Module Code: BIO0056I

Examination Candidate Number: __________
Desk Number: __________

BSc Degree Examinations 2018-9

Department:
BIOLOGY

Title of Exam:
Genes and Genomes in Populations and Evolution

Time Allowed:
1.5 hours

Marking Scheme:
Total marks available for this paper: 60
The marks available for each question are indicated on the paper

Instructions:
Answer all questions in the spaces provided on the examination paper

Materials Supplied:
CALCULATOR

For marker use only: Office use only:

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DO NOT WRITE ON THIS BOOKLET BEFORE THE EXAM BEGINS
DO NOT TURN OVER THIS PAGE UNTIL INSTRUCTED TO DO SO BY AN INVIGILATOR
1. There are two adult females in a group: one older and one younger. When both are reproductive at the same time, all of their offspring are in competition with each other for resources, and thus each female has lower reproductive success than when they are not in competition. Dispersal is male-biased, where younger males move into an older female’s group to mate for life with that older female’s daughter. Any reproductive competition is between those two females.

The following reproductive strategies are possible:

**Selfish**: Both females reproduce throughout their lives: both lose on average 1.9 offspring overall compared to no-competition.

**Altruist 1**: Females stop reproducing from mid-life: here females lose an average of 3 offspring during that later stage of their life.

**Altruist 2**: Females do not reproduce until mid-life: here younger females lose an average of 3 offspring during that earlier stage of their life.

Use Hamilton’s rule to calculate whether females in this diploid system could be selected to not reproduce at either of the life stages (young / old). (8 marks)

This is what the **pedigree** would look like (2 marks – can be verbally expressed)

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**Altruist 1 strategy: Hamilton’s rule**

Females stop reproducing from mid-life

- \( r \text{ (older}_f\rightarrow \text{own}_f\text{ offspring)} = 0.5 \)
- \( r \text{ (older}_f\rightarrow \text{younger}_f\text{ offspring)} = 0.25 \)

**B** = 1.9 (from reduced cost of competition for early life-stage) (1 mark)

**C** = 3 − 1.9 = 1.1 (1.9 being the cost if they are both reproducing) (1 mark)
\[
\frac{1.9}{1.1} > \frac{0.5}{0.25} = 1.73 > 2 \quad (1 \text{ mark})
\]
So females do not benefit from terminating reproduction mid-life \( (1 \text{ mark}) \)

**Altruist 2 strategy: Hamilton’s rule**

Females stop reproducing from mid-life

\[
r (\text{older}_f \rightarrow \text{own}_f \text{_offspring}) = 0.5
\]

\[
r (\text{older}_f \rightarrow \text{younger}_f \text{_offspring}) = 0.5
\]

B and C are as before

\[
\frac{1.9}{1.1} > \frac{0.5}{0.5} = 1.73 > 1 \quad (1 \text{ mark})
\]
So females do benefit from not reproducing until mid-life in this case \( (1 \text{ mark}) \)

LOs addressed:
1. Understand and describe key evolutionary processes that affect allele frequencies in populations
2. Understand and describe key evolutionary processes that affect behavioural strategies and macroevolution
3. Apply simple evolutionary models to problems related to LO1-3.

Feedback: I was pleasantly surprised to see so many students get full marks on this question. You may have noticed that this has a relation to one of the workshop questions, but with different costs and benefits and a different type of dispersal. Most people got the relatedness correct for this type of dispersal, and most people got the correct value for B. Calculating the cost seemed to understandably cause the most trouble, with some students forgetting to take off 1.9, which is the additional cost if they are both reproducing at the same time (as in the workshop). I gave marks for correct working out in cases where variables were incorrectly calculated. Overall well done.

