

## 18 The Effects of Randomness

*Grampa*: Put it all on 41. [nudges Homer] I've got a feeling about that number.

*Roulette man*: The wheel only goes to 36.

*Grampa*: Okay, put it all on 36. [nudges Homer] I've got a feeling about that number.

From: *The Simpsons*

### 18.1 Introduction

In Part I we discussed mathematical models of population growth that were based on continuous variation over time. Differential equations were the principal tool in such investigations. In the last chapter we considered models that can be used to describe growth in discrete time intervals. In both cases, however, our models are deterministic – the initial conditions and the mathematics of the model determine the future development of the system. Although random-like behavior may appear in these models, the “randomness” is intrinsic and is not due to truly random external effects. Of course, one could argue that external randomness is only a reflection of our ignorance. A larger, more complicated, model could incorporate deterministic models of climate change, geologic variation and other myriad influences on populations.

Whether such grand models will ever reach fruition is unknown. Yet even if they do, there is no doubt that they will exhibit the “deterministic chaos” that we have already seen in some of our simple discrete logistic models. In such cases, the models will only be useful in making probabilistic predictions about the future. However, without waiting for such grand theories we can study the effects of randomness in a much more simplified setting. Namely, all of our deterministic population models contain parameters such as the growth rate  $r$ , the carrying capacity  $K$ , competition coefficients, etc. In our treatment, we have assumed these quantities were either fixed throughout the time period under study, or varied in some predictable way (for example, density dependent growth). We can model the effects of external randomness on our system by subjecting these coefficients to random change over time. In implementing this program, we will restrict our attention to discrete systems, as it is easier to carry out simulations in that context. As you will see, our work in probability theory will help us to interpret and understand the results.

### 18.2 Environmental Variation

As in most scientific investigations, it is always best to begin by working with the simplest examples. Although often inaccurate in substance, these often can be analyzed completely thereby clarifying relevant features in more realistic models. Recall that our simplest model of discrete population growth is given by the difference equation  $N_{t+1} = rN_t$ . According to Theorem 17.3 (where we use  $k$  instead of  $r$  for the coefficient on the right side), the population will grow exponentially if  $r > 1$  and will exhibit exponential decay when  $r < 1$ . The difference equation is sometimes referred to as a *production equation*, since it specifies how many members of the population are produced in the next time period. The parameter  $r$  then measures the per capita

production. When  $r > 1$  each current member of the population produces more than one new member, so the population grows. When  $r < 1$  the reverse happens.

In the discrete model in Chapter 17 we considered that  $r$  was a constant. However,  $r$  is clearly dependent on environmental factors and as these change the value of  $r$  may change as well. Keeping with our theme of simplicity, let's suppose that our population encounters two types of environmental conditions, "good years" and "bad years". In the good years the per capita production rate is  $r = 2$ , while in the bad years the rate is  $r = \frac{1}{2}$ . Of course, whether a year is a good or bad one is not predictable. For starters, we will assume that the two are equally likely. Thus, whether a year turns out to be good or bad amounts to tossing a fair coin. We can then give the following probability distribution for the per capita production coefficient  $r$ .

|                                 |     |               |
|---------------------------------|-----|---------------|
| <b>Values of <math>r</math></b> | 2   | $\frac{1}{2}$ |
| <b>Probabilities</b>            | 0.5 | 0.5           |

**Table 18.1**

Let's see how to combine this probability model with our deterministic growth model  $N_{t+1} = rN_t$ . Notice that we are trying to combine the simplest model for population growth with the simplest probabilistic model.

**Example 18.1:** Suppose our initial population is  $N_0 = 100$ . Compute values for  $N_1, N_2, N_3, N_4$ , and  $N_5$ , if the coefficient  $r$  is selected randomly each year according to the probability distribution given in Table 18.1.

*Solution:*

We use *Excel* to select the values of  $r$  using its random number generator (see the Tech Notes to Chapter 13 for details). We obtained the sequence 2, 2, 0.5, 0.5, 0.5 (two good years followed by three bad ones). In each year starting with the first we use the value of  $r$  given by this sequence to generate the next value of  $N$ . We obtain the following results:

|                    |                    |                              |                              |                             |
|--------------------|--------------------|------------------------------|------------------------------|-----------------------------|
| $N_1 = 2N_0 = 200$ | $N_2 = 2N_1 = 400$ | $N_3 = \frac{1}{2}N_2 = 200$ | $N_4 = \frac{1}{2}N_3 = 100$ | $N_5 = \frac{1}{2}N_4 = 50$ |
|--------------------|--------------------|------------------------------|------------------------------|-----------------------------|

Of course, if we had done the simulation again, we might very well have obtained a different result. In fact, the population size after five years will be a random variable, taking on a certain number of possible values each with a definite probability. For example, it's clear that the largest possible value the population could reach is  $2^5 N_0 = 3200$ , if each of the 5 years turned out to be good. It is not hard to find the exact probability distribution for the population after 5 years.

