Evolutionary Game Theory

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Outline

1. Evolutionary Game Theory (EGT)
2. Evolutionary Stable Strategy (ESS)
3. Relationship between ESS and NE
4. Evolutionarily Stable Mixed Strategies

Introduction

- Basic ideas of game theory: individual players make decisions and the payoff to each player depends on the decisions made by all.
- A key question in game theory: to reason simultaneously or sequentially about the behavior we should expect to see when players take part in a given game.

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- Basic ideas of game theory: individual players make decisions and the payoff to each player depends on the decisions made by all.
- A key question in game theory: to reason <u>simultaneously or sequentially</u> about the behavior we should expect to see when players take part in a given game.
- Game-theoretic analysis will be applied here to settings in which individuals can exhibit different forms of behavior (may not be the result of conscious choices)
- We will consider which forms of behavior have the ability to persist in the nature and which forms of behavior have a tendency to be driven out by others.

Introduction

- In the area of evolutionary biology
- the idea was first articulated by John Maynard Smith and George R. Price in 1973.
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- the idea was first articulated by John Maynard Smith and George R. Price in 1973.
- GT as a powerful modeling tool, helps studying animal behavior and understanding population dynamics.
- Organisms that are more fit will tend to produce more offspring, causing genes that provide greater fitness to increase their representation in the population.
- Fitter genes tend to win over time.

Introduction

- Game theoretic ideas like equilibrium turn out to be a useful way to make predictions about the results of evolution on a population.
- The key insight of evolutionary game theory is that many behaviors involve the interaction of multiple organisms in a population, and the success of any one of these organisms depends on how its behavior interacts with that of others.
- So the fitness of an individual organism can’t be measured in isolation; rather it has to be evaluated in the context of the full population in which it lives.

Evolution

Chimpanzee

Bonobo

GT vs. EGT

Players	• Multiple organisms (spices) in a population
Strategies	• An organism’s genetically determined characteristics and behaviors
Payoffs	• Fitness depends on the strategies (behaviors) of the organisms with which it interacts.

Some Assumptions in EGT

1. Within spices competition
    - We assume no mixture of population: ants with ants, lions with lions.

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2. Random selection
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3. The player adopting the strategy yielding higher payoff will survive in population, whereas the player who “lost” the game, will die out.
4. The behavior of species is not necessarily based on rationality.

Some Assumptions in EGT

5. We suppose the entire population play strategy s.

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6. We then assume a mutation happens, and a small group of individuals start playing strategy s'.

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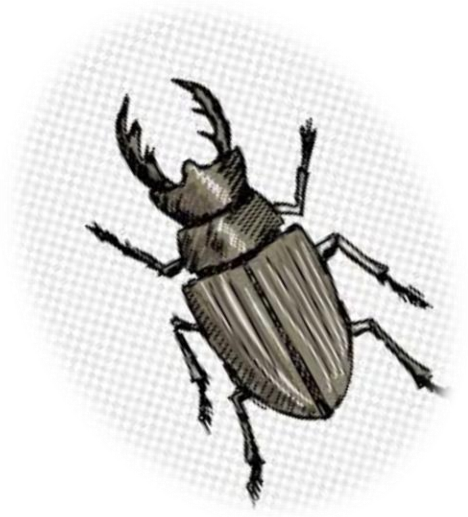
7. The probability for a player using s to meet another player using s is high, whereas meeting a player using s' is low.

Main Question in EGT

We will ask is whether the mutants s' will survive and grow in population or if they will eventually die out?

