

PLEASE SHOW YOUR WORK. However, you do not have to use all the space provided! All data in this exam are fictional.

1. (19 pts) In an aphid species, only females are present in the spring and summer. They reproduce by cloning themselves and give birth to live young. In the fall, some males are produced; sexual mating leads to eggs which will hatch into new females in the spring.
  - (a) (5 pts) On general principles, what sex ratio would you expect in these aphids during the fall mating season? Assume that male and female offspring are equally costly to produce.  
*Fifty-fifty, because if one sex is rarer, it will be advantageous to the mother to produce more of the rare sex, and mutations which increase this will tend to spread.*
  - (b) (4 pts) Would fixing a new chromosomal inversion be easier, harder, or about the same in this species compared to an aphid species of the same population size which always reproduces sexually? Explain briefly.  
*Easier. It can become common during the cloning period, where it does not have to go through meiosis and therefore has no disadvantage.*
  - (c) (5 pts) Due to a rare cross-species mating, the *Wolbachia* bacterium enters the aphid population. *Wolbachia* is transmitted from infected mother to all offspring, but cannot be transmitted by males. A mutation arises in *Wolbachia* which causes infected female aphids to produce only female offspring. Infected females are still able both to clone and to mate with males. While it is rare, will this mutation tend to spread in the *Wolbachia* population? Explain briefly.  
*Yes. Wolbachia without this mutation will sometimes find themselves in a male, and die out without leaving any offspring; Wolbachia with this mutation don't have that problem so they have a competitive advantage. It may be very bad for the aphids in the long run but evolution doesn't know this.*
  - (d) (5 pts) If the entire population becomes infected with this form of *Wolbachia*, so that males disappear completely, describe a long-term problem that the aphid species will encounter. (Assume that the short-term problem of how to produce overwintering eggs has been solved.)  
*They will have to reproduce only by cloning. They will not have as much genetic diversity, will suffer from Muller's Ratchet, and may eventually stop being diploid, which interferes with error correction and overdominance. I took points off if the answer evidently confused self-fertilization with cloning. Cloning does not increase homozygosity or pair up bad recessives.*

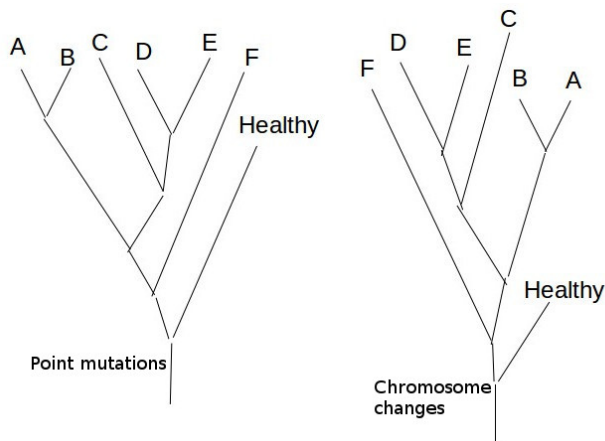
2. (29 pts) Tasmanian Devil Facial Tumor Disease (DFTD) is a contagious cancer which spreads when an infected Tasmanian devil bites another. (Typical devil mating behavior involves a lot of biting.) All samples of DFTD share multiple chromosome translocations compared to the normal devil chromosome set. Currently, devils infected with DFTD always die within a few months.

- (a) (5 pts) Chromosome translocations are usually harmful. What aspects of DFTD's life cycle probably make them less harmful to DFTD?

*They don't undergo meiosis and segregation, which gets rid of a major disadvantage. They may also need much less of their genome than the devil does so be more tolerant of genes damaged by translocation.*

*Several students said that the short life cycle makes translocations less harmful, but I can't see why, and no one explained.*

- (b) (5 pts) A researcher collects chromosome rearrangement and point mutation data from six samples of DFTD. She draws phylogenies separately from chromosomal data and point mutation (DNA base pair change) data, as shown below. The trees have been rooted using a healthy devil as the outgroup, and the branch lengths are proportional to inferred number of changes. Based on these trees she concludes that some of the chromosomal rearrangements must have happened independently multiple times. Explain what is wrong with her reasoning. You can assume that she used appropriate tree reconstruction methods in both cases.



*They are the same tree, so there are no discrepancies to explain.*

- (c) (4 pts) In both the chromosomal and point-mutation trees, the branch leading to the healthy devil appears much shorter than the others. What is a likely explanation for this?

*There are three possible reasons—all of them are likely true. DFTD may have an unstable genome which mutates and rearranges more readily. It is likely under weaker selection as it does not need its whole genome (for example, there are many tissues it does not have to make, so many genes are irrelevant to it). And it may be under directional selection, for example to become more contagious.*

## Problem 2 continued

- (d) (9 pts) Here is a list of traits that could evolve in the devil population in the presence of DFTD. (Note that these are genetic traits in the devils, not in the tumors.) For each trait, indicate if it would likely increase in the devil population, and if so, whether it would increase due to **individual selection** or only due to **kin selection**. It may be helpful to know that infected devils seldom successfully reproduce, and that devils seldom move far from where they were born, so tend to live near their close relatives.

