Modeling Altruism in Evolutionary Biology Using Game Theory

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MIT PRIMES Circle Final Project
May 2021

Abstract

Vampire bats demonstrate altruism by regurgitating blood to give to other vampire bats in order to prevent them from dying of hunger. In this paper, we model altruism in vampire bats using three different strategies based in classical game theory. First, we use a simple two-player matrix game and a utility function to observe how vampire bats value the health of a group over their own health. Building on our simple model, we use a CC-PP game model and a repeated game model to model more nuanced factors that affect how and when a vampire bat chooses to regurgitate blood. We notice how when bats get the chance to communicate with each other and play the game repeatedly, their productivity increases greatly.

1 Introduction

In this paper, we model altruism in vampire bats using 3 different models based in *classical game theory*, the study of games where the players make a decision without knowing the other player's choice. Definitions of terms used in game theory and an explanation of the altruism shown in vampire bats are located in section 2. In section 3, we use a two-player matrix game. Building on from our simple model, we use a CC-PP game model (in section 4) and a repeated game model (in section 5) to represent more complex situations.

We will start by defining altruism, and how it is exhibited in vampire bat populations:

Definition 1.1 [2, Pg. 67] Altruism is the behaviour whereby each individual provides aid as long as this aid has been reciprocated by the other in the previous encounter. It is also known as "tit for tat." Although termed *reciprocal altruism* by biologists, this behaviour is still self-regarding, because each individual's decisions depend only on the expected benefit the individual receives from the long-term relationship.

Vampire bats exhibit altruism by regurgitating blood and feeding it to other bats. This act is vital to vampire bat populations because a bat can die after just two days of not eating [3, par.4]. However, while this act of altruism provides a great benefit to the receiver, it also comes at a great cost to the donor. In other words, the decision to donate blood must be made with many factors kept in mind. We show these nuanced decisions through models using game theory.

2 Classical Game Theory

This section introduces concepts in game theory. As all three of our models utilize classical game theory, we will focus on that in this section.

Definition 2.1 [1, Pg. 89-90] *Classical game theory* is the study of games in which players choose a course of action independently without knowledge of the other player's decision. This results in one outcome.

2.1 Zero-Sum Matrix Games

Definition 2.2 [1, Pg. 90] A *zero-sum matrix game* is played between Rose and Colin. There is a fixed matrix that is known to both Rose and Colin. Rose will choose a row and Colin will choose a column without knowing the other person's choice. When Rose chooses some row, i and Colin chooses some column j, in some matrix A, the payoff is the (i, j) entry of matrix A. Rose wants the highest possible payoff and Colin wants the lowest possible payoff.

Example 2.3 Here is an example of a zero-sum matrix game:

$$\begin{bmatrix} 0 & -1 \\ 2 & 4 \end{bmatrix}$$

For example, if Rose chooses the top row and Colin chooses the right column, the payoff will be -1. If they played using dollars, this would mean Rose pays Colin $1.

If there is a row in which each value in the row is smaller than a corresponding value in another row of the matrix, Rose will never choose that row with smaller values. Similarly, Colin will never choose a column whose values are all larger than the corresponding values in a different column. We can use this phenomenon of *dominance* to simplify matrix games by eliminating rows and columns that the players would never rationally choose.

Example 2.4 Using the previous zero-sum matrix game, we can see that the strategy of playing row two for Rose dominates the strategy of playing row one, as the payoffs of 2 and 4 are strictly larger than the payoffs of 0 and -1.

As a result, we can remove row one from the matrix, leaving this matrix:

$$\begin{bmatrix} 2 & 4 \end{bmatrix}$$

Since Colin prefers as low of a payoff as possible, Colin will always play column one.

