Chapter 5

Single species, discrete time models

So far we have models where time is taken to be continuous and these have lead to simple odes. Now we consider models that lead to iterative maps.

6 Discrete generations

Recall that a generation is the expected time from the birth of a individual to the birth of its first offspring.

Definition 5 A population is said to have discrete (or non-overlapping) generations if the remaining expected lifespan of a sexually mature individual is less than or equal to one generation (see Figure 5.1)

Figure 5.1: Non-overlapping generations.
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Example: Insect lifecycle

Consider an insect that emerges from its egg in spring, lays eggs in summer and dies in the autumn. The number of insects in the \((k + 1)\)th generation depends only on the number of insects in the \(k\)th generation (since no other generations have survived). If \(N_k\) denotes the population density in generation \(k\) then we may write

\[
N_{k+1} = f(N_k), \quad k = 0, 1, 2, \ldots,
\]

(5.1)

This is a recursion relation. For general functions \(f\) these can be difficult to solve explicitly, except in a few simple cases.

7 Analyzing simple discrete time models

The evolution of models such as (5.1) can be investigated graphically using Cobweb maps. Basically one plots iterates \(N_{k+1}\) against \(N_k\) for \(k = 0, 1, 2, \ldots\). Figure 5.2 shows the construction. We first plot \(f(N)\)

![Cobweb map construction](image)

as a function of \(N\) and then draw a line \(L\) through the origin with gradient unity. Then we trace the development of a population with initial density as follows. Mark \(N_0\) on the \(N\)–axis. Draw a line vertically upwards till it meets the graph of \(f\). Draw a horizontal line through this point until it meets the vertical axis, which is at the value \(f(N_0) = N_1\). Now reflect this point in \(L\) onto the \(N\)–axis. Repeat the procedure with \(N_0\) replaced by \(N_1\) and so on. As a result we obtain the sequence of points \(N_0, N_1, N_2, \ldots\) on the \(N\)–axis that shows the evolution of \(N\) from generation to generation.
Location of steady states

A population $N^*$ is a steady state if and only if $N^* = F(N^*)$, i.e. they are the fixed points of the map $F$. They can be found in the cobweb map as the points where $L$ meets the graph of $f$.

Example: (Malthus)

The simplest case is $N_{k+1} = rN_k$ for $r > 0$. The explicit solution is $N_k = r^k N_0$. Thus if (i) $r > 1$ we get population explosion, (ii) $r < 1$ we get extinction, and (iii) $r = 1$ we get a steady population $N_k = N_0$ for all $k = 0, 1, \ldots$.

Example: (Verhulst, Beverton-Holt)

Here we introduce some density-dependent regulation.

$$N_{k+1} = f(N_k) = \frac{rN_k}{K + N_k}, \quad k = 0, 1, 2, \ldots$$

It is not easy to find an explicit solution of this recurrence (does one exist?). Thus we use cobwebbing. The function $f$ is hyperbolic: for small $N$, $f(N)$ looks linear, and then it saturates for large $N$. The only question is whether the graph of $f$ lifts above the “$y=x$” line $L$, and this depends on $r$. One finds that

$$f'(N) = \frac{rK}{(N+K)^2},$$

so that $f'(0) = r/K$. Therefore, if $r < K$ we have $f'(0) < 1$ and the graph of $f$ lies entirely below $L$, except at $N = 0$ where there is a steady state $N^* = 0$, and so there is no non-zero steady state in this case. However, when $r > K$ there is a positive steady state which we obtain from solving $N = f(N)$ when $N \neq 0$, i.e. $N^* = r - K$.

![Figure 5.3: Cobweb map construction for Verhulst example](image-url)
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Example: Birth rate vanishing at infinity

Now consider

\[ N_{k+1} = \frac{rN_k}{1+N_k^2}. \] (5.2)

To find any non-zero steady states we solve \( 1 = \frac{rN^*}{1+N^*_2} \), i.e. \( N^* = \sqrt{r-1} \) provided that \( r > 1 \). For small \( N \), again \( f \) is approximately linear, but then the graph of \( f \) curves over and starts to decrease as \( N \) passes a critical value where \( f' = 0 \), and then the curve curves back up and tends to zero as \( N \to \infty \). We therefore obtain the cobweb plots shown in figure 5.4. We see that if \( r < 1 \) all initial states converge to \( N^* = 0 \), whereas if \( r > 1 \) all non-zero initial states converge to \( N^* = \sqrt{r-1} \). (A little care is needed to draw this figure. The fact that \( f'(N^*) > -1 \) is needed to ensure that the oscillations do not grow (see below for more on this).)

