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DEMOGRAPHIC STOCHASTICITY

Objectives

- Evaluate effects of stochastic processes in small versus large populations.
- Develop a macro to simulate several trials.
- Compute standard statistics, such as means, variances, coefficients of variation.

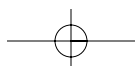
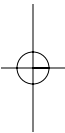
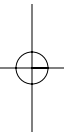
Suggested Preliminary Exercise: Geometric and Exponential Population Models; Statistical Distributions

INTRODUCTION

In a seminal book in conservation biology, Mark Shaffer (1987) wrote, “Given an expanding human population with rising economic expectations, competition for the use of the world’s remaining resources will be intense. Conservationists will often face the problem of determining just how little habitat a species can have and yet survive. At the same time, biologists are increasingly coming to recognize that extinction may often be the result of chance events and that the likelihood of extinction may increase dramatically as population size diminishes.”

Just how does chance play a role in the ability of a species to persist or go extinct, and how can we characterize the “risk of extinction” due to chance? This very question was asked by D. Saltz (1996), who was interested in determining how many Persian fallow deer (*Dama dama mesopotamica*), a critically endangered species, should be introduced into an area in western Asia as part of a species reintroduction program.

Stochasticity means random variation. In population biology, stochasticity refers to the random changes that influence the growth rate of a population (Akçakaya et al. 1997). Such variation is pervasive in the ecology of natural populations and operates at many levels. If you have completed the exercise on genetic drift, you know that chance plays a role in changing the *allele frequencies* in a population. Unpredictable changes in weather, food supply, and populations of competitors, predators, and parasites act on the *population as a whole* and may contribute to chance extinction. A third kind of chance event operates on *individuals*. This uncertainty is called “demographic stochasticity,” and in this exercise you will learn how demographic stochasticity can cause unpredictable population fluctuations and can lead to extinction.



Demographic stochasticity is the variation in average survivorship and reproduction that occurs because a population is made up of an integer number of individuals. For example, we might determine that a *population* has a birth rate b of 0.4 individuals per individual per year and a survival rate s of 0.6 individuals per individual per year. This indicates that, on average, individuals in the population produce 0.4 offspring per year and 0.6 individuals survive to the next year. But of course, an *individual* cannot partially die and there is no such thing as 0.4 of an offspring. The *population* has a growth rate, but *individuals* either live or die, and they reproduce an integer number of offspring. This interplay between the *finite* characteristics that describe individuals and the global characteristics that describe the collection of individuals in the population is the realm of demographic stochasticity.

Let's begin our explorations with a very brief review of modeling births and deaths in a population, and then discuss how demographic stochasticity can affect the population's growth over time. We will let

- N_t represent the size of the population at some arbitrary time t
- N_{t+1} represent population size one time-unit later
- B_t represent the total number of births in the interval from time t to time $t + 1$
- D_t represent the total number of deaths in the same time interval

We are assuming here, as we did in Exercise 7 on population growth, that the population is "closed" to immigration and emigration; thus we can write

$$N_{t+1} = N_t + B_t - D_t \tag{Equation 1}$$

If we assume that B (total births) and D (total deaths) are governed by the per capita birth and death rates, we can substitute bN_t for B_t and dN_t for D_t , and rewrite our equation as

$$N_{t+1} = N_t + bN_t - dN_t \tag{Equation 2}$$

Thus, if we know what the per capita birth and death rates (b and d) are at time step t , we can compute the total number of births and deaths (B and D) in Equation 1, and calculate the population size in the next time step, $t + 1$.

How does demographic stochasticity affect B and D , even if b , d , and N_t are known? Consider a population of 10 individuals, with $b = 0.4$ and $d = 0.4$ as described previously. The survival rate, s , equals $1 - d$, so $s = 0.6$. If there were no demographic stochasticity in this population, the total number of births would be

$$B = bN = 0.4 \times 10 = 4$$

and the total number of deaths would be

$$D = dN = 0.4 \times 10 = 4$$

The total number of survivors would be:

$$s = (1 - d)N = 0.6 \times 10 = 6$$

However, if we follow the fates of *individuals* in the population and determine whether each individual lives or produces offspring, we may not end up with B and D as computed because partial death and reproduction is generally not possible. We can evaluate this problem by modeling the fates of individuals, utilizing the per capita birth rate, b , and the per capita survival rate, s , in a process that determines whether an individual will live or die, and whether it will reproduce or not. This is often done with a random-number generator, where a random number between 0 and 1 is drawn from a uniform distribution. To determine whether an individual dies or survives, we can compare the random number to s and let all individuals with a random number less than s survive. To determine whether an individual reproduces offspring, we can compare a different random number to b and let all individuals with a random number less than b reproduce. This is quite easy to do on a spreadsheet such as the one shown in Figure 1.

