Adaptive dynamics of the continuous snow-drift game

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In the classical snowdrift game (a.k.a. chicken or hawk-dove game), there are only two strategies, cooperate (C) and defect (D). Under suitable conditions, there is a mixed ESS in which both strategies coexist. Today, we will look at an extension to the snowdrift game, in which individuals can choose from continuous range of strategies. This model has been developed by Doebeli, Hauert and Killingback (2004; Science 306: 859-862). An interactive version can be found at http://www.univie.ac.at/virtuallabs/Branching/.

Assume individuals are engaged in a costly task that produces a common good (e.g. yeast secreting digestive enzymes for hydrolyzing sugars, making them available for everyone as a food resource). An individual's strategy is the amount x of enzyme it produces, which ranges from 0 to some maximal value $x_{\max}$. Everybody can use the food, but only the producer of the enzyme pays the cost.

Formally, we can assume a two-player game, where the strategies of the players 1 and 2 are denoted by x_1 and x_2, respectively. Each player receives a benefit, which is a function of the combined investment $x_1 + x_2$, and pays a cost which is a function of the individual investment x_i. The pay-off for player 1 is given by

$$P(x_1, x_2) = B(x_1 + x_2) - C(x_1). \tag{1}$$

We will now use adaptive dynamics to investigate the evolution of x. That is, we assume that x is a heritable trait, that reproduction is asexual, that most of the time, the population is monomorphic for a single value of x, and that once in a while, the resident population is confronted with a rare mutant with stratey $y \neq x$. While rare, the growth rate of the mutant strategy (i.e. the invasion fitness) is equal to

$$s_x(y) = P(y, x) - P(x, x). \tag{2}$$

Exercise 0. From last week's lecture, recall the concepts of invasion fitness, invasion fitness gradient, evolutionarily singular strategy, convergence stability, ESS stability, evolutionary branching points and pairwise-invasibility plots.

Exercise 1. Give a verbal explanation for equation (2).

Answer: The invasion fitness is the difference in the pay-offs between mutants and residents, assuming both of them play only against residents. This assumes that fitness (i.e. life-time reproductive success) is directly proportional to the pay-off received in games played against random partners.

Exercise 2. Without specifying the functions B and C, derive a general expression for the invasion fitness gradient, which determines the evolutionary dynamics of x.

Answer: $D(x) = \frac{\partial s_x(y)}{\partial y}\Big|_{y=x} = B'(2x) - C'(x)$

Exercise 3. What is the condition for an evolutionarily singular strategy?

Answer: $D(x) = 0$, i.e., $B'(2x) = C'(x)$.

Exercise 4. Derive a general condition for converence stability of a singular strategy.

Answer: $\frac{dD}{dx}\Big|_{x=x^*} = 2B''(x*) - C''(x*) < 0$.

Exercise 5. Derive a general expression for evolutionary stability of a singular strategy.

Answer: $\frac{\partial^2 s_x(y)}{\partial y^2}\Big|_{y=x^*} = B''(2x*) - C''(x*) < 0$.

Exercise 6. To make things more explicit, we should now make explicit choices for the shape of the costs and benefit functions. The simplest possibility is to use linear functions

$$B(x) = b_2 x + b_1 \tag{3}$$
$$C(x) = c_2 x + c_1. \tag{4}$$

Explain why this leads to rather boring evolutionary dynamics.

Answer: The invasion fitness gradient $D(x) = b_2 - c_2$ is constant. That is, x decreases to 0 is $b_2 < c_2$ and increases to $x_{\max}$ if $b_2 > c_2$. (If $b_2 = c_2$, x is neutral.)

Exercise 7. The natural next choice is to try out quadratic functions

$$B(x) = b_2 x^2 + b_1 x \tag{5}$$
$$C(x) = c_2 x^2 + c_1 x. \tag{6}$$

This will turn out much more interesting. What does the singular strategy x^* look like? When does it exist (i.e. lie in the permissible range $[0; x_{\max}]$)?

Answer: $x^* = \frac{c_1 - b_1}{2(2b_2 - c_2)}$. Positive x^* requires that $c_1 - b_1$ and $2b_2 - c_2$ have the same sign. Furthermore, $|c_1 - b_1| < x_{\max} 2 |2b_2 - c_2|$.

Exercise 8. Determine the conditions under which x^* is convergence stable and/or evolutionarily stable. Classify and discuss the possible outcomes of the model.