Example 2.5 Consider the following matrix game played by Rose and Colin:

$$\begin{bmatrix} 0 & -1 \\ 2 & -1 \\ 1 & 2 \end{bmatrix}$$

Using our strategy of removing dominated rows, we can eliminate row one for Rose, since no matter what Colin plays, her payoff will always be strictly higher if she plays row three. This means that row one is *strictly dominated* and should not be played. Here is the updated matrix:

$$\begin{bmatrix} 2 & -1 \\ 1 & 2 \end{bmatrix}$$

Now, this matrix does not have any more dominated rows or columns. This means that Rose and Colin must play *mixed strategies* to achieve their highest respective payoffs. A mixed strategy is when a player does not always choose to play the same option. For example, a strategy of $[\frac{2}{5}\ \frac{3}{5}]$ would mean that Rose chooses to play the row one option $\frac{2}{5}$ of the time, and plays the row two option $\frac{3}{5}$ of the time.

Definition 2.6 [1, Pg. 113] For a zero-sum matrix game A, we say that a mixed strategy r for Rose *equates* Colin's results if all entries of rA are equal. Similarly, we say that a mixed strategy c for Colin equates Rose's results if all entries of Ac are equal.

Definition 2.7 [1, Pg. 103] The *von Neumann solution* is a pair of strategies where the guaranteed value, or minimum payoff from an optimal strategy regardless of the other player's choices, for Rose and Colin is the same. One way to find the von Neumann solution is to find the strategies that will equate each other's results.

Lemma 2.8 [1, Pg. 114] For every 2×2 zero-sum matrix game:

1. If Rose has no dominant row, Colin has a mixed strategy equating her results
2. If Colin has no dominant column, Rose has a mixed strategy equating his results.

According to the lemma, there exists a mixed strategy $r = \begin{bmatrix} p & 1-p \end{bmatrix}$ for Rose that equates Colin's results, and a mixed strategy $c = \begin{bmatrix} q \\ 1-q \end{bmatrix}$ for Colin that equates Rose's results. In Example 2.5, since there are no more dominated rows or columns in our matrix, we know that such r and c exist, and we can therefore find the von Neumann solutions.

We can solve for the von Neumann solution in a 2×2 matrix like so:

Example 2.9 Recall from above the following example of a zero-sum matrix game:

$$\begin{bmatrix} 2 & -1 \\ 1 & 2 \end{bmatrix}$$

Example 2.10 *Matrix Multiplication* Say we want to multiply the following two matrices together.

$$\begin{bmatrix} 1 & 2 & 3 \end{bmatrix} \begin{bmatrix} 0 & -1 \\ 2 & -1 \\ 1 & 2 \end{bmatrix} \quad \begin{bmatrix} 7 & 3 \end{bmatrix}$$

We employ the dot product to multiply these matrices – the process of multiplying matching members. For the above examples we would do (1, 2, 3) * (1, 4, 7). This gives (1*0) + (2*2) + (3*1), which gives us a total of 7 for the first element of the product.

We assume that Rose has a mixed strategy $\begin{bmatrix} p & 1-p \end{bmatrix}$ that will equate Colin's results. To do this, we multiply the two matrices and set the two entries in the new matrix equal to each other. This gives us $2p + (1-p) = -p + 2(1-p)$. Solving this equation gives $p = \frac{1}{4}$. It is important to note that the probabilities in a mixed strategy must sum to 1. So Rose's full mixed strategy is $r = \left[\frac{1}{4}, \frac{3}{4}\right]$.

Similarly, we can solve for Colin's mixed strategy:

$$\begin{bmatrix} 2 & -1 \\ 1 & 2 \end{bmatrix} \begin{bmatrix} q \\ 1-q \end{bmatrix}$$

Multiplying the matrices out gives us $q = \frac{3}{4}$. Colin's full mixed strategy is $c = \left[\frac{3}{4}, \frac{1}{4}\right]$.

Definition 2.11 [1, Pg. 98] The *expected payoff* is the average result of a player's strategy when played. The expected payoff of a strategy on a matrix can be found by multiplying the matrix with the strategy.

