

CHAPTER 1

Discrete population models

1.1. The basic model

The first example is based on a simple population model. Suppose that a population of rabbits lives on an island (so the population is not affected by immigration from the outside, or emigration to the outside). The population is observed once per year. We'll use x for the number of rabbits, and t for the time, measured in years.

In each year a certain number of rabbits die, and this number is proportional to the number that are present at the start of the year. The proportionality constant c is the “death rate” or “mortality rate”. That is, in one year cx rabbits die and are subtracted from the population of x . Similarly, a number of rabbits are born, and this number is also proportional to the number that are present at the start of the year. The proportionality constant b is the “birth rate”. That is, in one year bx rabbits are born and are added to the population of x rabbits. The net effect of this can be summarized as follows:

If the population at some time is x then the population one year later will be $x + bx - cx = (1 + b - c)x$. If we write $r = b - c$, the *net growth rate*, then we can rewrite this as $(1 + r)x$.

Thus we have a function F which specifies how the population changes during one year. In this case, $F(x) = (1 + r)x$. Once we know this function and we know the starting population x we can calculate the population any number of years later by *iterating* the function F . We will often use the alternate parameter $k = 1 + r$. For later reference we present this example as:

EXAMPLE 1.1. $F(x) = (1 + r)x = kx$, for real numbers x . The parameter r is the net growth rate; it must be > -1 . The alternate parameter is $k = 1 + r$, so $k > 0$.

For example, suppose the population is 1000 and the net growth rate is 0.1. Then, after one year, the population will be $F(1000) = (1 + .1) \cdot 1000 = 1100$. To find the population after another year just apply the function F to the population 1100, to get $F(1100) = (1 + .1) \cdot 1100 = 1210$. Then we can find the population after three years by another application: $F(1210) = 1.1 \cdot 1210 = 1331$. Thus if the population is x then, after three years, the population is obtained by iterating F three times, starting with x , so (using the general formula), we obtain $F(F(F(x)))$. We calculate

this by applying the function F three times, starting with x :

$$\begin{aligned}x &\rightarrow F(x) = (1+r)x \\(1+r)x &\rightarrow F((1+r)x) = (1+r) \cdot (1+r)x = (1+r)^2x \\(1+r)^2x &\rightarrow F((1+r)^2x) = (1+r) \cdot (1+r)^2x = (1+r)^3x.\end{aligned}$$

It should be clear (and it is easy to prove by induction) that, for any number of years t , the population after t years is $(1+r)^t x$, or $k^t x$. We will use the notation $F^t(x)$ for the t -fold iteration of F , so $F^t(x) = (1+r)^t x$ in this case. In terms of functional composition, $F^t = F \circ F \circ F \circ \dots \circ F$ (where there are t copies of F), so this really is, in a sense, “ F to the t^{th} power”. As special cases, F^1 is just F , and F^0 is the identity function; that is, $F^0(x) = x$.

Once we have this formula for $F^t(x)$ we can make some observations about population growth:

- (1) Although $(1+r)^t x$ makes mathematical sense for $x < 0$, this doesn't make sense in the model, since populations cannot be negative.
- (2) $(1+r)^t x$ is defined mathematically for all real numbers t (with some worries if $1+r$ is 0 or negative), but there is no meaningful sense in which we can iterate a function t times, where t is not a non-negative integer. [We can make sense of F^t when t is a negative integer, by iterating the inverse function F^{-1} , if it exists.]
- (3) $F^t(0) = 0$ for all t .
- (4) If $r > 0$ then $(1+r) > 1$, so $(1+r)^t \rightarrow \infty$ as $t \rightarrow \infty$. Hence $F^t(x) \rightarrow \infty$ as $t \rightarrow \infty$ if $x > 0$.
- (5) If $-1 \leq r < 0$ then $0 \leq (1+r) < 1$, so $(1+r)^t \rightarrow 0$ as $t \rightarrow \infty$. Hence $F^t(x) \rightarrow 0$ as $t \rightarrow \infty$.
- (6) If $r = 0$ then $F^t(x) = x$ for all t and all x .

This is a very simplistic model of population growth. Here are a few criticisms:

- (1) $F^t(x)$ will generally yield non-integer values.
- (2) $F^t(x) \rightarrow \infty$ can't happen: eventually there will be no space for the rabbits on the island.
- (3) No model can really predict exact numbers of rabbits, since there will always be some random fluctuations.
- (4) The model assumes that the net growth rate is constant, independent of both t and x .

1.2. Discrete dynamical systems

Before modifying this model we isolate the features of the model that constitute a *discrete dynamical system*:

In general, we will work with two variables, x and t . We always think of t as time, but the interpretation of x will depend on the particular application. In general, the values of x are called the *states* of the system. In most cases it will be necessary to specify more than just one number to describe the state of the system, so in most cases we will consider x to be a vector, and we'll refer to it as the *state vector* of the system. The *transition rule* for the system is a function F that transforms the state x at one time to the state $F(x)$ one time unit later. Then we can represent the state of the system t time units later by iterating F ; that is, we calculate $F^t(x)$.

