Discrete population Models
Chapter II
MTBI/SUMS

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1. Introduction: Linear Models

[1] The population size is described by the *red sequence* $\{x_n\}$ with x_0 the initial population size, $x_1 = x(t_1)$ the population size at the next generation (time t_1). The underlying assumption will always be that the population size at each stage is determined by the the population size in the past generations, but that intermediate population sizes between generations are not needed. Usually the time interval between generations is 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 rate 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 $n = 0, 1, 2, \cdots$, with x_0 as prescribed.

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[1] The title page Dodo *Raphus cucullatus* reconstruction at Oxford University Museum of Natural History

It is easy to solve the difference equation $x_{n+1} = rx_n$ algebraically. We begin by observing that

$$x_1 = rx_0, \quad x_2 = rx_1 = r^2 x_0, \quad x_3 = rx_2 = r^3 x_0$$

, and then we guess (and prove by induction) that the unique solution is $x_n = r^n x_0$ $(n = 0, 1, 2, \cdots)$. It follows that if $\mid r \mid < 1$ then $x_n \to 0$ as $n \to \infty$, while if $\mid r \mid > 1$ then x_n grows unbounded as $n \to \infty$. More precisely, if $0 \le r < 1$, x_n decreases monotonically to zero; if $-1 < r < 0$, x_n oscillates, alternating positive and negative values but tens 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 the 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

$$x_n = \begin{cases} rx_n & \text{for } x_n > 0 \\ 0 & \text{for } x_n \le 0 \end{cases}$$

which says that the population becomes extinct once it becomes zero in any generation. This will occur if and only if $r \le 0$. 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

Introduction: Linear . . .
Graphical Solutions of . . .
Equilibrium Analysis
Period-Doubling and . . .
Support and Reference . . .
Home Page
Title Page
◀◀ ▶▶
◀ ▶
Go Back
Full Screen
Close
Quit

leads to the linear nonhomogeneous 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

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

If $r > 1$, then x_n grows unbounded 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 unbounded. If $0 < r < 1$, 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 population except possible while the population size is small enough not to be subject to the effect

Introduction: Linear . . .
Graphical Solutions of . . .
Equilibrium Analysis
Period-Doubling and . . .
Support and Reference . . .
Home Page
Title Page
◀◀ ▶▶
◀ ▶
Page 3 of 23
Go Back
Full Screen
Close
Quit

of overcrowding. Various nonlinear difference equation models have been proposed as more realistic. For example, the difference equations

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

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 generations 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 at the end of next section 2, Graphical Solutions of Difference Equations), 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 as x_{n+1} becomes negative if x_n is too large. Another form, which could with some justification also be called logistic equations is

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

Here the growth rate decreases to zero as $x_n \to \infty$, 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

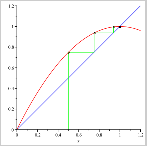
$$x_{n+1} = rx_n\left(1 + \alpha x_n\right)^{-\beta} \qquad \text{[Hassell (1975)]}$$

and

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

It should be recognized that none of these models is derived from actual population growth laws. Rather, they are attempts to give qualitative expressions 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).

Exercises



Introduction: Linear . . .
Graphical Solutions of . . .
Equilibrium Analysis
Period-Doubling and . . .
Support and Reference . . .

Home Page

Title Page

◀◀ ▶▶

◀ ▶

Go Back

Full Screen

Close

Quit

2. Graphical Solutions of Difference Equations

There is a way of solving difference equations graphically, called *cobwebbing method*, which we illustrate for the simple linear homogeneous example $x_{n+1} = rx_x$. 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 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 the information about the behavior of solutions. his is particularly useful for difference equations whose analytic solution is complicated. We give two more illustrative examples.

Example 1. *(Verhulst equation) For the equation*

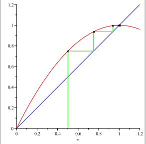
$$x_{n+1} = \frac{rx_n}{x_n + A}$$

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* $y = x$*intersect the reproduction curve (Figure 2).*

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*

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



Introduction: Linear . . .
Graphical Solutions of . . .
Equilibrium Analysis
Period-Doubling and . . .
Support and Reference . . .