**Example 18.2:** Find the probability distribution for  $N_5$ , the fifth year population, assuming the initial population was  $N_0 = 100$  and the per capita production coefficient  $r$  is selected according to the probability distribution Table 18.1.

*Solution:*

Mathematically, to find the next year's population we simply multiply the previous population by the new random  $r$ . After a specific number of years, the final result depends only on how many of the multiplicative factors  $r$  are equal to two and how many are equal to  $\frac{1}{2}$ . In particular therefore, the population size  $N_5$  depends only on the number of good and bad years that are experienced during the 5 years. The number of good years follows a binomial distribution with  $n = 5$  and success parameter  $p = \frac{1}{2}$ . The probability distribution is given below (see Section 13.3 and Table B.1):

| # Good Years $k$ | 0   | 1   | 2   | 3   | 4   | 5   |
|------------------|---|---|---|---|---|---|
| Probability      | ${}_5C_0 \left(\frac{1}{2}\right)^5$<br>=.031 | ${}_5C_1 \left(\frac{1}{2}\right)^5$<br>=.156 | ${}_5C_2 \left(\frac{1}{2}\right)^5$<br>=.313 | ${}_5C_3 \left(\frac{1}{2}\right)^5$<br>=.313 | ${}_5C_4 \left(\frac{1}{2}\right)^5$<br>=.156 | ${}_5C_5 \left(\frac{1}{2}\right)^5$<br>=.031 |

**Table 18.2**

From this we can derive the probability distribution for the population  $N_5$ . If there are  $k$  good years then there will be  $5 - k$  bad years. The population will be multiplied by  $2^k \left(\frac{1}{2}\right)^{5-k}$ . The probability distribution for  $N_5$  is then obtained by replacing the values in the top row of Table 18.2 by the factors  $2^k \left(\frac{1}{2}\right)^{5-k} N_0$ . This gives:

|                       |   |   |   |   |   |   |
|-----------------------|---|---|---|---|---|---|
| Population size $N_5$ | $\left(\frac{1}{2}\right)^5 N_0$<br>= 3.125   | $2\left(\frac{1}{2}\right)^4 N_0$<br>= 12.5   | $2^2 \left(\frac{1}{2}\right)^3 N_0$<br>= 50  | $2^3 \left(\frac{1}{2}\right)^2 N_0$<br>= 200 | $2^4 \left(\frac{1}{2}\right) N_0$<br>= 800   | $2^5 N_0$<br>= 3200                           |
| Probability           | ${}_5C_0 \left(\frac{1}{2}\right)^5$<br>=.031 | ${}_5C_1 \left(\frac{1}{2}\right)^5$<br>=.156 | ${}_5C_2 \left(\frac{1}{2}\right)^5$<br>=.313 | ${}_5C_3 \left(\frac{1}{2}\right)^5$<br>=.313 | ${}_5C_4 \left(\frac{1}{2}\right)^5$<br>=.156 | ${}_5C_5 \left(\frac{1}{2}\right)^5$<br>=.031 |

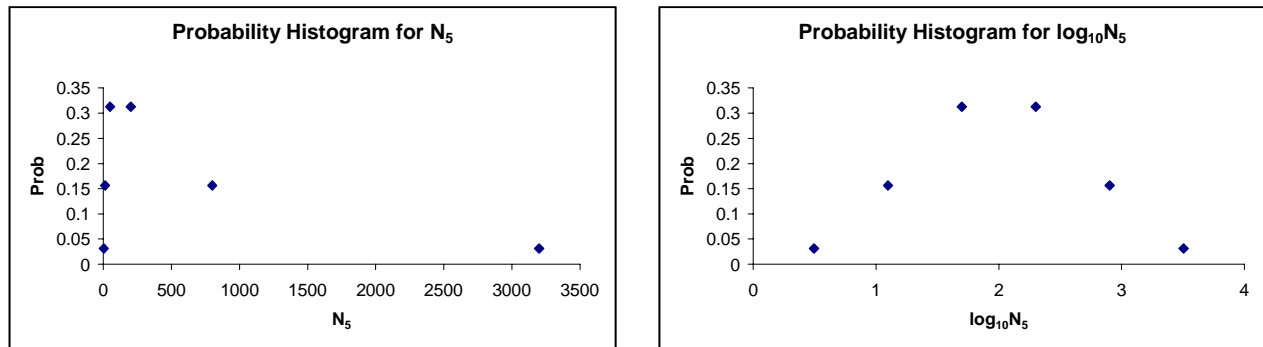
As we discussed in Chapter 13, the probability histogram for a random variable provides a useful visualization. Unfortunately, when we attempt to graph the histogram for the possible values of  $N_5$  we have to face the uncomfortable fact that the values of  $N_5$  are spread over approximately three orders of magnitude. We have seen in Section 9.5 that plotting such information on a linear

scale does not give a useful representation. Rather, we will get a more useful figure if we consider as our random quantity the logarithm of the population. For convenience we use base 10 logs:

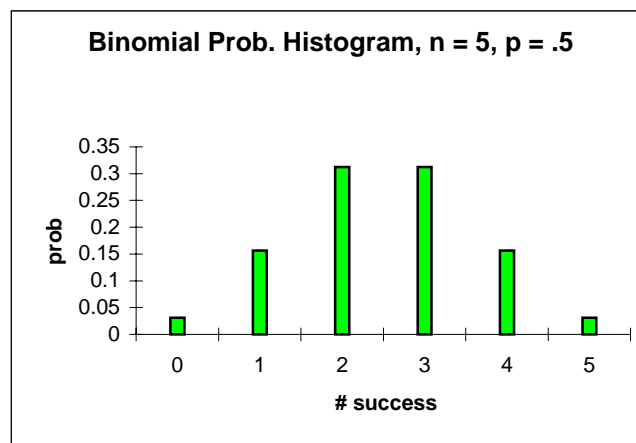
**Example 18.3:** Construct the probability histogram for the random variable  $\log_{10} N_5$ .

*Solution:*

We can use *Excel* to first construct the probability histogram for  $N_5$ , following the Tech notes in Chapter 13. The only modification we must make is that we should use a scatter plot for the probability histogram, rather than a bar chart. *Excel's* bar chart only plots the horizontal axis categorically rather than numerically, and here there are too many gaps between values for us to add empty positions as placeholders. We obtain the histogram shown on the left below:



The histogram of  $\log_{10} N_5$  on the right was obtained by computing  $\log_{10} N_5$  and using the same probabilities on the vertical axis. The pattern for the values of  $\log_{10} N_5$  resembles the histogram of the binomial distribution for  $n = 5$  and  $p = 0.5$ , but with a slight rescaling and translation of the horizontal axis. In fact the latter histogram is:



which clearly resembles the histogram for  $\log_{10} N_5$ . ■

Based on this limited exploration, we can make some conjectures about what will happen if we extend the model over a longer time period. When we use random elements in a mathematical model, we say the model is *stochastic*. Thus, we make the following conjecture for our stochastic model:

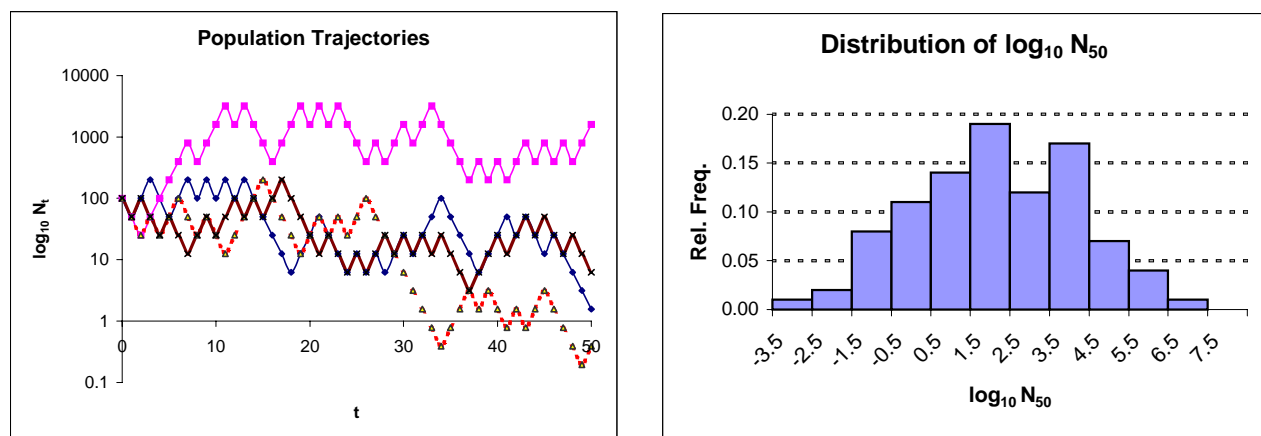
**Conjecture 18.1:** If for each  $t$  the per capita production coefficient  $r$  is selected according to the random variable given by Table 18.1 then the common logarithm of the population at time  $t$  will follow a rescaled binomial distribution. In particular,  $\log_{10} N_t$  will have an approximately normal distribution. ■

Before we verify this conjecture, we will study it empirically by looking at the distribution of values of  $\log_{10} N_{50}$  found from a simulation.

**Example 18.4:** Simulate 100 replications of the stochastic population model  $N_{t+1} = r_{t+1}N_t$ , where  $r_{t+1}$  is a value from the random variable described by Table 18.1,  $t = 0, 1, \dots, 49$ , and  $N_0 = 100$ . Plot several trajectories of  $\log_{10} N_t$  on the same graph and plot a histogram for the 100 values of  $\log_{10} N_{50}$ .

*Solution:*

The graph in the left panel shows four trajectories for  $\log_{10} N_t$ . The right panel shows the distribution of the values for  $\log_{10} N_{50}$  obtained from the 100 replications. The histogram graph is appropriately “mound-shaped,” consistent with the conjecture.



