BIOL 480: Animal Behavior **Fall 2011**

Writing Assignment #1
Digesting and Ruminating Game Theoretic Approaches to Understanding the Evolution of Cooperation
Due: October 21, 2011

In providing responses to the questions below, you must use your own words; you may not quote or copy directly from the published sources indicated or from any other sources. *Write your responses as if you were explaining them to another student in the class as an instructor or teaching assistant; do not write them to me specifically.* Responses must be written out in well organized essay form; do not use bulleted responses or lists or telegraphic sentences.

1. In terms of the IPD game, define both the "cooperator" (C) and the "defector" (D) behavioral tactics that any given individual may adopt. Also, define each of the payoffs as typically presented in the Prisoner's Dilemma matrix (S, P, T, and R), and indicate which of these payoffs are uniquely attributed to the focal player and which payoffs are equally shared by both players. Show a payoff matrix that presents a Prisoner's Dilemma situation where the payoffs to the focal player are labeled at the top and payoffs to the opponent are labeled down the side. Finally, provide a definition (not an equation) for the parameter "w" as presented in the lecture notes, by Axelrod and Hamilton (1981), and by Nowak (2006).

2. In Axelrod and Hamilton (1981), what minimum value of w is required for the stable evolution of cooperative behavior? What is the minimum value of w required for the stable evolution of cooperative behavior in Nowak (2006)? Note that w is defined the same way in both papers, but each paper presents a different equation for expressing the minimum value of w required for the stable evolution of cooperation. Thus, the equations presented in the two papers must somehow be conceptually equivalent.

Explain how one could claim that (T - R) from Axelrod and Hamilton is essentially biologically equivalent to the cost incurred by the cooperator (c) from Nowak. Justify the further claim that (R - S) (from one of Axelrod and Hamilton's inequalities) is biologically equivalent to the benefit to the recipient (b) from Nowak. As part of your answer, adjust Nowak's matrix (1) in the Supporting Online Material such that $S = 0$ as we've done in class (notice that he has $S = -c$); show this new matrix and explain how it corresponds to Axelrod and Hamilton's (T - R) and (R - S).

3. Provide definitions, in your own words, for the parameters r, q, and k as presented in Nowak (2006). In many cases, the parameters w, r, q, and k might all be expected to be positively correlated with each other; for example, w, r, q, and k probably all have higher values in social lions than they do in solitary cougars. Justify the claim, then, that w, r, q, and k can be considered, at some level, to be essentially describing the same biological concept. In other words, what conceptually unites all four of these seemingly disparate parameters? (Do not refer to cost/benefit ratios or equations involving them in your answer.)

4. Nowak (2006) presents a fifth model for the evolution of cooperation that is based on group selection. He concludes that cooperation can evolve through group selection, as long as:

$$b / c > 1 + (n/m)$$

where b = the benefit of cooperation to recipients, c = the cost of cooperation to actors, n = the largest size that a group can be in terms of the number of individuals contained in the group, and m = the number of such groups within the population.

For cooperation to evolve through this mechanism, and in a population of a given size, is it easier for cooperation to evolve in populations that are comprised of just a few, large groups or in populations comprised of a large number of small groups? Justify your response through both (a) evaluating Nowak's equation 5 (pg. 1562) for different combinations of n and m, and (b) explaining how population structure affects the level at which selection favors or does not favor the evolution of cooperation.

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IPD/Game Theory Grading Sheet

Name: ____ Score : _______ / 100

1. Definitions ____ / 21 **____ / 20**
   - Cooperator ___ / 2
     - Individual aids in securing resource
     - Decreases own fitness
   - Defector ___ / 2
     - Individual withholds aid
     - Gains fitness at expense of other
   - T, R, S, P ___ / 5
     - Accurately defined
     - Payoffs shared/unique to focal player
   - Presentation of PD payoff matrix ___ / 4
     - Focal top/opponent side
     - T>R>P>S
   - *w* ___ / 2
     - Prob. of meeting repeatedly
   - Clarity ___ / 2
   - Accessibility to students ___ / 2
   - Grammar ___ / 2

2. Exploration of *w*____ / 20 **____ / 35**
   - Min value re: Axelrod/Hamilton ___ / 1
   - Minimum value re: Nowak ___ / 1
   - (T - R) being equal to *c* ___ / 4
     - Fitness loss given cooperative behavior
     - Incurred by cooperator
   - (R - S) being equal to *b* ___ / 4
     - Fitness gain given cooperative behavior
     - Received by recipient
   - Adjusted Nowak matrix ___ / 4
     - Adding c to each term
     - Showing T-R= c and R-S = b
   - Clarity ___ / 2
   - Accessibility to students ___ / 2
   - Grammar ___ / 2

3. Additional Parameters ____ / 16 **___ / 20**
   - Accurate definitions for r, q, k ___ / 6
   - Linkage between w, r, q, k ___ / 4
     - Spatial / degree of relatedness structure embedded in each
     - Prob. of encountering individuals repeatedly

3. Additional Parameters (cont'd.)
   - Clarity ___ / 2
   - Accessibility to students ___ / 2
   - Grammar ___ / 2

4. Group Selection____ / 18 **____ / 25**
   - General conclusion about role of relative group size ___ / 3
   - Manipulating equation to show behavior of model ___ / 2
   - Recognition of threshold values re: b/c ___ / 1
   - Support of conclusion through equation ___ / 1
   - Recognition of levels of selection ___ / 3
   - Recognition of favored behavior at each level ___ / 1
   - Support of conclusion through selection levels ___ / 1
   - Clarity ___ / 2
   - Accessibility to students ___ / 2
   - Grammar ___ / 2