

Chapter 2

Discrete Population Models

2.1 Introduction: Linear Models

In this chapter we shall consider populations with a fixed interval between generations or possibly a fixed interval between measurements. Thus, we shall describe population size by a *sequence* $\{x_n\}$, with x_0 denoting the initial population size, x_1 the population size at the next generation (at time t_1), x_2 the population size at the second generation (at time t_2), and so on. The underlying assumption will always be that population size at each stage is determined by the population sizes in past generations, but that intermediate population sizes between generations are not needed. Usually the time interval between generations is taken to be a constant.

For example, suppose the population changes only through births and deaths, so that $x_{n+1} - x_n$ is the number of births minus the number of deaths over the time interval from t_n to t_{n+1} . Suppose further that the birth and death rates are constants b and d , respectively (that is, if the population size is x then there are bx births and dx deaths in that generation). Then

$$x_{n+1} - x_n = (b - d)x_n,$$

or

$$x_{n+1} = x_n + (b - d)x_n = (1 + b - d)x_n.$$

We let $r = 1 + b - d$ and obtain the *linear homogeneous difference equation*

$$x_{n+1} = rx_n.$$

This together with the prescribed initial population size x_0 determines the population size in each generation. By a *solution* of the difference equation $x_{n+1} = rx_n$ with initial value x_0 we mean a sequence $\{x_n\}$ such that $x_{n+1} = rx_n$ for $n = 0, 1, 2, \dots$, with x_0 as prescribed.

It is easy to solve the difference equation $x_{n+1} = rx_n$ algebraically. We begin by observing that $x_1 = rx_0$, $x_2 = rx_1 = r^2x_0$, $x_3 = rx_2 = r^3x_0$, and then we guess (and prove by induction) that the unique solution is $x_n = r^n x_0$ ($n = 0, 1, 2, \dots$). It follows

that if $|r| < 1$, then $x_n \rightarrow 0$ as $n \rightarrow \infty$, while if $|r| > 1$, then x_n grows unboundedly as $n \rightarrow \infty$. More precisely, if $0 \leq r < 1$, x_n decreases monotonically to zero; if $-1 < r < 0$, x_n oscillates, alternating between positive and negative values, but tends to zero; if $r > 1$, x_n increases to $+\infty$; if $r < -1$, x_n oscillates unboundedly. Negative values of x_n for this difference equation have no biological meaning, but we soon will consider difference equations in which the unknown is a deviation from equilibrium (which may be either positive or negative) rather than a population size. For this reason we have used the difference equation $x_{n+1} = rx_n$ as our first example, even though a more plausible model for a real population might be

$$x_{n+1} = \begin{cases} rx_n & \text{for } x_n > 0, \\ 0 & \text{for } x_n \leq 0, \end{cases}$$

which says that the population becomes extinct once it becomes zero in any generation. This will occur if and only if $r \leq 0$. The model $x_{n+1} = rx_n$ also arises under the assumption that all members of each generation die, but there is a constant birth rate b to form the next generation. In this case $d = 1$, so that $r = b$. We may form a different model by allowing migration and assuming a constant migration rate β per generation, with positive β denoting immigration and negative β denoting emigration. This leads to the linear inhomogeneous difference equation

$$x_{n+1} = rx_n + \beta,$$

which may also be solved iteratively,

$$\begin{aligned} x_1 &= rx_0 + \beta, \\ x_2 &= rx_1 + \beta = r(rx_0 + \beta) + \beta = r^2x_0 + r\beta + \beta, \\ x_3 &= rx_2 + \beta = r(r^2x_0 + r\beta + \beta) + \beta = r^3x_0 + r^2\beta + r\beta + \beta \\ &\vdots \end{aligned}$$

Again we may guess, and then prove by induction, that

$$\begin{aligned} x_n &= r^n x_0 + \beta(r^{n-1} + r^{n-2} + \dots + r + 1) \\ &= r^n x_0 + \frac{\beta(1 - r^n)}{1 - r} = \left(x_0 - \frac{\beta}{1 - r}\right)r^n + \frac{\beta}{1 - r}. \end{aligned}$$

If $r > 1$, then x_n grows unboundedly for $\beta > -(r - 1)x_0$, but x_n reaches zero if $\beta < -(r - 1)x_0$; thus sufficiently large emigration will wipe out a population that would otherwise grow unboundedly. If $0 < r < 1$, then x_n tends to the limit $\beta/(1 - r) > 0$ for $\beta > 0$, while x_n reaches zero for $\beta < 0$. Thus, immigration may produce survival of a population that would otherwise become extinct.

The assumption of a constant growth rate independent of population size is unlikely to be reasonable for real populations except possibly while the population size is small enough not to be subject to the effects of overcrowding. Various nonlinear

difference equation models have been proposed as more realistic. For example, the difference equations

$$x_{n+1} = \frac{rx_n}{x_n + A} \quad [\text{Verhulst (1845)}]$$

and

$$x_{n+1} = \frac{rx_n^2}{x_n^2 + A}$$

have been suggested as descriptions of populations that die out completely in each generation and have birth rates that saturate for large population sizes. The difference equations

$$x_{n+1} = x_n + rx_n \left(1 - \frac{x_n}{K}\right) \quad \text{and} \quad x_{n+1} = rx_n \left(1 - \frac{x_n}{K}\right),$$

both called the *logistic* difference equation, and essentially equivalent, describe populations with growth rates that decrease to zero as the population grows large. Neither should be taken too seriously for large population sizes since x_{n+1} becomes negative if x_n is too large. Another form, which could with some justification also be called the logistic equation, is

$$x_{n+1} = x_n e^{r(1-x_n/K)}.$$

Here the growth rate decreases to zero as $x_n \rightarrow \infty$, but x_{n+1} cannot become negative. Other difference equations, which have in fact been used as models to try to fit field data, are

$$x_{n+1} = rx_n(1 + \alpha x_n)^{-\beta} \quad [\text{Hassell (1975)}]$$

and

$$x_{n+1} = \begin{cases} r\epsilon^\beta x_n^{1-\beta} & \text{for } x_n > \epsilon \\ rx_n & \text{for } x_n < \epsilon. \end{cases}$$

It should be recognized that none of these models is derived from actual population growth laws. Rather, they are attempts to give quantitative expression to rough qualitative ideas about the biological laws governing the population. For this reason, we should be skeptical of the biological significance of any deduction from a specific model that holds only for that model. Our goal should be to formulate principles that are *robust*, that is, valid for a large class of models (ideally for all models that embody some set of qualitative hypotheses). In Section 2.5 we will describe some difference equation models that have been used to model fish populations and that are based on biological assumptions. Such models give some insight into the types of qualitative hypotheses that may be realistic.

Exercises

1. Find the solution of the difference equation $x_{n+1} = \frac{1}{2}x_n$, $x_0 = 2$.
2. Find the solution of the difference equation $x_{n+1} = \frac{1}{2}x_n + 1$, $x_0 = 2$.
3. Find by calculating recursively the solution of the second-order difference equation $x_{n+2} = \frac{1}{2}x_n$, $x_0 = 1$, $x_1 = -1$.
4. Consider the second order difference equation

$$x_{n+2} - 3x_{n+1} + 2x_n = 0.$$

- a. Show that the general solution to the equation is of the form

$$x_n = A_1 + 2^n A_2,$$

where A_1 and A_2 are any constants.

- b. Suppose that x_0 and x_1 are given. Then A_1 and A_2 must satisfy the system of equations

$$A_1 + A_2 = x_0,$$

$$A_1 + 2A_2 = x_1.$$

- c. From the general solution, solve for the specific solution with initial conditions $x_0 = 10$ and $x_1 = 20$.
5. Find by calculating recursively the solution of the second-order difference equation $x_{n+2} = rx_n$, $x_0 = 1$, $x_1 = -1$.
 6. Find the general form of the solution of the difference equation

$$x_{n+1} = c - x_n$$

with c arbitrary for an arbitrary initial value $x_0 = a$.

7. Consider the model

$$x_{n+1} = rx_n \left(1 - \frac{x_n}{K}\right), \quad r > 0.$$

- a. Show that $x_{n+1} < 0$ if and only if $x_n > K$.
 - b. Show that $x_{n+1} > K$ is possible with $0 < x_n < K$ only for $r > 4$.
 - c. What conditions on x_0 are necessary and sufficient to guarantee $x_n > 0$ for $n = 1, 2, 3, \dots$?
8. Find the general form of the solution of the difference equation

$$x_{n+1} = 1 - x_n$$

for an arbitrary initial value $x_0 = a$.

- 9*. The solution of the difference equation $x_{n+2} = x_n + x_{n+1}$, $x_0 = 0$, $x_1 = 1$ is called the *Fibonacci sequence* (originally formulated by Leonardo Fibonacci

(1202) to describe the number of pairs of rabbits under the hypothesis that each pair of rabbits reproduces only at age one month and age two months and produces exactly one pair of offspring on each of these two occasions, with all rabbits living exactly two months).

- Calculate the first eight terms of the Fibonacci sequence.
- Suppose it can be shown that the ratio of successive terms x_{n+1}/x_n of the Fibonacci sequence tends to a limit τ as $n \rightarrow \infty$. Show that $\tau = \frac{1}{\tau} + 1$.
- Deduce that $\tau = \frac{1+\sqrt{5}}{2}$.

10*. For a general, not necessarily linear, first-order difference equation

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

show that if a solution $\{x_n\}$ approaches a limit x_∞ as $n \rightarrow \infty$, then the limit x_∞ must satisfy the equation

$$x_\infty = f(x_\infty).$$

2.2 Graphical Solution of Difference Equations

There is a way of solving difference equations graphically, called the *cobwebbing method*, which we illustrate for the simple linear homogeneous example $x_{n+1} = rx_n$. We begin by drawing the *reproduction curve* $y = rx$ in the (x, y) -plane. Then we mark x_0 , go vertically to the reproduction curve, and from there horizontally to the line $y = x$ at the point (x_1, x_1) . Then we go vertically to the reproduction curve and from there horizontally to the line $y = x$ at the point (x_2, x_2) , and so on. There are four separate cases: $r > 1$, $0 < r < 1$, $-1 < r < 0$, and $r < -1$, corresponding to different relative positions of the reproduction curve $y = rx$ and the line $y = x$. In each case, the graphical solution illustrates the behavior already obtained analytically (Figure 2.1).

The cobwebbing method can be applied to any difference equation of the form $x_{n+1} = f(x_n)$ using the reproduction curve $y = f(x)$ and the line $y = x$; it gives information about the behavior of solutions. This is particularly useful for difference equations whose analytic solution is complicated. We give two more illustrative examples.

Example 1. (Verhulst equation) For the equation

$$x_{n+1} = \frac{rx_n}{x_n + A},$$

the reproduction curve is $y = rx/(x + A)$. Its slope is given by $dy/dx = rA/(x + A)^2$, which has the value r/A at $x = 0$. This means that we must distinguish the cases $r < A$, for which the line $y = x$ lies below the reproduction curve, and $r > A$, for which the line $y = x$ intersects the reproduction curve (Figure 2.2).

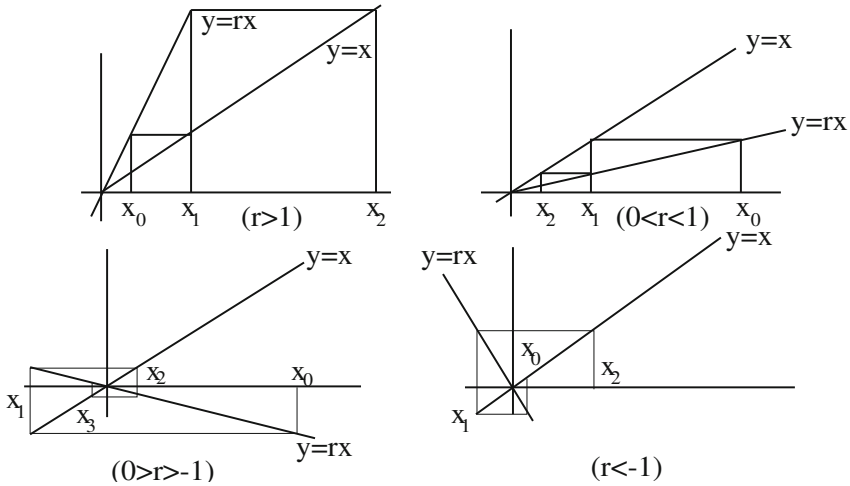


Fig. 2.1 Cobwebbing for a linear difference equation.

