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Exam 1

1. The annual morning glory, *Ipomoea purpurea*, exhibits a flower-color polymorphism at the *A* (albino) locus throughout the southeastern United States. Individuals that are *AA* have darkly pigmented flowers (purple or pink); individuals that are *Aa* have lightly pigmented flowers; and individuals that are *aa* are albino (have completely white flowers). In one study of a natural population, the following information was obtained:

- the population consisted of approximately 5000 flowering individuals.
- the number of flowering individuals of each genotype in 1991 was:
 - AA*: 2000
 - Aa*: 1000
 - aa*: 2000
- the number of flowering individuals of each genotype in 1992 was:
 - AA*: 2100
 - Aa*: 1100
 - aa*: 1800

Calculate the genotype and gene frequencies in both years, then calculate the change in gene frequency from 1991 to 1992. Is the observed change in gene frequency explainable by genetic drift? Why or why not?

ANSWER:

$$1991 \text{ gene freqs.:} \quad p_A = \frac{2000 + \frac{1}{2}1000}{5000} = 0.5 = p_a$$

$$\text{genotype freqs.:} \quad p_{AA} = \frac{2000}{5000} = 0.4$$

$$p_{Aa} = \frac{1000}{5000} = 0.2$$

$$p_{aa} = \frac{2000}{5000} = 0.4$$

$$1992 \text{ gene freqs.:} \quad p_A = \frac{2100 + \frac{1}{2}1100}{5000} = 0.53, \quad p_a = 0.47$$

$$\text{genotype freqs.:} \quad p_{AA} = \frac{2100}{5000} = 0.42$$

$$p_{Aa} = \frac{1100}{5000} = 0.22$$

$$p_{aa} = \frac{1800}{5000} = 0.36$$

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(answer to question 1 continued)

The change in gene frequency from 1991 to 1992 is $0.53 - 0.5 = 0.03$. In order to determine whether a change of this magnitude is consistent with only genetic drift operating, calculate

$$\sigma = \sqrt{\frac{p_A p_a}{2N}} = \sqrt{\frac{0.5 \times 0.5}{2 \times 5000}} = 0.005 .$$

Hence, $|\Delta p_A| \gg \sigma$ and therefore the null hypothesis that drift alone is responsible for the observed change in gene frequency must be rejected.

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2. Natural populations of *Drosophila pseudoobscura* commonly exhibit chromosomal inversion polymorphisms. In one population studied by Dobzhansky, two inversions were equally common and appeared to persist with very little gene frequency change for many years. Laboratory experiments designed to determine whether heterozygote superiority could account for the persistence of this polymorphism yielded the following data on survival and fecundity for the three inversion genotypes:

Genotype	l	m
ST,ST	0.9	60
ST,PP	0.8	80
PP,PP	0.6	90

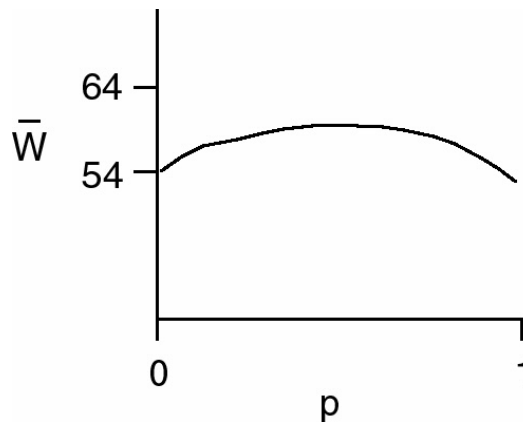
Using this data, answer the following questions:

- Calculate the fitness of each genotype.
- Sketch the adaptive topography associated with this locus.
- What is the expected equilibrium gene frequency of the ST inversion?
- Calculate the slope of the adaptive topography when the gene frequency of the ST inversion is 0.4.
- Calculate the expected change in gene frequency if the population starts with a gene frequency of ST of 0.4.
- Is heterozygote superiority a reasonable explanation for the persistence of the inversion polymorphism in nature? Explain.