	A	B	C	D	E
1	Demographic Stochasticity				
2	Survival rate = s =		0.6	Death rate = d =	0.4
3	Birth rate = b =		0.4		
4					
5	POPULATION 1				
6	Individual	Random #	Survive?	Random #	Reproduce?
7	1	0.38	1	0.11	1
8	2	0.91	0	0.86	0
9	3	0.16	1	0.56	0
10	4	0.78	0	0.78	0
11	5	0.98	0	0.62	0
12	6	0.59	1	0.44	0
13	7	0.23	1	0.89	0
14	8	0.61	0	0.28	1
15	9	0.48	1	0.44	0
16	10	0.61	0	0.94	0
17			5		2

Figure 1 In this population, $s = 0.6$ and we expect the total number of survivors to be 6, but we see that only 5 individuals actually survived. And although $b = 0.4$ and we expect B to be 4, only 2 individuals produced offspring. This variation or departure from the population birth and death rates is demographic stochasticity.

With $b = 0.4$ and $d = 0.4$, the population of 10 individuals in Figure 1 should theoretically remain at 10 individuals, since $r = 0$. (Remember that $r = b - d$.) However, in this instance, the population declined from time step 1 (10 individuals) to time step 2 (7 individuals). Occasionally, by chance, the total number of births will be 0 and the total number of survivors will be 0, in which case the population has gone extinct due to demographic stochasticity.

We can characterize the nature of demographic stochasticity under various population sizes, birth rates, and death (or survival) rates by simulating the fates of individuals as we have just done in Figure 1, and then recording the outcome (such as 5 total survivors and 2 total births). For instance, suppose that the probability of survival is 0.6, and we repeat the experiment in Figure 1 100 different times, recording only the total number of survivors for each trial. We will do this for two populations, the first of which consists of 10 individuals and the second of which consists of 25 individuals. Figure 2 shows the results of one such experiment. For population 1, 27 of the trials resulted in 6 survivors (the expected result), but the remaining trials deviated from this result. For population 2, 17 trials resulted in 15 survivors (60% of 25 individuals), but the remaining trials deviated from this expected result.

Which population shows a greater scatter, or more variation, in the trial results? If you have completed Exercise 3, "Statistical Distributions," you know that the **standard deviation** (S) is commonly used to measure the amount of variation from the mean in a data set. The standard deviation is calculated as

$$S = \sqrt{\frac{\sum (x - \bar{x})^2}{N - 1}} \quad \text{Equation 3}$$

where $(x - \bar{x})^2$ represents the square of the difference between each data point (x) and the mean (\bar{x}), and N is the total number of data points. In Figure 2, the standard deviation for population 1 turns out to be about 1.6, and the standard deviation for popu-

