EEB 245: Evolutionary Biology
Problem Set 6
Spring 2008

1. Compare the % sequence divergence observed in two genes in a pair of salamander species – one gene encoding a histone protein and the other encoding a hormone receptor. The **histone protein** requires a precise structure to function properly, while the structure of the **hormone receptor** depends on only a few key amino acids. You can assume that most of the observed variation in these genes has no effect on fitness.

a. Fill in the blanks below with >, < or = to indicate the relative difference in % divergence expected across species for each comparison.

3^{rd} codon positions in the histone gene		1^{st} codon positions in histone gene
3^{rd} codon positions in the histone gene		3^{rd} codon positions in the hormone receptor gene
1^{st} codon positions in the histone		1^{st} codon positions in the hormone receptor gene

b. Explain the reasoning that you used in filling in the blanks above.

>
</=
<

The histone protein gene is under strong selection to be conserved and functional, so you would expect more synonymous mutations than replacement (nonsynonymous) mutations to be fixed. Since changes in the third codon position are more likely to be synonymous, more of them will be fixed, resulting in more divergence in the third codon position across species than in the 1^{st} codon position in the histone gene. Changes to the 1^{st} codon position are more likely to change the amino acid present and, thus, more likely to be deleterious and selected against. For the second comparison, since changes in the third codon position are more likely to be synonymous and not change the amino acid sequence it is safe to assume that % divergence in the 3^{rd} codon for the histone protein gene and the hormone receptor gene are likely to be similar across species. For the third comparison, since only part of the hormone receptor gene is under strong selection, you would expect replacement changes to be neutral in some of the gene sequence. Thus more 1^{st} codon position changes would go to fixation in the hormone receptor gene sequence and you would see greater % divergence in this site across species than you would at the highly conserved 1^{st} codon site of the histone protein gene.

c. Suppose that you discover a gene in which most mutations that change the protein sequence increase fitness. How would you expect the rate of divergence at 1^{st} codon positions in the gene under selection compare to the rate of divergence at 1^{st} codon positions in the histone and hormone receptor genes? Why?

You would expect the most divergence in the 1st codon position of gene under strong selection, then in the histone or hormone receptor gene. Because changes in the protein sequence are beneficial in this gene, they nucleotide substitutions that cause amino acid substitutions have a higher probability of fixation than those that do not, leading to more divergence.

d. How would you expect the rate of divergence at 1st codon positions to compare to the rate of divergence at 3rd codon positions in the gene under selection for changes in protein sequence? Why?

You would expect a higher rate of divergence at the 1st codon position -- see 2c for explanation.

2. Why is the rate of fixation of neutral mutations (μ) independent of population size? (~ three sentences)

It is independent of population size because the rate of fixation = rate of production ($2N\mu$)*probability of fixation ($1/2N$). The 2N's cancel out. To clarify: In small populations the rate of production is small, but the probability of fixation is large. In large populations the rate of production is large, but the probability of fixation is small.

3. Height in human beings is influenced by many genes, i.e., it is polygenic or a quantitative trait. Like most quantitative traits, it is also influenced by environment. Thinking of the photographs showing heights of a haphazardly selected group of people at UConn that Dr. Holsinger discussed in class, answer the following questions:

a. What information about the two photographs we discussed allows you to infer that the environment individuals experience affects how tall they become?

The men in the older photograph (ca. 1900) were on average three inches shorter than the men in the current photograph. Because we don't have any evidence that there has been a genetic change (no selection, overwhelming migration, drift or mutation) we can conclude that this change in height is the result of a changed environment. Some of the most likely factors of this change are the nutritional and medical advances of the last century.

b. What is it about the distribution of heights in human populations that suggests many genes influence the height that an individual attains?

The fact that the distribution is continuous suggests that there are many genes influencing the height of an individual. The bell shape of this distribution corroborates this conclusion. If only one gene affected height in humans then there would only be a maximum of three different heights: short, medium, or tall. There would be twice as many people of medium height (heterozygotes). If there were two genes influencing height there would be five different heights with the most individuals being of medium height. Medium tall and medium short individuals would be moderately frequent and short and tall people would be rare. The more genes that have an influence on height the more the distribution of heights becomes continuous and resembles a bell curve.

