E1. Allozymes can be detected by gel electrophoresis. However, this technique underestimates the total amount of genetic variation because some sequence differences will not alter the mobility of an enzyme within a gel. By comparison, DNA sequencing will reveal all the sequence differences between different individuals.

E2. 1. One hypothesis is that the population having only two allozymes was founded from a small group that left the other population. When the small founding group left, it had less genetic diversity than the original population.

2. The population with more genetic diversity may be in a more diverse environment so it may select for a greater variety of phenotypes.

3. It may just be a matter of chance that one population had accumulated more neutral alleles than the other.

E3. A. At the DNA level, a clear-cut way to determine genetic variation is to clone and sequence genes. If the same gene is cloned from two different individuals and the sequences are different, this shows that there is genetic variation. In addition, several other methods can be used to detect genetic variation. For example, a comparison of Southern blots using samples from different individuals might reveal that a gene exists in different sizes or that it contains different restriction sites.

B. At the RNA level, a Northern blot may reveal genetic variation. If the RNA encoded by two different alleles has a different size, this can be detected in a Northern blot.

C. At the protein level, gel electrophoresis may reveal genetic variation. This method was described in your textbook. Different allozymes may migrate at different rates during gel electrophoresis. Another approach is to study the function of an enzyme using a biochemical assay of its activity. Allozymes may have different levels of enzymatic activity, and this may be detected using an enzyme assay.

E4. Glutamic acid is a negatively charged amino acid and valine is neutral. The Hb^A polypeptide has a glutamic acid at the sixth position while Hb^S has a valine. Therefore, the Hb^A polypeptide will move a little more quickly toward the positive end of the gel.

Lane 1—Hb^SHb^S
Lane 2—Hb^AHb^A
Lane 3—Hb^AHb^S

E5. Note: You need to look at solved problem S5 and realize that the Hardy-Weinberg equation can be extended to a gene existing in four alleles. In this case:

$$(p + q + r + s)^2 = 1$$

$$p^2 + q^2 + r^2 + s^2 + 2pq + 2qr + 2qs + 2rp + 2rs + 2sp = 1$$

Let $p = C$, $q = c^{ch}$, $r = c^h$, and $s = c$.

A. The frequency of albino rabbits is s^2.

$$s^2 = (0.05) = 0.0025 = 0.25\%$$

B. Himalayan is dominant to albino but recessive to full and chinchilla. Therefore, Himalayan rabbits would be represented by r^2 and by $2rs$.

$$r^2 + 2rs = (0.44)^2 + 2(0.44)(0.05) = 0.24 = 24\%$$

Among 1,000 rabbits, about 240 would have a Himalayan coat color.

C. Chinchilla is dominant to Himalayan and albino but recessive to full coat color. Therefore, heterozygotes with chinchilla coat color would be represented by $2qr$ and by $2qs$.

$$2qr + 2qs = 2(0.17)(0.44) + 2(0.17)(0.05) = 0.17, \text{ or } 17\%$$

Among 1,000 rabbits, about 170 would be heterozygotes with chinchilla fur.

E6. A. Let *W* represent the white fat allele and *w* represent the yellow fat allele. Assuming a Hardy-Weinberg equilibrium, we can let p^2 represent the genotype frequency of *WW* animals, and then *Ww* would be 2*pq* and *ww* would be q^2. The only genotype frequency we know is that of the *ww* animals.

$$ww = q^2 = \frac{76}{5,468}$$

$$q^2 = 0.014$$

$$q = 0.12, \text{ which is the allele frequency of } w$$

$$p = 1 - q$$

$$p = 0.88, \text{ which is the allele frequency of } W$$

B. The heterozygous carriers are represented by 2*pq*. If we use the values of *p* and *q*, which were calculated in part A:

$$2pq = 2(0.88)(012) = 0.21$$

Approximately 21% of the animals would be heterozygotes with white fat.

If we multiply 0.21 times the total number of animals in the herd:

$$0.21 \times 5,468 = 1,148 \text{ animals}$$

E7. A. Eskimo $M = 0.913$ $N = 0.087$

Navajo $M = 0.917$ $N = 0.083$

Finns $M = 0.673$ $N = 0.327$

Russians $M = 0.619$ $N = 0.381$

Aborigines $M = 0.176$ $N = 0.824$

B. To determine if these populations are in equilibrium, we can use the Hardy-Weinberg formula and calculate the expected number of individuals with each genotype.