- i. A mutation causing a devil not to bite during mating. This prevents the devil from transmitting the disease, but does not prevent it from becoming infected if bitten.

*It will increase by kin selection, because while it does not help the individual, if he mates with relatives while infected they will not catch the disease from him, and this will increase the frequency of the allele.*

- ii. A mutation causing male devils to prefer females at their first estrus (mating period) over older females.

*This will increase by individual selection, because a male with this preference is less likely to catch DFTD and has a survival advantage. (This has actually been seen in the real-life devils.) A female who has not mated before is unlikely to be infected.*

- iii. A mutation causing infected devils to die immediately rather than after several months.

*This clearly can't help the individual, but by dying quickly he may save his relatives, and it will spread by kin selection.*

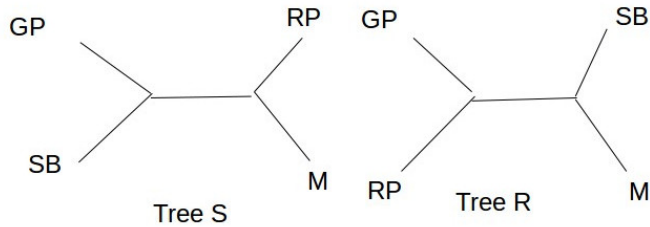
- (e) (6 pts) A researcher finds a mutation in devils which causes infected individuals to become extremely restless, so that they leave their birth area and travel long distances. She reasons that this mutation cannot spread, because it is harmful to the species and could even drive it extinct by rapidly spreading DFTD everywhere. Critique her reasoning.

*As far as the local population is concerned this is just like dropping dead, and will have the same kin-selection advantage. It's too bad that other populations may be infected by the roving individuals, but there is no selection pressure to save unrelated devils, so evolution can't recognize or deal with this problem.*

*Some students said that this mutation could save the population by driving out all infected devils, but if the mutation spreads, other populations will start sending their infected devils back here, so it's not really a solution unless the wandering devils fail to reach a new population (then it's equivalent to having them die).*

*In all of these subproblems I took off points if the answer clearly referred to mutations in DFTD, since the problem describes mutations in devils.*

3. (17 pts) A researcher wants to know whether giant pandas (GP) are more closely related to sun bears (SB) or to red pandas (RP); he also has data on mice (M). He draws the following two candidate trees (branch lengths are not meaningful):



He sequences a housekeeping gene, finding the following types of sites. To save time, he groups together sites which show the same pattern: for example, in the table below the first column represents any site where GP is different from the other species, and there were three such sites in the gene. The data are repeated on the tear-off sheet for your convenience.

Count	3	17	2	15	4	1	0	
GP	B	A	A	A	A	A	A	
RP	A	B	A	A	B	A	B	
SB	A	A	B	A	A	B	B	
M	A	A	A	B	B	B	A	
muts on S	3	17	2	15	4	2	0	Tree S Score: 43
muts on R	3	17	2	15	8	1	0	Tree R Score: 46

- (a) (6 pts) Under each column, write how many mutations are needed to explain a site of this type for the given tree. Write the total score of each tree in the space provided; be sure to use the information on the number of times each type of site was seen. Marking mutations on the tree may be helpful but is not required.  
*See above. I also accepted answers with correct 1's and 2's for single-site numbers of mutations in the row of boxes, as long as the totals reflected the information on number of times each type was seen.*
- (b) (4 pts) Which tree is preferred by parsimony? Draw the preferred tree as a rooted tree, using mouse as the outgroup. You do not need to indicate branch lengths.  
*Tree S. The tree should show GP and SB together, then RP, then mouse.*
- (c) (2 pts) Assuming that this rooted tree is correct, does it support grouping giant pandas with sun bears, or with red pandas?  
*Sun bears.*

## Problem 3 continued

- (d) (5 pts) The researcher examines the predicted protein for each of his gene sequences, and finds that the red panda sequence contains a STOP codon early in the gene. Explain how this additional information should change his evaluation of the experiment.

*This is probably a pseudogene in RP and a functional gene in the other species. At the very least, the part of the gene past the STOP in red panda is probably not under selection anymore. This makes the gene highly unreliable for use in a phylogeny because it will accumulate mutations much faster in RP (as can be seen in the data). He should find a different gene.*

- (e) (18 pts) In an insect species, the Mainland population has the following gene order on chromosome 1:

a-b-c-d-CEN-e-f-g

The Island population has a different gene order:

A-B-F-E-CEN-D-C-G

Upper and lower case represent different, but equally good, alleles. Assume that both gene orders have fully functional genes and there is no intrinsic advantage to either one.