2. Group-living howler monkeys use their howls in male-male competition over territory and females. The hyoid bone is enlarged in howler monkeys to increase the loudness of the howl. For 5 species of howler monkeys, male hyoid bone volume and testes volume are plotted against the mean number of males per group; the different species are denoted by letters A-E:
a) Using these graphs, compare the processes of sexual selection shaping male morphology in species A and species E.  
Answer: Species A has fewer males per group so multiple mating by females is lower (1 mark). This means that in species A reproduction success is mostly determined by the chances of securing a mating (1 mark). Hence pre-copulatory sexual selection (1 mark), as illustrated by the greater hyoid volume for competing by howling. Compared to A, E has increased chance of multiple mating by females, resulting in increased sperm competition (1 mark), so males invest more in testes production.

b) Monkeys with louder howls are better able to defend territories. What does this suggest about the evolution of female preference for louder howls?  
Suggests that howling indicates ability to provide for the female, hence is a reliable signal of quality.  

(1 mark)

(c) Howler monkeys calls are exceptionally low in pitch for their body size, compared to the calls of other monkeys. What does this suggest about the evolution of female preference for howls?  
This suggests that male howler monkeys have evolved to exploit a pre-existing sensory bias (1 mark) in primates to pay attention to low pitched noises, because these are often associated with predators (1 mark). Also accept because lower pitch is associated with increased body size

Feedback

This question was generally well-answered. Most people got 3 marks for part A). The mark that was most missed was the point that in species A, it is the chance of securing a mating that drives reproductive success, i.e. increased risk of missing out entirely. Some people wrote detailed descriptions of what the 2 graphs showed and listed values read off the graphs - this didn’t add any marks, as it wasn’t answering the question. Some answers failed to mention species A and E, which meant that though they did discuss pre- and post-copulatory selection, they weren’t answering the actual question that was asked; conversely, some answers included sections on species B, C, & D, which again, weren’t covered by the question, so this did not add any marks, even if what was written was accurate.
Part B) was answered correctly in most cases - common errors were to focus on sensory bias, which can't be inferred from the information here, or on cognitive processes rather than evolution which is the topic of the question. Most answers to part C) made the connection with sensory bias, but some answers got distracted onto the evolution of male calls, while the question is focussed on the evolution of female preference.

3.

a) Would you expect transposable elements to spread more easily in sexual or asexual organisms? Explain your reasoning. (4 marks)

Sexual, as they can spread to other lineages [2 marks]. In asexual species, lineages where they arise may be more likely to be lost due to drift and/or purifying selection [2 marks].

b) Give an example of a sex chromosome system. In what way can the structure of sex chromosomes differ to autosomes? (2 marks)

Human or Silene XY and bird ZW chromosomal systems [1 mark]. Sex chromosomes may become morphologically diverged, often with one becoming smaller [1 mark].

c) Explain the process by which sex chromosomes diverge. (7 marks)

[Unless otherwise stated, one mark for each]

· A mutation gives rise to a sex-determining factor
· Sex-specific genes become linked with this gene
· Suppression of recombination (by inversions) evolves in the heterozygous sex since it is advantageous for these genes to be inherited together [2 marks]
· Deleterious mutations and repetitive regions can also accumulate in these regions once recombination ceases
· Loss of degraded genes can occur, with the other chromosome increasing dosage of those genes to compensate
· Accumulation of additional sexually-antagonistic genes can lead to further cessation of recombination

d) How might the development of sex-linked chromosomes lead to changes in the appearance or behaviour of an organism? (2 marks)

If genes linked to behaviour or appearance are in close proximity to sex-specific genes [1 mark] when recombination ceases, they too may become fixed and co-inherited [1 mark].
LOs addressed:
2. Understand and describe evolutionary changes in genomes within and between species
3. Understand and describe key evolutionary processes that affect behavioural strategies and macroevolution

Feedback: Answers were variable for this question. Part A) Most students correctly identified that transposable elements would be expected to spread more easily in sexual organisms, but sometimes gave reasons more related to the abundance of TEs, rather than the spread across populations, and few described how they are more often lost from asexual lineages. Part B) Most students could give an example of a sex chromosome system and describe a major difference between them and autosomes. Part C) Most also picked up some marks when describing how sex-chromosomes diverge, although relatively few described inversions having happened multiple times in most systems. Part D) Only about half of the students were able to describe how the development sex chromosomes could lead to changes in behaviour or appearance due to genetic hitchhiking of linked genes also being co-inherited once recombination stops. Many lost marks for simply describing examples of secondary sexual characteristics, rather than focussing on how the development of sex chromosomes could cause this to happen.