ANSWER:

a. $W = lm$, so the fitnesses are 54, 64, and 54 for ST/ST, ST/PP and PP/PP respectively. You may also report the relative fitnesses: 0.844, 1, and 0.844 respectively.

b.



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(answer to question 2 continued)

Note: the value of the adaptive topography at $p = 0$ and $p = 1$ is 54 because mean fitness is just equal to the fitness of the fixed homozygote genotype, while its value at $p = 0.5$ is 59 ($\frac{1}{4}54 + \frac{1}{2}64 + \frac{1}{4}54$).

$$c. \hat{p} = \frac{W_{12} - W_{22}}{(W_{12} - W_{11}) + (W_{12} - W_{22})} = \frac{0.64 - 0.54}{(0.64 - 0.54) + (0.64 - 0.54)} = \frac{1}{2}.$$

$$d. \bar{W} = p^2a + 2pqb + q^2a,$$

where $a = 54$ and $b = 64$. Then

$$\frac{d\bar{W}}{dp} = 4p(a - b) + 2(b - a),$$

giving $\frac{d\bar{W}}{dp} = .064$. Or, if you used relative fitnesses, $a = .84$ and $b = 1$, giving $\frac{d\bar{W}}{dp} = .064$.

e. The expected change in gene frequency is given by

$$\Delta p = \frac{pq}{\bar{W}} \frac{d\bar{W}}{dp}.$$

At $p = 0.4$, $W = (.4)^2 54 + 2(.4)(.6) 64 + (.6)^2 54 = 58.8$. Hence,

$$\Delta p = \frac{(.4)(.6)}{58.8} 4 = 0.163.$$

f. Heterozygote superiority is a reasonable explanation for the maintenance of the polymorphism in nature if the fitnesses measured in the laboratory accurately reflect fitnesses in nature. However, there is no information on this, so the best we can say is that the heterozygote superiority observed in the lab is suggestive that it may explain the polymorphism observed in nature.

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3. Eckert and Barrett's investigation of the evolution of style-morph ratios in *Lythrum salicaria* provides one of the few definitive examples of genetic drift having a dominant influence on the evolution of an ecologically important character. Answer the following questions about their study:

- a. What is the expected morph-frequency equilibrium in large populations? Explain.
- b. Describe two patterns of deviation from this equilibrium that would be expected in small populations, and explain why those patterns are expected.
- c. Why is the short-styled morph eliminated more frequently than the other morphs in Canadian populations of this species?

ANSWER:

a. The expected morph frequencies are all equal to $\frac{1}{3}$. This is because the mating system generates a rare-morph advantage. In particular, because of intra-morph mating incompatibility, the rare morph, acting as a pollen parent, has a relatively greater number of potential mates than the more common morphs.

b. One type of deviation is that the actual morph frequencies would not be all exactly $\frac{1}{3}$. This is because genetic drift perturbs frequencies each generation and natural selection can not return the population to equal frequencies in one generation. The second type of deviation, is that one morph may be eliminated from the population. Drift again causes the elimination.

c. The bias is due to the fact that the "allele" for the short-style morph is dominant to the "alleles" for the other two morphs, which means that at the selection equilibrium the "short" allele is at lower frequency than the other two alleles. Since probability of elimination of an allele by drift is inversely proportional to initial allele frequency, the "short" allele, and hence the short-style morph, should be eliminated with greater probability.

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4. In the checkerspot butterfly, *Euphydryas editha*, populations in northern California are polymorphic at two electrophoretically detectable loci: *Pgm* (Phosphoglucomutase) and *Est* (Esterase), with two alleles (*F* and *S*) at each locus. A random sample of individuals in this population exhibited the following numbers of individuals of each genotype:

<i>Est</i> genotype	<i>Pgm</i> genotype		
	<i>FF</i>	<i>FS</i>	<i>SS</i>
<i>FF</i>	50	100	200
<i>FS</i>	75	0	75
<i>SS</i>	225	80	30

In addition, a set of crosses was performed to determine the degree of recombination between the two loci. Double heterozygote males were produced by crossing *FFFF* males with *SSSS* females. These double heterozygote males were then crossed with *FFFF* females and the following numbers of offspring were obtained:

Offspring genotype		Number of offspring
<i>Est</i>	<i>Pgm</i>	
<i>FF</i>	<i>FF</i>	90
<i>FS</i>	<i>FS</i>	90
<i>FF</i>	<i>FS</i>	10
<i>FS</i>	<i>FF</i>	10

Using this information, answer the following questions:

- Calculate the amount of linkage disequilibrium in the population.
- Calculate the recombination rate (fraction of gametes that result from recombination).
- Assuming that variation at both alleles is neutral (not subject to selection), what will the amount of linkage disequilibrium be after one generation?
- Twenty years (=20 generations) after the initial study the investigators returned and performed a similar study and found that the amount of linkage disequilibrium was $D = -0.10$. Propose a mechanism to explain the observed change, or lack thereof, in the magnitude of linkage disequilibrium. Briefly describe a set of experiments or observations that could be undertaken to evaluate your proposed explanation.

ANSWER:

- To calculate linkage disequilibrium, one needs to know the frequencies of the gamete genotypes. Assuming no differential mating success among genotypes and no differential fecundity, one can calculate the gamete frequencies from the diploid genotype frequencies. (Note, this can be done in this case because there are no double heterozygotes; hence, we don't need to worry about coupling and repulsion double heterozygote frequencies, nor about recombination.)

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(continuation of answer to question 4)

As an example, consider the frequency of the FF gamete, where the first F represents the allele at the *Est* locus and the second F represents the allele at the *Pgm* locus. Suppose each individual produces 1 gamete. Then the total number of FF gametes produced will be

$$50 + \frac{1}{2}(100) + \frac{1}{2}(75) = 137.5 \text{ .}$$

The total number of gametes produced is 835 (*i.e.* $50 + 100 + 200 + 75 + \dots + 80 + 30$). Therefore, the frequency of FF gametes is just

$$P_{FF} = \frac{137.5}{831} = 0.165 \text{ .}$$

In similar fashion, the frequencies of the other gamete types can be calculated:

$$P_{FS} = 0.344$$

$$P_{SF} = 0.362$$

$$P_{SS} = 0.129 \text{ .}$$

From these numbers, the allele frequencies can be calculated as

$$p_F = 0.165 + 0.344 = 0.509$$

$$q_F = 0.165 + 0.362 = 0.527 \text{ ,}$$

where p_F is the frequency of the F allele at the *Est* locus, and q_F is the frequency of the F allele at the *Pgm* locus.

Next, the magnitude of linkage disequilibrium for the population can be calculated using the formula

$$P_{FF} = p_F q_F + D \text{ , which rearranges to } D = P_{FF} - p_F q_F \text{ .}$$

Substituting the numbers above, one gets

$$D = 0.165 - (0.509)(0.527) = -0.103.$$

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b. To calculate the recombination rate, note that the FF FF and FS FS offspring are non-recombinants, while the other genotypes are recombinants. Thus the proportion of gametes that are recombinant, and hence the recombination rate, is

$$r = \frac{10+10}{10+10+90+90} = 0.1 .$$

c. After one generation without selection, the magnitude of linkage disequilibrium is

$$D' = (1 - r)D = (1 - 0.1) \times -0.103 = -0.0927$$

d. If there were no selection acting, then after 20 generations, the magnitude of linkage disequilibrium should be

$$D' = (1 - r)^{20} D = (1 - 0.1)^{20} \times -0.103 = -0.012$$

This value is much smaller than the observed -0.10 , which is not different from the initial value of D .

Hypothesis: Natural selection acts to maintain linkage disequilibrium. In particular, Selection favors both the FFFF and the SSSS genotype, while disfavoring others. (NOTE: Such a pattern of selection would lead to fixation of FFFF and SSSS, but could maintain significant linkage disequilibrium in the transient phase before fixation.)

An experiment would be to measure the fitness of each of the nine two-locus genotypes under natural conditions and determine whether the relative fitnesses were highest for the genotypes FFFF and SSSS.