

37

QUANTITATIVE GENETICS: EVOLUTION BY NATURAL SELECTION

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Objectives

- Set up a spreadsheet model for a population with a continuously varying trait.
- Understand the difference between selection and response to selection.
- Consider how differences in heritability and strength of selection can alter the response to selection.

Suggested Preliminary Exercises: Hardy Weinberg Equilibrium; Heritability

INTRODUCTION

To evolutionary biologists, *natural selection* and an *evolutionary response to natural selection* are different phenomena. For a population to experience **natural selection**, two conditions must be met: (1) individuals must vary from one another for a particular trait, and (2) an individual's survival and reproductive success must be affected by which of the traits it possesses.

Some traits will be well adapted to a given environment and some will not. For example, Darwin's finches are highly variable in beak size, and individuals with larger beaks tend to survive periods of drought more successfully than those with smaller beaks (Grant and Grant 1993). This is an example of natural selection: during drought, birds with small beaks are more likely to be eliminated from the population.

Note that selection happens *within* generations. However, natural selection says nothing about what happens to beak size in subsequent generations. Since evolution can be broadly defined as a change in genetic make-up over time, we need to examine future generations to determine if natural selection is a mechanism that causes an evolutionary change in organisms. If natural selection does indeed lead to changes in future generations, then you have observed an **evolutionary response to natural selection**, or **evolution by natural selection**.

Suppose you are studying butterflies that live just one summer. You find that the caterpillars vary in weight. Some are fat and some are skinny. At the end of the summer, you are able to show that many more fat caterpillars survived pupation than did skinny caterpillars. However, when you come back the next year, there are just as many skinny caterpillars as there were the previous year. How can that be? Perhaps the caterpillar population didn't fulfilled all *three* of the criteria

for evolution by natural selection:

1. Individuals in a population must vary from one another.
2. Survival and reproduction must be affected by that variation.
3. The variation must be heritable.

So in your population, caterpillars varied in weight and this variation influenced survival; but the variation in weight among individuals did not reflect *genetic* variation. Instead, it was probably due to environmental factors such as the particular plant that the caterpillar happened to eat. In other words, higher weight was not **heritable**.

Heritability is a concept best dealt with by quantitative genetics. The field of **quantitative genetics** examines quantitative (measurable) traits that vary **continuously**—over a range of values—such as beak size or caterpillar weight. All of the traits Mendel studied were *qualitative* traits in which individuals could be neatly lumped into two groups per trait, and a single gene controlled each trait. Pea color was either green or yellow; pea pods were either pinched or swollen; pea shapes were either wrinkled or smooth, and so on. What would Mendel have done if he had chosen to work with humans? Could he lump them by tall or short? Humans vary from short to tall and everything in between. Human height is a *quantitative* rather than a qualitative trait and is influenced by numerous genes and by the environment. When you consider that most traits are in fact quantitative, continuous, and affected by many genes, it is easy to understand why it took so long for scientists to understand that inheritance is caused by discrete factors called genes.

In the Hardy-Weinberg equilibrium exercise, you used a *population genetics* approach to studying evolution, where you were concerned with calculating specific changes in allele frequency over time. For example, we were interested in determining how p and q change over time. Quantitative geneticists also study evolution, but they use slightly different mathematical tools than population geneticists. In contrast to the population genetics approach, most of the mathematical equations used by a quantitative geneticist do not require knowing the genotype of individuals. A fundamental equation quantifies the **evolutionary response selection** (Falconer 1989). The formula is simple, yet wonderfully useful:

$$R = S \times h^2 \quad \text{Equation 1}$$

where R stands for evolutionary response to selection, a measure of how natural selection causes a population to evolve; S is the strength of selection (also known as the selection differential); and h^2 is heritability.

In order to understand R , let's first discuss the concepts of selection, selection differential, and heritability. Then we will return to Equation 1 and tie the concepts together.

Selection and the Strength of Selection

Natural selection occurs whenever survivorship or reproductive success is nonrandom with respect to a particular trait. Selection can be either *directional*, *stabilizing*, or *disruptive* (Figure 1). **Directional selection** occurs when the survivors are at either the high or the low end of the variation in a trait. In the caterpillar example, there was directional selection for weight of the caterpillars: the fattest caterpillars (those at the extreme high end of the population) survived.

