of females in the $(i + 1)$st age class at time t_k is equal to the number of females in the ith age class at time t_{k-1} who continue to survive to enter the $(i + 1)$st age class; hence,

$$x_{i+1}^{(k)} = c_i x_i^{(k-1)}.$$

Equations of the above form can be written in matrix form, and so

$$
\begin{pmatrix} x_1^{(k)} \\ x_2^{(k)} \\ x_3^{(k)} \\ \vdots \\ x_n^{(k)} \end{pmatrix} = \begin{pmatrix} b_1 & b_2 & b_3 & \cdots & b_{n-1} & b_n \\ c_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & c_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & c_{n-1} & 0 \end{pmatrix} \begin{pmatrix} x_1^{(k-1)} \\ x_2^{(k-2)} \\ x_3^{(k-1)} \\ \vdots \\ x_n^{(k-1)} \end{pmatrix},
$$

or

$$
X^{(k)} = LX^{(k-1)}, \quad k = 1, 2, \ldots,
$$

where $X \in \Re^n$ and the matrix L is called the *Leslie matrix*.

Suppose that $X^{(0)}$ is a vector giving the initial number of females in each of the n age classes, then

$$
X^{(1)} = LX^{(0)},
$$

$$
X^{(2)} = LX^{(1)} = L^2 X^{(0)},
$$

$$
\vdots
$$

$$
X^{(k)} = LX^{(k-1)} = L^k X^{(0)}.
$$

Therefore, given the initial age distribution and the Leslie matrix L, it is possible to determine the female age distribution at any later time interval.

Example 4. Consider a species of bird that can be split into three age groupings: those aged 0–1 year, those aged 1–2 years, and those aged 2–3 years. The population is observed once a year. Given that the Leslie matrix is equal to

$$
L = \begin{pmatrix} 0 & 3 & 1 \\ 0.3 & 0 & 0 \\ 0 & 0.5 & 0 \end{pmatrix},
$$

and the initial population distribution of females is $x_1^{(0)} = 1000$, $x_2^{(0)} = 2000$, and $x_3^{(0)} = 3000$, compute the number of females in each age group after

(a) 10 years;
(b) 20 years;
(c) 50 years.

Solution. Using the above,

$$\text{(a) } X^{(10)} = L^{10} X^{(0)} = \begin{pmatrix} 5383 \\ 2177 \\ 712 \end{pmatrix},$$

$$\text{(b) } X^{(20)} = L^{20} X^{(0)} = \begin{pmatrix} 7740 \\ 2388 \\ 1097 \end{pmatrix},$$

$$\text{(c) } X^{(50)} = L^{50} X^{(0)} = \begin{pmatrix} 15695 \\ 4603 \\ 2249 \end{pmatrix}.$$

The numbers are rounded down to whole numbers since it is not possible to have a fraction of a living bird. Obviously, the populations cannot keep on growing indefinitely. However, the model does give useful results for some species when the time periods are relatively short.

In order to investigate the limiting behavior of the system it is necessary to consider the eigenvalues and eigenvectors of the matrix L. These can be used to determine the eventual population distribution with respect to the age classes.

Theorem 3. *Let the Leslie matrix L be as defined above and assume that*

(a) *$b_i \geq 0$ for $1 \leq i \leq n$;*
(b) *at least two successive b_i are strictly positive; and*
(c) *$0 < c_i \leq 1$ for $1 \leq i < n$.*

Then,

  (i) *matrix L has a unique positive eigenvalue, say, λ_1;*
 (ii) *λ_1 is simple or has algebraic multiplicity one;*
(iii) *the eigenvector—X_1, say—corresponding to λ_1 has positive components;*
(iv) *any other eigenvalue, $\lambda_i \neq \lambda_1$, of L satisfies*

$$|\lambda_i| < \lambda_1,$$

and the positive eigenvalue λ_1 is called strictly dominant.