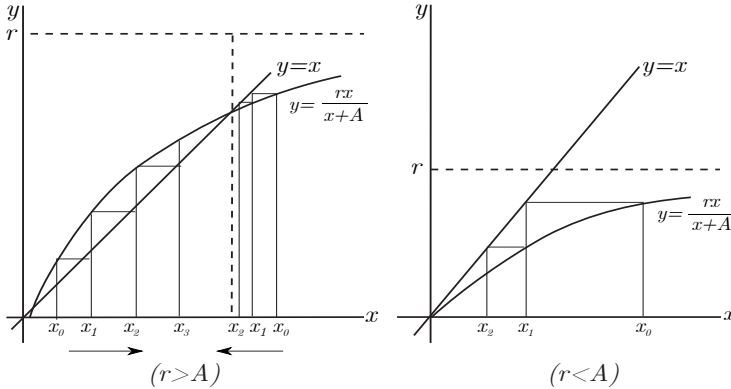


Fig. 2.2 Cobwebbing for the Verhulst equation

If $r > A$, every solution, regardless of the initial value x_0 , tends to the limit $x_\infty = r - A$ where the line $y = x$ and the reproduction curve $y = rx/(x + A)$ intersect. If $r < A$, every solution tends to the limit zero.

Example 2. For the equation

$$x_{n+1} = \frac{rx_n^2}{x_n^2 + A},$$

the reproduction curve is $y = rx^2/(x^2 + A)$, which intersects the line $y = x$ at $x = 0$ and at $x = (r \pm \sqrt{r^2 - 4A})/2$. Thus for $r > 2\sqrt{A}$ there are three real intersections, and for $r < 2\sqrt{A}$ the only real intersection is at $x = 0$ (Figure 2.3).

If $r > 2\sqrt{A}$, all solutions with $x_0 < (r - \sqrt{r^2 - 4A})/2$ tend to zero, and solutions with $x_0 > (r - \sqrt{r^2 - 4A})/2$ tend to the limit $x_\infty = (r + \sqrt{r^2 - 4A})/2$. If $r < 2\sqrt{A}$,

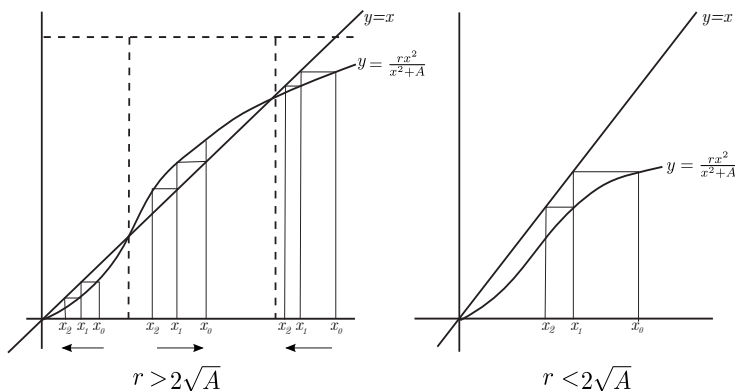


Fig. 2.3 Cobwebbing for model with Allee effect.

all solutions tend to the limit zero. This model attempts to describe populations that collapse if their initial size is too small but survive if their initial size is large enough. This is analogous to the critical depensation model, or Allee effect, described for continuous population models in Section 1.4.

Exercises

1. Use the cobwebbing method to sketch the first few terms of the solution of

$$x_{n+1} = x_n + x_n(1 - x_n), \quad x_0 = \frac{1}{2}.$$

2. Use the cobwebbing method to sketch the first few terms of the solution of

$$x_{n+1} = x_n + 2.2x_n(1 - x_n), \quad x_0 = \frac{1}{2}.$$

3. Use the cobwebbing method to sketch the first few terms of the solution of

$$x_{n+1} = x_n + 3x_n(1 - x_n), \quad x_0 = \frac{1}{2}.$$

4. Consider the difference equation

$$x_{n+1} = \begin{cases} x_n^{1/2} & \text{for } x_n > \frac{1}{4}, \\ 2x_n & \text{for } x_n < \frac{1}{4}. \end{cases}$$

Sketch the solutions for several different choices of x_0 between zero and one.

5. [Kaplan & Glass (1995)] Assume that the density of flies in a swamp is described by the equation

$$x_{n+1} = Rx_n - \frac{R}{2000}x_n^2.$$

Consider three values of R , where one value of R comes from each of the following ranges:

- (1) $1 \leq R < 3$,
- (2) $3 \leq R < 3.449$,
- (3) $3.57 \leq R < 4$.

For each value of R graph x_{n+1} as a function of x_n . Using the cobwebbing method, follow x_n for several generations. Describe the qualitative behavior found for $R = 2$.

2.3 Equilibrium Analysis

In the examples of the preceding section we observed a tendency for solutions to approach a limit that is the x -coordinate of an intersection of the reproduction curve and the line $y = x$. Such a value of x is a constant solution of the difference equation. This motivates the following definition of *equilibrium* of a difference equation:

$$x_{n+1} = f(x_n). \quad (2.1)$$

Definition 2.1. An *equilibrium* of a difference equation (2.1) is a value x_∞ such that $x_\infty = f(x_\infty)$, so that $x_n = x_\infty$ ($n = 0, 1, 2, \dots$) is a constant solution of the difference equation.

In order to describe the behavior of solutions near an equilibrium, we introduce the process of *linearization* just as we did in Section 1.4 for first-order differential equations. If x_∞ is an equilibrium of the difference equation $x_{n+1} = f(x_n)$, so that $x_\infty = f(x_\infty)$, we make the change of variable $u_n = x_n - x_\infty$ ($n = 0, 1, 2, \dots$). Thus u_n represents deviation from the equilibrium value. Substitution gives

$$x_\infty + u_{n+1} = f(x_\infty + u_n),$$

and application of Taylor's theorem gives

$$x_\infty + u_{n+1} = f(x_\infty + u_n) = f(x_\infty) + f'(x_\infty)u_n + \frac{f''(c_n)}{2!}u_n^2$$

for some c_n between x_∞ and $x_\infty + u_n$. We write $h(u_n) = f''(c_n)u_n^2/2!$ and use the relation $x_\infty = f(x_\infty)$ to form the difference equation equivalent to the original difference equation (2.1),

$$u_{n+1} = f'(x_\infty)u_n + h(u_n). \quad (2.2)$$

The function $h(u)$ is small for u , small in the sense that $|h(u)/u| \rightarrow 0$ as $|u| \rightarrow 0$; more precisely, for every $\varepsilon > 0$ there exists $\delta > 0$ such that $|h(u)| < \varepsilon|u|$ whenever $|u| < \delta$. The *linearization* of the difference equation $x_{n+1} = f(x_n)$ at the equilibrium

x_∞ is defined to be the linear homogeneous difference equation

$$v_{n+1} = f'(x_\infty)v_n, \quad (2.3)$$

obtained by neglecting the higher-order term $h(u_n)$ in (2.2). The importance of the linearization lies in the fact that the behavior of its solutions describes the behavior of solutions of the original equation (2.1) near the equilibrium. The behavior of solutions of the linearization has been described completely in Section 2.1. The following result explains the significance of the linearization at an equilibrium.

Theorem 2.1. *If all solutions of the linearization (2.3) at an equilibrium x_∞ tend to zero as $n \rightarrow \infty$, then all solutions of (2.1) with x_0 sufficiently close to x_∞ tend to the equilibrium x_∞ as $n \rightarrow \infty$.*

Proof. For convenience we write $\rho = |f'(x_\infty)|$. The assumption that all solutions of the linearization tend to zero is equivalent to $\rho < 1$. Now choose $\varepsilon > 0$ so that $\rho + \varepsilon < 1$. The difference equation $x_{n+1} = f(x_n)$ is equivalent to $u_{n+1} = f'(x_\infty)u_n + h(u_n)$. Then

$$|u_{n+1}| \leq |f'(x_\infty)||u_n| + |h(u_n)| < \rho|u_n| + \varepsilon|u_n|$$

provided $|u_n| < \delta$, where δ is determined by the condition that $|h(u)| < \varepsilon|u|$ for $|u| < \delta$. Thus, $|u_{n+1}| \leq (\rho + \varepsilon)|u_n|$ provided $|u_n| < \delta$. If $|u_0| < \delta$, it is easy to show by induction that $|u_{n+1}| < \delta$ for $n = 0, 1, 2, \dots$. This establishes $|u_{n+1}| \leq (\rho + \varepsilon)|u_n|$ for $n = 0, 1, 2, \dots$. Now it is easy to show, again by induction, that

$$|u_n| \leq (\rho + \varepsilon)^n |u_0|, \quad n = 0, 1, 2, \dots$$

Since $\rho + \varepsilon < 1$, it follows that $u_n \rightarrow 0$, and thus that $x_n \rightarrow x_\infty$ as $n \rightarrow \infty$.

In Section 2.1 we observed that if $|f'(x_\infty)| < 1$, then the solutions of $v_{n+1} = f'(x_\infty)v_n$ all tend to zero, and further that this approach is monotone if $0 < f'(x_\infty) < 1$ and oscillatory if $-1 < f'(x_\infty) < 0$. It is possible to refine Theorem 2.1 to show that the approach to an equilibrium x_∞ of $x_{n+1} = f(x_n)$ is monotone if $0 < f'(x_\infty) < 1$ and oscillatory if $-1 < f'(x_\infty) < 0$. That this is true is suggested by the cobwebbing method (Figure 2.4).

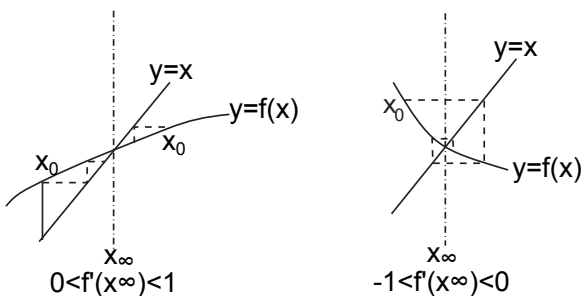


Fig. 2.4 Stability of equilibrium.

The content of Theorem 2.1 is that an equilibrium x_∞ with $|f'(x_\infty)| < 1$ has the property that every solution with x_0 close enough to x_∞ remains close to x_∞ and tends to x_∞ as $n \rightarrow \infty$. This property is called *asymptotic stability* of the equilibrium x_∞ . The condition $f'(x_\infty) < 1$ means that the curve $y = f(x)$ crosses the line $y = x$ from above to below as x increases, while the condition $f'(x_\infty) > -1$ means that the curve $y = f(x)$ cannot be too steep at the crossing. If $|f'(x_\infty)| > 1$, it is not difficult to show that except for the constant solution $x_n = x_\infty$ ($n = 0, 1, 2, \dots$), solutions cannot remain close to x_∞ . This property is called *instability* of the equilibrium x_∞ . An unstable equilibrium has no biological significance, since any deviation, however small, is enough to force solutions away.

We emphasize that Theorem 2.1 applies to solutions whose initial value x_0 is close enough to the equilibrium x_∞ . This is because the nonlinear term $h(u_n)$ in the difference equation $u_{n+1} = f'(x_\infty)u_n + h(u_n)$ is small enough to have an almost negligible effect on the solution only near the equilibrium x_∞ . Theorem 2.1 gives no explicit method of computing how close to x_∞ is close enough for the solution with a given initial value to tend to x_∞ . Often this can be seen in practice using the cobwebbing method of constructing solutions graphically, as we have shown in Section 2.2. Proofs of the theorems in this section may be found in such books as [Elaydi (1996)] and [Sandefur(1990)].

Example 1. For the *logistic* difference equation

$$x_{n+1} = x_n + rx_n \left(1 - \frac{x_n}{K}\right)$$

with $f(x) = (1+r)x - rx^2/K$ and $f'(x) = (1+r) - 2rx/K$, it is easy to find equilibria by solving the quadratic equation $x = x + rx(1 - x/K)$ and obtaining the roots $x = 0$ and $x = K$. Since $f'(0) = 1 + r$, the equilibrium $x = 0$ is asymptotically stable if $-1 < 1 + r < 1$, or $-2 < r < 0$. Since $r > 0$ in applications, this means that the equilibrium $x = 0$ is unstable. Since $f'(K) = 1 - r$, the equilibrium $x = K$ is asymptotically stable if $0 < r < 2$. It is not difficult to show that for $0 < r < 2$, every solution tends to the equilibrium K . If $r > 2$, the equilibrium $x = K$ is unstable and there is no asymptotically stable equilibrium to which solutions can tend. In the following section, we shall explore the behavior of solutions if $r > 2$ in more detail.

The logistic difference equation is sometimes presented in the form

$$x_{n+1} = rx_n \left(1 - \frac{x_n}{K}\right).$$

The study of the equation in this form is quite similar to the previous discussion; there is an equilibrium at $x = 0$ that is asymptotically stable if $r < 1$, in which case every solution tends to zero, and an equilibrium at $x = K(1 - 1/r)$ that is asymptotically stable if $1 < r < 3$, in which case every solution tends to $K(1 - 1/r)$, and if $r > 3$ there is no asymptotically stable equilibrium.

