

Ecology 101

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In the following article, Therese Donovan and James Goetz, College of Environmental Science and Forestry at SUNY in Syracuse, New York, have created a spreadsheet program that really helps to make comparisons between small and large populations regarding life and death and reproduction of individuals. At the end of the article, the authors indicate a willingness to publish a series of exercises through ESA. I encourage Ecology 101 readers to contact me and/or the authors if you see value in continuing their efforts.

EXPLORING DEMOGRAPHIC AND ENVIRONMENTAL STOCHASTICITY WITH SPREADSHEETS

Introduction

Models are an important tool for teaching and understanding (and predicting) ecological relationships, and commonly play a central role in ecology courses. However, students often struggle with the modeling process when aspects of the model are unknown to them or hidden within a packaged modeling program (Weldon 1999). Spreadsheet programs such as Excel or QuattroPro are readily available tools with excellent potential for teaching students about modeling, because there are no black boxes that conceal how numbers are generated. Spreadsheets allow students to start with a blank slate and develop their

own equations and graphs to determine relationships among variables. The mystery of modeling dissolves when students actively create and develop their own programs.

Spreadsheet programming teaches students to think quantitatively, to determine what parameters are needed to simulate an ecological process, and to assess the sensitivity of model results to input parameters (Weldon 1999). Additionally, a wide variety of ecological processes can be modeled with spreadsheets, and spreadsheet programs are widely available in computer clusters at many colleges and universities. By the end of a semester-long course that involves spreadsheet modeling, students view a blank spreadsheet as an artist's canvas, with vast potential for exploring a wide variety of ecological phenomena.

Here, we follow up on the article by Charles Weldon in a recent *ESA Bulletin* (1999), discussing how spreadsheets can be used to explore stochasticity in natural populations. Variation is pervasive in the ecology of natural populations, and stochasticity is the unpredictable variation that influences the growth rate of a population (Akçakaya et al. 1997). For example, a population may have a birth rate of 0.4 individuals per individual per year, and a survival rate of 0.6 individuals per individual per year, indicating that, on average, individuals produce 0.4 offspring per year, and 0.6 individuals survive to the next year. Of course, an individual cannot partially die and cannot produce 0.4 offspring; it either lives or dies, and produces an integer number of offspring. Thus, demographic stochasticity is the variation in average survivorship and reproduction that occurs because a population is made up of an integer number of individuals (May 1973). This concept, as well as the concept of environmental stochasticity, is easy for students to grasp when spreadsheet models are part of the lesson.

Prior to the modeling exercise, our students have completed several exer-

cises that cover the basics of spreadsheets, including relative and absolute cell addresses, functions, and graphs (charts). We discuss with students the concepts of demographic stochasticity and provide some general examples of how simulations are used by population ecologists, conservation biologists, and wildlife scientists (e.g., Shaffer 1981). We guide students through a simple demographic stochasticity model for a population of 10 individuals. Students then expand on the simple model and compare effects of demographic stochasticity in the small population with a larger population of 100 individuals. At the very end of the exercise, we ask students to add an environmental stochastic element to their model, and allow them to develop that portion of the model with minimal guidance.

Upon completion of the exercise, students are able to define demographic and environmental stochasticity and relate stochastic processes to population size. Students learn how to write a macro that generates "simulation trials," how to calculate means, variances, and coefficients of variation, how to graph frequency distributions of their results, and how to develop and examine binomial distributions. Here we outline the basic procedures that we use to model demographic stochasticity in the population of 10 individuals, and offer suggestions on expanding and modifying the basic model.

Methods

In this exercise, students use a Microsoft Excel spreadsheet to model the demographic stochasticity of two populations: *Population 1* has 10 individuals, and *Population 2* has 100 individuals. The demographic stochasticity model parameters include a fixed birth rate and a fixed survival rate. Time permitting, we have students select a scientific article that contains data on birth and death rates of a given organism for use in their model. In the