The reader will be asked to prove part (i) in the exercises at the end of the chapter. If the Leslie matrix L has a unique positive strictly dominant eigenvalue, then an eigenvector corresponding to λ_1 is a nonzero vector solution of

$$LX = \lambda_1 X.$$

Assume that $x_1 = 1$, then a possible eigenvector corresponding to λ_1 is given by

$$
X_1 = \begin{pmatrix} 1 \\ \frac{c_1}{\lambda_1} \\ \frac{c_1 c_2}{\lambda_1^2} \\ \vdots \\ \frac{c_1 c_2 \ldots c_{n-1}}{\lambda_1^{n-1}} \end{pmatrix}.
$$

Assume that L has n linearly independent eigenvectors, say, $X_1, X_2, \ldots, X_n$. Therefore, L is diagonizable. If the initial population distribution is given by $X^{(0)} = X_0$, then there exist constants $b_1, b_2, \ldots, b_n$, such that

$$
X_0 = b_1 X_1 + b_2 X_2 + \ldots + b_n X_n.
$$

Since

$$
X^{(k)} = L^k X_0 \quad \text{and} \quad L^k X_i = \lambda_i^k X_i,
$$

then

$$
X^{(k)} = L^k (b_1 X_1 + b_2 X_2 + \ldots + b_n X_n) = b_1 \lambda_1^k X_1 + b_2 \lambda_2^k X_2 + \ldots + b_n \lambda_n^k X_n.
$$

Therefore,

$$
X^{(k)} = \lambda_1^k \left(b_1 X_1 + b_2 \left(\frac{\lambda_2}{\lambda_1} \right)^k X_2 + \ldots + b_n \left(\frac{\lambda_n}{\lambda_1} \right)^k X_n \right).
$$

Since λ_1 is dominant, $\left| \frac{\lambda_i}{\lambda_1} \right| < 1$ for $\lambda_i \neq \lambda_1$, and $\left(\frac{\lambda_i}{\lambda_1} \right)^k \to 0$ as $k \to \infty$. Thus, for large k,

$$
X^{(k)} \approx b_1 \lambda_1^k X_1.
$$

In the long run, the age distribution stabilizes and is proportional to the vector X_1. Each age group will change by a factor of λ_1 in each time period. The vector X_1 can be normalized so that its components sum to one, the normalized vector then gives the eventual proportions of females in each of the n age groupings.

Note that if $\lambda_1 > 1$, the population eventually increases; if $\lambda_1 = 1$, the population stabilizes and if $\lambda_1 < 1$, the population eventually decreases.

Example 5. Determine the eventual distribution of the age classes for Example 4.

Solution. The characteristic equation is given by

$$
\det(L - \lambda I) = \begin{vmatrix} -\lambda & 3 & 1 \\ 0.3 & -\lambda & 0 \\ 0 & 0.5 & -\lambda \end{vmatrix} = -\lambda^3 + 0.9\lambda + 0.15 = 0.
$$

The roots of the characteristic equation are:

$$\lambda_1 = 1.023, \ \lambda_2 = -0.851, \ \text{and} \ \lambda_3 = -0.172,$$

to three decimal places. Note that λ_1 is the dominant eigenvalue.

To find the eigenvector corresponding to λ_1, solve

$$\begin{pmatrix} -1.023 & 3 & 1 \\ 0.3 & -1.023 & 0 \\ 0 & 0.5 & -1.023 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \\ x_3 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}.$$

One solution is $x_1 = 2.929$, $x_2 = 0.855$, and $x_3 = 0.420$. Divide each term by the sum to obtain the normalized eigenvectors

$$\hat{X}_1 = \begin{pmatrix} 0.696 \\ 0.204 \\ 0.1 \end{pmatrix}.$$

Hence, after a number of years, the population will increase by approximately 2.3 % every year. The percentage of females aged 0–1 year will be 69.6 %, aged 1–2 years will be 20.4 %, and aged 2–3 years will be 10 %.

2.3   Harvesting and Culling Policies

This section will be concerned with insect and fish populations only since they tend to be very large. The model has applications when considering insect species which survive on crops, for example. An insect population can be culled each year by applying either an insecticide or a predator species. Harvesting of fish populations is particularly important nowadays; certain policies have to be employed to avoid depletion and extinction of the fish species. Harvesting indiscriminately could cause extinction of certain species of fish from our oceans.