Example 2. For the Verhulst equation

$$x_{n+1} = \frac{rx_n}{x_n + A},$$

we have $f(x) = rx/(x+A)$; $f'(x) = rA/(x+A)^2$. The solution of $x = rx/(x+A)$ gives two roots, $x = 0$ and $x = r - A$. Thus, if $r < A$ the only equilibrium corresponding to a nonnegative population size is $x = 0$. Since $f'(0) = r/A < 1$, this equilibrium is asymptotically stable and every solution tends to zero. If $r > A$ there are two equilibria, $x = 0$, and $x = x_\infty = r - A$. Since $f'(0) = r/A > 1$, the equilibrium at $x = 0$ is unstable. Since $f'(x_\infty) = A/r < 1$, the equilibrium x_∞ is asymptotically stable. We have seen in Section 2.2 (graphically) that in fact every solution approaches x_∞ , that is, that the equilibrium x_∞ is globally asymptotically stable.

Exercises

In Exercises 1 through 9 find each equilibrium of the given difference equation and determine whether it is asymptotically stable or unstable.

1. $x_{n+1} = \frac{rx_n^2}{x_n^2 + A}$ (r and A are nonnegative).
2. $x_{n+1} = x_n e^{r(1-x_n/K)}$.
3. $x_{n+1} = rx_n(1 + \alpha x_n)^{-\beta}$.
4. $x_{n+1} = \begin{cases} x_n^{1/2} & \text{for } x_n > \frac{1}{4}, \\ 2x_n & \text{for } x_n < \frac{1}{4}. \end{cases}$
5. $x_{n+1} = \frac{2x_n}{1+x_n}$.
6. $x_{n+1} = x_n \log x_n$.
7. $x_{n+1} = \left(\frac{1}{\alpha x_n^b}\right)(\lambda x_n)$.
8. $x_{n+1} = x_n \exp(r(1 - \frac{x_n}{K}))$.
9. $x_{n+1} = \frac{\lambda x_n}{(1 + \alpha x_n)^b}$.
10. a. A population is governed by the difference equation

$$x_{n+1} = x_n e^{3-x_n}.$$

Show that all equilibria are unstable.

- b. The population of part (a) is to be stabilized by removing a fraction p ($0 < p < 1$) of the population in each time period after all births and deaths have taken place, to give the model

$$x_{n+1} = (1-p)x_n e^{3-(1-p)x_n}.$$

For what values of p does the population have an asymptotically stable positive equilibrium?

11. a. In the Fibonacci equation (see Exercise 9, Section 2.1) $x_{n+2} = x_n + x_{n+1}$, make the change of variable $u_n = x_{n+1}/x_n$ and obtain the transformed difference equation $u_{n+1} = 1 + 1/u_n$.
 b. Find all equilibria of the transformed difference equation of part (a) and determine which are asymptotically stable.
12. a. Find the nonnegative equilibria of a population governed by

$$x_{n+1} = \frac{3x_n^2}{x_n^2 + 2}$$

and check for stability.

- b. Suppose a fraction a is removed from the population in each generation, so that the model becomes

$$x_{n+1} = \frac{3x_n^2}{x_n^2 + 2} - ax_n.$$

For what values of a is there a stable equilibrium only at $x = 0$?

13. [Kaplan & Glass (1995)] The following equation plays a role in the analysis of nonlinear models of gene and neural networks:

$$x_{n+1} = \frac{\alpha x_n}{1 + \beta x_n},$$

where α and β are positive numbers and $x_n \geq 0$.

- a. Algebraically determine the fixed points. For each fixed point give the range of α and β for which it exists, indicate whether the fixed point is stable or unstable, and state whether the dynamics in the neighborhood of the fixed point are monotonic or oscillatory. For parts (b) and (c) assume $\alpha = \beta = 1$.
 - b. Sketch the graph of x_{n+1} as a function of x_n . Graphically iterate the equation starting from the initial condition $x_0 = 10$. What happens as the number of iterates approaches ∞ ?
 - c. Algebraically determine x_{n+2} as a function of x_n , and x_{n+3} as a function of x_n . Based on these computations what is the algebraic expression for x_{n+k} as a function of x_n ? What is the behavior of x_{n+k} as $k \rightarrow \infty$? This should agree with what you found in part (b).
14. Consider the following pair of difference equations:

$$\begin{aligned} x_{n+1} &= f(n, x_n), \\ y_{n+1} &= g(n, y_n), \end{aligned}$$

where f and g are nonnegative functions defined on $[0, \infty)$. Assume that $f(n, x_n) \leq g(n, x_n)$ for each nonnegative integer n and each nonnegative x_n and $g(n, y(n))$ is nondecreasing with respect to the second argument y_n . Prove that if $\{x_n\}_{n \geq 0}$ is a solution of the first equation and $\{y_n\}_{n \geq 0}$ is a solution of the

second equation with $x_0 \leq y_0$, then $x_n \leq y_n$ for all $n = 0, 1, 2, 3, \dots$.

15. Consider the single-species discrete-time population model

$$x_{n+1} = x_n e^{\beta \frac{1-x_n}{1+x_n}}$$

where $x_n \geq 0$ is the nonnegative population density in generation n , and the positive constant β is greater than 4. Let $\{x_1, x_2\}$ be a 2-cycle of this model, where $x_1 > 0$, $x_2 > 0$ and $x_1 \neq x_2$. Decide whether the 2-cycle $\{x_1, x_2\}$ is asymptotically stable. Explain.

2.4 Period-Doubling and Chaotic Behavior

For the logistic difference equation

$$x_{n+1} = x_n + rx_n \left(1 - \frac{x_n}{K}\right),$$

we have seen that the equilibrium $x_\infty = K$ is asymptotically stable for $0 < r < 2$. How do solutions behave if $r > 2$? We may think of r as a parameter that may be varied, and as r passes through the value 2, there must be a fundamental change in the behavior of solutions. While there is an equilibrium of K for all r , every solution tends to this equilibrium if $0 < r < 2$, but no solution other than the constant solution $x_n = K$ ($n = 0, 1, 2, \dots$) tends to this equilibrium if $r > 2$. What happens when r increases past 2 is that a solution of period 2 appears. By this we mean that there are two values, x^+ and x^- , with $f(x^+) = x^-$, $f(x^-) = x^+$ such that the alternating sequence x^+, x^-, x^+, \dots is a solution of the difference equation.

To establish the existence of this periodic solution, we take

$$f(x) = x + rx \left(1 - \frac{x}{K}\right) = (1+r)x - \frac{r}{K}x^2$$

and define

$$\begin{aligned} f_2(x) &= f(f(x)) = (1+r)f(x) - \frac{r}{K}(f(x))^2 \\ &= (1+r)^2x - \frac{r(1+r)}{K}x^2 - \frac{r}{K}\left((1+r)x - \frac{r}{K}x^2\right)^2 \\ &= (1+r)^2x - \frac{r(1+r)(2+r)}{K}x^2 + \frac{2r^2}{K^2}(1+r)x^3 - \frac{r^3}{K^3}x^4. \end{aligned}$$

We now look for equilibria of the second-order difference equation

$$x_{n+2} = f_2(x_n).$$

Such equilibria give solutions of period 2 for the original difference equation $x_{n+1} = f(x_n)$. These equilibria are solutions of the fourth-degree polynomial equation

$$x = (1+r)^2x - \frac{r(r+1)(r+2)}{K}x^2 + \frac{2r^2(1+r)}{K^2}x^3 - \frac{r^3}{K^3}x^4,$$

giving

$$x \left(r^3 \left(\frac{x}{K} \right)^3 - 2r^2(1+r) \left(\frac{x}{K} \right)^2 + r(r+1)(r+2) \left(\frac{x}{K} \right) - r(r+2) \right) = 0$$

or

$$x \left(\left(\frac{x}{K} \right) - 1 \right) \left(r^2 \left(\frac{x}{K} \right)^2 - r(r+2) \left(\frac{x}{K} \right) + (r+2) \right) = 0.$$

There are four roots, namely $x = 0$, $x = K$, and the roots x_+ , x_- of the quadratic equation $r^2(x/K)^2 - r(r+2)(x/K) + (r+2) = 0$. Thus

$$x_+ = \frac{(r+2) + \sqrt{r^2-4}}{2r}K, \quad x_- = \frac{(r+2) - \sqrt{r^2-4}}{2r}K,$$

and these roots are real if $r \geq 2$. We also have

$$\begin{aligned} f(x_+) &= (1+r)x_+ - \frac{r}{K}x_+^2 \\ &= (r+1)\frac{r+2}{2r}K + (r+1)\frac{\sqrt{r^2-4}}{2r}K \\ &\quad - \frac{r}{K}\frac{K^2}{4r^2} \left((r+2)^2 + r^2 - 4 + 2(r+2)\sqrt{r^2-4} \right) \\ \frac{2r}{K}f(x_+) &= (r+1)(r+2) + (r+1)\sqrt{r^2-4} \\ &\quad - \frac{1}{2} \left(r^2 + 4r + 4 + r^2 - 4 + 2(r+2)\sqrt{r^2-4} \right) \\ &= (r+2) - \sqrt{r^2-4} = \frac{2r}{K}x_-. \end{aligned}$$

Thus $f(x_+) = x_-$, and since $f_2(x_+) = f(f(x_+)) = x_+$, we have $f(x_-) = x_+$. We have now shown that if $r > 2$, there is a periodic solution of period 2 of $x_{n+1} = f(x_n)$ given by $x_n = x_+$ (if n is odd), $x_n = x_-$ (if n is even).

In order to test the stability of this periodic solution, we must compute $f_2'(x_+)$, which may be done by starting with

$$\begin{aligned} f_2(x) - x &= -rx \left(\left(\frac{x}{K} \right) - 1 \right) \left(r^2 \left(\frac{x}{K} \right)^2 - r(r+2) \left(\frac{x}{K} \right) + (r+2) \right) \\ &= r \left(x - \frac{x^2}{K} \right) \left(r^2 \left(\frac{x}{K} \right)^2 - r(r+2) \left(\frac{x}{K} \right) + (r+2) \right). \end{aligned}$$

Differentiation (using the product rule) gives

$$\begin{aligned} f'_2(x) - 1 &= r \left(1 - \frac{2x}{K} \right) \left(r^2 \left(\frac{x}{K} \right)^2 - r(r+2) \left(\frac{x}{K} \right) + (r+2) \right) \\ &\quad + r \left(x - \frac{x^2}{K} \right) \left(2r \frac{x}{K^2} - \frac{r(r+2)}{K} \right). \end{aligned}$$

Since $r^2(x_+/K)^2 - r(r+2)(x_+/K)r(r+2) = 0$, we have

$$\begin{aligned} f'_2(x_+) - 1 &= r \left(x_+ - \frac{x_+^2}{K} \right) \left(2r \frac{x_+}{K^2} - \frac{r(r+2)}{K} \right) \\ &= \frac{r(r+2) + r\sqrt{r^2-4}}{2} \left(1 - \frac{(r+2) + \sqrt{r^2-4}}{2r} \right) \sqrt{r^2-4} \\ &= \frac{1}{4} \left((r+2) + \sqrt{r^2-4} \right) \left((r-2) - \sqrt{r^2-4} \right) \sqrt{r^2-4} \\ &= 4 - r^2. \end{aligned}$$

We now have $f'_2(x_+) = 5 - r^2$. If we accept the theorem that a constant solution $x_n = \bar{x}$ ($n = 1, 2, \dots$) of the second-order difference equation $x_{n+2} = f_2(x_n)$ is asymptotically stable if $|f'_2(\bar{x})| < 1$, a theorem analogous to the one established in Section 2.3 for first-order difference equations (which will be described further in Exercises 2 and 3 below), then we see that this periodic solution is asymptotically stable if $-1 < 5 - r^2 < 1$, or $2 < r < \sqrt{6} = 2.449$. Thus, if $2 < r < 2.449$, there is a solution of period 2 to which every solution of $x_{n+1} = f(x_n)$ tends.

For $r > \sqrt{6}$, the solution of period 2 is unstable, but it can be shown that a solution of period 4 appears and that this solution is asymptotically stable if $\sqrt{6} < r < 2.544$. When it becomes unstable, a solution of period 8 appears, which is asymptotically stable for $2.544 < r < 2.564$. This *period-doubling* phenomenon continues until $r = 2.570$, when periodic solutions whose periods are not powers of 2 begin to appear, but these solutions are unstable. In addition, for many values of $r > 2.570$ solutions are *aperiodic*, that is, they never settle down to either an equilibrium or a periodic orbit [Strogatz (1994)]. It is possible to show analytically that a solution of period 3 appears when $r = \sqrt{8} = 2.828$ [Saha and Strogatz (1995)]. For $r > \sqrt{8}$ there is a periodic solution of period k for every integer k , but different initial values give different solutions. There are also solutions whose behavior is apparently random; such solutions are called *chaotic* (see Figure 2.5, a bifurcation diagram generated by a program in (the virtual) Appendix C). The existence of a solution of period 3 implies chaotic behavior [Li and Yorke (1975)].