	A	B	C	D	E	F	G	H	I
1	survival rate =	0.5	birth rate =	0.17					
2									
3	POP 1								
4	individual	random #	survival	reproduce?					
5		1	0.72	0	0	random #	survival	reproduce?	
6		2	0.52	0	0	=RAND()	=IF(B5<B\$1,1,0)	=IF(B5<D\$1,1,0)	
7		3	0.24	1	0	=RAND()	=IF(B6<B\$1,1,0)	=IF(B6<D\$1,1,0)	
8		4	0.19	1	0	=RAND()	=IF(B7<B\$1,1,0)	=IF(B7<D\$1,1,0)	
9		5	0.80	0	0	=RAND()	=IF(B8<B\$1,1,0)	=IF(B8<D\$1,1,0)	
10		6	0.43	1	0	=RAND()	=IF(B9<B\$1,1,0)	=IF(B9<D\$1,1,0)	
11		7	0.16	1	1	=RAND()	=IF(B10<B\$1,1,0)	=IF(B10<D\$1,1,0)	
12		8	0.06	1	1	=RAND()	=IF(B11<B\$1,1,0)	=IF(B11<D\$1,1,0)	
13		9	0.12	1	1	=RAND()	=IF(B12<B\$1,1,0)	=IF(B12<D\$1,1,0)	
14		10	0.94	0	0	=RAND()	=IF(B13<B\$1,1,0)	=IF(B13<D\$1,1,0)	
15				6	3	=RAND()	=IF(B14<B\$1,1,0)	=IF(B14<D\$1,1,0)	
16		population 1	population 1						
17	Trial	survivors	births						
18	1	4	1						
19	2	6	0						
20	3	5	3						
21	4	4	2						
22	5	7	3						
23	6	5	1						
24	7	6	2						
25	8	6	2						
26	9	5	1						
27	10	6	2						
28	11	6	3						
29	12	7	2						
30	13	7	2						
164	147	7	0						
165	148	4	0						
166	149	5	2						
167	150	1	1						
168	mean	5.134228188	1.66442953		=AVERAGE(B18:B167)				
169	sd	1.445672565	1.06295571		=STDEV(B18:B167)				
170	cv	0.281575441	0.638630648		=B169/B168				

```

random #      survival      reproduce?
=RAND()      =IF(B5<B$1,1,0)  =IF(B5<D$1,1,0)
=RAND()      =IF(B6<B$1,1,0)  =IF(B6<D$1,1,0)
=RAND()      =IF(B7<B$1,1,0)  =IF(B7<D$1,1,0)
=RAND()      =IF(B8<B$1,1,0)  =IF(B8<D$1,1,0)
=RAND()      =IF(B9<B$1,1,0)  =IF(B9<D$1,1,0)
=RAND()      =IF(B10<B$1,1,0) =IF(B10<D$1,1,0)
=RAND()      =IF(B11<B$1,1,0) =IF(B11<D$1,1,0)
=RAND()      =IF(B12<B$1,1,0) =IF(B12<D$1,1,0)
=RAND()      =IF(B13<B$1,1,0) =IF(B13<D$1,1,0)
=RAND()      =IF(B14<B$1,1,0) =IF(B14<D$1,1,0)

```

```

Macro recorded 3/10/99 by Authorized User
*
* Keyboard Shortcut: Ctrl+d
*
Application.Goto Reference:="R18C2:R18C3"
Selection.Insert Shift:=xlDown
Application.Goto Reference:="R15C3:R15C4"
Selection.Copy
Application.Goto Reference:="R18C2:R18C3"
Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone, SkipBlanks:=
False, Transpose:=False
End Sub

```

Fig. 1. Appearance of part of a spreadsheet model of demographic stochasticity. Shaded cells contain formulae for calculating the spreadsheet values and the Visual Basic macro that is recorded for simulating trials.

example shown (Fig. 1), birth rate is 0.17 individuals per individual per year (Column D, Row 1) and survival rate is 0.5 individuals per individual per year (Column B, Row 1). The individuals in *Population 1* are assigned numbers 1–10, and are listed in Column A, Rows 5–14.

A major concept in demographic stochasticity is that *populations* have death and birth rates, but *individuals* either live or die, and *individuals* reproduce an integer number of offspring. This can be demonstrated by generating a random number for each individual in the population. The Excel function `=rand()` generates a random number between 0 and 1. A random number function is entered for each individual in column B, Rows 5–14. Excel recalculates random numbers each time either **return** or the calculate shortcut, **F9**, is pressed.