Home Page
Title Page
◀◀ ▶▶
◀ ▶
Page 6 of 23
Go Back
Full Screen
Close
Quit

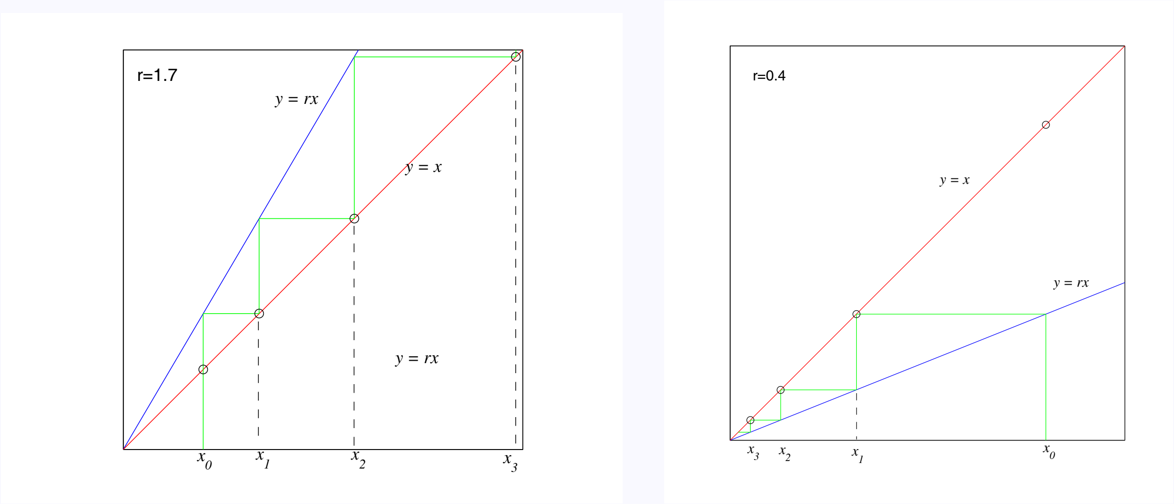
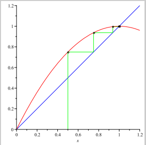


Figure 1: Cobweb graphs: (a) $r > 1$ and (b) $0 < r < 1$

the reproduction curve $y = rx^2/(x^2 + A)$, *which intersect the line* $y = x$ *at* $x = 0$ *and at* $x = \left(r \pm \sqrt{r^2 - 4A}\right)/2$. *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 3).*

If $r > 2\sqrt{A}$, *all solutions with* $x_0 < \left(r - \sqrt{r^2 - 4A}\right)/2$ *tend to zero and the solutions with* $x_0 > \left(r - \sqrt{r^2 - 4A}\right)/2$ *tend to the limit* $x_\infty = \left(r + \sqrt{r^2 - 4A}\right)/2$. *If* $r < 2\sqrt{A}$, *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 depensation model, or* Allee effect, *described for continuous population model in section 1.4.*



