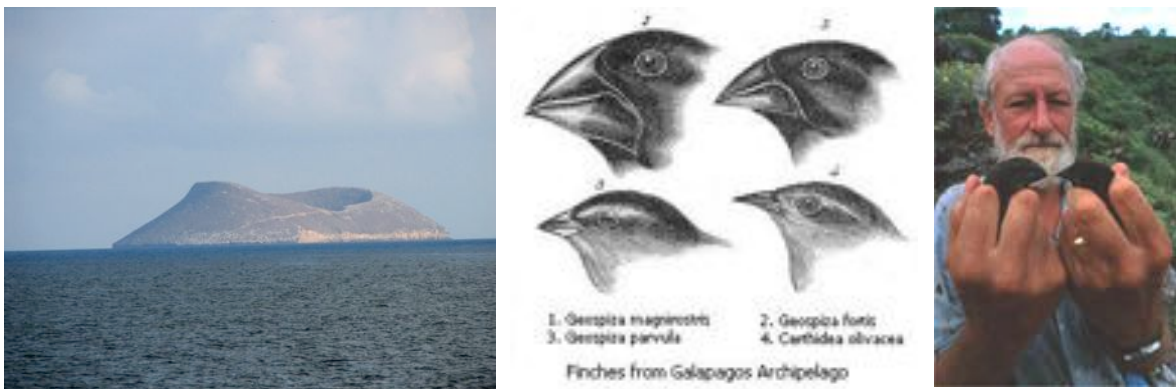


8 The Evolution of Phenotypes

Charles Darwin visited the Galapagos toward the end of his voyage on the HMS Beagle. By that time he was already beginning to think about the process of the formation of species but he had not yet developed his idea of natural selection. What he did notice on the islands, however, was that each island in the archipelago had a slightly different set of species. He looked at the various mockingbirds and found that although they were clearly in the same group the birds looked slightly different on each island and slightly different from the birds on the mainland. He also collected many species of finches and brought them back to London. There, when he showed them to other taxonomists he realized that he was looking at several different species. One feature in particular that set them apart was the size and shape of their bills. Some had large, deep, bills such as are used for cracking large seeds. Others had slender bills more suited for small seeds and insects. Although the finches eventually helped Darwin understand the patterns of species variation they were not even mentioned in the *Origin of Species*.¹

A century later the British evolutionary biologist David Lack visited the Galapagos and published a very influential book entitled “*Darwin’s Finches*”. In it he described the variation in beak size and shape and interpreted those differences as a result of natural selection for efficiency of feeding on different types of food. That research was then continued by Drs. Peter and Rosemary Grant who have provided the most complete description of the process of evolution of beak size.



Daphne Island in the Galapagos

Four species of Galapagos finches

Peter Grant with finches

Figure 8.1 photos: http://www.lpi.usra.edu/science/treiman/heatwithin/galapagos1/galapagos1_imgs/img_0196_sm.jpg;
<http://www.abc.net.au/nature/vampire/img/grantfinches.jpg>

¹ The closest Darwin comes to talking about the finches in the *Origin* is this single sentence in chapter 2 where he is talking about variation in nature: “Many years ago, when comparing, and seeing others compare, the birds from the separate islands of the Galapagos Archipelago, both one with another, and with those from the American mainland, I was much struck how entirely vague and arbitrary is the distinction between species and varieties.”.

The Galapagos Archipelago is a series of small volcanic islands in the Pacific Ocean off the coast of Ecuador. In his journal Darwin described them as ugly and lifeless. But those islands have a number of advantages that helped the Grants' in their study of evolution. The islands are small and the diversity of species on each island is low, making it a fairly simple system to understand. There are only a few suitable seed types on each island. The habitat is open so it is relatively easy to spot the birds, and the lack of predators makes the birds relatively tame. Through repeated captures and exhaustive searching on the small island they were able to tag each adult finch with unique leg bands and therefore follow the fate of each and every bird.

Their first big surprise came in 1977 when there was an especially severe drought on the islands. That year the rains did not arrive and there was a period of 20 months with almost no rain. Eventually the finches ate most of the seeds that were available. Different plants produce seeds of different sizes. The smaller seeds were the first to disappear until by the end of the drought all that were left were the larger, harder, *Tribulus* seeds. Those seeds were particularly difficult for finches with small bills to crack and as a result many of the birds with small beaks died of starvation.

