Evolutionary Genetics Midterm 2008

Name_____ Student #_____

Signature_____

P1:	/10
P2:	/10
P3:	/12
P4:	/18
P5:	/23
P6:	/12
TOT:	/85

The Rules:

(1) Before you start, make sure you've got all six pages of the exam, and write your name legibly on each page.

(2) Show your work on calculation questions. Use the back of the paper if needed, but make sure to tell us when to look on the back. *Calculations are **required** for full credit.*

(3) If a calculation question requires you to start with the result from a previous calculation, and you were unable to answer the earlier question, you may make up a reasonable number to start with and still potentially get full credit on the second question.

(4) State any required assumptions you have made to complete the question.

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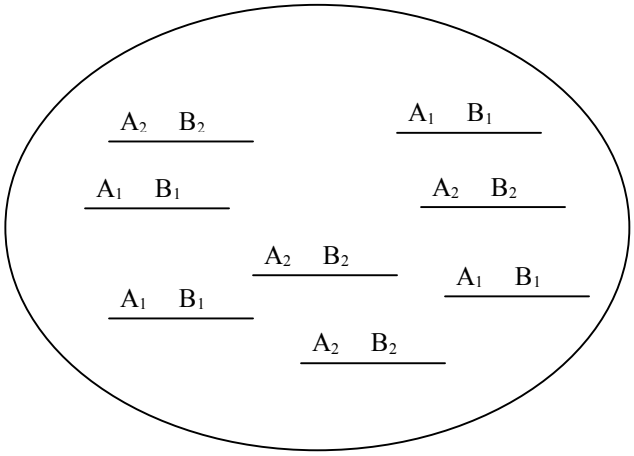
1. Match the scientist in the left column with one of their major contribution on the right. (Use the letter corresponding to each biologist only once.) (6 points)

a) Lamarck	___ Uniformitarianism
b) Haldane	_a_ Inheritance of acquired characters
c) Malthus	_f__ Binomial system of nomenclature
d) Wallace	_b_ Mutation-Selection balance
e) Fisher	_c_ Theory of overpopulation
f) Linnaeus	___ the 'Scala Naturae' or chain of being
	_e_ Linking Mendelian inheritance to quantitative variation
	_d_ Evolution by natural selection

2. Genetic drift leads to loss of genetic variation in populations through random sampling effects. A rare species of marmots exists in 10 small mountain top populations (<100 mature individuals). While these populations are isolated, they do occasionally exchange migrants (averaging 1 new migrant into each population every 2 years). Consider a neutral locus (in which all alleles are equally fit) subject to drift in this set of populations. In 1-2 sentences, describe what you think the relative contribution of mutation versus gene flow (via migration of individuals between populations) will be on levels of genetic variation at this neutral locus within populations of this species. (4 points)

Gene flow is likely to be more important than mutation in this type of situation. We know that mutation rates per locus are quite low (10^{-4} - 10^{-6}). Given the migration rates described here, migration is more important.

3. The circle below represents a gamete pool for an organism with a single chromosome. There are two loci, A and B, physically linked on this chromosome. Each locus has two alleles, A_1 and A_2 at the A locus, and B_1 and B_2 at the B locus. (10 points)



a) Calculate D for this gamete pool.

$f(A_1B_1)=1/2, \quad f(A_2B_2)=1/2$
$f(A_1B_2)=0, \quad f(A_2B_2)=0$

$D=x_{11}*x_{22}-x_{12}*x_{21}$
$D=(1/2)(1/2)-0=1/4$

b) If the two loci are 10 map units apart, how many generations would it take for D to reach 0.000001?
If the two loci were separated by >45 map units do you predict it will take longer for D to reach 0.000001? Why?

$D[t]=(1-r)^t D[0]$
$0.000001=(1-0.1)^t 0.25$
$\ln(0.000001)=t\ln(0.9)+\ln(0.25)$
$t=-13.81551=t(-0.1053605)-1.386294$
$t=118$

If the loci were > 45 map units apart? Anything along the lines of: With higher rates of recombination disequilibrium decays faster because crossing over breaks apart the association created by physical linkage. You can also give marks if they can work it out and show that t=21.

c) In general, which of the following factors can cause gametic disequilibrium? (Circle all that apply.)

i. Physical linkage - **yes**
ii. The random death of a large fraction of the population. - **yes**
iii. Mating among relatives - **yes**
iv. Selection on a multi-locus trait - **yes**
v. High rates of recombination – **no will decouple an association**

4. The common morning glory (*Ipomoea purpurea*) is polymorphic for flower colour. The anthocyanin biosynthetic gene (*ABG*) that underlies colour polymorphism in flowers has two alleles *ABG-1* and *ABG-2*. Individuals that are homozygous ABG-2/ABG-2 are white, while individuals that are ABG-1/ABG-1 are red, and ABG-1/ABG-2 are pink. Anthocyanins are known to play a role in water relations in plants. Researchers surveyed the numbers of each genotype in a population in 2006 and 2007. A drought occurred in 2007 and researchers were able to estimate the relative fitnesses of the three flower types under drought conditions. The relevant data are given in the table below: (12 points)

YEAR	RED	PINK	WHITE
2006: Numbers of adults	611	989	400
2007: Relative Fitnesses	0.632	1	0.815

a) Is the adult population of *Ipomoea purpurea* surveyed in 2006 at Hardy-Weinberg equilibrium for the ABG locus? Show your work.)

