BioMath

Evolutionary Game Theory: The Game of Life

Student Edition

COMAP

Funded by the National Science Foundation,
Proposal No. ESI-06-28091

This material was prepared with the support of the National Science Foundation. However, any opinions, findings, conclusions, and/or recommendations herein are those of the authors and do not necessarily reflect the views of the NSF.

At the time of publishing, all included URLs were checked and active. We make every effort to make sure all links stay active, but we cannot make any guaranties that they will remain so. If you find a URL that is inactive, please inform us at info@comap.com.

Published by COMAP, Inc. in conjunction with DIMACS, Rutgers University.

COMAP, Inc.
175 Middlesex Turnpike, Suite 3B
Bedford, MA 01730
www.comap.com

ISBN: 1 933223 58 8

Evolutionary Game Theory: The Game of Life

Overview

This unit examines the role that behavior plays in evolutionary fitness. Through studying and playing games, you will develop an understanding of natural selection as organisms compete for limiting resources (e.g. food, water, space, mates, safety, etc.). You may have previously considered adaptations due to the physical phenotype of the organisms. This unit will look specifically at behavioral choices made to obtain the resources organisms need for survival and for reproduction. You will develop different strategies under different conditions in various games and examine the effects of these strategies on survival. If the behavioral traits you see are due to a genetically inherited variation, then these genes may be passed to the next generation. Those who are more successful will survive to live another day and perhaps even go on to reproduce, passing their genes on to their descendants and thereby having only genes of the successful represented in the next generation. Unsuccessful individuals will not reproduce and will die before passing their genes on to the next generation. Building on all of this, the concept of evolutionary fitness is being both successful at surviving and successful at reproducing.

Unit Goals and Objectives

Goal: Understand the role of natural selection in the evolution of a species.
Objectives:

- Explain the term natural selection and relate natural selection to variation.
- Describe the role of competition for limited resources with regard to natural selection.
- Explain how natural selection acts as a possible mechanism for evolutionary change.
- Explain the role of kin selection in natural selection.

Goal: Understand the basic concepts of game theory.
Objectives:

- Summarize what game theory entails.
- Explain what is meant by a game strategy.
- Contrast pure strategy with dominant strategy.
- Explain and provide examples of a Nash equilibrium.

Goal: Be able to analyze a game and the strategies available.
Objectives:

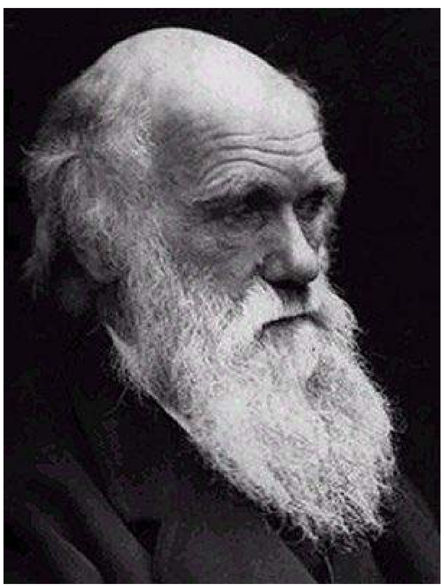
- Analyze how a player can maximize his/her outcome in a 2-player game.
- Differentiate between various payoff structures.
- Evaluate a players' choice of strategy in different game situations.
- Design a payoff structure consistent with a given situation.
- Compute how relatedness may affect how the game is played.

Lesson 1 Survival of the Fittest

Biology Background

You have probably heard the phrase "**survival of the fittest**". What does it really mean?

Charles Darwin originated this phrase in the 1850's. Darwin realized that there are not enough resources in the environment for every organism to survive. As a result, there will be **competition** for these resources. Darwin also realized that within any group of similar organisms there are **variations**, and certain variations may result in some organisms being better competitors for limited resources. The individuals least successful at getting resources will fail to obtain those needed to be healthy and to survive. If this lack of success is due to a genetically inherited variation, individuals with the less beneficial **genes** will die before passing these genes to the next generation. Those that are more successful will survive to live another day and perhaps even go on to reproduce. These successful individuals will pass their genes on to their descendants; therefore, having only the genes of successful individuals represented in the next generation.



FATHER OF EVOLUTION
Charles Robert Darwin, FRS (Born 12 February 1809 – 19 April 1882) was an English naturalist and geologist, best known for his contributions to evolutionary theory. He established that all species of life have descended over time from common ancestors, and in a joint publication with Alfred Russel Wallace introduced his scientific theory that this branching pattern of evolution resulted from a process that he called natural selection, in which the struggle for existence has a similar effect to the artificial selection involved in selective breeding.

Darwin published his theory of evolution with compelling evidence in his 1859 book *On the Origin of Species*, overcoming scientific rejection of earlier concepts of transmutation of species. By the 1870s the scientific community and much of the general public had accepted evolution as a fact. However, many favoured competing explanations and it was not until the emergence of the modern evolutionary synthesis from the 1930s to the 1950s that a broad consensus developed in which natural selection was the basic mechanism of evolution. In modified form, Darwin's scientific discovery is the unifying theory of the life sciences, explaining the diversity of life.

Text from Wikipedia. Photograph: By J. Cameron (Unknown) [Public domain], via Wikimedia Commons

Building on all of this, the concept of **evolutionary fitness** describes being both successful at surviving and successful at reproducing. So, in a resource-limited environment, those that are least evolutionary fit should be the first to die without having reproduced. This is the essence of the idea of survival of the fittest.

Limiting resources can take many forms. They include, but are not limited to, food, water, space and mates. If food is the limiting factor, large size might be an advantage. For example, being a large boa constrictor allows the snake to have more food options and strength to squeeze. But, survival of the fittest does not always mean being the biggest or the strongest. For cheetahs being the fastest helps the large cat catch more prey. If food is really limiting, a slower metabolism may be an advantage since your energy requirements will not be as great. For bears in winter, being able to hibernate through the winter when food is very scarce gives this animal an advantage. Camouflage could be another advantage. Alligators use camouflage to get close enough to their prey to have an advantage in catching them. Can you see the two moths in each picture in Figure 1.1? The characteristic of camouflage is of benefit to one species or another depending upon the environment.

Figure 1.1: Camouflage

Left: By Gilles San Martin from Namur, Belgium (Moth camouflage Uploaded by Jacopo Werther) [CC-BY-SA-2.0 (http://creativecommons.org/licenses/by-sa/2.0)], via Wikimedia Commons.
Right: By Jerzy Strzelecki (Own work) [GFDL (http://www.gnu.org/copyleft/fdl.html) or CC-BY-3.0 (http://creativecommons.org/licenses/by/3.0)], via Wikimedia Commons.

Other less obvious things can also be thought of as limiting factors. Take safety for an example. There may be enough food for plant eating rabbits, but if they cannot get to it because of coyote predators, food becomes a limiting factor. Birds and squirrels cannot safely survive in an area where there are not enough trees to house and hide them.

If the environment stays the same, each generation would have to compete for the limited resources available, setting the bar higher and higher. But, the environment is always changing so what makes an organism the "fittest" today may not be the most evolutionarily successful in the future. The weeding out of individuals with traits that are less fit (because of how those traits make the individuals that have them interact with the environment, including interactions with other species) is called **Natural Selection**. The aspect of the environment that causes the trait to make the individual less fit than those that don't have that trait is called the **selective pressure** or the **mechanism of selection**.

Biologists study the relationships between organisms (or species) that are competing for limited resources as having a behavioral relationship to each other. An organism (Organism 1) can act in a way that will help, harm, or have no effect on another organism (Organism 2). Each action will result in a cost, benefit, or neutral outcome for Organism 1. These relationships and behaviors are characterized by the combination of actions and results. Some of these relationships have names in biology as shown in Table 1.1.