Eskimo $MM = (0.913)^2 = 83.3$

$MN = 2\ (0.913)(0.087) = 15.9$

$NN = (0.087)^2 = 0.76$

In general, the values agree pretty well with an equilibrium. The same is true for the other four populations.

C. Based on similar allele frequencies, the Eskimo and Navajo Indians seem to have interbred as well as the Finns and Russians.

E8. The first thing we need to do is to determine the allele frequencies. Let's let *p* represent *i*, *q* represent I^A, and *r* represent I^B.

p^2 is the genotype frequency of *ii*
q^2 is the genotype frequency of I^AI^A
r^2 is the genotype frequency of I^BI^B
2*pq* is the genotype frequency of I^Ai
2*pr* is the genotype frequency of I^Bi
2*qr* is the genotype frequency of I^AI^B

$$p^2 = \frac{721}{721 + 932 + 235 + 112}$$

$$p^2 = 0.36$$

$$p = 0.6$$

Next, we can calculate the allele frequency of I^A. Keep in mind that there are two genotypes (I^AI^A and I^Ai) that result in type A blood.

$$q^2 + 2pq = \frac{932}{721 + 932 + 235 + 12}$$

$$q^2 + 2(0.6)q = 0.47$$

$$q = 0.31$$

Now it is easy to solve for *r*,

$$p + q + r = 1$$

$$0.6 + 0.31 + r = 1$$

$$r = 0.09$$

Based on these allele frequencies, we can compare the observed and expected values. To determine the expected values, we multiply the genotype frequencies times 2,000, which was the total number of individuals in this population.

p^2 is the genotype frequency of $ii = (0.6)^2(2{,}000) = 720$
q^2 is the genotype frequency of $I^AI^A = (0.31)^2(2{,}000) = 192$
r^2 is the genotype frequency of $I^BI^B = (0.09)^2(2{,}000) = 16$
$2pq$ is the genotype frequency of $I^Ai = 2(0.31)(0.6)(2{,}000) = 744$
$2pr$ is the genotype frequency of $I^Bi = 2(0.09)(0.6)(2{,}000) = 216$
$2qr$ is the genotype frequency of $I^AI^B = 2(0.31)(0.09)(2{,}000) = 111$

	Expected Numbers	**Observed Numbers**
Type O	720	721
Type A	192 + 744 = 936	932
Type B	16 + 216 = 232	235
Type AB	111	112

The observed and expected values agree quite well. Therefore, it does appear that this population is in Hardy-Weinberg equilibrium.

E9. A. $\Delta p_C = m(p_D - p_R)$

With regard to the sickle-cell allele:

$$\Delta p_C = (550/10{,}550)(0.1 - 0.01) = 0.0047$$

$$p_C = p_R + \Delta p_C = 0.01 + 0.0047 = 0.0147$$

B. We need to calculate the genotypes separately:

For the 550 migrating individuals,

$Hb^AHb^A = (0.9)^2 = 0.81$, or 81% We expect (0.81)550 = 445.5 individuals to have this genotype

$Hb^AHb^S = 2(0.9)(0.1) = 0.18$ We expect (0.18)550 = 99 heterozygotes

$Hb^SHb^S = (0.1)^2 = 0.01$ We expect (0.01)550 = 5.5 Hb^SHb^S

For the original recipient population,

$Hb^AHb^A = (0.99)^2 = 0.98$ We expect 9,801 individuals to have this genotype

$Hb^AHb^S = 2(0.99)(0.01) = 0.0198$ We expect 198 with this genotype

$Hb^SHb^S = (0.01)^2 = 0.0001$ We expect 1 with this genotype

To calculate the overall population:

$$(445.5 + 9801)/10{,}550 = 0.971\ Hb^AHb^A \text{ homozygotes}$$

$$(99 + 198)/10{,}550 = 0.028 \text{ heterozygotes}$$

$$(5.5 + 1)/10{,}550 = 0.00062\ Hb^SHb^S \text{ homozygotes}$$

C. After one round of mating, the allele frequencies in the conglomerate (calculated in part A), should yield the expected genotype frequencies according to the Hardy-Weinberg equilibrium.

