

36

HERITABILITY

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Objectives

- Understand the concept of heritability.
- Differentiate between broad-sense heritability and narrow-sense heritability.
- Learn different methods for computing heritability.
- Understand the conditions that lead to high heritability and low heritability.

INTRODUCTION

Can you think of a physical trait that makes you different from your brother or sister? You may be taller than your sibling or have darker skin or have a different hair color. Can you think of a trait in which you and your sibling are similar? Were either of these traits inherited from your parents, or were they controlled more by environmental factors?

Most people have a good general concept of **heritability**. Surprisingly, the strict scientific definition of heritability is a much more difficult concept to grasp than our everyday use of the word. This is partly because heritability has a theoretical definition that is impossible to directly measure in the field, and there are several different ways to estimate heritability in practice (e.g., twin studies, breeding experiments, offspring-parent regressions, and selection experiments). These different ways of estimating heritability have assumptions. As such, it is not uncommon that two different methods of estimating heritability might lead to quite different values even in the same population in the same environment.

Possibly the most important key to understanding the scientific definition of heritability is to realize that the trait itself is almost completely unimportant to the definition of heritability. Rather, it is the *variation* in the trait that is important. If you repeatedly remind yourself that heritability is defined by the variation in a trait and not by the trait itself, you will avoid falling into many pitfalls with your understanding of the term.

The Theoretical Definition of Heritability

Imagine that you take a black-and-white photograph of people you know and you “score” the darkness of their hair with a single value. The lightest-haired people would receive a zero and the darkest-haired people would receive a 100. Everyone else would receive values between these. You could describe the vari-

ation among individuals by calculating the **variance**, a common statistic that you are likely to have calculated in your science, math, or statistics courses. This statistic is (approximately) the average squared deviation from the mean, and we calculate it to measure the amount of variation in a collection of observations. For a sample taken from a population, variance (abbreviated V in this exercise) is calculated as

$$V = \frac{\sum (X_i - \bar{X})^2}{N - 1} \quad \text{Equation 1}$$

N is used when the computations are for a population, and $N - 1$ is used when the computations are for a sample of the population.

For a set of observations, the variance is easily computed with a spreadsheet function. Individuals vary in their hair color for at least two different reasons. One is that they inherited different kinds of genes for hair color, and the other reason is that they've experienced different environments. For example, hair color may depend on a chemical environment (a hair dye or bleach), or on time spent (or not spent) exposed to the sun. Theoretically, the variance in hair color (abbreviated V_p ; the "p" subscript comes from term "phenotype") can be divided into the variance that is due to genetic differences among individuals (V_g) and the variance due to differences among the environments of the individuals (V_e). Thus,

$$V_p = V_g + V_e \quad \text{Equation 2}$$

Heritability (abbreviated here as h^2) in a strict genetic sense is the proportion of total phenotypic variance in a trait that is explained by genetic differences among individuals. Theoretically, heritability can vary between 0 and 1.

$$h^2 = V_g / V_p \quad \text{Equation 3}$$

Let us look more closely at the V_g and V_e components of total variation. How do we determine the deviations from which these variance components are calculated? If you could take the mean hair color of the population and then ask how much a *particular individual* differs from that *population* mean due to particular alleles it has, and then how much that individual differed from the population mean due to its environment, you could express these deviations with quantities called G and E , respectively, for each individual in the population (Hartl 2000). G represents a deviation of that individual's phenotype from the population mean (μ) due to the particular genotype that individual has, and E represents the deviation of that individual's phenotype from the population mean that is due the environment in which the individual was raised. Once you had a G and E for every individual, the variance in the G and E are the phenotypic variance due to environmental and genotypic effects, respectively. The variance in G would be calculated as

$$V_g = \sum \frac{G^2}{N}$$

and the variance in E would be calculated as

$$V_e = \sum \frac{E^2}{N}$$

Note that capital letters G and E are used for individuals. Provided that individuals were randomly occurring in different environments, $V_g + V_e$ would equal V_p as in Equation 2. Furthermore, you can now define the phenotype of each *individual* in a population in a particular environment (Equation 4). In this equation, the P stands for the phenotype of the particular individual. In theory, all the G 's in the population should add to zero, and likewise all the E 's should add to zero. Notice that if you took the variance of each variable in the equation below, you would recreate Equation 2 because the variance in μ is zero.

$$P = \mu + G + E \quad \text{Equation 4}$$

One of the advantages of using modeling is that it can allow you to investigate a process that is not directly measurable in reality. In this exercise, you will construct a

population and define the G 's and E 's, two variables that can not be directly measured in real life, so that you can investigate many aspects of the definition of heritability that are virtually impossible to investigate any other way.