Behavior	Outcome	Relationship
Organism 1 Helps Organism 2	Benefits Organism 1	Mutualism
	Costs Organism 1	Altruism
Organism 1 Harms Organism 2	Benefits Organism 1	Selfish
	Costs Organism 1	Spite
Organism 1 Has no Effect on Organism 2	Benefits Organism 1	Commensalism
	Costs Organism 1	Stupid

Table 1.1: Biological Relationships

The choice of action made by Organism 1 can be thought of as a strategy for Organism 1 in a **game** (even if the choice is not conscious one). The results of the game are the **payoff** for both organisms. Questions may arise about the relative outcome of results of the chosen action by Organism 1. More importantly, games can be studied where both organisms have choices. In these two player games, it is possible to see how each player can maximize its own results, no matter how the other organism plays the game. The game being played here is competition for the same resources and survival of ones' genes. Ultimately, the point of the game is to outcompete the other players and ensure one's evolutionary fitness.

This unit will explore how math is used to study the game, its rules, and the payoffs.

Questions For Discussion

1. Why are variations within similar organisms and limiting resources the basis for the survival of the fittest?

2. Explain what is meant by evolutionary fitness.

3. Will certain traits that make an organism more fit at one point in time, necessarily make that organism more fit at a point in time in the future? Explain.

Game Theory Background

Game theory is the mathematics of how people, typically called "players" in the context of a game, consider conflicts and opportunities for cooperation when making decisions about how to behave in situations with each other. The mathematics we use assumes that all the players understand the situation and that each knows that the others understand the situation too. An important assumption that is made in game theory is that each player works to maximize her or her own benefit. Later in this unit we will use game theory to model situations in which it seems - at first - that players are *not* working to maximize their own benefits.

A game defines the number of players, the possible actions that each player can take, whether players must move at the same time. If not moving simultaneously, the game will define the order in which players will choose their moves. Once all the players have chosen their actions, the combination of the chosen actions is called an **outcome**. The game must also define how much each player gains or loses from each outcome. This gain or loss is called the **payoff** to the player from the outcome.

Example #1

Our first game has two players, Tina and Sahar. Each player chooses between the same two actions: 1 finger or 2 fingers. The two players make their choices at the same time and cannot discuss them beforehand.

In this game, there are 4 possible outcomes:

1. Tina chooses 1 finger and Sahar chooses 1 finger,
2. Tina chooses 1 finger and Sahar chooses 2 fingers,
3. Tina chooses 2 fingers and Sahar chooses 1 finger, and
4. Tina chooses 2 fingers and Sahar chooses 2 fingers.

We still need to know the payoffs for these outcomes. An easy way to represent these is with a table with two rows (the number of possible actions Tina has) and two columns (the number of possible actions Sahar has). Then the payoff can be written as an ordered pair (x, y), where x is the payoff for Tina and y is the outcome for Sahar.

Sahar's Choice (y)

Tina's Choice (x)	**(x, y) Payoff**	1 Finger	2 Fingers
	1 Finger	(2, 2)	(1, 0)
	2 Fingers	(0, 1)	(0, 0)

Table 1.2: Finger Game Payoff - Example #1

Question For Discussion

4. If you were going to play this game as Tina, would you pick one finger or two fingers? Why?

A plan for how to play in every possible situation in a game where you might need to make a decision is called a **strategy**. A more formal definition is:

> A strategy is a complete contingent plan, or decision rule, that specifies how the player will act in every possible distinguishable circumstance in which she might be called upon to move.[1, pg.228]

In the game we just defined, each player has only two strategies: play one finger, or play two fingers. Because the players have only one choice to make and they make their choices at the same time, without knowing what the other player is choosing, the strategies are the same as the actions. If we changed the rules of the game to have Tina announce her choice first, then one of Sahar's possible strategies would be "If Tina plays one finger, play one finger; if Tina plays two fingers, play two fingers." This provides a rule that determines Sahar's decision in every possible scenario - that is, for every possible action that Tina might have chosen before he has to choose his action. Another strategy for Sahar in that game would be "If Tina plays one finger, play one finger; if Tina plays two fingers, play one finger."

Let's now think about which strategy in the game we defined above, in which the players choose their actions simultaneously without knowing the other player's choice, each player might choose. When Tina has to decide whether to choose one finger or two fingers, she might think about what she would do to maximize her payoff if she knew what Sahar's choice would be. Her thought process might be something like: "If Sahar plays one finger, should I choose one finger or two fingers? Since a payoff of 2 is better for me than 0, I should play one finger also because that will give me a payoff of 2. Also, if Sahar plays two fingers, should I choose one finger or two fingers? Since a payoff 1 is better than 0, I should play one finger because that will give me a payoff of 1." Even though Tina does not know what Sahar will choose, she knows that she will maximize her payoff (remember that we assumed that is the goal for every player) if she chooses one finger. This does not mean that Tina knows what her payoff will be; that depends on what Sahar chooses. She only knows that, regardless of what Sahar chooses, she will maximize her payoff by choosing one finger.

There is something important that we should notice here. No matter what Sahar chooses to do, Tina should choose one finger in order to maximize her payoff. This is called a **dominant strategy** for Tina—it's the best choice for her no matter what Sahar does. When a player has a dominant strategy, that player should choose that strategy. Based on our assumptions that players know everything about the game and try to maximize their payoffs, they will choose a dominant strategy.

What about Sahar's choice? If Tina plays one finger, a payoff of 2 is better than 0, so Sahar would be better off picking one finger. Similarly, if Tina plays two fingers, a payoff of 1 is better than 0, so Sahar would again be better off picking one finger. Just like Tina, Sahar has a dominant strategy of playing one finger.

Notice that both Tina and Sahar have determined that they each should pick one finger in this game. This seems to make sense because those are the highest payoffs for both players, but is it always true that the players will play in such a way to get the best possible outcome?

Example #2

Let's consider a new game with different payoffs for Tina and Sahar. Suppose that the players are playing to decide how much money they will each get from a bank. If the payoff is positive, they get money, but if the payoff is negative, they have to pay money to the bank.

		Sahar's Choice (y)	
	(x, y) Payoff	1 Finger	2 Fingers
Tina's Choice (x)	1 Finger	(-1, -1)	(-9, 0)
	2 Fingers	(0, -9)	(-6, -6)

Table 1.3: Finger Game Payoff - Example #2

The same analysis we used before now has a different outcome.

Tina thinks: “If Sahar plays one finger, should I choose one finger or two fingers? Because getting 0 is better for me than having to pay 1, I should pick two fingers because that will give me a payoff of 0. Also, if Sahar plays two fingers, should I choose one finger or two fingers? Because paying 6 is better than paying 9, I should pick two fingers because that will give me a payoff of -6.”

Similarly, Sahar thinks: “If Tina plays one finger, should I choose one finger or two fingers? Because a payoff of 0 is better for me than having to pay 1, I should pick two fingers because that will give me a payoff of 0. Also, if Tina plays two fingers, should I choose one finger or two fingers? Because paying 6 is better than paying 9, I should pick two fingers because that will give me a payoff of -6.”

Thus, both players have a dominant strategy; playing two fingers. When the players follow their dominant strategies, they both will receive a payoff of -6, meaning that they will both pay the bank 6 dollars. This is a bit curious, because there is an outcome in the game (if each player had played one finger) where they would have each owed the bank only 1 dollar.

It is important to observe that this better outcome for both players (in which each player picks one finger) requires both players to change their strategies. It is not something that either player can bring about simply by changing only his or her own strategy.

