Math Circle
University of Arizona

Evolutionary Game Theory

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Section 1 : Introduction

Video Link: https://www.youtube.com/watch?v=YMzNkNoFzG4

In the context of evolution, *payoff* often refers to the increase of an organism's fitness or reproductive advantage. For instance, consider two equally matched male kangaroos competing over three potential mates. Access to mates follows a status-based hierarchy in kangaroo life: a female will choose to mate with the male who has the greatest success in combat. Thus, these male kangaroos each face an important decision– Challenge his opponent and potentially fight, or make a display of fitness and back down. If the kangaroos fight, they may each end up hurt with little energy to participate in mating. If one kangaroo challenges and the other merely displays, the female kangaroos will be more admiring of the challenger, and likely to mate with him. If the kangaroos choose not to challenge each-other, they share the mates. The scenario might give us a payoff matrix as follows:

		Male Kangaroo 2	
		Challenge	*Display*
Male Kangaroo 1	*Challenge*	$(0.5, 0.5)$	$(3, 0)$
	Display	$(0, 3)$	$(2, 2)$

Games are often represented by a *payoff matrix*, where each player wants the greatest payoff they can get.
Payoff Matrix Example: Hawk-Dove

		Bird 2	
		Hawk	*Dove*
Bird 1	*Hawk*	$(-1, -1)$	$(5, 0)$
	Dove	$(0, 5)$	$(2.5, 2.5)$

Round #	Strategy Chosen	Opponent's Strategy	Payoff
1	*H D*	*H D*	
2	*H D*	*H D*	
3	*H D*	*H D*	
4	*H D*	*H D*	
5	*H D*	*H D*	
6	*H D*	*H D*	
7	*H D*	*H D*	
8	*H D*	*H D*	
9	*H D*	*H D*	
10	*H D*	*H D*	

Section 2 : Relatedness, A Gene's Eye View

Recall that a *strategy* can be thought of as your move in the game. In this case the strategies are Greedy and Moderate.

		Player 2	
		Greedy	*Moderate*
Player 1	*Greedy*	$(6, 6)$	$(10, 2.5)$
	Moderate	$(2.5, 10)$	$(8, 8)$

Problem 0.1: *Which strategy would you choose in the game above? If you are unsure, play 5-10 rounds with a friend, keeping track of the strategies you choose each round and the associated payoffs.*
Problem 0.2: *Imagine you are playing as both player 1 and player 2. Which strategies do you choose (as both player 1 and player 2)?*

At its heart, evolution is about replication. We often hear the phrase 'survival of the fittest', originally coined by Charles Darwin. We might take it to mean 'survival of the fittest *individual*'. However, evolution is not about the individuals that survive, but about the genes that persist (replicate). Therefor genetic material itself, the very genetic codes that make up our DNA, can be thought of as forming the collection of individuals that we care about in an evolutionary context. That is to say: genes themselves are the individuals that succeed in replicating, or fail to produce descendants. In mathematics, as in science, we will often take a course grained view of a highly detailed and complex picture in order to gain greater insights.

Suppose A is a gene carried by Harmony, and let $p \in [0, 1]$ be the probability that Fred also carries gene A. Gene A 'cares' only about its own fitness, meaning the replication or replication potential of its particular molecular structure. The copies of Gene A residing in Harmony are, practically speaking, no more valuable to its fitness than the its copies that appear in any other human or non-human organism.

Problem 1: *How does gene A weight the reproductive success (fitness) of Fred relative to that of Harmony?*
Problem 2: *Joseph and Erman are brothers. Overall, how does Erman weigh the reproductive success (fitness) of Joseph relative to his own?*
Problem 3: *What if they are cousins?*
Problem 4: *Grandfather and grandson?*
Problem 5: *What could be a flaw or shortcoming of this perspective?*

Problem 6: *Fill out the payoff matrix below for the Greedy-Moderate game where Player 1 and Player 2 are siblings. What strategy do you choose? Is this the same as before? Feel free to play 5-10 rounds with a friend.*

		Player 2 (you)	
		Greedy	*Moderate*
Player 1 (you)	*Greedy*		
	Moderate		

Problem 7: *You are playing your sibling in the following game. What strategy do you choose?*

		Player 2	
		Greedy	*Moderate*
Player 1	*Greedy*	$(3, 3)$	$(5, 3)$
	Moderate	$(3, 5)$	$(5, 5)$

Section 3: Hawk-Dove (Evolutionary Strategy Selection)

The Hawk-Dove game represents the interaction outcomes between two organisms. A hawk is an organism that tries to gain resources with aggression and even violence. A dove is a pacifist organism that generally minds its own business, and will flee in the face of danger.