**Figure 18.1**

■

Notice that the vertical scale on the trajectory graph in Figure 18.1 has logarithmic scaling. This means that while the tick marks refer to the values of  $N$  rather than their logarithms, it is powers of

10 that are equally spaced, rather than multiples of 10. There is of course an enormous variation in the range of possible values of  $N_{50}$ . In fact, the histogram shows that the base 10 logarithm of the population  $N_{50}$  can range from about  $-3$  to  $7$ , so  $N_{50}$  can range from about  $10^{-3}$  to  $10^7$ . Of course, small values of  $N$  are only mathematical fictions. The modeled population has ceased to exist.

Before we consider proving and amplifying the results in Conjecture 18.1, we perhaps ought to consider what this excursion into stochastic models has revealed. Recall that we started with a deterministic model  $N_{t+1} = rN_t$  that leads either to a population explosion or extinction. The simple introduction of randomness in the production factor  $r$  gives us a model which may behave in either way, depending on chance. A reasonable question to ask here is how likely is it that an initial population will become extinct under this scenario, where extinction means that the population drops below some critical level. Is a large population more ecologically secure against such external variation than a smaller one?

The answer to these questions is provided by the following Theorem. The proof uses properties of the binomial distribution discussed in Chapter 13.

**Theorem 18.1:** Suppose  $N_t$  follows the stochastic model  $N_{t+1} = r_{t+1}N_t$ , where  $r_{t+1}$  is a random variable with distribution given by Table 18.1. When  $t$  is large, the quantity  $\log_{10} N_t$  will have an approximately normal distribution with expected value  $E(\log_{10} N_t) = \log_{10} N_0$  and standard deviation  $\sigma_{\log_{10} N_t} = (\log_{10} 2)\sqrt{t} \approx 0.3\sqrt{t}$ .

*Proof:*

We have  $N_1 = r_1N_0$ ,  $N_2 = r_2N_1 = r_2(r_1N_0)$ , and more generally  $N_t = r_t r_{t-1} \cdots r_2 r_1 N_0$ . Taking logs of this equation gives

$$\log_{10} N_t = (\log_{10} r_t + \cdots + \log_{10} r_1) + \log_{10} N_0. \quad (18.1)$$

Suppose there are  $k$  good years, and therefore  $t-k$  bad ones. Then the quantity  $D_t = \log_{10} r_t + \cdots + \log_{10} r_1$ , which measures the “drift” of the log population through time  $t$ , has value

$$k \log_{10} 2 + (t-k) \log_{10} \left(\frac{1}{2}\right) = k \log_{10} 2 - (t-k) \log_{10} 2 = (2 \log_{10} 2)k - t \log_{10} 2.$$

Moreover, the probability that  $D_t$  has the latter value is precisely the chance that  $k$  good years will be selected out of the  $t$  years. This probability is just the binomial probability  ${}_t C_k \left(\frac{1}{2}\right)^t$ . If we let  $X = X_{t, \frac{1}{2}}$  denote the binomial random variable with  $t$  trials and probability  $\frac{1}{2}$  of success, then we

have shown that the random variable  $D_t$  satisfies  $D_t = aX + b$ , where  $a = 2 \log_{10} 2$ , and  $b = -t \log_{10} 2$ . Therefore, we have from (18.1) that

$$\log_{10} N_t = aX + b + \log_{10} N_0. \quad (18.2)$$

A relationship between random variables of the sort given by (18.2) is similar to relationships between data sets that we examined in the exercises of Chapter 7 (see Exercise 5 in particular). The results discussed there apply as well for random variables, so that

$$\begin{aligned} E(aX) &= aE(X) \text{ and } \sigma_{aX} = a\sigma_X \text{ if } a > 0, \\ E(Y + b) &= E(Y) + b \text{ and } \sigma_{Y+b} = \sigma_Y. \end{aligned} \quad (18.3)$$

Since  $X$  has a binomial distribution, the formulas for the mean and standard deviation of the binomial distribution give  $E(X) = np = \frac{1}{2}t$  and  $\sigma_X = \sqrt{npq} = \frac{\sqrt{t}}{2}$ . Combining this result with (18.3) gives:

$$E(\log_{10} N_t) = aE(X) + b + \log_{10} N_0 = \frac{(2 \log_{10} 2)t}{2} - t \log_{10} 2 + \log_{10} N_0 = \log_{10} N_0 \quad (18.4)$$

and

$$\sigma_{\log_{10} N_t} = a\sigma_X = \frac{(2 \log_{10} 2)\sqrt{t}}{2} = (\log_{10} 2)\sqrt{t}. \quad (18.5)$$

This establishes the formulas for the mean and standard deviation of  $\log_{10} N_t$ . Since  $X$  has a binomial distribution, its distribution is approximately normal when the number of trials  $t$  is large. Since  $\log_{10} N_t$  involves only a stretching and translation of  $X$ , it will also have a bell-shaped density curve that is approximately normal. ■

Theorem 18.1 is a powerful and important result. To illustrate its consequences consider the following example.

