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	:	**09-MAY-02**
TIME	:	**10.00**
TIME ALLOWED	:	**2 hours**

02-C0929-3-40

TURN OVER

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. A single autosomal locus in a large, randomly mating, diploid population admits n alleles, $A_1, A_2, \ldots, A_n$, with associated vector of gene frequencies, $\mathbf{p} = (p_1, p_2, \ldots, p_n)$. Define the following terms:

   (i) *viability fitness*, w_{ij}, of the genotype A_iA_j,

   (ii) *allelic fitness*, $w_i(\mathbf{p})$, of the allele A_i,

   (iii) *mean fitness*, $\bar{w}(\mathbf{p})$, of the population,

   (iv) *additive* and *dominance* fitness components of w_{ij}.

   (a) Show that the total genetic variance, V, decomposes as $V = V_a + V_d$, where V_a is the additive genetic variance and V_d is the dominance variance.

   (b) State, without proof, Fisher's Fundamental Theorem of Natural Selection.

   (c) All individuals in a given population at evolutionary equilibrium have homozygous geneotype A_1A_1 at a given autosomal locus. A rare mutant allele, A_2, appears in the population, with fitnesses of the possible genotypes,

   $$w_{11} = 1 + s_1, \qquad w_{12} = 1 + hs_1 + (1-h)s_2, \qquad w_{22} = 1 + s_2,$$

   where $s_1, s_2 > 0$ and $0 < h < 1$. Show that A_2 can invade the population, and eventually completely displace A_1, only if $s_2 > s_1$.

2. (a) State, without proof, the Hardy-Weinberg Law for an autosomal locus with n alleles, and explain at what stage of the life cycle it can be expected to hold.

(b) Write down the discrete-generation Replicator dynamics, and explain the terms involved.

(c) A population of a certain animal species contains two distinct phenotypes, *Fast* and *Slow*. Fast individuals escape predators better than Slow individuals, so that their respective probabilities of survival from zygote to adult are $1-d_F$ and $1-d_S$, with $d_S - d_F = \rho > 0$.

The Fast/Slow phenotypic character is determined at a single autosomal locus admitting two alleles, A_1 and A_2, with A_1 purely dominant over A_2. Thus, A_1A_1 and A_1A_2 genotypes are Fast, and A_2A_2 genotypes are Slow.

In some generations, the population experiences a disease epidemic carried by a virus. Thus, a given generation experiences an epidemic with probability q, and is disease free with probability $1-q$, where $0 < q < 1$. The recessive allele A_2 offers some protection against this virus, so that the probability that an individual dies from the disease before reaching adulthood is m_2 if it posseses allele A_2, and m_1 if it does not, with $m_1 - m_2 = \sigma > 0$.

Assuming that death from predation and death from the disease are independent events, show that there is an evolutionarily stable equilibrium in which both Fast and Slow phenotypes are present, and that the frequencies of A_1 and A_2 at this equilibrium are

$$p_1^* = \frac{\rho}{\rho + \sigma q}, \qquad p_2^* = \frac{\sigma q}{\rho + \sigma q}.$$

3. In a certain species of bird, male and female adults pair at random at the beginning of each season and produce two fertilized eggs, with one laid earlier than the other. Each egg in a pair is fertilized independently.

The two offspring in a pair compete with each other to be fed by their parents. The firstborn offspring has an advantage, because it hatches first and benefits from being the sole recipent of food before the second hatches, and therefore can become bigger and heavier. This means that when the secondborn hatches, the firstborn is able to grab more of the food provided by the parents. Because of this, the firstborn's probability of surviving to adulthood is S and the secondborn's is s, with $S > s$.

The feeding behaviour of the offspring is controlled at a single autosomal locus, with common genotype aa. A rare mutant allele A arises in the population, with the effect that firstborn Aa genotypes are more generous to their secondborn sibling, and allow the latter to obtain more of the available food. The behaviour of secondborn offspring is unaffected by the A allele, and AA genotypes can be assumed to be too rare to be significant. Thus, a firstborn Aa has a decreased probability $S - c$ of survival to adulthood, and its secondborn sibling has an increased survival probability $s + b$.

(a) The numerical entries in the following table are the probabilities with which the indicated parental crosses produce offspring pairs of the indicated genotypes (firstborn first). $Aa \times Aa$ parental crosses are assumed to be negligibly rare, so are not included. Explain the entries in this table.

		Parental cross		
		aa×aa	aa×Aa	Aa×aa
Offspring pair	aa, aa	1	$\frac{1}{4}$	$\frac{1}{4}$
	aa, Aa	0	$\frac{1}{4}$	$\frac{1}{4}$
	Aa, aa	0	$\frac{1}{4}$	$\frac{1}{4}$
	Aa, Aa	0	$\frac{1}{4}$	$\frac{1}{4}$

(b) If x is the frequency of Aa genotypes in the parent population, show that the frequency x' of Aa genotypes in the next generation of adults is, to first order in x,

$$x' = \left\{1 + \frac{\frac{1}{2}b - c}{S + s}\right\} x.$$

Deduce that the rare allele A can invade the population only if $\frac{1}{2}b > c$.

4. A symmetric, 2-player game with n strategies labelled $1, 2, \ldots, n$, has payoff matrix $\Pi = (\ \pi_{ij}\ )$, where π_{ij} is the payoff to an agent who plays strategy i against an agent who plays strategy j. Define the following terms associated with this game:

   (i) *Mixed strategy Nash equilibrium.*

   (ii) *Symmetric Nash equilibrium.*

   (iii) *Evolutionarily stable strategy* (ESS).

   Show that an ESS is equivalent to a *non-invadable* equilibrium.

   (b) Two animals use display signals to bargain over how to share a piece of food between them. The strategies each animal may adopt are labelled 0, which means "I don't want it", 1, which means "I want half of it", and 2, which means "I want all of it". If the animals play the pair of strategies (i, j), then they each receive their request, provided that what they jointly ask for is a possible split; i.e. provided $i + j \leqslant 2$. If $i + j > 2$, then the requested split is not possible, and the animals will proceed to fight each other. Under these circumstances, neither animal gets a share, because the food is stolen by outsiders while they are fighting. The payoff matrix for this 3-strategy, symmetric game is shown below.

   Show that there are exactly four pure-strategy Nash equilibria, but that only two of them are symmetric, and only one of these is an ESS.

5. In a 2-player, asymmetric game, players can adopt one of two possible roles, with the roles recognized by both players. Define the terms:

   (i) *Mixed strategy Nash equilibrium.*

   (ii) *Conditional mixed strategy.*

   (iii) *The associated symmetrized game.*

   (a) Show that an ESS of the symmetrized game is a mixed strategy Nash equilibrium of the underlying asymmetric game.

   (b) State, and prove Selten's Theorem concerning the nature of ESSs in such an asymmetric game.

END OF PAPER

ERRATUM

MATHEMATICS C398

The pay off matrix in Question 4 p. 4 has been accidentally omitted. It should be:

	0	1	2
0	0 0	1 0	2 0
1	0 1	1 1	0 0
2	0 2	0 0	0 0