4. A reptile enthusiast is attempting to increase the size of individuals in his cricket colony in order to provide bigger better meals for his scaly friends. He is using an artificial selection set up to select for increased body weight in his crickets and has determined the overall phenotypic variance ($V_P = 0.25$ mg^2) and how much of the phenotypic variance in body weight is due to nutrition ($V_E = 0.05$mg^2).

a. How much of the variance is genetic?

$V_P = V_G + V_E$ | **$V_G = 0.25\text{mg}^2 - 0.05\text{mg}^2$**
$V_P = 0.25\text{ mg}^2$ | **$\underline{V_G = 0.20\text{ mg}^2}$**
$V_E = 0.05\text{mg}^2$

b. What proportion of the phenotypic variance is due to genotypic differences (i.e. what is the heritability?)

$h^2 = V_G / V_P$ | **$h^2 = 0.20\text{ mg}^2/0.25\text{mg}^2$**

$h^2 = 0.8$

5. Under artificial selection for increased body weight, what will be the response to selection (R), after one generation, for the following values of phenotypic variance (V_P), additive variance (V_A), environmental variance (V_E), and selection differential (S)?
a. $(V_P) = 2.00$ grams^2, $(V_G) = 1.25$ g^2, $(V_E) = 0.75$ g^2, (S) = 1.33 g
b. $(V_P) = 2.00$ grams^2, $(V_G) = 0.95$ g^2, $(V_E) = 1.05$ g^2, (S) = 1.33 g
c. $(V_P) = 2.00$ grams^2, $(V_G) = 1.25$ g^2, $(V_E) = 0.75$ g^2, (S) = 2.67 g
If the parameters remain the same for the successive generations of selection and the initial mean weight is 10 grams, what is the expected mean after two generation of selection in each case?
(Futuyma)

a. **R = (1.33)(1.25/2.00) = 0.83; after two generation of selection mean = 10 + 0.83 + 0.83 = 11.66**
b. **a. R = (1.33)(0.95/2.00) = 0.63; after two generation of selection mean = 10 + 0.63 + 0.63 = 11.26**

c. **a. $R = (2.67)(1.25/2.00) = 1.67$; after two generation of selection mean = $10 + 1.67 + 1.67 = 13.34$**
(recall $R = h^2 S$; $h^2 = V_G / V_P$)

6. Large tadpoles of the common toad (*Bufo bufo*) are able to outcompete smaller individuals for resources resulting in low survival of small individuals to metamorphosis and adulthood. Small body size and low energy stores are traits correlated with low post-metamorphic survival in many amphibian species (Scott et al. 2007). Studies suggest that the heritability of body weight in a Connecticut population of toads is 0.3. Body weight measurements were taken on a sample of newly emerging metamorphic toads and the mean body weight was found to be 2.42 g/cm. Several weeks later, toads were sampled at random and mean body weight was recorded at 3.74 g/cm. Assume individuals maintain a constant weight between first weight sampling and second weight sampling. What do you predict will be the mean body weight will be of newly emerging metamorphs of the next generation?

$R = h^2S$, where
R = response to selection (mean offspring phenotype – mean parental phenotype)
S = selection differential (population mean after selection – mean before selection)
h^2= heritability

$R = (0.3)\ (3.74\text{g/cm} – 2.42\text{g/cm})$
$R = 0.396\text{g/cm}$
Mean body weight of newly emerging metamorphs = 2.42g/cm* + 0.396g/cm
= <u>2.816g/cm</u>

***add response to mean of current generation BEFORE selection**

7.
Imagine a species in which brothers are often able to increase the reproductive success of their sisters by delaying their own attempts to reproduce.
Suppose that a brother delays reproducing and helps his sister rear her 6 offspring. The following year he reproduces 4 of his own offspring.
Meanwhile, another male in the population does not help his sister. The sister raises her 3 offspring alone and the male produces 6 offspring.
The relatedness, *r*, between full-siblings is 0.5. Using what you know about the evolution of altruism, would you expect evolution to favor delayed reproduction of brothers, i.e., would this behavior be favored by natural selection?

First, we need to figure out what the COST (c) and BENEFIT (b) of the delay strategy for the brother. If the brother delays reproduction, his own reproductive output changes from 6 to 4 offspring; at the same time he gains 3 offspring via his sister. So, c = 2, b =3. We need to include the element of relatedness, r, which equals 0.5.