A harvesting or culling policy should only be used if the population is increasing.

Definition 1. A harvesting or culling policy is said to be *sustainable* if the number of fish, or insects, killed and the age distribution of the population remaining are the same after each time period.

Assume that the fish or insects are killed in short sharp bursts at the end of each time period. Let X be the population distribution vector for the species just before the harvesting or culling is applied. Suppose that a fraction of the females about to enter the $(i + 1)$st class are killed, giving a matrix

$$D = \begin{pmatrix} d_1 & 0 & 0 & \cdots & 0 \\ 0 & d_2 & 0 & \cdots & 0 \\ 0 & 0 & d_3 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \cdots & d_n \end{pmatrix}.$$

By definition, $0 \leq d_i \leq 1$, where $1 \leq i \leq n$. The numbers killed will be given by DLX and the population distribution of those remaining will be

$$LX - DLX = (I - D)LX.$$

In order for the policy to be sustainable one must have

$$(I - D)LX = X. \tag{2.6}$$

If the dominant eigenvalue of $(I - D)L$ is one, then X will be an eigenvector for this eigenvalue and the population will stabilize. This will impose certain conditions on the matrix D. Hence

$$I - D = \begin{pmatrix} (1-d_1) & 0 & 0 & \cdots & 0 \\ 0 & (1-d_2) & 0 & \cdots & 0 \\ 0 & 0 & (1-d_3) & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \cdots & (1-d_n) \end{pmatrix}$$

and the matrix, say, $M = (I - D)L$, is easily computed. The matrix M is also a Leslie matrix and hence has an eigenvalue $\lambda_1 = 1$ if and only if

$$(1 - d_1)(b_1 + b_2 c_1(1 - d_1) + b_3 c_1 c_2(1 - d_2)(1 - d_3)$$
$$+ \ldots + b_n c_1 \ldots c_{n-1}(1 - d_1) \ldots (1 - d_n)) = 1. \tag{2.7}$$

Only values of $0 \leq d_i \leq 1$, which satisfy (2.7) can produce a sustainable policy.

A possible eigenvector corresponding to $\lambda_1 = 1$ is given by

$$X_1 = \begin{pmatrix} 1 \\ (1-d_2)c_1 \\ (1-d_2)(1-d_3)c_1 c_2 \\ \vdots \\ (1-d_2) \ldots (1-d_n)c_1 c_2 \ldots c_{n-1} \end{pmatrix}.$$

The sustainable population will be $C_1 X_1$, where C_1 is a constant. Consider the following policies

Sustainable Uniform Harvesting or Culling. Let $d = d_1 = d_2 = \ldots = d_n$, then (2.6) becomes

$$(1 - d)LX = X,$$

which means that $\lambda_1 = \frac{1}{1-d}$. Hence a possible eigenvector corresponding to λ_1 is given by

$$X_1 = \begin{pmatrix} 1 \\ \frac{c_1}{\lambda_1} \\ \frac{c_1 c_2}{\lambda_1^2} \\ \vdots \\ \frac{c_1 c_2 \dots c_{n-1}}{\lambda_1^{n-1}} \end{pmatrix}.$$

Sustainable Harvesting or Culling of the Youngest Class. Let $d_1 = d$ and $d_2 = d_3 = \dots = d_n = 0$; therefore, (2.7) becomes

$$(1 - d)(b_1 + b_2 c_1 + b_3 c_1 c_2 + \dots + b_n c_1 c_2 \dots c_{n-1}) = 1,$$

or, equivalently,

$$(1 - d)R = 1,$$

where R is known as the *net reproduction rate*. Harvesting or culling is only viable if $R > 1$, unless you wish to eliminate an insect species. The age distribution after each harvest or cull is then given by

$$X_1 = \begin{pmatrix} 1 \\ c_1 \\ c_1 c_2 \\ \vdots \\ c_1 c_2 \dots c_{n-1} \end{pmatrix}.$$

Definition 2. An *optimal sustainable* harvesting or culling policy is one in which either one or two age classes are killed. If two classes are killed, then the older age class is completely killed.