Types of Genetic Variation

Before reviewing some of the practical methods of measuring heritability, it is useful to briefly discuss what types of genetic variation exist. The V_g that you have just reviewed above can also be partitioned into two parts: the phenotypic variances owing to additive genotypic effects (V_a) and the phenotypic variances owing to non-additive genotypic effects (V_{na}). Thus,

$$V_g = V_a + V_{na} \quad \text{Equation 5}$$

In the exercise to follow, we will assume that $V_{na} = 0$. We will do this by constructing individuals with genotypes for two genes (A and B). For these genes, there will be only two alleles (a "1" allele and a "2" allele, each with a frequency of 0.5). Each allele will have a given affect on the phenotype of the individual regardless of what other allele occurs at that gene and regardless of what alleles occur at other genes. In other words, an A_1 allele will always be worth "+1" units from the mean in terms of your phenotype, an A_2 will be worth "-1"; a B_1 will be worth "+1" and a B_2 will be worth "-1". Thus an individual who is $A_1A_2B_2B_2$ will differ from the mean population phenotype by -2 units because the deviation of this individual's phenotype from the mean is $1 - 1 - 1 - 1 = -2$. In real life, the A_1 and A_2 alleles might interact—for example, A_2 might be dominant over A_1 (in which case the A_1 allele would be worth nothing in the presence of A_2). Likewise, it is not uncommon for **epistasis** to occur, meaning that the effect of an allele at the B gene depends on what alleles are at the A gene.

Thus, in the scientific literature, there are two types of heritability: **broad-sense heritability** (V_g/V_p where V_g includes the nonadditive component) and **narrow-sense heritability** (V_a/V_p where the numerator is only the additive component of genetic variance). In this exercise, all V_g is additive, so the broad- and narrow-sense heritabilities are the same. Narrow-sense heritability is a more useful measure of heritability as it is the variance in a population that will respond predictably to selection. In the next exercise on quantitative genetics, you will see how heritability is related to a response to selection.

Practical Methods of Estimating Heritability

How does one go about estimating heritability if you cannot measure V_g and V_e directly? Probably the most conceptually simple way is to compare offspring to their parents. The more closely the offspring's phenotype is predicted by their parents' appearances, the more the variation among individuals in a population is due to genetic variation. Specifically, you can measure the trait in an offspring and graph it against the mean of the trait in the two parents (the **midparent trait value**; Figure 1). The slope

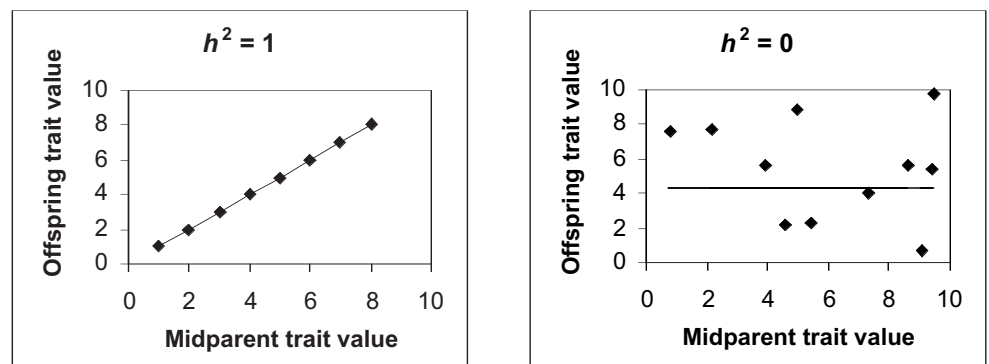


Figure 1 Parent-offspring regressions showing high (left) and low (right) heritability.

