# UNIVERSITY COLLEGE LONDON 

University of London

## EXAMINATION FOR INTERNAL STUDENTS

## For The Following Qualification:-

## M.Sc.

## Mathematics in Biology

COURSE CODE : MATHG505

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 $A_{1}, A_{2}, \ldots, A_{n}$ in a large, randomly mating, diploid population:
a) How do the frequencies $p_{1}, p_{2}, \ldots, p_{n}$ 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 $w_{k k}>w_{k i}$ for all $i \neq k$, and is unstable if $w_{k k}<w_{k i}$ for at least one $i$.
e) Consider the fitness matrix $W=\left(\begin{array}{ccc}0 & \frac{2}{3} & 1 \\ \frac{2}{3} & \frac{1}{3} & 0 \\ 1 & 0 & 0\end{array}\right)$ 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 $n p$ ).
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

$$
p^{\prime}-p=\frac{p(1-p)}{2 V(p)} \frac{d V(p)}{d p}
$$

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 $A_{1} A_{1}, A_{1} A_{2}, A_{2} A_{2}$ 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 $A=\left(a_{i j}\right)$ and $B^{T}=\left(b_{i j}\right)$.
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 $1,2, \ldots, n$ and payoff matrix $A=\left(a_{i j}\right)$.
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 $p \cdot A x>x \cdot A x$ 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 ( $\mathrm{S}, \mathrm{M}, \mathrm{L}$ ). 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 is globally superior?
f) Sketch the phase portrait of the replicator dynamics for this game. Is the NE globally asymptotically stable?

