3 The first principle: exponential growth

I think I may fairly make two postula. First, that food is necessary to the existence of man. Second, that the passion between the sexes is necessary and will remain nearly in its present state. Assuming then, my postula as granted, I say, that the power of population is indefinitely greater than the power in the earth to produce subsistence for man. (T. R. Malthus, 1798)

Malthus' *Essay on the Principle of Population* was one of the earliest explorations into the theory of population dynamics. What Malthus realized is that populations of humans, and in fact any self-replicating entity, can grow exponentially or geometrically, and that this kind of growth can overwhelm finite or arithmetically increasing resources. Exponential growth is most easily visualized by considering a single amoeba which, we assume, reproduces by division once every day. After 2 days there will be two amoebas, after 3 days four, then eight, then 16, then 32, then 64, then 128 and so on. In 10 days there will be 1024 amoebas, in 20 days a million, and in a month a trillion. As Malthus realized, exponential population growth is indeed a powerful force.

Exponential growth will be known henceforth as the *first principle of population dynamics.* By using the term "principle" we imply that exponential growth is a fundamental, if somewhat obvious, property of all population systems.

3.1 MATHEMATICAL INTERPRETATION

The first principle can be derived mathematically from the step-ahead forecasting equation (2.8)

$$N_t = N_{t-1}G. \tag{3.1}$$

where $G = 1 + B - D$ is the finite per capita rate of change, with B and D the per capita birth and death rates, respectively. This equation is called a finite *difference equation* because it computes the growth of the population over a finite period of time, like a year or a generation.

The growth of a population can be computed from equation (3.1) by starting with a population of N_0 individuals at time zero. After one time period, say a year, there will be

$$N_1 = N_0G, \tag{3.2}$$

individuals, after 2 years

$$N_2 = N_1G, \tag{3.3}$$

and so on.

Substituting the right-hand side of equation (3.2) for N_1 in equation (3.3) we have

$$N_2 = (N_0G)G = N_0G^2. \tag{3.4}$$

In fact it is possible to solve the equation for any length of time t

$$N_t = N_0G^t. \tag{3.5}$$

to arrive at a finite difference equation describing the first principle of population dynamics.

The first principle can also be derived as a *differential* or continuous-time equation. For example, the *instantaneous* rate of growth of a population, dN/dt, is obtained from the instantaneous per capita rate of change, R, multiplied by the density of the population, N, so that

$$\frac{dN}{dt} = RN. \tag{3.6}$$

Note that the instantaneous rate of change is measured when the time step is very small (i.e. when $dt \to 0$). Rearranging equation (3.6) so that only N appears on the left-hand side

$$\frac{1}{N}dN = R\,dt, \tag{3.7}$$

and integrating over time, yields

$$N_t = N_0e^{Rt}, \tag{3.8}$$

where e is the base of the natural logarithm (e = 2.71828 . . .). Converting to natural logarithms gives the linear relationship

$$\ln N_t = \ln N_0 + Rt. \tag{3.9}$$

Transforming equation (3.5) to natural logarithms,

$$\ln N_t = \ln N_0 + (\ln G)t, \tag{3.10}$$

we see that equations (3.5) and (3.8) are identical with

$$R = \ln G. \tag{3.11}$$

Equations (3.5), (3.8), (3.9) and (3.10) are all precise mathematical statements of the first principle of population dynamics. This principle is truly general in that it applies to all populations and, in fact, to all self-replicating entities, including your compound interest savings account. It is sometimes called the "law of population growth" or the "Malthusian law". These equations will be used, in one form or another, whenever we want to calculate the *trajectory* that a population takes over time, or to predict the future growth of a population when the per capita rate of change and current population size are known.