**Example 18.5:** Using Theorem 18.1 estimate the likelihood that when  $N_0 = 100$  the population will be extinct after 50 generations. (This is the scenario plotted in Figure 18.1.).

*Solution:*

We take extinction to mean that the population  $N_{50} < 1$  or in terms of logarithms,  $\log_{10} N_{50} < 0$ . After 50 generations the random quantity  $\log_{10} N_{50}$  will have a normal distribution with mean  $\log_{10} N_0 = 2$  and standard deviation  $\sigma = (\log_{10} 2)\sqrt{50} \approx 2.13$ . We can now use  $z$  scores to compute the probability of extinction in generation  $t = 50$ . We want

$$P(\log_{10} N_{50} < 0) = P\left(Z < \frac{0 - \log_{10} N_0}{\sigma}\right) = P\left(Z < \frac{-2}{2.13}\right) \approx 17\%$$

This agrees fairly closely with the frequency distribution given in Figure 18.1. Note, however, that this is only a lower bound on the extinction probability. Some trajectories that were “knocked out” before  $t = 50$  may have recovered mathematically, even though in reality they should have been eliminated. Thus the 17% is only a lower bound on the desired probability. In fact, more advanced methods show that the actual extinction probability is about double this bound, or 34%. ■

Notice that because the expected value of  $\log_{10} N_t$  is constant for all  $t$ , but the standard deviation grows approximately as  $.3\sqrt{t}$ , as time progresses a population of any initial size will be at greater and greater risk of extinction. Indeed, it may be shown that extinction is inevitable under this model. Since extinction seems to occur rather rarely (except during certain known geologic periods), this model must be overstating the effects of randomness. In particular, the assumption that good and bad years are equally likely seems to imply that the environment is more volatile than seems to be the case, or that species are only adapted to a rather narrow spectrum of environmental conditions. In the exercises we consider modifications to the model.

### 18.3 Demographic Variation

In Section 18.2 we considered how the basic discrete time exponential model  $N_{t+1} = rN_t$  is affected when the per capita production coefficient is subjected to random variation. The variation we considered was environmental in the sense that all members of the population were equally affected. The per capita production number  $r$  changed for all members of the population. This type of change affects both large and small populations, though the latter may be endangered more quickly.

We can incorporate demographic variation into our model by considering the reproductive fate of each member of the population as a random variable. Some individuals may produce no offspring, others one or two, etc. The quantity  $r$  in our basic model  $N_{t+1} = rN_t$  should be viewed as an average or mean production of individuals. Again, let’s begin with an easy example and try to understand some of its features. So we will assume that individuals either have zero or two offspring with equal probability. Letting  $X$  denote the number of offspring for an individual we are assuming the following probability distribution for  $X$ :

|            |     |     |
|------------|-----|-----|
| $X$        | 0   | 2   |
| $P(X = x)$ | 0.5 | 0.5 |