ABG-1/ABG-1=red
ABG-1/ABG-2=pink
ABG-2/ABG-2=white

observed
f(red)=611/2000=0.306
f(pink)=989/2000= 0.494
f(white)=0.2

under HWEq expected
f(red)=p^2= 0.333
f(pink)=2pq= 0.488
f(white)=q^2= 0.179

f(ABG-1)=0.3055+1/2(0.4945)= 0.577
f(ABG-2)=1-f(ABG-1)= 0.423

Comparing observed and expected, they look similar, therefore, yes population surveyed in 2006 is in HW equilibrium

b) Given the relative fitnesses, what form of selection is acting on this population? What is the magnitude of the selection coefficient in the genotypes ABG-1/ABG-1 and ABG-2/ABG-2? Are these genotypes at an equal advantage/disadvantage? How much do they differ in their selective advantage/disadvantage?

Heterozygote advantage (overdominance or stabilizing selection are also answers)
The selection coefficient for ABG-1/ABG-1:
$1+s_1=0.632$, thus s= -0.368, red flowers are at a selective disadvantage
The selection coefficient for ABG-2/ABG-2:
$1+s_2=0.815$, thus s= -0.185, white flowers are at a selective disadvantage
These two genotypes are not at an equal disadvantage but rather ABG-1/ABG-1 is at an almost two fold disadvantage. They can also say they differ by a magnitude of s=0.183.

c) Assuming relative fitness is constant over time, sketch the frequency of the ABG-1 allele over time. Do not calculate the equilibrium frequency, but just sketch the general shape of the graph.

Key points to look for in the graph:
They must be plotting f(ABG-1) allele.
They must use the starting frequency of 0.577, not some (or several) random starting frequency(ies).
All axes should be clearly labeled.

d) Confirm your predictions by determining the equilibrium frequency of ABG-1. How does the magnitude of the selection coefficients described in b) affect the value of the equilibrium frequency of ABG-1?

Using $\hat{p} = \frac{W_{Aa} - W_{aa}}{2W_{Aa} - W_{AA} - W_{aa}} = 0.3345$

The selective disadvantage faced by the homozygote ABG-1/ABG-1 is larger than the selective disadvantage faced by the homozygote ABG-2/ABG-2, thus the equilibrium frequency should be lower. If the two were equivalent then, $\hat{p}=0.5$, but in this case $\hat{p}<0$.

5. Provide three reasons why the frequency of allele *A* might increase from one generation to the next within a haploid population. [**Explain each answer in one sentence.**] (6 points)

a) Reason: higher relative fitness of A Explanation: If the relative fitness of A is greater, it will rise in frequency and go to fixation.

b) Reason: hitchhiking Explanation: By association with another selected locus (including due to physical linkage).

c) Reason: Genetic Drift Explanation: Chance sampling effects could lead to a rise in frequencydue to chance alone.

6. Answer either **a) or b).** Do not answer both. (If you answer both, we will count the **lower** grade.)

   a) Derive the expression: $\Delta p = p_{t+1} - p_t = \frac{(W_A - W_a) p_t q_t}{\overline{w}_t}$

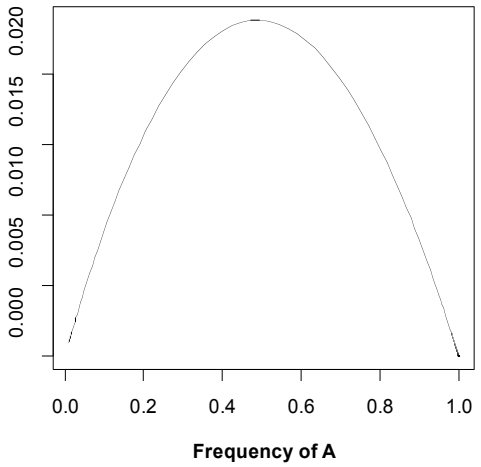
   b) Given relative fitnesses of W(A)=1.1 and W(a)=1 and a starting frequency of p[t]=0.01, sketch the change in allele frequency as a function of p[t].