The expected payoff of Colin will be

$$\begin{bmatrix} 2 & -1 \\ 1 & 2 \end{bmatrix} \begin{bmatrix} \frac{3}{4} \\ \frac{1}{4} \end{bmatrix}$$

Using matrix multiplication, we find that the expected payoff for Colin will be $\frac{5}{4}$. Similarly, we can find that Rose's payoff will also be $\frac{5}{4}$.

We can note that each player's expected payoff is the same for the von Neumann solution. The full von Neumann solution can be listed as Rose's strategy r, Colin's strategy c, and then the expected payoff v. The von Neumann solution for this game would be $r = \begin{bmatrix} \frac{1}{4} & \frac{3}{4} \end{bmatrix}$, $c = \begin{bmatrix} 3/4 \\ 1/4 \end{bmatrix}$, $v = \frac{5}{4}$.

2.2 General Matrix Games

Having discussed zero-sum matrix games, we now discuss more general matrix games.

Definition 2.12 [1, Pg. 134] A *general matrix game* is a game played between two players, who can be named Rose and Colin. The game is played on a fixed matrix A, where each entry of A has an ordered pair (a, b) where a is the payoff for Rose and b is the payoff for Colin. To play, Rose selects a row and Colin selects a column without knowing the other's selection. Additionally, each player wants the highest payoff possible. Note that the condition $a = -b$ gives us a zero-sum matrix game.

Next we will examine the process of finding optimal strategies for for two players in a two by two matrix game.

Example 2.13 Here is a well-known example of a matrix game, known as the *Prisoner's Dilemma*. Imagine that Rose and Colin are caught committing a crime, and they are given the option to cooperate with the authorities and reveal their involvement, or deny the crime. C is the option to cooperate, while D is the option to defect.

Colin

Rose		C	D
	C	$-1, -1$	$-10, 0$
	D	$0, -10$	$-5, -5$

For example, if Rose chooses to cooperate and Colin chooses to defect, Rose will receive a payoff of -10 and Colin receives a payoff of 0.

Definition 2.14 [1, Pg. 162] Each player has their own *payoff matrix*, which takes just their own payoffs and puts them into a matrix.

Remark 2.15 Individual payoff matrices look similar to a zero-sum matrix game, but Colin will also want as large of a payoff as possible.

Example 2.16 Rose's payoff matrix in the Prisoner's Dilemma would be $\begin{bmatrix} -1 & -10 \\ 0 & -5 \end{bmatrix}$ and Colin's payoff matrix would be $\begin{bmatrix} -1 & 0 \\ -10 & -5 \end{bmatrix}$.

Each player's best choice is to defect. From Rose's perspective, defecting will yield a higher payoff for her no matter which option Colin chooses. The strategy of choosing row two dominates row one. Similarly, defecting is a dominating strategy for Colin. Therefore, Rosa and Colin (playing rationally) will both defect, each getting a payoff of -5. While $(-1, -1)$ is a better outcome for both Rosa and Colin, cooperating leaves the players susceptible to being taken advantage of, so defecting is a stabler strategy. Both players defecting is an example of *Nash equilibrium*.

Definition 2.17 [1, Pg. 166] *Nash equilibrium* is the idea of two players' strategies that are the best response to each other. It will not necessarily give the two players the highest possible payoff, but at this point, neither player has an incentive to change their strategy.

Theorem 2.18 [1, Pg. 166] In every 2×2 matrix game, there is a Nash equilibrium. There are two ways to find a Nash equilibrium:

1. Removing dominated strategies reduces the matrix to a 1×1 matrix. This forms a pure Nash Equilibrium.
2. Rose and Colin have mixed strategies that equate each other's results. This results in a Nash Equilibrium.

3 Simple Model

Section 3.1 Modeling a Vampire Bat Encounter

A simple model of altruism can be modeled with the vampire bat species. As previously mentioned, vampire bats exhibit altruism by regurgitating blood, and feeding it to other bats (for simplicity's sake, we call this process "donating").

