Summer 2005: Exam 1 Key **Name _____KEY__________________________**

Part I: Definitions. *[5 points for each term]* For each term, provide a brief definition *that also indicates why the term is important in evolutionary biology*. Where I've provided two terms, choose one to define. *Circle the one that you're defining.* Where appropriate, feel free to provide an example or draw a diagram to accompany your written answer.

1. Natural selection **or** the struggle for existence

   Natural selection: the process by which individuals in a species that have a phenotype that is better suited to a particular environment either survive or reproduce at a higher rate than other individuals having different phenotypes. Important because it is the mechanism proposed by Darwin (in combination with heritability of the traits and a struggle for existence) which could explain how organisms become adapted to a particular environment

   Struggle for existence: the fact that all organisms produce more offspring than the resources in the environment can support. Important because this struggle sets up the circumstances where individuals with better phenotypes for a particular environment will be more fit under natural selection.

2. Parsimony **or** positional homology

   Parsimony: generally, the rule that the simplest explanation is the best. In the context of phylogenetic reconstruction we use it as an optimality criterion for choosing the best phylogenetic reconstruction, i.e., the tree requiring the least number of steps (evolutionary changes) is considered the best

   Positional homology: when aligning sequences (DNA or protein) for phylogenetic reconstruction, we strive to have each column represent the true evolutionary history of a particular position in a sequence. This is positional homology. Important because only if our alignment has positional homology can we build the best possible phylogenetic tree.

3. Vicariance event

   A large-scale geological or geographical event, such as mountain building, plate tectonics, or a river changing course. Important because these sort of events can subdivide populations and isolate them, leading to allopatric speciation

4. Tension zone **or** reinforcement

   Tension zone: a special type of hybrid zone where the hybrids are less fit than their parents. Important because a tension zone sets up the conditions where assortative mating is selectively favored, which could lead to reinforcement and speciation of the different types on either side of the tension zone

   Reinforcement: a process by which incipient speciation, often in a hybrid zone, might be driven by natural selection to full speciation. It consists of two ecotypes that produce hybrids that are less fit than either of the parental types, leading to selection for assortative mating. If sufficient genetic variation for mating preference exists and the hybrids are sufficiently unfit, this could lead to prezygotic isolation of the two types, hence speciation

5. Hardy-Weinberg equilibrium

   The neutral or null model for how genes in at a locus in a population go from one generation to the next when the population is infinitely large, has random mating, no mutation, no migration, and no selection. Important because it is the foundation for all of population genetics and is used for adding other factors that are evolutionarily important

6. Concentrated changes test **or** Phylogenetically independent contrasts

Concentrated changes test: a statistical test for discrete characters, which assesses the probability of a particular combination of putative adaptive events and their hypothesized selective agent on a particular phylogenetic tree. Important because it is a modern comparative method for assessing the support for a character being an adaptation.

Phylogenetically independent contrasts: a statistical test for continuous characters, which assesses whether the association between a putative adaptive character and its hypothesized selective agent is significant. Important because it gives us way of assessing the support for an adaptive hypothesis that takes account of the character's phylogenetic history

7. Fitness (in a population genetic context) **or** genetic drift

Fitness: w or 1-s, that is, the probability that a particular genotype will survive and reproduce relative to the other genotypes in the population. Important because it is the essential concept in population genetics that allows us to determine how adaptive evolution will take place.

Genetic drift: a population genetic process where the genotypes in the previous generation are sampled at random leading to changes in gene frequencies from one generation to the next that are created by chance events, i.e, it is a form of evolution that is neutral or not due to selection.

Part II: Short answer. Make your answers economical and to the point. Draw a labeled diagram if that will help you to make your point.

8. Why is the phrase "struggle for existence" more appropriate to describe what happens under natural selection than "survival of the fittest"? *[6 points]*

"Survival of the fittest" implies that natural selection is producing an absolutely most optimal phenotype, whereas we know that, instead, the survivors of natural selection are just the individuals with the best phenotype given the particular gene combinations available at the time and the requirements for survival and reproduction in a particular environment. The "struggle for existence" better reflects the conditional relationship between genotypes and an environment without implying an absolutely most optimal phenotype is being produced by evolution.

9. In a situation of dominant advantage, what is the fate of the recessive allele after many rounds of selection (assume the population size is very large)? Why? *[6 points]*

After many rounds of natural selection if the dominant allele is favored, both the dominant and the recessive alleles will still be in the population although the recessive allele will be at a lower frequency. The recessive allele cannot be removed entirely from the population because as its frequency decreases, the majority of the individuals carrying the recessive allele will be heterozygous, where the dominant allele will mask the presence of the recessive allele, effectively shielding it from removal by natural selection.