This last example shows that extra information on the slope of the growth \( f \) is necessary to determine the precise behaviour close to a steady state, since the slope determines the local stability of a steady state.

8 Local stability of steady states

We consider a small perturbation \( n_0 \) from \( N^* \) as see how this evolves. Let \( N_0 = N^* + n_0 \) where \( n_0 \ll 1 \). Let \( N_k \) denote the iterates generated by \( N_{k+1} = F(N_k) \), and let \( n_k = N_k - N^* \). Then we have

\[
\begin{align*}
N_{k+1} &= F(N_k) \\
N^* + n_{k+1} &= F(N^* + n_k) \\
&= F(N^*) + F'(N^*)n_k + O(n_k^2)
\end{align*}
\]

Figure 5.4: Cobweb map construction for equation 5.2
Since $N^* = F(N^*)$, we therefore obtain
\[ n_{k+1} = F'(N^*)n_k, \] (5.3)
to first order. This equation remains a valid approximation to the full nonlinear system provided that $n_k$ is small. Usually we write $\lambda = F'(N^*)$ as the eigenvalue for this linearised system. The solution of (5.3) is
\[ n_k = \lambda^k n_0, \]
and so perturbations go to zero as $k \to \infty$ only if $|\lambda| < 1$, i.e the condition for local stability is
\[ |F'(N^*)| < 1. \]
There are 4 distinct types of stability around a steady state which are shown in figure 5.5. In the first case (i), $0 < \lambda < 1$ so that $n_k > 0$ for all $k$ and since $\lambda < 1$ we have $n_k \to 0$ as $k \to \infty$.

\[ \begin{align*}
\text{(i) } & \ 0 < \lambda < 1 \\
& \text{monotonic stable}
\end{align*} \quad \begin{align*}
\text{(ii) } & \ -1 < \lambda < 0 \\
& \text{stable with oscillations}
\end{align*} \quad \begin{align*}
\text{(iii) } & \ 1 < \lambda \\
& \text{monotonic unstable}
\end{align*} \quad \begin{align*}
\text{(iv) } & \ \lambda < -1 \\
& \text{unstable with oscillations}
\end{align*}

Figure 5.5: The 4 types of cobweb map close to a steady state

**Example:** $F(N) = rN/(1+N^2)$ revisited

Here
\[ F'(N) = \frac{r(1-N^2)}{(1+N^2)^2}, \]
so that

1. $\lambda = F'(0) = r$, so that $N^* = 0$ is stable for $r < 1$ and unstable for $r > 1$. 

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2. When $r > 1$, \( \lambda = F'(\sqrt{r-1}) = \frac{2}{r} - 1 \), so that \( \lambda < 1 \) if \( r > 1 \). Hence the second steady state, when it exists, is always stable.

These results are illustrated in Figure 5.6

**Example:** \( f(N) = N \exp \left[ r \left( 1 - \frac{N}{K} \right) \right] \)

Let \( u = \frac{N}{K} \). Then the steady states satisfy \( u = h(u) := u \exp \left[ r \left( 1 - u \right) \right] \), so that \( u^* = 0 \) and \( u^* = 1 \) are the only steady states. Also

\[
h'(u) = (1 - ru) \exp r(1 - u),
\]

so that \( h'(0) = e^r > 1 \) for \( r > 0 \), so that \( u^* = 0 \) is always unstable. At \( u^* = 1 \) we have \( h'(1) = 1 - r \), so that \( u^* \) is unstable with oscillations for \( r > 2 \), stable with damped oscillations if \( 1 < r < 2 \) and monotonically stable for \( 0 < r < 1 \). See figure 5.7 for the cobweb plots.