First, we can model the choice to donate blood in vampire bats by only considering the effect on each bat's individual health. The matrix depicts the actions and associated payoffs (Bat 1, Bat 2) for two bats. Each of the bats has the option to cooperate (donate blood) or defect (not donate blood). We assume that the two bats are deciding whether to donate blood.

Bat 2

Bat 1		C	D
	C	$-1, -1$	$-10, 10$
	D	$10, -10$	$0, 0$

In this scenario, each bat would prefer to defect, as the strategy to defect dominates the option to cooperate. However, this clearly contradicts the idea of altruism in vampire bats. Next, we will look at how other factors beside individual gain/loss affect the bat's decision.

Definition 3.1 [1, Pg. 135] This introduces *utility* in games – the concept that a decision criteria is based off of more factors than just expected monetary values.

In our vampire bat example, a game in which utility did not exist would allow the bats to focus on simply maximizing their own expected payoffs (by not donating at all). Some other factors that affect the utility of the matrix for vampire bats include the health of the overall population (which would improve chances for reproduction) and being able to improve their relationships with other bats.

In our updated model, the two bats will be donating blood to each other at some point in their lives. So, if a bat cooperates, they will donate blood to the other player, but if a bat defects, they choose not to donate blood to the other player.

If both bats cooperate, the payoff is -1 for each, since the action is reciprocated and nothing really changes, while the action of donating blood wastes time. If one bat cooperates and the other defects, the cooperating bat receives a payoff of -3 (since they are losing blood) and the defecting bat receives a payoff of $+7$ (since they are gaining blood). If both bats defect, the payoff is -5 for each.

Here is the updated matrix with these new assigned utilities:

Bat 2

Bat 1

	C	D
C	$-1, -1$	$-3, 7$
D	$7, -3$	$-5, -5$

With the introduction of utility to this model we see the more nuanced ways in which a certain set of decisions made by the bats can affect both of their payoffs. While cooperating seems to be the most beneficial option, we cannot guarantee that both bats will choose to cooperate. What if one bat suspects the other will defect? That can cause the cooperating bat to suffer a much harsher comparative payoff.

Next, we will identify the optimal strategies both bats should use in this model.

As there are no dominated strategies in this matrix game, we will use the method of equating Bat 1 and Bat 2's results to find the Nash Equilibrium.

Bat 1's payoff matrix is $\begin{bmatrix} -1 & -3 \\ 7 & -5 \end{bmatrix}$ and Bat 2's payoff matrix is $\begin{bmatrix} -1 & 7 \\ -3 & -5 \end{bmatrix}$. First, we find a strategy $\begin{bmatrix} p & 1-p \end{bmatrix}$ for Bat 1 that equates Bat 2's results. Equating Bat 2's payoffs results in this equation:

$$-1(p) - 7(1-p) = -3p - 5(1-p)$$

Solving this equation gives $p = \frac{1}{5}$, which means that Bat 2 will choose to cooperate $\frac{1}{5}$ of the time, and choose to defect $\frac{4}{5}$ of the time.

Equating Bat 1's payoffs will result in the same equation:

$$-1(q) - 3(1-q) = 7q - 5(1-q)$$

This makes sense, as the matrix is symmetrical.

Conclusion In our simple matrix game model, each bat will choose to cooperate about $\frac{1}{5}$ of the time and defect $\frac{4}{5}$ of the time in order to secure themselves the maximum payoff.

Each bat will have an expected payoff of $7(\frac{1}{5}) - 5(\frac{4}{5}) = \boxed{-\frac{13}{5}}$

Section 3.2 Disadvantages of the Simple Model

While the matrix game model provides some good insight into how utility can affect decisions, the game does not take into account many other factors. The matrix game model is unable to model how desperate a bat is in need of food, or how previous encounters with another bat will affect the bats' decisions on whether to donate.

Example 3.2 [3, par. 10] A researcher named Gerald Carter who studied vampire bats made this observation: "Carter noticed that when a fasting female bat had previously shared her food with other females, she received more total sustenance than a selfish one."

