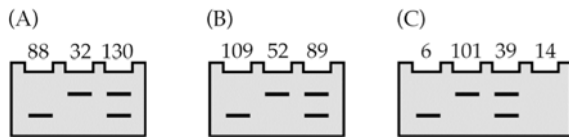


Chapter 2



2.1. Spitze (1993) reported the following numbers of genotypes at the *PGI* locus in his *Daphnia* population in Nothing Pond:

SS	11	$11/127 = 0.087$
SS-	55	$55/127 = 0.433$
S-S-	61	$61/127 = 0.480$
	127	1.000

a. What are the observed genotype and allele frequencies? See above and:

$$f(S) = p = \frac{(2 \times 11) + 55}{2 \times 127} = 0.30$$

These sum to one.

$$f(S-) = q = \frac{(2 \times 61) + 55}{2 \times 127} = 0.70$$

b. Given the observed allele frequencies, what are the genotypic frequencies expected under Hardy-Weinberg? Using a chi-square test, how well do the observed genotypic frequencies agree with the Hardy-Weinberg expectations?

$$p^2 = 0.09$$

$$2pq = 0.42$$

$$q^2 = 0.49$$

$$1.00$$

$$\chi^2 = \sum \frac{(O - E)^2}{E} = \frac{(11 - 11.43)^2}{11.43} + \frac{(55 - 53.34)^2}{53.34} + \frac{(61 - 62.23)^2}{62.23} = 0.09, 1 \text{ d.f.}, P = 0.77$$

Therefore, there is no evidence for deviation from Hardy-Weinberg frequencies, and thus no evidence for lack of random mating.

2.2 Calculate F for the *Daphnia PGI* locus in the Ojibway Pond (page 35; note that there are data for *PGM* in the text as well) and the Nothing Pond (problem 2.1 above) populations. What is a possible biological interpretation of these data? Explain your reasoning.

$$F_{NP} = \frac{0.42 - 0.433}{0.42} = -0.03$$

$$F_{OJ} = \frac{0.5 - 0.375}{0.5} = 0.25$$

The Nothing Pond population is in HWE and thus is likely to be random mating, but the Ojibway Pond population shows an excess of homozygotes suggesting inbreeding.

2.3 Gels A and B show banding patterns from RFLP markers in two related plant species.

a. Estimate allele and genotypic frequencies and test for HWE in each species.

For both species $p = 0.61$, $q = 0.39$.

	Species A			Species B		
	Observed	Frequency	Expected	Observed	Frequency	Expected
<i>FF</i>	88	0.352	93	109	0.436	93
<i>FS</i>	130	0.520	119	89	0.356	119
<i>SS</i>	32	0.128	38	52	0.208	38
Sum	250	1.000	250	250	1.000	250

Species A $\chi^2 = 2.23$, $P=0.15$. Species B $\chi^2 = 15.47$, $P < 0.0001$.

b. Estimate F for each species.

$$F_{SpA} = \frac{0.476 - 0.520}{0.476} = -0.09$$

$$F_{SpB} = \frac{0.476 - 0.356}{0.476} = 0.25$$

c. What is a possible biological interpretation of the data from parts a and b? Explain your reasoning.

Species A is close to HWE, so is likely close to random mating, whereas Species B is inbred. Species A may have adaptations to promote outcrossing such as self-incompatibility (see Chapter 3).

2.4 RAPD and AFLP markers have only two genotypes—presence or absence of a band. When a band is present, it can be homozygous or heterozygous. Therefore, only the band-absent (null) genotype can be scored definitively. In a study of a selfing plant (*Medicago truncatula*), Bonnin et al. (1996) reported band-presence at a frequency of 0.59 at their RAPD locus B6-600 in a population from Aude, France.

a. Assuming HWE, what are the frequencies of the two alleles and three genotypes?

Frequency of null homozygote (Q) = $1 - 0.59 = 0.41 = q^2$ assuming HWE.

So $q = \sqrt{0.41} = 0.64$. $p = 1 - 0.64 = 0.36$; $H = 2pq = 0.46$; $P = p^2 = 0.13$ ($P + H + Q = 1$).

b. Because this is a selfing plant, assuming HWE is not valid. Is your estimate of the frequency of the band-present allele an over- or underestimate? Explain your reasoning.