Eventually the rains did return and the Grants continued to follow the population of finches as it recovered. The surviving large-beaked birds had offspring that also had larger-than-average beaks: the drought had caused the average beak size of birds on the island to increase. In other words they had seen evolution in action. In this chapter we'll explore the process of phenotypic evolution in more detail to understand how to predict the change in trait means as a result of natural selection.

8.1 A simple model of selection:

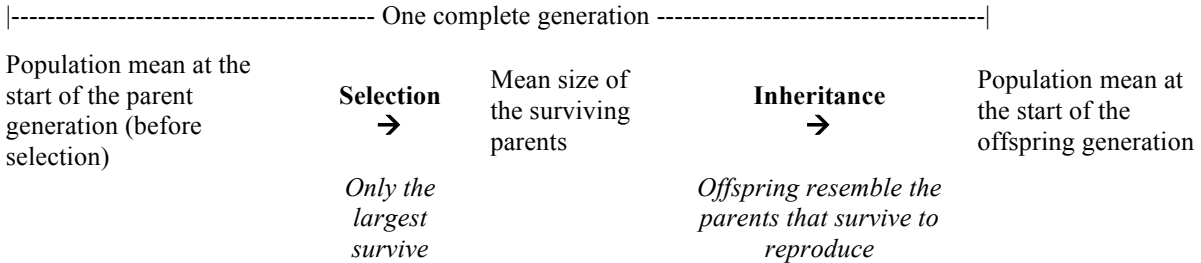
In previous chapters we examined the evolutionary dynamics of individual alleles at a single genetic locus. However many traits of ecological importance are determined by the joint effects of many genes acting together to produce a complex trait. Such traits might include body size and shape, behavior, longevity, etc. Indeed for those kinds of traits we usually have no idea what the underlying genes are. Nevertheless those complex traits are precisely the traits that are most often cited as the spectacular examples of natural selection and adaptation. It turns out that the theory of *quantitative genetics* allows us to study the evolution of phenotypes on the basis of statistical similarities among relatives, even without identifying the individual genes.

For example, Darwin and Wallace presented their theory of evolution by natural selection before scientists even knew that genes existed. All that is required is that traits are somehow inherited from parents to offspring. Even without knowing precisely why, they could look at the results from plant and animal breeders to see how traits can be modified from one generation to the next.

Darwin and Wallace's theory of evolution by natural selection can be summarized by four steps:

1. There is variation in some trait of interest.

2. Individuals with traits that best match their particular environment will on average leave more descendants than others, either because they have higher survival or higher reproductive output.
3. Some of that variation is heritable, so offspring tend to resemble their parents.
4. The result is that the population mean will shift toward the better-adapted phenotype.



In the case of the finches, the drought causes only some of the birds to survive to reproduction, so the average beak size of the parents is slightly larger than the average beak size at the beginning of the generation (because many of the birds with small beaks died). We call that difference in size between the actual parents and the original population the “**selection differential**”. Those parents then produce offspring. Normally the offspring will resemble their parents somewhat, but the resemblance is not perfect. Only to the extent that the beak size is caused by additive effects of alleles, will it can be inherited. Thus there will be a scaling coefficient (that we will call the “**heritability**”) that reflects the degree to which offspring resemble their parents. The overall change in phenotype as a result of selection will be a change due to the differential survival of parents times the degree to which that change is inherited. That change in population mean from one generation to the next is called the selection “**response**”. We’ll examine selection, heritability, and response in more detail in the following sections.

8.2 Selection:

The drought of 1977 caused massive mortality among the finches. The limited seed supply was soon depleted, leaving only the large seeds that were difficult for small-beaked birds to crack. The result was that birds with larger beaks survived at a higher rate than birds with small beaks. The average beak depth of survivors was 9.84 mm, compared to 9.31 mm in the general population before selection. Nevertheless some of the small birds did survive, and some of the birds with the very largest beaks did not.

Differential survival of individuals represents the action of natural selection favoring birds with large beaks, but that is not evolution. Evolution requires a change in the average beak size from one generation to the next. How will the increase in the number of large-beaked survivors show up in the offspring generation? For that we also need to consider the heritability of beak depth.