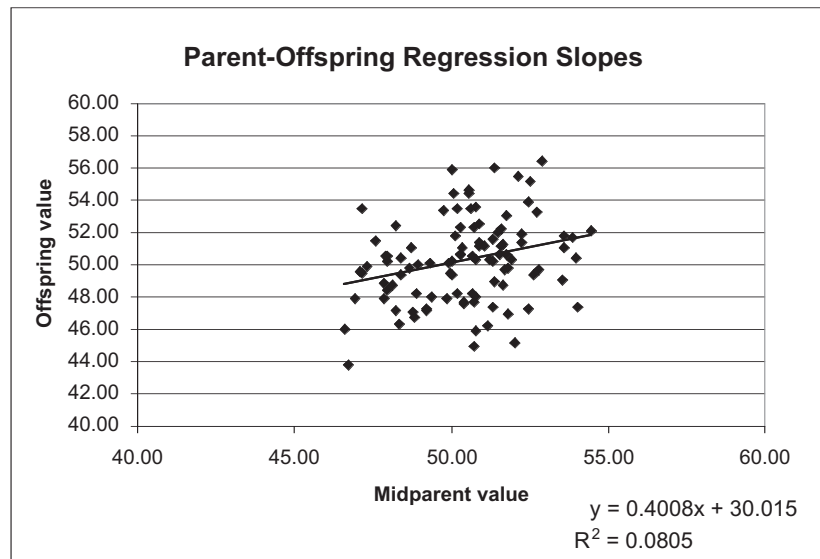


Figure 2 A parent-offspring regression in which heritability is somewhere between 0 and 1. The graph illustrates the typical scatter that you might find around a regression line.

of that plot of offspring values against midparent values is exactly narrow-sense heritability. In this exercise you will see that the slope really does accurately estimate the heritability that you can also calculate as V_g/V_p , if you know V_g .

When an offspring's trait is perfectly matched to the average of its two parents, $h^2 = 1$ (Figure 1, left). Small parents will have small offspring, and large parents will have large offspring. The slope of the line is 1, and $h^2 = 1$. When an offspring's trait cannot be predicted by the traits of its parents, $h^2 = 0$ (Figure 1, right). Parents of any size can have offspring of any size. In this case, the slope of the regression line is 0, and $h^2 = 0$.

In many cases, the parent-offspring graph for a given trait might look like Figure 2. 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. This suggests that h^2 would fall between 0 and 1.

There are other ways to measure heritability that we will not explore in this exercise. One commonly used method in human studies is to investigate twins. This method is based on the idea that monozygotic (identical) twins are more similar genetically than dizygotic (non-identical) twins. Other methods of estimating heritability involve estimating V_g and V_e through carefully planned breeding experiments (Falconer 1989). Finally, **realized heritability** (the degree to which a trait responds to selection in a population) can be estimated through a selection experiment. You will investigate this method in the "Quantitative Genetics" exercise that follows.

Take-Home Messages about Heritability

It is easy to get mired in the details of heritability and forget the big picture. If you recall, we began this exercise by emphasizing that heritability in a scientific sense is defined by the *variation* among individuals. This fact has two important consequences:

- Variation is a *population level trait* and is undefined at the level of an individual.
- Heritability is *not fixed*. It depends on the genetic variation in a population and the environment in which the population occurs. In other words, a population with exactly the same genetic composition as another population can have a different heritability if the two populations are in different environments.

Likewise, if the genetic composition of a population changes, even if the environment stays the same, estimates of heritability for that population will also change.

Let us return for a moment to the hair color example. Suppose cloning had advanced to the point that we could clone all the people you knew and split them into two groups. If we prevent the clones in one group from going out in the sun or using any hair dyes or bleaches, we might be able to eliminate most of variation among individuals in hair color that is due to environment (i.e., we could reduce V_e). If we allow the clones in the other group to go out in the sun and color their hair as they please, the variation in hair color due to environment will be greater, and heritability will be lower. To reiterate, even though the two populations would be identical genetically, the heritability would be different! Perhaps you can begin to see why heritability in a strict scientific sense has some nuances that make it quite different from the way we use the term in everyday conversation.

PROCEDURES

In this exercise, you will explore the theoretical definition of heritability. At the same time you will see that the practical method of constructing a regression of offspring against midparent values can also be used to estimate heritability. Two consequences of the theoretical definition of heritability (that heritability is a population level trait, and that it depends on both the genetic composition and environment of the population) will also be illustrated.