Home Page
Title Page
◀◀ ▶▶
◀ ▶

Go Back
Full Screen
Close
Quit

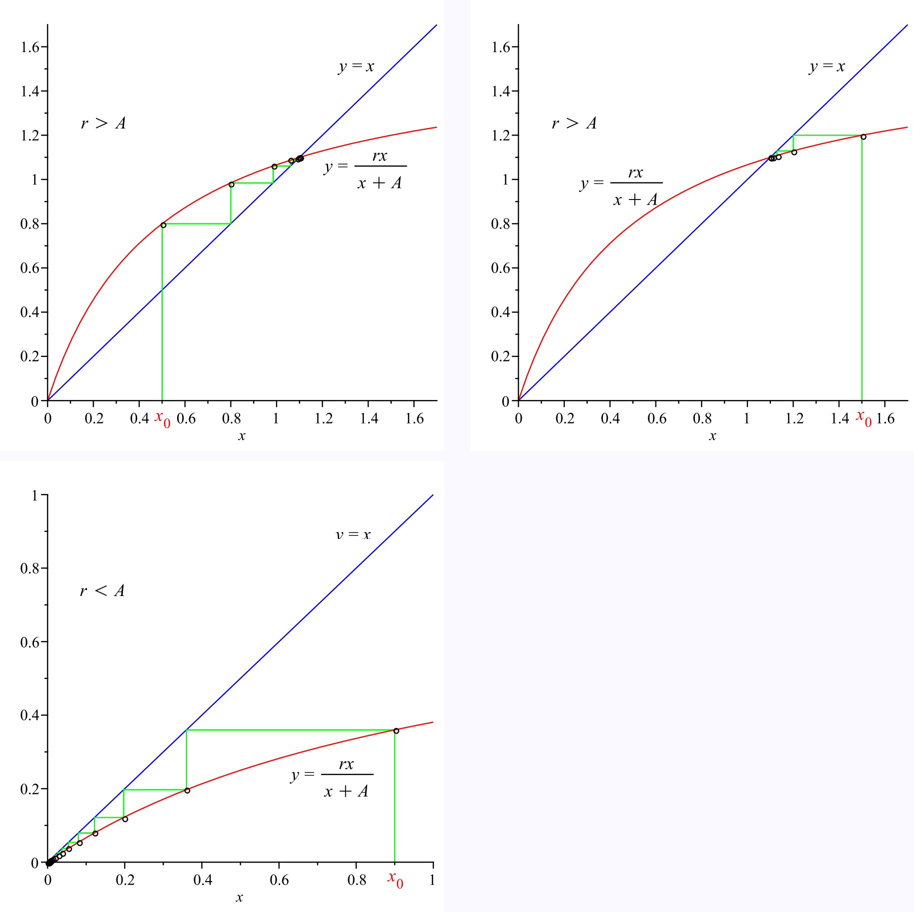
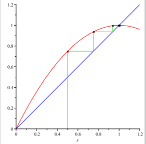


Figure 2: Cobweb graph with different initial values x_0 for Example 1.



Introduction: Linear . . .
Graphical Solutions of . . .
Equilibrium Analysis
Period-Doubling and . . .
Support and Reference . . .

Home Page
Title Page
◀◀ ▶▶
◀ ▶
Page 8 of 23
Go Back
Full Screen
Close
Quit

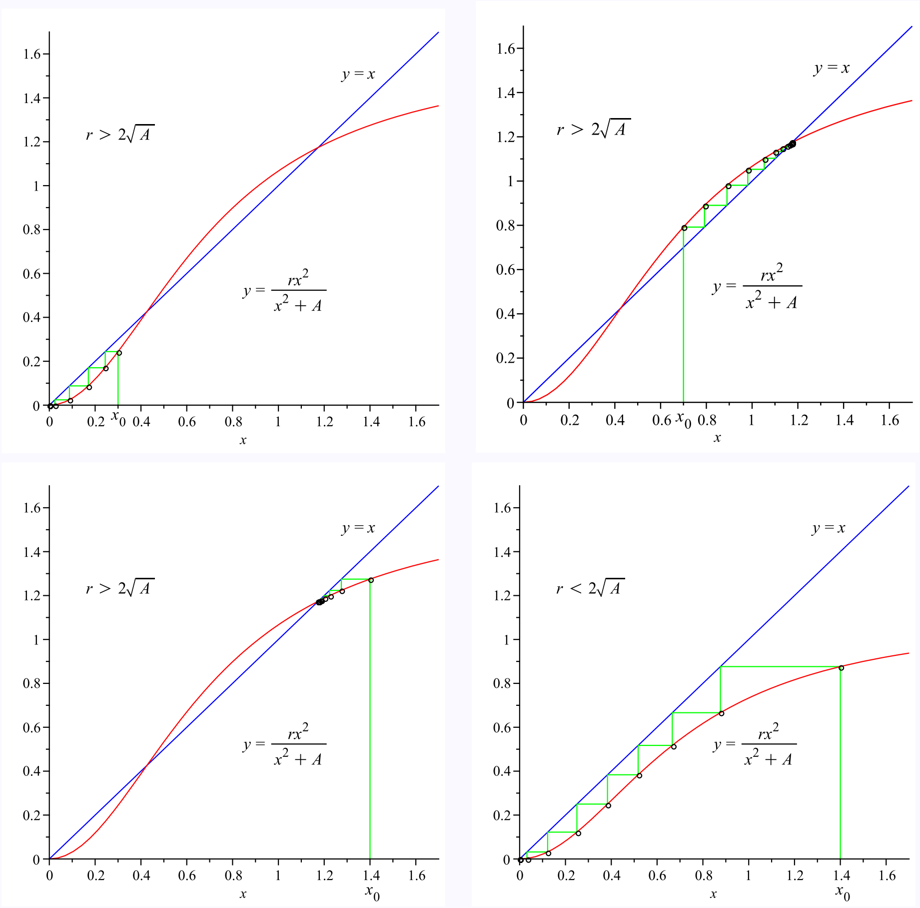
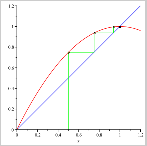


Figure 3: Cobweb graph with different initial values x_0 for Example 2.



