QUEEN'S UNIVERSITY

FACULTY OF ARTS AND SCIENCE

DEPARTMENT OF MATHEMATICS AND STATISTICS

MATH 239

FINAL EXAMINATION

APRIL 2007

SAMUEL ALIZON

INSTRUCTIONS

This examination is **three hours** in length. No aids or calculators are allowed.

There are three sections to this examination. Sections 1, 2 and 3 are worth approximately **14**, **10** and **6** points respectively. Do not spend too much time on a section: try to follow the suggested time allocation.

Please answer all questions in the space provided. If you need more room, continue your answer on the back of the previous page.

Justify all your answers and keep in mind that markers always appreciate the clarity and concision.

Good luck!

Please note: Proctors are unable to respond to any queries about the interpretation of the exam questions. Do your best to answer exam questions as written.

Section 1: Parental care, a conflict between the sexes

(Suggested time: 1 hr 20 min)

Bi-parenthood is rare in nature (humans are one of the rare examples). In most species, there is no parental care at all. The offspring can sometimes be raised by females alone and (more rarely) by males alone (in seahorses for instance).

Which sex should take care of the offspring? Trivers (1974) argues that females should: first because they invested a lot of energy to make an egg and second because they are sure of the offspring is from them. Dawkins (1976) argues that the parent who releases its gametes first should leave first. Following Maynard-Smith (1982), we will use a game theory approach to try to answer this question.

Consider a species where each female lays V eggs if she deserts and v eggs if she stays ($V > v$). She thus compensates the lack of parental care by increasing the number of eggs. All females are identical and only mate once per season. A male can mate again R times if he deserts and r if he stays ($r < R$). A male always keep the same behaviour and always mates with the same type of females. Without any parental care, the probability the egg will survive is g_0. If only one parent invests in parental care, this probability becomes g_1. Finally, with bi-parental care, the probability is g_2. Of course, $g_0 < g_1 < g_2$.

We assume this game is a one-shot game between two players (i.e. the players cannot change strategies). The fitness of a bird is assumed to be proportional to the number of youngs.

1.1 Find the payoff matrix for this game between males and females and justify the use of a normal form game.

1.2 Find all pure strategy Nash equilibria and specify under which parameter values they are valid.

1.3 Give a brief biological interpretation for each of these Nash equilibria (no more than one sentence for each case).

From now on <u>and until the end of the section</u>, we make some simplifying assumptions. First, we assume that a male cannot reproduce again during the same season if he stays and he may only reproduce once more if he deserts. Second, a female lays three times more eggs when she deserts than when she stays. Finally, an egg can only develop if at least one of the parents invests in parental care.

1.4 Write down the new payoff matrix. At which condition on g_1 and g_2 is there a completely mixed strategy Nash equilibrium? Write this Nash equilibrium.

We denote p the proportion of males investing in parental care and q the proportion of females investing in parental care. From now on <u>and until the end of the exercise</u>, we assume that g_2 is equal to 1 and that g_1 is 0.75. Also, we assume that v is equal to 4.

1.5 Find the replicator dynamic equations for this game (factorising the expressions will help).

1.6 Find all the fixed points.

1.7 Write the Jacobian of the dynamical system.

1.8 Find the nature of each of the fixed points.

1.9 Draw a phase diagram of the dynamical system. Be sure to indicate the fixed points, the isoclines, a vector indicating the direction of change in each region of the diagram and one or more trajectories illustrating the nature of the fixed points.

1.10 Based on the replicator dynamics, what conclusions can you draw concerning the game?

1.11 Could the results of this game be applied to humans? Why? Why not?

References

Trivers, RL (1974) Parent-Offspring Conflict, *Integrative and Comparative Biology*, **14**(1):249

Dawkins, R and Carlisle, TR (1976) Parental investment, mate desertion and a fallacy, *Nature*, **262**:131

Maynard-Smith, J (1982) Evolution and the Theory of Games, *Cambridge University Press*

Section 2: Siderophore production in bacteria

(Suggested time: 1 hr)

One of the main constraints limiting bacteria growth in vivo *(i.e. in real-life conditions) is the abundance of iron. In aerobic conditions (i.e. in presence of O_2), iron exists in an insoluble form (Fe III) and many host species actively take away iron from infectious bacteria by using proteins with high affinity to iron. As a response, bacteria have elaborated several mechanisms to steal iron from their host. One of the mechanisms shared by several bacterial species is the production and uptake of siderophores. These compounds fix iron and make it soluble. The complex [siderophore+iron] can then be actively transported into the bacteria. Bacteria release siderophores in the host as a response to a lack of iron.*

One of the key aspects of siderophore production is that they may potentially benefit any bacteria in the neighbourhood.