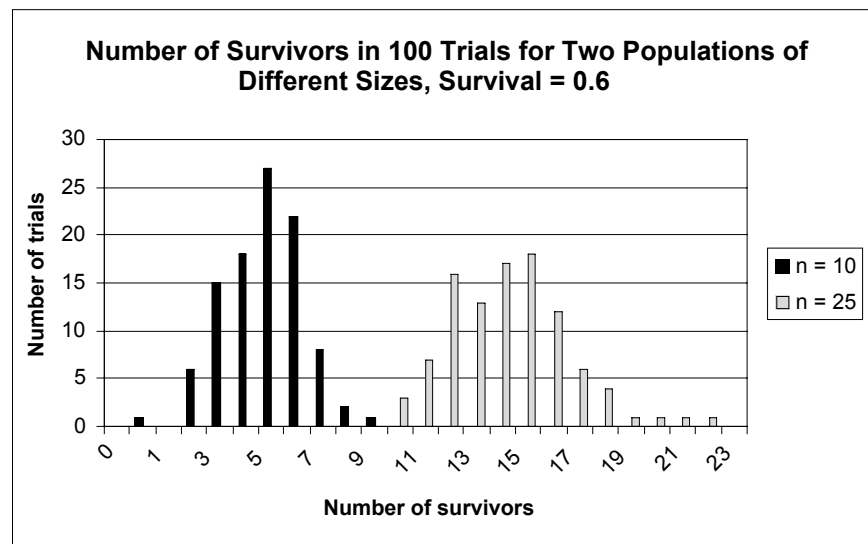


Figure 2

lation 2 is about 2.3, so by this measure, population 2 shows more variation than population 1. But let's think about this for a moment. Note that for each trial, population 1 had only 11 possible outcomes (0–10 survivors), almost all of which occurred, but population 2 had 26 possible outcomes (0–25 survivors), only half of which occurred. In fact, a general property of data sets is that the mean and standard deviation tend to change together—the lower the mean, the lower the standard deviation, and the higher the mean, the higher the standard deviation. Population 2 has a higher mean than population 1, so the difference in their standard deviations might not be as significant as it at first appears. To compare populations whose means are quite different, we “adjust” the standard deviations by dividing each one by its corresponding mean to get the **coefficient of variation (CV)**:

$$CV = \frac{S}{\bar{x}} \quad \text{Equation 4}$$

The coefficient of variation is the ratio of the standard deviation to the mean, and it provides a relative measure of data dispersion compared to the mean. The CV has no units. It may be reported as a simple decimal value or it may be reported as a percentage by multiplying by 100. In the example presented in Figure 2, the CV for population 1 is about 0.27, and the CV for population 2 is about 0.15, so by this measure (which takes into account that we *expect* less data scatter when the mean is small than when it is large), population 1 showed *more* variation than population 2.

Demographic stochasticity has important biological implications. Shaffer (1987) has demonstrated that the chance of extinction through demographic stochasticity increases dramatically as population size diminishes. Mating systems (Legendre et al. 1999) and age structure (Saltz 1996) have also been shown to be affected by demographic stochasticity.

PROCEDURES

In this exercise, you will set up a spreadsheet model to investigate the effects of demographic stochasticity on two populations. Population 1 is a small population (10 individuals), while population 2 is large (100 individuals). The values of b and d remain fixed throughout the exercise. After the exercise is completed, Questions 1 and 2 will ask you to change the values of b and d to explore how their relative differences, and absolute values, affect demographic stochasticity.

As always, save your work frequently to disk.

INSTRUCTIONS

A. Calculate birth and survival rates for population 1.

1. Open a new spreadsheet and set up titles and column headings as shown in Figure 3.

2. In cells C2 and C3, enter the values shown for s and b .

3. In cells A7–A16, set up a linear series from 1 to 10.

4. In cells B7–B16, use the **RAND** function to assign a random number between 0 and 1 to each individual in population 1.

5. In cells C7–C16 enter an **IF** formula to determine whether each individual survives (1) or dies (0).

6. Enter a random number in cells D7–D16.

ANNOTATION

	A	B	C	D	E
1	Demographic Stochasticity				
2	Survival rate = s =		0.6	Death rate = d =	0.4
3	Birth rate = b =		0.2		
4					
5	POPULATION 1				
6	Individual	Random #	Survive?	Random #	Reproduce?
7	1				
8	2				
9	3				
10	4				
11	5				
12	6				
13	7				
14	8				
15	9				
16	10				
17					

Figure 3

Enter 0.6 in cell C2.
Enter 0.2 in cell C3.

Here the survival rate, s , is 0.6 (individuals/individual/year) and the per capita birth rate, b , 0.2 (individuals/individual/year). Remember that the death rate, d , is $1 - s$, so $d = 0.4$. These values will remain fixed for the purposes of this exercise. You will vary them to answer the questions at the end of the exercise.

Enter 1 in cell A7.
Enter the formula `=A7+1` in cell A8. Copy this formula down to cell A16.
These numbers designate the 10 individuals that make up population 1.

Enter `=RAND()` in cells B7–B16
This formula generates a random number between 0 and 1. Note that the spreadsheet generates new random numbers each time the calculate shortcut key, **F9**, is pressed.