- i. (6 pts) Diagram the structure formed in meiosis by a heterozygote for the Mainland and Island gene orders, showing a crossover in the region between genes E and F. Please draw it LARGE and clearly label the genes. *This diagram should show four chromatids (I did not take off if it showed only two as long as the gametes below were correct, but there should really be four). One pair is laid out in a U shape, and the other twists around to keep the loci together. There's a crossing-over event between loci E and F.*
- ii. (2 pts) Show the four gametes that would be produced by this crossover.

*a-b-c-d-CEN-e-f-g*

*A-B-F-E-CEN-D-C-G*

*a-b-c-d-CEN-e-F-B-A*

*G-C-D-CEN-E-f-g*

*I took off one point if any gamete was wrong, and two points if they were all wrong.*

## Problem 4 continued

- iii. (5 pts) We test these heterozygotes and find that they produce only 80% as many viable offspring as either homozygote. What is the critical frequency of invading Mainland chromosomes in the Island population above which we would expect the Island chromosome type to be lost? Assume that the populations are large and drift is not significant. Please show your work.

*This is underdominance with fitnesses 1.0, 0.8, 1.0. You can plug into the formula  $pA = t/(s + t)$  or just remember that when both homozygotes are equally good the equilibrium is in the middle ( $pA = 0.5$ ). So if the Mainland chromosomes outnumber the Island ones, Island is likely to be lost.*

*This was apparently the hardest problem on the exam.*

- iv. (5 pts) Assuming that some insects do start to move from Mainland to Island, but not enough to overwhelm the unique Island chromosomal type, suggest a reproductive trait that might rapidly evolve in the Island population, and briefly explain why it would be favored.

*Some form of pre-mating or cheap post-mating reproductive isolation: different mating season, different mating behavior, genital differences, or even early miscarriage of hybrid young. All of these will avoid wasting effort making low-fertility hybrid offspring, and individuals who have them will therefore have more grandchildren, so such traits will tend to increase.*

4. (17 pts) Fossils of very small hominids have been found on the Indonesian island of Flores. I will call individuals of this population “halfings.” (If they are a species, their proper name is *Homo floresiensis*.) An advance in ancient DNA sequencing enables us to obtain whole-genome sequences from seven halfing specimens and an equal number of mainland *H. sapiens* (human) specimens from the same time period.

(a) (12 pts) One hypothesis for these fossils is that *H. floresiensis* was a distinct species that evolved by peripatric (“island”) speciation after splitting from the mainland population. If this hypothesis is true, predict whether halfings will be higher, lower, or about the same as humans for the following measurements, and explain briefly:

i. Average time back to the common ancestor of gene copies from two random individuals. (Assume that the gene is evolving neutrally.)

*Lower in halfings, because peripatric speciation involves a small population and small populations have short times back to common ancestors.*

*A few students misinterpreted this as the time back to the common ancestor of the two **populations** but the text is clearly referring to individual gene copies.*

ii. Number of mildly harmful mutations fixed.

*Higher in halfings. Small population size makes it easier to fix a bad mutation by drift. (Current data on Neanderthals suggests that they had fitness issues due to this.)*

iii. Number of new chromosomal rearrangements fixed.

*Higher in halfings, again because of the small population size. There might also be stronger selection for novelty as the halfings had to adapt to their new physiology.*

(b) (5 pts) If halfings are found to be homozygous for a recessive mutation that is known to cause dwarfism in modern humans, does this mean that they are definitely not a separate species? Explain your answer.

*No. The mutation could have been present in the human population but become part of the new species' unique set of adaptations, or could have happened independently in a halfing ancestor. As many students pointed out, we'd want to know if the populations were partly or completely reproductively isolated in order to decide if they were species. The bottom line is that there is no clear distinction between “genetic disease” and “adaptation”—it all depends on the organism and environment, and what might be a genetic disease in humans could be an adaptive trait in other circumstances.*

[Sadly, DNA breaks down rapidly in a hot, wet climate and it is unlikely *H. floresiensis* DNA will ever be recovered.]

You may tear this sheet off to use as scratch paper if you wish. Nothing on it will be graded. You will probably not need most of these formulas.

$\chi^2$  table for 5% significance:

df	cutoff value
1	3.84
2	5.99
3	7.81

Data for Problem 3 (write your answers on the exam page, not just here!):

Count	3	17	2	15	4	1	0	
GP	B	A	A	A	A	A	A	
RP	A	B	A	A	B	A	B	
SB	A	A	B	A	A	B	B	
M	A	A	A	B	B	B	A	
muts on S								Tree S Score:
muts on R								Tree R Score:

$$p^2 + 2pq + q^2 \quad p(A) = \frac{t}{s+t}$$

$$p(A) = \frac{\nu}{\mu+\nu} \quad C < Br$$

$$\omega = \frac{D_N}{D_S} \quad \hat{w} = p(AA)f(AA) + p(Aa)f(Aa) + p(aa)f(aa)$$

$$\frac{1}{N_e} = \sum \frac{1}{N} / k \quad V_T = V_G + V_E = V_A + V_D + V_{GE} + V_E$$

$$h^2 = \frac{V_A}{V_T} \quad 2g$$

$$R = h^2 S$$