In **stabilizing selection**, individuals with intermediate values survive best; individuals at both extremes do not survive as well. For example, suppose that small caterpillars did not survive due to insufficient resources to survive pupation, but that very large caterpillars also did not survive well because predators such as birds were better able to see and eat them. Then the best survivors would be caterpillars with an intermediate size. In this case, the caterpillar population is experiencing stabilizing selection.

The third and final type of selection is **disruptive selection**, where individuals in the population with *either* high or low extremes for a trait survive better than individuals with an intermediate-sized trait. Suppose that the caterpillars varied in their degree of melanism (pigmentation), with some caterpillars being quite dark, some being

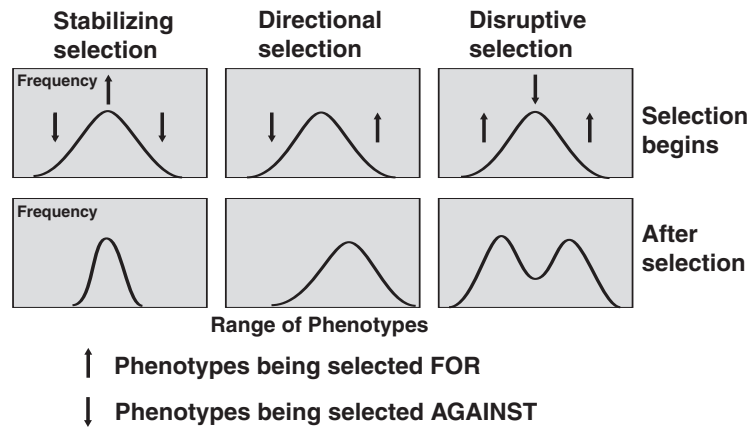


Figure 1 The effects of directional, stabilizing, and disruptive selection on a population before and after a selection event.

very light-colored, and some caterpillars having an in-between color. Now suppose that the caterpillars were found on both the white bark of birch and the darker bark of walnut trees. The light caterpillars would be protected from predators because they would be hidden on the white bark of the birch trees. The dark caterpillars would be protected on the bark of the walnut trees. However, the caterpillars with intermediate coloring would be visible to predators on both types of tree, and so they would not survive as well as either of the extreme colors.

Suppose that the only those caterpillars at the extreme high end of a trait's value in the population survived (directional selection). How would you measure the impact of natural selection on the population? You could take the mean weight of the population before any individuals died, and then compare it to the mean weight of those individuals that survived natural selection. This is what S , the **strength of selection** or **selection differential**, measures—the difference in a population's trait before and after natural selection. If $S = 0$, then survivors and nonsurvivors did not differ in this trait, and the offspring of survivors should not differ from the previous generation. The larger the value of S , the more intense the action of natural selection on the population.

Heritability

Another important component of Equation 1 is heritability, h^2 . You were introduced to the concept of heritability in the previous exercise, and we will briefly review the important concepts here because knowledge of heritability is required to determine how natural selection can give rise to evolutionary change.

Heritability in a scientific sense is not the degree to which a trait is genetic, nor is it the proportion of an individual's phenotype that is controlled by genes (rather than environment). These concepts are often mistaken for h^2 , which in reality has a much more specific meaning. **Heritability** is the proportion of variation for a trait that is explained by genetic variation among individuals, abbreviated V_g . The variation in a trait that is due to variation in *environmental* conditions is V_e . The total variation in population is thus $V_g + V_e$. Heritability, h^2 , has the formula

$$h^2 = \frac{V_g}{(V_g + V_e)} \quad \text{Equation 2}$$

Theoretically, h^2 can only vary between 0 and 1. When variation among individuals in a population is due entirely to differences in environmental conditions, $h^2 = 0$. When the total variation among individuals in a population is due solely to differences in the genotypes of individuals, $h^2 = 1$. Note that h^2 is a specific measure for a specific population at a specific point in time.