Nash Equilibrium

When neither player can improve his or her payoff by making a change only to his or her own strategy, that collection of strategies is called a **pure-strategy Nash equilibrium** (or just a "Nash equilibrium"). As we saw in our most recent example, a Nash equilibrium is not necessarily the best possible outcome for either player. However, if the players are playing strategies that form a Nash equilibrium, then neither player can improve his or her payoff without the other player also changing his or her strategy.

AMERICAN MATHEMATICIAN AND NOBEL PRIZE WINNER

John Forbes Nash, Jr. (born June 13, 1928) is an American mathematician whose works in game theory, differential geometry, and partial differential equations have provided insight into the factors that govern chance and events inside complex systems in daily life. His theories are used in market economics, computing, evolutionary biology, artificial intelligence, accounting, politics and military theory. Serving as a Senior Research Mathematician at Princeton University during the latter part of his life, he shared the 1994 Nobel Memorial Prize in Economic Sciences with game theorists Reinhard Selten and John Harsanyi.

Nash is the subject of the 2001 Hollywood movie *A Beautiful Mind*. The film, loosely based on the biography of the same name, focuses on Nash's mathematical genius and also his schizophrenia.

If, as in our first two games, neither player can improve his or her payoff by changing only his or her own strategy, then that collection of strategies forms a Nash equilibrium. For example, Tina's dominant strategy in the Example #2 of playing two fingers was her best choice regardless of what strategy Sahar chose. In particular, if he chose his dominant strategy - or any other strategy - then Tina could not do better by choosing a different strategy.

Example #3

Let's look at another game that Tina and Sahar could play. The rules will be the same as before - both players choose one or two fingers, and they make their choices simultaneously and without communication - but the payoffs will be given by the following table.

Sahar's Choice (y)

	(x, y) Payoff	1 Finger	2 Fingers
Tina's Choice (x)	1 Finger	(1, 1)	(1, 0)
	2 Fingers	(0, 0)	(0, 2)

Table 1.4: Finger Game Payoff - Example #3

Questions for Discussion

5. Do the players have dominant strategies? Describe the thought processes of Tina and Sahar.

6. Is there a Nash equilibrium in this game? If so, what is it? Explain.

7. Choose another strategy combination and explain why it is not a Nash equilibrium.

We have already looked at how to think about games in a way that lets us find dominant strategies. Let's think a bit more about how to find combinations of strategies that form Nash equilibria.

Activity 1-1 Finding the Nash Equilibrium

Objective: Use the payoff matrix to identify all Nash equilibria.
Materials:

Handout GT-H1: Finding the Nash Equilibrium Activity Worksheet
Colored pencil or marker

1. Start with a payoff matrix showing the payoffs for all combinations of strategies and the corresponding payoffs for each player. Use the following payoff matrix from Example 3.

Sahar's Choice (y)

	(x, y) Payoff	1 Finger	2 Fingers
Tina's Choice (x)	1 Finger	(1, 1)	(1, 0)
	2 Fingers	(0, 0)	(0, 2)

Table 1.4: Finger Game Payoff - Example #3

a. The first step is to pick a box (that is, a combination of strategies). For this matrix, start with the box corresponding to each player playing two fingers (the lower-right corner of this table with a (0, 2) payoff). For each other box in the same column, use your colored pencil or marker to draw an arrow *from* the box in which Tina has a lower payoff *to* the box in which she has a higher payoff. If Tina has the same payoff in both boxes, do not draw any arrow.

b. Now, do the same thing with the other boxes in the same *row*, except now draw an arrow from the box in which *Sahar* has a lower payoff to the box in which he has a higher payoff. If Sahar's payoff is the same in both boxes, do not draw an arrow.

c. Keep doing this for all of the boxes in the payoff matrix. Remember to only compare boxes in the same row or in the same column. When comparing boxes in the same row, look at *Sahar's* payoffs; when comparing boxes in the same column, look at *Tina's* payoffs. You might sometimes compare two boxes between which you've already drawn an arrow; you don't need to draw a second arrow.

Remember that we drew an arrow from one box to another box in the same column if Tina had a higher payoff in the second box. This means (because the boxes are in the same column) that Tina could change her strategy, without Sahar changing his, in order to increase her payoff. This means that the strategy combinations in which Tina cannot improve her payoff are the boxes that do not have any arrows *to* another box in the same column. Similarly, the strategy combinations in which Sahar cannot improve his payoff are exactly the boxes that do not have any arrows to another box in the same *row*.

This means that the Nash equilibria in a game are exactly those boxes that do not have *any* arrows drawn *from* them, either in the same row or in the same column.

d. In Lesson 1, we said that each player playing one finger was the unique Nash equilibrium in this game. Look at the arrows you have drawn. Describe using your matrix with arrows why this is a Nash equilibrium and the only one in this matrix.

2. Use the following payoff matrix and identify any Nash equilibria. Assume that Tina and Sahar make their choices simultaneously and without discussing them.

		Sahar's Choice (y)	
	(x, y) Payoff	1 Finger	2 Fingers
Tina's Choice (x)	1 Finger	(1, -1)	(-1, 1)
	2 Fingers	(-1, 1)	(1, -1)

Table 1.5: Finger Game Payoff – Activity 1-1, 2

a. Discuss this game in your group and describe the strategies available to Tina and Sahar.

b. Use the method of drawing arrows to find any Nash equilibria. Describe what you find.

3. Use the following payoff matrix and identify any Nash equilibria. Assume that Tina and Sahar make their choices simultaneously and without discussing them.

		Sahar's Choice (y)	
	(x, y) Payoff	1 Finger	2 Fingers
Tina's Choice (x)	1 Finger	(1, 1)	(0, 0)
	2 Fingers	(0, 0)	(1, 1)

Table 1.6: Finger Game Payoff – Activity 1-1, 3

a. Discuss this game in your group and describe the strategies available to Tina and Sahar.

b. Use the method of drawing arrows to find any Nash equilibria. Describe what you find.

Practice

1. Explain what is meant by game theory.

2. What is the "payoff" in a game?

3. Describe what is meant by a "strategy" in a game.

4. How is a (pure-strategy) Nash equilibrium different from a collection of dominant strategies (one for each player)?

5. If each player has a dominant strategy and plays it, will each player always receive his or her maximum possible payoff (considering all the possible strategy combinations)? Explain.

6. Draw a payoff matrix (different from ones already presented) with only 1 Nash equilibrium.

7. Draw a payoff matrix (different from ones already presented) with 2 Nash Equilibria.

Lesson 2 Resource Advantage

We can device games to help improve our understanding of evolutionary fitness. In a two-player game, the outcomes can indicate control of a specific resource. To begin, we will examine a well-known two-player game used to model business, economics and nature.

Prisoner's Dilemma

Imagine that the police capture two suspects and accuse them of a crime. Using the terminology of game theory, we can describe the scenario and determine a strategy for each of the suspects. The police know they do not have enough evidence to convict either of the suspects of the crime they are accused of committing, but do have enough to convict them both of a lesser crime. The police make each of the suspects, individually, an offer.

This scenario is the two-player game commonly known as the **Prisoner's Dilemma**. Each of the suspects plays against the other for an advantage. If either suspect betrays his compatriot to the police, he will receive a lesser sentence, but his partner will be convicted of the greater crime. If the partners cooperate with each other, both will get 1 year in prison. If only one betrays his partner, he will be set free and his partner, after a trial, will be sentenced to 10 years in prison. If both betray, they will each be sentenced to 5 years.