Introduction: Linear . . .
Graphical Solutions of . . .
Equilibrium Analysis
Period-Doubling and . . .
Support and Reference . . .
Home Page
Title Page
◀◀ ▶▶
◀ ▶

Go Back
Full Screen
Close
Quit

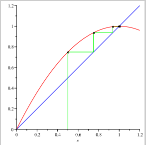
A Maple code

Here is a simple MAPLE code to experiment with the difference equations from this section

```
restart:with(plots):
f:=x -> x+r*x*(1-x);
xmin:=0: xmax:=1
x[0]:=0.5:nmax:=40:
# The loop
for n from 1 to nmax do
x[n+1]:= evalf(f(x[n])):
P[2*n]:=[[x[n],x[n+1]]:
P[2*n+1]:=[x[n+1],x[n+1]]:
end:
# The graph:
L:=[P[k]$ k=1..2*nmax]:
L2:=[P[2*k]$k=1..nmax]
cobweb:=pointplot(L,style=line,color=green):
cobwebP:=pointplot(L2,style=circle,color=black):
diag:=plot(x,x=xmin..xmax,,color=blue):
graphf:=plot(f(x),x=xmin..xmax,,color=red, title="Logistic Equation"):
display(diag,graphf,cobweb,cobwebP);
```

A link to a Maple worksheet with this code is at the course web page here.

Exercises



Home Page

Title Page

◀◀ ▶▶

◀ ▶

Page 10 of 23

Go Back

Full Screen

Close

Quit

3. Equilibrium Analysis

In the examples of the preceding section 2 we observed a tendency for solutions to approach a limit that is the $x - coordinates$ 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:

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

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

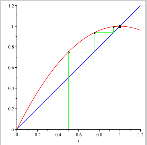
In order to describe the behavior of solutions near an equilibrium, we introduce the process of *linearization* just as we did in Section 1.4 for the first order differential equations. If x_∞ is an equilibrium of the difference equation $x_{n+1} = f(x_n)$, so that $x_\infty = f(x_\infty)$, we make the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



Introduction: Linear . . .
Graphical Solutions of . . .
Equilibrium Analysis
Period-Doubling and . . .
Support and Reference . . .

Home Page
Title Page
◀◀ ▶▶
◀ ▶
Page 11 of 23
Go Back
Full Screen
Close
Quit

$x_\infty = f(x_\infty)$ to form the difference equation equivalent to the original difference equation (1),

$$u_{n+1} = f'(x_\infty)u_n + h(u_n). \tag{2}$$

The function $h(u)$ is small for u small in the sense that $\mid h(u)/u \mid \to 0$ as $\mid u \mid \to 0$; more precisely, for every $\epsilon > 0$ there exists $\delta > 0$ such that $\mid h(u) \mid < \epsilon \mid u \mid$ whenever $\mid u \mid < \delta$. 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

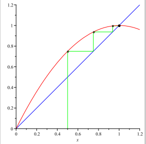
$$v_{n+1} = f'(x_\infty)v_n, \tag{3}$$

obtained by neglecting the higher order term $h(u_n)$ in (2). The importance of the linearization lies in the fact that the behavior of its solutions describes the behavior of the original equations (1) near the equilibrium. The behavior of solutions of the linearization has been described completely in section 1 Introduction: Linear Models. The following result explains the significance of the linearization at the equilibrium.

Theorem 1. *If all the solutions of the linearization* (3) *at an equilibrium* x_∞ *tend to zero as* $n \to \infty$*, then all solutions of* (1) *with* x_0 *sufficiently close to* x_∞ *tend to the equilibrium* x_∞ *as* $n \to \infty$.