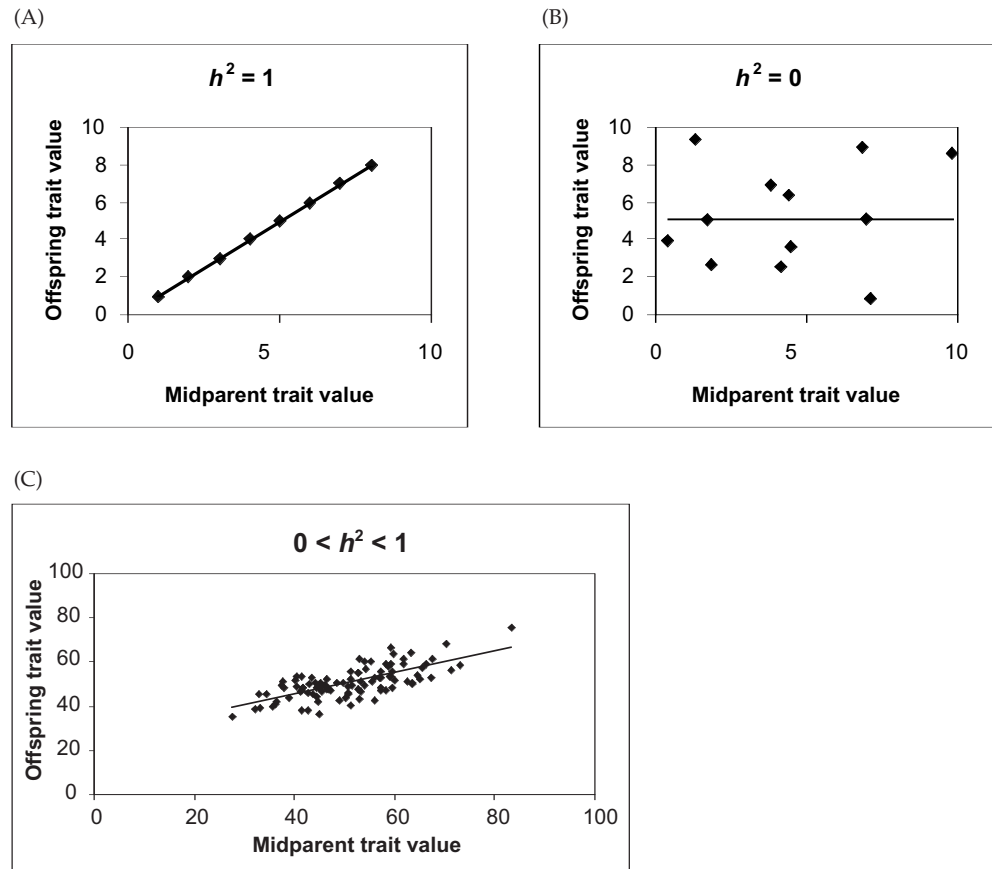


Figure 2 (A) When an offspring's trait is perfectly matched to the average of its two parents, $h^2 = 1$. Small parents will have small offspring, and large parents will have large offspring. The slope of the line is 1, and $h^2 = 1$. (B) When an offspring's trait cannot be predicted by the traits of its parents, $h^2 = 0$. Parents of any size can have offspring of any size. In this case, the slope of the regression line is 0, and $h^2 = 0$. (C) This graph shows a tendency for larger parents to have larger offspring and for smaller parents to have smaller offspring, but there is substantial scatter, suggesting that h^2 here falls between 0 and 1.

Quantitative geneticists calculate heritability in two ways. By manipulating Equation 1, you can solve for heritability as

$$h^2 = R/S$$

This is the **realized heritability**, or heritability defined by the degree to which a trait responds to selection in a population. We'll return to this equation after we learn more about R .

A second way to solve for heritability is to graph the trait in a set of offspring against the mean of the trait of each of their two parents (called the **midparent value**; Figure 2). The slope of the regression line for such a plot is one way to estimate heritability.

Putting S , h^2 , and R Together

Now that we have a little background on S and h^2 , let's return to Equation 1 and our discussion of how populations can evolve as a result of natural selection. Recall that

$$R = S \times h^2$$

R measures the evolutionary response to selection, or how natural selection will cause a population to evolve. Recall that there will be a response to selection only if three criteria are fulfilled:

1. Individuals in a population must vary from one another.
2. Survival and reproduction must be affected by that variation.
3. The variation must be heritable.