We first address this problem as a two-player game. We assume that a player is a bacterium and that mixed-strategies are not allowed. We also assume that the gain in fitness of a bacterium is the number of siderophores it gets. Sideophores are shared equally among all the players.

We consider two genotypes:

- co-operators (***C***): they pay a cost ***g*** to produce ***b*** siderophores
- defectors (***D***): they don't produce siderophores

2.1 If there are only two bacteria in the population and if a co-operator plays a defector, what are their respective payoffs?

2.2 Write the payoff matrix of this game.

2.3 In which case can ***C*** be an evolutionary stable population state?

2.4 Is it possible to observe an evolutionary stable population state with more than one genotype?

We now work with a colony of N bacteria (N large) each of which produces an amount x_i ($i \in [1,N]$) of siderophores. We assume the cost paid by a bacterium is proportional to the amount of siderophores produced (bacteria i pays $a\, x_i$).

2.5 Find the total amount of siderophores produced by the colony.

2.6 Assuming that siderophores are shared equally among the bacteria of the colony, find the payoff of a bacterium i.

2.7 Which game does this biological situation corresponds to?

2.8 Give the mathematical definition of a Nash equilibrium for this N-bacteria population where each individual i produces x_i siderophores.

2.9 Using questions 2.6 and 2.8, find the optimal genotype (*i.e.* the best strategy) when $1 < a\, N$.

2.10 Describe in words the effect of N on the optimal investment.

2.11 What modifications of the model could you think of to explain high levels of cooperation (which are sometimes observed)?

References

West, SA and Buckling, A (2003) Cooperation, virulence and siderophore production in bacterial parasites, *Proc. R. Soc. Lond. B* , **270**:37-44

Griffin, AS and West, SA and Buckling, A (2004) Cooperation and competition in pathogenic bacteria, *Nature*, **430**:1024

Harrison, F, Browning, LE, Vos, M and Buckling, A (2006) Cooperation and virulence in acute *Pseudomonas aeruginosa* infections, *BMC Biology*, **4**:21

Section 3: The pirate game

(Suggested time: 40 min)

For this section, a verbal reasoning is accepted (as long as it is logical) and diagrams are expected.

‘Ten pirates have gotten their hands on a hoard of 100 gold pieces and wish to divide the loot. They are democratic pirates, in their own way, and it is their custom to make such divisions in the following manner: The fiercest pirate makes a proposal about the division, and everybody votes on it, including the proposer.

If 50 percent or more are in favor, the proposal passes and is implemented forthwith. Otherwise the proposer is thrown overboard, and the procedure is repeated with the next fiercest pirate. All the pirates enjoy throwing one of their fellows overboard, but if given a choice they prefer cold, hard cash. They dislike being thrown overboard themselves. All pirates are rational and know that the other pirates are also rational.

Moreover, no two pirates are equally fierce, so there is a precise pecking order—and it is known to them all. The gold pieces are indivisible, and arrangements to share pieces are not permitted, because no pirate trusts his fellows to stick to such an arrangement. It’s every man for himself. What proposal should the fiercest pirate make to get the most gold? For convenience, number the pirates in order of meekness, so that the least fierce is number 1, the next least fierce number 2 and so on. The fiercest pirate thus gets the biggest number, and proposals proceed in reverse order from the top down. […]’

This game is difficult so before solving a 10-players game we will study simpler cases.

3.1 Find what proposal the fiercest pirate should make to get the most gold in the case where there are only 2 pirates playing the game.

3.2 Same question as question 3.1 but for a 3-pirate game.

3.3 Same question as question 3.1 but for a 5-pirate game.

3.4 Same question as question 3.1 but for a 10-pirate game (you do not need to justify this answer).

3.5 Bonus question: What happens if 204 pirates are playing the game?

Do not spend time on this (very difficult) question unless you have done the whole exam.

Reference

Ian Stewart (May 1999) A Puzzle for Pirates, *Scientific American* (p.98-99)