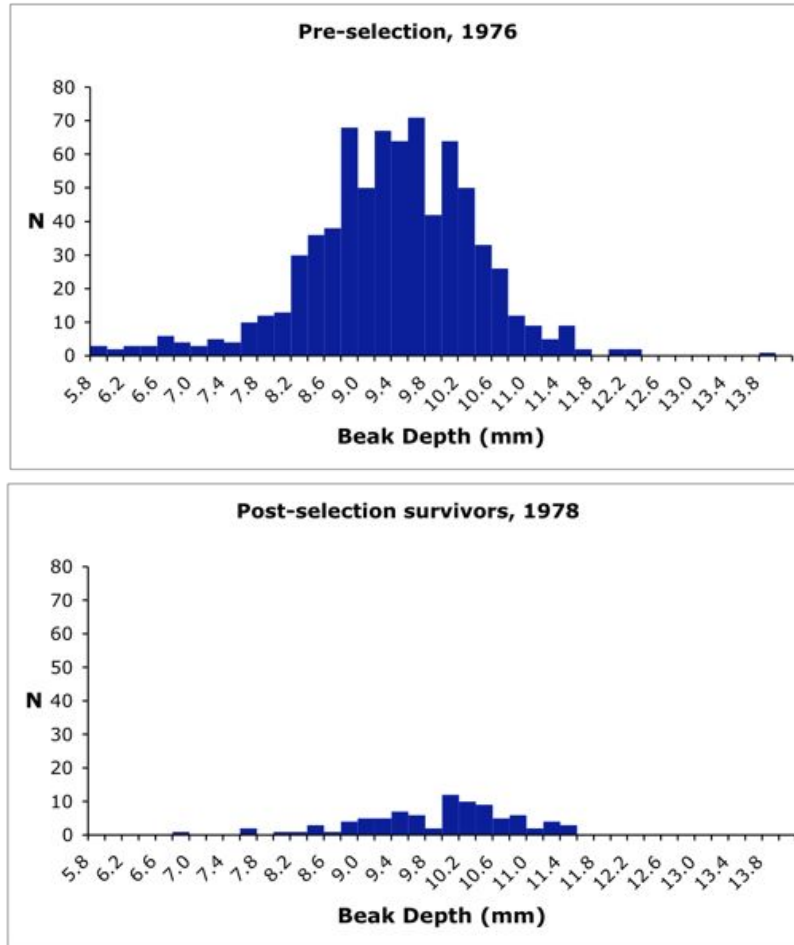


Figure 8.2 Distribution of beak sizes before and after the drought of 1977. Mortality during the drought dramatically decreased the overall number of birds, but it also shifted the phenotypic distribution to the right because most of the survivors had larger than average beaks. *Data from Grant 1986.*

8.3 Heritability

One of the other researchers on the finch team, graduate student Peter Boag, studied the inheritance of beak depth in Galapagos finches by looking at the relationship between parent beak depth and that of their offspring. He collected two sets of parent offspring data, once in 1976 and again in 1978. For both years he followed birds to determine which pairs belonged to which nests. Most of the parents had been previously captured so their beak depths were known. He then captured the offspring when they fledged and measured their beak depth. He calculated the "midparent" beak depth (the average beak depth of the two parents) and then compared that to beak depth of their offspring.

Here is what he found:

1976		1978	
"Midparent" Average beak depth of the two parents	Offspring beak depth	Midparent beak depth	Offspring beak depth
8.2	8.0	8.9	8.9
8.3	7.8	9.0	9.4
8.4	8.2	9.6	9.2
9.3	7.8	9.1	9.5
8.9	8.3	9.5	9.5
8.8	8.6	9.8	9.5
9.9	8.7	10.1	9.6
10.9	8.8	9.5	10.0
9.1	8.9	9.6	9.9
9.1	9.0	9.9	9.8
9.3	9.2	10.0	10.0
9.2	9.5	10.2	10.2
9.7	9.2	10.1	10.4
9.4	9.7	10.4	10.2
9.7	9.7	10.6	10.4
9.9	9.6	10.6	10.5
10.4	9.8	10.3	10.9
10.0	9.9		
10.2	10.1		
10.7	10.9		