Enter the formula `=IF(B7<C2,1,0)` in cell C7. Copy this formula down to cell C16.
Whether an individual survives or dies is based on the population survival rate in cell C2 and the random number associated with each individual in cells B7–B16. In cell C7, if the random number in cell B7 is less than the survival rate in cell C2, the individual receives a score of 1 (survives); otherwise it receives a score of 0 (dies). Copy this formula down for the remaining nine individuals in population 1.

Enter `=RAND()` in cells D7–D16.

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7. In cells E7–E16, enter an **IF** formula to determine whether each individual reproduces (1) or not (0), based on the birth rate given in cell C3.

8. In cells C17 and E17, use the **SUM** function to tabulate the total number of survivors and births, respectively.

9. Press the F9 key to generate a new set of random numbers, and hence a new total number of survivors and total number of births in population 1.

10. Save your work.

B. Write a macro to simulate 150 trials.

1. Set up new column headings as shown in Figure 4, but extend the trial numbers to 150 (cell A170).

2. Repeat your “experiment” 150 times.

Enter the formula `=IF(D7<C3,1,0)` in cell E7. Copy this formula down to cell E16. In this exercise, you will assume that individuals that reproduce have just one offspring. Whether an individual reproduces is based on the birth rate given in cell C3 and the random numbers in column D; the formula is analogous to the one in Step 5.

Enter the formula `=SUM(C7:C16)` in cell C17.

Enter the formula `=SUM(E7:E16)` in cell E17.

You can also use the “Autosum” button on your toolbar, which looks like a sigma (Σ). Based on the survival and birth rates entered in cells C2 and C3, how many total survivors and total births do you expect for population 1?

How did your total survivors and total births change with the new set of random numbers? The difference between your results and the population’s birth and survival rates is an example of demographic stochasticity. Although the rates are “fixed” in cells C2 and C3, the numbers of survivors and births vary due to chance and because individuals cannot reproduce 0.2 individuals, nor can they partially die. What is the likelihood of obtaining the same results again? Characterize the nature of demographic stochasticity based on your two “trials.”

By conducting a great number of trials, you can determine how likely a certain outcome is by calculating the means and variances of the survivors and births produced in population 1 and characterize the nature of demographic stochasticity more effectively.

Enter the number 1 in cell A21.

In cell A22, enter `=1+A21`. Copy this formula down to cell A170.

	A	B	C
18	POPULATION 1		
19	Trial	Total	Total
20	number	survivors	births
21	1		
22	2		
23	3		

Figure 4

You can either push F9, the calculate key, 150 more times and manually enter how many individuals survived and reproduced in each trial (keeping track of your results in the appropriate cell labeled “trial”), or you can write a macro to do this for you.

From the menu, select Tools | Options | Calculations. Select Manual Calculation. (In Macintosh programs, the sequence is Tools and then Preferences.) From this point on you will need to press F9 when you want the spreadsheet to recalculate numbers generated by your macro. Then open the Macro function to the Record mode and assign a shortcut key (see Exercise 2 for details). Enter the following steps in your macro:

- Press F9 to obtain a new set of random numbers, and hence a new set of total survivors and total births.
- Select cell C17, then open Edit | Copy.
- Select cell B20, the column labeled “Total Survivors.”

- Open Edit | Find. The dialog box in Figure 5 will appear. Leave the Find What box empty, searching by columns and formulas, and then select Find Next and Close.

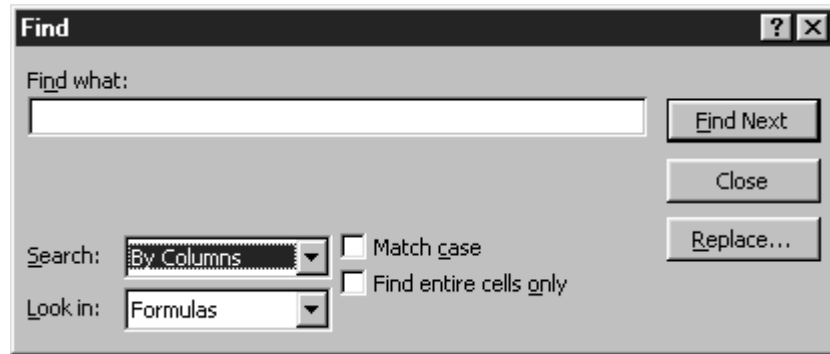


Figure 5

- Open Edit | Paste Special | Paste Values. Click OK.
- Select cell E17.
- Open Edit | Copy.
- Select cell C20, the column labeled "Total Births."
- Open Edit | Find. Leave the Find What box empty, searching by columns and formulas. Select Find Next and Close.
- Open Edit | Paste Special | Paste Values. Click OK.