These facts, whose proofs require a close examination of the properties of continuous functions and fixed points of iterates of continuous functions, are not restricted to the logistic difference equation. It is a remarkably robust fact that for every difference equation $x_{n+1} = rf(x_n)$ with $f(x)$ a function increasing to a unique maximum and then decreasing, the period-doubling phenomenon and the onset of chaos occur. In fact, if r_n is the value of r for which the asymptotically stable solution of period

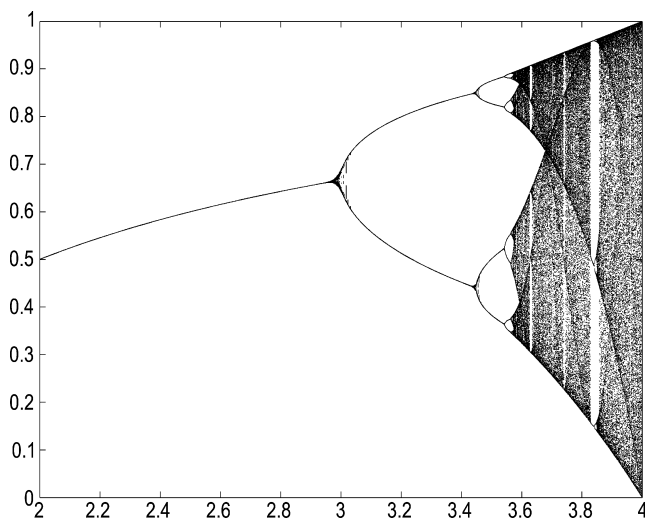


Fig. 2.5 Bifurcation diagram

2^n appears, then

$$\lim_{n \rightarrow \infty} \frac{r_{n+1} - r_n}{r_{n+2} - r_{n+1}} = 4.6692016\dots,$$

the *Feigenbaum constant*. For the logistic equation, $r_1 = 2.000$, $r_2 = 2.449$, $r_3 = 2.544$, and $(r_2 - r_1)/(r_3 - r_2) = 4.73$; usually the limiting value is approached very rapidly. This says that the period-doubling values of r occur closer and closer together [Feigenbaum (1980)].

From a biological point of view, these results are also remarkable. One interpretation is that even very simple models can produce apparently unpredictable behavior and this suggests the possibility that the governing laws may be relatively simple and therefore discoverable [May (1976)]. There do appear to be experimental observations supporting the possibility of chaotic behavior [Gurney, Blythe, and Nisbet (1980)]. On the other hand, the fact that such simple models lead to unpredictable results suggests that experimental results and observations may not be repeatable. This suggests that one should focus on the range of values of r in which the behavior is predictable and in the chaotic ranges look for properties of solutions, such as upper and lower bounds, that are verifiable.

For models of the form $x_{n+1} = rf(x_n)$ with $f(x)$ a bounded monotone increasing functions, such as the Verhulst equation

$$x_{n+1} = \frac{rx_n}{x_n + A},$$

it is easy to verify that since $rf(x)$ is bounded while x is not, there is a largest equilibrium x_∞ at which $y = rf(x)$ crosses the line $y = x$ from above to below. This implies $0 < rf'(x_\infty) < 1$, and shows that the equilibrium x_∞ is asymptotically stable; in fact solutions approach x_∞ monotonically. Thus, there is no possibility of period-

doubling or chaotic behavior, or even of stable oscillations. This fact is also robust in that it is valid for all bounded increasing recruitment functions $f(x)$. The biological significance of the difference between recruitment functions that are monotone increasing and recruitment functions that rise to a maximum and then fall involves the nature of the intraspecies competition for resources. Recruitment functions with a maximum correspond to *scramble* competition, in which resources are divided among all members and excessive population sizes reduce the survival rate, while monotone recruitment functions correspond to *contest* competition, in which some members obtain enough resources for survival, while others do not and die as a result. We now have a legitimate example of a biological assumption leading to qualitative predictions of behavior that might be experimentally observable.

Exercises

1. For what value of r does a solution of period 2 appear for the difference equation

$$x_{n+1} = rx_n e^{1-x_n}?$$

2. Let $\{x_+, x_-\}$ be a solution of period 2 of the difference equation

$$x_{n+1} = f(x_n).$$

Show that both x_+ and x_- are equilibria of the second-order difference equation

$$x_{n+2} = f(f(x_n)).$$

3. Define a new index $k = n/2$ for n even and the iterated function

$$f_2(x) = f(f(x)).$$

Show that x_+ and x_- from Exercise 2 are equilibria of the first order difference equation

$$x_{k+1} = f_2(x_k).$$

[*Remark:* Exercise 3 together with Theorem 2.1 of Section 2.3 shows that an equilibrium x^* of the second order equation $x_{n+2} = f_2(x_n)$ is asymptotically stable if $|f_2'(x^*)| < 1$. Exercise 8 below gives another stability criterion for the asymptotic stability of a solution of period 2 of the difference equation $x_{n+1} = f(x_n)$.]

4. [Kaplan & Glass(1995)] Consider an ecological system described by the finite difference equation

$$x_{n+1} = Cx_n^2(2 - x_n), \quad \text{for } 0 \leq x_n \leq 2,$$

where x_n is the population density in year n and C is a positive constant that we assume is equal to $25/16$.

- a. Sketch the graph of the right hand side of this equation. Indicate the maxima, minima, and inflection points.
 - b. Determine the fixed points of this system.
 - c. Determine the stability at each fixed point and describe the dynamics in a neighborhood of the fixed points.
 - d. In a brief sentence or two describe the expected dynamics starting from initial values of $x_0 = 1/3$ and also $x_0 = 1$ in the limit as $n \rightarrow \infty$. In particular, comment on the possibility that the population may go to extinction or to chaotic dynamics in the limit $n \rightarrow \infty$.
5. [Kaplan and Glass(1995)] The following finite difference equation has been considered as a mathematical model for a periodically stimulated biological oscillator [Bélair and Glass (1983)].

$$\phi_{n+1} = \begin{cases} 6\phi_n - 12\phi_n^2 & \text{for } 0 \leq \phi_n < 0.5, \\ 12\phi_n^2 - 18\phi_n + 7 & \text{for } 0.5 \leq \phi_n \leq 1. \end{cases}$$

- a. Sketch ϕ_{n+1} as a function of ϕ_n for $0 \leq \phi_n \leq 1$. Be sure to show all maxima and minima and compute the values of ϕ_{n+1} at these extreme points.
 - b. Compute all fixed points. What are the qualitative dynamics in a neighborhood of each fixed point?
 - c. If you have done part (a) right, you should be able to find a cycle of period 2. What is this cycle? Show it on your sketch.
6. For the logistic difference equation $x_{n+1} = x_n + rx_n(1 - x_n/K)$ with $r > 2$, show that

$$0 < x_- < x_\infty < x_+ < K.$$

- 7*. a. Let $\{x_+, x_-\}$ be a solution of period 2 of the difference equation $x_{n+1} = f(x_n)$. Use the chain rule of calculus to show that if $f_2(x) = f(f(x))$, then

$$f'_2(x_+) = \frac{d}{dx}f(f(x)) \Big|_{x=x_+} = f'(x_-)f'(x_+).$$

- b. Deduce from part (a) that the solution of period 2 is asymptotically stable if

$$|f'(x_-)| \cdot |f'(x_+)| < 1.$$

8. [Kaplan and Glass (1995)] The finite difference equation

$$x_{n+1} = 0.5 + \alpha \sin(2\pi x_n), \quad 0 \leq x < 1,$$

where $0 \leq \alpha < 0.5$, has been used as a mathematical model for periodic stimulation of biological oscillators .

- a. There is one steady state. Determine this steady state and its stability as a function of α .
 - b. Sketch x_{n+1} as a function of x_n for $\alpha = 0.25$. Be sure to indicate all maxima, minima, and inflection points.
 - c. For $\alpha = 0.25$ there is a stable orbit of period 2. What is it?
- 9*. For what value of r does a solution of period 2 appear for the difference equation

$$x_{n+1} = rx_n e^{1-x_n}?$$

Hint: Let $f(x)$ be the right-hand side function, i.e., $f(x) = rxe^{1-x}$. Find the condition for r under which $f(f(x))$ has fixed points. If you find that the condition is $r > e$, you will find the solution.

10. The population of a species is described by the finite difference equation

$$x_{n+1} = ax_n \exp(-x_n) \text{ for } x_n \geq 0,$$

where a is a positive constant.

- a. Determine the fixed points.
 - b. Evaluate the stability of the fixed points.
 - c. For what value of a is there a period-doubling bifurcation (using the conclusion of the previous exercise).
 - d. For what values of a will the population become extinct starting from any initial condition?
11. The objective of this problem is to get you to read and think about some of the work on difference-equation models in population biology. Read [May (1976)]. Write a summary that deals with critical ideas, methods, and presentation in that article. The questions you might wish to answer are these:
- a. What is the main focus of this article? Is a particular question being addressed?
 - b. Do the mathematical models help illuminate the topics? If so, in what ways?
 - c. Are there alternative methods or approaches that might have been suitable for answering the questions the author addressed?

2.5 Discrete-Time Metered Models

In many populations there is a recruitment cycle in which the population size at each stage is a function of the population size at the previous stage, but the form of this function is determined by a continuous birth and death process. In this case the population size is given by a difference equation

$$x_{n+1} = f(x_n)$$

describing what may be called the long-term dynamics of the model. The function $f(x)$ is constructed from assumptions on births and deaths occurring continuously in the intervals between stages and incorporates the short-term dynamics of the model. Such models are called *metered models*. As difference equations they may be analyzed by the methods of this chapter. What is new in this section is the use of models of the type considered in Chapter 1 to establish specific forms for the reproductive curve $y = f(x)$. In many fish populations there is an annual birth process, with the number of births depending on the adult population size at the time, followed by a continuous death rate until the next birth cycle, at which time the survivors make up the adult population. Such populations lend themselves naturally to metered models.

To describe the general form of a metered model, we let x_n be the size of the adult population at the n th stage. Suppose this parent stock gives rise to B_n young and the survivors of this class at time T (often one year for fish populations) are the x_{n+1} adults at the next stage. More generally, we may assume that there are R_n surviving recruits of whom H_n are harvested with the remainder $R_n - H_n$ forming the adult population x_{n+1} at the next stage. This parent stock x_{n+1} is often called the *escapement* by fishery biologists. This description assumes that none of the adults' x_n parents survive to the next stage, but it is not difficult to relax this restriction. It also assumes that harvesting occurs just before the reproductive stage.

We shall assume constant fertility, that is, that the number of births B_n is proportional to the number of adults x_n , that is,

$$B_n = \alpha x_n.$$

We also assume that between birth times there is a per capita death rate that is a function of the number of survivors from the B_n newborn members. This means that if there are $z(t)$ survivors at time t then there is a function $\phi(z)$ (the per capita death rate) such that

$$\frac{dz}{dt} = -z\phi(z).$$

Then the recruitment R_n is the value for $t = T$ of the solution of the initial value problem

$$\frac{dz}{dt} = -z\phi(z), \quad z(0) = B_n = \alpha x_n. \quad (2.4)$$

Formally, we can solve by separation of variables, obtaining

$$\int_{\alpha x_n}^{R_n} \frac{dz}{z\phi(z)} = -T.$$

The function f in the metered model $x_{n+1} = f(x_n)$ is given implicitly by the relation

$$\int_{\alpha x_n}^{f(x_n)} \frac{dz}{z\phi(z)} = -T.$$

Under harvesting, the model is

$$x_{n+1} = R_n - H_n = f(x_n) - H_n,$$

with the same function f .

Example 1. (The Beverton and Holt stock recruitment model) In some bottom-feeding fish populations, including the North Atlantic plaice and haddock studied by Beverton and Holt (1957), recruitment appears to be essentially unaffected by fishing, and this is true over a wide range of fishing effort. These species have very high fertility rates and very low survivorship to adulthood. The Beverton and Holt model assumes a linear per capita mortality rate, so that the differential equation describing survivorship has the form

$$\frac{dz}{dt} = -z(\mu_1 + \mu_2 z),$$

with μ_1 and μ_2 positive constants. Explicit solution of the initial value problem (2.4) leads to a recruitment function of the form

$$R_n = \frac{ax_n}{1 + bx_n},$$

where a and b are positive constants related to μ_1 and μ_2 . In fact, the same form is valid if μ_1 and μ_2 are arbitrary nonnegative functions of t . This leads to the Beverton and Holt metered model

$$x_{n+1} = \frac{ax_n}{1 + bx_n}.$$

The reader should observe that this is equivalent to the Verhulst model

$$x_{n+1} = \frac{rx_n}{x_n + A}$$

described earlier with $a = r/A$, $b = 1/A$. As we have seen for the Verhulst equation, there is an asymptotically stable positive equilibrium only if $r > A$, or equivalently if $a > 1$.

