

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) Consider the model with n alleles in a large, randomly mating, diploid population. Show that the allele frequencies remain unchanged from generation to generation (the Hardy-Weinberg law).
 - (b) Suppose that in sex-linked genes sex is determined by a pair of nonhomologous chromosomes: females XX and males XY. Consider a locus on the X chromosome with two alleles A_1 and A_2 so that female genotypes are A_1A_1 , A_1A_2 , A_2A_2 and males genotypes are A_1 , A_2 . Show that genotype frequencies in females converge to Hardy-Weinberg proportions.
 - (c) Now suppose that the model includes the selection. State, without proof, the fundamental theorem of natural selection.
 - (d) If $n = 3$, what can be said about the number of fixed points?
 - (e) Consider the fitness matrix $W = \begin{pmatrix} 0 & 1 & \frac{1}{3} \\ 1 & 0 & \frac{1}{3} \\ \frac{1}{3} & \frac{1}{3} & 0 \end{pmatrix}$ for three alleles. Determine all fixed points and their stability properties.
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2. (a) Consider the selection-mutation model with 2 alleles A_1, A_2 in a large, randomly mating, diploid population. How does the frequency p of allele A_1 evolve from one generation to the next? Explain the relevant parameters introduced in the derivation.
 - (b) Consider the selection mutation model with 2 alleles A_1, A_2 , allele frequencies $p, 1 - p$, mutation rates μ from A_1 to A_2 , and ν from A_2 to A_1 . Let the function $\bar{w}(p)$ be the mean fitness function. Which role is played by the function $V(p) = p^{2\nu}(1 - p)^{2\mu}\bar{w}(p)^{1-\mu-\nu}$ in this model?
 - (c) Consider the selection mutation model for 2 alleles, with fitnesses for A_1A_1 , A_1A_2 , A_2A_2 given as $1 - s, 1, 1$, and mutation rates $\mu = 0, \nu > 0$ (i.e., only mutations to the less fit allele A_1 occur). Show that there is a unique fixed point \hat{p} describing selection-mutation balance, which is (approximately) given by $\hat{p} \approx \sqrt{\frac{\nu}{s}}$.
 - (d) A neutral mutant individual (genotype Aa) enters a genetically uniform (genotypes AA) population of size $N - 1$ (N including the newcomer). Assuming random mating and non-overlapping generations, what is the probability that the mutant gene, a , will dominate the population?

3. (a) Explain the process of crossover and recombination. Consider alleles A_1, A_2, \dots, A_n at one locus and alleles B_1, B_2, \dots, B_m at another locus, and let x_{ij} be the frequency of gametes $A_i B_j$. If the probability for recombination between these two loci is r derive the frequencies x'_{ij} in the next generation. Show that the allele frequencies stay the same.
- (b) What values can r take?
- (c) Show that x_{ij} converges over generations, and determine the limit.
- (d) Consider the model with recombination and selection. Show that in a special case of additive fitness ($w_{ij,kl} = a_{ik} + b_{jl}$, $a_{ik} = a_{ki}$, $b_{jl} = b_{lj}$) the average fitness function and allele frequencies in the next generation do not depend on r . Which theorem can then be used for an analysis?

4. For a game with $n \times n$ payoff matrix A :

- (a) Define the following terms: Nash equilibrium (NE), evolutionary stable strategy (ESS), locally superior strategy, strict equilibrium.
- (b) State without proof which of the above equilibrium concepts imply one another.
- (c) Write down the replicator equation.
- (d) Give examples of 2×2 matrix A such that the game has:
- only one NE (find it) which is ESS;
 - three NE (find them), two of which are strict;
 - infinitely many NE, none of which is ESS.

(e) For

$$A = \begin{pmatrix} 0 & -1 & 2 \\ 2 & 0 & -1 \\ -1 & 2 & 0 \end{pmatrix} \quad (1)$$

describe Nash equilibria and evolutionary stable strategies.

- (f) Characterise the behaviour of solutions to the replicator equation with payoff matrix (1) for large time ($t \rightarrow \infty$) depending on the initial combination of frequencies.

5. Consider an asymmetric (bimatrix) game with payoff matrices

$$A = \begin{pmatrix} 3 & 0 \\ 0 & 2 \end{pmatrix} \quad \text{and} \quad B = \begin{pmatrix} 2 & 0 \\ 0 & 3 \end{pmatrix}.$$

- (a) Define the following terms: Nash equilibrium, strict equilibrium.
- (b) Find all Nash equilibria. Find out, if any of them are strict.
- (c) Write down the equation of replicator dynamics for this game.
- (d) Sketch the phase diagram.
- (e) Define the concept of asymptotically stable pair of strategies.
- (f) Determine which of the equilibria are asymptotically stable for the game in question.