Example 6. A certain species of fish can be divided into three 6-month age classes and has Leslie matrix

$$L = \begin{pmatrix} 0 & 4 & 3 \\ 0.5 & 0 & 0 \\ 0 & 0.25 & 0 \end{pmatrix}.$$

The species of fish is to be harvested by fishermen using one of four different policies which are uniform harvesting or harvesting one of the three age classes, respectively. Which of these four policies are sustainable? Decide which of the sustainable policies the fishermen should use.

Solution. The characteristic equation is given by

$$\det(L - \lambda I) = \begin{vmatrix} -\lambda & 4 & 3 \\ 0.5 & -\lambda & 0 \\ 0 & 0.25 & -\lambda \end{vmatrix} = -\lambda^3 + 2\lambda + 0.375 = 0.$$

The eigenvalues are given by $\lambda_1 = 1.5$, $\lambda_2 = -0.191$, and $\lambda_3 = -1.309$, to three decimal places. The eigenvalue λ_1 is dominant and the population will eventually increase by 50 % every 6 months. The normalized eigenvector corresponding to λ_1 is given by

$$\hat{X}_1 = \begin{pmatrix} 0.529 \\ 0.177 \\ 0.294 \end{pmatrix}.$$

So, after a number of years there will be 52.9 % of females aged 0–6 months, 17.7 % of females aged 6–12 months, and 29.4 % of females aged 12–18 months.

If the harvesting policy is to be sustainable, then (2.7) becomes

$$(1 - d_1)(b_1 + b_2 c_1(1 - d_2) + b_3 c_1 c_2(1 - d_2)(1 - d_3)) = 1.$$

Suppose that $h_i = (1 - d_i)$, then

$$h_1 h_2(2 + 0.375 h_3) = 1. \tag{2.8}$$

Consider the four policies separately.

(i) *Uniform harvesting*: let $\mathbf{h} = (h, h, h)$. Equation (2.8) becomes

$$h^2(2 + 0.375h) = 1,$$

which has solutions $h = 0.667$ and $d = 0.333$. The normalized eigenvector is given by

$$\hat{X}_U = \begin{pmatrix} 0.720 \\ 0.240 \\ 0.040 \end{pmatrix}.$$

(ii) *Harvesting the youngest age class*: let $\mathbf{h} = (h_1, 1, 1)$. Equation (2.8) becomes

$$h_1(2 + 0.375) = 1,$$

which has solutions $h_1 = 0.421$ and $d_1 = 0.579$. The normalized eigenvector is given by

$$\hat{X}_{A_1} = \begin{pmatrix} 0.615 \\ 0.308 \\ 0.077 \end{pmatrix}.$$

(iii) *Harvesting the middle age class*: let $\mathbf{h} = (1, h_2, 1)$. Equation (2.8) becomes

$$h_2(2 + 0.375) = 1,$$

which has solutions $h_2 = 0.421$ and $d_2 = 0.579$. The normalized eigenvector is given by

$$\hat{X}_{A_2} = \begin{pmatrix} 0.791 \\ 0.167 \\ 0.042 \end{pmatrix}.$$

(iv) *Harvesting the oldest age class*: let $\mathbf{h} = (1, 1, h_3)$. Equation (2.8) becomes

$$1(2 + 0.375h_3) = 1,$$

which has no solutions if $0 \le h_3 \le 1$.

Therefore, harvesting policies (i)–(iii) are sustainable and policy (iv) is not. The long-term distributions of the populations of fish are determined by the normalized eigenvectors $\hat{X}_U$, $\hat{X}_{A_1}$, and $\hat{X}_{A_2}$, given above. If, for example, the fishermen wanted to leave as many fish as possible in the youngest age class, then the policy which should be adopted is the second age class harvesting. Then 79.1 % of the females would be in the youngest age class after a number of years.