Our estimate of p , the frequency of the band present allele, is an underestimate because it is based on our estimate of q , which is an overestimate. Recall that there is an excess of homozygotes relative to HWE expectations with inbreeding, so that Q , the frequency of recessive homozygotes, is greater than q^2 , the expectation under HWE. Thus with inbreeding the actual q is less than our estimate of $\sqrt{0.41}$, meaning that the actual p is larger.

2.5 Gel C shows the banding patterns from two AFLP markers (the upper and lower sets of bands).

a. Estimate the frequency q of the null allele of each of the two AFLP markers assuming HWE.

Upper set of bands: Band-present frequency $P + H = (101 + 39)/160 = 0.875$, so frequency of band-absent $Q = 1 - 0.875 = 0.125$. Assuming HWE, $q = \sqrt{0.125} = 0.354$.

Lower bands: $P + H = 45/160 = 0.281$ so $Q = 0.719$ and $q = \sqrt{0.719} = 0.848$.

b. Estimate the percentage of *band-present* individuals (not the overall frequencies) that are heterozygous at each of the two markers. What biological principle does the difference between these two percentages illustrate?

Upper bands: $2pq/(p^2 + 2pq) = 0.523$

Lower bands: 0.918.

This illustrates that as the band-present allele becomes rarer, a greater proportion of them are heterozygotes at HWE.

Chapter 3

3.1. The fly *Eurosta solidaginis* forms galls (enlarged areas) on goldenrod plants within which the fly larvae feed and develop. A study of allozyme frequencies in 21 subpopulations of *E. solidaginis* on two different species of goldenrod distributed from Minnesota to Maine (Waring et al. 1990) produced the following estimates of F_{ST} :

Locus	F_{ST}	$N_e m$
<i>GAP-1</i>	0.10	2.25
<i>TPI-1</i>	0.11	2.02
<i>IDH-1</i>	0.02	12.25
<i>HBDH-1</i>	0.62	0.15
<i>GPD-1</i>	0.11	2.02
<i>PGM-1</i>	0.14	1.54

a. Calculate the expected number of migrants per generation for each locus. What is your interpretation of these data? Do you think differentiation at these loci is caused solely by a balance between migration and drift? Why or why not?

See table above for $N_e m$ values calculated using Equation 3.19. It appears that differentiation is likely to be due to a balance between migration and drift at all loci except *IDH-1* and *HBDH-1*. The other loci appear to be selectively neutral, and all agree on about 2 migrants per generation. The F_{ST} data suggest the possibility of selection for local adaptation at *HBDH-1* and homogenizing selection at *IDH-1*, but this would need to be confirmed by further study.

b. Most of the differentiation at *HBDH-1* shown in the data above occurs between the two species of host plants; nine of the subpopulations occurred on *Solidago altissima* and the other 12 subpopulations were on *S. gigantea*. The frequency of one of the two *HBDH* alleles is 0.84 on *Solidago altissima* and 0.13 on *S. gigantea*. How does this fact affect your interpretation of the results?

This is further evidence for selection for local adaptation at *HBDH-1* or a locus linked with it, with the selection generated by differences between the two species of host plant.

3.2 Levin (1978) studied allele frequencies at the *6-pgd* allozyme locus in 73 subpopulations of the self-incompatible species *Phlox drummondii*. Of these 73, 66 were fixed for the *a* allele, with allele frequencies and observed heterozygosities at the other loci given below (Levin's original subpopulation numbering altered for simplicity):

Subpopulation	p	H_I
1-66	1	0
67	0.86	0.06
68	0.8	0.12
69	0.7	0.2
70	0.96	0.03
71	0.96	0.09
72	0.73	0.15
73	0.91	0.06

a. Calculate the three F -statistics for these data and check to make sure they have the correct mathematical relationship. Compare them with those calculated for the self-compatible *P. cuspidata* calculated in the text box (pp. 60-61). Do these comparisons fit your expectations based on the mating systems of these two species? Why or why not? If not, do you have a possible explanation for the lack of fit?