10. How do ring species serve as examples of population genetic variation within a single species eventually becoming so great that two species are formed? *[8 points]*

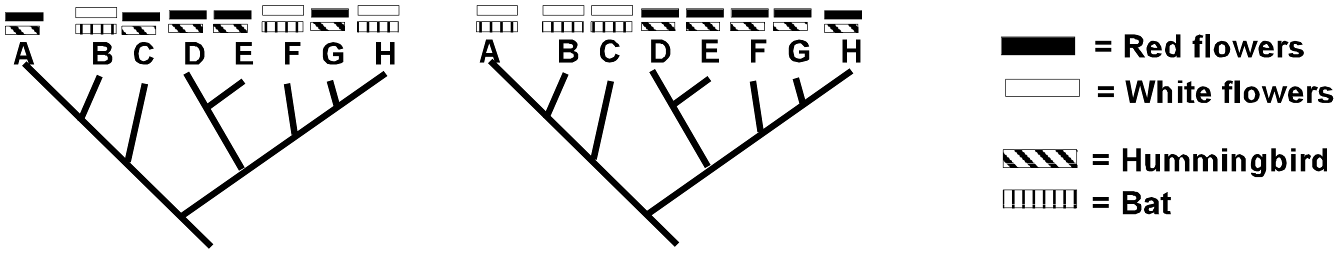
Ring species are just a special case of species that have evolved to be different along an environmental gradient. Geographically the gradient runs in a circle or a ring rather than being linear, e.g., from north to south. In many cases, species experiencing an environmental gradient will evolve different characteristics that make them better suited to the environment at that point on the gradient. In the case of a ring species, the populations of the species along the different sides of the gradient evolve independently until the ring comes back upon itself. In some cases, e.g., the salamanders in California, the populations from either side of the ring have evolved to the point that they no longer recognize each other as appropriate mates and preferentially mate only with members of their own population. Since all the evolution that took place along the gradient occurred by ordinary microevolutionary processes, this shows that sufficient variation can evolve by these mechanisms to cause isolation between populations that arise from a single species.

11. Why might host shifts by endoparasites provide the opportunity for sympatric speciation? *[7 points]*
Sympatric speciation requires two morphological types to speciate due to reinforcement brought about by being better adapted to two sympatric environments. Because endoparasites live in close association with their hosts and each host species is likely to provide a different environment for the parasite, it is reasonable to expect that a host switch will lead to selection that favors different genotypes of the endoparasite in each host. Because the endoparasites on the host live and often mate in the host, this should lead to ample opportunity for reinforcement to take place and hence sympatric speciation.

12. Remember that we divided homologies into symplesiomorphies, synapomorphies and autapomorphies. Why is it that we can only use synapomorphies to unambiguously group all of the descendants from a common ancestor? *[7 points]*
[You could have drawn diagrams to illustrate your points.] Synapomorphies are the only type of homology that include all of the descendants from a single common ancestor. Therefore they are the only type of homology that will guarantee that when we group a set of species into a clade (monophyletic group) we will have all of the members of the clade. Symplesiomorphies only include some of the descendants of a common ancestor, so different Symplesiomorphies can lead to different and inconsistent groupings of species. Autapomorphies are only found in a single species and therefore cannot be used to determine membership in a clade.

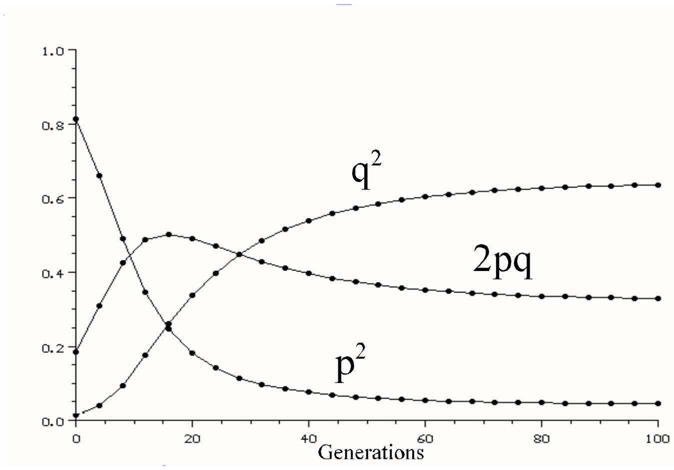
13. How do we distinguish homologies from analogies (homoplasies)? Which of these can we use to distinguish homologies and analogies when we use DNA sequence data? *[7 points]*
There are three methods for distinguishing homologies from analogies
– Determine whether a feature is made up of the same underlying parts, e.g., bones
–Determine whether the underlying parts in the same relationship to one another, e.g., are the bones in the same relative positions to one another
–Determine whether the features have the same developmental sequence and arise from the same origin during development
Unfortunately, none of these can be used to determine homology when using DNA sequence data. Instead we have to assign homology and analogy after the fact or aposteriori.