$$\text{Allele frequency of } Hb^S = 0.0147, \text{ so } Hb^A = 0.985$$

$$Hb^AHb^A = (0.985)^2 = 0.97$$

$$Hb^AHb^S = 2(0.985)(0.0147) = 0.029$$

$$Hb^SHb^S = (0.0147)^2 = 0.0002$$

E10. Let's assume that the relative fitness values are 1.0 for the dominant homozygote and the heterozygote and 0 for the recessive homozygote. The first thing we need to do is to calculate the mean fitness for the population.

$$p^2W_{AA} + 2pqW_{Aa} + q^2W_{aa} = \bar{W}$$
$$(0.78)^2 + 2(0.78)(0.22) = \bar{W}$$
$$\bar{W} = 0.95$$

The genotype frequency in the next generation for AA equals

$$\frac{p^2W_{AA}}{\bar{W}}$$
$$\frac{(0.78)^2}{0.95} = 0.64$$
$$p = \sqrt{0.64} = 0.80 \text{ and } q = 0.20$$

For the second generation, we first need to calculate the mean fitness of the population, which now equals 0.96. Using the preceding equation, the genotype frequency of *AA* in the second generation equals 0.67 and the allele frequency equals 0.816. The frequency of the recessive allele in the second generation would equal 0.184 and the mean fitness would now equal 0.967. The genotype frequency of *AA* in the third generation would be 0.688 and the allele frequency would be 0.83. The frequency of the recessive allele would be 0.17.

E11. A. Probability of fixation = $1/2N$ (Assuming equal numbers of males and females contributing to the next generation)

Probability of fixation = 1/2(2,000,000)

= 1 in 4,000,000 chance

B. where t = the average number of generations to achieve fixation

N = the number of individuals in population, assuming that males and females contribute equally to each succeeding generation

C. If the blue allele had a selective advantage, the value calculated in part A would be slightly larger; there would be a higher chance of allele fixation. The value calculated in part B would be smaller; it would take a shorter period of time to reach fixation.

E12. If we let *C* represent the *carbonaria* allele and *c* represent the *typical* allele:

$$W_{CC} = 1.0$$
$$W_{Cc} = 1.0$$
$$W_{cc} = 0.47$$

In the next generation, we expect that the Hardy-Weinberg equilibrium will be modified by the following amount:

$$p^2W_{CC} + 2pqW_{Cc} + q^2W_{cc}$$

In a population that is changing due to natural selection, these three genotypes will not add up to 1.0 as in the Hardy-Weinberg equilibrium. Instead, the three genotypes will add up to the mean fitness of the population.

$$p^2W_{CC} + 2pqW_{Aa} + q^2W_{aa} = \bar{W}$$
$$(0.7)^2(1.0) + 2(0.7)(0.3)(1.0) + (0.3)^2(0.47) = \bar{W}$$
$$\bar{W} = 0.95$$

After one generation of selection:

Allele frequency of *C:*

$$p = \frac{p^2 W_{CC}}{\bar{W}} + \frac{pqW_{Cc}}{\bar{W}}$$
$$p = \frac{(0.7)^2(1.0)}{0.95} + \frac{(0.7)(0.3)(1.0)}{0.95}$$
$$p = 0.74$$

Allele frequency of *c:*

$$q = \frac{q^2 Wcc}{\bar{W}} + \frac{pqW_{Cc}}{\bar{W}}$$
$$q = \frac{(0.3)^2(0.47)}{0.95} + \frac{(0.7)(0.3)(1.0)}{0.95}$$
$$q = 0.27$$

After one generation, the allele frequency of *C* has increased from 0.7 to about 0.74 while the frequency of *c* has decreased from 0.3 to about 0.27. This is because the homozygous, *cc,* genotype has a lower fitness compared to the heterozygous, *Cc,* and homozygous, *CC*, genotypes.

E13. The selection coefficients are

$$s_{ww} = 1 - 0.19 = 0.81$$
$$s_{WW} = 1 - 0.37 = 0.63$$

If the rats are not exposed to warfarin, the equilibrium will no longer exist and natural selection will tend to eliminate the warfarin-resistance allele because the homozygotes are vitamin K deficient.