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

$$\begin{aligned} \mid u_{n+1} \mid &\le \mid f'(x_\infty) \mid \mid u_n \mid + \mid h(u_n) \mid \\ &< \rho \mid u_n \mid + \epsilon \mid u_n \mid \end{aligned}$$



Introduction: Linear . . .
Graphical Solutions of . . .
Equilibrium Analysis
Period-Doubling and . . .
Support and Reference . . .
Home Page
Title Page
◀◀ ▶▶
◀ ▶
Page 12 of 23
Go Back
Full Screen
Close
Quit

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

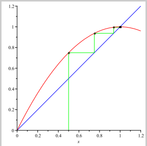
$$| u_n |\leq (\rho+\epsilon)^n | u_0 |, n = 0, 1, 2, \cdots .$$

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

In section 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 (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 **??**).

The content of Theorem (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 $n \to \infty$. This property is called *asymptotic stability* of the equilibria 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 $x_n = x_\infty$ $(n = 0, 1, 2, \cdots)$, solutions cannot remain close to x_∞. This property is called *instability* of the equilibria x_∞. An unstable equilibrium has no biological significance since any deviation, however small, is enough to force solutions away.

We emphasize that Theorem 1 applies to solutions whose initial value x_0 is close enough to the equilibrium x_∞. This is because the nonlinear term $h(u)$ 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 (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 by using the cobwebbing method of constructing solutions graphically, as we have shown in Section 2, Graphical



Introduction: Linear . . .
Graphical Solutions of . . .
Equilibrium Analysis
Period-Doubling and . . .
Support and Reference . . .

Home Page
Title Page
◀◀ ▶▶
◀ ▶
Page 13 of 23
Go Back
Full Screen
Close
Quit

Solutions of Difference Equations. Proofs of the theorems in this section may be found in such books as [Elaydi (1996)] or [Sandefur (1990)].

Example 3. *For the logistic equation*

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

with $f(x) = (1+r)x - rx^2/K$ *and* $f'(x) = (1+r) - 2rx/K$*, it is easy to find the equilibria by solving the quadratic equation* $x = x + rx\big(1 - x/K\big)$ *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* $x_\infty = 0$ *is unstable. Since* $f'(K) = 1 - r$*, the equilibrium* $x_\infty = K$ *is asymptotically stable if* $0 < r < 2$*. It is not difficult to show that for* $0 < r < 2$ *every solution tends to the equilibrium* $x_\infty = K$*. If* $r > 2$*, the equilibrium* $x_\infty = K$ *is unstable and there is no asymptotically stable equilibrium to which solutions can tend. In the following section 4, we shall explore the behavior of solutions if* $r > 2$ *in more details.*

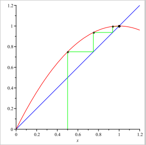
The logistic difference equation is sometime presented in the form

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

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

Example 4. *For the Verhulst equation*

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



Introduction: Linear . . .
Graphical Solutions of . . .
Equilibrium Analysis
Period-Doubling and . . .
Support and Reference . . .

Home Page

Title Page

◀◀ ▶▶

◀ ▶

Page 14 of 23

Go Back

Full Screen

Close

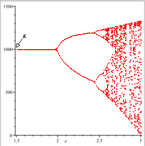
Quit

where

$$f(x) = rx/(x+A); \qquad f'(x) = rA/(x+A)^2$$

. *The solution of* $x = rx/(x+A)$ *gives two roots,* $x = 0$ *and* $x = r - A$. *Thus, if* $r < A$ *the only equilibria 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 (graphically) that in fact every solution approaches* x_∞, *that is, the equilibrium* x_∞ *is globally asymptotically stable.*

Exercises



Introduction: Linear . . .
Graphical Solutions of . . .
Equilibrium Analysis
Period-Doubling and . . .
Support and Reference . . .
Home Page
Title Page
◀◀ ▶▶
◀ ▶

Go Back
Full Screen
Close
Quit

4. Period-Doubling and Chaotic Behavior

For the logistic difference equation

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

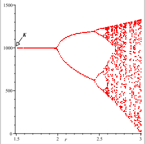
we have seen that the equilibrium $x_\infty = K$ is asymptotically stable for $0 < r < 2$. How do solutions behave for $r > 2$? We might think of r as a parameter that may be varied, and as r passes through the value 2 there must be a fundamental change in the behavior of the solutions. While there is 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 $x_n = K \ (n = 0, 1, 2, \cdots)$ 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 $f(x_+) = x_-$, $f(x_-) = x_+$ so that the alternating sequence $x_+, x_-, x_+, \cdots$ 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