A Simple Example

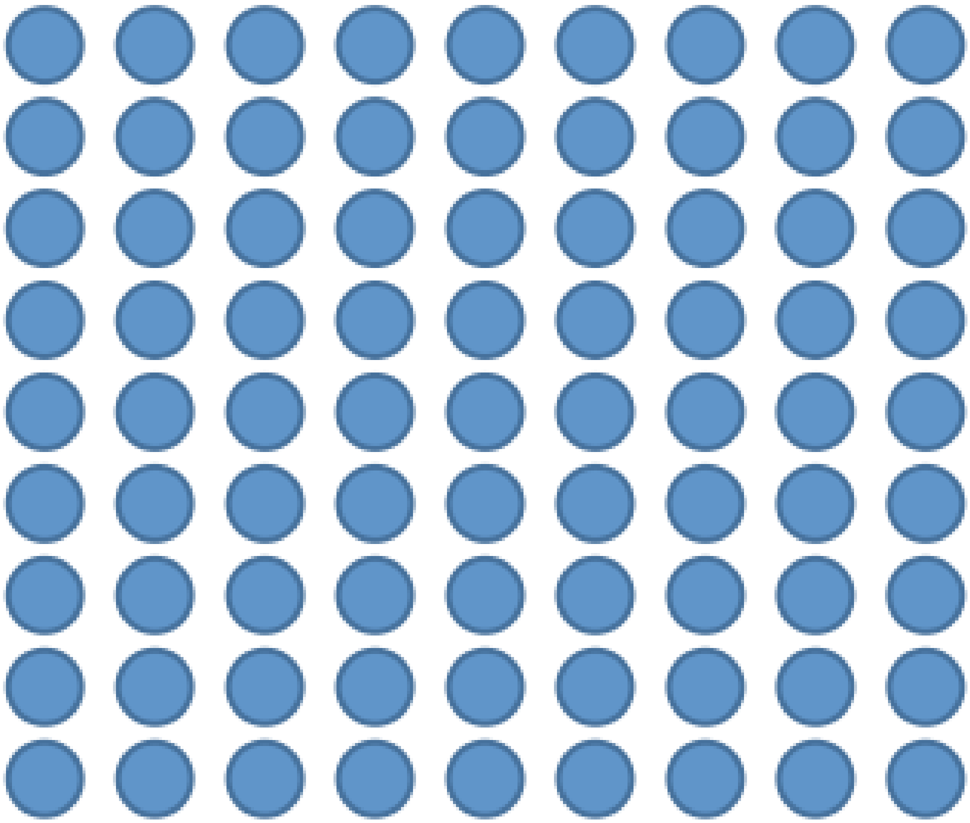
- Interaction among some species of beetles.
- A population with small species of beetle (s)
- A particular mutation causing beetles with the mutation to grow a significantly larger body size (s’).
- two distinct kinds of beetles in the population: small and large
- When beetles of the same size compete, they get equal shares of the food.
- When a large beetle competes with a small beetle, the large beetle gets the majority of the food.

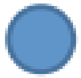


A Simple Example

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

A Population

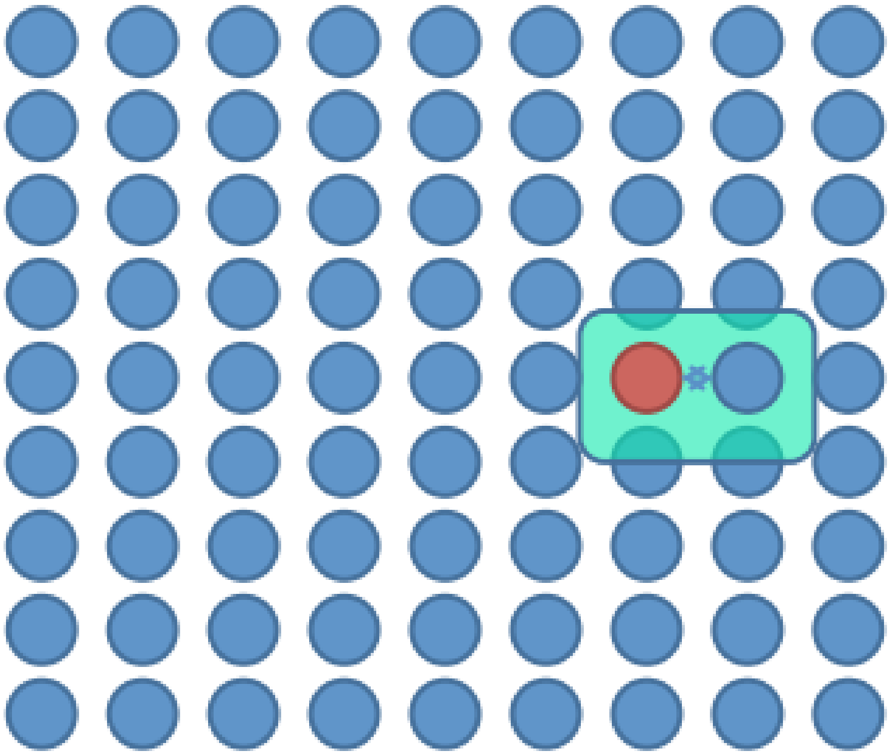


 beetles with small size.