The macro is finished; stop recording (Tools | Macro | Stop Recording). Now when press your shortcut key 150 times; each trial will run automatically.

From the menu, select Tools | Options | Calculations. Select Automatic Calculation.

3. Switch back to Automatic Calculation. Save your work

C. Calculate birth and survival rates for population 2.

1. Enter the column headings shown in Figure 6.

Population 2 is larger, consisting of 100 individuals. In this section, we will repeat the steps you've just completed for the larger population.

	F	G	H	I	J
5	POPULATION 2				
6	Individual	Random #	Survive?	Random #	Reproduce?

Figure 6

2. Set up a linear series from 1 to 100 in cells F7–F106.

Enter 1 in cell F7.
Enter =1+F7 in cell F8. Copy your formula down to cell F106.

3. Repeat the steps in Part A to fill in survival and birth outcomes for population 2, and sum the total survivors and total births.

You should generate numbers and outcomes in cells G7–J106.

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4. Enter column headings as shown in Figure 7.

Count the total number of survivors and total number of births for population 2, and record the results of each “simulation” as we did for population 1.

	D	E
18	POPULATION 2	
19	Total	Total
20	survivors	births

Figure 7

5. Record a macro to track the total survivors and total births and run 150 trials with population 2.

Follow the instructions in Section B. Make sure your macro for population 2 has a *different name and shortcut key* from the ones you used in population 1. Press your new macro 150 times to run 150 trials.

6. Switch back to Automatic Calculation. Save your work.

From the menu, select Tools | Options | Calculations. Select Automatic Calculation.

D. Construct a frequency histogram of results.

1. Set up column headings as shown in Figure 8.

These are the headings for a frequency histogram for population 1, which consists of 10 individuals. For any trial, the number of survivors could be between 0 and 10, and the total number of births could be between 0 and 10.

	A	B	C	D
175	# of survivors and breeders in 150 trials for population 1			
176	# Survivors	Frequency	# Births	Frequency
177	0		0	
178	1		1	
179	2		2	
180	3		3	
181	4		4	
182	5		5	
183	6		6	
184	7		7	
185	8		8	
186	9		9	
187	10		10	

Figure 8

2. In cells B177–B187, enter a COUNTIF formula to count the number of trials in which there were 0 survivors, 1 survivor, etc.

Enter the formula =COUNTIF(\$B\$21:\$B\$170,A177) in cell B177. Copy the formula down to cell B187.

This formula examines the range of numbers in cells \$B\$21:\$B\$170 and counts the number of times 0 (listed in cell A177) appears. Fill this formula down to obtain frequency counts for the number of trials in which 1, 2, 3 ... 10 survivors were recorded. Double-check your results upon completion; the sum of the numbers generated by the cells with the COUNTIF formula should be 150 because there were 150 trials.

3. In cells D177–D187, enter a **COUNTIF** formula to count the number individuals that reproduced a single offspring in the various trials.

4. Construct a frequency histogram of the number of survivors and the number of breeders for population 1.

Enter the formula `=COUNTIF(C21:C170,C177)` in cell D177. Copy the formula down to cell D187.

Your histogram should resemble Figure 9.

