

1 Piggy litters. The parental mean is 11 and the variance is 1.2. The offspring mean is 10.5 and the variance is 1.05. The selection differential S is $9.67 - 11 = -1.33$ and the response to selection R is $10.5 - 11 = -0.5$, so the heritability h^2 is $-0.5/-1.33 = 0.375$. This is narrow-sense heritability, so we can estimate the additive variance as $V_A = h^2 * V_P = 0.375 * 1.2 = 0.45$.

2 Sluggy fecundity. Please see "The Parable of the Slugs", on the other side of this sheet.

3 Mousy cholesterol. The response was $(2.01 - 2.15)/5 = -0.14/5 = -0.028$ mg/100 ml. The selection differential was -0.07 . So the realized heritability was $-0.028/-0.07 = 0.4$.

4 Tobacco leaves. The F_1 plants are genetically homogeneous, so their variance for leaf number (1.5) is a direct estimate of the environmental variance V_E . In the F_2 generation, the phenotypic variance (6.0) includes both genetic and environmental components, so we can estimate V_G as $6.0 - 1.5 = 4.5$ and the broad-sense heritability as $4.5/6.0 = 0.75$.

5 Flour beetle pupal weights. The heritability is $100/400 = 0.25$. The phenotypic standard deviation is the square root of $400 = 20$, so the selected parents are $2 * 20 = 40$ μg above the mean. The response to selection will therefore be $0.25 * 40 = 10$ μg , so the offspring mean will be $2000 + 10 = 2010$ μg .

6 Chicky yearly eggs. With a selection differential of 20 eggs per year and a heritability of 0.20, we will increase egg production by 4 eggs per generation. To get an increase of $220 - 180 = 40$, we will therefore need to select for $40/4 = 10$ generations.

7 Poppy flower size. A bimodal distribution could be caused by selection against plants with mid-sized flowers, but this seems unlikely here because you got a similar distribution when you raised plants from seed in the greenhouse, where there should be little if any selection.

Given this fact, the simplest hypothesis would seem to be that there is a locus with two alleles that make a very large difference to petal length. (For example, **AA** and **Aa** might make larger flowers, while **aa** makes smaller flowers.) Several or many other loci might have smaller effects on flower size, and of course there is likely to be some environmental variance as well. The result would be *two* overlapping normal distributions, one centered on the average flower size of **AA/Aa** genotypes, and one centered on the average flower size of **aa** individuals.

An alternative hypothesis would be that the large-flower mode and the small-flower mode arise from a *developmental switch* that sends individual plants (more or less at random) down one developmental pathway or another. In this case the modes would represent environmental variation, not genetic variation.

You could test these alternatives by breeding from the extreme lower and extreme upper tails of the distribution. On the major-locus hypothesis, the offspring would come out as almost pure lower-mode and pure upper-mode populations. But on the environmental-variation hypothesis, each set of offspring would include roughly equal numbers of lower-mode and upper-mode plants.

8 Eensy populations. Small populations tend to have less genetic variation than large ones, because drift is much stronger in small population, and variation is therefore lost at higher rates. If there is less genetic variation, there will tend to be less genetic variance (including *additive* genetic variance) for most quantitative traits. The environmental variance should be roughly as great in small populations as in large ones, however. So the total phenotypic variance will be less in small populations, but a larger fraction is likely to be environmental, resulting in lower heritability. At least that seems like the most straightforward argument. But to be contrary, you could argue that there will be less environmental variance in small populations because they will tend to have simpler (less complex, hence less variable) environments, hence just as much or even more heritability, despite lower levels of genetic variation.

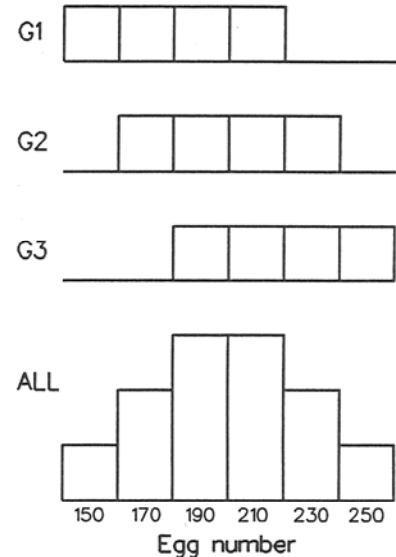
The Parable of the Slugs (Key to quantitative-genetics problem #2)

