UNIVERSITY OF TORONTO

Faculty of Arts and Science
Department of Ecology and Evolutionary Biology

Mathematical modeling in ecology and evolution

(EEB314/1430)

Test 4 – December 2, 2025

Available Time: 50m

Permitted Materials: Pen/pencil

Question 1 (10/10 points) Let's use evolutionary invasion analysis to examine the evolution of cooperation in a classic game theory model.

This model is based on the so-called Snowdrift Game, also called Hawk-Dove. The anthropogenic interpretation of the game is that two drivers (or bicyclists!) are caught on either side of a snowdrift and can either wait for the other driver to shovel out a path or do it themselves. If the other driver shovels it is best to stay put and save energy, but if the other driver stays put it is best to get out and shovel so that you get home eventually. So whether shovelling (cooperation) is advantageous depends on the strategies of other individuals on the road. A more ecological interpretation could be that some microbes need to secrete enzymes to break down compounds in the environment before being able to consume them – it is then best if others break them down for you, but if they don't it's best to do it yourself. Here we'll assume the evolving trait is essentially the amount of enzyme secreted, which is a continuous trait (rather than a discrete trait: secrete or not), and so this is called the Continuous Snowdrift Game.

Following Doebeli (2011), we'll define $C(x)$ as the cost of employing strategy x and $B(x+y)$ the benefit accrued from playing strategy x with a partner who is playing strategy y (and vice versa). So the payoffs from a pairwise interaction between individuals with strategies x and y are $P_x = B(x+y) - C(x)$ and $P_y = B(x+y) - C(y)$, respectively. We use the so-called replicator equation to describe the change in the frequency of strategy y in a population of individuals playing strategy x,

$$\frac{\mathrm{d}q}{\mathrm{d}t} = q(P_y - \bar{P}),$$

where $\bar{P}$ is the average payoff in the population. When y is rare the average payoff is just the payoff of strategy x against itself, $\bar{P} = B(x+x) - C(x) = B(2x) - C(x)$. The invasion fitness (in continuous time) of a rare mutant with strategy y is then given by

$$r(y,x) = \frac{\mathrm{d}}{\mathrm{d}q}\frac{\mathrm{d}q}{\mathrm{d}t} = (B(x+y) - C(y)) - (B(2x) - C(x)).$$

Now assume the benefit and cost functions are quadratic, $B(z) = b_2 z^2 + b_1 z$ and $C(z) = c_2 z^2 + c_1 z$, with the b_i and c_i arbitrary constants. Let $x = 0$ imply no cooperation and assume some cooperation will evolve so that we can restrict our attention to $x \geq 0$ (this requires $B'(0) > C'(0)$, i.e., $b_1 > c_1$).

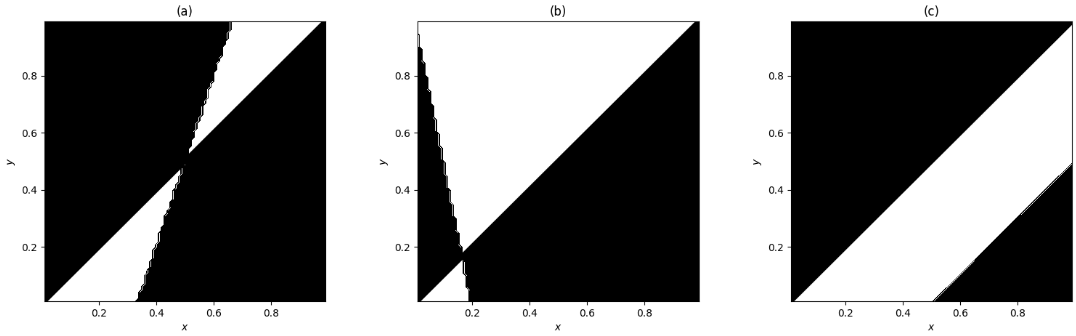
a) (2 points) Show that the selection gradient is $2(2b_2 - c_2)x + b_1 - c_1$.

b) (2 points) Show how to find the evolutionarily singular strategy, $\hat{x} = \frac{c_1 - b_1}{2(2b_2 - c_2)}$. Given $c_1 < b_1$, what needs to be true for $\hat{x}$ to be biologically valid ($x \geq 0$)?

c) (2 points) Show that the singular strategy is convergence stable whenever $2b_2 < c_2$.

d) (2 points) Show that we also require $c_2 < b_2$ for the singular strategy to be an evolutionary branching point.

e) (1 points) Which one of the following could be the pairwise invasibility plot when $c_2 < b_2 < c_2/2$? The black shading indicates where $r(y,x) > 0$.



f) (1 points) Say that after branching, one group of individuals evolves to play strategy $x = 0$ and the other evolves to play some strategy $x > 0$. In 1-2 sentences, describe what this means in terms of a population of microbes secreting enzymes to break down compounds for consumption.

——— *End of Exam* ———