Example 2. (The Ricker stock recruitment model) It was observed by Ricker (1954, 1958) that some species of fish, including salmon, habitually cannibalize their eggs and young. The Ricker model assumes a per capita death rate proportional to the initial size of the young population. Then the survivorship differential equation has the form

$$\frac{dz}{dt} = -zB_n = -\alpha x_n z, \quad z(0) = \alpha x_n.$$

This has the solution

$$z = \alpha x_n e^{-\alpha x_n t}$$

and therefore

$$R_n = \alpha x_n e^{-\alpha T x_n},$$

which we write

$$R_n = \alpha x_n e^{-\beta x_n}$$

by letting $\beta = \alpha T$. This leads to the Ricker metered model

$$x_{n+1} = \alpha x_n e^{-\beta x_n}.$$

Exercises

1. a. Show that the Ricker model $x_{n+1} = \alpha x_n e^{-\beta x_n}$ has an equilibrium $x = 0$ and a positive equilibrium $x_\infty = \log \alpha / \beta$ if $\alpha > 1$.
 b. Determine the range of values of the parameter α for which each of these equilibria is asymptotically stable.
2. In the Beverton and Holt model

$$x_{n+1} = \frac{ax_n}{1 + bx_n},$$

determine the constants a and b in terms of α and T if the survivorship differential equation is

$$\frac{dz}{dt} = -dz^2.$$

(Or $\mu_1 = 0, \mu_2 = d$.)

3. Analyze the behavior of the continuous analogue of the metered Ricker model,

$$\frac{dx}{dt} = \alpha x e^{-\beta x} - x,$$

and compare with the behavior of the metered model.

4. Analyze the behavior of the continuous analogue of the metered Beverton and Holt model

$$\frac{dx}{dt} = \frac{ax}{1 + bx} - x.$$

2.6 A Two-Age Group Model and Delayed Recruitment

Suppose we are interested in studying a population that in the n th generation contains x_n immature members and y_n adult members, with a birth rate depending on the number of adult members and a transition rate from immature to adult members depending on the number of immature members. If the birth rate is α and the rate of transition is β , we are led to a system of two difference equations,

$$\begin{aligned} x_{n+1} &= \alpha y_n \\ y_{n+1} &= \beta x_n, \end{aligned}$$

assuming no survival of adult members to the next generation. Graphical methods of solving this system are cumbersome, but the method of analytic solution is easy. Iteration gives $x_1 = \alpha y_0$, $y_1 = \beta x_0$; $x_2 = \alpha y_1 = \alpha\beta x_0$, $y_2 = \beta x_1 = \alpha\beta y_0$, $x_3 = \alpha y_2 = \alpha^2\beta y_0$, $y_3 = \beta x_2 = \alpha\beta^2 x_0$. The pattern becomes apparent if we introduce vector–matrix notation. Define the two-dimensional column vector

$$\mathbf{z}_n = \begin{pmatrix} x_n \\ y_n \end{pmatrix}$$

and the *reproduction matrix*

$$A = \begin{pmatrix} 0 & \alpha \\ \beta & 0 \end{pmatrix}.$$

Then the system can be written

$$\mathbf{z}_{n+1} = A\mathbf{z}_n,$$

and now iterative solution gives

$$\mathbf{z}_n = A^n \mathbf{z}_0,$$

where A^n is the n th power of the matrix A . More generally, we could assume a nonlinear birth function $B(y)$ and a nonlinear mortality function $D(y)$, that is, a nonlinear system

$$\begin{aligned} x_{n+1} &= B(y_n) \\ y_{n+1} &= \alpha x_n - D(y_n). \end{aligned}$$

An equilibrium of this system is a solution (x_∞, y_∞) of the system $x_\infty = B(y_\infty)$, $y_\infty = \alpha x_\infty - D(y_\infty)$. We may linearize about the equilibrium and examine the asymptotic stability of the equilibrium by studying the linearized system

$$\begin{aligned} u_{n+1} &= B'(y_\infty)v_n, \\ v_{n+1} &= \alpha u_n - D'(y_\infty)v_n, \end{aligned}$$

with coefficient matrix

$$A = \begin{pmatrix} 0 & B'(y_\infty) \\ \alpha & -D'(y_\infty) \end{pmatrix}.$$

Such a study requires the machinery of linear algebra, which we shall not undertake here. Models with a larger number of age groups are also natural and their study leads to systems of difference equations each with dimension equal to the number of age groups. Again, the use of linear algebra is essential. In order to study a two-age group model such as

$$x_{n+1} = B(y_n), \quad y_{n+1} = \alpha x_n - D(y_n),$$

without being forced to use linear algebra, we may eliminate by substituting $B(y_{n-1})$ for x_n in the second equation. We then obtain a single *second-order* difference equation

$$y_{n+1} = \alpha B(y_{n-1}) - D(y_n),$$

using the relation $x_{n+1} = B(y_n)$ to determine x_n once this second-order equation has been solved. An equilibrium of this second order equation is a value y_∞ such that

$$y_\infty = \alpha B(y_\infty) - D(y_\infty).$$

The linearization at the equilibrium is the second-order linear homogeneous difference equation

$$u_{n+1} = \alpha B'(y_\infty)u_{n-1} - D'(y_\infty)u_n.$$

In order to study the stability of an equilibrium of a difference equation of order higher than one, we first state the following linearization theorem without proof.

Theorem 2.2. *If x_∞ is an equilibrium of the difference equation*

$$x_{n+k} = f(x_{n+k-1}, x_{n+k-2}, \dots, x_{n+1}, x_n)$$

of order k , so that

$$x_\infty = f(x_\infty, x_\infty, \dots, x_\infty),$$

the equilibrium is asymptotically stable if all solutions of the linearization at the equilibrium

$$u_{n+k} = \sum_{j=1}^k a_j u_{n+k-j}$$

(with $a_j = f_j(x_\infty, x_\infty, \dots, x_\infty)$ and f_j denoting the partial derivative with respect to the j th variable) tend to zero.

In order to determine whether all solutions of a linear difference equation tend to zero, we look for solutions of the form $x_n = \lambda^n x_0$ and obtain a *characteristic equation*—a polynomial equation of degree k —for λ . For the difference equation $u_{n+k} = \sum_{j=1}^k a_j u_{n+k-j}$, this characteristic equation is $\lambda^{n+k} = \sum_{j=1}^k a_j \lambda^{n+k-j}$, or

$$\lambda^k - \sum_{j=1}^k a_j \lambda^{k-j} = 0.$$

If the roots of this characteristic equation, say $\lambda_1, \lambda_2, \dots, \lambda_k$, are distinct, then every solution of the difference equation $u_{n+k} = \sum_{j=1}^k a_j u_{n+k-j}$ is a linear combination of $\lambda_1^n, \lambda_2^n, \dots, \lambda_k^n$. If the characteristic equation has multiple roots, then there are also terms $\lambda_j^n \log \lambda_j$, but in any case the condition that all solutions of a linear homogeneous difference equation tend to zero is that all roots λ_j of the characteristic equation satisfy $|\lambda_j| < 1$.

Combination of this information about the solutions of linear difference equations with Theorem 2.2 gives the following extension of Theorem 2.1 of Section 2.3.

Theorem 2.3. *Let x_∞ be an equilibrium of the following difference equation of order k :*

$$x_{n+k} = f(x_{n+k-1}, x_{n+k-2}, \dots, x_{n+1}, x_n).$$

If all roots of the characteristic equation

$$\lambda^k - \sum_{j=1}^k f_j(x_\infty, x_\infty, \dots, x_\infty) \lambda^{k-j} = 0$$

of the linearization at this equilibrium satisfy $|\lambda| < 1$, then the equilibrium x_∞ is asymptotically stable.

For a first-order difference equation $x_{n+1} = f(x_n)$ the characteristic equation is $\lambda - f'(x_\infty) = 0$, and thus the condition for asymptotic stability is $|f'(x_\infty)| < 1$, as given in Theorem 2.1 of Section 2.3. For the equilibrium x_+ of the second order difference equation

$$x_{n+2} = f_2(x_n)$$

considered in Section 2.4 the characteristic equation is $\lambda^2 - f'_2(x_+) = 0$, with roots $\lambda = \pm \sqrt{|f'_2(x_+)|}$ or $\lambda = \pm i \sqrt{|f'_2(x_+)|}$, depending on whether $f'_2(x_+) > 0$ or $f'_2(x_+) < 0$. In either case the condition for asymptotic stability is $|f'_2(x_+)| < 1$, a fact used without proof in Section 2.4.

The results developed in Theorem 2.3 would enable us to study the delayed recruitment model $y_{n+1} = \alpha B(y_{n-1}) - D(y_n)$ formulated at the beginning of this section. However, we shall instead consider the model

$$x_{n+1} = ax_n + F(x_{n-\tau}),$$

which is often used to study whale populations. Here x_n represents the adult breeding population, a ($0 \leq a \leq 1$) the survival coefficient, and $F(x_{n-\tau})$ the recruitment to the adult stage with a delay of τ years. Equilibrium population size is obtained by solving

$$x_\infty = ax_\infty + F(x_\infty),$$

or $F(x_\infty) = (1-a)x_\infty = Mx_\infty$, where $M = 1-a$ is the annual mortality rate. More generally, we could consider a model of the form $x_{n+1} = G(x_n) + F(x_{n-\tau})$ with equilibrium population size determined from $x_\infty = G(x_\infty) + F(x_\infty)$. To study the stability of equilibrium, we linearize about the equilibrium by setting $x_n = u_n + x_\infty$ and neglecting higher order terms, obtaining

$$u_{n+1} = au_n + F'(x_\infty)u_{n-\tau}.$$

We let $b = F'(x_\infty)$ to write this in the form

$$u_{n+1} = au_n + bu_{n-\tau}.$$

The characteristic equation is

$$\lambda^{\tau+1} - a\lambda^\tau - b = 0,$$

and asymptotic stability of equilibrium requires $|\lambda| < 1$ for all roots of this equation.

If $\tau = 0$, the characteristic equation is $\lambda - a - b = 0$ and the stability condition is $|a + b| < 1$, or $-1 - a < b < 1 - a$.

If $\tau = 1$, the characteristic equation is $\lambda^2 - a\lambda - b = 0$, which has roots

$$\lambda = a \pm \frac{\sqrt{a^2 + 4b}}{2}.$$

If $a^2 + 4b \geq 0$, these roots are real, and the condition $|\lambda| < 1$ is equivalent to $a + \sqrt{a^2 + 4b} < 2$ and $a - \sqrt{a^2 + 4b} > -2$. These conditions give $\sqrt{a^2 + 4b} < 2 - a$ and $\sqrt{a^2 + 4b} < 2 + a$. Since $2 - a \leq 2 + a$, we have the single condition $\sqrt{a^2 + 4b} < 2 - a$, or $b < 1 - a$. If $a^2 + 4b < 0$, the roots are complex and $|\lambda|^2 = a^2/4 + (-a^2 - 4b)/4 = -b$. Since $b < 0$, we must have $-1 < b < 0$. Combining the cases $a^2 + 4b < 0$ and $a^2 + 4b \geq 0$, we see that for $\tau = 1$, the equilibrium x_∞ is asymptotically stable if $-1 < b < 1 - a$.

For values of $\tau > 1$, the stability condition is more difficult to analyze, but it is possible to establish the following result [Levin and May (1976)].

Theorem 2.4. *There is a function $z_\tau(a) \leq -1 + a$ with $z_\tau(a) \nearrow -1 + a$ as $\tau \rightarrow \infty$ such that the equilibrium x_∞ is asymptotically stable if*

$$z_\tau(a) < b < 1 - a.$$

We have shown that $z_0(a) = -1 - a$, $z_1(a) = -1$. Since $z_\tau(a) < -1 + a$ for all τ , the equilibrium is certainly asymptotically stable if $-1 + a < b < 1 - a$, or $|b| < 1 - a$.

The population of the Antarctic fin whale has been studied using this model with $F(x) = rx(1 - x/K)$, $r = 0.12$, $a = 0.96$, $k = 600,000$, $\beta = 5$. The equilibrium population size is given by $rx_\infty(1 - x_\infty/K) = (1 - a)x_\infty$, or $x_\infty = K(1 - (1 - a)/r)$. If we use $M = 1 - a$, we have $x_\infty = K(1 - M/r)$. Since $F'(x) = 4 - 2rx/K$, $F'(x_\infty) = 2M - r$. The equilibrium is certainly asymptotically stable if $|2M - r| < 1 - a = M$, or $M < r < 3M$. With $K = 600,000$, $M = 0.04$, $r = 0.12$, this condition is not satisfied, since $r = 3M$. However, since $z_\tau(a)$ is actually less than $-1 + a$, the stability condition is satisfied.

Discrete single-species models do not involve merely first-order difference equations. As we have seen, age-class models lead to systems of difference equations and delayed-recruitment models lead to higher-order difference equations. For a unified treatment, we would have to show how to write a difference equation of order k as a system of k first-order difference equations, and then use vector-matrix notation and methods of linear algebra to develop the theory of equilibria and asymptotic stability.

Exercises

1. Convert the system of difference equations

$$x_{n+1} = 2y_n, \quad y_{n+1} = 3x_n$$

to a second-order difference equation and find the first three terms of the solution with $x_0 = y_0 = 1$.

2. Solve the second order difference equation

$$x_{n+2} - x_n = 0$$

with $x_0 = 1, x_1 = -1$.

3. Solve the second-order difference equation

$$x_{n+2} + x_n = 0$$

with $x_0 = 1, x_1 = -1$.

The Jury criterion states that the eigenvalues of a 2×2 matrix M have magnitude less than one if and only if $|tr(M)| < det(M) + 1 < 2$. Use it in problems 4 and 5.