$$\bar{H}_I = \frac{(66 \times 0) + 0.06 + 0.12 + 0.2 + 0.03 + 0.09 + 0.15 + 0.06}{73} = 0.0097$$

$$\bar{H}_S = \frac{(66 \times 0) + 0.24 + 0.32 + 0.42 + 0.08 + 0.08 + 0.39 + 0.16}{73} = 0.0232$$

$$\bar{p} = \frac{(66 \times 1) + 0.86 + 0.8 + 0.7 + 0.96 + 0.96 + 0.73 + 0.91}{73} = 0.985$$

$$\bar{q} = 1 - \bar{p} = 0.015$$

$$H_T = 2\bar{p}\bar{q} = 0.0296$$

$$F_{IS} = \frac{\bar{H}_S - \bar{H}_I}{\bar{H}_S} = \frac{0.0232 - 0.0097}{0.0232} = 0.582$$

$$F_{ST} = \frac{H_T - \bar{H}_S}{H_T} = \frac{0.0296 - 0.0232}{0.0296} = 0.216$$

$$F_{IT} = \frac{H_T - \bar{H}_I}{H_T} = \frac{0.0296 - 0.0097}{0.0296} = 0.672$$

$$1 - F_{IT} = (1 - F_{IS})(1 - F_{ST})$$

$$0.328 = 0.418 \times 0.784 = 0.328$$

Both F_{IS} and F_{ST} are substantially less than those estimated for *P. cuspidata*, which makes sense because the self-incompatibility of *Phlox drummondii* should decrease inbreeding and increase gene flow between subpopulations. However, the F_{IS} is still very large for a non-selfing species. It could be explained partly by “bi-parental” inbreeding, that is mating with close relatives, but the F_{IS} value is probably too big to be explained entirely by inbreeding. Another good possibility is the **Wahlund effect**, which is the appearance of inbreeding from inadvertently lumping several differentiated subpopulations together. If some of these subpopulations are actually made up of more than one, then drift would cause an excess of homozygotes when the cryptic subpopulations are combined.

- b. Calculate $N_e m$ from these data. If the migration rate m was found to be 0.1, what would your estimate of N_e be?

$$N_e m = \frac{1}{4 \times 0.216} - 0.25 = 0.91$$

$$N_e = 0.91/0.1 = 9.1$$

- c. Now assume that N_e is very large, *6-pgd* is neutral in these subpopulations, and the migration rate is still 0.1. What would the frequencies of the *a* allele in subpopulations 68 and 69 after 10 generations be? After 25 generations? What biological principle is illustrated by these results?

Using Equation 3.4: $p_t = \bar{p} + (p_0 - \bar{p})(1 - m)^t$. Here $m = 0.1$, $\bar{p} = 0.985$, $p_0 = 0.8$ for subpopulation 68 and 0.7 for 69.

$$\text{Subpopulation 68: } p_{10} = 0.985 + (0.8 - 0.985)(1 - 0.1)^{10} = 0.92$$

$$p_{25} = 0.97$$

$$\text{Subpopulation 69: } p_{10} = 0.985 + (0.7 - 0.985)(1 - 0.1)^{10} = 0.88$$

$$p_{25} = 0.96$$

This illustrates migration reducing differentiation, as both subpopulations are converging on the average allele frequency in the metapopulation.

3.3. A rare triggerplant from Australia (*Stylidium coroniforme*) has only five known populations (Coates 1992). One of these populations has been monitored for several years, and over five years in the early 1980s, 2, 3, 25, 32, and 86 plants were recorded. Assuming that N_e in each year equals N_a in that year, estimate N_e as well as the average N_a over this period. What biological principle is illustrated by the difference between the two?

$$\frac{1}{N_e} = \frac{1}{5} \left(\frac{1}{2} + \frac{1}{3} + \frac{1}{25} + \frac{1}{32} + \frac{1}{86} \right)$$

$$N_e = 5.46$$

$$\bar{N}_a = 29.6$$

The bottleneck in the first two years disproportionately decreased N_e and would thus increase drift greatly.

3.4. Due to suburban development, a large panmictic population of moles is split into a metapopulation of five subpopulations of 20 males and 20 females each, with no migration among subpopulations. The variance in reproductive success is equal to 2 in females but is 8 in males, due to a few dominant males fathering most of the offspring.

a. Estimate N_e within each of these subpopulations.

$$N_e = \frac{8 \times 40}{8 + 2 + 4} = 22.86 \text{ in each subpopulation.}$$

b. Calculate what F_{ST} will be at 5 and 10 generations after the split if the subpopulations remain at the N_e you estimated in part (a). Also describe in words what has happened.

$$\Delta F_{ST} = \frac{1}{2N_e} = \frac{1}{2 \times 22.86} = 0.022$$

$$F_5 = 1 - (1 - 0.022)^5 = 0.105$$

$$F_{10} = 1 - (1 - 0.022)^{10} = 0.199$$

Due to the small population sizes and high variance in male reproductive success, drift has created a high degree of differentiation between these populations in 10 generations.