		Sahar's Choice (y)	
	(x, y) Payoff	Cooperate	Betray
Tina's Choice (x)	Cooperate	(-1, -1)	(-10, 0)
	Betray	(0, -10)	(-5, -5)

Table 2.1: Prisoner's Dilemma

If Tina and Sahar analyze this game as they did the previous games, one thought process might be something like this: "If my partner chooses to betray, I am better off if I also betray (-5 is better than -10). Likewise, if my partner chooses to cooperate, I am still better off betraying (0 is better than -1). Therefore, I will betray." Both players have a dominant strategy of betray, and therefore both players betraying is thus a Nash equilibrium. The "dilemma" of the game is that by betraying, both will serve more time than they would by cooperating. However, the dominant strategy tells them both to betray.

ACTIVITY 2-1 Moderate or Greedy

Objective: Understand Dilemmas Involved in Strategies

Materials:

Handout GT-H2: Moderate or Greedy Activity Worksheet

Consider the following payoff matrix. Each player MUST choose a strategy without knowledge of the other player's strategy and players are not allowed to communicate with each other. The winning player is the one with the most tokens.

		Player 2 Choice (y)	
	(x, y) Payoff	Moderate	Greedy
Player 1 Choice (x)	Moderate	(2, 2)	(0, 4)
	Greedy	(4, 0)	(1, 1)

Table 2.2: Moderate or Greedy Payoff in Tokens

1. Describe the payoff structure for each of the four outcomes.

2. The choice each player must make is "Moderate" or "Greedy." Define these choices in terms of resources, confrontation with the other player and payoff.

3. Consider the choice you will make in the first round of this game. (Do not share with your opponent.) Indicate your choice (Moderate or Greedy) here and provide a short explanation of your choice.

4. Playing the Game.
Your teacher will instruct the class on the method players will use to indicate Moderate or Greedy simultaneously. You will play several rounds of the game. After each round, choose a new opponent. No communication is allowed about the game. Play the game and record your choices and payoff.

Round	My Choice	Opponent’s Choice	My Tokens this Round	My Total Tokens
1	Moderate / Greedy	Moderate / Greedy		
2	Moderate / Greedy	Moderate / Greedy		
3	Moderate / Greedy	Moderate / Greedy		
4	Moderate / Greedy	Moderate / Greedy		
5	Moderate / Greedy	Moderate / Greedy		

5. How many times did you get more tokens than your opponent? (How many times did you receive 4 tokens?) Which strategy(ies) did you use? Did you get more tokens than your opponent more often with one strategy over another?

6. Who in the class received the greatest number of tokens overall? What was their strategy?

Practice

As an example of a Prisoner’s Dilemma game in nature, consider two rams hoping to mate with some ewes. Both rams could ignore each other and mate with three ewes. Alternatively, one of the rams could be more aggressive and challenge the other ram to a fight in order to impress all the ewes. If the other ram backs down from the challenge, then more of the ewes watching will be impressed with the aggressive ram than with the passive ram. As a result, the aggressive ram will get to mate with more ewes than if he had not challenged the other ram to the fight, and the passive ram will get to mate with fewer ewes. However, if the other ram, instead of being passive, meets the challenge and fights, both rams lose time and energy, and take the chance of getting hurt. Since both of the rams have less time and energy to mate with ewes, there will be some ewes with whom neither ram has time nor energy to mate, even though all the ewes are impressed with the bravery of both rams and would be willing to mate with either of them.

1. Design a payoff structure that is consistent with the scenario above. The numbers in the payoff will represent the number of ewes mated with. Be prepared to defend you choices in a class discussion.

Ram 2 Choice (y)

	(x, y) Payoff	Passive	Aggressive
Ram 1 Choice (x)	Passive		
	Aggressive		

Table 2.3: Moderate or Greedy Payoff in Tokens

Lesson 3 Payoff Structure Changes

If the payoff structure in the game changes, will the strategy that gives the best payoff also change? To explore this possibility we play a new game called Hawk-Dove with different types of strategies.

ACTIVITY 3-1 The Hawk-Dove Game

Objective: Explore changes in payoff structure of games.
Materials:

Handout GT-H3: Exploring the Hawk-Dove Game Activity Worksheet

1. Consider the game defined by the following payoff matrix. The two players will decide on an action simultaneously and independently.

Player 2 Choice (y)

	(x, y) Payoff	Hawk	Dove
Player 1 Choice (x)	Hawk	(1, 1)	(4, 2)
	Dove	(2, 4)	(3, 3)

Table 3.1: Hawk-Dove

The strategy labeled “Hawk” means that the player will escalate a conflict (if there is one); the strategy labeled “Dove” means that the player will back down. If both players choose Dove, or if one player chooses Dove and the other player chooses Hawk, then the total payoff is 6. It is split evenly between the two players if both choose Dove, while the majority of it is given to the player who chooses Hawk if the players choose different strategies. If both players choose Hawk, then the escalation of the conflict has a cost that reduces the value of the resource for both. In this case, each player gets the same payoff, but it is only a payoff of 1.

a. Your teacher will instruct the class on the method players will use to indicate Hawk or Dove simultaneously. You will play 10 rounds of the game. After each round, choose a new opponent. No communication is allowed about the game. Play the game and record your choices and payoff.

Round	**My Choice**	**Opponent's Choice**	**My Payoff this Round**	**My Total Payoff**
1	Hawk / Dove	Hawk / Dove		
2	Hawk / Dove	Hawk / Dove		
3	Hawk / Dove	Hawk / Dove		
4	Hawk / Dove	Hawk / Dove		
5	Hawk / Dove	Hawk / Dove		
6	Hawk / Dove	Hawk / Dove		
7	Hawk / Dove	Hawk / Dove		
8	Hawk / Dove	Hawk / Dove		
9	Hawk / Dove	Hawk / Dove		
10	Hawk / Dove	Hawk / Dove		

b. Is there a Nash Equilibrium, and, if so, what is it?

2. The following is the payoff matrix for another game. The two players will decide on an action simultaneously and independently.

Player 2 Choice (y)

	(x, y) Payoff	A	B
Player 1 Choice (x)	A	(3, 3)	(0, 0)
	B	(0, 0)	(4, 4)

Table 3.2: A and B

a. Your teacher will instruct the class on the method players will use to indicate A or B simultaneously and how many rounds to play. After each round, choose a new opponent. No communication is allowed about the game. Play the game and record your choices and payoff.

Round	**My Choice**	**Opponent's Choice**	**My Payoff this Round**	**My Total Payoff**
1	A / B	A / B		
2	A / B	A / B		
3	A / B	A / B		
4	A / B	A / B		
5	A / B	A / B		
6	A / B	A / B		
7	A / B	A / B		
8	A / B	A / B		

b. Is it a Nash equilibrium if both players choose A?

c. How many Nash equilibria are there in this game?

3. The following is the payoff matrix for another game. The two players will decide on an action simultaneously and independently.

		Player 2 Choice (y)	
	(x, y) Payoff	C	D
Player 1 Choice (x)	C	(2,4)	(2,4)
	D	(4,2)	(4,2)

Table 3.3: C and D

a. Your teacher will instruct the class on the method players will use to indicate C or D simultaneously and how many rounds to play. After each round, choose a new opponent. No communication is allowed about the game. Play the game and record your choices and payoff.

Round	**My Choice**	**Opponent's Choice**	**My Payoff this Round**	**My Total Payoff**
1	C / D	C / D		
2	C / D	C / D		
3	C / D	C / D		
4	C / D	C / D		
5	C / D	C / D		
6	C / D	C / D		
7	C / D	C / D		
8	C / D	C / D		

b. Is there a Nash equilibrium in a game with this payoff matrix?

c. Is there a strategy that can be used to determine what choice you would make in this game?