- n_H is the number of hawks
- n_D is the number of doves
- N is the total number of birds, $N >> 1$
- c_H is the damage that a hawk takes when it scuffles with another hawk
- v is the amount of resource held by each bird before any interaction occurs

When two doves encounter each-other they peacefully part ways, each keeping the resources they started with. When a hawk encounters a dove, it steals whatever the dove has (e.g food and territory resources), and the dove flees. When two hawks meet, they compete over resources and both take damage, gaining nothing. In this game, payoffs represent changes in fitness: a positive payoff means the bird gains fitness, a negative payoff means the bird loses fitness, etc...

Problem 8: *Come up with a 2x2 payoff matrix for Hawk-Dove based on the information above. What parameter values were used in the game we played together at the start of the session?*

Now that we have a game describing interactions between any two organisms, we can consider the case of many organisms interacting within an ecosystem. In this simple model we consider only birds playing the strategies hawk or dove. All birds look the same and are not aware of each-other's behavioral strategies until they interact. On each turn, birds are paired up randomly to play Hawk-Dove.

Problem 9: *Suppose you are a hawk (you play the hawk strategy). What is the probability that you encounter another hawk? What about the probability that a given dove encounters any hawk?*
Problem 10: *On each turn, what is the expected fitness payoff to a hawk, $f_H(n_D, n_H)$? What is the expected fitness payoff to a dove, $f_D(n_D, n_H)$? Hint: expected is another way of saying average or mean.*
Problem 11: *For what sizes of the hawk population would you prefer to be a hawk to a dove?*
Problem 12: *Could coexistence of the species be possible in this model? Why or why not?*

Section 4: The Replicator Equation

Each bird in the population has a default strategy. A given bird might change its strategy over time. There are at least two interpretations for this. A bird might notice that it is doing rather poorly compared to the rest of the population, and try to mimic a strategy employed by the more successful birds in order to succeed in kind. In other words, the bird receives a below average payoff and decides to change strategy. A more realistic interpretation is as follows.

Each strategy is the expression of a replicator. Examples include genes that promote aggressive behavior among birds, genes that promote timid behavior among male kangaroos, or even learned foraging behaviors that are passed down from one generation of lemurs to the next. An organism's fitness is a function of the strategies it employs (and of the strategies employed by each other organism in the ecosystem!). Organisms with low fitness will reproduce less and decline in population. Consequently, the replicators responsible suffer also. More fit organisms whose strategies were generally superior will increase in population and 'fill the void' left by the declining populations of low fitness organisms.

> ***Problem 13:*** *How does a replicator's effectiveness result in changes to its presence in a given population or ecosystem?*

The replicator equation models how population levels change over time through continuous interactions like those described above in the simple Hawk-Dove model.

The Replicator Equation

$$\dot{x_i} = x_i(f_i(x) - \Phi(x))$$

where

$$\Phi(x) = \Sigma_{i=1}^{n} x_i f_i(x)$$

- $x = (x_1, x_2, ..., x_n)$ is the population of organisms
- x_i is the fraction of type i organisms in the population
- $\dot{x_i}$ denotes the instantaneous rate of change of the quantity x_i
- $f_i(x)$ is the fitness of population x_i

In Hawk-Dove, these equations become:

$$(\dot{\frac{n_D}{N}}) = \frac{n_D}{N}(f_D(n_H, n_D) - \Phi(n_H, n_D))$$
$$(\dot{\frac{n_H}{N}}) = \frac{n_H}{N}(f_H(n_H, n_D) - \Phi(n_H, n_D))$$
$$\Phi(n_H, n_D) = \frac{n_D}{N} f_D(n_H, n_D) + \frac{n_H}{N} f_H(n_H, n_D)$$

> ***Problem 13:*** *How might you interpret the function Φ? Hint: what does each term represent?*
> ***Problem 14:*** *Using the replicator equation and the new model below, can hawks and doves coexist?*
> ***Problem 15:*** *Find the equilibrium number of hawks and doves.*

Hawks and doves at the watering hole, from a paper published not too long ago in Nature:
https://www.nature.com/articles/s41598-017-04284-6

- c_H is the cost to a single hawk from aggressive behavior with other hawks

- R is the collectively shared resource, the watering hole

Let $R = 1$ and $c_H = \frac{2}{N-1}$.

$$f_H = \frac{R-(n_H-1)c_H}{n_H}$$

$f_D = \frac{R}{N}$ if $n_H = 0$ and $f_D = 0$ otherwise.

Section 5: Bonus!

https://playgameoflife.com/
Create a still life and two different 2-periodic oscillators.