Students then model survival of the 10 individuals by entering an **IF** function, which uses the survival rate to convert the random number into a binary “survive” or “die” for each individual. An **IF** function has the form `IF(logical test, value if true, value if false)`, and is entered in column C for survival and in column D for reproduction. In cell C5, students enter `=IF(B5<B$1,1,0)`, where B5 references the random number generated for individual 1, and B\$1 is an absolute reference that refers to the survival rate specified in cell B1. If the random number in cell B5 is less than the survival rate in cell B1, the individual receives a score of 1 and survives; otherwise it receives a score of 0 and dies. Similarly, students use an **IF** statement to determine if individuals reproduced (Fig. 1, column D). In this exercise, we assume that indi-

viduals that reproduced had just 1 offspring. In columns F, G, and H, we show the functions that underlie the cells in columns B, C, and D as a reference for the reader.

Next, using the **SUM** function, students tabulate the total number of deaths and total number of births. In our example, 4 of the 10 individuals survived the sampling period, and 1 of the 10 individuals produced 1 offspring (Fig. 1, cells C15 and D15). Because half of the 10 individuals on average will die when the survival rate is 0.5, the total of deaths is expected to be around 5, but will vary due to the demographic stochasticity simulated by the random number function. In fact, the total deaths can assume any value from 0 to 10; values that deviate more strongly from 5 have lower outcome probabilities, as we will see with the binomial distri-

bution. The total number of births is expected to be around 2, but may vary widely. (In many trials with 10 individuals, 1.7 individuals, on average, are expected to be produced.)

We then engage the students in a discussion about the meaning of their results. Ultimately, students realize that in order to gauge how reliable their outcome is, they need to run a series of trials enabling them to evaluate the probability of different outcomes. That is, students need to repeat the experiment a number of times and calculate the average and the variance of many different trials. By conducting a great number of trials, students can be reasonably certain that they know the mean and the variation of survivors and births produced by stochastic processes. For this exercise, we ask students to run 150 trials and record trial results in the spreadsheet.

We discuss various ways of running 150 trials and recording the results. The most common suggestion is to generate a new set of random numbers for each trial, and then to copy the values for total survivors and births and paste them into the appropriate trial outcome column. (Fig. 1: Trials 1–150 in column A, results in columns B and C.) Of course, this process is a bit tedious for 150 trials! It is much more efficient to write a macro, a small computer program that automates any series of commands and functions that you choose. The macro described here combines and automates three tasks: (1) generating a random number, (2) calculating survival and reproduction values, and (3) transferring the calculated values to a designated set of cells. Although we encourage all students to learn how to write macros, this step is not essential, since macros can easily be copied from another spreadsheet. However, most students quickly catch on and are very enthusiastic once they recognize the potential of spreadsheet macros in modeling ecological processes.

The easiest way to record a macro is to go through the steps with a mouse, while Excel records the series of keystrokes used. Each time you run the macro, Excel will use this record to carry out the commands. Here we

suggest one way to program the macro:

- From the menu, select “Tools,” then “Macro,” and then “Record new macro.”

- In the dialog box that appears, enter a macro name (e.g., trial#1) and a shortcut key (e.g., control t). The macro is now in record mode. If you make a mistake when you record the macro, the corrections you make will also be recorded.

- From the menu, select “Edit,” then select “Go To” (or use the shortcut key F5). A dialog box will prompt you for a cell reference for the cursor position. Use your mouse to highlight cells B18 and C18, or enter R18C2:R18C3. This moves the cursor down the survival and reproduction columns associated with Trial 1. Click OK, and those cells are then highlighted (Fig. 1).

- From the menu, select “Insert,” then select “cells” and then select “move cells down.”

- Use the “Go To” (F5) again and go to cells C15 and D15, or type in R15C3:R15C4, the newly calculated results (total number of survivors and total births).

- From the menu, select “Edit,” then select “Copy,” and then “Go To” (F5) to return to the newly inserted, blank cells in R18C2:R18C3. Again, these cells can be highlighted with the mouse or entered by hand.

- From the menu, select “Edit,” and select “Paste Special.” A dialog box appears. Select “paste values” to paste the new calculated values from the source cell (do not paste the function that generates the values).

- Finally, select “Tools,” then “macro” and then select “stop recording.”

- Run the macro by pressing **control t**. If the macro was correctly recorded, trial results will be inserted in row 18, in columns B and C, shifting the cells with previous trial results downward. Simply press **control t** 150 times to calculate and record the results of 150 trials.