Questions for Discussion

1. Describe the differences in the three payoff structures in Activity 3-1.

2. If the payoff structure in a game changes, will the strategy that gives the best payoff also change?

Lesson 4 Cooperation

In some real life situations players only play the game against each other one time. The prisoner doesn't have the opportunity to say "Since my partner betrayed me last time, I'll betray him this time." This is the situation we have investigated in the previous lessons. What if you had another opportunity to play the game again?

Questions for Discussion

1. What would be your strategy if you played multiple rounds of a game with the same partner?

2. In general, do you think people are more apt to cooperate for a moderate payoff or be more adversarial to try to get a better payoff?

Strategies Over Time

We now return to the token game from Lesson 2, but we'll play it for multiple rounds with the same opponent. The actions will be the same as before—you may choose Moderate or Greedy—and the payoffs in each round will be the same as before. However, instead of just making one choice, comparing it with your partner's choice, and ending the game, now you'll repeat this process multiple times. You do not need to choose the same action each time, and your goal is to maximize the total number of tokens that you have at the end of all of the rounds.

ACTIVITY 4-1 Cooperate or Not?

Objective: Determine if and how strategies change in multiple rounds of a game.
Materials:

Handout GT-H4: Cooperate or Not? Activity Worksheet
Calculator or spreadsheet

In all rounds of the following games, you and your opponent will both choose an action simultaneously and without communicating. After the first round, you will be able to base your decisions on what has happened already in the game.

Player 2 Choice (y)

	(x, y) Payoff	Moderate	Greedy
Player 1 Choice (x)	Moderate	(2, 2)	(0, 4)
	Greedy	(4, 0)	(1, 1)

Table 4.1: Moderate or Greedy Payoff in Tokens

1. Privately write a few sentences about whether or not you think you will change your strategy during the game. If so, how do you think you will you change and why?

2. Matchup #1 - Play the game for five rounds with the same opponent. Use the payoff structure above, but note that players who do not earn at least 10 tokens in the five rounds, will pay a fine equal to their tokens and not survive. Do not talk to your opponent about your strategy.

a. Record each player's choice and the payoff for each round on Table 4.2. At the end of the game, total each player's number of tokens, assess any fine and determine each player’s earnings.

Round	Player 1 Choice	Player 1 Payoff	Player 2 Choice	Player 2 Payoff
1				
2				
3				
4				
5				
Total				
Fine				
Earnings				

Table 4.2: Payoff Table – Matchup #1

b. After playing five rounds and totaling earnings, discuss with your partner whether changes in strategy improved or damaged your performance. What action (or actions) did you choose? Why?

3. Matchup #2 - For this matchup, switch opponents and play the game again for 10 rounds. Any player scoring less than 20 total tokens will be fined all of their tokens and not survive. No communication is allowed between partners. The next game will be played for ten rounds.

a. Given the change in rounds and the increase in tokens needed for survival, what changes in strategy would you use?

b. Record each player’s choice and the payoff for each round on Table 4.3. At the end of the game, total each player's number of tokens, assess any fine and determine each player’s earnings.

Round	Player 1 Choice	Player 1 Payoff	Player 2 Choice	Player 2 Payoff
1				
2				
3				
4				
5				
6				
7				
8				
9				
10				
Total				
Fine				
Earnings				

Table 4.3: Payoff Table – Matchup #2

c. After totaling earnings, discuss with your partner whether changes in strategy improved or damaged your performance. What action (or actions) did you choose? Why?

Questions for Discussion

3. For the players who received the highest payoff, what strategies (rule for choosing) did they use?

4. Did these strategies or their outcomes depend upon the choices made by the player's opponent on earlier rounds?

5. Does the success of a strategy depend upon the strategy used by a player's opponent?

6. If the number of tokens needed to survive were 25 instead of 20, could changes be made to a strategy to make it more effective?

7. What is the purpose of the fine to determine survival? How does this relate to real world game outcomes?

8. Imagine playing the game again with a new opponent. For this matchup, you will play until told to stop. You will not know how many rounds you will play. It is important to acquire, on average, more than 2 tokens per round in order for you to survive. Acquiring an average of 2 or less per round will result in elimination and therefore extinction.

a. Which strategy do you think is the safest to ensure survival?

b. Which strategy do you think would result in the most tokens?

Playing by Genetic Profile

Individuals played the previous games on a time-constrained basis representing the daily, weekly or seasonal struggle of an organism to gain resources. Another way of playing is where each round of the game is played by successive generations of a **population**. In this new way of playing, the individual's choice of how to play against all other individuals is determined by its genes and passed on to its offspring. Those who play successfully, as a result of the genes they carry, gather enough resources to survive and reproduce. Those who do not make a successful enough choice don't live to reproduce. Therefore, in the next generation of organisms, only those genes that lead to making sufficiently successful choices are represented.

This new generation then plays the next round of the game according to the genes they inherited from their parents. This way of playing the game represents genetically based evolutionary fitness. Since evolutionary fitness involves the survival of one's genes over time (and therefore over many generations), those genes that never die out are fit. In the remainder of this lesson, "survival" of an organism shall mean that the organism survives long enough to pass its genetic profile on to its progeny.

Suppose that each strategy is no longer a matter of choice, but is controlled by a single genetic profile that determines how the organism will play. In this scenario there are two genetic profiles; one that determines “Always be Moderate” and one that determines “Always be Greedy.”

Now imagine a population that only has these two genetic profiles; call them “moderate” and “greedy,” and that the payoffs are given by the following matrix:

		Organism 2 (y)	
	(x, y) Payoff	Moderate	Greedy
Organism 1 (x)	Moderate	(8, 8)	(2, 4)
	Greedy	(4, 2)	(3, 3)

Table 4.4: Moderate or Greedy - Organisms

Question for Discussion

9. If half of the population has one genetic profile and the other half has the other profile, and they pair up randomly to play, what do you expect to happen?

ACTIVITY 4-2 Once and Done

Objective: Explore variations in a game that may result in elimination.

Materials:

Handout GT-H5: Once and Done Activity Worksheet

1. Suppose a game is played only once in each individual organism's life and that the outcome of the game determines whether or not the organism survives. Each organism has either the "moderate" or the "greedy" gene. In a population of 100, half of the population has the moderate gene. Pairings in the game are random. Each individual organism that survives has a single offspring with the same genetic profile as the parent, but individuals that do not survive have no offspring.

a. Given the payoff structure in Table 4.4 and the minimum payoff needed for survival is 3, what percentage of the next generation is expected to have the moderate genetic profile?

b. Complete the table below to determine the population after seven generations.

GEN	# of Always Moderate	# of Always Greedy	Total Population	% of Always Moderate	% of Always Greedy
1	50	50	100	50/100 * 100% = 50.0%	50/100 * 100% = 50.0%
2	50*.5 = 25	50	75	25/75 * 100% = 33.3%	50/75 * 100% = 66.7%
3	25*.5 = 12.5	50	62.5		
4	12.5*.5 = 6.25				
5					
6					
7					

Table 4.5: Seven Generations of Moderate and Greedy – Scenario #1

c. If the minimum payoff needed for survival is 4, how does this change the percentage of the next generation expected to have the moderate genetic profile?

d. What will happen with a required payoff of 4 for survival after seven generations?

2. Start again with a population of 10 organisms; half with the moderate genetic profile. Imagine that, instead of having one offspring, the number of offspring an organism has is determined by its payoff in the game (i.e., a payoff of 1 means the organism has 1 offspring, a payoff of 2 means the organism has 2 offspring, etc.).

a. Given this payoff structure, what percentage of the next generation is expected to have the moderate genetic profile? As an example for the first generation, the answer would be: Half of the moderate will have 8 children each and the other half of moderate will have 2 children. Half of the greedy will have 3 children each, and the other half of greedy will have 4 children each. The first three generations are shown in the table below. Complete the table for the next seven generations.