2.4 MATLAB Commands

```
% Program 2a: Recurrence relations.
% Solving a first order recurrence relation (Example 1).
% Call a MuPAD command using the evalin command.
% Commands are short enough for the Command Window.
xn=solve(rec(x(n+1)=(1+(3/(100)))*x(n),x(n),{x(0) = 10000}))
n=5
savings=vpa(eval(xn),7)
%Solving a second order recurrence relation (Example 2(i)).
clear
xn=solve(rec(x(n+2)-x(n+1)=6*x(n),x(n),{x(0)=1,x(1)=2}))
% Solving a characteristic equation (Example 2(iii)).
syms lambda
CE=lambda^2-lambda+1
lambda=solve(CE)
```

```
% Program 2b: Leslie matrix.
% Define a 3x3 Leslie Matrix (Example 4).
L=[0 3 1; 0.3 0 0; 0 0.5 0]
% Set initial conditions.
X0=[1000;2000;3000]
```

```
% After 10 years the population distribution will be:
X10=L^10*X0
% Find the eigenvectors and eigenvalues of L (Example 5).
[v,d]=eig(L)
```

2.5   Exercises

1. The difference equation used to model the length of a carpet, say, l_n, rolled n times is given by

$$l_{n+1} = l_n + \pi(4 + 2cn), \quad n = 0, 1, 2, 3, \ldots,$$

   where c is the thickness of the carpet. Solve this recurrence relation.

2. Solve the following second-order linear difference equations:

   (a) $x_{n+2} = 5x_{n+1} - 6x_n$, $n = 0, 1, 2, 3, \ldots$, if $x_0 = 1, x_1 = 4$;
   (b) $x_{n+2} = x_{n+1} - \frac{1}{4}x_n$, $n = 0, 1, 2, 3, \ldots$, if $x_0 = 1, x_1 = 2$;
   (c) $x_{n+2} = 2x_{n+1} - 2x_n$, $n = 0, 1, 2, 3, \ldots$, if $x_0 = 1, x_1 = 2$;
   (d) $F_{n+2} = F_{n+1} + F_n$, $n = 0, 1, 2, 3, \ldots$, if $F_1 = 1$ and $F_2 = 1$ (the sequence of numbers is known as the Fibonacci sequence);
   (e) $x_{n+2} = x_{n+1} + 2x_n - f(n)$, $n = 0, 1, 2, \ldots$, given that $x_0 = 2$ and $x_1 = 3$, when (i) $f(n) = 2$, (ii) $f(n) = 2n$ and (iii) $f(n) = e^n$ (use MATLAB for part (iii) only).

3. Consider a human population that is divided into three age classes: those aged 0–15 years, those aged 15–30 years, and those aged 30–45 years. The Leslie matrix for the female population is given by

$$L = \begin{pmatrix} 0 & 1 & 0.5 \\ 0.9 & 0 & 0 \\ 0 & 0.8 & 0 \end{pmatrix}.$$

   Given that the initial population distribution of females is $x_1^{(0)} = 10,000, x_2^{(0)} = 15,000$, and $x_3^{(0)} = 8,000$, compute the number of females in each of these groupings after

   (a) 225 years;
   (b) 750 years;
   (c) 1,500 years.

4. Consider the following Leslie matrix used to model the female portion of a species

$$L = \begin{pmatrix} 0 & 0 & 6 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{pmatrix}.$$

Determine the eigenvalues and eigenvectors of L. Show that there is no dominant eigenvalue and describe how the population would develop in the long term.

5. Consider a human population that is divided into five age classes: those aged 0–15 years, those aged 15–30 years, those aged 30–45 years, those aged 45–60 years, and those aged 60–75 years. The Leslie matrix for the female population is given by

$$L = \begin{pmatrix} 0 & 1 & 1.5 & 0 & 0 \\ 0.9 & 0 & 0 & 0 & 0 \\ 0 & 0.8 & 0 & 0 & 0 \\ 0 & 0 & 0.7 & 0 & 0 \\ 0 & 0 & 0 & 0.5 & 0 \end{pmatrix}.$$

Determine the eigenvalues and eigenvectors of L and describe how the population distribution develops.