Essentially, it is the iterated function F^t which constitutes the dynamical system, although we often simply refer to the transition rule F as the dynamical system. It is called a *discrete dynamical system* to emphasize the fact that t is measured in discrete steps, so the values of t are restricted to integers – usually positive integers.

Note that the transition rule must be a function of x alone; it does not depend on t . We will see later how to accommodate transition rules that do depend on t . Also, the transition rule is a well-defined function. Hence, the dynamical system is *deterministic*, in the sense that the values of x and t uniquely determine the value of $F^t(x)$.

The first example above illustrates these features. The state vector x is one dimensional – that is, it is just a number. The transition rule is $F(x) = (1 + r)x$, and the state at time t is given by $F^t(x) = (1 + r)^t x$ for $t = 0, 1, 2, 3, \dots$.

The first example illustrates some common features of dynamical systems:

First, the domain of x is usually restricted. That is, state vectors cannot be arbitrary, but are limited to a particular set of values, sometimes called the *state space*. For example, in our population model the values of x cannot be negative.

Second, the transition rule usually incorporates one or more *parameters*. These are quantities that are constant for a specific instance of the dynamical system, and which, in applications, are either determined empirically or are adjusted externally. For example, in our original population model the birth and death rates are parameters. The model only depends on their difference, so it is reasonable to talk of just one parameter, the net growth rate, r .

Here's an important property of dynamical systems:

PROPOSITION 1.2. $F^t \circ F^s = F^{t+s}$.

1.3. Some variations

We now consider two variations on the original model.

The first variation involves external interaction with the population. We envision a yearly addition to (or subtraction from) the population. For example, if $r < 0$, so the population is dying out, we might add a number of rabbits each year to stabilize the population. If $r > 0$, so the population is increasing without limit, we

might remove a number of rabbits each year in order to keep the population from exploding. This gives the following example:

EXAMPLE 1.3. $F(x) = (1+r)x + A = kx + A$, for real numbers x . The parameter A is any real number, and k and $1+r$ are defined as in Example 1.1.

The effect of this model is that, each year, A rabbits are added to the population. In this model the addition occurs at the end of the year, just before the population is counted. [If the addition occurred at the beginning of the year then the transition rule would be $F(x) = (1+r)(x+A)$. Of course A might be negative, in which case rabbits are removed rather than added.

Iterating a few times gives

$$\begin{aligned} F^1(x) &= kx + A \\ F^2(x) &= F(F(x)) = F(kx + A) = k(kx + A) + A = k^2x + A + Ak \\ F^3(x) &= F(F^2(x)) = F(k^2x + A + Ak) = k(k^2x + A + Ak) + A \\ &= k^3x + A + Ak + Ak^2 \\ F^4(x) &= k^4x + A + Ak + Ak^2 + Ak^3. \end{aligned}$$

The pattern should now be clear; the general form is

$$F^t(x) = k^t x + A(1 + k + k^2 + \cdots + k^{t-1}).$$

If you look up the *geometric series* you will find a formula for the sum in parentheses. If $k \neq 1$ this allows us to write

$$(1.1) \quad F^t(x) = k^t x + A \cdot \frac{k^t - 1}{k - 1} = k^t x + A \cdot \frac{1 - k^t}{1 - k}.$$

We now look at a second variation on the basic model.

Instead of looking at the effect of adding population from the outside we consider a way of adjusting the growth rate r to take into account the effects of overcrowding. The idea is that if the population x becomes too large then the rabbits on our island will not be able to find enough to eat, so we expect that the death rate will go up. Also, they will be less healthy, so we expect the birth rate to go down. In other words, we expect that the net growth rate will decrease as the population increases.

Our new variation amounts to replacing the constant growth rate r with a function of x , which is approximately equal to r for small values of x but which decreases as x increases. The simplest function that satisfies these conditions is a linear function of the form $r - \alpha x$ where α is a positive constant. There are many other candidates for a variable growth rate, but we will concentrate on this one because of its simplicity. This gives us the next example:

EXAMPLE 1.4. $F(x) = (1 + r - \alpha x)x = (k - \alpha x)x = kx - \alpha x^2$ for real numbers x . The parameter α is a positive real number, and k and $1 + r$ are defined as in Example 1.1.

We can iterate this:

$$\begin{aligned} F^1(x) &= kx - \alpha x^2 \\ F^2(x) &= F(F(x)) = k(kx - \alpha x^2) - \alpha(kx - \alpha x^2)^2 \\ &= k^2x - \alpha(k + k^2)x^2 + 2\alpha^2kx^3 - \alpha^3x^4. \end{aligned}$$

However, the calculations rapidly become very messy – in fact, $F^t(x)$ is a complicated polynomial of degree 2^t in x , and there is no simple general form for it.