4. Assume that the population (P) of a parasite and that of its host population (H) are modeled by the difference equations

$$\begin{aligned} P_{t+1} &= \alpha H_t (1 - e^{-aP_t}), \\ H_{t+1} &= \alpha H_t e^{-aP_t}, \end{aligned}$$

where α, a are positive.

- a. Calculate the equilibrium population sizes and show that they are positive only if $\alpha > 1$.
- b. Use the Jury criterion to show that if $\alpha > 1$, then the equilibrium is unstable. *Hint:* The following relation holds:

$$\frac{\alpha}{\alpha - 1} \ln \alpha > 1 \text{ for all } \alpha > 1.$$

- 5*. Determine all equilibria and the stability of each equilibrium for the system

$$\begin{aligned} x_{n+1} &= \alpha x_n e^{-by_n}, \\ y_{n+1} &= cx_n (1 - e^{-by_n}). \end{aligned}$$

(This system is known as the Nicholson and Bailey model (1935) for a host-parasite system; x_n denotes the number of hosts and y_n the number of parasites.)

6. One of the common discrete-time models for the growth of a single species is the Pielou logistic equation

$$x_{n+1} = \frac{\alpha x_n}{1 + \beta x_n},$$

where $x_n \geq 0$ is the size of the population at generation n , $\alpha > 1$, and $\beta > 0$. If we assume that there is a delay of time period 1 in the response of growth rate per individual to density change, we obtain the delay difference equation model

$$x_{n+1} = \frac{\alpha x_n}{1 + \beta x_{n-1}}.$$

Determine the stability of all the nonnegative fixed points of this equation.

2.7 Systems of Two Difference Equations

In Section 2.6, we examined a system of two difference equations by reducing it to a single second order difference equation. In Section 2.8 we shall examine a system that cannot be reduced to a single equation of higher order. In this section, we shall outline the main results of the analysis of stability of an equilibrium of a system of two first-order difference equations.

We begin with a system of two difference equations,

$$\begin{aligned} x_{n+1} &= f(x_n, y_n), \\ y_{n+1} &= g(x_n, y_n). \end{aligned} \tag{2.5}$$

An equilibrium of the system (2.5) is a solution (x_∞, y_∞) of the system

$$f(x, y) = x, \quad g(x, y) = y.$$

Generally, $f(x, y) = x$ and $g(x, y) = y$ are represented by curves in the (x, y) -plane, and an equilibrium is an intersection of the two curves. If (x_∞, y_∞) is an equilibrium of (2.5), then the system (2.5) has a constant solution $x_n = x_\infty, y_n = y_\infty$ ($n = 1, 2, \dots$).

The description of the behavior of solutions near an equilibrium parallels the description given in Section 2.3 for a single first-order difference equation. If (x_∞, y_∞) is an equilibrium of the system (2.5), we make the change of variables $u_n = x_n - x_\infty, v_n = y_n - y_\infty$ ($n = 0, 1, 2, \dots$), so that (u_n, v_n) represents deviation from the equilibrium. We then have the system

$$\begin{aligned} u_{n+1} &= f(x_\infty + u_n, y_\infty + v_n) - x_\infty = f(x_\infty + u_n, y_\infty + v_n) - f(x_\infty, y_\infty) \\ v_{n+1} &= g(x_\infty + u_n, y_\infty + v_n) - y_\infty = g(x_\infty + u_n, y_\infty + v_n) - g(x_\infty, y_\infty). \end{aligned} \tag{2.6}$$

If we use Taylor's theorem to approximate the functions $f(x_\infty + u_n, y_\infty + v_n)$ and $g(x_\infty + u_n, y_\infty + v_n)$ by their linear terms and neglect the remainder terms, we obtain a linear system

$$\begin{aligned} u_{n+1} &= f_x(x_\infty, y_\infty)u_n + f_y(x_\infty, y_\infty)v_n, \\ v_{n+1} &= g_x(x_\infty, y_\infty)u_n + g_y(x_\infty, y_\infty)v_n. \end{aligned} \quad (2.7)$$

called *the linearization of the system (2.5) at the equilibrium (x_∞, y_∞)* , which approximates the system (2.5) near the equilibrium. The analogue of Theorem 2.1, Section 2.3, which explains the significance of the linearization at an equilibrium, is valid.

Theorem 2.5. *If all solutions of the linearization (2.7) of the system (2.5) at an equilibrium (x_∞, y_∞) tend to zero as $n \rightarrow \infty$, then all solutions of (2.7) with x_0 and y_0 sufficiently close to x_∞ and y_∞ respectively tend to the equilibrium (x_∞, y_∞) as $n \rightarrow \infty$.*

The proof is more complicated than that given in Section 2.3 for $n = 1$, and we shall omit it.

The next problem is to determine conditions under which all solutions of the linear system (2.7) approach zero. The idea behind the solution of this problem, although there are some technical complications, is to look for solutions of the form $u_n = u_0\lambda^n$, $v_n = v_0\lambda^n$ and then determine conditions under which all values of λ for which this is possible satisfy $|\lambda| < 1$. (Recall that if $|\lambda| < 1$, then $\lambda^n \rightarrow 0$ as $n \rightarrow \infty$.) The basic fact is that all solutions of the linear system (2.7) approach zero if all roots of the characteristic equation

$$\lambda^2 - \text{tr}A(x_\infty, y_\infty)\lambda + \det A(x_\infty, y_\infty) = 0$$

satisfy $|\lambda| < 1$. Here, $\text{tr}A$ and $\det A$ are the trace and determinant of the 2×2 matrix

$$A(x_\infty, y_\infty) = \begin{pmatrix} f_x(x_\infty, y_\infty) & f_y(x_\infty, y_\infty) \\ g_x(x_\infty, y_\infty) & g_y(x_\infty, y_\infty) \end{pmatrix}.$$

This characteristic equation may also be written as a determinant, namely as

$$\det(A(x_\infty, y_\infty) - \lambda I) = 0, \quad (2.8)$$

where

$$I = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix},$$

the identity matrix. It arises from the condition that

$$A(x_\infty, y_\infty) \begin{pmatrix} u \\ v \end{pmatrix} = \lambda \begin{pmatrix} u \\ v \end{pmatrix}$$

has a nontrivial solution for the vector

$$\begin{pmatrix} u \\ v \end{pmatrix}.$$

In this vector–matrix form, the stability result generalizes to systems of arbitrary order.

Theorem 2.6. *If all roots of the characteristic equation (2.8) at an equilibrium satisfy $|\lambda| < 1$, then all solutions of the system (2.5) with initial values sufficiently close to an equilibrium approach the equilibrium.*

A proof of this result may be found in books that explore the theory of difference equations, such as Elaydi (1996) and Sandefur (1990).

The characteristic equation for a system of k difference equations at an equilibrium is a polynomial equation of degree k . Conditions are known under which all roots of a polynomial equation have absolute value less than 1. These conditions were originally derived to analyze some economic models [Samuelson (1941)]. For a quadratic equation

$$f(\lambda) = \lambda^2 + a_1\lambda + a_2 = 0, \quad (2.9)$$

both roots satisfy $|\lambda| < 1$ if and only if

$$1 + a_1 + a_2 > 0, \quad 1 - a_1 + a_2 > 0, \quad 1 + a_2 > 0.$$

These three conditions can be combined and written as

$$0 < |a_1| < a_2 + 1 < 2, \quad (2.10)$$

which is the *Jury criterion* (Exercise 3, Section 2.6).

To establish the Jury criterion, we begin by noting that $f(\lambda) \rightarrow +\infty$ as $\lambda \rightarrow \infty$ and $\lambda \rightarrow -\infty$. If $f(-1) < 0$, there is a root less than -1 , and if $f(1) < 0$ there is a root greater than 1. Further, the product of the roots of (2.9) is a_2 ; thus we must have $|a_2| < 1$, $f(-1) > 0$, $f(1) > 0$ in order to have all roots of (2.9) satisfy $|\lambda| < 1$. We may rewrite these conditions as $-1 < a_2 < 1$, or $0 < a_2 + 1 < 2$, $f(-1) = 1 - a_1 + a_2 > 0$, $f(1) = 1 + a_1 + a_2 > 0$. The conditions $f(-1) > 0$ and $f(1) > 0$ may be combined to give

$$-(1 + a_2) < a_1 < 1 + a_2,$$

or $|a_1| < 1 + a_2$. Thus, in order to have the roots of (2.9) satisfy $|\lambda| < 1$, the conditions in (2.10) must be satisfied.

To prove that the conditions in (2.10) imply that the roots of (2.9) satisfy $|\lambda| < 1$, we consider first the case that the roots of (2.9) are complex conjugate. In this case, both roots have the same absolute value, and $|a_2| < 1$ implies that this absolute value is less than 1. If the roots of (2.9) are real and $f(-1) > 0$, $f(1) > 0$, then either both roots are less than -1 (contradicted by $|a_2| < 1$), or both roots are greater than 1 (contradicted by $|a_2| < 1$), or both roots are between -1 and 1. Thus the conditions in (2.10) imply that both roots satisfy $|\lambda| < 1$, and the Jury criterion is established.

In the next section, we will examine a system of three first order-difference equations. It can be shown that the conditions under which the roots of a cubic equation

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$$

satisfy $|\lambda| < 1$ are

$$\begin{aligned} 1 + a_1 + a_2 + a_3 &> 0, & 1 - a_1 + a_2 - a_3 &> 0, \\ 3 + a_1 - a_2 - 3a_3 &> 0, & 1 + a_1a_3 - a_2 - a_3^2 &> 0 \end{aligned} \quad (2.11)$$

[Samuelson (1941)]. We will make use of this result.

Exercises

1. Find all equilibria of the system

$$\begin{aligned} x_{n+1} &= B(y_n), \\ y_{n+1} &= \alpha x_n - D(y_n), \end{aligned}$$

treated as a single second-order difference equation in Section 2.6, and establish conditions for their stability.

2. For the delayed-recruitment model

$$x_{n+1} = ax_n + F(x_{n-r}),$$

with $0 \leq a \leq 1$, considered in Section 2.6, the characteristic equation at an equilibrium x_∞ , that is, a solution of $F(x_\infty) = (1 - a)x_\infty$, is

$$\lambda^{r+1} - a\lambda^r - F'(x_\infty) = 0.$$

Determine the conditions on a and $F'(x_\infty)$ for stability of equilibrium if $r = 2$ and write them in the form

$$z_r(a) < F'(x_\infty) < 1 - a,$$

i.e., determine the function $z_r(a)$.

3. Consider the two-dimensional system

$$\begin{aligned} x_{n+1} &= \frac{\alpha y_n}{1 + (x_n)^2}, \\ y_{n+1} &= \frac{\beta x_n}{1 + (y_n)^2}, \end{aligned}$$

where α and β are positive constants. If $\alpha^2 < 1$ and $\beta^2 < 1$, prove that the origin $(0, 0)$ is globally asymptotically stable. [Global asymptotic stability means that every solution approaches the origin, not just solutions starting close to the origin.]

4. Consider the single-species, age-structured population model

$$\begin{aligned}x_{n+1} &= y_n \exp(r - ax_n - y_n) \\ y_{n+1} &= x_n,\end{aligned}$$

where $x_n \geq 0$, $y_n \geq 0$, and the constants a , r are positive. Show that all the solutions are bounded. Interpret your result.

2.8 Oscillation in Flour Beetle Populations: A Case Study

Some recent experimental studies of flour beetles (*Tribolium castaneum*) have indicated a possibility of behavior in the laboratory that appears to be chaotic [R.F. Costantino, R.A. Desharnais, J.M. Cushing, B. Dennis, (1997), (1995)]. We shall describe and attempt to analyze a model for such behavior, taking note of the properties of the life cycle of the flour beetle.

The life cycle consists of larval and pupal stages, each lasting approximately two weeks, followed by an adult stage. Both larvae and adults are cannibalistic, consuming eggs and thus reducing larval recruitment. In addition, there is adult cannibalism of pupae. We take two weeks as the unit of time and formulate a discrete model describing the larval population L , pupal population P , and adult population A at two-week intervals.

If there were no cannibalism, we could begin with a linear model

$$\begin{aligned}L_{n+1} &= bA_n, \\ P_{n+1} &= (1 - \mu_L)L_n, \\ A_{n+1} &= (1 - \mu_P)P_n + (1 - \mu_A)A_n,\end{aligned}$$

where b is the larval recruitment rate per adult in unit time, and μ_L , μ_P , μ_A are the death rates in the respective stages. However, in practice, $\mu_P = 0$ since there is no pupal mortality except for cannibalism. We assume that cannibalistic acts occur randomly as the organisms move through the container of flour that forms their environment. This suggests a metered model with cannibalism rates proportional to the original size of the group being cannibalized, as in the Ricker fish model (Section 2.5). We are led to a model

$$\begin{aligned}L_{n+1} &= bA_n e^{-c_{EA}A_n} e^{-c_{EL}L_n}, \\ P_{n+1} &= (1 - \mu_L)L_n, \\ A_{n+1} &= P_n e^{-c_{PA}A_n} + (1 - \mu_A)A_n,\end{aligned} \tag{2.12}$$

with “cannibalism coefficients” c_{EA} , c_{EL} , c_{PA} . The fractions $e^{-c_{EA}A_n}$ and $e^{-c_{EL}L_n}$ are the probabilities that an egg is not eaten in the presence of A_n adults and L_n larvae

through the larval stage. The fraction $e^{-c_{PA}A_n}$ is the survival probability of a pupa through the pupal stage in the presence of A_n adults.