As always, save your work frequently to disk.

INSTRUCTIONS

A. Set up the population parameters.

1. Open a new spreadsheet as shown in Figure 3. Enter the values shown in cells B6–E6.

ANNOTATION

	A	B	C	D	E
1	Heritability				
2					
3	Model inputs				
4					
5	Genotype	A1	A2	B1	B2
6	G	1	-1	1	-1
7	Freq.	0.5	0.5	0.5	0.5
8					
9					Population traits
10				Parents	Offspring
11	Average phenotype =			50.00	50.00
12	Environmental heterogeneity =			0.01	0.01

Figure 3

We will assume that genes at two loci control the trait, the A locus and the B locus. Thus, we are dealing with a **polygenic trait**. We will also assume that each locus has just two alleles, A_1 and A_2 , and B_1 and B_2 . In the simplest case, each allele makes a contribution to

2. Enter 0.5 in cells B7–E7.

3. Enter 50 in cells D11–E11.

4. Enter 0.01 in cells D12–E12.

5. Save your work.

B. Set up the parental population.

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

2. Generate a linear series from 1 to 1000 in cells A19–A1018.

3. In cells B19–B1018, enter a formula to generate a genotype for parent 1 based on the allele frequencies in cells B7–E7.

the expressed trait. For example, if an individual inherits an A_1 or B_1 allele from its parents, it “inherits” a +1 unit contribution in the trait size. If it inherits an A_2 or B_2 allele from its parents, it “inherits” –1 units in the trait size. Thus, $A_1A_1B_1B_1$ individuals will have a +4 phenotype, $A_2A_2B_2B_2$ genotypes will have a –4 phenotype. Because $A_1A_2B_1B_2$ (heterozygotes) will have a phenotype of 0, they are the “standard” upon which other genotypes are compared. Note that since two loci contribute to the trait size, the population will tend to exhibit **continuous variation** in trait size, ranging between –4 and +4 units.

Cells B7–E7 give the frequencies of each allele. Remember that the frequencies must add to 1. You will be able to change these frequencies later in the exercise. You may wish to enter the formula =1-B7 in cell C7 and =1-D7 in cell E7.

This represents the average phenotype of the parental population. In our example, the parents are currently located in an environment and have genotypes that confer, on average, 50 units to trait size (cell D11).

Cells D12–E12 set how variable the environmental conditions are for the parental and offspring populations, respectively. Each individual will experience its own set of environmental conditions that will cause its phenotype to deviate from the population’s average phenotype, μ . In this model, a very low score (standard deviation) such as 0.01 suggests that the deviation from the mean phenotype due to the environment is very low—in other words, most individuals occupy the same kind of environment. High numbers, such as 10 or greater, suggest that individuals experience dramatically different environments; some will be located in low-quality environments, some in high-quality environments, and some will be found in an “average” environment. If our environmental conditions can be described with a normal distribution, and cell D12 is set to 0.1, then approximately 68% of the adults in the population experience environments that alter their phenotypes by 0.01 units, and 95% of the individuals will experience environments that alter their phenotypes by 0.02 units (± 2 standard deviations) from the population mean.

Now we will generate genotypes and phenotypes for a population of individuals (parents) who will then mate and produce offspring. Columns B–E will focus on the first parent, and columns F–I will focus on the second parent of each pair.

	A	B	C	D	E	F	G	H	I	J
16	PARENTAL POPULATION									
17	Individual	Genotype parent 1	G parent 1	E parent 1	Phenotype parent 1	Genotype parent 2	G parent 2	E parent 2	Phenotype parent 2	Midparent value
18										

Figure 4

- Enter 1 in cell A19.
- Enter =1+A19 in cell A20. Copy the formula down to cell A1018.

In cell B19, enter the formula =IF(RAND()<\$B\$7,"A1","A2")&IF(RAND()<\$B\$7,"A1","A2")&IF(RAND()<\$D\$7,"B1","B2")&IF(RAND()<\$D\$7,"B1","B2"). Copy the formula down to cell B1018. This formula follows the nested formula used in the Hardy-Weinberg exercise. It uses the & function to join the results of 4 separate IF functions together, because each individual requires four alleles (two A alleles and two B alleles) to make up its geno-

4. In cells C19–C1018, use a **LOOKUP** formula to generate a trait size for individual 1, based on individual 1's genotype (cell B19) and the contribution of each allele to trait size (cells B6–E6).