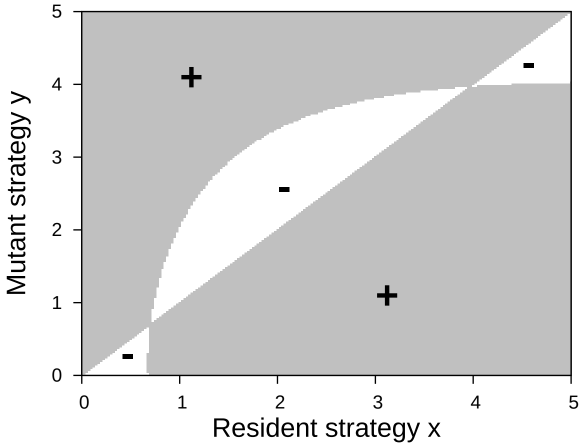
Answer: Convergence stability requires $2b_2 < c_2$ (see Exercise 4). Evolutionary stability requires $b_2 < c_2$ (see Exercise 5). Depending on parametes, there are five possible outcomes: Evolution of $x = 0$, evolution of $x = x_{\max}$, evolution of $x = 0$ or $x = x_{\max}$ depending on initial conditions (in this case, x^* is not convergence stable), evolution towards x^* as an ESS, and evolution towards x^*, followed by evolutionary branching. In the latter case, the two branches evolve to $x = 0$ and $x = x_{\max}$, respectively, thus recovering the simple two-strategy version of the game with only defectors and cooperators. See Figure 1 of Doebeli et al. (2004).

Exercise 9. With more complicated choices for $B(x)$ and $C(x)$, the model shows an even richer behavior, but typically, it is no longer analytically tractable. In this case, a useful graphical approach is to use pairwise invasibility plots. For example, for

$$B(x) = b\sqrt{x} \tag{7}$$

$$C(x) = \ln(cx + 1) \tag{8}$$

and the parameters $b = 1, c = 0.6$, the PIP looks like this:



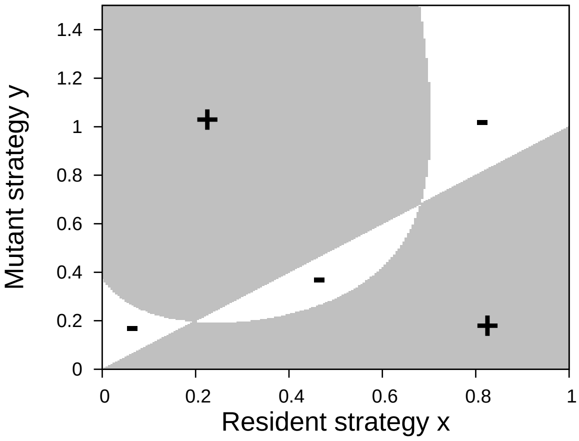
What would you have done to produce this plot? Discuss what it reveals about the evoluationary dynamics.

Answer: The plot can be produced by either calculating the sign of $s_x(y)$ for a range of x and y values, or by numerically determining the line where $s_x(y) = 0$. In this version of the model, there are two evoluationarily singular strategies. The one on the left-hand side is an evoluationary branching point, whereas the one on the right-hand side is a repellor.

Exercise 10. Another choice for the functions is

$$B(x) = b(1 - e^{-x}) \tag{9}$$
$$C(x) = \ln(cx + 1). \tag{10}$$

With $b = 5$ and $c = 10$, this yields the following PIP:



What is the behavior of this model?

Answer: Again, there are two singular strategies. Now, the left-hand one is a repellor and the right-hand one a branching point.

Exercise 11. As you will have noticed, some of the singular strategies in the models above are evolutionary branching points. Determining the dynamics after branching is more difficult (but see below). A quick way to see what happens (and to verify the analytical results), is to use simulations. Assume that reproduction is asexual with occasional mutation, that individuals are characterized only by their strategy x, and that individual fitness is determined by the pay-off from games played against random opponents. What would a simple individual-based model look like?

Answer: A simple individual-based model could go like this: The population consists of a fixed number N of individuals characterized by their strategy x_i (i.e. and array of x_i values). Each time-step, a random individual (I_1) is chosen to die (by drawing a random number between 1 and N). This individual may be replaced by its own offspring, or by the offspring of another randomly drawn individual (I_2). To decide between these two possibilities, two more random individuals (I_3 and I_4) are drawn. Then I_1 plays a game against I_3, and I_2 plays a game against I_4. I_1 and I_2 receive pay-offs P_1 and P_2 according to equation (1), and I_1 reproduces with probabilities $P_1/(P_1 + P_2)$. Repeating this process N times equals one generation.

Exercise 12. A more sophisticated simulation tool with a nice web-interface is available at http://www.univie.ac.at/virtuallabs/Branching/. Use this to verify your previous results, and to explore some additional model variants.

Exercise 13. Maybe you find that relying on simulations is not fully satisfying. To get analytical results about evolution after branching, we need to derive the invasion fitness of a mutant in resident population made up of two coexisting strategies x_1 and x_2 (with $x_1 < x^* < x_2$). For given values of x_1 and x_2), we first need to determine the equilibrium frequency p^* of, say, x_1. How can this be done, and what is the solution for the quadratic costs and benefits functions? Next, we can define the invasion fitness gradient for each branch separately. What does is look like for the quadratic functions, and what does this mean biologically?

Answer. See section 1.1.2 of supporting online material to Doebeli et al. (2004).