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



Introduction: Linear . . .
Graphical Solutions of . . .
Equilibrium Analysis
Period-Doubling and . . .
Support and Reference . . .
Home Page
Title Page
◀◀ ▶▶
◀ ▶

Go Back
Full Screen
Close
Quit

We look for the equilibria of the second order difference equation

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

Such equilibria gives 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

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

giving,

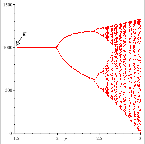
$$x\left(r^3\left(\frac{x}{K}\right)^3 - 2r^2(1+r)\left(\frac{x}{K}\right)^2 + r(r+1)(r+2)\left(\frac{x}{K}\right) - r(r+2)\right) = 0$$

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 root, 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

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



Introduction: Linear . . .
Graphical Solutions of . . .
Equilibrium Analysis
Period-Doubling and . . .
Support and Reference . . .

Home Page

Title Page

◀◀ ▶▶

◀ ▶

Go Back

Full Screen

Close

Quit

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

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

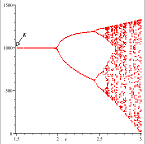
Thus $f(x_+) = x_-$, and since $f_2(x_+) = f\big(f(x_+)\big) = x_+$, we have $f(x_-) = x_+$. We have shown that if $r > 2$ there is a periodic solution of period 2 of $x_{n+1} = f(x_n)$ given by $x_n = x_+$ (if n is odd), $x_n = x_-$ (if n is even).

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

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

Differentiating (using the product rule) gives

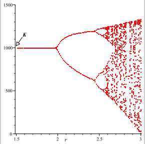
$$f_2'(x) - 1 = r\left(1 - \frac{2x}{K}\right)\left(r^2\left(\frac{x}{K}\right)^2 - r(r+2)\left(\frac{x}{K}\right) + (r+2)\right) + r\left(x - \frac{x^2}{K}\right)\left(2r\frac{x}{K^2} - \frac{r(r+2)}{K}\right).$$



Since $r^2\left(x_+/K\right)^2 - r(r+2)\left(x_+/K\right) + (r+2) = 0$, 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 $x_n = \bar{x}$ $(n = 1, 2, \cdots)$ of the second order difference equation $x_{n+2} = f_2(x_n)$ is asymptotically stable if $\mid f_2'(\bar{x}) \mid < 1$, a theorem analogous to the one established in Section 3 for the 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 $2 < r < \sqrt{6}$. 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 become 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 power of 2 begin to appears, 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 $r = \sqrt{8} = 2.828$. For $r > \sqrt{8}$ there is a periodic solution f period k for every integer k , but different initial values give different solutions. There are also solutions whose behavior in apparently random; such solutions are called *chaotic* (see

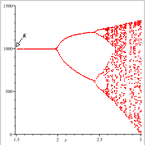


Home Page
Title Page
◀◀ ▶▶
◀ ▶

Go Back
Full Screen
Close
Quit

Figure 4, a bifurcation diagram generated by a program in Maple) The existence of a solution of period three implies chaotic behavior [Li and Yorke (19750].

Exercises



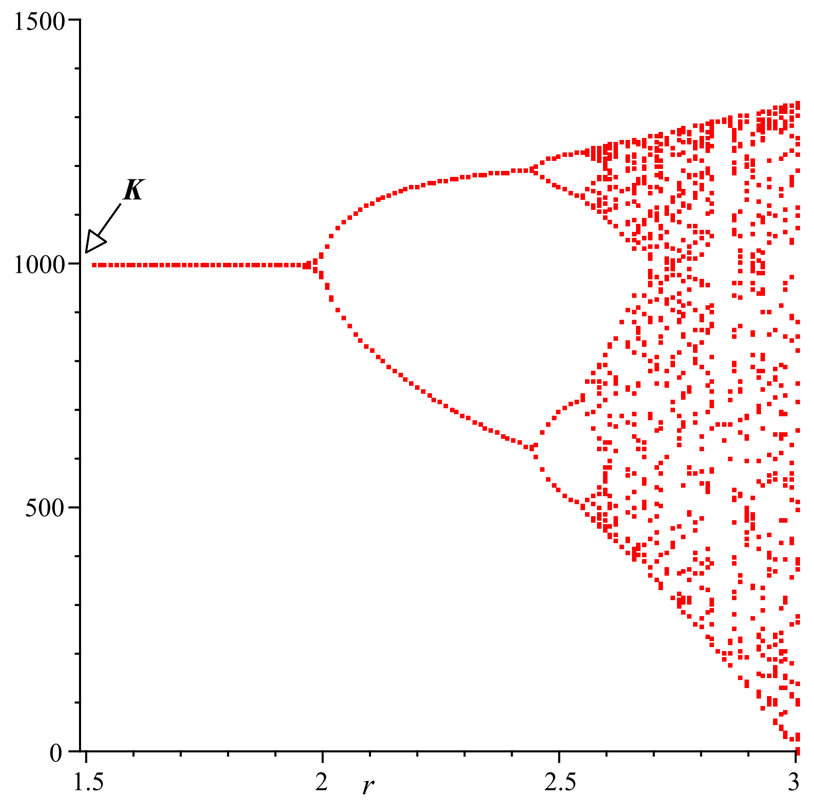
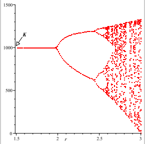