14. You are studying adaptation in a group of plants and have a phylogeny from independent evidence. Given the following two trees and relationships between flower color and pollinators, which of the two provides stronger evidence for adaptation? Explain your answer. *[5 points]*



The left tree offers better evidence for adaptation because there have been at least three transitions between red and white flowers and their respective pollinators. On the right there has only been one transition (of red to white or white to red; we can't tell which). When we are trying to infer whether their has been an adaptation to a particular environmental variable in a phylogenetic context, we have to take a statistical approach. The larger the number of independent events where the character changes with the environment, the stronger the support for the association being significant.

15. If you were presented with the following graph of genotype frequencies in a population, what type of selection would you say is operating. Justify your answer. *[5 points]*



Ok, this was a tough one. It might look like this is a case of recessive advantage because the recessive homozygote is increasing in frequency, but note that it is not asymptotically approaching a frequency of 1.0, which it should be doing if this is a case of recessive advantage. Instead, it is approaching an equilibrium frequency of approximately 0.7. In fact, all of the frequencies are approaching equilibria. We only know of two things that reach equilibrium frequencies for both alleles that are non-zero: Hardy-Weinberg equilibrium and heterozygous advantage. This can't be H-W equilibrium because it is taking more than one generation to get to the equilibrium, so this is more likely to be heterozygous advantage.

Part III: Essay.

Answer *one* of the two choices (A or B) for each of the two essay questions that follow. *[15 points each]*

16. You want to study whether blood types in a group of primates evolved as an adaptation for resistance to variants of rhinoviruses. Answer how you might go about the parts the analysis in either A or B below.
A. What steps would you go through to generate a phylogeny of the primates? Assume you're going to use DNA sequence data to generate the phylogeny. Why do you need a phylogeny anyway?
B. Assume you've already generated the phylogeny. How would you go about assessing whether you have evidence that the blood types are possibly adaptations for resistance to different types of rhinoviruses? Explain why you chose to use a method for discrete or continuous characters.

A. To generate the phylogeny, I would

1. Attempt to choose a region of DNA that is evolving at the right rate to meet the assumptions of maximum parsimony as well as possible, i.e., that evolutionary change is rare and hence there is a low chance of a character changing multiple times on a branch of the tree.
2. Having chosen the DNA sequence, I would generate the sequence for each of the species of primates of interest.
3. Align the sequences to have maximum positional homology. If some areas cannot be aligned with confidence, they will be left out of the analysis.
4. Use the aligned sequences to find the most parsimonious tree among all of the possible trees that could be reconstructed with the species of interest. [If there are too many taxa in the analysis to search all of the trees exhaustively, I'll use a heuristic to try and search through tree space to find the best tree.]

5. Having found the most parsimonious tree, I'll root it using an outgroup consisting of the closest know relatives.

B. Blood types (A, B, AB, O) are discrete characters and rhinoviruses also fall into discrete types, so to test whether blood types are an adaptation to different types of rhinoviruses, I'll map the blood types and the rhinoviruses onto the primate phylogenetic tree and then use parsimony to determine the number of times blood types have changed and the number of times the rhinoviruses have changed type. Then to test whether the number of changes of each is significantly correlated, I would use the concentrated changes test to assess the probability of the blood types and rhinoviruses being associated by chance. If there is a low probability of them having been associated by chance then it may be that the blood types have evolved as adaptations against rhinoviruses.

17. **A.** You come upon a hybrid zone and think that the different individuals on either side of the zone may be in the process of speciating. What evidence could you collect to test whether that might be true and what patterns in the data would support your hypothesis?

B. A population of lions, isolated in the Ngorongoro Crater in Kenya, has the following genotype frequencies at the α-hemoglobin locus.

AA	AB	BB
0.1296	0.4608	0.4096

Is the population in Hardy-Weinberg equilibrium? Why?

A. I would first determine whether the hybrid zone is a tension zone. I would test for this by measuring whether the hybrids have lower fitness (decreased survival and/or fecundity) relative to their parents. If there is a tension zone, I would then try to determine whether there is evidence for assortative mating developing in the region of the hybrid zone. I would expect there to be greater evidence for assortative mating close to the hybrid zone than away from it because the individuals living closer to the zone are more likely to produce hybrids, which means they are more likely to produce offspring of reduced fitness without assortative mating than individuals living far from the hybrid zone.

B. First we need to determine the gene frequencies in the population from the genotype frequencies. There are several ways you can do this mathematically. I'll just present one. We know the frequency of the AA genotype is 0.1296, and it has only the A allele. We also know that the frequency of the AB genotype is 0.4608, but it has both the A and the B alleles, so we have to halve its value to get the frequency of the A allele in it. Therefore the frequency of the A allele is

$$\begin{array}{r} 0.1296 \\ \underline{+\ (0.4608*0.5)} \\ 0.36 = p \end{array}$$

Since the H-W equation is $p^2 + 2pq + q^2$, we can check if the population is in equilibrium by squaring p.

$(0.36)^2 = 0.1296$, which matches the frequency of the AA genotype. Hence, the population is in H-W equilibrium.