4. Imagine there are two closely related eukaryotic parasite species in one location (one city, for example).
   a) List the main sample collection methods, laboratory methods and bioinformatics methods you would use to perform a population genomics study of these two parasite species? Include brief strategies for sample collection, DNA sequencing and bioinformatics methods.  
   (4 marks)

   Of the order of 10-100 parasite samples will be collected from throughout the range for each parasite, depending on sequencing budget (1 mark). DNA will be extracted from parasites, and sequencing with short read Illumina technology (1 mark). Assuming there is a reference genome for each species, reads will be mapped to these reference genomes (1 mark) and genetic variants identified from the read alignments (1 mark).

   b) Describe summary statistics and other analyses that would characterise the populations and evolutionary forces at play.  
   (4 marks)

   Average pairwise diversity (\(\pi\)) indicates how genetically diverse the populations are (1 mark). Tajima’s D gives some indication of population expansion (1 mark), selection selective sweeps and/or balancing selection (1 mark). Analysis of
population structure will describe whether populations contain sub-populations or not (1 mark).

(c) Describe what information the relationship $\Theta = 4N_e\mu$ would provide, if mutation rates could be assumed to be the same. \hspace{1cm} (2 marks)

Since diversity ($\pi$) is an estimator of $\Theta$, we will have an estimate of this quantity (1 mark). Rearranging this formula produces this formula for the effective population size: $N_e = \Theta/4\mu$. So, if mutation rates are assumed to be the same the relative $\pi$ between populations gives an estimate of the relative population sizes ($N_e$) of the two parasites (1 mark).

LOs addressed:
1. Understand and describe key evolutionary processes that affect allele frequencies in populations
2. Understand and describe evolutionary changes in genomes within and between species
5. Understand experimental design, data collection and analysis of data and be able to design simple experiments related to LO1-3.
6. Apply simple evolutionary models to problems related to LO1-3.

Feedback

There were a wide range of answers for this question. Over all parts (A,B,C) some people were a little confused between population genomics, where we examine the whole-genome diversity within one or two species and metagenomics where we examine many species, usually using PCR. Population genomics will generally not use PCR because this amplifies only one region of the genome (hence not whole genome). Sometimes quantitative genetics (GWAS) was also included, which is related, but not exactly what we were aiming at here - which is the information you can gain from sequence data alone.

Part A was generally well-understood. With the small exception that we generally don’t use BLAST to align sequences. Part B was almost binary, with some people understanding the concept of summary statistics to describe genetic variation, and some not. Some people understood this very well, and descriptions of the meaning of Tajima’s D and MK tests were particularly good. Part C was a challenging question, and few people obtained full marks. It depended on both remembering the meaning of the letters in the formula, and reading the question very carefully.

5.

a) What sequencing methods can be employed to study the diversity, composition and functioning of microbiomes? \hspace{1cm} (5 marks)
Diversity and composition of microbiomes can be studied by using 16S rRNA (1 mark) or 18S rRNA/ITS (1 mark) amplicon sequencing for detecting different prokaryote and eukaryote taxa, respectively.

Functioning of microbiomes can be studied by using targeted amplicon sequencing and/or metagenomics (1 mark), transcriptomics (1 mark) and metabolomics (1 mark).

Feedback: This question was answered quite well in general. In the case of diversity estimation, most answers forgot to mention 18S rRNA/ITS amplicon sequencing for eukaryotic organisms. Similarly, while most answers mentioned metagenomics and transcriptomics, metabolomics (or proteomics) was often forgotten in the case of studying microbiome functioning. Some answers were more focused and detailed but only focused on one or two specific methods losing some marks. Only a few answers scored full marks.

b) You are planning to start an experimental evolution experiment to study adaptation of the bacterium *Pseudomonas aeruginosa* to glucose medium. You need to transfer a proportion of the evolved replicate bacterial populations to new fresh media everyday. How would your results be affected by transferring 1% or 80% of the populations? (5 marks)

1% serial transfer regime will introduce more severe bottlenecking that reduces stochastic genetic variation (1 mark) and creates a stronger selection for the most abundant genotypes (1 mark). Also, bacteria will be spending more time at reproducing clonally in 1% transfer regime where they are kept further away from their carrying capacity (1 mark). As a result, bacteria will go through a higher number of generations in 1% transfer regime (1 mark) leading to higher supply rate of mutations and faster adaptation to the growth media (1 mark).