3.2 POPULATION DYNAMICS UNDER THE FIRST PRINCIPLE

Let us examine the dynamic consequences of the first principle by calculating the growth of a population obeying equation (3.8). First write equation (3.8) in step-ahead forecasting form by setting the time step to unity ($dt = 1$) so that

$$N_t = N_{t-1}e^R. \tag{3.12}$$

Then set the initial population density at $N_0 = 10$ and assume an average per capita rate of change of $R = 0.5$ per year. After 1 year the population will be

$$N_t = 10e^{0.5}.$$

The value of $e^{0.5} = 1.6487$ can be found in a table of exponents or from a pocket calculator, and so

$$N_1 = 10 \times 1.6487 = 16.5$$
$$N_2 = 16.5 \times 1.6487 = 27.2,$$

and so on. This is what is called a numerical solution of the growth equation, or a simulation of the growth process. Numerical solutions for three different values for R are shown in Figure 3.1. As expected, populations with $R > 0$ (or the birth rate greater than the death rate) grow at an increasing rate (exponentially), those with $R = 0$ (or the birth rate equal to the death rate) remain unchanged, while those with $R < 0$ (or the birth rate less than the death rate) decay exponentially towards zero (Figure 3.1, left). If the logarithm of population density is plotted against time, a straight line or linear relationship is obtained with the slope equal to the per capita rate of change (Figure 3.1, right). [Note that logarithmic transformation of the exponential growth curve is a straight line as shown by equation (3.10).]

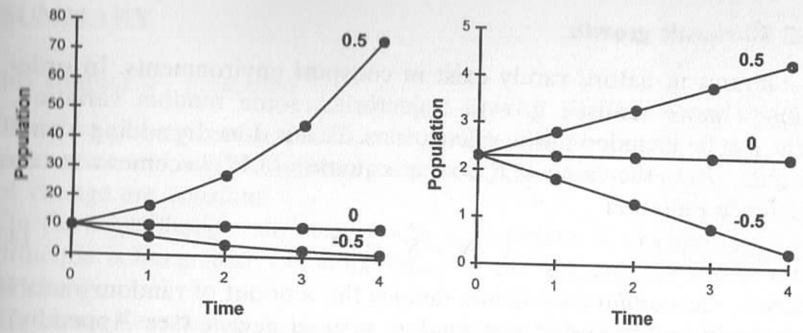

Figure 3.1 Simulation of population growth according to the first principle; equation (3.12) with $N_0 = 10$ and $R = 0.5$, 0, and –0.5, plotted on the arithmetic (left) and logarithmic (right) scales.

Populations growing or declining exponentially are said to be *unstable* because they tend to move away from their original, or initial, conditions. They are also said to be exhibiting *transient* or *non-equilibrium* dynamics – they are in transition, or in the process of going somewhere else, perhaps to extinction. The reason for this instability is that the first principle defines a first-order +feedback process because larger populations give rise to higher growth rates; i.e. the rate of population growth is determined by the product RN [see equation (3.6)]. Notice, however, that the population can be in equilibrium if the exact condition $R = 0$ is met, or the birth rate exactly equals the death rate, but this condition is unlikely to occur for very long in nature where variation is the norm.

3.2.1 Sensitive dependence

One of the characteristics of systems governed by +feedback growth processes is that their current states depend critically on their initial, or starting, states. This is called *sensitivity to*, or *sensitive dependence on*, initial conditions. Let us illustrate this with the differential equation (3.8). Suppose there are two isolated populations, both with the same per capita rate of change ($R = 0.5$) but one containing 10 individuals and the other 11. After five time steps the first population will have 316 individuals and the second one 401, a difference of 85. However, by the 10th time step the difference will be 61,051 and by the 20th this difference will have grown to over 15 billion. In fact it is easy to show that the initial difference between the two populations grows exponentially with time[8]. The phenomenon of sensitive dependence is important, for it means that small errors made when estimating population size can be amplified with time so that long-range predictions become almost impossible, at least for exponentially expanding populations.