Equation 1 reflects all three criteria:

1. If individuals do not vary for a trait, then the denominator of Equation 2 is 0 and h^2 is undefined, so Equation 1 is undefined.
2. If S is 0, then R is 0, and natural selection did not impact the population.
3. If h^2 is 0, then R is 0.

If both S and h^2 are greater than 0, then you can expect the offspring will have a different mean trait than the previous generation's population before selection. Thus, R can be measured directly as the mean of the offspring population minus the mean of the original parental population before any individuals died.

PROCEDURES

In this exercise, you will develop a spreadsheet model of a population of 100 individuals that undergoes natural selection. You can imagine that the trait you are following is beak size in birds. (For real data on such a trait, see Grant and Grant 1993 or read Jonathan Weiner's *The Beak of the Finch*, one of our all-time favorite books.) In this exercise, you can manipulate several variables: the mean and variance of a trait in the parental population, the "quality" of breeding habitat, how the individuals are distributed across breeding habitats, the degree of environmental and genetic influence on the offspring trait (a modeling surrogate for heritability), and how natural selection favors individuals of various traits. You'll be able to manipulate these values to see how they affect S , R , and the course of evolution.

As always, save your work frequently to disk.

INSTRUCTIONS

A. Set up the model parental population.

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

2. Enter the values shown in cells C4 and C5 for mean size and standard deviation.

ANNOTATION

	A	B	C	D	E
1	Quantitative Genetics				
2					
3	Initial population trait		Offspring trait		
4	Mean trait value ==>		50	"Heritability factor" ==>	0.5
5	Variation in trait ==>		10	"Environmental factor" ==>	0.5
6					
7	Environmental conditions		Selection values		
8	Mean condition ==>		50	Select parents above ==>	0
9	Variation in environment ==>		10	Select parents below ==>	0
10					

Figure 3

Enter 50 in cell C4.

Enter 10 in cell C5.

First we'll define the parental population to have a particular mean and standard deviation for the trait. Let's suppose the birds in our study population have a mean beak size of 50 mm. Keep in mind that evolution requires variation in the parental population; this is the standard deviation of beak size. For now, enter a standard deviation of 10 in cell C5.

- 3. Enter the values shown in cells C8 and C9 to represent the mean and variation in environmental conditions.
- 4. Enter the selection values shown in cells E8 and E9.
- 5. Enter the values shown in cells E4 and E5 for the heritability and environmental contributions to offspring phenotype.
- 6. Save your work.

B. Establish parental traits before and after selection.

1. Set up new column headings as shown in Figure 4.

2. Set up a linear series from 0 to 99 in cells A20–A119.

3. In cells B20–B119, use the **NORMINV** and **RAND** functions to assign average beak sizes to each pair in the parental population.

Enter 50 in cell C8.
Enter 10 in cell C9.
Cells C8 and C9 establish the environmental conditions in which the parents breed and produce offspring. Set cell C8 to 50, suggesting that on average (genetics aside), most parents nest in environments that produce offspring with 50 mm beak size. The variation in the environment is set by cell C9, which is currently set to 10. This means that the population is nesting in a very heterogeneous environment; some individuals will nest in high-quality environments that generate large offspring with big beaks, while others will nest in lower-quality environments that generate smaller offspring with smaller beaks. If the value in cell C9 were small, such as 1, it would indicate that parents are breeding in a similar (homogeneous) environment.

Enter 0 in cells E8 and E9.
Cells E8 and E9 establish how natural selection will “select” or pick which parents will breed. You can set these cells so that only large or small parents breed (directional selection), both small and large parents breed (disruptive selection), or only medium-sized parents breed (stabilizing selection). For now, cells E8 and E9 are set to 0, which indicates that all parents are able to breed, and natural selection will not discriminate among the parent trait size. In the Questions section, you will be asked to modify these cells to see how natural selection affects *S* and *R*.

Enter 0.5 in cells E4 and E5.
Cells E4 and E5 define the extent to which an offspring’s trait size will be controlled by its parental genotype or by the environment in which it was raised. For lack of a better term, we call these cells the “heritability factor” and the “environmental factor,” respectively. Remember that *heritability* measures the amount of variation in a population that can be explained by genetic variation among individuals. In this exercise, we use the term “heritability factor” to shape each offspring’s phenotype. In this sense, the word “heritability” is not correct because heritability is not a phenomenon that happens to individuals, but is a population-level measure. We trust that you have completed the heritability exercise for a true interpretation of the term.