2 A population of asexually reproducing slugs shows genetic variance for fecundity (egg number, which translates directly into fitness) in a certain back yard in Seattle. There are, at the moment, three *equally frequent* genotypes in this population, with distributions of fecundity (lifetime egg number) as given in the table. These samples of four individuals are representative of the population as a whole. What is the mean fecundity in *this* generation? What will it be *next* generation? (*Hints:* You must find the heritability and the selection gradient or differential; there are *several* ways to find the heritability; for example, you could figure out the parent-offspring regression by noting that these slugs are *asexual*; what other approaches could you use?) What will the *equilibrium* fecundity be in this population? (Assume that there is no significant immigration or mutation for many generations.) At equilibrium, what is the additive genetic variance? The phenotypic variance?

Genotype	Fecundities
1	150, 170, 190, 210
2	170, 190, 210, 230
3	190, 210, 230, 250

This problem brings together most of the key ideas about selection on alleles at a single locus *and* about quantitative traits.

The trait is egg number (fecundity), which amounts to fitness. The three genotypes (1,2,3) vary in average egg number. Obviously, selection is going to increase the frequency of the fittest genotype (3). But there is also a lot of variation in egg number *within* genotypes, so not all of the variation is genetic. The graph at the right shows how egg number is distributed by genotype and overall within the population.



What are the genotype frequencies next generation? The *average* egg numbers of the three genotypes are 180, 200, and 220, respectively, and the genotypes are equally frequent, so the population *mean* fitness is 200. Thus the genotype frequencies next generation will be

$$p'_1 = p_1(\bar{W}_1/\bar{W}) = (0.333)(180/200) = 0.300$$

$$p'_2 = p_2(\bar{W}_2/\bar{W}) = (0.333)(200/200) = 0.333$$

$$p'_3 = p_3(\bar{W}_3/\bar{W}) = (0.333)(220/200) = 0.367$$

What's the mean fitness of these offspring? The genotype-specific means are unchanged, so $\bar{W}' = 0.300 \cdot 180 + 0.333 \cdot 200 + 0.367 \cdot 220 = 201.333$, an increase of 1.333 eggs, or 0.67%. This population-genetics approach is easy because we know the genotypes. It turns out that the quantitative-genetics approach is *just* as easy.

We can calculate the environmental variance directly as the variance of egg number *within* any one of the three genotypes, since they are all the same. (They deviate from their means by -30, -10, +10 and +30 eggs, so the squared deviations are 900, 100, 100 and 900; the average of these is $V_E = 500$.) The total phenotypic variance (for the population as a whole, as shown in the bottom distribution) is the average squared deviation of all twelve numbers in the table from the population mean of 200; this gives $V_P = 766.67$. So now we know $V_G = 766.67 - 500 = 266.67$ and the heritability $h^2 = 266.67/766.67 = 0.348$. (There's no sex here, so we can forget about dominance and epistatic interactions; it's as if the whole slug genome were just one giant haploid locus.)

But note that we can also calculate V_G *directly* as the variance of the *genotypic values* themselves, which are the average phenotypes of the three genotypes. (We can do this because the problem reveals the genotypes to us.) The variance of 180, 200 and 220 is the average of $(-20)^2$, 0^2 and 20^2 , which is $(400 + 0 + 400)/3 = 266.67$. *Yes!* $V_P = V_G + V_E$.

What's the selection gradient? The phenotypes *weighted* by relative fitness are $150 \cdot (150/200)$, $170 \cdot (170/200)$, and so on, up to $250 \cdot (250/200)$. Multiplying these by their frequencies (1/12, 2/12, etc.), we find that the average fecundity of the "selected" parents (*the average fecundity of the mother of an egg*) is 203.83. Thus $S = 203.83 - 200 = 3.83$. The predicted response to selection is $R = h^2 S = 0.348 \cdot 3.83 = 1.33$ eggs, just as we found by the first approach.

We could also calculate the heritability from the parent-offspring regression, as shown graphically on the right. *Average* offspring egg number is plotted against parental egg number. The regression slope is (of course!) 0.348.

Question. How will the heritability change as genotype 3 increases in frequency? How would it change if the environmental variance decreased?