3.5. The sex ratio in fig wasps becomes even more female-biased as the number of females laying eggs in one fig declines. In figs with only one wasp mother, there were an average of 72 wasps per fig but only 10% were male. Calculate N_e in this case, and explain why this answer is different than the fig wasp example in the text (see pg. 62).

$$N_e = \frac{4 \times 7.2 \times 64.8}{7.2 + 64.8} = 25.92$$

This represents a reduction of 64% from N_a compared to only a 29% reduction in the text example, due to a more highly female-biased sex ratio here.

3.6. Selander and Yang (1969) trapped wild mice (*Mus musculus*) from four large chicken barns near Ramona, California and performed electrophoresis on a number of loci. F_{ST} values for three of these loci (hexose-6-phosphate dehydrogenase, NADP-isocitrate dehydrogenase, and hemoglobin) were 0.10, 0.16, and 0.11, respectively, for an average $F_{ST} = 0.12$. Assuming that the four subpopulations in each barn were founded at the same time from the same large panmictic population, there is no migration among the barns, and the effective subpopulation size has been the same in each barn since they were founded, estimate how many years ago the subpopulations were established if $N_e = 20$. How long ago if $N_e = 100$? Explain the biological reason for the difference between the two.

Substituting Equation 3.13 into Equation 3.14:

$$F_t = 1 - \left(1 - \frac{1}{2N_e}\right)^t \text{ Now solve for } t:$$

$$1 - F_t = \left(1 - \frac{1}{2N_e}\right)^t$$

$$\ln(1 - F_t) = t \ln\left(1 - \frac{1}{2N_e}\right)$$

$$t = \frac{\ln(1 - F_t)}{\ln\left(1 - \frac{1}{2N_e}\right)}$$

$N_e = 20$:

$$t = \frac{\ln(1 - 0.12)}{\ln\left(1 - \frac{1}{2 \times 20}\right)} = 5$$

$N_e = 100$:

$$t = \frac{\ln(1 - 0.12)}{\ln\left(1 - \frac{1}{2 \times 100}\right)} = 25.5$$

With a larger N_e of 100 there is less drift, so it takes longer (25.5 generations) to produce the same amount of divergence than it would at the smaller population size (only 5 generations with $N_e = 20$).

3.7. Stanton et al. (1986) studied selection on a floral color polymorphism in wild radish (*Raphanus raphanistrum*). Pollinators preferred yellow-flowered plants, so average total fitness (estimated seed production and seed siring) was 88.3 for yellow-flowered plants and 56.6 for white-flowered plants. Floral color is determined by a single locus with the white allele completely dominant to the yellow allele.

a. Calculate relative fitness for the three genotypes and the selection coefficient. What is unusual about this case?

Genotype	Absolute fitness	w (relative fitness)	s
WW	56.6	0.64	0.36
Ww	56.6	0.64	0.36
ww	88.3	1	0

This is unusual because the recessive allele is favored and the dominant allele is deleterious.

b. The frequency of yellow-flowered plants in this study population averaged 0.85. Assuming that this frequency results from an equilibrium between mutation and selection, and the population is in HWE, what is the mutation rate to the white allele? Do you think that the assumption of an equilibrium between mutation and selection is reasonable here? Why or why not? Give one alternative explanation for the frequency of yellow plants.

Because the deleterious allele is dominant, use $\hat{q} \approx \frac{\mu}{hs}$ (see Equation 3.17) where q is the frequency of the deleterious dominant and $h = 1$. Assuming HWE, $p = \sqrt{0.85} = 0.92$, so $q = 0.08$. Rearranging Equation 3.17 yields:

$$\mu = \hat{q}hs = 0.08 \times 1 \times 0.36 = 0.03$$

This is an extraordinarily high estimated mutation rate for a single locus, so it seems that the high frequency of the white allele must be due to something else. Possibilities include: (1) migration from another subpopulation in which selection favors white alleles, (2) selection varies from year to year, (3) the population is not at equilibrium and thus the white allele is still declining, and (4) there is a small effective population size and the white allele has drifted to high frequency.

c. What would the mutation rate be if the white allele was completely recessive, assuming the same allele frequencies as above? What biological principle is illustrated by the difference among these two mutation rates?

