

Evolution of Cooperation

In last week's lab we created hermaphroditic turtles with two alleles "A" and "B". We then assigned a constant fitness to each of the genotypes to investigate how allele frequencies changed with different fitness values. We also examined how removing random mating resulted in quantitatively different long-term behavior. In practice, fitness is not a constant, but varies according to the frequency of different phenotypes. In this lab we will allow turtles to play a game with each neighbor before mating. The fitness will be determined by the score of the game. The game the turtles will play is the prisoner's dilemma. In this game the reward for defecting against a cooperative player is higher than the reward for cooperating, but two cooperators have a higher reward than two defectors. The rational choice in such a game is to defect. Indeed, in evolutionary game theory defecting is an evolutionary stable strategy – that is defectors cannot be invaded by cooperators. The assumptions in evolutionary game theory are that individuals reproduce asexually and each individual plays against every other individual. We will relax both these assumptions in this model and show that under such circumstances cooperative behavior can gain a foothold, and in some circumstances it can even take over.

The Model

Here are the parameters for your model:

We will use last week's model so make sure it is working. Remove references to slider assigned fitness values. Let each turtle have a variable called `defecting?`. AA turtles will have `defecting?` set to true. These are the defectors. BB turtles will have `defecting?` set to false. These are the cooperators. Let heterozygotes have `defecting?` set to true with some probability `defecting-probability`, which is set with a slider, and otherwise let them have `defecting?` set to false. In this way you can investigate the case where defecting is a dominant allele or the case where cooperating is dominant allele.

Before mating, get each turtle to play the prisoners dilemma game with each of its neighbours. Write a `play` procedure:

To simplify matters, let's assume a payoff matrix :

	C	D
C	1	0
D	b	0

With this matrix, cooperators get a point for each neighbor who is cooperating, and defectors get `b` points for each neighbor who is cooperating. The reward parameter `b` can be determined by a slider with values ranging from 0 to 3. The prisoner's dilemma assumes $b > 1$. Let the fitness of the turtle be the total score divided by the total number of its neighbors. If the number of neighbors is zero, the fitness will be zero.

Now, let turtles mate with probability determined by given by the ratio of their fitness to the maximum fitness of all the turtles.

This should complete the model. Do make sure that new turtles are hatched with the appropriate value for the `defecting?`

For homework you will explore how the parameters of the model affect the survival rates of cooperators and defectors. You should compare the results of the model with predictions from evolutionary game theory. Answer homework questions in the information section of your model.

Homework

1. Run the simulation with your screen-edge set at 25 by 25, p set at 0.5, initial population 2000 and the random walk steps to be about 10 (which should ensure random mating). Set the defector reward parameter b to be 2. Run the simulation several times with these parameter values. Try both the defecting as dominant allele and cooperating as dominant allele cases. Do you obtain the results you expect? Explain your observations.
2. The above results are quite sensitive to the density of turtles on the screen. Repeat the experiment with turtle numbers varying from 500 to 5000. In which cases do cooperators fare better. Can you find population values at which the defectors take-over? Explain your observations.
3. Now investigate the reward parameter b . Set the population parameter back to 2000. Find the critical value for b , below which cooperators end up taking over. Does it depend on which type of allele is dominant? Evolutionary game theory predicts this should happen at $b=1$. If you get a different result explain why. Can you find a critical value above which the defectors take over? Explain why or why not.
4. While the above examples may bring out some interesting behavior, it is the case where turtles do not move around to mate that is most interesting. This is because defectors do well in an environment where they can find cooperators, but if they do too well, local cooperators may die out and the fitness of the defectors will suffer. Repeat questions 1-3 above, but this time set the random-walk distance to zero. Compare the parameter values where transitions between cooperator take-over and defector take-over occur. You should see that cooperators fare better in an environment where there is less movement. Use your results to explain why. You may have to run some of these models for a while to see interesting behavior emerge.
5. If you reflect on the mating part of our model, you may think of one change that make sense. We have used the score in the prisoner's dilemma game as means to determine a probability of mating, however, turtles not take into account the fitness of its neighbors when choosing a mate. Change your program to so that turtles choose the fittest neighbor as a mate. How does this change the results of your previous experiments? Would you recommend choosing selfish, but successful individuals as your mate? Would your offspring fair better or worse? Would the population as a whole be better of or worse off?
6. In question 4 you will have seen that cooperators which establish themselves in colonies, are globally fit and reproduced fast, but are susceptible to local invasions by opportunistic defectors. Defectors do well for themselves, but rely on cooperators to survive. In many ways defectors are like parasites. We could enhance this model by introducing a mutant strategy that punishes defectors by defecting against them, but is kind to cooperators by cooperating with them. However, the only fair way to determine if a player is a defector is by playing against them (no fair looking at their genes!). Therefore, in order to punish them you have to play against them a second time, and remember what they did the first time. This leads us to the iterated prisoner's dilemma game. We could change our model to do this, but instead lets actually play the game. In the models library under Hubnet Computer Activities, open up the prisoner's dilemma hubnet, under unverified models. This is an interactive demonstration that will allow you to play the prisoner's dilemma with your classmates. You choose a strategy, and see how you do.
7. Save your file as "lastname_firstname_week9.nlogo. Add comments to your code, include answers to the homework questions and then copy your file to the dropbox.