	A	B	C	D
16	PARENTAL POPULATION		NATURAL SELECTION	
17				
18		Midparent	Survive	Midparent
19	Pair #	trait	selection?	trait

Figure 4

We will track the fates of 100 pairs of individuals (male and female breeders) and their offspring.

Enter 0 in cell A20.
Enter **=1+A20** in cell A21. Copy your formula down to cell A119.

Enter the formula **=NORMINV(RAND(),\$C\$4,\$C\$5)** in cell B20. Copy this formula down to cell B119.
The formula in cell B20 tells the spreadsheet to draw a random cumulative probability (the **RAND()** portion of the formula) from a distribution whose mean is given in cell C4 and whose standard deviation is given in cell C5. This probability is converted

into an actual data point by the **NORMINV** function. We'll assume that this data point represents the average of the male and female beak size. Copy the formula down to obtain midparent beak sizes for the remaining pairs in the population.

Each parent will vary in beak size, but we'll keep track of the average value from the two individuals. Remember that our population has an average beak size of 50 mm and a standard deviation of 10 mm. If our population is normally distributed (see Exercise 3, "Statistical Distributions") with respect to beak size, 68% of the population will have beak sizes between the mean and ± 1 standard deviation. That is, 68% of the population will have beak sizes between 40 and 60 mm. About 95% of the population will have beak sizes between the mean and ± 2 standard deviations. That is, 95% of the population will have beak sizes between 30 and 70 mm. Thus, our initial population is quite variable with respect to beak size.

4. In cells C20–C119, enter an **IF(OR)** formula to see which breeding pairs survive.

Enter the formula **=IF(OR(B20>=\$E\$8,B20<=\$E\$9),1,0)** in cell C20. Copy this formula down to cell C119.

We'll now subject our population to natural selection in which only certain breeding pairs survive. The **IF** formula returns one value if a condition you specify is true, and another value if the condition you specify is false. The **OR** formula returns the word "true" if any of the conditions specified are true. For example, the section **OR(B20>=\$E\$8,B20<=\$E\$9)** tells the program to evaluate two conditions: first, Is the value in cell B20 greater than the value in cell E8? and second, Is the value in cell B20 less than the value in cell E9? If either of these conditions is true, the program returns the word "true"; otherwise, it returns the word "false." The **IF** formula tells the program to evaluate the **OR** function, and if it is true, return the number 1; if false, return the number 0.

Because cells E8 and E9 are both set to 0, all pairs of parents will survive natural selection, and column C should be filled with the number 1.

5. In cells D20–D119, enter a formula to return the mid-trait of those parents that survived the selection event.

Enter the formula **=IF(C20=1,B20)** in cell D20. Copy this formula down to cell D119. Cell D20 simply returns the midparent trait if the parents survived the selection event. It tells the program to evaluate cell D20, and if the value is 1, then return the traits of the parents given in cell B20.

Your spreadsheet should now look something like Figure 5, although your midparent trait values will be different due to the nature of random sampling.

6. Save your work.

	A	B	C	D
16	PARENTAL POPULATION		NATURAL SELECTION	
17				
18		Midparent	Survive	Midparent
19	Pair #	trait	selection?	trait
20	1	52.5	1	52.5
21	2	49.1	1	49.1
22	3	46.6	1	46.6
23	4	72.3	1	72.3
24	5	58.7	1	58.7

Figure 5

C. Calculate selection statistics.

1. Set up new column headings as shown in Figure 6.

	G	H	I
1	Selection statistics		
2		Parents	Offspring
3	Average_i =		
4	N_s =		
5	Average_s =		
6	S =		
7	Average_o =		
8	R =		

Figure 6

2. In cell H3, use the **AVERAGE** function to obtain the mean initial parental trait (designated as Average_i).

3. In cell H4, use a **SUM** formula to count the number of surviving pairs of parents, designated as N_s.

4. In cell H5, use the **AVERAGE** formula to obtain the mean parental trait after natural selection (designated as Average_s).