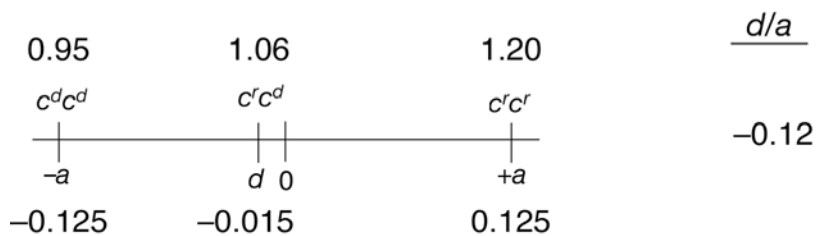
Rearranging Equation 3.16 gives $\mu = q^2s = 0.08^2 \times 0.36 = 0.002$. This illustrates that a lower mutation rate is needed to maintain the same frequency of the deleterious white allele,

because selection is less effective against the allele when it is recessive (due to the heterozygotes having a relative fitness of one and most of the rarer allele in the heterozygotes).

Chapter 4

4.1. Sewall Wright studied the genetics of coat color in guinea pigs. He reported the following scores for degree of black coloration for the three genotypes at the c locus: $c^r c^r = 1.20$, $c^r c^d = 1.06$, $c^d c^d = 0.95$.

a. Calculate a , d , and d/a for this trait, and place these values, the genotypes, and the raw genotypic values (G) on a line graph, using Figures 4.6 and 4.7 as a guide.



b. Calculate the population mean, additive genetic variance, and dominance variance for this trait, assuming the c locus is the only locus that affects this trait and that the frequency of the c^r allele is $p = 0.5$.

$$\text{Mean} = -0.008, V_A = 0.008, V_D = 5.6 \times 10^{-5}.$$

c. Calculate the population mean, additive genetic variance, and dominance variance for the case where $p = 0.25$. What important principle is illustrated by the difference between these answers and your answers for part (b)?

Mean = -0.07 , $V_A = 0.005$, $V_D = 3.2 \times 10^{-5}$. This illustrates that population mean and variance (both additive and dominance) depend on allele frequencies. Note that since this locus is almost additive (d/a is small because the heterozygote phenotype is almost intermediate between the two homozygotes), V_D is always small and the additive variance peaks near $p = q = 0.5$. Also note that the mean becomes more negative as the frequency of the c^d allele increases; the mean is negative because the midpoint between the homozygotes is set to zero. We can convert it back to the raw genotypic value by adding it to the raw midpoint: $-0.07 + 1.075 = 1.005$.

4.2. Merila (1997) performed a cross-fostering experiment with collared flycatchers in which unequal numbers of offspring were moved, so that half of the nests had reduced numbers of nestlings and half had enlarged brood sizes. The regression slopes of the offspring tarsus length on their genetic midparent values (not the foster parents that raised them) were 0.48 in the nests with reduced brood sizes and 0.22 in the nests with

enlarged numbers of young. What do these slopes represent? What are two possible reasons for the differences in slopes between the two treatments? What role do you think maternal and paternal effects played in determining these slopes?

These slopes are the narrow-sense heritabilities. The decrease in heritability with increased brood size could be due to increased environmental variance and/or decreased expression of additive variance. Maternal and paternal effects likely had little influence on these estimates because the genetic parents did not raise the offspring.

4.3. The study by Futuyma et al. (see Tables 4.7 and 4.8) also examined genetic variance for adult feeding rate using their nested half-sibling design. The ANOVA table for the amount of leaf consumed by *Ophraella* adults on feeding on marsh elder is below. Calculate the sire and dam variance components, V_A and h^2 for these data. Is there evidence for additive variance, dominance variance, or common environmental effects? Compare the results to the larval feeding data for the same species in Table 4.7; what similarities and differences do you see?