**Table 18.3**

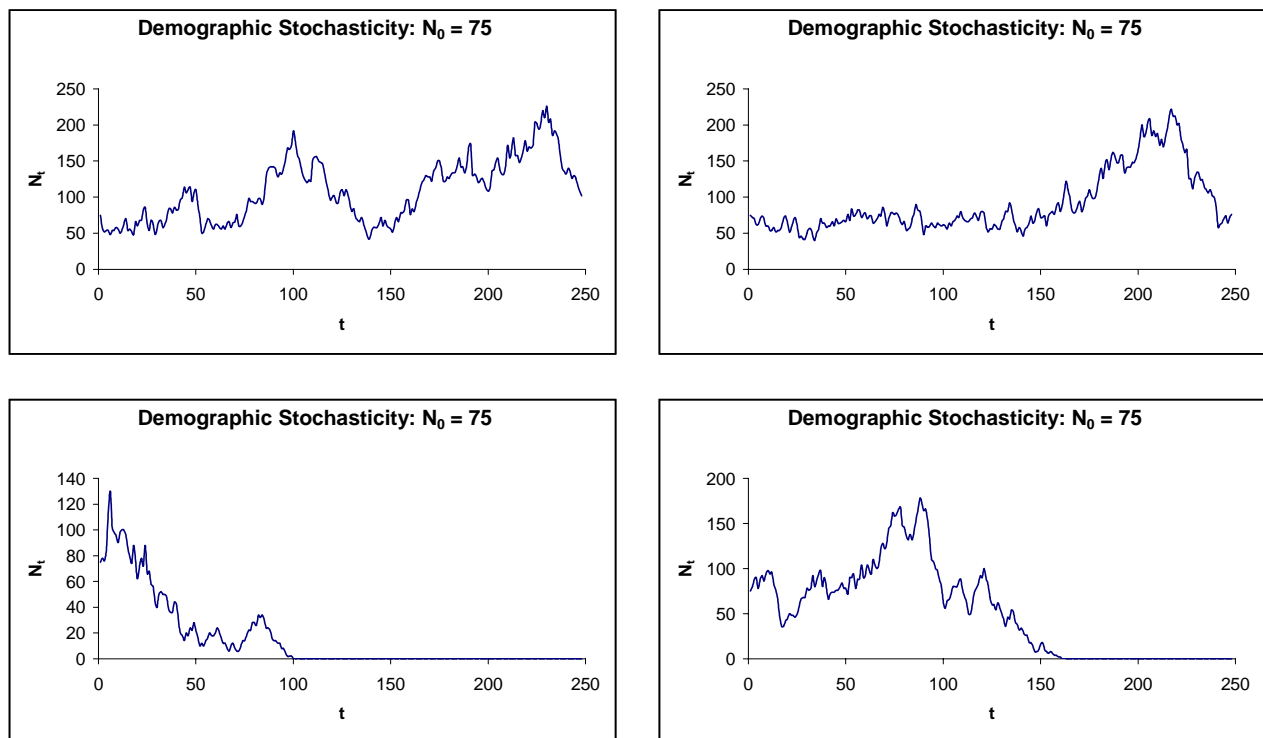


**Example 18.6:** Suppose we start with an initial population of  $N_0 = 3$ . Compute values of  $N_1, N_2$ , and  $N_3$  if the number of offspring of each individual is selected randomly according to Table 18.3.

*Solution:*

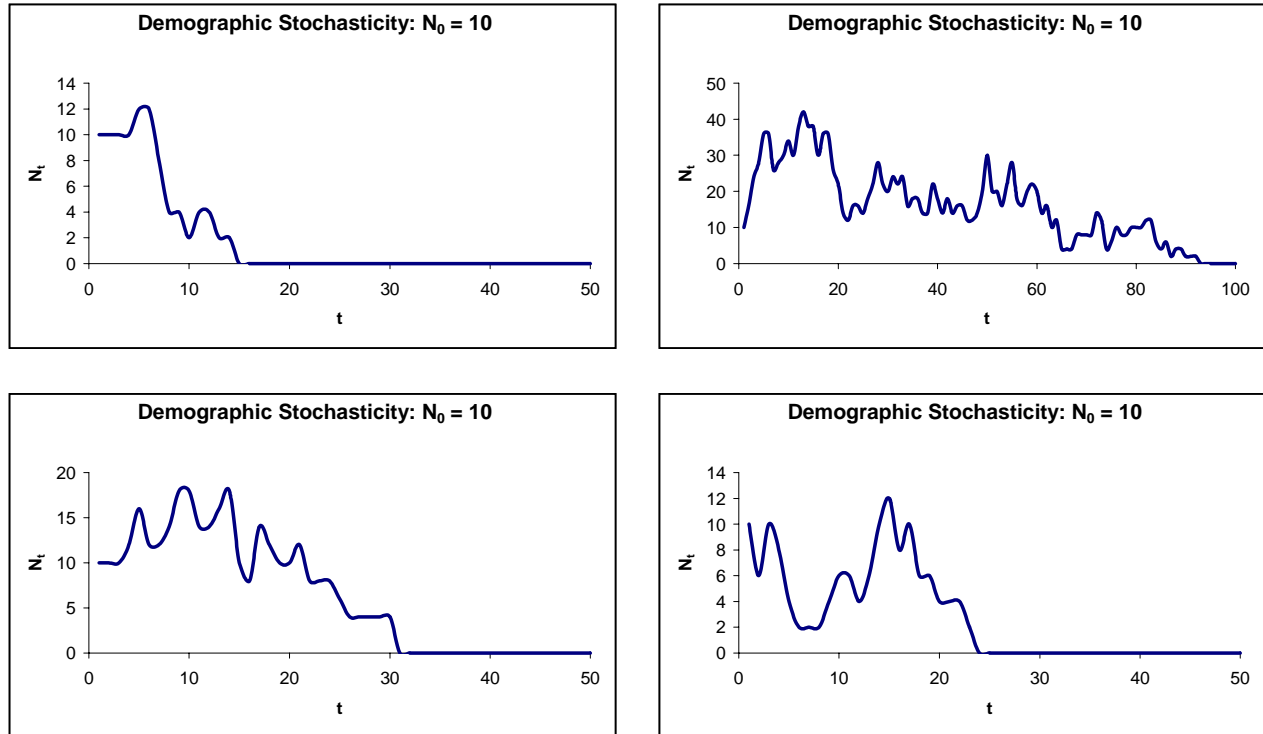
We first draw three values for the number of offspring of the initial three individuals. Excel generated the values 2, 0, and 0. Therefore,  $N_1 = 2$ . We continue by selecting the number of offspring for each individual in the first generation. Excel generated the values 2, and 0, so  $N_2 = 2$ . For each of these two members we select the random number of offspring according to Table 18.3. We obtained the values 2, and 2, so that  $N_3 = 4$ . We could continue, generating 4 more values for the offspring of third generation, etc. ■

Notice that the expected value of our random variable  $X$  is simply one. If the population were large to begin with, on average every member would have one offspring and we would expect the population size to remain more or less constant. In fact, the population size fluctuates quite a bit, but the large initial size provides a substantial cushion against these stochastic shocks. The population can persist for quite a long time, although extinction via random variation is not impossible. Below are four trajectories showing population variation with initial populations of  $N_0 = 75$ . Notice that two of the trajectories result in extinction after 100 or 150 generations.