3.2.2 Stochastic growth

Populations in nature rarely exist in constant environments. In order to simulate more realistic growth trajectories, some random variation, or *noise*, can be included in the calculations. This is done by adding a random variable, sZ, to the value of R, so that equation (3.12) becomes a *stochastic* difference equation

$$N_t = N_{t-1}e^{R+sZ}, \tag{3.13}$$

where s, the *standard deviation*, defines the amount of random variability in the value of R, and Z is a *random normal deviate* (see Appendix). A random normal deviate is a value selected at random from a *normal distribution* with mean $\bar{Z} = 0$ and standard deviation $s = 1$. Because the mean of the distribution is zero, most of the numbers chosen will be close to zero and, therefore, the value of $R + sZ$ will usually be close to R. The probability of selecting large negative or positive numbers is directly proportional to the standard deviation.

Let us now examine transient dynamics in a noisy world: starting with 10 organisms, an average per capita rate of change 0.5, and standard deviation 0.1, we read the first value of $Z = 0.614$ from the table of random normal deviates (Appendix; pick a number with your eyes closed). Inserting these values in equation (3.13) gives us

$$N_1 = 10 \times e^{0.5+0.1\times0.641} = 17.5,$$

then, taking the next random deviate, $Z = -0.66$,

$$N_2 = 17.5 \times e^{0.5+0.1\times(-0.66)} = 27,$$

and so on. Figure 3.2 illustrates the transient dynamics of a population inhabiting a noisy environment. Notice that the population still grows exponentially and, when plotted as logarithms, retains its basic linear form.

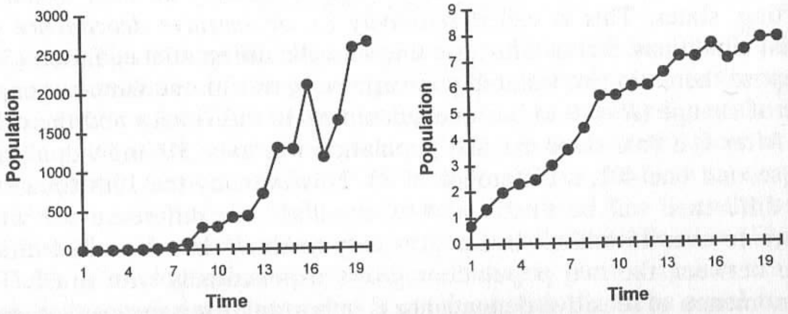

Figure 3.2 Population growth according to the stochastic equation (3.13) with parameters the same as in Figure 3.1 and $s = 0.1$, plotted on arithmetic (left) and logarithmic (right) scales.

3.3 SUMMARY

In this chapter we presented

1. The first principle of population dynamics, which states that populations grow and decline geometrically or exponentially when their rates of change are constant.
2. On the logarithmic scale, the growth of populations obeying the first principle is linear with the slope equal to the average per capita rate of change.
3. The basic forecasting equations were derived in terms of finite per capita rate of change, G (i.e. $N_t = N_{t-1}G$) and the instantaneous per capita rate of change, R (i.e. $N_t = N_{t-1}\,e^R$) with $R = \ln G$.
4. The first principle defines a first-order $^+$feedback loop because the rate of change of the population is directly related to its own size.
5. This $^+$feedback loop gives rise to unstable dynamics; accelerating growth when $G > 1$ or $R > 0$, decay to extinction when $G < 1$ or $R < 0$, and equilibrium under the unlikely condition that $G = 1$ or $R = 0$.
6. Exponential growth processes are sensitive to their initial conditions so that accurate long-term forecasts are virtually impossible.
7. Numerical solutions show that these transient patterns are manifested in both constant and noisy environments.

3.4 EXERCISES

1. If you have $10,000 in the bank at 10% annual interest rate, how much will you have in 10 years if the interest is compounded at the end of each year? What is the relationship between the interest rate and the population parameters G, R, B and D?
2. Simulate the dynamics* of a population for 10 years using equation (3.13) when the initial density is 10 individuals, the per capita rate of change is $R = 0.8$ and the standard deviation is zero. Plot the trajectory on both arithmetic and logarithmic scales.
3. Simulate the dynamics* of a population governed by equation (3.13) under the same conditions as before but with the standard deviation 0.2. Plot the trajectory on arithmetic and logarithmic scales.

*These problems can be done by hand or on a typical computer spreadsheet.