4 CC-PP Game Model

Now that we have established a simple model, we will now explore more nuanced instances of altruism in evolutionary biology through more advanced models. We will start with the CC-PP model:

Definition 4.1 A *CC-PP Game Model*, or the Commonize Costs-Privatize Profits game is a model in which the aim is to commonize a resource across a wider community than just the individual, while privatizing, or maximizing the profits (monetary or resource) to the individual.

Simply put, this model assumes that there is a certain amount of resource that must be divided amongst a community. However, each individual is trying to earn as much profit as possible.

Before we examine the CC-PP model in the context of our vampire bat game, we will first introduce a common game theory example of the model.

Example 4.2 [1, Pg. 246] The *Tragedy of the Commons* is a game played between 100 farmers who share a field for grazing cattle. Each farmer can decide either to put one or two cows on the field. Each farmer gets +50 for each cow she has on the field. However, the field only sustainably supports 100 cows, and each cow beyond that depletes the field's nutrients. This costs everyone. Every farmer gets −1 for each extra cow.

We can depict the payoff for a farmer that chooses to either cooperate (putting only one cow on the field) or defect (putting two cows on the field) with the following 2×1 matrix:

		k other D's
Farmer i	C	$50 - k$
	D	$100 - (k+1)$

As you can see from the matrix, no matter what, farmer i will achieve their highest payoff if they defect, by putting two cows on the field. While this is great for the individual, we must not forget that the field only sustainably supports 100 cows, so if every farmer were to defect, each person gets a payoff of $100 - 100 = 0$, which is worse than the payoff each farmer would get (+50) if everyone chose to cooperate.

Tragedy of the Commons is an example of a CC-PP model because players are required to actively regulate the condition of the community as a whole, while simultaneously maximizing their own profit.

The Tragedy of the Commons game is a common CC-PP example in game theory. Now that we have an idea of what this model is and how it is used to model situations, let's apply it to our study of altruism in vampire bats.

Section 4.2 CC-PP Model of Altruism in Vampire Bats

Suppose a population of 20 vampire bats live in an area where there is a fixed amount of blood resource to be found each day. The area can sustainably feed 10 bats each night, providing them each with +10 of the blood resource). Each bat only need +5 to survive. In this game, each bat has the choice to cooperate (by donating some blood to a starving bat) or defect (by not donating). A bat that donates has a payoff of -5, and a bat that defects keeps their full amount of blood resource, $+10$. Blood is pivotal to the survival of vampire bats, as many can die within just two days of not eating. To represent this, each remaining bat in the population suffers a -1 payoff for each bat that dies from starvation.

We can depict the payoff to each bat based on their choice to cooperate or defect with the following 2×1 matrix:

k other D's

bat x		
	C	$5 - k$
	D	$10 - (k + 1)$

If we isolate bat x in the CC-PP model, we find that defecting is better, since bat x receives a $+10$ payoff. However, in this model we must consider the actions of the other bats as well as their impacts on the population as a whole. If every bat chooses the defect along with bat x, according to the model, each bat would receive a payoff of 0 ($100 - 100 = 0$). However, if every bat chooses to cooperate, each bat would receive a payoff of $+50$.

As you can see from the matrix analysis, the ideal choice for bat x, and all the other bats in the population for that matter, to cooperate, since doing so secures the highest possible payoff for each bat while also ensuring that members of the population don't die out of starvation. You can view this as the stable point of the CC-PP model.

The CC-PP model is ideal in modeling situations where a player must evaluate the condition of the group as a whole, while also maximizing individual benefits. The CC-PP model is also ideal in understanding why and how animals exhibit altruistic behaviors.

5 Repeated Game Model

Next, we will use a Repeated Game Model to model how bats interact with each other over multiple encounters.

Definition 5.1 [1, Pg. 229] In a *Repeated Game Model*, the two players play the game more than once. This allows players to consider more than just the immediate results of one game, usually resulting in more cooperation.