5. In cell H6, calculate the strength of selection (S) as the mean trait after selection minus the mean trait before selection.

6. Save your work.

D. Establish offspring traits.

Enter the formula **=AVERAGE(B20:B119)** in cell H3.

Enter the formula **=SUM(C20:C119)** in cell H4.

Enter the formula **=AVERAGE(D20:D119)** in cell H5.

We used the formula **=H5-H3** in cell H6.

Note that since we haven't considered offspring yet, we cannot measure the response to selection, R.

Now that we've exposed the population to natural selection, we need to determine if the population *evolved* as a result. Since an evolutionary response is a change in trait over generations, we'll let the surviving pairs of parents mate and produce a single offspring, and see if the offspring beak sizes have changed as a result of natural selection. The traits in the offspring are controlled by cells E4 and E5. **The values in cells E4 and E5 must sum to 1.** If cell E4 is set to 1, an offspring will be identical to its parents. If cell E5 is set to 1, the beak size will be determined solely by the environment in which the offspring was raised.

1. Set up new column headings as shown in Figure 7.

	F	G	H
16	OFFSPRING TRAIT		
17			
18	Genetic	Environmental	Offspring
19	factor	factor	trait

Figure 7

2. In cells F20–F119, enter a formula to determine the genetic component of the offspring’s beak size.

Enter the formula `=IF(C20=1,E4*B20)` in cell F20. Copy this formula down to cell F119.

The formula in cell F20 evaluates first whether the value in cell C20 is 1 (the pair survived natural selection and were able to breed). If the pair survived, the spreadsheet will compute `E4*B20`, or the genetic “component” multiplied by the midparent beak size. Notice that the last part of the IF function was omitted; by default, the spreadsheet will return the word “false” if the last part of the IF function is not specified.

3. In cells G20–G119, enter a formula to determine how the environment affects the offspring’s phenotype.

Enter the formula `=IF(C20=1,E5*NORMINV(RAND(),C8,C9))` in cell G20. Copy this formula down to cell G119.

How much the environment will affect the offspring’s phenotype depends on three things: first, the pair must survive to breed; second, the mean of the environment in which the offspring are produced needs to be specified; and third, the standard deviation of that environment needs to be specified. The formula in cell H20 is another IF function that evaluates whether the pair of adults survived to reproduce. If so, the spreadsheet will use the **NORMINV** function to draw a random cumulative probability from a normal distribution whose mean is given in cell `C8` and whose standard deviation is given by cell `C9`. This number is then multiplied by the value in cell `E5`, which is the environmental component of the offspring’s phenotype. Note again that the last part of the IF function was not specified, so the word “false” will be returned if the pair failed to breed.

4. In cell H20, enter a formula to compute the offspring’s beak size.

Enter the formula `=IF(C20=1,F20+G20)` in cell H20. Copy this formula down to cell H119.

The offspring’s final beak size is determined by the genetic component plus the environmental component. The IF function is used again so that only parents that survive to breed can generate offspring.

5. Save your work.

E. Construct histograms.

We’ll now examine the effect of the selection event on the population visually. The most common way to depict a population’s values is through a **frequency distribution**—a plot of the raw data (in this case, beak sizes) against the frequency that values appear in the population. We will calculate the frequencies of adult traits before and after natural selection, as well as offspring traits.

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

	J	K	L	M	N
16	FREQUENCY DISTRIBUTION				
17					
18			Frequency of parents	Frequency	
19	"Bin"	Trait size	Before	After	of offspring
20	9	<10			
21	19	<20			
22	29	<30			
23	39	<40			
24	49	<50			
25	59	<60			
26	69	<70			
27	79	<80			
28	89	<90			
29		<100			

Figure 8

2. Use the **FREQUENCY** function in cells L20–L29 to count the number of adult pairs with trait sizes <10, <20, etc. before natural selection.

The **FREQUENCY** function calculates how often values occur within a range of values, and then returns a vertical array of numbers. You will use the **FREQUENCY** function to count the number of beaks in cells B20–B119 that fall below 10 mm, within 10 and 19 mm, within 20 and 29 mm, and so on. These are the “bins” in which numbers will be grouped.