Data from Boag 1983, Figure 1

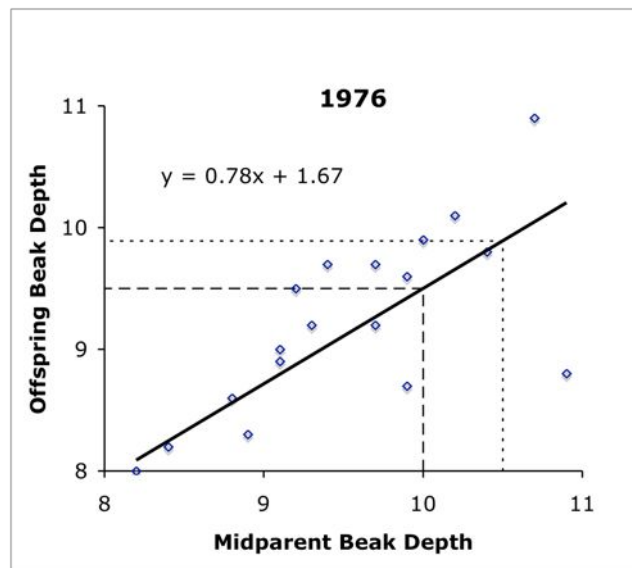


Figure 8.3 The heritability of beak depth in 1976. Data from Boag 1983. The “midparent” is the average of the two parents.

How can we use this information? The parent-offspring regression shows the way beak depth is (on average) inherited across generations. In particular, the heritability of a trait is the *slope* of the regression line of the midparent-offspring regression. It allows us to predict how a particular change in phenotype among the parents will be translated into a response among the offspring. For example, if the average beak depth of the parents increases from 10.0 mm to 10.5 mm, we can use the parent-offspring regression to see how much of a change we would expect in the offspring generation.

In 1976, the best-fit slope of offspring beak size on mid-parent beak size is 0.78. That means that the heritability of this trait is 0.78.

Notice that the slope of this line is less than 1.0. For each unit increase in the size of the parents there is a slightly lower gain in the offspring. Why? Because the parents beak depth is determined in part by genetics and in part by the environment. Only the genetic component of that variation can be inherited. Therefore the heritability will always be less than 1.0.

If the phenotypic variation is determined strictly by their environment then there will be no necessary relationship between the parent and offspring phenotype and the slope of the line (heritability) will be 0. That leads to a second definition of heritability: heritability is the proportion of the total phenotypic variance that is attributable to additive genetic variance.

Optional: Repeat the analysis for the 1978 parent offspring data by graphing the offspring vs. midparent beak sizes and finding the slope of the best-fit line.

What is the heritability for beak depth in 1978? _____

Are those data consistent with the heritability estimate from 1976? _____

8.4 Response to selection

Following the drought, the few surviving birds bred and the Grant's and their coworkers were there to measure the beak size of the offspring they produced. The average beak depth in the new generation of offspring was 9.7 mm. There was still a lot of variation in beak size, but on average, the size had increased. Beak size had evolved.

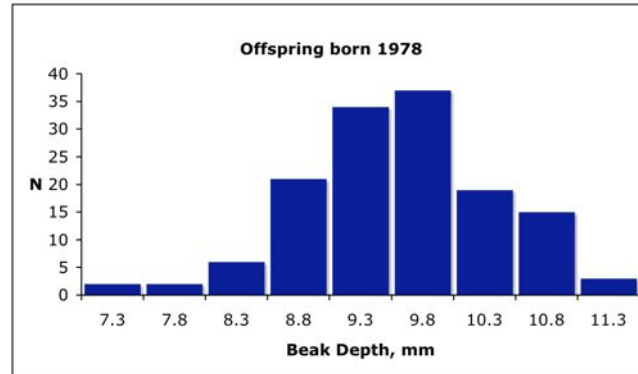


Figure 3. Evolutionary response, after the drought

8.5 The “breeders equation”:

The theoretical understanding of the evolution of polygenic traits was actually first worked out by plant and animal breeders trying to predict the yield increases for various breeding programs. They developed the “breeders equation” that still forms the basis of our understanding of quantitative trait evolution:

$$R = h^2 S \quad \text{eq. 8.1}$$

In words, that says that the response to selection (R) is equal to heritability (h^2) times the selection differential (S).

The selection differential (S) is just the difference between the mean of the population and the mean of the individuals that reproduce. If selection is weak, then the parents who actually breed will have a similar mean to the mean of the overall population. S will be small. If the parents are very different from the base population then the selection differential will be large (i.e. selection is strong).