In our repeated game model, we explore Nash equilibria and determine how vampire bats behave when they are able to negotiate with the bats over multiple encounters. Additionally, we will observe how the hunger level of a bat affects how likely they are to donate blood.

To do this, we must create a new matrix game. We label the hungry bat as Bat H, and the full bat as Bat F.

Bat F

Bat H		C	D
	C	$-1, 1$	$-5, 5$
	D	$9, -1$	$-7, -3$

Here, we can see that the full bat is more inclined to donate blood than the hungry bat, and it is not as bothered when the hungry bat chooses to defect.

Definition 5.2 [1, Pg. 215] The *security level* of a player in a matrix game is the maximum expected payoff they can guarantee themselves.

Theorem 5.3 [1, Pg. 215] The security level of Bat H is the von Neumann value of their payoff matrix. Bat H's payoff matrix is $\begin{bmatrix} -1 & -5 \\ 9 & -7 \end{bmatrix}$. We can use the method of equating the results to find the von Neumann solution. If Bat F uses the strategy $\begin{bmatrix} q \\ 1-q \end{bmatrix}$, we can multiply the strategy with the matrix to get

$$-1(q) - 5(1-q) = 9q - 7(1-q)$$

Simplifying this equation gives $4q = 16q - 2$, and that $q = \frac{1}{6}$. Bat H's security level will be $-\frac{13}{3}$.

Theorem 5.4 [1, Pg. 216] The security level of Bat F is the von Neumann value of their transposed payoff matrix.

Definition 5.5 *A transposed matrix* means a matrix that has been flipped across the diagonal from the top left to the bottom right of the matrix.

In order to figure out Bat F's security level, we transpose its payoff matrix $\begin{bmatrix} 1 & 5 \\ -1 & -3 \end{bmatrix}$ into the matrix:

$$\begin{bmatrix} 1 & -1 \\ 5 & -3 \end{bmatrix}$$

To find the von Neumann value, we can use the same method that we used for Bat H. The equation will be:

$$1(q) - 1(1-q) = 5q - 3(1-q)$$

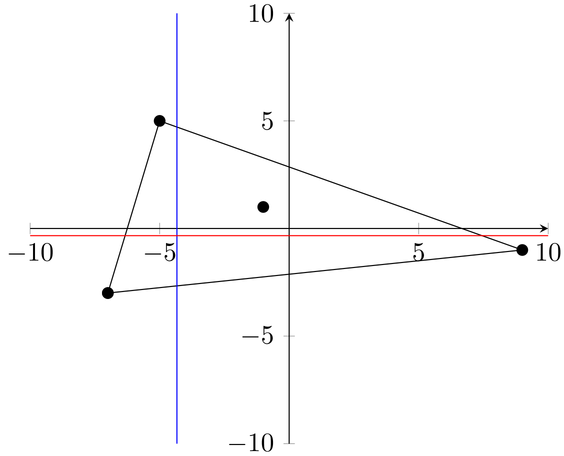
Simplifying this equation gives us $6q = 2$, so $q = 1/3$. Plugging this value in for q, the security level of Bat F will be $\boxed{-\frac{1}{3}}$.

Definition 5.6 [1, Pg. 218] The *payoff polygon* of a matrix game A is the convex hull of the ordered pairs in the matrix game.

The payoff polygon is useful because it provides a visual representation of the possible outcomes of a repeated matrix game.

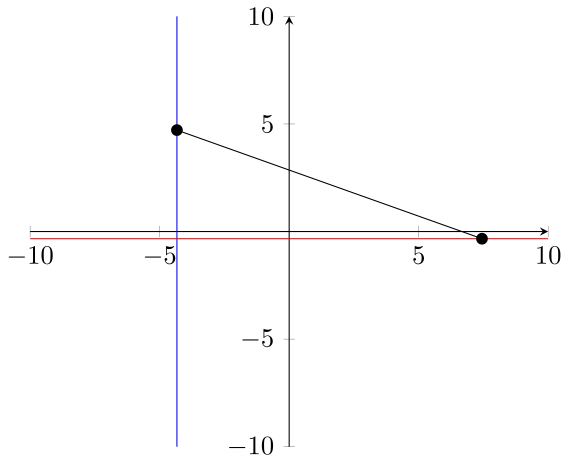
In the graph below, the payoff polygon is graphed, along with the security levels of the two bats. (Bat H in blue and Bat F in red.)