5. In cells D19–D1018, enter a **NORMINV** function to obtain the deviation in trait size for individual 1 as determined by individual 1's environment.

type. Each **IF** function draws a random number between 0 and 1 (the **RAND()** portion). For the *A* locus, if the random number is less than the frequency of the A_1 allele given in cell B7, the individual gets an A_1 allele; otherwise it gets an A_2 allele.

Enter the formula **=LOOKUP(MID(B19,1,2),\$B\$5:\$E\$5,\$B\$6:\$E\$6)+LOOKUP(MID(B19,3,2),\$B\$5:\$E\$5,\$B\$6:\$E\$6)+LOOKUP(MID(B19,5,2),\$B\$5:\$E\$5,\$B\$6:\$E\$6)+LOOKUP(MID(B19,7,2),\$B\$5:\$E\$5,\$B\$6:\$E\$6)** in cell C19. Copy the formula down to cell C1018.

This long formula is really quite simple; it is just four **LOOKUP** equations added together. The first part of the formula, **=LOOKUP(MID(B19,1,2),\$B\$5:\$E\$5,\$B\$6:\$E\$6)**, is a nested function because within the **LOOKUP** function is the **MID** function. The **LOOKUP** function looks up the value given by the function **MID(B19,1,2)**. This function examines the first *A* allele for individual 1, which will be either A_1 or A_2 . It examines the text in cell B19 (individual 1's genotype), and starting with the first character, returns two characters from the text given in cell B19. The result will be either A_1 or A_2 . The program then returns to the lookup function, finds this value in the range of cells B5–E5, and returns the number associated with the appropriate value in cells B6–E6. When this procedure is done for each of the alleles in individual 1's genotype, and the results are added together, it generates the genetic contribution to trait size.

Double-check your results. You should be able to examine a genotype and make sure that the function is generating the proper trait size. Technically, this computation provides the contribution to the phenotype for individuals, rather than the *deviation* of the genotype from the population mean phenotype, which is the correct computation of *G*. Since p and $q = 0.5$ for both loci, the average trait should in fact be 0, so the *G*'s represent deviations from this mean and also the phenotypic contribution.

Enter the formula **=NORMINV(RAND(),0,\$D\$12)** in cell D19. Copy the formula down to cell D1018.

Remember that the **NORMINV** function draws a random cumulative probability from a distribution whose mean and standard deviation are specified, and then converts that probability to an actual number from the distribution. Here we are interested in how much individual 1 deviates from the average phenotype because of the environment in which it lives, so the mean of 0 and the standard deviation from cell D12 is used. The result shows, generally speaking, what kind of environment each individual is located in. For example, Figure 5 shows that individual 1 has a genotype of $A_2A_2B_2B_2$ and so the genetic contribution to a trait is -4 units (it is 4 units smaller than the heterozygous "standard" in terms of genetic trait size). But this individual is located in an environment that is somewhat better in quality than average (deviation = 0.01 in cell D19). Its phenotype (computed in the next step) will be the genetic trait, plus the environmental deviation, plus the average phenotype of the population. In contrast, individual 4 is 2 units larger than an $A_1A_2B_1B_2$ heterozygote, but it is located in an average environment (0.00), so the deviation in its phenotype is not due to the environment.

	A	B	C	D	E	F
17	Individual	Genotype parent 1	<i>G</i> parent 1	<i>E</i> parent 1	Phenotype parent 1	Genotype parent 2
18						
19	1	A2A2B2B2	-4	0.01	46.01	A1A1B2B2
20	2	A2A2B2B1	-2	0.02	48.02	A2A1B2B2
21	3	A1A2B2B1	0	-0.01	49.99	A1A1B2B2
22	4	A2A1B1B1	2	0.00	52.00	A2A1B2B1

Figure 5

6. Enter a formula in cells E19–E1018 to generate the phenotype for individual 1 (parent 1).

7. Enter formulae in cells F19–I19 to generate *G*, *E*, and *P* (steps 3–6) for the *second* parent. Copy your formulae down to row 1018.