The response to selection (R) is just the difference between the mean of the parents *before selection* and the mean of the offspring produced to *start* the next generation. Sometimes, we will use the variable z to indicate the value of a particular trait. In that case $R = \Delta \bar{z}$ or the *change* in the trait mean across generations.

Finally the heritability (h^2). is a scaling factor that translates the strength of selection into a realized response². As we’ll see below, the heritability can be defined by either the slope of the regression relating midparent to offspring, or by the ratio of additive genetic variance to total phenotypic variance.

² You may wonder why the symbol h^2 is used for the heritability. The practice dates back to Sewall Wright’s original derivation, where h was a ratio of standard deviations. Therefore, the ratio of variances (V_a/V_p) must be h^2 . When using breeders equation it is most useful to think of h^2 as a single symbol, not $h \cdot h$.

The breeder's equation (eq 8.1) is simple, but it is very powerful because it allows a quantitative prediction of the response to selection from a couple of easily measured parameters.

Use the breeder's equation and the definitions above to complete the following table: What is the selection differential? What is the predicted response? How does that compare to the observed response?

Average Beak Depth at start of 1976 (before selection)	9.31 mm
Beak Depth of survivors, who lived to breed in 1978	9.84 mm
Selection Differential	
Heritability	0.78
Predicted response to selection	
Predicted mean of the offspring born 1978	
Average Beak Depth of the offspring born in 1978	9.70 mm

8.6 More about the genetic basis of quantitative traits

Natural selection acts on the *variation* that is present in the population. The total phenotypic variance can be partitioned into a genetic plus an environmental component. In turn, the genetic variance is composed an additive genetic component (caused by the average effects of alleles) and a non-additive or dominance component, caused by particular combinations of alleles.

Total Phenotypic Variance (V_P)		
Genetic Variance		Environmental Variance
Additive Variance (V_A)	Dominance Variance (V_D)	V_E

If we wanted, we could also partition the environmental component into effects of the rearing environment, developmental defects, nutritional status, etc, but for now we will just leave it as is.

We can express the partitioning of total variance in symbols as $V_P = V_G + V_E$ or, we we subdivide the genetic component into additive and dominance variance then $V_P = V_A + V_D + V_E$.

Parents only pass a single allele on to their offspring, so only the additive or average effects of the alleles can be inherited. Effects due to particular combinations of alleles (dominance) are broken up each generation. Therefore the evolutionary response to selection will depend upon the magnitude of the additive component of genetic variance, symbolized V_A .

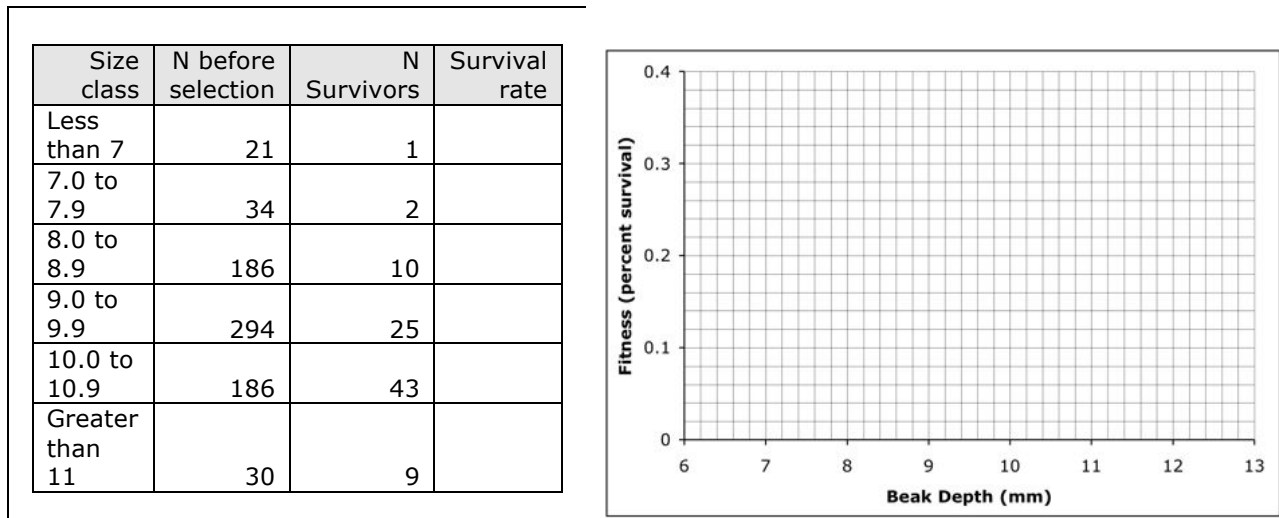
The ratio of additive genetic variance to total phenotypic variance is another way to define the heritability³.