Payoff Polygon Graph



Definition 5.7 [1, Pg. 219] The *Negotiation Set* of a payoff polygon is the set of all points that are greater than both players' security levels.

Negotiation Set Graph



Definition 5.8 [1, Pg. 224] *Nash Arbitration* is a strategy for determining how to choose a "fair" outcome on the negotiation set. If there is a point (x, y) in the polygon where $x > x_0$ and $y > y_0$, choose the point where $(x - x_0)(y - y_0)$ is a maximum. (Note: x_0 is the security level of Bat H, and y_0 is the security level of Bat F.)

The linear equation for the negotiation set is $y = -\frac{6}{14}x + \frac{27}{7}$. Substituting this into the expression $(x - x_0)(y - y_0)$, we get $(x + \frac{13}{3})(\frac{6}{14}x + \frac{27}{7} + \frac{1}{3})$ To maximize this expression, we can take the derivative. Taking the derivative gives this expression

$$\frac{-18x + 49}{21}$$

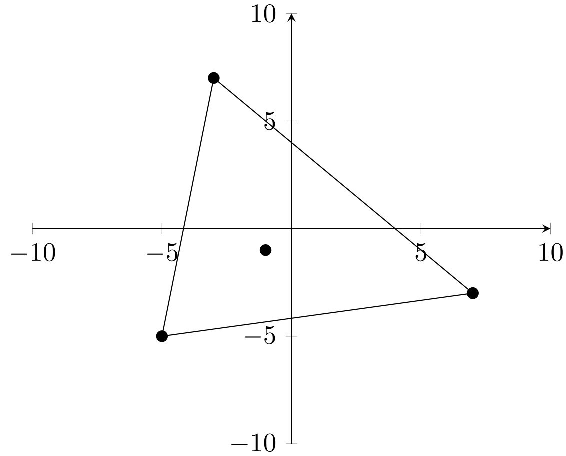
By setting this expression equal to zero, we find that the Nash Arbitration point is when $\boxed{x = 2.72}$ and $\boxed{y = 2.69}$. Clearly, these payoffs are much higher than the security levels, proving that working together can be much more effective.

We also find that the point is roughly 55 percent of the way from the point (-5,5) to the point (9,1). This means that the optimal strategy for the two bats in this model would be:

Conclusion: The hungry bat defects and the full bat cooperates 55 percent of the time. The full bat defects and the hungry bat cooperates 45 percent of the time.

In fact, we can even quickly graph the original matrix from section 3 and see how a repeated game could lead to better results for both bats.

Payoff Polygon Graph (Bat 1 and Bat 2)



Because this graph is symmetrical, the point where $(x - x_0)(y - y_0)$ must be the midpoint of $(7, -3)$ and $(-3, 7)$, which is $(2, 2)$. That means that by cooperating during a repeated game, each bat will have an expected payoff of 2, which is much higher than the payoff of $-\frac{13}{5}$ we calculated in section 3.

This model is clearly more accurate than the simple model because it takes into account that the bats can communicate with each other before deciding to donate blood. For example, it is very unlikely that two bats will choose to donate blood to each other, since this simply wastes time and nothing is accomplished. However, in our simple model, the two bats donate blood to each other $\frac{1}{16}$ of the time.

Acknowledgements

We would like to thank our mentor, Ariana Park, for teaching us this semester, and for guiding us through our final project with kindness, patience, and enthusiasm. We would also like to acknowledge and thank Peter Haine, Marisa Gaetz, and everyone at Primes Circle for coordinating the program and helping us finalize this paper.

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