

Evolution of Cooperative Behavior

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In many instances in nature we see examples of **altruism**; that is, animals appear to help each other at their own expense. This seems to create a problem for the idea of natural selection: if more successful organisms are those that transmit their characteristics to future generations, shouldn't organisms always be selfish and behave in ways that benefit only themselves and not others? One factor to consider is the possibility of common interests between individuals. Two theories that consider such shared interests are **kin selection** (discussed in lecture) and **reciprocal altruism**: that individuals might help non-related individuals in the hopes that they will reciprocate; i.e. they will help in return at some future date. This lab will focus on the latter theory, as it seems counter intuitive to the idea of natural selection: why incur a cost for a non-related individual when there is no guarantee they will return the favor?

Situations where interactions can harm or benefit both individuals can be modeled as **non zero-sum games**, in which one player's gain is NOT NECESSARILY the other's loss (this is in contrast to zero-sum games such as checkers, where one player's gain is by definition a loss for the opponent). The goal in such situations is to maximize your own points, regardless of the opponent's points. A common example of such a game is called the "Prisoner's Dilemma." It also appears in theories about criminal justice, sociology, politics, psychology, philosophy, and athletics, and so may be helpful to you outside of this class.

The name "Prisoner's Dilemma" comes from the following imaginary situation: Two prisoners are in jail in different cells, with no possibility of communication. They have both been charged for a small crime for which they would have to spend 2 years in jail. The authorities suspect (but have no evidence) that they are also guilty of a major crime for which they could spend 8 years in jail. To extract convictions for the major crime, the authorities offer a reduced sentence to each prisoner (charges will be dropped on the small crime) if they will betray the other prisoner and implicate them in the major crime (**defect**). If, on the other hand, the prisoners **cooperate** with each other and both remain silent, the authorities can only keep them in jail for 2 years. Imagine you are Prisoner 1. You do not know what your partner in crime is going to do, so what should you do?

If you decide to remain silent (cooperating with your partner), but your partner defects, you have been suckered and you get jailed for 10 years while your partner goes free. If you both remain silent both of you will only get the 2-year sentence. If you both tell on each other (defect), you both get jailed for 8 years (both collaborate with authorities and so do not get charged for the small crime) what should your choice be? If your partner cooperates by remaining silent, then your best move is to defect and go free. Alternatively, if your partner defects then your best move is to also defect and you remain jailed for 8 years. And herein lies the dilemma: no matter what your partner chooses, you would do better by defecting, and the same is true for your partner. But if you both betray each other, you are both worse off than if you had cooperated and remained silent.

A number of natural encounters mimic this dilemma. Many species of birds and mammals engage in mutual grooming, where individuals alternate removing parasites from the other. There are obvious benefits to be gained from getting someone else to pull off parasites from places that are not easily accessible to one, and therefore one can see the benefits of mutual grooming. However, one individual might do even better by not cooperating: letting other individuals get rid of its parasites without paying the costs of time and energy in reciprocating. Even such seemingly competitive interactions, such as between a parasite and its host, may have an aspect of cooperative behavior; it may benefit the parasite to maintain a healthy host and thus continue to benefit from it.

- How might this dilemma play out in nature? Does natural selection mean that nice guys finish last? Or does cooperation make sense?

A. Evolution of cooperative behavior pre-quiz

- List three examples of behaviors that are genetically determined
- Define reciprocal altruism.
- Define natural selection.

B. Single move game

GOALS: In a single turn non zero-sum game, is it better to cooperate or defect?

In studies of animal behavior, rather than prison sentences, the payoff is based on the costs of performing a behavior and the benefits that behavior derives. The costs could be measured in energetic terms, or in terms of reduced reproduction or survivorship, etc. Similarly the benefits could be measured in terms of number of offspring, energy gain, increased probability of survival, economic gain, etc.

1. Raw Payoff Matrix

Let's assume that the benefit for an interaction is four points, and the cost is two points. If you cooperate, you each get the benefit and bear the cost. If one cooperates and one defects, the cooperator bears the cost and the defector gets the benefit. If you both defect, you both get nothing. These outcomes are summarized in the table below.