	<i>d.f.</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Sire	49	1.07	1.2	>0.25
Dam (Sire)	25	0.90	2.0	0.005
Error	150	0.44		

$s = 50, d = 1.5, k = 3.$

Sire VC = 0.038, Dam VC = 0.15, $V_A = 0.15$, and $h^2 = 0.24$. There is not strong evidence for additive variance, in contrast to the larval data, because the sire VC and heritability are much lower and the sire term in the ANOVA is not statistically significant. There is much stronger evidence for dominance variance and/or common environment effects than in the larval data, because the dam variance component is four times the sire variance component (compare Equations 4.16 and 4.17), and the dam term in the ANOVA is highly significant and the sire term is not.

Chapter 5

5.1 On the facing page are reaction norm plots and summaries of ANOVA results for four traits of the weed *Polygonum persicaria* grown under three different light intensities (Sultan and Bazzaz 1993). Each line in the reaction norms represents means for replicates of one clone. For each trait, describe whether or not these data provide evidence for:

- Overall genetic variance for the trait.
- Overall plasticity for the trait. If so, is this plasticity likely to be adaptive? Why or why not?
- Genotype by environment interaction. Could adaptive plasticity evolve?

a. There is evidence for significant overall genetic variance for mean leaf size and mean fruit weight—the genotype main effect is highly significant for both these traits, and the reaction norms show differences among the genotypes at each light level. The genotype

main effect is not significant for the other two traits, and the reaction norms for total fruit biomass show little difference among the genotypes at each light level. The reaction norms for total leaf area also show little variance among genotypes at 8% sunlight. There is more variance among the genotypes at the higher light levels for total leaf area, but the crossing of the reaction norms reduces the variance averaged across light levels.

b. There is strong evidence for overall plasticity for each trait. In all cases the environment main effect is highly significant, and the reaction norms show large differences among the overall means produced at each light level. Total fruit biomass shows a fairly steady increase with increasing light, while most of the difference in total leaf area and mean fruit weight is accounted for by the lower values seen at 8% sunlight compared to the two higher levels. The plasticity for these three traits seems unlikely to be adaptive, but rather we see reduced total plant size and reduced fitness with lower light levels, especially at the lowest light, because of reduced photosynthesis (total fruit biomass is likely to be very closely related to fitness in this annual plant). The plasticity in mean leaf size may be partly adaptive. The lower mean leaf size at 8% sunlight is likely maladaptive, as larger leaves would increase light capture. The reduced leaf size at 100% light as compared to 37% could be adaptive, as smaller leaf size would conserve resources needed to produce leaves and reduce water loss; due to the abundant light at the 100% treatment, photosynthetic rates are not likely to be limited very strongly by leaf size.

c. There was evidence for genotype by environment interaction for total leaf area and mean leaf size, but not for total fruit mass or mean fruit weight. For the first two traits the $G \times E$ term in the ANOVA was significant, and the reaction norms often cross each other, indicating that the genotypes have different relative sizes at the different environments. There is also some evidence for variance $G \times E$, as there appears to be more genetic variance (difference between genotypes) in total leaf area at the two higher light levels compared to 8% light, and more variance in mean leaf size at 37% light compared to the two extremes. Thus, further evolution of adaptive plasticity could evolve for total leaf area and mean leaf size if selection for plasticity occurred, but not for total fruit biomass or mean fruit weight.

2. The accompanying table shows heritabilities and genetic and environmental correlations for pairs of traits from three of the same studies in Table 5.4. Different traits from those in Table 5.4 are shown for snakes and finches, while the same traits measured at a different age are given for mice. Calculate the phenotypic correlation in each case, and describe how each of the parameters in the table affected each of the correlations you calculated.

Species	Trait 1	Trait 2	h^2_1	h^2_2	r_A or r_G	r_E	r_P
Garter snake	Color pattern	Sprint speed	0.71	0.53	0.28	-0.23	0.09
Darwin's finch	Weight	Bill depth	0.91	0.79	0.87	0.19	0.76

House mouse	Brain size	Body size	0.16	0.20	-0.43	0.31	0.18
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See above table. In the garter snakes, the genetic and environmental correlations were in opposite directions, and the heritabilities were moderate, so the phenotypic correlation is very low. It is positive because the positive genetic correlation was slightly greater than the negative environmental correlation, and because the average heritability was a bit higher than 0.5, meaning that the genetic correlation was weighted slightly more than the environmental correlation.