All players are small size
and get a payoff of 5.

What happens in a mutations?

A Population



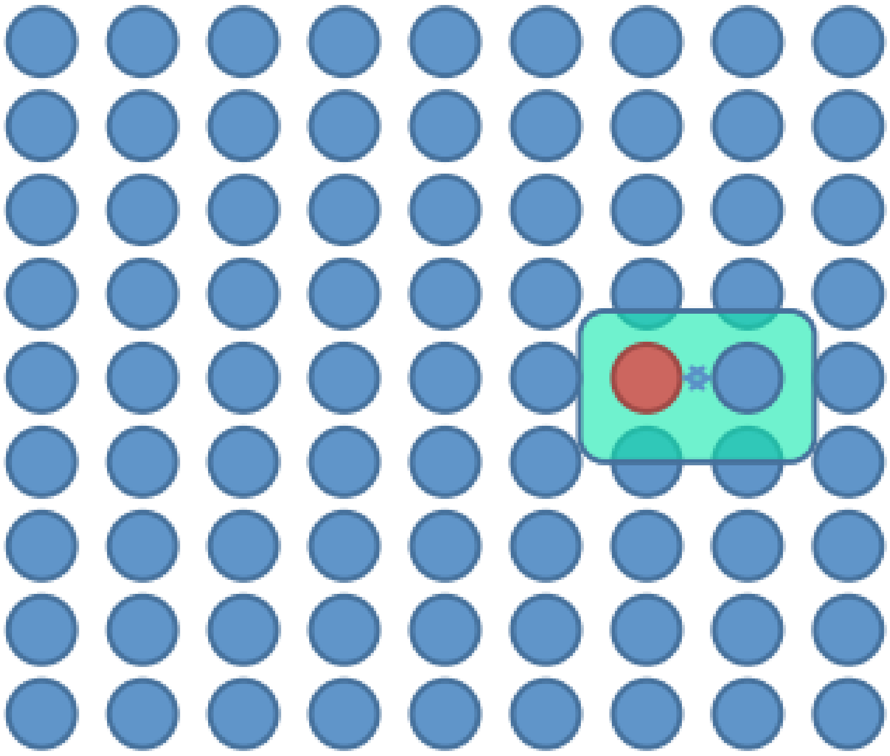
Players with small size

beetles with large size

Small beetle obtain a payoff of 1
Large beetle obtain a payoff of 8

Survival of the fittest?