E14. Each area that he tested had its own endogenous population of moths. For example, the polluted areas had many more darkly colored moths, so we would expect to capture many more of these simply because there are more of them in the first place. Kettlewell wanted to release an equal number of moths of both types and then recapture them as a way to examine how well each type of moth could survive in polluted and unpolluted environments.

E15. Let's use the data for bird predation, but we could also carry out a chi square analysis for the percentage of recapture.

Hypothesis: Color has nothing to do with predation by birds. Note: We need to propose this hypothesis to obtain expected values. According to this hypothesis, we would expect an equal number of dark and light moths to be eaten by birds.

$$\chi^2 = \frac{\Sigma(O - E)^2}{E}$$

In the Dorset woods, there were (43 + 15) = 58 moths that were eaten. We would expect 29 to be *carbonaria* and 29 to be *typical* according to our hypothesis. In the Birmingham woods, there were (26 + 164) = 190 moths eaten, so we would expect 95 to be *carbonaria* and 95 to be *typical.*

$$\chi^2 = \frac{(43 - 29)^2}{29} + \frac{(15 - 29)^2}{29} + \frac{(26 - 95)^2}{95} + \frac{(164 - 95)^2}{95}$$
$$\chi^2 = 113.8$$

If we look in the chi square table in Chapter 2 with 3 degrees of freedom, this rather high chi square value is very unlikely to occur as a matter of chance (less than 1% of the time). Therefore, we reject our hypothesis that color does not affect predation. As an alternative, we would propose that the color of the moths does have a significant effect on their likelihood of predation.

E16. Fitness based on the number eaten by birds:

The number of moths eaten by birds is really a measure of the selection coefficient (*s*), not a measure of fitness. $s = 1 - W$

We first need to compare the *carbonaria* and the *typicals.*

$$carbonaria = \frac{43}{43+15}$$
$$carbonaria = 0.74$$
$$typical = \frac{15}{43+15}$$
$$typcial = 0.26$$

If we wish to give the *typical* moths a fitness value of 1.0, this means the selection coefficient for *typical* moths must be zero. Therefore, to calculate the selection coefficient for the *carbonaria* moths:

$$s_{carbonaria} = 0.74 - 0.26 = 0.48$$
$$W_{carbonaria} = 1 - 0.48 = 0.52$$

Fitness based on the number of moths recaptured:

$$W_{carbonaria} = \frac{7.0}{12.5}$$
$$W_{carbonaria} = 0.56$$

The two values (0.52 and 0.56) agree reasonably well. The fitness value based on recapture data is probably more reliable since it seems to be an unbiased measure of the survival rate. The fitness based on the number eaten by birds is somewhat biased because it assumes that this is the only factor that affects the survival of the two types of moths. However, there could be other factors. For example, animals other than birds may eat moths.

E17. If we assume that the different phenotypes of snails have the same level of fertility, we can estimate their fitness values by determining their survival percentages in the different habitats. This calculation assumes that the snails freely migrate through these different environments during their lifetimes, and that the percentages of snails in any given environment reflect their likelihood of survival. This assumption may not be valid if the snails are fairly sedentary and do not migrate very far from where they were born.

A. In beechwoods, the pink snails have the greatest survival rate. If we assign a fitness value of 1 for the pink snails, then the brown snails have a fitness of 0.23/0.61 = 0.38, and the yellow snails have a fitness value of 0.16/0.61 = 0.26.

B. In deciduous woods, the pink snails also have the greatest survival rate. If we assign a fitness value of 1 for the pink snails, then the brown snails have a fitness of 0.05/0.68 = 0.07, and the yellow snails have a fitness value of 0.27/0.68 = 0.40.

C. In hedgerows, the yellow snails have the greatest survival rate. If we assign a fitness value of 1 for the yellow snails, then the brown snails have a fitness of 0.05/0.64 = 0.08, and the pink snails have a fitness value of 0.31/0.64 = 0.48.

E18. One could follow an analogous protocol as conducted by Kettlewell. You could mark snails with a dye and release equal numbers of dark and light snails into dimly lit forested regions and sunny fields. At a later time, recapture the snails and count them. It would be important to have a method of unbiased recapture because the experimenter would have an easier time locating the light snails in a forest and the dark snails in a field. Perhaps one could bait the region with something that the snails like to eat and only collect snails that are at the bait. In addition to this type of experiment, one could also sit in a blind and observe predation as it occurs.