In the Darwin's finch example, heritabilities were very high, so the phenotypic correlation is dominated by, and very similar to, the genetic correlation. The environmental correlation was also positive. In contrast, the heritabilities of the house mouse traits were very low, so that the larger negative genetic correlation was outweighed by the smaller positive environmental correlation. Still, as in the garter snakes, the opposing signs of the genetic and environmental correlations leads to a small overall phenotypic correlation.

3. Endler et al. (2001) artificially selected guppies (*Poecilia reticulata*) for increased sensitivity to red light in two replicate selection lines (R1 and R2) for seven generations. The results, plotted as the cumulative response (R) versus the negative of the cumulative selection differential ($-S$), are shown below.

a. Is there evidence for a selection plateau? If so, describe this evidence and briefly outline two experiments that could be done to examine possible causes of the plateau. Be sure to explain how results of these experiments could be interpreted.

The guppy lines seem to reach a plateau after three generations, because there was a rapid and fairly consistent response to selection for the first three generations, but no consistent response for the last three. To test whether this plateau was caused by opposing natural selection, selection could be relaxed and the population followed for a few more generations. If opposing selection was the cause, then the population should evolve back toward the phenotypic value of the founding population. If opposing natural selection was not the cause, no consistent phenotypic change should occur.

To test whether the plateau was caused by a depletion of genetic variance, reverse selection back toward the founder population mean could be implemented. If the population responds and evolves back toward the original mean phenotype, then genetic variance was still present in the lines. If the populations remain at the new selected phenotype, then this suggests a depletion of additive genetic variance for the trait. Of course, if the mean reverts back toward the original under relaxed selection (above) then this also is excellent evidence for remaining genetic variance.

b. Endler and colleagues calculated the realized heritability of sensitivity to red light from regressions on these data as 0.39 and 0.30 in R1 and R2, respectively. Estimate the realized heritability using the breeder's equation,

but leaving out the last three generations in the figure (that is, use only the data up to the generation marked with the arrow). Give a possible reason for any discrepancy between your estimate and that of the authors.

The cumulative R over the first three generations is approximately 0.8 in both lines, and the cumulative S is approximately one. Since realized heritability is R/S , the estimate for the first three generations is approximately 0.8, over twice the estimate from all six generations. The reason is the possible selection plateau. Response to selection was very rapid for three generations, leading to a high realized heritability, but was essentially zero for the last three generations. Averaging over all six leads to a lower estimate of realized heritability. If the plateau was due to a depletion of variance, then there was a high heritability initially, but this heritability decreased to very low levels after three generations. If the plateau was caused by opposing natural selection, then the early estimate of 0.8 better reflects actual levels of additive variance in the populations.

4. The accompanying figure shows a portion of the QTL map from the cross between *Mimulus lewisii* and *M. cardinalis* discussed in the text (Bradshaw et al. 1998). Shown are the QTL positions for four floral traits on three of the linkage groups.

a. How many gene loci for each of the traits did they find in these three linkage groups?

Two gene loci for each of the four traits.

b. Is there evidence for pleiotropic effects of any of these loci? If so, describe this evidence.

Yes, on both linkage groups A_C and B_C , the QTL for stamen length, pistil length, and aperture width map very close to each other; this is particularly true for the first two traits. Pleiotropy would not be surprising for these traits, as they are lengths of closely related floral parts. However, because standard errors for map position are not given, and because there are at least dozens of genes in the chromosomal regions these traits are mapping to, the association could be due to close linkage rather than pleiotropy.

c. What are the approximate map distance and recombination rate between the loci affecting aperture height and pistil length in linkage group A? What is the recombination rate between the two loci that affect aperture height?

The first part of the question cannot be answered, because due to an error no scale in map units was provided in the figure. The recombination rate between the two aperture height loci is 0.5, because they are on different linkage groups.

Chapter 6

6.1 Johnston (1991) measured selection on several traits in cardinal flowers (*Lobelia cardinalis*). The standardized selection gradients for these traits are

given in the top part of the accompanying table, and the phenotypic correlations among them are given in the bottom part of the table.

a. Calculate the selection differentials for these traits.