A Population



Players with small size

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Small beetle obtain a payoff of 1
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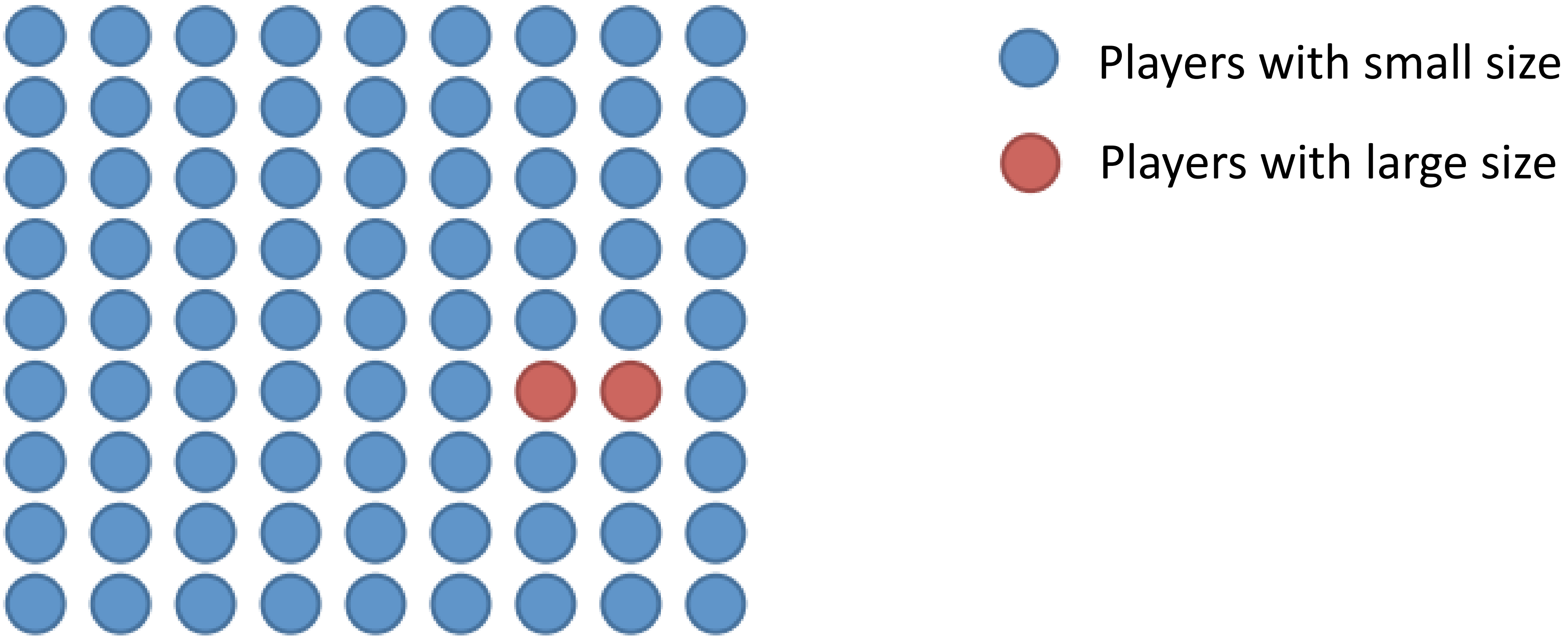
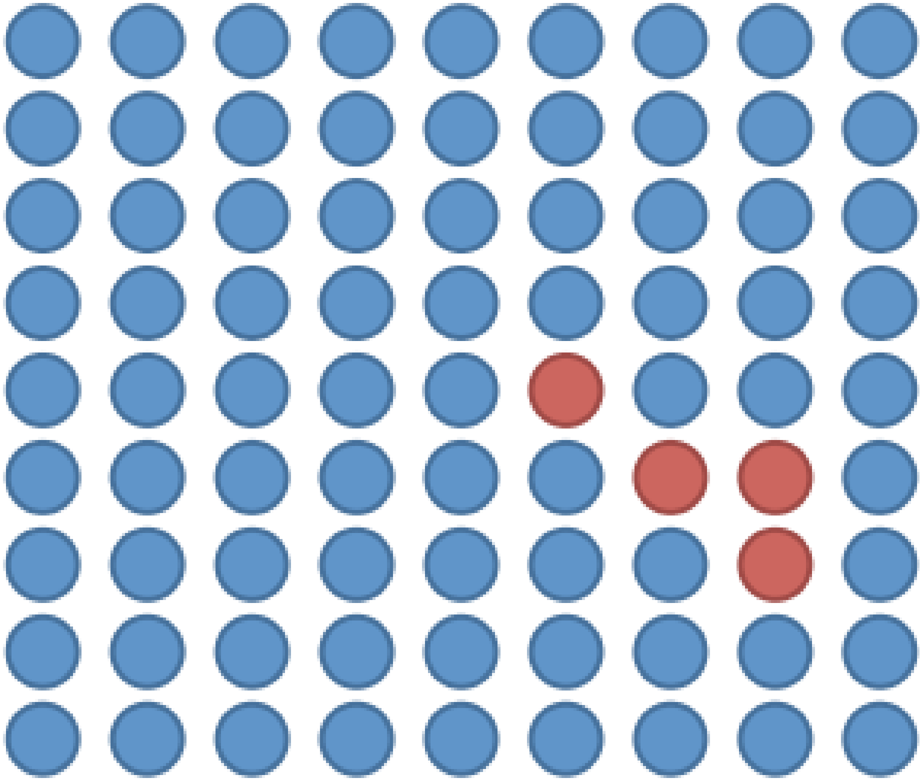
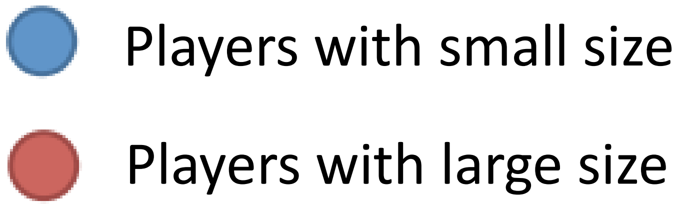
Survival of the fittest?
Large wins over Small