Equilibria of our basic model (2.12) are solutions (L, P, A) of the system of equations

$$\begin{aligned} L e^{c_{EL}L} &= b A e^{-c_{EA}A}, \\ P &= (1 - \mu_L)L, \\ \mu_A e^{c_{PA}A} &= P. \end{aligned} \tag{2.13}$$

This system has a solution $(0, 0, 0)$ corresponding to extinction and also has a solution with $L > 0$, $P > 0$, $A > 0$ corresponding to survival for some sets of parameter values. We are unable to find this survival equilibrium analytically, but we may solve numerically for a given choice of parameters.

We may rewrite the equilibrium conditions by eliminating P as

$$\begin{aligned} (1 - \mu_L)L &= \mu_A A e^{c_{PA}A}, \\ L e^{c_{EL}L} &= b A e^{-c_{EA}A}. \end{aligned}$$

Division of the second equation by the first gives

$$e^{c_{EL}L} = \frac{b(1 - \mu_L)}{\mu_A} e^{-(c_{EA} + c_{PA})A}. \tag{2.14}$$

The left side of (2.14) increases with L and is greater than one for all positive L , while the right side of (2.14) decreases with A and is between $b(1 - \mu_L)/\mu_A$ and zero. Thus, if the quantity θ , defined by

$$\theta = \frac{b(1 - \mu_L)}{\mu_A}, \tag{2.15}$$

is less than one, there cannot be a solution of (2.14) and thus there cannot be a survival equilibrium. On the other hand, if θ is greater than one, the equation (2.14) represents a straight line from $(0, \log \theta / c_{EL})$ to $(\log \theta / (c_{EA} + c_{PA}), 0)$ in the (A, L) -plane. An equilibrium is an intersection of this line with the curve $(1 - \mu_L)L = \mu_A e^{c_{PA}A}$, which starts from the origin and grows as A increases. Thus if $\theta > 1$, there is always a survival equilibrium.

Some experiments have been carried out with flour beetle populations and fit to the model (2.12) with the parameter values $b = 7$, $c_{EA} = c_{EL} = 0.01$, $c_{PA} = 0.005$, $\mu_L = 0.2$, $\mu_A = 0.01$ [Costantino, Desharnais, Cushing, and Dennis (1997), (1995)]. Since experimental data are inevitably noisy, it is not possible to determine parameters exactly, but it is possible to obtain a confidence interval for the parameters. We take these values as a baseline and then compare the model with the experiment when some of the parameters are manipulated. For example, we may remove (harvest) some adults at each census and thus set μ_A arbitrarily. In real life outside the laboratory, adult mortality may be changed by spraying with a pesticide. It is also

possible to manipulate the cannibalism coefficient c_{PA} by changing the supply of food; increasing the food supply reduces the rate of cannibalism of pupae by adults.

With the parameter values given above, we find $\theta = 560$, and there is a survival equilibrium $L = 36$, $P = 29$, $A = 398$, as well as the extinction equilibrium $L = 0$, $P = 0$, $A = 0$. In order to determine the stability of these equilibria, we must compute the matrix of partial derivatives at an equilibrium and form the characteristic equation as in Section 2.7.

At an equilibrium (L, P, A) this matrix is

$$\begin{pmatrix} -c_{EL}bAe^{-c_{EA}A}e^{-c_{EL}L} & 0 & be^{-c_{EL}L}e^{-c_{EA}A}(1-c_{EA}A) \\ 1-\mu_L & 0 & 0 \\ 0 & e^{-c_{PA}A} & 1-\mu_A-c_{PA}Pe^{-c_{PA}A} \end{pmatrix}. \quad (2.16)$$

At the extinction equilibrium $(0, 0, 0)$, it reduces to

$$\begin{pmatrix} 0 & 0 & b \\ 1-\mu_L & 0 & 0 \\ 0 & 1 & 1-\mu_A \end{pmatrix}.$$

The characteristic equation at $(0, 0, 0)$ is (after some manipulation of signs)

$$\det \begin{pmatrix} -\lambda & 0 & b \\ 1-\mu_L & -\lambda & 0 \\ 0 & 1 & 1-\mu_A-\lambda \end{pmatrix} = \lambda^2(\lambda - (1-\mu_A)) - b(1-\mu_L) = 0,$$

or $\lambda^3 - (1-\mu_A)\lambda^2 - b(1-\mu_L) = 0$. Thus, it has the form $\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$ with $a_1 = -(1-\mu_A)$, $a_2 = 0$, $a_3 = -b(1-\mu_L)$. The conditions for asymptotic stability ((2.11), Section 2.7) are

$$\begin{aligned} 1 + a_1 + a_2 + a_3 &> 0, & 1 - a_1 + a_2 - a_3 &> 0, \\ 3 + a_1 - a_2 - 3a_3 &> 0, & 1 + a_1a_3 - a_2 - a_3^2 &> 0, \end{aligned} \quad (2.17)$$

and these become

$$\begin{aligned} \mu_A - b(1-\mu_L) &> 0, \\ 2 - \mu_A + b(1-\mu_L) &> 0, \\ 3 - (1-\mu_A) + 3b(1-\mu_L) &> 0, \\ 1 + b(1-\mu_L)(1-\mu_A) - b^2(1-\mu_L)^2 &> 0. \end{aligned}$$

Because $0 \leq \mu_A \leq 1$, $0 \leq \mu_L \leq 1$, the second and third of these conditions are satisfied automatically. The first condition is satisfied if and only if $\mu_A > b(1-\mu_L)$, which is equivalent to $\theta < 1$.

The last condition,

$$(b(1-\mu_L))^2 - b(1-\mu_L)(1-\mu_A) < 1,$$

is satisfied as well, since

$$(b(1 - \mu_L))^2 - b(1 - \mu_L)(1 - \mu_A) < \mu_A^2 - b(1 - \mu_L)(1 - \mu_A) < \mu_A^2 < 1.$$

Thus, the extinction equilibrium is asymptotically stable if and only if $\theta < 1$, that is, if and only if the extinction equilibrium is the only equilibrium.

At a survival equilibrium we may use the equilibrium conditions (2.13) to simplify the coefficient matrix (2.16) to

$$\begin{pmatrix} -c_{EL}L & 0 & \frac{L}{A} - c_{EA}L \\ 1 - \mu_L & 0 & 0 \\ 0 & e^{c_{PA}A} & 1 - \mu_A - \mu_A c_{PA}A \end{pmatrix}.$$

In this case, the characteristic equation is

$$\lambda(\lambda + c_{EL}L)(\lambda - (1 - \mu_A - \mu_A c_{PA}A)) - \left(\frac{L}{A} - c_{EA}L\right)(1 - \mu_L)e^{-c_{PA}A} = 0,$$

or

$$\begin{aligned} \lambda^3 + (c_{EL}L + \mu_A c_{PA}A - (1 - \mu_A))\lambda^2 \\ - c_{EL}L(1 - \mu_A)\lambda - \left(\frac{L}{A} - c_{EA}L\right)(1 - \mu_L)e^{-c_{PA}A} = 0, \end{aligned}$$

that is, a cubic equation $\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$ with coefficients

$$\begin{aligned} a_1 &= c_{EL}L + \mu_A c_{PA}A - (1 - \mu_A), \\ a_2 &= -c_{EL}L(1 - \mu_A), \\ a_3 &= -\left(\frac{L}{A} - c_{EA}L\right)(1 - \mu_L)e^{-c_{PA}A}. \end{aligned} \tag{2.18}$$

We are unable to analyze the stability of the survival equilibrium in general, but for a particular choice of parameters $b, c_{EA}, c_{EL}, c_{PA}, \mu_L, \mu_A$ we can calculate the survival equilibrium (L, P, A) numerically and then use the values given by (2.18) to check the stability condition (2.17).

With the baseline parameters $b = 7, c_{EA} = c_{EL} = 0.01, c_{PA} = 0.005, \mu_L = 0.2, \mu_A = 0.01$, the survival equilibrium is $(36, 29, 398)$, and we find from (2.18) that $a_1 = -0.61, a_2 = -0.36, a_3 = 0.43$. The stability conditions (2.17) are satisfied, and thus the survival equilibrium is asymptotically stable. This agrees with experimental observations. However, this does not validate the model, since the parameter values were chosen to fit the experimental data.

To obtain some validation of the basic model, we must manipulate some of the parameter values and see whether experimental observations still agree with model predictions. Thus, we set $\mu_A = 0.96, c_{PA} = 0.5$ by harvesting adults and reducing the flour supply. With these parameter values, the model predicts a survival equilibrium $(12, 10, 3)$, and (2.18) gives $a_1 = 1.52, a_2 = -0.005, a_3 = -0.69$ in the cubic

characteristic equation. Now the stability condition $1 + a_1 a_3 - a_2 - a_3^2 > 0$ is violated, and our model predicts instability of the survival equilibrium. A more detailed study of the model indicates that with $\mu_A = 0.96$, the dynamics are very sensitive to changes in the cannibalism rate c_{PA} . For $c_{PA} = 0.5$ there is a solution of period 3 and a chaotic attractor, while for $c_{PA} = 0.55$ there are two attractors and a solution of period 8. Experimental observations indicate chaotic behavior, but it is not possible to be specific about the nature of the dynamics. Nevertheless, this does indicate some validity for the model and supplies what appears to be genuinely chaotic behavior in the laboratory.

Another way in which it is possible to perturb the model is to introduce periodic forcing by varying the volume of flour. Experiments indicate that cannibalism rates are inversely proportional to flour volume. Thus we may assume

$$c_{EL} = \frac{k_{EL}}{V}, \quad c_{EA} = \frac{k_{EA}}{V}, \quad c_{PA} = \frac{k_{PA}}{V},$$

where V is the volume of flour. We make flour volume oscillate with period 2 and amplitude αV_0 about a mean V_0 , so that $V_n = V_0(1 + \alpha(-1)^n)$. Then the cannibalism coefficients at stage n are

$$c_{EL} = \frac{k_{EL}}{V_0(1 + \alpha(-1)^n)}, \quad c_{EA} = \frac{k_{EA}}{V_0(1 + \alpha(-1)^n)}, \quad c_{PA} = \frac{k_{PA}}{V_0(1 + \alpha(-1)^n)}.$$

If we let c_{EL} , c_{EA} , c_{PA} denote the cannibalism coefficients in the average flour volume, $c_{EL} = k_{EL}/V_0$, $c_{EA} = k_{EA}/V_0$, $c_{PA} = k_{PA}/V_0$, we obtain the periodic model

$$\begin{aligned} L_{n+1} &= bA_n \exp\left(-\frac{c_{EL}L_n + c_{EA}A_n}{1 + \alpha(-1)^n}\right), \\ P_{n+1} &= (1 - \mu_L)L_n, \\ A_{n+1} &= P_n \exp\left(-\frac{c_{PA}A_n}{1 + \alpha(-1)^n}\right) + (1 - \mu_A)A_n. \end{aligned} \tag{2.19}$$

This model has an extinction equilibrium $(0, 0, 0)$, which may be shown to be asymptotically stable if $\theta < 1$. If $\theta > 1$, there is a solution of period 2 that is asymptotically stable if θ is close to 1, but for larger values of θ the dynamics may be chaotic. In addition, population sizes are considerably larger than in the unforced case, and this is borne out by experiment.

There are two important lessons that may be drawn from this model. The first is that trying to control a pest population by removing adults may have unintended consequences such as large fluctuations in the pest population size. The second is that periodic variation in the environment may produce substantial increases in population size.

The analysis of the model (2.12) becomes considerably simpler if we neglect cannibalism of eggs by larvae. Mathematically, this means taking $c_{EL} = 0$. The recruitment of larvae at equilibrium is then changed from $bA_n e^{-c_{EA}A_n} e^{-c_{EL}L_n}$ to $bA_n e^{-c_{EA}A_n}$. In order to make the parameter values correspond, we should replace

b by $be^{-c_{EL}L^*}$, where c_{EL} is the original cannibalism coefficient and L^* is the equilibrium larval population. With our baseline parameters this would mean replacing $b = 7$ by $b^* = 7e^{-0.36} = 4.88$. We will not carry out the analysis of this reduced model

$$\begin{aligned} L_{n+1} &= b^* A_n e^{c_{EA} A_n}, \\ P_{n+1} &= (1 - \mu_L) L_n, \\ A_{n+1} &= P_n e^{-c_{PA} A_n} + (1 - \mu_A) A_n, \end{aligned} \tag{2.20}$$

but will indicate it in a sequence of exercises.