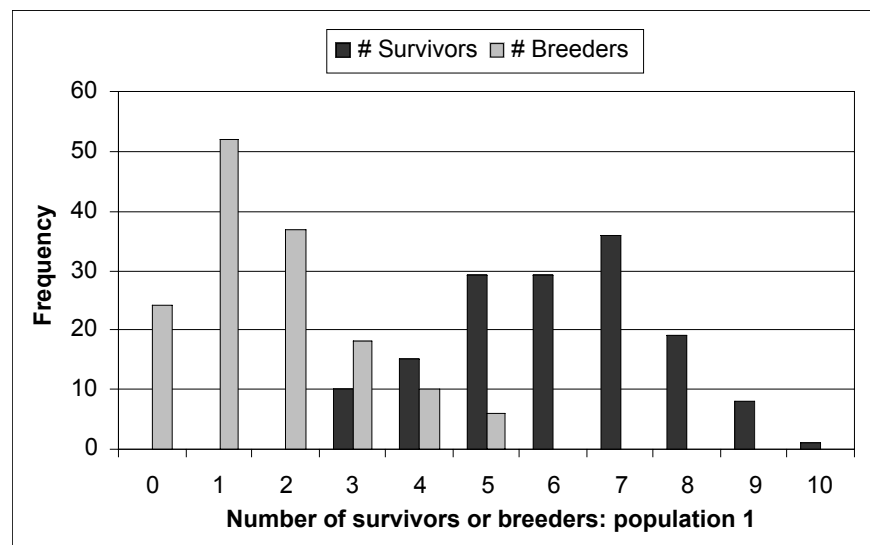


Figure 9

5. Construct a frequency histogram for population 2.

E. Compute means and standard deviations.

1. In cells B171 and B172, enter **AVERAGE** and **STDEV** formulae, respectively, to calculate the mean and standard deviation of the number of survivors in population 1.

2. In cells C171–E172, enter **AVERAGE** and **STDEV** formulae to calculate the mean and standard deviation of the number of breeders in population 1, and the number of breeders in population 1 and the number of survivors and breeders in population 2.

Adapt the preceding steps (1–4) to the values for population 2. Remember that population 2 consists of 100 individuals, so the total number of survivors or births in any trial can range between 0 and 100. Interpret your results.

Review Exercise 3, “Statistical Distributions,” if you are unsure about the use of means and standard deviations.

Enter the formula `=AVERAGE(B21:B170)` in cell B171.
Enter the formula `=STDEV(B21:B170)` in cell B172.

Select cells B171–B172 and copy them over to cells E171–E172. The resulting formulae should be:

- C171 =**AVERAGE**(C21:C170)
- D171 =**AVERAGE**(D21:D170)
- E171 =**AVERAGE**(E21:E170)
- C172 =**STDEV**(C21:C170)
- D172 =**STDEV**(D21:D170)
- E172 =**STDEV**(E21:E170)

3. Examine the histograms you made for each population in Section D and answer the questions at right.

F. Calculate and graph coefficients of variation.

1. In cells B173 and C173, compute the CVs for population 1.

2. In cells D173 and E173, compute the CVs for population 2.

3. Create a graph to compare the CVs, a standardized measure of variation, for the two populations.

Which population appears to exhibit greater stochasticity (i.e., greater variation in the number of births and survivors)? Pay attention to the standard deviations, which measure dispersion of variation in results. Now reflect on the mean values you computed in the previous two steps. Is it useful to compare the variation in two populations that have such different mean values? Why or why not?

The **coefficient of variation**, or **CV**, is calculated as standard deviation divided by the mean, which is then multiplied by 100. We perform this calculation for both the number of survivors and the number of breeders. Analysis of the CV will allow you to directly compare populations 1 and 2 by adjusting for their means.

Enter the formula $=\text{(B172/B171)}*100$ in cell B173 to compute the CV for the number of survivors in population 1.

Enter the formula $=\text{(C172/C171)}*100$ in cell C173 to compute the CV for the number of breeders in population 1.

Enter the formula $=\text{(D172/D171)}*100$ in cell D173 to compute the CV for the number of survivors in population 2.

Enter the formula $=\text{(E172/E171)}*100$ in cell E173 to compute the CV for the number of breeders in population 2.

Your graph should resemble Figure 10.