A Population



A Population





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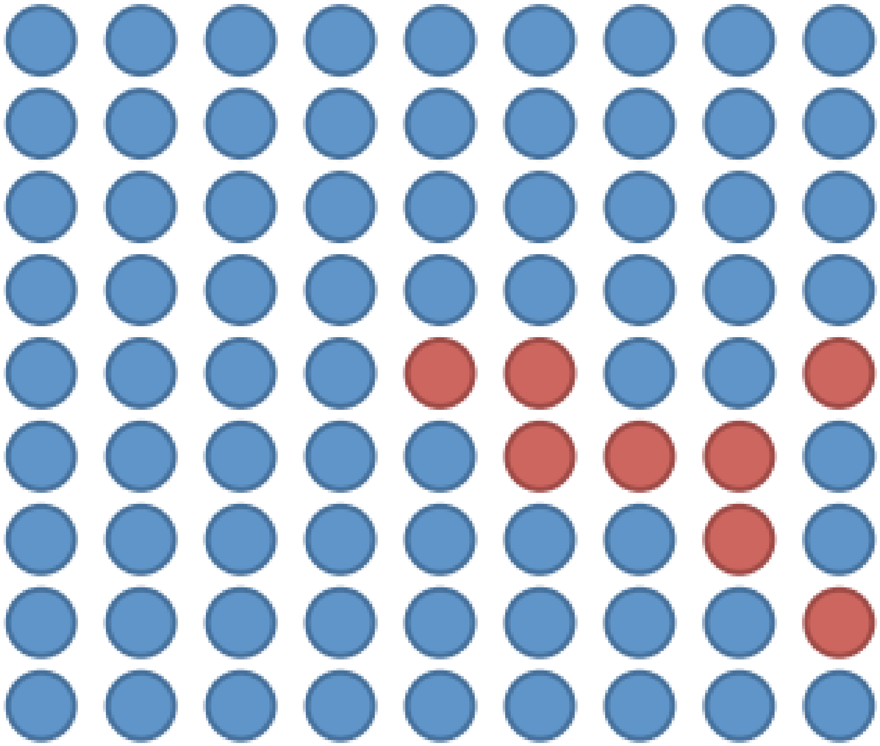

Players with small size

Players with large size

A small initial mutation is rapidly expanding instead of dying out.

A Main Question

- Let's now try to be a little bit more formal.

Is "Large" beetle (s') evolutionarily stable or not?

Is “Small” Evolutionary Stable?

- Entire population with the behavior of “Small”,
- A mutation happens with size of ϵ and a small group of individuals start the behavior of “Large”.

		Beetle 2	
		Small	*Large*
Beetle 1	*Small*	5, 5	1, 8
	Large	8, 1	3, 3
		$1 - \epsilon$	ϵ

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		$1 - \epsilon$	ϵ

"Small" vs. total population: $5(1-\epsilon) + 1(\epsilon)$

"Large" vs. total population: $8(1-\epsilon) + 3(\epsilon)$

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“Large” vs. total population: $8(1-\epsilon) + 3(\epsilon)$

$8(1-\epsilon) + 3(\epsilon) > 5(1-\epsilon) + 1(\epsilon)$

“Small” is not ES.