8. In cells J19–J1018, enter a formula to compute the average phenotype for parent 1 and parent 2 (the **midparent value**).

9. Save your work.

C. Generate offspring.

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

2. In cells K19–K1018, enter formulae to randomly obtain an *A* and a *B* allele from each parent to generate a zygote.

3. Enter formulae in cells L19–N19 to generate *G*, *E*, and *P* for offspring 1. Copy your formula down to row 1018. Be sure to reference cells E11–E12 in your formulae.

Enter the formula = $\$D\$11+D19+C19$ in cell E19. Copy the formula down to cell E1018. This formula is the spreadsheet version of the Equation 4, $P = u + G + E$.

The formulae are the same except that cell references should refer to columns F, G, H, and I. We entered the formulae

- F19 =IF(RAND()<\$B\$7,"A1","A2")&IF(RAND()<\$B\$7,"A1","A2")&IF(RAND()<\$D\$7,"B1","B2")&IF(RAND()<\$D\$7,"B1","B2")
- G19 =LOOKUP(MID(F19,1,2),\$B\$5:\$E\$5,\$B\$6:\$E\$6)+LOOKUP(MID(F19,3,2),\$B\$5:\$E\$5,\$B\$6:\$E\$6)+LOOKUP(MID(F19,5,2),\$B\$5:\$E\$5,\$B\$6:\$E\$6)+LOOKUP(MID(F19,7,2),\$B\$5:\$E\$5,\$B\$6:\$E\$6)
- H19 =NORMINV(RAND(),0,\$D\$12)
- I19 = $\$D\$11+H19+G19$

Enter the formula =AVERAGE(E19,I19) in cell J19. Copy the formula down to J1018. Review your entries to this point to make sure you fully comprehend the model thus far.

	K	L	M	N
16	OFFSPRING POPULATION			
17	Genotype	G	E	P
18	offspring	offspring	offspring	offspring

Figure 6

Enter the formula =IF(RAND()<0.5,MID(B19,1,2),MID(B19,3,2))&IF(RAND()<0.5,MID(F19,1,2),MID(F19,3,2))&IF(RAND()<0.5,MID(B19,5,2),MID(B19,7,2))&IF(RAND()<0.5,MID(F19,5,2),MID(F19,7,2)) in cell K19. Copy the formula down to cell K1018.

With this formula, we simulate gamete formation and independent assortment so that each parent contributes a single *A* allele and a single *B* allele. The alleles from both parents are then joined with the & function to specify the offspring’s genotype. The first portion of the formula, =IF(RAND()<0.5,MID(B19,1,2),MID(B19,3,2)) , specifies the *A* allele for parent 1. If a random number is less than 0.5, parent 1 will contribute the first *A* allele listed in its genotype (given by the first and second characters in cell B19). Otherwise, parent 1 will contribute the second *A* allele listed in its genotype (given by the third and fourth characters in cell B19). The second IF function concentrates on the *A* allele for parent 2. The third and fourth IF functions concentrate on the *B* allele contributions from parents 1 and 2, respectively.

Double-check your results:

- L19 =LOOKUP(MID(K19,1,2),\$B\$5:\$E\$5,\$B\$6:\$E\$6)+LOOKUP(MID(K19,3,2),\$B\$5:\$E\$5,\$B\$6:\$E\$6)+LOOKUP(MID(K19,5,2),\$B\$5:\$E\$5,\$B\$6:\$E\$6)+LOOKUP(MID(K19,7,2),\$B\$5:\$E\$5,\$B\$6:\$E\$6)
- M19 =NORMINV(RAND(),0,\$E\$12)
- N19 = $\$E\$11+M19+L19$

4. Save your work.

D. Obtain frequencies and make graphs.

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

	P	Q	R
17	Frequency		
18	Bins	Parents	Offspring
19	40		
20	41		
21	42		
22	43		
23	44		
24	45		
25	46		
26	47		
27	48		
28	49		
29	50		
30	51		
31	52		
32	53		
33	54		
34	55		
35	56		
36	57		
37	58		
38	59		
39	60		

Figure 7

2. In cells Q19–Q39, use the **FREQUENCY** function to generate frequencies of average parent phenotypes.

3. In cells R19–R39, use the **FREQUENCY** function to generate frequencies of average offspring phenotypes.

4. Make a frequency histogram of midparent and offspring phenotypes.

Remember that the frequency function is an array function, so must be entered differently than a standard function. (Refer to Exercise 2 for information on how to use array functions.) This function computes the frequency of the average parent phenotype (cells J19–J1018) and uses cells P19–P39 as bins. When you are finished, your formula in cells Q19–Q39 should read **{=FREQUENCY(J19:J1018,P19:P39)}**.