Figure 4: Bifurcation diagram for the logistic difference equation



Introduction: Linear . . .
Graphical Solutions of . . .
Equilibrium Analysis
Period-Doubling and . . .
Support and Reference . . .

Home Page
Title Page
◀◀ ▶▶
◀ ▶

Go Back
Full Screen
Close
Quit

5. Support and Reference Materials

There is a huge amount of information on population dynamic on the web. There are also a large variety of texts written on Population Ecology. Let's begin with a basic list of the books which are good references for the course.

1. *Mathematical Models in Population Biology and Epidemiology*, F. Brauer and C. Castillo-Chavez, Springer 2000. This is our textbook for the course.
2. *Mathematical Modelling with Case of Studies.* A Differential Equation Approach Using Maple and Matlab, by *Belinda Barnes* and *Glenn R. Fulford.* Taylor and Francis, 2008. Good and basic reference
3. *Mathematical Models in Biology*, L. Edelstein-Keshet, McGraw-Hill 1988. A classic in Mathematical Biology.
4. *Ecological Dynamics*, Gurney W.S.C. and Nisbet R.M. , Oxford University Press 1998. A more theoretical book.
5. *Discrete Chaos* with Applications in Science and Engineering, by *Saber N. Elaydi.* Second Edition, Chapman & Hall/CRC 2008.

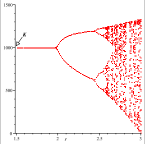
Some web sites with related material are:

1. *Population Ecology* Alexei Sharov, Department of Entomology at Virginia Tech. One of the complete and very good sites on the Web.

   http://home.comcast.net/ sharov/popechome/welcome.html

2. *Introduction to Population Ecology* Edward B. Radcliffe at University of Minnesota. Excellent site with a lot of material in IPM (Integrated Pest Management) In English and Español.

   http://ipmworld.umn.edu/chapters/ecology.htm



Introduction: Linear . . .
Graphical Solutions of . . .
Equilibrium Analysis
Period-Doubling and . . .
Support and Reference . . .

Home Page

Title Page

◀◀ ▶▶

◀ ▶

Page 22 of 23

Go Back

Full Screen

Close

Quit

3. *Population Ecology* David B. McDonald, Department of Zoology at The University of Wyoming.

http://www.uwyo.edu/dbmcd/popecol/

and web pages with essential software tools:

- For phase plane analysis using *MATLAB* there is no finer tools than Pplane by John Polking at Rice University.

  http://math.rice.edu/ dfield/dfpp.html

- Another excellent tool for phase plane analysis is the Bard Ermentrout’s package *XppAut*.

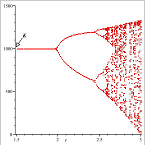
  http://www.math.pitt.edu/ bard/xpp/xpp.html

- The *Maple* Application Center of *Maplesoft* is a good resource material.

  http://www.maplesoft.com/applications/index.aspx

- The list will be incomplete without mentioning the powerful Computer Algebra System *Mathematica* by *Wolfram Research*.

  http://www.wolfram.com/



Home Page
Title Page
◀◀ ▶▶
◀ ▶
Page 23 of 23
Go Back
Full Screen
Close
Quit