

# Evolutionary Game Theory

# Evolutionary game theory

Game theory can still be applied when the players aren't making explicit decisions.

- John Maynard Smith and George Robert Price: "The logic of animal conflict" 1973



- Based on the idea that an organism's genes largely determine its fitness in a given environment.
- Organisms interact. The success of an organism depends on how it interacts with other organisms.

# Evolutionary game theory

## Analogy to game theory

- An organism's genetically determined traits and behaviors are like the strategy in a game.
- Its fitness is like its payoff.
- This payoff depends on the traits and behaviors of the organisms with which it interacts.

# Beetle game



Drugstore beetle



Titan beetle

# Beetle game

Disclaimer: Very simplified game!

- Most beetles in the population are small, then a mutation is introduced and large beetles are introduced to the population.
- When beetles of the same size compete, they split the food equally.
- When a large beetle competes with a small beetle, the large beetle gets most of the food.
- In all cases the large beetle experiences less fitness from a given quantity of food.

		Beetle 2	
		Small	Large
Beetle 1	Small	5, 5	1, 8
	Large	8, 1	3, 3

# Beetle game

		Beetle 2	
		Small	Large
Beetle 1	Small	5, 5	1, 8
	Large	8, 1	3, 3

Nash equilibria?

No personal strategies!

# Evolutionary stable strategies

The analogy to a Nash equilibria is an *evolutionarily stable strategy*.

## Definition

An *evolutionarily stable strategy* is a genetically determined strategy that tends to persist once it is prevalent in a population.

We expect that a beetle will interact with many other beetles over the course of its lifetime. The beetle's overall fitness will be equal to the average fitness that it experiences from its many pairwise interactions with other beetles. This determines the beetle's reproductive success. How many beetles with its strategy (genes).

# Evolutionary stable strategies

## Definition

A strategy is *evolutionarily stable* if, when the whole population is using this strategy, any small group of invaders (mutants) using a different strategy will eventually die off over multiple generations.

More formally,

- Suppose the whole population is using strategy  $S$  and a small group of invaders is using strategy  $T$ .
- The *fitness* of an organism is the expected payoff it receives from an interaction with a random member of the population.
- $T$  invades  $S$  at level  $x$  for some small positive number  $x$ , if an  $x$  fraction of the population uses strategy  $T$  and a  $1 - x$  fraction of the population uses  $S$ .
- A strategy  $S$  is *evolutionarily stable* if there is a small positive number  $y$  such that, when any other strategy  $T$  invades  $S$  at any level  $x < y$ , the fitness of an organism playing  $S$  is strictly greater than the fitness of an organism playing  $T$ .

# Evolutionary stable strategies - back to the beetles

## Is Small evolutionarily stable?

- Suppose a  $1 - x$  fraction of the population uses Small and an  $x$  fraction of the population uses Large.
  - What is the expected payoff for Small in a random interaction in this population? With probability  $1 - x$  it will meet another Small for a payoff of 5. With probability  $x$  it will meet a Large for a payoff of 1.

$$5(1 - x) + 1(x) = 5 - 4x$$

- What is the expected payoff for Large in a random interaction in this population? With probability  $1 - x$  it will meet a Small for a payoff of 8. With probability  $x$  it will meet another Large for a payoff of 3.

$$8(1 - x) + 3(x) = 8 - 5x$$

- For reasonably small values of  $x$ :  
Expected payoff (fitness) of Small < Expected fitness of Large
- Therefore Small is not evolutionarily stable.