Use Equation 6.4, e.g., for Flower number:

$$S = 1.35 + (0.11 \times 0.71) + (0.19 \times -0.35) = 1.34$$

Trait	β	S
Flower number	1.35***	1.34
Plant height	0.11	0.98
Median flower date	0.19*	-0.33

Phenotypic correlations:	Flower number	Plant height
Plant height	0.71***	
Median flower date	-0.35***	-0.47***

b. Which traits are likely targets of selection? Which trait is most strongly affected by indirect selection? How would having only the differentials and not the gradients mislead interpretations about adaptation?

Flower number is definitely a target of selection, as the β estimating the strength of direct selection is strongly positive and highly significant. Median flower date also seems to be under direct selection and is thus a target, with weaker direct selection for later flowering. There is no evidence that plant height is a target, as the β for that trait is not significant, but it is the trait that is most strongly affected by indirect selection. The strong direct selection on flower number coupled with the strong positive correlation between these traits (0.71) results in a selection differential for plant height that is almost as large as the differential for flower number. Thus, from the differentials alone one might conclude that increased plant height is adaptive, but the selection gradients provide no support for this conclusion. The negative correlations between flower date and the other two traits, coupled with the positive direct selection on the other traits (especially flower number) resulted in negative total selection on flower date. This negative differential for flower date would also mislead interpretations, as it might be concluded that earlier flowering is adaptive when in fact the opposite is the case.

c. For one of the targets of selection that you mentioned in your answer to part b, briefly describe an experiment designed to prove that this trait is a cause of fitness differences.

To prove that flower number and date are causally related to fitness, these traits need to be manipulated experimentally. Flower number could easily be reduced by clipping, but increasing functional flower number could be difficult. Flower date might be manipulated by starting plants at different times in the greenhouse and planting them out in the field at the same time, so flower date differs experimentally. Both these traits could be manipulated by artificial selection or perhaps genetic engineering.

6.2. A hypothetical G -matrix for the traits in Problem 6.1 is shown below.

Calculate $\Delta\bar{z}$ for the traits. Is there any evidence for constraints on the evolution of any of these traits? Describe these constraints, and be specific!

Trait	β	$\Delta\bar{z}$	$\Delta\bar{z}$ direct	$\Delta\bar{z}$ CR
Flower number	1.35	0.02	0.03	-0.01
Plant height	0.11	0.18	0.10	0.08
Median flower date	0.19	-0.02	0.16	-0.18

There is strong evidence for constraints on flower number evolution; despite very strong selection for an increase (1.35), the predicted change in the mean is small (0.02), due both to a low additive genetic variance (0.02) and a negative covariance between flower number and flower date (-0.10), a trait that itself is under positive selection (0.19).

There is no evidence for a constraint on plant height—there is adequate additive genetic variation and adaptive evolution of this trait is augmented by the positive correlated response (CR). The positive CR is caused by the strong positive selection on flower number and the positive correlation between flower number and height; this outweighs the negative component of the CR caused by the negative covariance between flower date and height.

There is evidence for a constraint on adaptive evolution of flowering date. The predicted change is slightly negative, despite direct selection for an increase. The negative $\Delta\bar{z}$ is caused by the negative covariances between flowering date and the other two traits, both of which are under positive selection.

6.3 The table below shows hypothetical selection gradients for leaf thickness in a plant that was grown experimentally at three different watering levels and three different light levels. Are water, light, both, or neither selective agents on leaf thickness in this experiment? Explain your reasoning.

There is good evidence in the table that water is a selective agent on leaf thickness, because as the amount of water provided to the plants declines, selection for increased leaf thickness becomes stronger (higher selection gradients). Thus, thick leaves are likely an adaptation to conserve water in drier habitats in this species. There is no evidence that light is a selective agent on leaf thickness, as selection gradients are very similar across the three light levels. Note that light could easily be a selective agent on a different trait in this species.

6.4 In a study of a hypothetical butterfly, linear and quadratic selection gradients were estimated for three traits. These are shown below, with asterisks denoting statistical significance (gradient greater than zero) at $P < 0.001$. What can you infer about the shape of the fitness function for each? Make a sketch of what each fitness might look like based on these gradients. What other information would help further your understanding of the shape of the fitness functions?

Fitness increases with increasing wing length, but the rate of increase slows at the longer wing values. Selection on proboscis length is likely disruptive, and there is negative

directional selection on wing spot size (see sketches below). To strengthen these interpretations, the fitness functions should be fitted from the actual data, preferably using a method like loess or cubic splines to accurately characterize the relationship between fitness and the phenotype.

