Bio 417 Homework 5

(for the weeks of Mar 25th and April 1st, due April 18th)

1. (Non-additive Hamilton's Rule): Take the model in the beginning of the lecture notes "Selection in structured populations," where each genotype has probability r of interacting with its own type and probability $1-r$ to interact with a random genotype. Assume a non-additive Prisoner's Dilemma game (eq. 11 in the notes, with non-zero d). Calculate the total regression coefficient $\beta_{wg_\bullet}$, remembering the fact that the regression is defined as $\beta_{XY} = \text{cov}(x,y)/\text{var}(y)$, and confirm the the condition for cooperation to increase is given by equation 16 in the notes (Hint: consider the discrete probability distribution of all possible pairings, and take expectations over that distribution.)

We first want to write the covariance $\text{cov}(w, g_\bullet) = \text{E}[wg_\bullet] - \text{E}[w]\,\text{E}[g_\bullet]$. For that, we write down the probability for each possible pairing (CC, CD, DC, DD), and write the payoff of the focal individual (which we can take to be the first one in the pair, without loss of generality): Now, when the focal individual is a cooperator,

Pairing	CC	CD	DC	DD
Probability	$p(r+(1-r)p)$	$p(1-r)(1-p)$	$(1-p)(1-r)p$	$(1-p)(r+(1-r)(1-p))$
Payoff	$b-c+d$	$-c$	b	0

we have $g_\bullet = 1$; $g_\bullet = 0$ otherwise. So, we have

$$\text{E}[wg_\bullet] = p(r+(1-r)p)(b-c+d) - p(1-r)(1-p)c \tag{1}$$
$$\text{E}[w] = p(r+(1-r)p)(b-c+d) - p(1-r)(1-p)c + (1-p)(1-r)pb \tag{2}$$
$$\text{E}[g_\bullet] = p\,. \tag{3}$$

Thus:

$$\text{cov}(w, g_\bullet) = p(1-p)((r+(1-r)p)(b-c+d) - (1-r)(1-p)c) - (1-p)(1-r)p^2 b \tag{4}$$

The variance of $g_\bullet$ on the other hand is $p(1-p)$, so we have:

$$\beta_{wg_\bullet} = (r+(1-r)p)(b-c+d) - (1-r)(1-p)c) - (1-r)pb \tag{5}$$
$$= rb - c + d(r+(1-r)p)\,, \tag{6}$$

which is the same condition we obtained in class (equation 16 of the notes).

2. (Evolutionary branching in continuous Prisoner's Dilemma) Take the following continuous Prisoner's Dilemma game: two players, i and j, make contributions a_i and a_j to a public good, respectively. The payoff to player i is then given by:

$$\pi_i(a_i, a_j) = b(a_i + a_j) - c(a_i) \; ,$$

where $b(\cdot)$ denoted the common benefit from the public good, and is an increasing function of the total contribution, and $c(\cdot)$, the private cost of contributing, is an increasing function of the individual contribution. Assume that all interactions in the population take place completely randomly. (Hint for all the questions below: notice that although the fitness function doesn't have dependence on N in this case as we assumed for our adaptive dynamics model, you can still consider it as a special case of adaptive dynamics theory and apply the same conditions.)

a) Write down the first order condition for the evolutionarily stable contributions.

$$\left.\frac{\partial \pi_i}{\partial a_i}\right|_{a_i=a_j=a^*} = 0 = b'(2a^*) - c'(a^*) = 0 \tag{7}$$

b) Write down the second order evolutionary stability condition.

$$\left.\frac{\partial^2 \pi_i}{\partial a_i^2}\right|_{a_i=a_j=a^*} = b''(2a^*) - c''(a^*) < 0 \tag{8}$$

c) Write down the convergence stability condition.

$$\frac{\partial}{\partial a^*}\left[\frac{\partial \pi_i}{\partial a_i}\right]_{a_i=a_j=a^*} = 2b''(2a^*) - c''(a^*) < 0 \tag{9}$$

d) Consider the following cost and benefit functions: $c(a) = c_2 a^2 + c_1 a$ and $b(a) = b_2 a^2 + b_1 a$. Evaluate the first order evolutionary stability conditions, solve it for the candidate ESS contribution. Then using this candidate ESS, write down the second order ES and convergence stability conditions. Say when a positive candidate ESS exist, when the candidate ESS will satisfy the second order conditions, and when it is convergent stable. What is a necessary condition for a candidate ESS to exist that is convergent stable but does not satisfy the second order ES condition? Interpret this necessary condition. 1st order ESS:

$$4b_2 a^* + b_1 - 2c_2 a^* - c_1 = 0 \tag{10}$$

$$a^* = \frac{c_1 - b_1}{4b_2 - 2c_2} \tag{11}$$

This is positive when the denominator and the numerator have the same signs. The second order ESS condition is given by:

$$2b_2 - 2c_2 < 0 \,, \tag{12}$$

whereas the convergence stability condition is given by

$$4b_2 - 2c_2 < 0 \,. \tag{13}$$

The latter condition says the denominator of the first order condition must be negative, so it implies that a positive candidate ESS is only convergent stable when $c_1 - b_1 < 0$. Satisfying convergent stability but not the second order ES happens when the last condition holds, but not the second. A necessary condition for this is for $b_2 < 0$, which means that the marginal benefit from contributing to the public good is decreasing.