# Evolutionary stable strategies - back to the beetles

## Is Large evolutionarily stable?

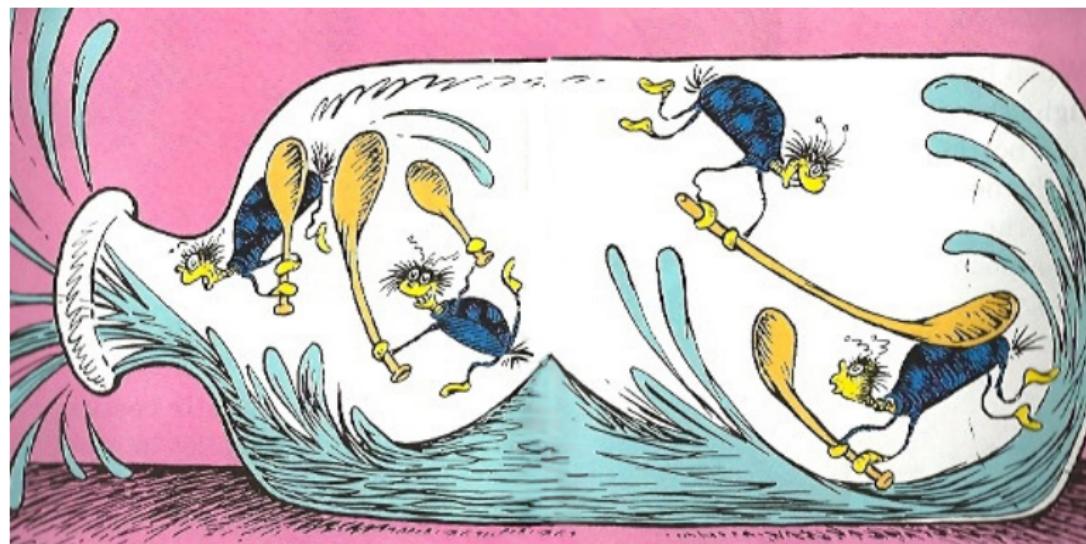
- Suppose a  $1 - x$  fraction of the population uses Large and an  $x$  fraction of the population uses Small.
  - What is the expected payoff for Large in a random interaction in this population? With probability  $1 - x$  it will meet another Large for a payoff of 3. With probability  $x$  it will meet a Small for a payoff of 8.
$$3(1 - x) + 8(x) = 3 + 5x$$
  - What is the expected payoff for Small in a random interaction in this population? With probability  $1 - x$  it will meet a Large for a payoff of 1. With probability  $x$  it will meet another Small for a payoff of 5.
$$(1 - x) + 5(x) = 1 + 4x$$
- Expected fitness of Large  $>$  Expected fitness of Small
- Therefore Large is evolutionarily stable.

## Evolutionary stable strategies - back to the beetles

Summarize:

- If a small group of large beetles is introduced to a large group of small beetles, the small beetles cannot drive out the large ones.
- If a small group of small beetles is introduced to a large group of large beetles, the large beetles can drive out the small ones. Therefore the large beetles form an evolutionarily stable strategy.

# Beetle Battle - Dr. Seuss



# Natural selection?

The fitness of individuals is decreasing!

This is analogous to:

- The prisoners dilemma
- Arms races
- Athletes deciding whether or not to use drugs.
- Many more...short and tall trees

## Natural selection? - Tree height

- If two trees are short, they share the sunlight equally.
- If two trees are tall, they share the sunlight equally, but experience less fitness because of the energy taken to grow.
- If there is one tall tree and one short tree, the tall tree gets most of the sunlight.

There is a similar game for root systems.

## Generalize evolutionarily stable strategies

Restrict to 2-player, 2-strategy, symmetric games.

		Organism 2	
		S	T
Organism 1	S	a, a	b, c
	T	c, b	d, d

As before, suppose that for some small  $x$ , a  $1 - x$  fraction of the population uses  $S$  and an  $x$  fraction of the population uses  $T$ .

## Generalize evolutionarily stable strategies

		Organism 2	
		S	T
Organism 1	S	a, a	b, c
	T	c, b	d, d

- What is the expected payoff for  $S$ ?

$$a(1 - x) + bx$$

- What is the expected payoff for  $T$ ?

$$c(1 - x) + dx$$

- Therefore  $S$  is evolutionarily stable if:

$$a(1 - x) + bx > c(1 - x) + dx$$

In a two-player, two-strategy, symmetric game,  $S$  is evolutionarily stable when either  $a > c$  or  $a = c$  AND  $b > d$ .

# Evolutionary and Nash equilibria

When is  $(S, S)$  a Nash equilibria?

		Organism 2	
		S	T
Organism 1	S	a, a	b, c
	T	c, b	d, d

When  $S$  is the best response to  $S$ :

$$a \geq c$$

## Theorem

*If  $S$  is evolutionarily stable, then  $(S, S)$  is a Nash equilibrium.*

The other direction does not hold.

# Evolutionary and Nash equilibria

		Organism 2	
		S	T
Organism 1	S	a, a	b, c
	T	c, b	d, d

Find an example of when the Nash equilibria is not evolutionarily stable.

Need  $a = c$  and  $b < d$ .

Modified stag hunt game:

		Hunter 2	
		Hunt Stag	Hunt Hare
Hunter 1	Hunt Stag	4, 4	0, 4
	Hunt Hare	4, 0	3, 3

## Evolutionarily stable mixed strategies

The notion of mixed strategies can be applied to evolutionary game theory in two ways:

- Either a portion  $q$  of the total population plays strategy  $X$  while the remaining  $1 - q$  portion of the population plays the other strategy.
- Or each individual in a species plays strategy  $X$   $q$  of the time and the other strategy  $1 - q$  of the time