**Figure 18.2**

A small population is much more susceptible to extinction through demographic stochasticity. For example, the graphs below show four trajectories in which  $N_0 = 10$ .



If the population is lucky and has an initial rapid increase it may of course persist for a considerable time, as if it started with a large population. However, in most cases a small population is doomed to rapid extinction. These examples illustrate an essential difference between environmental and demographic stochasticity. Random changes in the environment affect all population members. Large populations may have only a marginal factor of safety against such effects, especially if they are prolonged. On the contrary, random demographic variation caused by individual reproductive differences is unlikely to affect the overall viability of a large population.

### 18.4 Tech Notes

We give some ideas to the reader as to how to carry out the simulations presented in this chapter. The techniques rely heavily on *Excel*'s random number generator, described in the Tech Notes in Chapter 13.

**Example 18.7:** Set up an *Excel* spreadsheet to simulate the stochastic environmental model discussed in Section 18.2.

*Solution:*

You need to compute the random numbers in advance. It is best if they are stored on a separate sheet, since they are uninteresting and take up useful real estate. If you are using your own random variable for the quantity  $r$ , enter the probability distribution table in the first two columns of Sheet1, with headings for the values and probabilities. Use *Excel's* random number generator to generate values of your random variable on Sheet2. For example, if you want to do 10 replications each one going through 50 generations you will need to generate 10 columns (# of variables), each with 50 values.

To create a simulation of 50 generations you might first enter the numbers 0 to 50 in column A of sheet 1. Next, enter the initial population size in a separate cell. You will refer to this by reference, so that changing the initial size does not involve redoing the entire worksheet. The basic formulas are quite straightforward and follow the principles for writing ordinary difference equations. Figure 18.3 below shows the beginning of this table. The entries "Sheet2!B5" etc. refer to the random numbers on Sheet2. Each row after row 5 is obtained from the previous one by multiplying the old population by the next random number in the appropriate column from Sheet 2.

|   | A | B      | C   |
|---|---|--------|-----|
| 1 |   | Init N | 100 |
| 2 |   |        |     |
| 3 |   |        |     |
| 4 | 0 | 100    | 100 |
| 5 | 1 | 50     | 50  |
| 6 | 2 | 100    | 25  |

|   | A | B                     | C                     |
|---|---|-----------------------|-----------------------|
| 1 |   | Init N                | 100                   |
| 2 |   |                       |                       |
| 3 |   |                       |                       |
| 4 | 0 | = $\$C\$1$            | = $\$C\$1$            |
| 5 | 1 | = $\$C\$1$ *Sheet2!A5 | = $\$C\$1$ *Sheet2!B5 |
| 6 | 2 | =B5*Sheet2!A6         | =C5*Sheet2!B6         |

Figure 18.3

■

**Example 18.8:** Set up an *Excel* spreadsheet to simulate the stochastic demographic model discussed in Section 18.3.

*Solution:*

This is more difficult (and less efficient) to do (without programming) because the action required in a given step depends in a more complicated way on the results obtained in the previous step. As in Example 18.7, you first must generate values of the random variable that characterizes the birth demographics. If your initial population is greater than 50 and you wish to trace the trajectory over 100 generations then you may easily need 10,000 values of the random variable!

The basic idea is of course quite simple. If the initial population is say, 10, we have to add the first ten values in the column of random variables on Sheet2. This gives  $N_1$ . We must then add the next  $N_1$  values in the random variable column to get  $N_2$ , then add the next  $N_2$  values, etc. Now

the SUM() function can add the random numbers for us, provided we can specify the range. Since this range varies, we need a way of constructing it at each step. *Excel* has one worksheet function that allows the user to construct ranges. This is the OFFSET() function. The reader who wishes to understand the formulas that follow should read the help page on that function. Basically, we use the OFFSET function to tell *Excel* what range of random numbers must be added at each step. The formulas are shown below. Pay close attention to the mix of absolute and relative references. The entries referred to on Sheet2 are random numbers generated according to the distribution in Table 18.3. The last statement in A4 can be copied to all cells below and then column A (except for A1) can be duplicated for as many replications as is desired.

|   | A                 |   | A   |
|---|-------------------|---|---|
| 1 | 10 (initial $N$ ) | 1 | 10  |
| 2 | 10                | 2 | = $\$A\$1$                                    |
| 3 | 6                 | 3 | =SUM(OFFSET(Sheet2!A\$1,0,0,A2,1))            |
| 4 | 10                | 4 | =SUM(OFFSET(Sheet2!A\$1,A2,0,A3,1))           |
| 5 | 8                 | 5 | =SUM(OFFSET(Sheet2!A\$1,SUM(A\$2:A3),0,A4,1)) |

■

### 18.5 Summary

Population models can potentially gain greater realism by incorporating randomness. This can be done by modifying deterministic models so that one or more parameters vary randomly. The selection of appropriate random models is an important aspect of such investigations. The resulting models can be used to estimate the likely development of the system, as well as the possible variability in outcomes. Such probabilistic models have been used in developing harvesting protocols for fisheries and other natural resources where supply depends on environmental conditions that are as yet unpredictable. Many of the probabilistic models cannot be analyzed in any explicit manner. Conclusions about these models are often made on the basis of extensive computer simulation using random number generators.