GEN	# of Always Moderate	# of Always Greedy	Total Population	% of Always Moderate	% of Always Greedy
1	5	5	10	50%	50%
2	5*.5*8+5*.5*2=25	5*.5*3+5*.5*4=17	42	25/42 *100% = 60%	175/42 *100% = 40%
3	25*.5*8+25*.5*2=125	17*.5*3+17*.5*4=60	185	125/185 *100% = 68%	61/185 = 32%
4					
5					
6					
7					
8					
9					
10					

Table 4.6: Ten Generations of Moderate and Greedy – Scenario #2

b. Describe the trend that occurs over 10 generations.

c. If the game is played over many more generations, what do you expect to happen to the population?

d. Is this trend different than what was seen when it was just based on survival? Explain.

3. Now suppose the available resources can only support a population of 1000 organisms. The percentage in the chart now not only represents the percentage of the population, but also the percentage of the available resources allocated to each genetic profile. For example, in the first generation, the moderate profile organisms will receive 50% of the resources and the greedy profile organisms will receive the remaining 50% of the resources. Since there are only 10 organisms total, resources for a population of 1000 are plenty to support both types of organisms.

a. How do you predict this allocation of resources with a population limit of 1000 will affect the greedy profile organisms in the long term?

b. In what generation is the first impact of this resource restriction felt by the organisms? Explain.

c. Complete the table below to determine the impact of the resource restriction in the seventh generation.

GEN	# of Always Moderate	# of Always Greedy	Total Population without limitation	% of Always Moderate	% of Always Greedy	# of Always Moderate w/Resource Limitation	# of Always Greedy w/Resource Limitation
1	5	5	10	50%	50%	5	5
2	25	17	42	60%	40%	25	17
3	125	60	185	68%	32%	125	60
4	625	214	839	74%	26%	625	214
5	625*.5*8+625*.5*2 = 3125	214*.5*3+214*.5*4 = 749	3874	3125/3874 = 80.7%	749/3874 = 19.3%	1000*.807= 807	1000*.193 = 193
6							
7							

Table 4.7: Ten Generations of Moderate and Greedy – Scenario #3

Gene Strategy

In some of the earlier games, your strategy was dependent on how many times you anticipated playing the game against the same opponent. In the games being considered now, each of the generations is only playing once. The ultimate goal from an evolutionary perspective is to continue the survival and reproduction of the genes. From this perspective, it can be said that the genes are actually the players playing each round of a game that will continue over all the generations to come.

Thinking in this way, it's clear that the strategy a gene might take could allow it to survive for a generation or two, but still not be a successful strategy for the whole, continuing game over many generations. Think about some other strategies and consider which are better within a single round and which might be more evolutionarily successful over many generations.

Consider the situation in which the “Always Moderate” and “Always Greedy” profiles still exist in the population, but the population includes other organisms possessing two additional profiles. One of the additional genetic profiles is "Play Moderate First and then Choose Whichever Choice the Other Player Chose Last Time" (called "Tit for Tat"). The other additional genetic profile plays "Choose at Random" each time a choice is made.

Question for Discussion

10. Predict what will happen to the genetic profile of an organism population with these four different profiles.

Practice

1. Use the situation from Activity 4-2, #3 for the following.

   a. In the seventh generation, the moderate profile was almost 90% of the population and the greedy was about 10%. Predict when the greedy profile organisms will be extinct in the population. Explain.

   b. What will happen to the moderate population in the long run?

   c. Continue Table 4.7 to check your prediction.

2. The plain old white clover that grows in your yard could be poisonous! The key word here is “could”. It depends on where you live. If you live in a colder climate like Wisconsin, then you probably have nothing to worry about. But, if you live in the southern states, do not indiscriminately put clover on your salad. They could be laced with cyanide. You can find both forms living together, but the toxic forms are more prevalent in warmer climates and the non-toxic forms are more prevalent in cooler climates. Scientists are studying the two different forms, toxic and non-toxic, of clover to learn more about their survival strategies. The toxic form has a gene that codes for the production of a sugar with cyanide attached to it to be present in clover cells. Another gene codes for a specific enzyme found in the cell wall. If the cell wall is damaged, the enzyme is released and causes the cyanide to hydrolyze making it poisonous. The non-toxic form does not make this enzyme.

Scientists think the environment is at play in this situation. In the south, there are more herbivores (snails, slugs, and voles). If they eat the toxic clover, they break the cell wall releasing the enzyme, and the cyanide is activated killing the herbivore. In the north the cold temperatures result in fewer herbivores, so there is not as much need for the cyanide. Also, the freezing temperatures may result in the cell walls breaking and releasing the enzyme. In this case the activated cyanide would act like a suicide pill, and the clover would die.

   a. Does one strategy (toxic or non-toxic) appear more "fit" overall? Explain.

   b. Do you think that variation in genetic make-up that control these types of traits would be under selective pressure? Explain.

Lesson 5 Playing Games with Kin Selection

In Lessons 2 and 3, the games played were against strangers (either of the same species, or of a different species). In general, much in biology theory points to the advantages of being selfish without thinking about anyone else and just outcompeting others. The games played earlier demonstrated how and why cooperation among strangers can still have a selfish evolutionary benefit. But is this the only way that evolution can lead to cooperation?

Relative Impact

When a player cooperates with a stranger, the only benefits to the player happen in the payoff received. It may be that there are times when a player can actually benefit by getting not only their own payoff, but also a part of the payoffs from the other players. In biology, since the only real, measurable payoff is evolutionary fitness (as discussed in Lesson 1); the question becomes "are there other players whose evolutionary fitness can increase your own fitness, no matter what your individual payoff is"?

Questions for Discussion

1. Who else could add to the player's evolutionary fitness? Explain.

2. It is reported that when asked if he would give his life to save a drowning brother, J.B.S. Haldane replied “No, but I would to save two brothers or eight cousins.” Why would Haldane say ***two*** brothers or ***eight*** cousins? Does ***two*** really equal ***eight***?

The Cleverest Man

John Burdon Sanderson Haldane, (Born 5 November 1892 – Died December 1964), known as Jack (but who used 'J. B. S.' in his printed works), was a British-born naturalised Indian scientist. He was a polymath well known for his works in physiology, genetics and evolutionary biology. He was also a mathematician making innovative contributions to statistics and biometry education in India. In addition he was an avid politician and science populariser. He was the recipient of National Order of the Legion of Honour (1937), Darwin Medal (1952), Feltrinelli Prize (1961), and Darwin–Wallace Medal (1958). Nobel laureate Peter Medawar, himself recognised as the "wittiest" or "cleverest man", called Haldane "the cleverest man I ever knew". Arthur C. Clarke credited him as "perhaps the most brilliant scientific populariser of his generation".

He was born of an aristocratic and secular Scottish family. A precocious boy, he was able to read at age three and was well versed with scientific terminology. His higher education was in mathematics and classics at New College, Oxford. He had no formal degree in science, but was an accomplished biologist. Since he was eight years old he worked with his physiologist father John Scott Haldane in their home laboratory. With his father he published his first scientific paper at age 20, while he was only a graduate student. His education was interrupted by the First

World War during which he fought in the British Army. When the war ended he resumed as research fellow at Oxford. Between 1922 and 1932 he taught biochemistry at Trinity College, Cambridge. After a year as visiting professor at University of California at Berkeley, in 1933 he became full Professor of Genetics at University College London. He emigrated to India in 1956 to enjoy a lifetime opportunity of not "wearing socks". He worked at the Indian Statistical Institute in Calcutta (now Kolkata) and later in Orissa (now Odisha), where he spent the rest of his life.