We use this opportunity to discuss with students the various kinds of computer languages, and then scrutinize the Visual Basic Editor Code in which the macro is recorded. To view

or edit this code, select “Tools,” then select “Macro.” The code from our example is shown in columns E through I, rows 18–29, as a reference to the reader (Fig. 1). Students can inspect the Visual Basic Code to follow how the program carried out the commands specified in the macro. This simple step demystifies computer programming for those students who have not been exposed to any kind of programming language.

After 150 trials are conducted, we ask students to calculate the mean and standard deviation of the 150 trials. We ask them to make some educated guesses about what their mean should be, based on the model’s birth and survival rates. The mean number of survivors for *Population 1* should be around 5 individuals, and the mean number of births should be between 1 and 2. In our example, our mean values for *Population 1* were 5.13 survivors and 1.66 births. This would translate to a survival rate for *Population 1* of 0.513 individuals per individual per year (mortality rate = 0.487) and birth rate of 0.166 individuals per individual per year. Each trial produces different results, but these are the averages of 150 trials. The functions used for calculating means and standard deviations in rows 168 and 169, columns B and C, are shown in column E.

At this point, we ask students to independently develop a demographic stochasticity model for *Population 2*, which consists of 100 individuals. We provide over-the-shoulder guidance, but most students can carry out the steps of the exercise independently, and are quite pleased to see how writing macros can increase efficiency in constructing models. After computing means and standard deviations of the 150 trials for *Population 2*, we then discuss two important statistical concepts in ecology: the frequency histogram and the binomial distribution. Students can use the spreadsheet program to make a frequency distribution of their results (Fig. 2).

The frequency distribution of survivors and births from the 150 trials can be constructed in one of two ways. The first way is to simply go through