Using the either of the two equations:

$$Br - c > 0$$

or

$$(b/c)*r > 1$$

Using the first equation, we find that: 3(0.5) – 2 = -0.5 which is NOT greater than 0. Thus we do not expect the delay strategy to evolve. It's simply too costly for the brother. For practice, figure out what the minimum benefit has to be in order for this strategy to evolve.

8. Crows (*Corvus brachyrhynchos*) will mob, work together, to chase away predators and some young will help their parents raise their siblings. Which behavior would you predict to be favored by kin selection. Suggest a hypothesis to explain why young crows in some populations might help at the nest while in other populations they nest on their own. (Freeman & Herron)

A researcher observing young crows helping their parents raise siblings could hypothesize this is due to kin selection.
Young crows in populations with limited nest sites might help their parents until a nest site is available. They would increase their indirect fitness by helping raise siblings. They could potentially increase their chances of inheriting the parents' nest site.
Crows in other populations could nest on their own if nest sites are available, thereby increasing their direct fitness.

9. Blue jays (*Cyanocitta cristata*) seem to be better than American robins (*Turdus migratorius*) at recognizing individuals. In one study (Schimmel & Wasserman 1994), blue jays raised with American robins could distinguish strange from familiar robins better than the robins themselves. Do you think these species differ in occurrence of kin selection or reciprocal altruism (or both)? Why?
(Freeman & Herron)

Reciprocal altruism requires animals to be able to recognize individuals. (This allows them to "keep track" of 1) those who they have donated to and thus can expect a donation from in return and 2) those who have given and thus the act should be reciprocated.)
We should not be surprised to observe reciprocal altruism in blue jays but we would not expect to observe it in robins.
Kin selection in robins would be unlikely as they cannot distinguish between strange (non-relatives) and familiar (relatives) robins. Kin selection in blue jays would be more likely as they have demonstrated the ability to distinguish between strange (non-relatives) and familiar (relatives) individuals.

10. Males of many species often attempt to mate with inappropriate partners. Ryan (1985), for example, describes male túngara frogs clasping other males. Anecdotally, male sage grouses have been observed to attempt to mate with cow patties if they

slightly resemble a receptive female sage grouse (see 'What Females Want and What Males Will Do' on PBS, http://www.pbs.org/wnet/nature/females/). Would a female túngara frog or a female sage grouse make the same mistake? Why or why not? (A general answer – applicable to a wide range of sexually reproducing species – is best). (adapted from Freeman & Herron 2001)

It is generally assumed that it is cheap and easy for males to produce sperm so males of many species can afford the mistake of mating with the wrong sex or wrong species or, in some cases, inanimate objects. Since the energetic costs of sperm production are low, the benefits of potentially mating with females of the correct species outweigh potential costs related to instances of mistaken identity. Females, on the other hand, are generally considered to require a lot of resources and energy to make eggs and brood or rear young. If there is a restriction on the number of mating opportunities for the female of a species, females that are selective will have greater reproductive success than females that mate indiscriminately. Species recognition signals have evolved in many species because females who can recognize conspecific males have higher reproductive success than those females who are less discriminate and potentially wasted important reproductive resources. If such a recognition system has a heritable basis, a female's offspring will also mate discriminately with members of their own species – increasing the frequency of those alleles in the gene pool.

11. In three-spine sticklebacks (a small fish common in marine and freshwater environments in North America), males search out a territory in shallow water and construct a nest in which females lay eggs. The males mate with a few females over a span of several days and then guard the nest until the eggs hatch and the young leave the nest. The females leave the nest as soon as the eggs are laid and may mate with several different males over the course of the breeding season. Females choose to mate with males based on many factors – three of the most important being: (1) territory quality, (2) male nuptial coloration, and (3) courtship vigor. Given what you know about sexual selection, would you expect male-male competition to be an important evolutionary force in this species? Explain why or why not.

One of characteristics on which females base their choice is territory quality. Males can potentially compete for females INDIRECTLY by acquiring a high quality territory in order to attract females to their nest. Males may potential use combat (fighting) or threat signals to set up territory boundaries in which they will make a nest. If females are more apt to search out good territories and then choose among the males on good territories it could increase a male's reproductive fitness to obtain a preferred nesting area.