Text and Photograph: Wikipedia. Com

Was J.B.S. Haldane biologically insightful? To answer this questions consider what happens when you could cooperate with someone whose success is also your success. In biology, this happens when you are genetically related!

The relatedness between players within families can be quantified. Since evolutionary fitness means the success of the survival of your genes, and how related you are to other individuals represents how many genes you have in common, then the survival of your relatives actually increases your own evolutionary fitness. It is no longer the case that the only contribution to your evolutionary fitness comes from your own payoff in the game you are playing. The more related to the other individual with whom you are playing, the more their payoff contributes to your evolutionary fitness. Understanding evolution from the perspective of these inclusive payoffs is called **kin selection**. Think of the fitness of your genes as your own payoff plus a percentage of your kin's payoff based on the closeness of relatedness.

Relatedness

In all of the games played in Lessons 2 and 3, Player 1 and Player 2 were unrelated. The figure in Case 1 below represents that game scenario. In Cases 2 and 3, the two players are related. In the following figures a square represent a male and a circle represents a female.

Case 1

There are two players in this game, player 1 (P1) and player 2 (P2). The gray square represents a man (P1) playing the game against a man, represented by the white square (P2), who is not a relative.

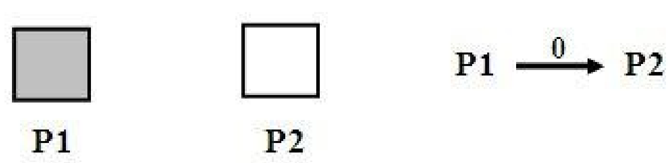


Figure 5.1: Two Unrelated Male Players

Since there is no relationship between P1 and P2 in Case 1, the value of relatedness (r) is 0. This is shown above the arrow.

Case 2
In Case 2, P1 and P2 are brothers. To calculate the value of r from P1 to P2, look first at the relationship from each of P1's parents to P1. In the case shown in the figure below, a female and a male have 2 male offspring, brothers.

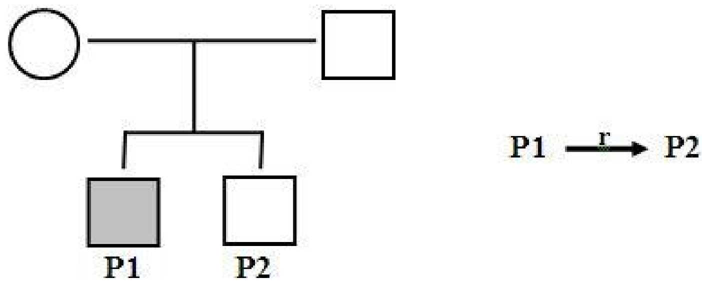


Figure 5.2: Parents and Two Brothers

Each parent donates half of P1's genes. This gives the mother to P1 relationship an r-value of ½ and the father to P1 an r-value of ½. This is illustrated below.

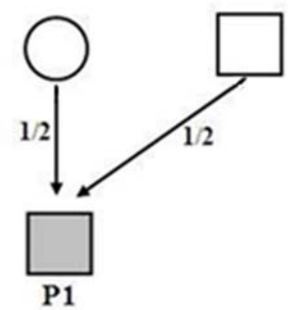


Figure 5.3: Mother and Father Gene Relationship to Son

If this is extended to P2, note that mother to P2 and father to P2 have relatedness values of ½ also.

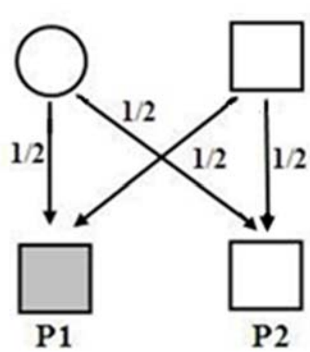


Figure 5.4: Parents and Gene Relationship to Two Sons

To calculate the relatedness of **P1 to P2,** follow the yellow lines in the figures below. The yellow lines show the paths of relatedness between P1 and P2. P2 is related to P1 through both his father and his mother.

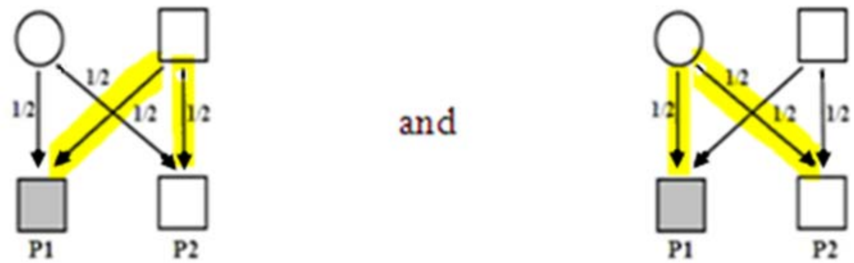


Figure 5.5: Paths of Relatedness

It is important to realize that it is not possible to predict the exact proportion of genes that two siblings share. This is due to the random assortment of chromosomes that occurs during sex-cell formation. It is possible, but highly improbable, that two siblings share all of their genes in common. It is also possible, but again highly improbable, that they share no genes in common. On average, though, siblings will share 50% of their genes. This is based on the probability that 25% of the genes they received from their mother are the same (1/2 × 1/2) and 25% of the genes that they received from their father are the same (1/2 × 1/2). Adding the relatedness through the father to the relatedness through the mother results in their total relatedness: **r = (½ × ½) + (½ × ½) = ¼ + ¼ = ½**

Case 3

Let's now consider the relatedness of cousins. Each of the brothers from Case 2 marry and have 1 child. One of the brothers has a son (P1) while the other has a daughter (P2). P1 and P2 are cousins in this case.

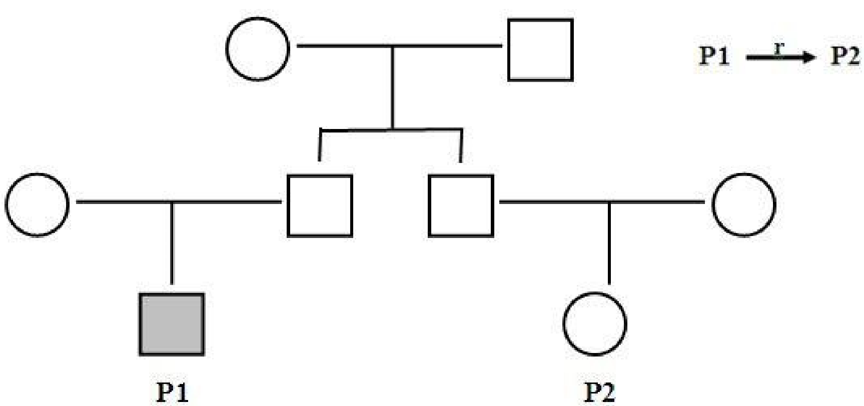


Figure 5.6: Parents, Two Brothers and Two Cousins

The relatedness of the 2 brothers remains the same. To calculate the relatedness of the cousins, the relatedness of P1 to his father and P2 to her father must be added into the equation.