Is “Large” Evolutionary Stable?

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

“Large” vs. total population: $8(\epsilon) + 3(1-\epsilon)$

“Small” vs. total population: $5(\epsilon) + 1(1-\epsilon)$

$8(\epsilon) + 3(1-\epsilon) > 5(\epsilon) + 1(1-\epsilon)$

“Large” is ES: any mutation from “large” gets wiped out!

Lesson

If a strategy is strictly dominated, then
it is not Evolutionarily Stable.
(The strictly dominant strategy will be a successful Mutation)

Another Example

- 2-player symmetric game with 3 strategies.

- Is “c” ESS?

	a	b	c
a	2,2	0,0	0,0
b	0,0	0,0	1,1
c	0,0	1,1	0,0

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$\epsilon \quad 1 - \epsilon$

c vs. $[(1-\varepsilon)c + \varepsilon b] \rightarrow (1-\varepsilon)\,0 + \varepsilon\,1 = \varepsilon$

b vs. $[(1-\varepsilon)c + \varepsilon b] \rightarrow (1-\varepsilon)\,1 + \varepsilon\,0 = 1-\varepsilon$

$1-\varepsilon > \varepsilon$

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$$c \text{ vs. } [(1-\varepsilon)c + \varepsilon b] \rightarrow (1-\varepsilon)\,0 + \varepsilon\,1 = \varepsilon$$
$$b \text{ vs. } [(1-\varepsilon)c + \varepsilon b] \rightarrow (1-\varepsilon)\,1 + \varepsilon\,0 = 1-\varepsilon$$
$$1-\varepsilon > \varepsilon$$

"c" is not evolutionary stable, as "b" can invade it

Another Example

- 2-player symmetric game with 3 strategies.

- Is (c,c) NE?

	a	b	c
a	2,2	0,0	0,0
b	0,0	0,0	1,1
c	0,0	1,1	0,0

Another Example

- 2-player symmetric game with 3 strategies.
- Is (c,c) NE?
  - No!

	a	b	c
a	2,2	0,0	0,0
b	0,0	0,0	1,1
c	0,0	1,1	0,0

Another Example

- 2-player symmetric game with 3 strategies.

	a	b	c
a	2,2	0,0	0,0
b	0,0	0,0	1,1
c	0,0	1,1	0,0

- Is (c,c) NE?
  - No!

- NE vs. ESS?

Relationship between ESS and NE

If s is **not Nash** (i.e., (s,s) is not a NE),
then s is **not evolutionary stable** (ES)

If s **is ES**, then (s,s) **is a NE**

Relationship between ESS and NE

If s is **not Nash** (i.e., (s,s) is not a NE),
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Question: Is the opposite true?

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⇕

If s **is ES**, then (s,s) **is a NE**

Question: Is the opposite true? No

Yet Another Example

- NE?
  - (a,a) and (b,b)

- Is b ES?

	a	b
a	2,2	0,0
b	0,0	0,0

Yet Another Example

- NE?
  - (a,a) and (b,b)
- Is b ES?

	a	b
a	2,2	0,0
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ϵ $\quad 1 - \epsilon$

$b \rightarrow 0$

$a \rightarrow (1-\varepsilon)\,0 + \varepsilon\, 2 = 2\epsilon$

$2\epsilon > 0$

Yet Another Example

- NE?
  - (a,a) and (b,b)

	a	b
a	2,2	0,0
b	0,0	0,0

ϵ $1 - \epsilon$

- Is b ES?

b → 0
a → $(1 - \varepsilon)\, 0 + \varepsilon\, 2 = 2\epsilon$
$2\epsilon > 0$

→ *(b,b)* is a NE, but it is not ES!

Why NE but not ES?

- Why is “b” not ES despite it is a NE?

Why NE but not ES?

- Why is “b” not ES despite it is a NE?
    - This relates to the idea of a weak NE

Why NE but not ES?