The expansion of human economic activity has shrunk and partially fragmented many ecosystems. As a result, many populations live in environments in which they are much more isolated than they were in the past. The study of such isolated communities has therefore taken on renewed interest to ecologists. In small communities, stochastic variation in population size can play an important role in population survival. Similar effects occur in the gene pool, with the result that genetic variation may be lost solely because of the relatively greater variability of small samples.


**18.6 Exercises**

1. Suppose that in the stochastic population model  $N_{t+1} = rN_t$ , the production coefficient  $r$  has the following distribution:

|                    |      |               |
|--------------------|------|---------------|
| $r$                | 2    | $\frac{1}{2}$ |
| Probability of $r$ | 0.75 | 0.25          |

**Table 18.4**

In such a model, “good years” occur more frequently than “bad years”.

- Suppose the first four values of  $r$  selected from this distribution are 2,  $\frac{1}{2}$ , 2, and 2. If the initial population is 50, find  $N_1, N_2, N_3$  and  $N_4$ .
- Determine the probability distribution for  $N_4$  and  $\log_{10} N_4$ ? Is either of these symmetric? Contrast with the example based on Table 18.1.
- What is the expected value of  $N_4$  and  $\log_{10} N_4$ ? What is the standard deviation of  $N_4$  and  $\log_{10} N_4$ ?
- Show that  $\log_{10} N_t$  satisfies (18.2), where  $X$  is a binomial distribution with  $t$  trials and probability of success  $p = \frac{3}{4}$ .
- Using d) show that  $E(\log_{10} N_t) = (\frac{1}{2} \log_{10} 2)t + \log_{10} N_0$ . Explain the significance of the contrast between this result and (18.4).
- Using d) show that  $\sigma_{\log_{10} N_t} = \frac{\sqrt{3}}{2} \log_{10} 2 \sqrt{t} \approx .26 \sqrt{t}$ . What do the results in e) and f) imply about the likelihood of extinction based on this model? Explain.
-  Generate and graph a number of trajectories of  $\log_{10} N_t$  using values of  $r$  drawn from the distribution in Table 18.4 for  $t = 0, 1, 2, \dots, 20$ . Use initial values  $N_0 = 10, 20$ , and 40. Does extinction ( $N_t < 1$ ) ever occur in your examples? Are the results in line with your predictions in f)?

2. Suppose good years and bad years occur equally often, but good years are relatively more productive than the bad years are detrimental. For example the distribution for  $r$  might be




|                    |     |               |
|--------------------|-----|---------------|
| $r$                | 3   | $\frac{1}{2}$ |
| Probability of $r$ | 0.5 | 0.5           |

Find  $E(\log_{10} N_t)$  and  $\sigma_{\log_{10} N_t}$  using this model for  $r$ . What do your results imply about the possibility of extinction?

3. a) Compute the mean and standard deviation for the random variable defined by Table 18.3.
- b) Suppose the birth demographics are given by the following distribution, where  $X$  represents the number of offspring for an individual: Find  $E(X)$  and  $\sigma_X$ .

|            |     |    |     |
|------------|-----|----|-----|
| $X$        | 0   | 1  | 2   |
| $P(X = x)$ | .25 | .5 | .25 |

**Table 18.5**

- c) Suppose we consider demographic growth models based on the distributions in Table 18.3 and Table 18.5. Which one do you think will have a greater tendency to produce extinction in small populations? Justify your answer.
-  d) Create several simulations for the demographic models based on Table 18.3 and Table 18.5. Using small initial values for  $N$ , try to confirm your answer to c).
4. a) Suppose that a population has an average per capita production of 2. It is then plausible to consider as a deterministic model the exponential growth equation  $N_{t+1} = 2N_t$ . Why is the Poisson distribution  $X$  (see sections 13.3 and 14.2) with  $\lambda = 2$  a reasonable choice for the individual birth demographics?
-  b) Suppose  $N_0 = 4$ . Use *Excel* to generate enough values of the Poisson distribution  $X$  defined in a) so as to compute  $N_1, N_2, N_3$ , and  $N_4$ .
-  c) Following the procedure in Example 18.8, construct trajectories for  $t = 0, 1, \dots, 25$ , using the initial conditions  $N_0 = 5$ , with the birth demographics described by Poisson distribution in part a). Repeat with  $N_0 = 10$  and contrast the behaviors in the two cases.