ANSWER PART 6 marks a)

The main relationship required for this derivation is q[t]=1-p[t]. They can examine the numerator only as long as they indicate that's what they're doing and include it back at the end.

ANSWER PART 6 marks b)

The correct graph *must* have Δp on the y-axis and p on the x-axis. No marks for showing the allele frequency as a function of time. They must use the starting frequency of p=0.01.
The change in allele frequency is the greatest when p=0.5, in other words when there is the maximum genetic variance.



7. In the Grant and Grant (2002) article discussed in tutorial, the authors state, "Evolution of a population is contingent upon environmental change, which may be highly irregular, as well as on its demography and genetic architecture." Briefly discuss this statement given the findings of their 30 year study. (6 points)

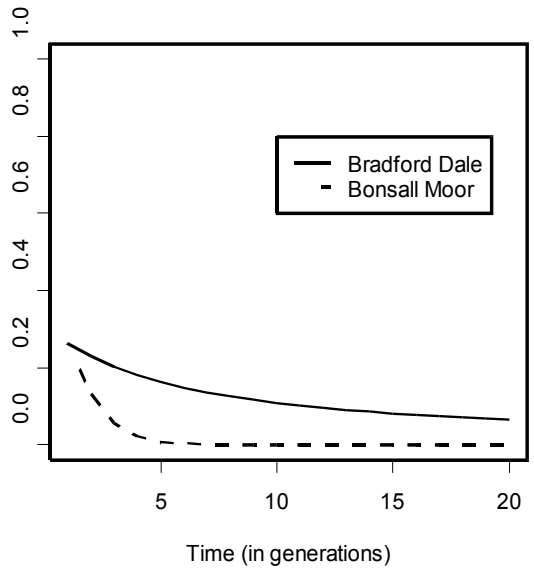
Answer should reflect an understanding of the synergistic effects of environmental change (e.g. effects of el-nino and el-nina on selection on beak shape and size), as well as the effects of demographic changes on the likelihood of hybridization.

8. *Thlaspi caerulescens* (Brassicaceae) grows in soils enriched with heavy metals. A friend is studying this plant and has surveyed variation at a single locus in two different populations (Bradford Dale and Bonsall Moor) in the British Isles. She surveyed seedlings and then followed the plants to adulthood. In addition, she took soil samples and found that Bradford Dale soils were extremely high in zinc, while in Bonsall Moor soils were high in lead. The number of seedlings and surviving adults of each genotype are given below for each populations. (15 points)

POPULATION	Heavy metal found in soil	Life History Stage	BB	Bb	bb
Bradford Dale	Zinc	Seedlings	491	418	91
		Adults	245	209	16
Bonsall Moor	Lead	Seedlings	682	409	409
		Adults	227	48	48

a. Assuming relative fitness for each genotype at each location is constant over the next 20 generations, sketch a graph of f(b) vs. time for each of the populations. (Do not calculate the actual frequencies for all 20 generations instead just sketch the general shape of the graph). Remember to label your x and y axis.

For your starting allele frequency, either starting allele frequencies in adults or seedlings was acceptable.
in Bradford Dale: SEEDLINGS: f(b)=0.3 or ADULTS: f(b)=0.284
in Bonsall Moor: SEEDLINGS: f(b)=0.41 or ADULTS: f(b)=0.264



b. List three factors that affect the rate of evolution at this locus, and compare their effects in the two different populations. Explain the pattern.

Three factors that affect the rate of evolution at locus B are:

1. initial allele frequency: In BD the initial allele frequency was $f(b_{t=0})=0.284$ while in BM it was $f(b_{t=0})=0.264$.
2. selection coefficient: In BD, the selection coefficient was s= 1.84 while in BM it was s=1.83
3. dominance coefficient: In BD, the dominance coefficient was h=1 and in BM it was h=0.

The rate of decrease of the b allele is faster in BM and it is ultimately lost from the population (i.e., f(b)=0). The selection coefficients in the two populations were approximately the same, but the dominance coefficient and the starting allele frequencies were different. In BM the allele starts at a lower frequency and this may contribute in a small way to difference in the rate of decrease. It is the dominance coefficient, however, that causes the difference in the rate of evolution. Because h=0 in BM, the heterozygote has the same fitness as the disfavoured homozygote bb, selection acts against both genotypes driving the allele b to extinction. On the other hand, because h=1, in BD, the heterozygote has the same fitness as the selectively advantageous homozygote BB, thus the allele never goes completely to extinction.

NOTE: The h's will be reversed if you scaled by BB and the selection coefficients will be s~-0.65 see below.