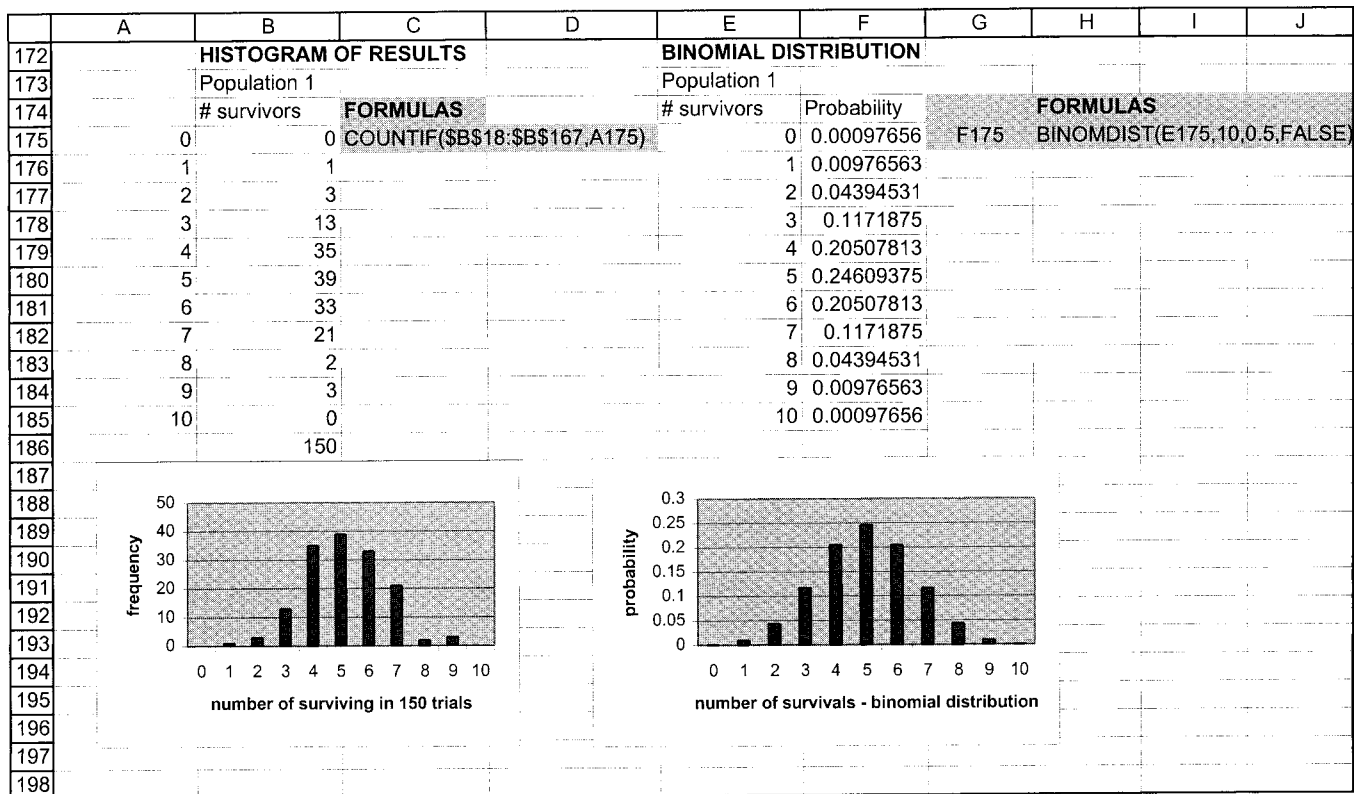


Fig. 2. Data and formulae (shaded) for constructing frequency histogram of number of survivors from 150 trials, and associated binomial distribution.

the 150 trials and count how many times there were 0 survivors, how many times there were 1 survivors, how many times there were 2 survivors, etc., and then graph the values. The other way is to use the **COUNTIF** formula in Excel. This little formula counts all of the 0s, 1s, 2s, 3s, and so on, which can then be graphed (Fig. 2).

Spreadsheet programs also allow students to examine properties of the binomial distribution, which is used to determine probabilities of a certain event happening when there are only two outcomes (e.g., survive or die). We can make use of the binomial distribution function to determine the probability of a specific number of individuals surviving one trial. For our population of 10 individuals, and a survival rate of 0.5, the Excel function looks like this: **BINOMDIST(0, 10, 0.5, FALSE)**, which calculates the probability 0 individuals of a population of 10 individuals would survive when the survivorship is 0.5. The number that Excel returns is 0.00097656. What is the probability

that exactly 5 of 10 would survive? It is 0.24609375.

We ask students to use the **BINOMDIST** function to obtain probabilities for each of the possible outcomes (0, 1, 2, 3 ... 10) given a survival rate of 0.5. Using this distribution also allows students to examine other interesting questions, such as determining the probability that 5 or fewer individuals survive (by adding the probabilities of each individual outcome from 0 to 5), determining the probability that the population will go extinct (0 survivors), and examining the distribution of probabilities in a histogram. We have found that this simple step helps students understand simple statistical distributions because they can visualize the outcome and compare the frequency distributions of the trials to the binomial distribution. We ask them to generate a binomial distribution when the survival rate is 0.8 or some other value so that they can see that the distribution takes on different shapes depending on the probabilities entered in the function.

Next, we ask students to compare the means and standard deviations of survivors for Population 1 and Population 2. Students should have a mean number of survivors of around 5 and 50 for Populations 1 and 2, respectively. (This is because we kept our survival rate at 0.5 and our birth rate at 0.17.) We then ask students to evaluate which of the two populations shows greater stochasticity, or greater variation due to stochastic processes. We try to engage students in a discussion about making comparisons between two populations that have vastly different means, and examine how mean values can influence variances. We then introduce coefficient of variation, or CV, which is simply the standard deviation divided by the mean. Analysis of the CV allows us to directly compare *Population 1* and 2 by adjusting for their means. In our example, the CV for survivors in *Population 1* was 0.28, and the CV for survivors in *Population 2* was 0.09. This tells us that the small population is much more variable ... and is a clear ex-

ample of how stochasticity has its greatest effects on small populations.

With the basic model in place, there are several directions in which to lead students. We typically challenge students to add an element of environmental stochasticity to their model. That is, we challenge them to design a way to let the birth and death rates incorporate a random effect. If they are stuck, we give them some hints such as "what if your population experiences an El Niño event just once every 10 years, and during that time the survival rate increases to 0.6?" In time, most students figure out a way to add this element to their model.

In short, spreadsheet modeling can be a very positive way of teaching concepts such as stochasticity, and challenges students to think creatively and quantitatively. In collaboration with Charles Weldon, we

hope to make available a set of spreadsheet exercises that cover a wide variety of ecological and evolutionary topics that will be available through ESA in the near future. We welcome any comments and suggestions.

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