**Example: Harvesting**

Consider the following model:

\[
N_{k+1} = \frac{b N_k}{1 + N_k^2} - H N_k = f(N_k), \quad k = 0, 1, 2, \ldots,
\]

(5.4)

where \( b > 1, H > 0 \). This models population growth with a harvesting term \(-H N_k\). Let us see what the effect of the harvesting is.

\[
f'(N) = \frac{b(1 - N^2)}{(1 + N^2)^2} - H,
\]
so that $f'(0) = b - H$. Hence if $b < H$ then the graph of $f$ goes negative for $N$ small and positive (in fact for all $N > 0$), which gives an unrealistic model. Hence for realism we need $b > H$. First we find the steady states. These are $N^* = 0$ and solutions to

$$\frac{b}{1+N^2} - H = 1.$$  

Firstly, note that if there is no harvesting, so that $H = 0$, then $N^* = 0$ is the only steady state. Non-zero steady states must be positive solutions to

$$HN^2 - b + H + 1 = 0,$$

which has one positive solution $N^* = \sqrt{\frac{b-H-1}{H+1}}$ if $b > H + 1$. Now $f'(0) = b - H > 0$, so that $N^* = 0$ is stable if $H > b - 1$, but otherwise is unstable. At the second steady state,

$$f'(N^*) = \frac{b(1-N^*^2)}{(1+N^2)^2} - H.$$
There is no need in substituting in the value for $N^*$ and then simplifying. Since $N^*$ is a steady state, $1 + N^{*2} = b/(H + 1)$, so that

$$f'(N^*) = \frac{(H + 1)^2}{b} - H = \frac{2(1 + H)^2 - b(1 + 2H)}{b}.$$ 

Now we can solve $f'(N^*) = -1$ to find $b = b^* = \frac{(H + 1)^2}{H + 1}$ and if $b > b^*$ then $f'(N^*) < -1$. Also $f'(N^*) = 1$ when $b = H + 1$. Thus $N^*$ is stable when $H + 1 < b < \frac{(H + 1)^2}{H + 1}$. Actually, as $b$ increases through $b^*$ we get a periodic orbit appearing around $N^*$ (see Figure 5.8).

**Example: The Logistic Map**

This is the famous model due to May and can be written as

$$N_{k+1} = rN_k[1 - bN_k], \quad r, b > 0.$$  

We let $u(t) = bN(t)$ so that we are solving

$$u_{k+1} = ru_k(1 - u_k) = f(u_k), \quad \text{where } f(u) = ru(1 - u).$$

The steady states $u^*$ are solutions of

$$ru(1 - u) = u,$$

so that $u^* = 0$ and $u^* = 1 - \frac{1}{r}$ are the two possible steady states. The second steady state only exists when $r > 1$. Figure 5.9 shows how the steady states change as $r$ change. To study the stability of these steady
states, note that

\[ f'(u) = r(1 - 2u). \]

Then \( f'(0) = r \) and so \( u^* = 0 \) is stable for \( r < 1 \). When \( r > 1 \) the second steady state \( u^* = 1 - \frac{1}{r} \) exists and \( f'(u^*) = 2 - r \). Thus \( u^* = 1 - \frac{1}{r} \) is stable when \( 1 < r < 3 \).

What about periodic cycles? Let us consider cycles of length 2. These pairs \( \{u_1, u_2\} \) satisfy

\[ u_1 = f(u_2), \ u_2 = f(u_1), \]

and so \( u_1 = f^2(u_1) = f(f(u_1)), u_2 = f^2(u_2) = f(f(u_2)) \), where \( f^2(u) = f(f(u)) \). Hence each of \( u_1, u_2 \) is a fixed point of the map \( f^2 \), i.e. a solution of

\[ f^2(u) = r^2u(1 - u)(ru^2 - ru + 1) = u. \]

Notice that if \( u^* \) is a steady state of \( f \) then \( f(u^*) = u^* \), so that \( f^2(u^*) = f(f(u^*)) = f(u^*) = u^* \), so that in order to locate the 2-cycle we must throw away the 2 steady states \( u^* = 0, 1 - 1/r \). Thus we first remove the root \( u = 0 \) and solve

\[ r^2(1 - u)(ru^2 - ru + 1) - 1 = 0. \]

This last equation can be factored

\[ r^2(1 - u)(ru^2 - ru + 1) - 1 = -(1 - r + ru)(1 + r - (r + r^2)u + r^2u^2) = 0. \]

Discarding the steady state \( u = 1 - 1/r \) yields \( 1 + r - (r + r^2)u + r^2u^2 = 0 \), which has roots \( u_{-u}, u_+ \) where \( u_{-u} = (1 + r)/r^2 \) and \( u_+ + u_- = (1 + 1/r) > 0 \). Hence both roots \( u_{\pm} \) have positive real part. Moreover, these roots are real positive and distinct when \( (r + r^2)^2 - 4r^2(1 + r) > 0 \) which gives \( r > 3 \).
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Figure 5.10: Logistic equation - location of 2-cycles. Notice that at \( r = 3 \) there is a tangency at the positive steady state and at this point two new intersections of the line \( L \) and \( f^2 = f \circ f \) appear.