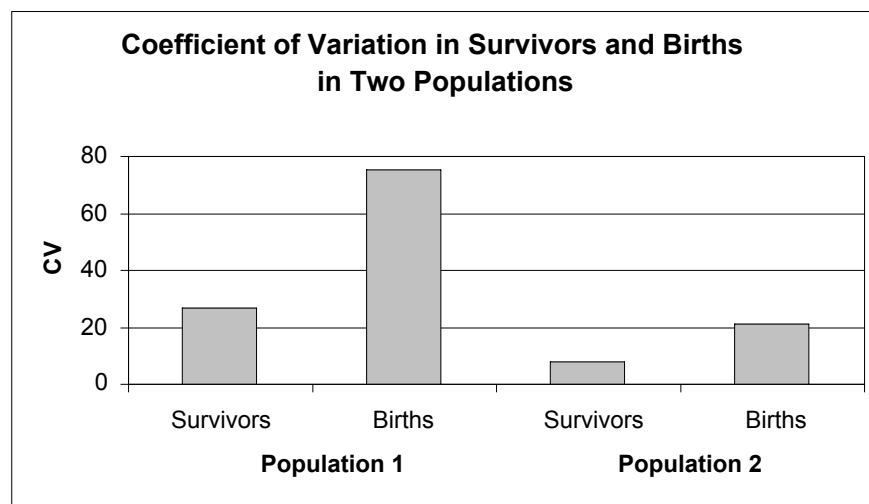


Figure 10

You should see that the smaller population, population 1, has a much higher CV in both number of survivors and number of births than population 2. This reflects a greater amount of unpredictable variation (demographic stochasticity) in small populations.

QUESTIONS

1. Focus on population 1 (the small population), cells C17 and E17 (the total survivors and total births). Press F9 20 times and record the number of times the population goes extinct (number of survivors *and* number of births = 0) Then compute the extinction risk, $P(\text{extinction})$, as the number of times the population went extinct divided by 20 trials. (Your result is likely to be 0). Enter differing values of s and b in cells C2 and C3 (except 0). What levels of s and b are likely to produce higher extinction rates due to demographic stochasticity?

2. Compare the stochasticity in the larger population, population 2, under different survival and birth rates, while keeping r constant (remember that $r = b - d$). In the first scenario, let the population have a high birth rate ($b = 0.9$) and low survival rate ($s = 0.1$). In the second scenario, let the population have a low birth rate ($b = 0.1$) and a high survival ($s = 0.9$). Note that in both cases, $r = 0$. Set up spreadsheet headings as shown, and modify the survival and birth rates in cells C2 and C3. For each scenario, develop a macro in which the number of survivors and births are recorded in 100 trials. For each trial, compute ΔN as the change in population size (number of births minus number of deaths). (You can generate the delta symbol, Δ , by typing in a capital D and then changing the font to "Symbol.") Then compare the coefficient of variation in ΔN over 100 trials when the population size is 100. How do the *absolute* birth and death rates affect stochasticity when population size is relatively large?

	L	M	N	O	P	Q	R
2		High birth and low survival ($b = 0.9, s = 0.1$)			Low birth and high survival ($b = 0.1, s = 0.9$)		
3	Trial	# survivors	# births	ΔN	# survivors	# births	ΔN

3. Variation is pervasive in nature. For example, birth rates and death rates are rarely constant over time. How do you think demographic stochasticity differs from a more commonly noted type of variation, environmental stochasticity? With environmental stochasticity, b , s , and d vary with some randomness as opposed to remaining fixed (cells C2, E2, C3). Can you think of ways in which you might add an element of environmental stochasticity to your model?

*4. (Advanced) In your model, you've discovered that demographic stochasticity is different between populations consisting of 10 and 100 individuals. As population size increases, in what fashion do the effects of demographic stochasticity decrease? (For example, does it decrease linearly as population size increases, or is there some threshold at which increasing population size has little effect on stochastic processes?) Develop your model more fully to answer this question (you may want to copy your entire model onto a new sheet for this question, so that you do not alter your original model).

*5. (Advanced) Examine the Visual Basic for Applications code that was used to write your macro. See if you can follow through the code and match the action of your keystrokes outlined in step 2 of Section B to the code. It should look something like this:

MACROS

```
Sub trial()
    \
    \ trial Macro
    \ Macro recorded 8/31/99 by Authorized User
    \
    \ Keyboard Shortcut: Ctrl+t
    \
    Application.Goto Reference:="R21C2:R21C3"
    Selection.Insert Shift:=xlDown
    Application.Goto Reference:="R17C3:R17C4"
    Calculate
    Selection.Copy
    Application.Goto Reference:="R21C2:R21C3"
    Selection.PasteSpecial Paste:=xlValues, Operation:=xlNone,
        SkipBlanks:= _
        False, Transpose:=False
End Sub
```

- *6. (Advanced) The binomial distribution could have been used to estimate the various probabilities that x number of survivors and x number of breeders would have occurred in the 150 trials (see Exercise 3, “Statistical Distributions”). Use the **BINOMDIST** function to obtain survivorship probabilities for Population 1, and compare your trial results with those predicted by the binomial distribution. Does the binomial distribution also reflect greater “stochasticity” when sample sizes are small?

LITERATURE CITED

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