Feedback: It was nice to see that most of the people were able to answer this question and score at least 1 mark. Most of the answers clearly described a link between bacterial growth and the emergence of novel and potentially adaptive mutations into the population for the selection to act on. The effect of transfer volume on genetic variation was also described quite often in sufficient detail: bottlenecking and reduction of variation in 1%, and maintenance of variation at 80% transfer regime, respectively. Some answers mixed these two and concluded that evolution would be faster at 80% transfer regime due to a higher genetic variation. However, as experimental evolution studies are traditionally initiated from a single genetically uniform clone, there will be no standing variation present and all the variation is generated via *de novo* mutations. More mutations will emerge just by a chance in 1%
transfer regime populations that will reproduce more as they are further away from their carrying capacity compared to 80% transfer regime populations.

Learning outcomes addressed:
1. Understand and describe key evolutionary processes that affect allele frequencies in populations
2. Understand and describe evolutionary changes in genomes within and between species
5. Understand experimental design, data collection and analysis of data and be able to design simple experiments related to LO1-3.

6. The figure below shows, across a number of different shark species, how their diet breadth relates to the number of tapeworm (parasite) species identified inside them. For both axes, the numbers are residual values from the relationship between the number of tapeworm species or prey families counted, plotted against sampling effort. The straight line represents the linear regression through the data, and the slope is significantly different from zero.

Explain why this regression is problematic as a test of evolutionary association between shark diet breadth and tapeworm species richness; how you would more convincingly demonstrate if there was such an association; and speculate on why a positive evolutionary association might exist. (10 marks)
The regression assumes independence of species traits (1 mark), but species which are related might share characteristics, which might make them non-independent, which is a form of pseudoreplication (1 mark). An alternative way of saying the above is that it assumes a star-phylology. For a more convincing test, one could use a phylogenetically controlled test as independent contrasts (1 mark). A phylogeny illustrating how species in the dataset are related would need to be assembled (1 mark), and contrasts between sister groups estimated for both traits (1 mark), which are then standardized by their standard deviations (1 mark). This assumes a Brownian model of evolution (1 mark). The contrasts can then be subjected to regression through the origin (1 mark). Credit will be given for discussion on how sampling effort should be dealt with here. Diet breadth might be correlated with other variables that might enhance species richness such as abundance or range size, which might help promote parasite persistence (1 mark), or it might directly promote richness via for example increasing the rate at which tapeworms are acquired, perhaps from prey themselves (1 mark). Up to 2 marks for the first part, six for the second and 2 for the third, with marks available for any well explained credible explanation in the latter.

LOs addressed:
3. Understand and describe key evolutionary processes that affect behavioural strategies and macroevolution
5. Understand experimental design, data collection and analysis of data and be able to design simple experiments related to LO1-3

Feedback: Many people did very well here, which was pleasing, as they had clearly engaged with the macroevolution material either in the workshops and/or on the VLE. There were, in contrast, a fair minority who had also clearly not done so, which was unsurprising given the low turnout for the workshops and practicals, and so the mark distribution was somewhat bimodal. People who had engaged with the material generally did best at the first two points about independence and tended to lose marks by a less full explanation of how contrasts work. There were two types of answer that scored well at the last part, including the model answer, and also the idea that wider diets might allow greater niche breadth in the gut so more tapeworms could coexist. I actually think this is fairly unlikely, since tapeworms are macroscopic, not microscopic, organisms, hence are unlikely to show niche separation on the scales found in the gut based on host diet breadth, but I thought it was at least an hypothesis worth ruling out. I didn’t give credit for explanations that posited that higher tapeworm richness allows increased host diet breadth; apart from being a bit of a stretch biologically, the graph has the axes the other way around, so the authors are willing you to think about how x affects y.