		Partner's move	
		Cooperate	Defect
My move	Cooperate	2	-2
	Defect	4	0

2. Normalized payoff matrix

We are going to play a couple versions of this game, and add up the points earned by various strategies. To simplify things, use the following matrix; it is the same as above, but normalized by adding 2 to everything so there are no negative values.

		Partner's move	
		Cooperate	Defect
My move	Cooperate	4	0
	Defect	6	2

3. Single moves game procedure

1. Pair with one other student at random. Each of you will have two cards, one marked C (for Cooperate) and the other marked D (for Defect)
2. Decide what card you will play, but do not give your partner any clue of your intended move.
3. When the instructor says "ready" put your chosen card with the letter side down on the desk.
4. When the instructor says "go" turn your card over.
5. Record your move, your partner's move, and the points each of you made from the play in the table provided.
6. Tabulate the data from the entire class on the board, copy the data into the table provided. As a class, you will tally up the points and calculate the average points for cooperators, and the average for defectors.

4. Single move game data table

	Total Points for strategy	# students	Avg. Points
C			
D			

5. In a *single* interaction such as this, what is the best move in a Prisoner's Dilemma game?

C. Multiple moves game

GOAL: To see whether the same strategy that wins for the single move game applies when there are multiple interactions between the same two individuals.

Why is this so different than the single round game? As before, cooperating earns you both more points on average but leaves you open to a bigger loss if your partner defects.

You now know what won the first round. But your partner knows that you know that. And you know that they know that you know that. There's more of a head game when there is the chance to build long term trust, or for revenge!

While you play, try to think of a winning long term strategy.

1. Multiple moves game procedure

1. Pair randomly again. You will be playing the same game, this time between 20 to 30 times with the same person.

2. Follow the same procedure as before for each move: When the instructor says “ready” put your chosen card on the table, and when the instructor says “go” turn it over.
3. After each play, record your move and your partner's and the number of points you obtained in the table provided.
4. The instructor will stop the game after somewhere between 20 and 30 times.
5. Tally up your points. The instructor will tabulate each player's points on the board. Now you can compare how you did relative to others in the class.

2. Multiple moves game data table

	My move	Their move	My points		My move	Their move	My points
1				16			
2				17			
3				18			
4				19			
5				20			
6				21			
7				22			
8				23			
9				24			
10				25			
11				26			
12				27			
13				28			
14				29			
15				30			

3. **Why might it be important that you do not know when the game is going to finish?**
4. **What was the strategy of the player getting the highest points? The lowest points?**
5. **Now that you have played the iterated version, can you think of improvements to your strategy that would increase your score?**

D. Evolutionary game

GOALS: To see whether natural selection would allow "nice" strategies to survive in a population.

Now suppose that within any population, individuals adopt one of a number of possible game plans or strategies, and that strategies are transmitted between individuals across generations. We are going to assume that behaviors are genetically fixed for a simple case, so individuals cannot modify the program with which they were born. Some strategies are "nasty" in that they defect without provocation, others are "nice" and do not. Will the "nice guys" be edited out of the population?

1. Evolutionary game procedure

1. You will be given a card with the name and a brief description of one of the four possible strategies. All strategies will be represented by about the same number of players (for example, if there are 16 students in the class, each strategy will be played by 4 students).
2. Play the game 20 times with your partner using your assigned strategy. As before, record all moves as well as the number of points that you make at each move. Record your moves in the table provided.
3. When you finish, tally up your points and give them to the TA who will then tally up the total number of points for each strategy.
4. *Calculate Strategies for the Next Generation* The number of strategies playing in the 2nd generation is based on the points each strategy made in the 1st generation. As an example, suppose that the total points amassed by the players using the "Always defect" strategy was 410 and together with the three other strategies there was a class total of 820 points. The relative success of the Always defect strategy is expressed as a frequency; that is, $410/820 = 0.50$. So, one-half of the players in the 2nd round will be using the "Always defect" strategy.
5. *2nd Generation and Onward* Strategies are now reassigned to players by the instructor, based on each strategies' success in the previous generation, as described above.
6. Players pair up with a new partner.
7. Play 20 times with your new partner using your strategy (which may be a different one from the previous generation).
8. Tally up points as before, and the instructor will calculate the success of each strategy after at the end of the generation.
9. This procedure will be repeated for a total of FIVE generations (including the first) and you should record the number of individuals playing each strategy in each generation in the table provided.