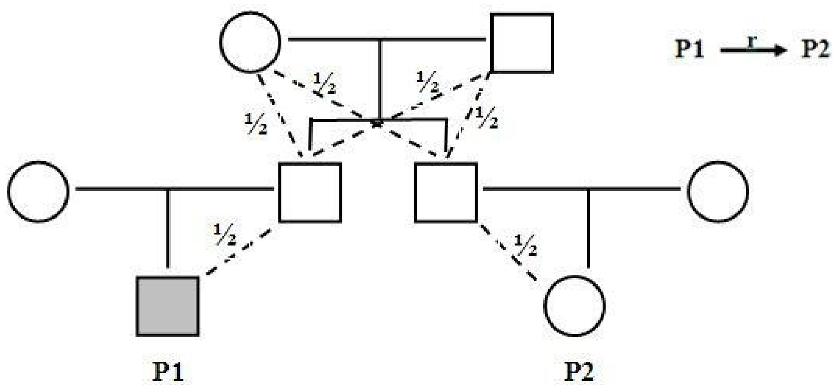


Figure 5.7: Gene Relatedness of Parents to Brothers to Cousins

The relatedness of P1 to P2 is 1/8:

r **= ½ x {(½ x ½) + (½ x ½)} x ½**
=½ x {¼ + ¼} x ½
= ½ x ½ x ½
= 1/8

Beneficially Related

Reconsider now the games in the previous lesson. How do they change if 1 the players are brothers or the players are cousins?

Consider this payoff matrix with two strangers playing our original game. Both players choosing Greedy is the Nash equilibrium.

		Player 2 Choice (y)	
	(x, y) Payoff	Moderate	Greedy
Player 1 Choice (x)	Moderate	(3, 3)	(1, 4)
	Greedy	(4, 1)	(2, 2)

Table 5.1: Moderate or Greedy Payoff

The payoff matrix for two brothers playing would be the following where bold indicates the contribution to the payoff from the relationship.

Player 2 Choice (y)

Player 1 Choice (x)	**(x, y) Payoff**	Moderate	Greedy
	Moderate	(3+**(1/2)3**, 3+**(1/2)3**)	(1+**(1/2)4**, 4+**(1/2)1**)
	Greedy	(4+**(1/2)1**, 1+**(1/2)4**)	(2+**(1/2)2**, 2+**(1/2)2**)

Table 5.2: Moderate or Greedy Payoff for Brothers

Or

Player 2 Choice (y)

Player 1 Choice (x)	**(x, y) Payoff**	Moderate	Greedy
	Moderate	(4.5, 4.5)	(3, 4.5)
	Greedy	(4.5, 3)	(3, 3)

Question for Discussion

3. If you are playing against a brother, is there a reason to pick greedy? Explain.

In the case of a cousin the payoff matrix is

Player 2 Choice (y)

Player 1 Choice (x)	**(x, y) Payoff**	Moderate	Greedy
	Moderate	(3+**(1/8)3**, 3+**(1/8)3**)	(1+**(1/8)4**, 4+**(1/8)1**)
	Greedy	(4+**(1/8)1**, 1+**(1/8)4**)	(2+**(1/8)2**, 2+**(1/8)1**)

which is

Player 2 Choice (y)

Player 1 Choice (x)	**(x, y) Payoff**	Moderate	Greedy
	Moderate	(3.375, 3.375)	(1.5, 4.125)
	Greedy	(4.125, 1.5)	(2.25, 2.25)

Question for Discussion

4. Will this have an effect on the strategy chosen when cousins are playing? Remember that the genes that cousins share are playing this game with cousins for every generation of the family.

Remember that the genes that lead to successful choices in these games are passed on to the next generation. The genes that lead to unsuccessful choices did not allow the individuals who carried them to survive and reproduce. Therefore, we can think of each of these games as being played between the genes, over and over again, once in each generation. From this perspective, Haldane's idea about how much relatives contribute to a payoff still makes perfect sense because relatedness is a measure of how much of the genetic makeup is shared among individuals. Therefore the inclusion of relatedness into the payoff structure demonstrates how these games can reinforce the evolution of cooperation among relatives.

Cooperation is not only seen in the natural world among related individuals. By looking at evolution as a game played by genetic profiles, we can see how a seemingly altruistic behavior could evolve among unrelated players. Remember from Lesson 3, as the payoffs enable greater or lesser success in survival and reproduction, the success of the different genes can be affected by competition with each other, leading to the possible extinction of particular genetically determined behaviors. If the payoff structure of the game is such that cooperation is favored under cases of resource limitation, we would expect that unrelated individuals should still cooperate because those that did not would not have survived to pass along their genes over the generations. Going even further, this doesn't just apply within populations. Not only can cooperative choices within families and single populations be explained, we can look across species and show how different species can evolve to cooperate. It's important, however, to remember that cooperation is only favored under evolutionary constraint for some games. It's the payoff structure that determines which of the choices will be successful over time, and which genes governing the choices for how to behave in interactions will be selected for by nature.

Practice

1. Consider the original game of Hawk-Dove.

Player 2 Choice (y)

	(x, y) Payoff	Hawk	Dove
Player 1 Choice (x)	Hawk	(1, 1)	(4, 2)
	Dove	(2, 4)	(3, 3)

a. Fill in the contribution from the relationship of brothers.

Player 2 Choice (y)

	(x, y) Payoff	Hawk	Dove
Player 1 Choice (x)	Hawk	1 + ( ),1 + ( )	4 + ( ),2 + ( )
	Dove	2 + ( ),4 + ( )	3 + ( ),3 + ( )

b. Determine the final payoff matrix for brothers.

Player 2 Choice (y)

	(x, y) Payoff	Hawk	Dove
Player 1 Choice (x)	Hawk		
	Dove		

c. Fill in the contribution from the relationship of cousins.

Player 2 Choice (y)

	(x, y) Payoff	Hawk	Dove
Player 1 Choice (x)	Hawk	1 + ( ), 1 + ( )	4 + ( ), 2 + ( )
	Dove	2 + ( ), 4 + ( )	3 + ( ), 3 + ( )

d. Determine the final payoff matrix for cousins.

Player 2 Choice (y)

	(x, y) Payoff	Hawk	Dove
Player 1 Choice (x)	Hawk		
	Dove		

2. Does Hawk-Dove favor brothers over cousins and cousins over strangers in the same way that our previous game did?

Glossary

Competition – the act or process of competing usually for a prize or advantage.

Dominant strategy – the best choice for a player in a game to get the highest payoff, regardless of the choices of the other players.

Evolutionary fitness – the ability of a species or organism to be successful at both survival and reproduction.

Game theory – the mathematics of how people, typically called “players” in the context of a game, consider conflicts and opportunities for cooperation when making decisions about how to behave in situations with each other.

Genes – the basic physical unit of heredity that provides the coded instructions that lead to the expression of hereditary character.

Kin selection – understanding the impact on evolutionary fitness from the perspective of the interrelationships of payoffs resulting from heredity connections to other players.

Mechanism of selection – the aspect of the environment that causes the trait to make the individual less fit than those that don't have that trait. (selective process)

Nash equilibrium – the collection of strategies that result in neither player being able to improve his or her payoff by making a change only to his or her own strategy.

Natural selection – the weeding out of individuals from a species that are less fit (because of how those traits make the individuals that have them interact with the environment, including interactions with other species).

Outcome – the combination of chosen actions of all players in a game.

Payoff – the gain or loss to a player of a game based on the outcome of the game.

Population – all individuals a species or a group of organisms in aggregate living in one area.

Prisoner’s dilemma – a scenario where the outcome of one person’s actions is determined by another person’s actions and the result of each acting in self

Selective pressure – the aspect of the environment that causes the trait to make the individual less fit than those that don't have that trait. (mechanism of selection)

Survival of the fittest – a description of natural selection in terms of evolutionary fitness.

Variations (evolution) – differences that occur in individual members of a species or among a group of similar organisms.

References

[1] Mas Colell, A., Whinton, M.D., & Green, J.R. (1995). *Microeconomic theory*. Oxford: Oxford University Press.