

**UNIVERSITY COLLEGE LONDON**

University of London

**EXAMINATION FOR INTERNAL STUDENTS**

For The Following Qualifications:-

*B.Sc.*    *M.Sci.*

**Mathematics C398: Mathematics in Biology 2**

**COURSE CODE            :    MATHC398**

**UNIT VALUE             :    0.50**

**DATE                     :    18-MAY-06**

**TIME                     :    14.30**

**TIME ALLOWED         :    2 Hours**

All questions may be attempted but only marks obtained on the best **four** solutions will count.

The use of an electronic calculator is **not** permitted in this examination.

1. Consider the selection model with  $n$  alleles  $A_1, A_2, \dots, A_n$  in a large, randomly mating, diploid population:
  - a) How do the frequencies  $p_1, p_2, \dots, p_n$  evolve from one generation to the next? Explain the relevant parameters (fitness of a genotype, etc.)
  - b) State, without proof, the fundamental theorem of natural selection.
  - c) For given  $n$ , how many fixed points can the selection map have?
  - d) Show that the monomorphism corresponding to allele  $A_k$  only, is asymptotically stable if  $w_{kk} > w_{ki}$  for all  $i \neq k$ , and is unstable if  $w_{kk} < w_{ki}$  for at least one  $i$ .
  - e) Consider the fitness matrix  $W = \begin{pmatrix} 0 & \frac{2}{3} & 1 \\ \frac{2}{3} & \frac{1}{3} & 0 \\ 1 & 0 & 0 \end{pmatrix}$  for three alleles. Determine all fixed points and their invasion and stability properties.
  
2. a) Formulate the Hardy-Weinberg Law in the case of 2 alleles. List the main assumptions for this law.  
b) Explain the Wright-Fisher model for a finite population (of diploid  $N$  individuals) with 2 alleles.  
Write down the transition probabilities for this stochastic process.  
Show that the expected number of allele  $A_1$  in the population does not change from one generation to the next. (Recall that the mean value of a binomially distributed random variable with order  $n$  and parameter  $p$  is given by  $np$ ).  
Explain what happens to the actual number of alleles. Determine the fixation probability in terms of the initial frequency.

3. Consider the selection-mutation model with 2 alleles  $A_1, A_2$  in a large, randomly mating, diploid population:

a) How does the frequency  $p$  of allele  $A_1$  evolve from one generation to the next? Explain the relevant parameters (fitness of a genotype, mutation rate, etc.)

b) Recall that this selection-mutation model is equivalent to the difference equation

$$p' - p = \frac{p(1-p)}{2V(p)} \frac{dV(p)}{dp}$$

with  $V(p) = p^{2\nu}(1-p)^{2\mu}\bar{w}(p)^{1-\nu-\mu}$ , where  $\bar{w}(p)$  is mean fitness and  $\mu, \nu$  are mutation rates. Explain how this implies an analogue to the fundamental theorem of natural selection for this model. Explain why each orbit converges to a fixed point.

c) What can be said about the number of fixed points of this model?

d) Show that in the case of overdominance (ie, the heterozygote has a higher fitness than the homozygotes),  $\log V$  is concave and there is a unique fixed point.

e) Consider genotypes  $A_1A_1, A_1A_2, A_2A_2$  with fitnesses given by  $1, 1-s, 1$ , respectively, and equal mutation rates ( $\mu = \nu$ ). Show that for small mutation rates there are three fixed points and compute them to lowest order approximation.

4. Consider an asymmetric, two-player game with  $n \times m$  payoff matrices  $A = (a_{ij})$  and  $B^T = (b_{ij})$ .

a) Define the following terms associated with this game: Nash equilibrium, strict equilibrium, strictly dominated strategy.

b) Write down the (standard) replicator dynamics for such games.

c) Show that a strictly dominated strategy is eliminated along every interior solution of the replicator dynamics.

d) Show that in a zero-sum game, a Nash equilibrium is stable under the replicator dynamics.

e) For the following  $2 \times 2$  bimatrix game

1,-1	2,-2
2,-2	-1,1

write down the replicator dynamics, determine all Nash equilibria and sketch the phase portrait of the replicator dynamics.

5. Consider a symmetric, two-player game with  $n$  strategies labelled  $1, 2, \dots, n$  and payoff matrix  $A = (a_{ij})$ .

a) Define the following terms associated with this game: Nash equilibrium (NE), strict equilibrium, evolutionarily stable strategy (ESS).

b) What is the logical relation between these equilibrium concepts?

c) Show that  $p$  is an ESS if it is globally superior, i.e., if  $p \cdot Ax > x \cdot Ax$  holds for all mixed strategies  $x \neq p$ .

d) Write down the replicator dynamics. Which of the equilibrium concepts mentioned in a) give rise to asymptotically stable equilibria?

e) Consider the following war-of-attrition game:

Each player is prepared to wait for a short, medium or long time (S,M,L). If he outwaits his opponent, he wins an object of value  $v$ , while the opponent gains nothing. If they leave at the same time, they share the object:  $\frac{v}{2}$  for each player. There are increasing costs for waiting:  $c_1 = 0 < c_2 < c_3$ .

This leads to the payoff matrix

	S	M	L
S	$\frac{v}{2}$	0	0
M	$v$	$\frac{v}{2} - c_2$	$-c_2$
L	$v$	$v - c_2$	$\frac{v}{2} - c_3$

Assume  $v = 6$ ,  $c_2 = 2$ ,  $c_3 = 4$ . Show that this game has a unique Nash equilibrium. Is it an ESS? Is it globally superior?

f) Sketch the phase portrait of the replicator dynamics for this game. Is the NE globally asymptotically stable?