$$h^2 = \frac{V_A}{V_P} \quad \text{eq 8.2}$$

Although we won't prove it here, that definition is equivalent to the definition based on the offspring-midparent regression.

8.7 More about selection

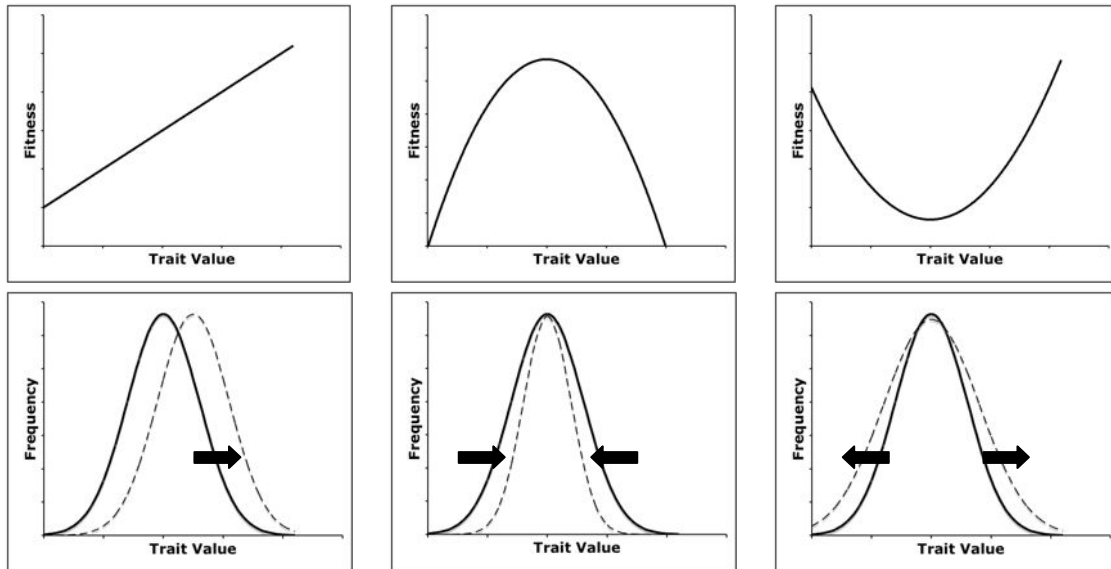
To see the pattern of survival more clearly, it helps to combine the data into larger size categories so some of the random variation is averaged out. What proportion of each size class survived the drought? Use those data to graph fitness (survival) vs. beak size.



That graph is called the "fitness function". Fitness functions describe the way fitness relates to a particular trait, in this case the relationship between survival during drought and beak depth. Fitness functions with positive slopes mean that selection favors an increase in the trait. Fitness functions with negative slopes mean that selection favors a decrease in the trait. Curved fitness functions can indicate stabilizing selection or disruptive selection as shown in Fig 8.4.

³ Although we won't derive it, this definition is mathematically equivalent to the offspring-midparent regression.

Figure 8.4. Fitness functions and their effects on phenotypes. The solid line shows the frequency distribution before selection and the dashed line is the distribution after selection.



Directional selection causes a change in the mean value of a trait.

Stabilizing selection causes a decrease in the variance of the trait, with no change in mean.

Disruptive selection causes an increase in the variance of the trait.

8.8 More about heritability.

When only one of the two parents is measured, the slope of the regression estimates only $\frac{1}{2}h^2$. (Intuitively, you can say that's because each parent contributes only half of the offspring's genes). Therefore you need to double the slope of the mother-offspring or father-offspring regression to obtain the heritability.

For example, Boag compared his midparent-offspring regression to the father-offspring and mother-offspring regressions. Notice how the regressions on single parents both have much lower slope than the midparent regression. What is the estimate of heritability for each of those regressions?