To get above answer you could have worked out the following:

Population	**Bradford Dale**			**Bonsall Moor**		
genotype	BB	Bb	bb	BB	Bb	bb
Freq before selection (seedling stage)	0.491	0.418	0.091	0.455	0.273	0.273
Freq after selection (Adult stage)	0.521	0.500	0.034	0.703	0.149	0.19
Absolute Fitness	0.521/0.491=1.061	1.063	0.374	1.545	0.545	0.545
Relative Fitness	2.84	2.84	1	2.83	1	1

Relative Fitness (Scaled by bb)	1+s (s=1.84) selective advantage	1+s (h=1)	1	1+s (s=1.83) selective advantage	1 (h=0)	1

OR

Population	**Bradford Dale**			**Bonsall Moor**		
genotype	BB	Bb	bb	BB	Bb	bb
Freq before selection (seedling stage)	0.491	0.418	0.091	0.455	0.273	0.273
Freq after selection (Adult stage)	0.521	0.500	0.034	0.703	0.149	0.19
Absolute Fitness	0.521/0.491 =1.061	1.063	0.374	1.545	0.545	0.545
Relative Fitness	1	1	0.352	1	1	0.352
Relative Fitness (Scaled by BB)	1	1+hs (h=0)	1+s (s=- 0.648) selective disadvantage	1	1+hs	1+s (s=-0.647) selective disadvantage

9. What is the equilibrium frequency of a completely recessive allele arising with a mutation rate of $4x10^{-6}$ and a relative reproductive fitness in homozygotes of 0.8. What would the equilibrium frequency be if the allele was partially dominant, with h=0.05? How does dominance (the heterozygous effect) affect the equilibrium frequency of a harmful allele? (8 points)

complete recessivity h=0

$\hat{q} = \sqrt{\frac{\mu}{s}}$ = sqrt(4x10^{-6}/0.2)=4.5x10^{-3}

h=0.05

$\hat{q} = \frac{\mu}{hs}$ =4x10^{-6}/(0.05)*(0.2)=4x10^{-4}

The five percent heterozygous effect reduces the equilibrium frequency by more than an order magnitude.

10. A strain of mice was selected for decreased blood cholesterol levels. Over five generations, the mean blood cholesterol level of the mouse population decreased from 2.26 mg/ 100 ml to 2.11 mg/ 100 ml. The selection differential over this time period averaged 0.06 mg/ 100 ml per generation. (12 points)

a) What is the narrow sense heritability, h^2, for blood cholesterol levels in this strain?

R = h^2S

R = 0.15

S = 0.06 X 5 = 0.30

h^2 = R/S = 0.5

Note that if you didn't multiply by 5, you obtained a heritability > 1, which is not possibl

b) If the phenotypic variance in the population at the start of the experiment is 8.35, what is the estimated additive genetic variance for blood cholesterol levels?

$h^2 = V_A/V_P$ $V_A = 0.5 \times 8.35 = 4.17$

$h^2 \times V_P = V_A$

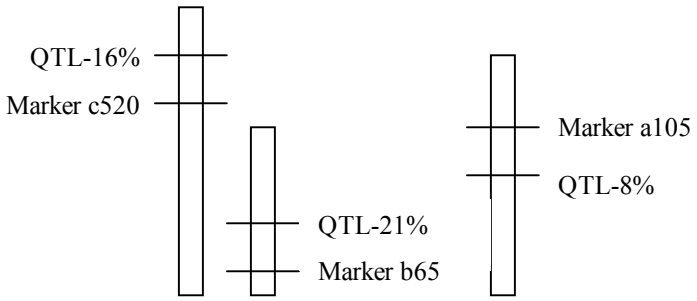
Again, if you used the wrong heritability from above, you would get additive genetic variance greater than the total phenotypic variance, which is not possible

c) After another 100 generations of selection using the same selection differential, the strain shows no further response to selection, and blood cholesterol levels plateau at around 1.92 mg/ 100 ml. In two sentences, explain what could account for this phenomenon and what might allow the population to respond to selection once again.

This observation suggests that V_A has been exhausted. Among the possible ways to get a response once again are:

- bring in new genetic variation by crossing the mice with other mice.
- change the environment (because this may change the phenotypic variance)
- change the direction of selection.

d) In a subsequent study, this same research team undertook a QTL analysis of a number of traits, including blood cholesterol levels in mice. They found three significant QTLs, explaining 8%, 16% and 21% of the phenotypic variance in blood cholesterol in an F2 population. They now have the option of using marker assisted selection, in which they can choose mice with a particular genotype at a marker locus to aid in selection for lower blood cholesterol levels. How might they use the QTL information to aid in selection?



Knowledge of the location of QTL affecting the trait would allow researchers to use associated markers to inform crossing schemes. For example, mice with markers that are associated with lower blood cholesterol can be chosen for interbreeding.