The **FREQUENCY** function works best when you use the f_x key and follow the cues for entering a formula. Remember that since you will be entering this formula for an array of cells, the mechanics of entering this formula is a bit different than the typical formula entry. **Instead of selecting a single cell to enter a formula, you need to select a series of cells, then enter a formula, and then press <Control><Shift><Enter> (Windows machines) or ⌘ + <Return> (Macintosh) to enter the formula for all of the cells you have selected.**

To determine the frequencies of beak lengths before selection, select cells L20–L29, then select the **FREQUENCY** function. To define the Data Array, use your mouse to highlight all 100 pairs of individuals before the selection event in cells B20–B119. To define the Bins Array, select cells J20–J28. Instead of clicking OK, press <Control><Shift><Enter>. The program will return your frequencies of beak sizes before the selection event.

After you’ve obtained your results, examine the formulas in cells L20–L29. Your formula should be {=FREQUENCY(B20:B119,J20:J28)}. The { } symbols indicate that the formula is part of an array. If for some reason you get “stuck” in an array formula, press the escape key and start over.

3. Use the **FREQUENCY** function in cells M20–M29 to count the number of adults pairs with trait sizes <10, <20, etc. after natural selection.

The formula that calculates frequencies after the selection event is {=FREQUENCY(D20:D119,J20:J28)}.

4. Use the **FREQUENCY** function in cells N20–N29 to count the number of

The formula that calculates frequencies of offspring is {=FREQUENCY(H20:H119,J20:J28)}.

offspring with trait sizes <10, <20, etc.

5. Graph your frequency distributions of beak sizes for parents before and after the selection event, and for offspring of surviving parents.

Now you can visually examine strength of selection (S). (You've already calculated S in cell H6). It's the difference in the trait before and after selection—that is, the shift in the distribution as a result of natural selection. In this case, because natural selection did not kill off any adults, S is 0.

Use the column graph option, and label your graph fully. Your graph should resemble Figure 9, but your values may be different.

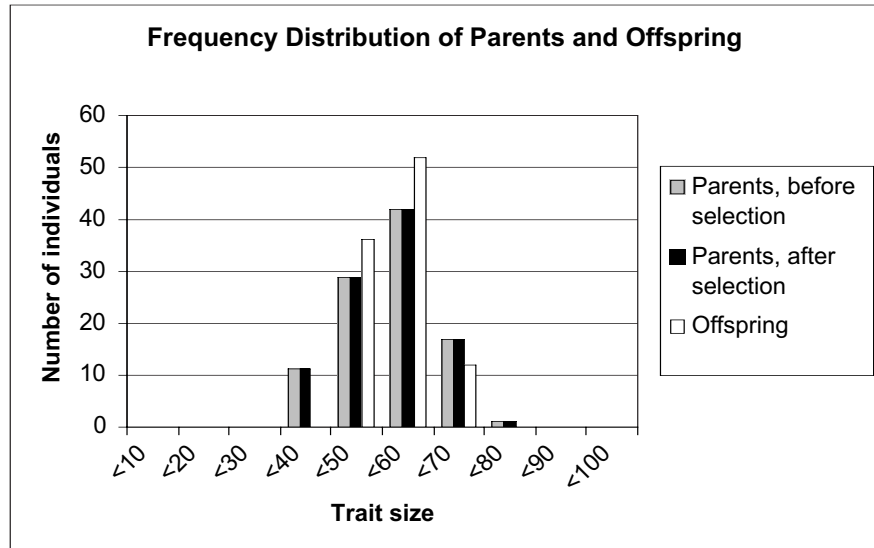


Figure 9

Interpret your graph. You should see that the frequency distribution of parents before and after natural selection is identical because all of the parents survived to breed. The offspring traits are a bit different than the parents because the environment played a role in shaping their beak sizes. Press F9, the calculate key, and you will see the offspring traits can be quite variable from calculation to calculation. This is because the environment plays an equal role in shaping beak sizes of offspring, and the environment for breeding is quite variable at the moment. If natural selection “picked” only adults with beak sizes larger than 50 mm (cell E8), our graph would look like Figure 10.