Beak depth	Midparent-Offspring	Father-Offspring	Mother Offspring
Regression slope	0.72	0.22	0.39
Heritability			

Why do you think the estimate of heritability using fathers is so much lower than the estimate using the mother-offspring regression?

One of the assumptions of using parent-offspring regressions to estimate the heritability is that the *only* source of resemblance is shared genes. In many organisms it is common to see "maternal effects". For example, well fed, females may lay large eggs, which produce large offspring. That produces a resemblance between mothers and offspring that is strictly environmental. That kind of environmental correlation is less common through males, who generally provide only sperm.

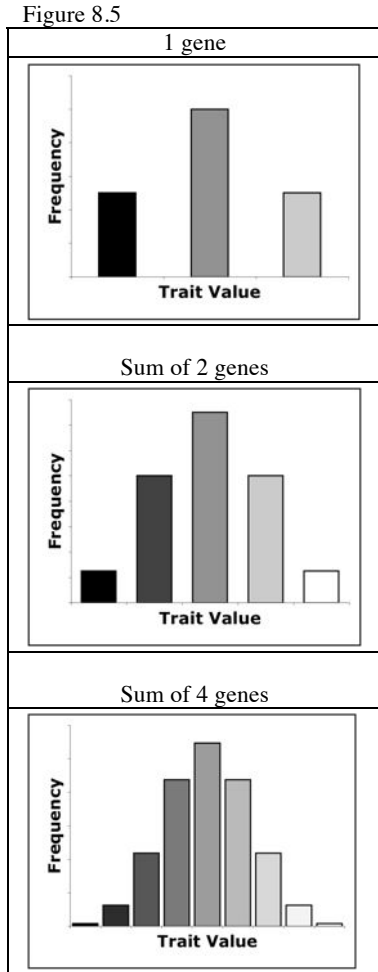
Second, the fathers at the nest aren't always the birds that actually sired the offspring. In *G. fortis* approximately 20% of the offspring are produced through extra-pair matings. DNA samples revealed that 44 of 223 offspring did not match their putative father's genotype and must have been sired by another male. If the non-genetic fathers are excluded from the father-offspring regression, then the slope increases to $b=0.36$.

8.8.1 Some common misconceptions about heritability:

- Heritability of zero does not mean the trait is not determined by genes. It means that the *variation* in the trait does not have a genetic basis. Some traits that are universal (e.g. presence of two eyes in humans) are still determined by our genes. However there is no variation in that trait so the heritability would be zero.
- Heritability applies only to a particular population and a particular environment.
- Two populations with the same genetic variance may have very different heritabilities if one is subject to more environmental variance than the other.

8.9 **EXTRA** (read this if you are interested): **The relationship between selection on single loci and the breeders equation:**

To understand the genetic basis of quantitative traits, it is important to think about the effect of a particular allele, not simply its presence or absence. A single locus can produce three discrete phenotypes, but as more and more loci contribute to a trait the phenotypic distribution comes closer and closer to a normal (bell shaped) distribution.



Any normal distribution can be described by the mean and variance. The breeder's equation uses those aggregate measures of the trait to predict the response to selection without explicitly following individual alleles. Nevertheless it is important to realize that at each of the underlying loci selection will change allele frequencies following exactly the same model that we used for other Mendelian loci.

Let's imagine that we are studying the size of some organism. To keep things simple, we will assume that size is controlled by a large number of independent genes, each with equal effect. We'll assume that there are two alleles, "big" (B) and "small" (b). The "big" allele at each locus adds 2 units of size and the "small" allele subtracts 2 units. We say that the "value" of this allele is $a=2$. Each individual has two alleles at this locus so the net effect on size for each locus will be the sum of the values of the two alleles: the net effect will be -4 if both copies are the "small" allele, 0 if the individual is heterozygous, and +4 for the other homozygote where there are two doses of the "big" allele.

Allelic values at one locus. In this case there is no dominance so the heterozygote is exactly intermediate between the two homozygotes.

Genotype	bb	Bb	BB
Value	-2a	0	+2a

Finally the overall trait value (in this case size) will be determined by the total dosage of "big" alleles summed over all loci.