On the other hand, it is easy to calculate as many iterations as we need in a specific case. For example, let $r = .1$ and $\alpha = .0001$. Starting with $x = 2000$ we calculate

$$\begin{aligned} (1.2) \quad F^1(x) &= 1800 \\ F^2(x) &= 1656 \\ F^3(x) &= 1547 \\ F^4(x) &= 1462 \\ F^5(x) &= 1394 \\ F^6(x) &= 1339 \\ F^7(x) &= 1294 \\ F^8(x) &= 1256 \\ F^9(x) &= 1224 \\ F^{10}(x) &= 1196 \end{aligned}$$

Notice that $F^t(2000)$ is decreasing as t increases, although $r > 0$. It is not clear, without further analysis, whether this decrease continues, or what the limiting value is.

1.4. Steady states and limit states

A *steady state* of a dynamical system is a state x_0 so that $F^t(x_0) = x_0$ for all values of t . For example, in our original model, 0 is a steady state, since $F^t(0) = (1 + r)^t \cdot 0 = 0$ for all t .

Since F^t is defined by iterating F this is the same as finding a state for which $F(x_0) = x_0$. In general, such a value x_0 is called a *fixed point* for F . Often such fixed points can be found by just solving an algebraic equation. For example, in

our second model, $F(x) = kx + A$, so we can find the fixed points of F by solving $F(x) = x$ for x , as follows:

$$\begin{aligned} kx + A &= x \\ A &= x - kx = (1 - k)x \\ x &= \frac{A}{1 - k} \end{aligned}$$

If A and $1 - k = r$ both have the same sign then $x_0 = \frac{A}{1 - k} > 0$ so it represents a population, and this population will not change with time.

Next, suppose that x_1 is a state of a dynamical system. If $F^t(x_1)$ converges to a state x_2 as $t \rightarrow \infty$ and $x_2 \neq x_1$ then x_2 is called a *limit state* of the system. We will need to modify this definition later, but this is sufficient for simple examples. For example, in our original model, 0 is a limit state if $-1 \leq r < 0$ since in that case $k = 1 + r < 1$ so $F^t(x) = k^t x \rightarrow \infty$ for any x . On the other hand, if $k > 1$ then 0 is not a limit state, since $F^t(x) = k^t x \rightarrow \pm\infty$ as $t \rightarrow \infty$ if $x \neq 0$. It is true that $F^t(0) \rightarrow 0$ as $t \rightarrow \infty$ in this case, since 0 is a steady state; but 0 is not a limit state of the system since we required $x_2 \neq x_1$ in the definition.

The examples above show that a steady state may – or may not – be a limit state. In the other direction we have:

PROPOSITION 1.5. *If F is continuous then any limit state is a steady state.*

PROOF. Suppose that $F^t(x_1) \rightarrow x_2$ as $t \rightarrow \infty$. Then, if we replace t with $t + 1$, we also have $F^{t+1}(x_1) \rightarrow x_2$. But we can write $F^{t+1}(x_1) = F(F^t(x_1))$. If we take the limit in this equation as $t \rightarrow \infty$ and use the fact that F is continuous we get

$$x_2 = \lim_{t \rightarrow \infty} F^t(x_1) = \lim_{t \rightarrow \infty} F(F^t(x_1)) = F\left(\lim_{t \rightarrow \infty} F^t(x_1)\right) = F(x_2),$$

so $F(x_2) = x_2$. Since x_2 is a fixed point of F it is a steady state. \square

Exercises

- 1.1. Find the limit states (if any) of Example 1.3. Compare with the steady states. You should get different answers depending on the sign of r .
- 1.2. Use a calculator to compute several values of $F^t(x)$ for $x = 500$, using the same system as for (1.2). You should find that the states are now *increasing*, rather than decreasing as in (1.2).
- 1.3. Find the steady states of Example 1.4, using the same parameters as for (1.2).

- 1.4. Example 1.4 has two states x which satisfy $F(x) = 0$. One is 0. Find the other one, in terms of k and α ; call this state M . In a population model we need to restrict x to be between 0 and M , since $F(x) < 0$ if $x < 0$ or $x > M$. Demonstrate this graphically, by plotting the equation $y = F(x)$. [This is a parabola. Where does it cross the axis? Is it concave up or down?]
- 1.5. Example 1.4 has two steady states; one is 0. Find the other in terms of k and α . Is the second steady state between 0 and M ?
- 1.6. Using Example 1.4: Find the maximum value of $F(x)$ in terms of k and α .
- 1.7. Consider the discrete dynamical system defined by the transition rule $F(x) = kx^2$, where k is a positive constant. Find $F^2(x)$, $F^3(x)$, $F^4(x)$. Can you see the general form for $F^t(x)$? What can you say about limit states?