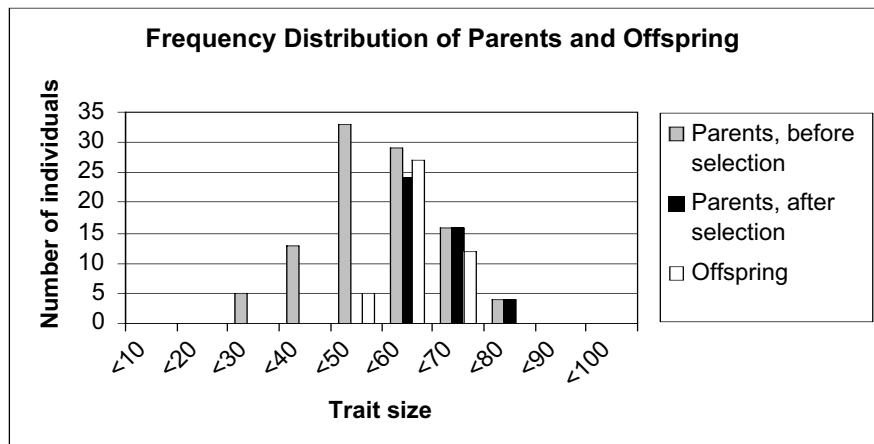


Figure 10

F. Calculate offspring statistics and R .

1. In cell I7, compute the average of the offspring's trait size.
2. In cell I8, calculate R , the response to selection, as the mean offspring trait minus the mean parental trait.
3. Save your work.

Enter the formula **=AVERAGE(H20:H119)** in cell I7.

Enter the formula **=I7-H3** in cell I8.

Take time now to fully interpret your graphs and calculations, keeping in mind the model entries given at the beginning of the exercise.

QUESTIONS

1. Although the model is currently set so that all parents survive to breed ($S = 0$), occasionally you will see that R does not equal 0. Fill in the table below by striking the F9 key 5 times. After each strike, record your results, and then describe the pattern you see. After filling in the table, continue to hit the F9 key many more times. Are your offspring ever smaller than your parents? In other words, do you ever get a negative response to selection? Are they ever larger than the parents are? Why? Interpret S and R .

Trial	Mean Offspring Trait	Response to Selection
1		
2		
3		
4		
5		

2. Let's continue to let all parents breed, but we will alter how the offspring's phenotypes are generated. Set cell E4 to 1 (and cell E5 to 0) so that offspring are identical to their parents in phenotype. Press F9 several times and interpret R . Then set cell E4 to 0 and cell E5 to 1 so that an offspring's phenotype is controlled strictly by the environment in which it was raised. Under what conditions is it possible to see a change in R ? Why?
3. Now let's let only some parents survive to breed. If you were trying to commercially breed these birds to obtain birds with a mean beak size of 70 mm, what conditions would you modify in your spreadsheet to consistently generate birds with the desired traits? Answer this question first for a population with a heritability factor (cell E4) of 1. Answer this question a second time for a population with heritability factor (cell E4) of 0.6. Assume that you cannot control the environment in which the birds are living (C8 and C9), but you can change the selection values (cells E8 and E9). Discuss your answer in terms of S and R , and interpret your updated graphs.
4. Now that you have tried the above (and perhaps looked at the answer), let us try to use a population with a heritability factor of 0.6 again, but this time try to breed for birds with a mean beak size of 55 mm. Discuss your answer in terms of S and R .

5. In questions 3 and 4, you explored directional selection. Alter the values in cells E8–E9 to model the effects of disruptive selection. How does changing E4–E5 affect the distribution of the offspring population, R , and S ? Compare your results with earlier answers from directional selection.
6. Explore your spreadsheet in new ways, and ask an interesting question and answer it. Modify parents original traits (variable or not variable, cells C4–C5), the environment of the nest (C8–C9) in which the offspring is raised, the genetic and environmental influence on offspring traits (cells E4–E5), and selection of parents (cells E8 and E9).

LITERATURE CITED

- Falconer, D. S. 1989. *Introduction to Quantitative Genetics*, 3rd Edition. Longman Scientific & Technical, Essex.
- Grant, B. R. and P. R. Grant. 1993. Evolution of Darwin's finches caused by a rare climatic event. *Proceedings of the Royal Society of London (B)* 251: 111–117.
- Weiner, J. 1995. *The Beak of the Finch*. Vintage Books, New York.