At each locus the additive genetic variance will be

$$V_A = 2pqa^2 \tag{eq. 8.3}$$

What this equation makes clear is that the additive genetic variance depends on the allele frequencies (p and q) as well as the squared value of the alleles (a^2). If one of the alleles goes to fixation ($p=0$ or $q=0$) then there will be no genetic variation at this locus.

Why are we only concerned with the *additive* component of genetic variance?

Example: We'll continue to imagine that a particular locus has two alleles B and b. Each copy of the B allele increases the size of an organism by 2 mm (in other words the allelic effect is $a=2$) and there is no dominance. Large individuals have a fitness advantage, so allele B gradually increases to fixation. What happens to the genetic variance as B increases in frequency? Use equation 8.3 to complete the table:

Frequency of B allele	V_A
0.50	2.0
0.75	
0.95	
1.00	

This represents a general phenomenon that *directional selection acts to decrease the genetic variance* for a trait. After many generations of selection, if there is no new source of genetic variation by mutation, the additive variance will decline to zero and there will no longer be any response to selection. A corollary to this is that for traits that under strong selection, there should be little genetic variation remaining in the population.

The genetic variation in this figure is shown by the different distributions for the three genotypes. There is also an environmental contribution to the variance so there is variation around the mean of each genotype. The dotted line then shows the overall variation attributable to both the genetic variation at this locus and the environmental variation. When the allele frequency is 0.5 each of the three possible genotypes is abundant and there is a large genetic contribution to the variance. When the allele frequency increases to 0.95 then one genotype (the BB homozygote) dominates. The genetic variation is close to zero and the overall variance simply reflects the environmental component.

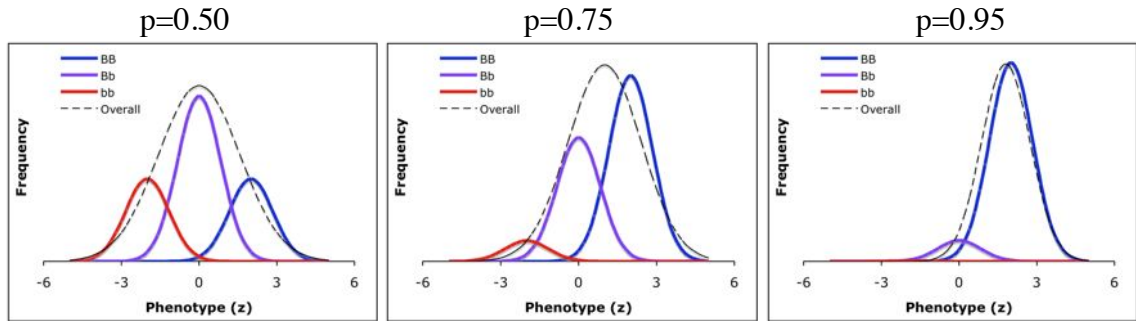


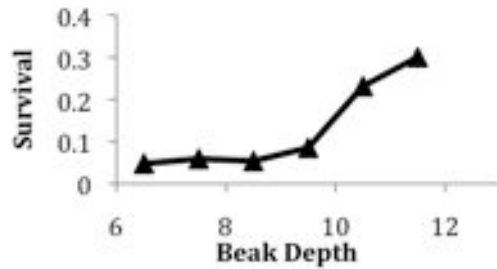
Figure 8.6. Allelic contribution to genetic variance. In this example the allele “b” has a phenotypic effect of -2 units and allele “B” has an effect of +2. As allele B goes to fixation the genetic variation contributed by this locus declines. Note that there is some variation in the phenotype of each of the three genotypes, because of environmental variation.

(parameters: $a=2$, $d=0$, $V_e=0.5$)

Answers:

p 6. The heritability for beak depth in 1978 is 0.80, which is very similar to the estimate from 1976.

p 8. $S=9.84-9.31=0.53$ $R=0.78*0.53=0.41$ Predicted offspring mean = $9.31+0.41=9.72$, which is very close to the observed mean of 9.7



p 10 Heritability estimates. Midparent-offspring $h^2=0.72$; Father-offspring $h^2=0.44$; Mother-offspring $h^2=0.78$

p 13. The additive component of variance is important because parents transmit only one allele to their offspring. Therefore only the average effects of alleles can be inherited, not the particular combinations of alleles.

p	V_A
0.50	2.0
0.75	1.5
0.95	0.38
1.00	0