Exercises

1. a. Show that the survival equilibrium of (2.20) has

$$A = \frac{1}{c_{EA} + c_{PA}} \log \theta,$$

and once A has been calculated,

$$L = b^* A e^{-c_{EA} A}, \quad P = b^* (1 - \mu_L) A e^{-c_{EA} A}.$$

- b. Calculate the equilibrium population sizes for the parameter values $b^* = 4.88$, $c_{EA} = 0.01$, $\mu_L = 0.2$, and (i) $\mu_A = 0.81$, $c_{PA} = 0.005$, (ii) $\mu_A = 0.96$, $c_{PA} = 0.5$.
2. Show that the extinction equilibrium of the model (2.20) is asymptotically stable if and only if $\theta < 1$.
3. Show that at a survival equilibrium of (2.20) the characteristic equation is a cubic polynomial with

$$\begin{aligned} a_1 &= \mu_A c_{PA} A - (1 - \mu_A), \\ a_2 &= 0, \\ a_3 &= - \left(\frac{L}{A} - c_{EA} L \right) (1 - \mu_L) e^{-c_{PA} A}. \end{aligned}$$

4. Show that with parameter values $b^* = 4.88$, $c_{EA} = 0.01$, $\mu_L = 0.2$, the survival equilibrium of (2.20) is asymptotically stable if $\mu_A = 0.01$, $c_{PA} = 0.005$, and unstable if $\mu_A = 0.96$, $c_{PA} = 0.5$.
5. Run simulations to compare the behaviors of the models (2.12) and (2.20) with the two sets of parameter values used in this section and a variety of initial values.
6. Show that it is possible to eliminate L and P from the model (2.20) and obtain a single third-order difference equation,

$$A_{n+3} = b^*(1 - \mu_L)A_n e^{-c_{EA}A_n} e^{-c_{PA}A_{n+2}} + (1 - \mu_A)A_{n+2}.$$

2.9 Project: A Discrete SIS Epidemic Model

In this project we outline of analysis of an *SIS* (susceptible infective suceptible) discrete epidemic model in a human population with variable size. The *SIS* model is given by the system

$$\begin{aligned} S_{n+1} &= f(T_n) + S_n\pi(n, n+1)h(I_n) + I_n\pi(n, n+1)[1 - \xi(n, n+1)], \\ I_{n+1} &= S_n\pi(n, n+1)[1 - h(I_n)] + I_n\pi(n, n+1)\xi(n, n+1)\zeta(n, n+1), \end{aligned}$$

with

$$T_n = S_n + I_n = f(T_n) + T_n\pi(n, n+1) + I_n\pi(n, n+1)[\zeta(n, n+1) - 1],$$

where $\pi(n, n+1)$, $\xi(n, n+1)$, $\zeta(n, n+1)$ are assumed to be constants with α, μ, σ positive constants, that is,

$$1 - \pi(n, n+1) = 1 - e^{-\mu}$$

is the probability of death due to natural causes,

$$1 - \xi(n, n+1) = 1 - e^{-\sigma}$$

is the probability of recovering,

$$1 - \zeta(n, n+1) = 1 - e^{-\rho}$$

is the probability of death due to infection,

$$h(I_n) = e^{-\alpha I_n}$$

is the probability of not becoming infected, and $f(T_n)$ is the birth or immigration rate (two cases). In this project we take $\rho = 0$, that is, the disease is not fatal.

The model assumes that the time step is one generation; from generation n to $n+1$, infections occur before deaths; there are no infected offspring, that is, all newborns or recruits enter into the susceptible class; in the case of nonconstant recruitment, if there are no people, then there are no births, that is, $f(0) = 0$; if there are too many people, then there are not enough resources to sustain further reproduction, that is, $\lim_{T_n \rightarrow \infty} f(T_n) = 0$; the probability of not becoming infected when there are no people is one, that is, $h(0) = 1$; the probability of not becoming infected as the number of infected increases is a strictly decreasing function, $h'(I_n) < 0$; as the number of infected people increases, the probability of not becoming infected goes to zero, that is, $\lim_{I_n \rightarrow \infty} h(I_n) = 0$.

Case A. Assume a constant recruitment rate, that is, let

$$f(T_n) = \Lambda > 0,$$

where Λ is a constant (immigration rate).

1. Show that the model becomes:

$$\begin{aligned} S_{n+1} &= \Lambda + S_n e^{-\mu} e^{-\alpha I_n} + I_n e^{-\mu} [1 - e^{-\sigma}] \\ I_{n+1} &= S_n e^{-\mu} [1 - e^{-\alpha I_n}] + I_n e^{-\mu} e^{-\sigma}, \end{aligned} \quad (2.21)$$

with

$$T_{n+1} = \Lambda + T_n e^{-\mu}.$$

2. Show that

$$T_n = e^{-\mu n} \left(T_0 - \frac{\Lambda}{1 - e^{-\mu}} \right) + \frac{\Lambda}{1 - e^{-\mu}}$$

and that

$$\lim_{n \rightarrow \infty} T_n = \frac{\Lambda}{1 - e^{-\mu}} \equiv T_\infty.$$

3. Set $T_0 = T_\infty$ (initial population size). This simply means that the population starts at its asymptotic limit, that is, the population is at a demographic equilibrium. Now substitute S_n by $S_n = T_\infty - I_n$ into (2.21) and show that

$$I_{n+1} = (T_\infty - I_n) e^{-\mu} [1 - e^{-\alpha I_n}] + I_n e^{-(\mu + \sigma)}. \quad (2.22)$$

4. Show that $I^* = 0$ is a fixed point of (2.22) and also show that the basic reproductive number is

$$R_0 = \frac{\alpha T_\infty e^{-\mu}}{1 - e^{-(\mu + \sigma)}}.$$

5. Explain the biological meaning of \mathcal{R}_0 .
6. Show that if $\mathcal{R}_0 < 1$, then $I^* = 0$ is a global attractor of $u(I_n)$.
7. Show that if $\mathcal{R}_0 > 1$, then the disease-free equilibrium is unstable.
8. Show that there exists a unique fixed point $I^* > 0$ of $v(I_n)$ for $\mathcal{R}_0 > 1$.

Case B. Assume a nonconstant recruitment rate of Ricker type, that is, let

$$f(T_n) = \beta T_n e^{-\gamma T_n}.$$

Then

$$\begin{aligned} S_{n+1} &= \beta T_n e^{-\gamma T_n} + S_n e^{-\alpha I_n} e^{-\mu} + e^{-\mu} [1 - e^{-\sigma}] I_n, \\ I_{n+1} &= S_n e^{-\mu} [1 - e^{-\alpha I_n}] + I_n e^{-\mu} e^{-\sigma}, \\ T_{n+1} &= S_{n+1} + I_{n+1} = \beta T_n e^{-\gamma T_n} + T_n e^{-\mu} \end{aligned} \quad (2.23)$$

where β = maximal birth rate/person/generation

Let $\mathcal{R}_d = \beta / (1 - e^{-\mu})$.

1. Show that if $\mathcal{R}_d < 1$, then there is no positive fixed point.
2. Show that if $\mathcal{R}_d > 1$, then there exist two fixed points, $T'_\infty = 0$ and $T_\infty^2 > 0$.
3. Show that if $1 < \mathcal{R}_d < e^{2/(1-e^{-\mu})}$, then T_∞^2 is locally stable.
4. What is the biological interpretation of \mathcal{R}_d ? Assume that (2.23) can be “reduced” to a single “equivalent” limiting equation

$$I_{n+1} = (T_\infty - I_n)e^{-\mu}(1 - e^{-\alpha I_n}) + I_n e^{-\mu} e^{-\sigma} \quad (2.24)$$

when $1 < \mathcal{R}_d < e^{2/(1-e^{-\mu})}$ and where $T_\infty^2 = \frac{1}{\gamma} \log(\mathcal{R}_d)$.

5. Show that the basic reproductive number is

$$\mathcal{R}_0 = \frac{\alpha e^{-\mu} \frac{1}{\gamma} \log R_d}{1 - e^{-(\mu+\sigma)}}.$$

6. Show that T_∞^2 is a global attractor if $\mathcal{R}_0 < 1$. Show that if $\mathcal{R}_0 > 1$, then the endemic equilibrium of (2.24) is a global attractor.
7. Simulate the full system (2.23) in the region $1 < R_d < e^{2/(1-e^{-\mu})}$, where T_∞ is a fixed point, and in the regions $R_d > e^{2/(1-e^{-\mu})}$, where period-doubling bifurcation occurs on the route to chaos. Does the demography drive the disease dynamics?

References: Castillo-Chavez and Yakubu (2000b, 2000c, 2000d), Barrera, Cintron-Arias, Davidenko, Denogean, and Franco (2000).

2.10 Project: A Discrete-Time Two-Sex Pair-Formation Model

1. Consider the following discrete-time two-sex pair-formation model:

$$\begin{aligned} x(t+1) &= (\beta_x \mu_x \mu_y + (1 - \mu_y) \mu_x + (1 - \sigma) \mu_x \mu_y) p(t) \\ &\quad + \mu_x x(t) G(x(t), y(t), p(t)), \\ y(t+1) &= (\beta_y \mu_y \mu_x + (1 - \mu_x) \mu_y + (1 - \sigma) \mu_x \mu_y) p(t) \\ &\quad + \mu_y y(t) H(x(t), y(t), p(t)), \\ p(t+1) &= \sigma \mu_x \mu_y p(t) + \mu_x x(t) (1 - G(x(t), y(t), p(t))), \end{aligned}$$

where the functions $G : [0, \infty) \times [0, \infty) \times [0, \infty) \rightarrow [0, 1]$ and $H : [0, \infty) \times [0, \infty) \times [0, \infty) \rightarrow [0, 1]$ denote the state-dependent probability functions and satisfy the equation

$$\mu_x x(t) (1 - G(x(t), y(t), p(t))) = \mu_y y(t) (1 - H(x(t), y(t), p(t)))$$

and where $\beta_x, \beta_y, \mu_x, \mu_y$, and σ are constants in the interval $[0, 1]$.

(a) Given that

$$G(x(t), y(t), p(t)) = \frac{p(t)}{y(t) + p(t)},$$

where $(x(t), y(t), p(t))$ belong to the set Ω , where

$$\Omega := \left\{ (x(t), y(t), p(t)) \mid 0 \leq \frac{x(t)}{y(t)} \leq \frac{\mu_y}{\mu_x(1 - G(x(t), y(t), p(t)))} \right\}$$

find

$$H(x(t), y(t), p(t)).$$

(b) For the given function in (a) find the marriage function $\phi : [0, \infty) \times [0, \infty) \times [0, \infty) \rightarrow [0, 1]$ that satisfies the equation

$$\begin{aligned} \phi(x(t), y(t), p(t)) &\equiv \mu_x x(t)(1 - G(x(t), y(t), p(t))) \\ &= \mu_y y(t)(1 - H(x(t), y(t), p(t))). \end{aligned}$$

(c) Show that the marriage function in (b) satisfies the following properties for all $(x(t), y(t), p(t)) \in \Omega$ and the constant $k \in [0, \infty)$:

(i)

$$\phi(x(t), y(t), p(t)) \geq 0,$$

(ii)

$$\phi(kx(t), ky(t), kp(t)) = k\phi(x(t), y(t), p(t)),$$

(iii)

$$\phi(x(t), 0, p(t)) = \phi(0, y(t), p(t)) = 0.$$

(d) If $\beta_x = \beta_y = \mu_x = \mu_y = \sigma$, use the marriage function in (b) to solve the following equation for the characteristic equation $\lambda = \lambda^*$:

$$-\sigma\mu_x\mu_y + \lambda = \phi\left(\frac{\beta_x\mu_x\mu_y}{\lambda - \mu_x} - 1, \frac{\beta_y\mu_y\mu_x}{\lambda - \mu_y} - 1, 1\right),$$

where

$$\frac{\beta_x\mu_x\mu_y}{\lambda - \mu_x} - 1 > 0 \quad \text{and} \quad \frac{\beta_y\mu_y\mu_x}{\lambda - \mu_y} - 1 > 0.$$

2. Use the marriage function in (b) with $\varepsilon = 0$ and $\beta_x = \beta_y = \mu_x = \mu_y = \sigma$ to find a positive fixed point $[\xi_0, \eta_0, 1] \in \Omega$ of the following system (if one exists):

$$\begin{aligned} \xi(t+1) &= \frac{\beta_x\mu_x\mu_y + \mu_x + \mu_x\xi(t)}{\sigma\mu_x\mu_y + \phi(\xi(t), \eta(t), 1)} - 1, \\ \eta(t+1) &= \frac{\beta_y\mu_x\mu_y + \mu_y + \mu_y\eta(t)}{\sigma\mu_x\mu_y + \phi(\xi(t), \eta(t), 1)} - 1, \\ \varsigma(t+1) &= 1. \end{aligned}$$

3. Use the Jury test to find values of σ (if any exist) for which the fixed point $[\xi_0, \eta_0, 1]$ is stable.

References: Castillo-Chavez and Yakubu (2000e, 2000f).

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