This is illustrated in Figure 5.10, which shows how the number of solutions of \( f^2(u) = u \) varies with \( r \). What actually happens here is that the non-zero solution \( u^* = 1 - 1/r \) loses stability at \( r = 3 \) and simultaneously a period 2 cycle emerges. As \( r \) increases, eventually at \( r = 1 + \sqrt{6} \) this 2 cycle becomes unstable and gives rise to a period 4 cycle, and so on. Progressively longer cycles of period \( 2^n \) appear as \( r \) increases, until at a critical value of \( r = r_c \approx 3.57 \) all even period cycles are present and we get chaos. Here there are periodic points of every period \( k \in \mathbb{N} \), yet an uncountable number of initial points are not attracted to some periodic orbit. At around \( r \approx 3.6786 \), the first odd periodic orbit occurs. As \( r \) is increased further periodic points with small odd periods are picked up, and eventually at \( r \approx 3.8248 \) a period three orbit occurs. Figure 5.12 summarises these results through a bifurcation diagram.

9 Appendix: Mathematica code

Code for plotting cobweb map for logistic map

\[
(* \text{Mathematica code for plotting a cobweb map for Logistic Map} *)
\]

\[
(* \text{start code} *)
\]

\[
f[x_, r_] := r \times (1-x)
\]

\[
\text{its} = 20; (* \text{total number of iterations} *)
\]

\[
y = .1; (* \text{initial value of iterates} *);
\]

\[
r = 3.1; (* \text{bifurcation parameter} *);
\]

\[
r = 1.0+\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\!\![
\]

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Figure 5.11: Cobweb plots for the logistic map for various values of $r$. Top left $r = 2.9$, stable positive steady state. Right top, $r = 3$ a 2-cycle is just about to appear, and it grows as $r$ increases (bottom left, $r = 3.1$). Bottom right at $r = 1 + \sqrt{5}$ a 4-cycle appears.

```mathematica
dat = {{y, 0.}, {y, f[y, r]}};

i = 0;
While[i < its,
y = f[y, r];
AppendTo[dat, {y, y}];
AppendTo[dat, {y, f[y, r]}];
i++;

AppendTo[dat, {f[y, r], f[y, r]}];

plot1 = ListPlot[dat,
PlotJoined -> True,
PlotRange -> {{0, 1.}, {0., 1.}}]
```
Figure 5.12: Bifurcation diagram for the Logistic equation. As $r$ increases to $r = 3$ the stable steady state bifurcates into a stable 2-cycle where the population cycles between the two branches of the plot. As $r$ increases further, the 2-cycle becomes unstable where the two branches bifurcate into 4 branches giving a stable 4-cycle and so on.

```mathematica
AspectRatio -> 1, DisplayFunction -> Identity];

plot2 = Plot[{f[t,r],0},{t,0.1},
PlotRange -> {0.1},
AspectRatio -> 1, DisplayFunction -> Identity];

plot1=Show[plot1,plot2,DisplayFunction -> $DisplayFunction];

(* end code *)

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Code for plotting bifurcation diagram for logistic map

(* Mathematica code for plotting bifurcation diagram for Logistic Map *)

(* start code *)

Clear[f, x0, It0, its, seed, pmin, pmax, p, psteps, step, bifurcList, data];

f[x_, p_] = Chop[p x (1-x)];

It0 = 250;
its = 150;
seed = .5;
pmin = 2; pmax = 4; psteps = 400;

p = N[pmin];
step = N[(pmax - pmin)/psteps];

bifurcList[p_] := Module[
{x0 = Nest[f[#, p]&, seed, It0]},
Map[{p, #} &, FixedPointList[f[#, p] &, x0, its, SameTest -> (#2 == x0 &)]]]

data = Partition[Flatten[
Table[bifurcList[t], {t, pmin, pmax, step}], 2];
plot = ListPlot[data, PlotRange -> {{pmin, pmax}, {0., 1.}}, AxesOrigin -> {pmin, 0.0}, PlotStyle -> {PointSize[.002]}, Frame -> True];

(* end code *)