For offspring, the formula in cell R19–R39 should read **{=FREQUENCY(N19:N1018,P19:P39)}**.

Use the column graph option and label your axes fully. Your graph should resemble Figure 8.

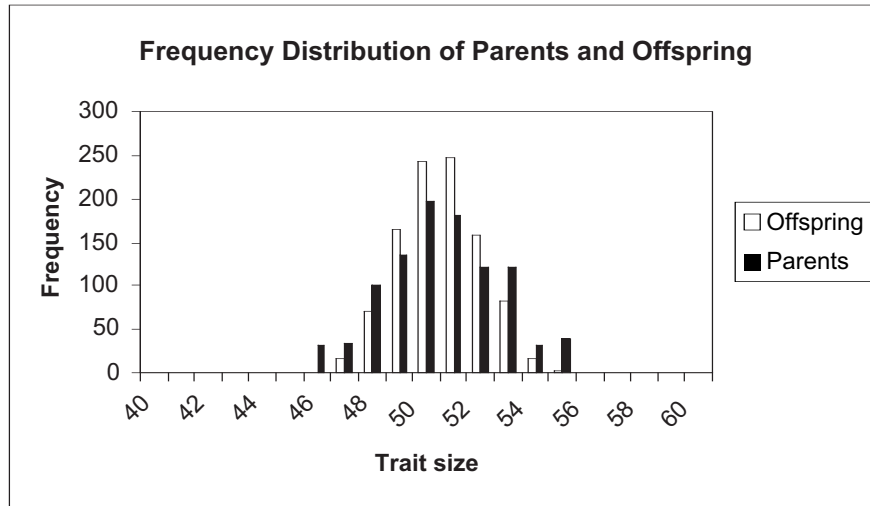


Figure 8

5. Graph the midparent versus the offspring trait size. Use the scattergraph option and add the regression equation to the graph. Adjust your axes so that the each axis ranges from 40–60 units in trait size.

Your graph should resemble Figure 9. To add the trendline, select the Chart Menu, then go to Chart | Add Trendline. Select the Linear option, then click on the Options tab. Select Display equation on the chart.

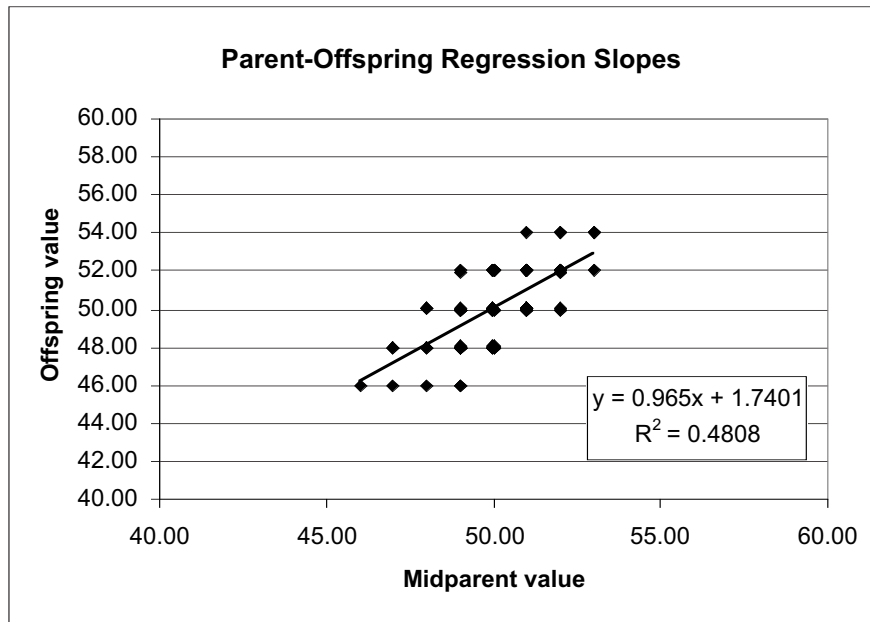


Figure 9

6. Save your work.

E. Compute heritability statistics.

The heritability statistics are based on offspring traits, as well as on parent-offspring regressions.