6. Given that

$$L = \begin{pmatrix} b_1 & b_2 & b_3 & \cdots & b_{n-1} & b_n \\ c_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & c_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & c_{n-1} & 0 \end{pmatrix},$$

where $b_i \geq 0, 0 < c_i \leq 1$, and at least two successive b_i are strictly positive, prove that $p(\lambda) = 1$, if λ is an eigenvalue of L, where

$$p(\lambda) = \frac{b_1}{\lambda} + \frac{b_2 c_1}{\lambda^2} + \ldots + \frac{b_n c_1 c_2 \ldots c_{n-1}}{\lambda^n}.$$

Show the following:

(a) $p(\lambda)$ is strictly decreasing;
(b) $p(\lambda)$ has a vertical asymptote at $\lambda = 0$;
(c) $p(\lambda) \rightarrow 0$ as $\lambda \rightarrow \infty$.

Prove that a general Leslie matrix has a unique positive eigenvalue.

7. A certain species of insect can be divided into three age classes: 0–6 months, 6–12 months, and 12–18 months. A Leslie matrix for the female population is given by

$$L = \begin{pmatrix} 0 & 4 & 10 \\ 0.4 & 0 & 0 \\ 0 & 0.2 & 0 \end{pmatrix}.$$

Determine the long-term distribution of the insect population. An insecticide is applied which kills off 50 % of the youngest age class. Determine the long-term distribution if the insecticide is applied every 6 months.

8. Assuming the same model for the insects as in Exercise 7, determine the long-term distribution if an insecticide is applied every 6 months which kills 10% of the youngest age class, 40% of the middle age class, and 60% of the oldest age class.

9. In a fishery, a certain species of fish can be divided into three age groups each 1 year long. The Leslie matrix for the female portion of the population is given by

$$L = \begin{pmatrix} 0 & 3 & 36 \\ \frac{1}{3} & 0 & 0 \\ 0 & \frac{1}{2} & 0 \end{pmatrix}.$$

Show that without harvesting, the fish population would double each year. Describe the long-term behavior of the system if the following policies are applied:

(a) harvest 50 % from each age class;
(b) harvest the youngest fish only, using a sustainable policy;
(c) harvest 50 % of the youngest fish;
(d) harvest 50 % of the whole population from the youngest class only;
(e) harvest 50 % of the oldest fish.

10. Determine an optimal sustainable harvesting policy for the system given in Exercise 9 if the youngest age class is left untouched.

References

1. H. Anton, C. Rorres, *Elementary Linear Algebra* (Wiley, New York, 2005)
2. S. Barnet, *Discrete Mathematics* (Addison-Wesley, New York, 1998)
3. E. Chambon-Dubreuil, P. Auger, J.M. Gaillard, M. Khaladi, Effect of aggressive behaviour on age-structured population dynamics. Ecol. Model. **193**, 777–786 (2006)
4. S. Jal, T.G. Hallam, Effects of delay, truncations and density dependence in reproduction schedules on stability of nonlinear Leslie matrix models. J. Math. Biol. **31**, 367–395 (1993)
5. M.R.S Kulenovic, O. Merino, *Discrete Dynamical Systems and Difference Equations with Mathematica* (Chapman & Hall, London, 2002)
6. V.N. Lopatin, S.V. Rosolovsky, *Evaluation of the State and Productivity of Moose Populations using Leslie Matrix Analyses. An article from: Alces [HTML] (Digital)*, Alces, 2002
7. L. Monte, Characterisation of a nonlinear Leslie matrix model for predicting the dynamics of biological populations in polluted environments: applications to radioecology. Ecol. Model. **248**, 174–183 (2013)
8. E. Otumba, *The Extended Leslie Matrix Model: Estimation of Population Sizes of Migrating Sizes* (LAP LAMBERT Academic Publishing, Saarbrücken, 2011)

Springer