

BIOL2007 - TUTORIAL 2, 2008 - ASPECTS OF PHENOTYPIC EVOLUTION

Use lecture scripts/handouts to help. Contact tutor or, if all else fails, K. Fowler (k.fowler@ucl.ac.uk).

a) EVOLUTIONARY GAMES

This tutorial is related to my lecture on frequency dependent selection in which you learned about the use of game theory to study the outcome of evolutionary conflicts of interest between individuals. **The first part of the tutorial includes background material and a worked example from my lecture.**

Game theory and the evolution of fighting

When there are evolutionary conflicts between individuals (such as competition for resources) the best strategy to use may depend upon strategies used by other competitors. Game theory is used to make theoretical models of these situations which are usually subject to **frequency-dependent selection** where the fitness of a morph varies with its frequency in the population.

The procedure is a) specify the **strategy set** (the array of tactics): b) set up a **pay-off matrix** based on the costs and benefits that accrue to individuals that play the different strategies when they meet: c) work out the **evolutionarily stable strategy** (ESS), the uninvadable strategy at evolutionary equilibrium.

The hawk-dove game has been used to study the evolution of fighting behaviour. "Hawk" and "Dove" are the strategy set for this game. An animal playing **dove** is a conventional fighter. If its opponent shows any sign of aggression it runs away, so it never gets injured. Two doves have a problem when they meet; they both waste time trying to settle the contest before one wins. An animal playing **hawk** fights unconventionally, in that it keeps going until it wins (its opponent gives in or runs away) or until it is so seriously injured itself that it cannot continue. The individuals meet in pairs at random according to their frequencies in the population; they get the payoffs associated with victory, injury or wasting time, and the outcome is recorded in a payoff matrix. **The matrix shows the payoffs to an individual playing the strategy on the left when it meets an individual playing the strategy at the top of the matrix.**

PAYOFFS: Serious injury = -20, Victory = +10, Time wasting = -3

Matrix of average outcomes

	when meeting Hawk	when meeting Dove
Payoff to Hawk	$-20/2 + 10/2 = -5$	+10
Payoff to Dove	0	$(+10 - 3)/2 + (-3)/2 = +2$

We look for the ESS for this game. Neither 'pure' strategy is an ESS; if all opponents are dove, hawk invades: if all opponents are hawk, dove invades. Is there a mixed ESS? The test is whether there is a frequency of the two strategies at which they would receive equal payoffs.

Let the ESS frequency of dove be Y and let the ESS frequency of hawk be X. At equilibrium: Dove will receive payoff of 0 at frequency X and payoff +2 at frequency Y giving a total payoff of 2Y

Hawk will receive payoff of -5 at frequency X and payoff +10 at frequency Y giving a total payoff of -5X and 10Y.

At equilibrium $-5X + 10Y = 2Y$

Therefore $5X = 8Y$ and the ESS is play 5/13 dove 8/13 hawk.

This is a mixed ESS.

The values chosen for victory, injury and time-wasting have important effects on the outcome of this game. In the exercise below you must determine the consequences of changes to values of various parameters.

- 1) Investigate what happens to the ESS if the value of serious injury changes to -3 leaving the values of victory at +10 and of time-wasting at -3.
- 2) Investigate what happens to the ESS if the value of victory changes to +2, keeping the value of serious injury at -3 and of time-wasting at -3.

For 1) and 2), give details of your calculations, construct new payoff matrices and explain whether the new ESS is a pure or a mixed one. What do you conclude from your results? in each case, give a brief description of an example of a simple animal contest that can be explained in this way. **[15 marks for answer to 1) and 15 marks for answer to 2)]**

3) Here you must work out the evolutionary fate of a new strategy in the game. This strategy respects ownership of a resource. It plays hawk when it is the owner and dove when it is the interloper. This strategy is called "Bourgeois". Assume that on half the occasions when an individual playing bourgeois meets another individual that it is the owner and the other individual is the interloper, while on the other half of the occasions the reverse relationship is the case. Obviously both individuals cannot be the owner.

Construct a new pay-off matrix for all three strategies. Use the values from part 2) of +2, -3 and -3 for victory, serious injury, and time-wasting respectively. Using the same rules as above, determine whether bourgeois is an ESS? Justify your conclusion and suggest some explanations for it. Can you think of any cases in nature where ownership conventions are evident? **[15 marks]**

b) QUANTITATIVE GENETICS

A farmer measures the body weight of her herd of pigs when they are 180 days old. Their mean weight is 200 kg, and their phenotypic variance is 625 kg². She conducts rigorously controlled experiments with the herd-members and establishes that the total genetic variance of body weight is 195 kg², the variance due to dominance is 50 kg² and the epistatic variance is 20 kg².

a) What is the heritability estimate of this trait? **[5 marks]**

b) In a response to quality perceptions of the average consumer, the farmer wishes to produce heavier individuals. If she breeds from the heaviest pigs, with an average weight of 250 kg, calculate the response to selection **[4 marks]** and hence

c) predict the average weight of the offspring. **[1 mark]**