1. Set up new column headings as shown in Figure 10.

	G	H	I
3	Model outputs		
4			
5	Offspring	V_e	
6	Variance	V_g	
7	Values	$V_e + V_g$	
8		V_p	
9	Heritability	V_g/V_p	
10		Slope	
11			

Figure 10

2. In cell I5, use the **VAR** function to compute the variance in offspring's environmental conditions.

Enter the formula `=VAR(M19:M1018)` in cell I5.

3. In cell I6, use the **VAR** function to compute the variance in offspring's genetic traits.

Enter the formula `=VAR(L19:L1018)` in cell I6.

4. In cell I7, add $V_e + V_g$.

Enter the formula `=I6+I5` in cell I7.

5. In cell H8, use the **VAR** function to compute the total phenotypic variation in offspring.

Enter the formula `=VAR(N19:N1018)` in cell H8.

6. In cell I9, compute heritability as V_g/V_p .

Enter the formula `=I6/I8` in cell I9.

7. In cell I10, compute heritability as the slope of the parent-offspring regression.

Enter the formula `=SLOPE(N19:N1018,J19:J1018)` in cell I10.

8. Save your work.

QUESTIONS

1. Why do you suppose that the slope is sometimes not exactly equal to V_g/V_p ?
2. How does the mean affect heritability? Using the initial conditions you entered upon setting up the spreadsheet model (top of next page) hit the F9 key several times to examine the heritability. Your heritability measures as shown in cells I9 and I10 should be very close to 1. Now, change the mean of the parental and offspring population to 10 (change cells D11 and E11 both to 10). Hit the F9 key several more times. Leave cell D11 as 10 but change cell E11 to 50. Again hit the F9 key and observe the effect on the heritability estimates. You may want to examine the parent-offspring regression as well.

	A	B	C	D	E
3	Model inputs				
4					
5	Genotype	A1	A2	B1	B2
6	G	1	-1	1	-1
7	Freq.	0.5	0.5	0.5	0.5
8					
9				Population traits	
10				Parents	Offspring
11	Average phenotype =			50.00	50.00
12	Environmental heterogeneity =			0.01	0.01

3. How does environmental variation affect heritability? Return cells D11 and E11 to 50. Hit the F9 key five times, and fill in the first column of the table below. Repeat this but this time change *both* cells D12 and E12 to 1, then to 5 and then to 20. Observe changes in cells I9 and I10. How do the graphs change? How do the V_e and V_g change? What can you conclude about the effect of the environment on estimates of heritability? Is heritability really constant for a population with a specific genetic composition? What does this exercise suggest to you about studies in which people attempt to make conclusions about heritability of traits in a natural/wild population, but they measure heritability in a greenhouse or growth chamber setting? What happens to the slope if the parental population has a different environmental variation than the offspring?

Trial	Heritability when Environmental Variation was 0.01	Heritability when Environmental Variation was 1	Heritability when Environmental Variation was 5	Heritability when Environmental Variation was 20
1				
2				
3				

4. How does heritability change if there is very little or no genetic variation in the population? Return the environmental heterogeneity to 0.01, and change the frequencies of the alleles so that they look like those below. Hit the F9 key several times to see how the heritability changes.

	A	B	C	D	E
3	Model inputs				
4					
5	Genotype	A1	A2	B1	B2
6	G	1	-1	1	-1
7	Freq.	0.001	0.999	0.001	0.999
8					
9				Population traits	
10				Parents	Offspring
11	Average phenotype =			50.00	50.00
12	Environmental heterogeneity =			1.00	1.00

5. What do you think might happen if we changed our model so that genotypes were no longer randomly assigned to different environments? (You do not need to try to change the model to do this, treat this instead as a thought question.)
6. Consider what might happen if there were effects of the maternal environment on the offspring (for example, if mothers in resource rich microhabitats bore larger babies). (You do not need to try to change the model to do this; treat this instead as a thought question.)

LITERATURE CITED

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