- Why is “b” not ES despite it is a NE?
  - This relates to the idea of a weak NE

- Observation:

If (s,s) is a ***strict NE*** then s is ES

Informal Definition: ESS

- Entire population with the behavior of s
- suddenly a mutation happens and a small group of individuals start the behavior of s' (ϵ).
- s is evolutionarily stable Strategy (ESS), if for all sufficiently small values of $\epsilon > 0$:

Expected fitness of any mutant s' << Expected fitness of normal organism.

Formal Definition 1: ESS

In a symmetric 2 player game, the pure strategy ŝ is ES (in **pure** strategies) if there exists an $\varepsilon_0 > 0$ such as:

$$\underbrace{(1-\varepsilon)\left[u(\hat{s},\hat{s})\right]+\varepsilon\left[u(\hat{s},s')\right]}_{\text{Payoff to ES } \hat{s}} > \underbrace{(1-\varepsilon)\left[u(s',\hat{s})\right]+\varepsilon\left[u(s',s')\right]}_{\text{Payoff to mutant } s'}$$

for all possible deviations s' and for all mutation sizes $\varepsilon < \varepsilon_0$

Formal Definition 2: ESS

- In a symmetric 2 player game, the pure strategy $\hat{s}$ is ES (in **pure** strategies) if:

A) $(\hat{s},\hat{s})$ is a symmetric Nash Equilibrium

$$u(\hat{s},\hat{s}) \geq u(s',\hat{s}) \quad \forall s'$$

and

B) if $u(\hat{s},\hat{s}) = u(s',\hat{s})$ then

$$u(\hat{s},s') > u(s',s')$$

Theorem

Definition 1 $\Leftrightarrow$ Definition 2

Theorem

Definition 1 $\Leftrightarrow$ Definition 2

- Let's see Def. 2 $\Rightarrow$ Def. 1

<u>Sketch of proof:</u>

- Fix a $\hat{s}$ and suppose $(\hat{s},\hat{s})$ is NE, that is

$$u(\hat{s},\hat{s}) \geq u(s',\hat{s}) \quad \forall s'$$

- There are two possibilities

Theorem

- **Case 1:**
  $u(\hat{s},\hat{s}) > u(\hat{s},s') \quad \forall s'$
  the mutant dies out because she meets $\hat{s}$ often
- **Case 2:**
  $u(\hat{s},\hat{s}) = u(\hat{s},s') \quad \forall s'$ but
  $u(\hat{s},s') > u(s',s')$
  the mutant does "ok" against $\hat{s}$ (the mass) but badly against s' (itself)

Conclusion

– First check if $(\hat{s},\hat{s})$ is a ***symmetric*** Nash Equilibrium

– If it is a ***strict*** NE, we're done

– Otherwise, we need to compare how $\hat{s}$ performs against a mutation, and how a mutation performs against a mutation

– If $\hat{s}$ performs better, then we're done

Evolution in Social Sciences

- Let’s have a look at how driving to the left or right hand side of the road might evolve

- NE?
  - (L,L) , (R,R) and symmetric NE.
- Strict NE?

		Player 2	
		L	R
Player 1	L	2,2	0,0
	R	0,0	1,1

Evolution in Social Sciences

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  - Yes, they are strict.

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- ESS?

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Evolution in Social Sciences

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- NE?
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- Strict NE?
  - Yes, they are strict.
- ESS?
  - L and R are both ESS.

		Player 2	
		L	R
Player 1	L	2,2	0,0
	R	0,0	1,1

New Lesson

We can have multiple ESS.
Multiple ESS need not to be equally good.
Remember coordination game!

Let’s go to study Evolutionarily Stable Mixed Strategies

The Game of Chicken

- This is just a symmetric version of the Battle of the Sexes game.

	a	b
a	0,0	2,1
b	1,2	0,0

- Biology interpretation:
  - “a” : Individuals that are aggressive
  - “b” : Individuals that are non-aggressive

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- Pure NE?
  - (a,b) , (b,a)
- Symmetric NE?
  - No
- ESS?
  - Neither the pure strategy “a” not “b” can be ESS.
  - If you had only aggressive genes, they had do very badly against each other, hence they could be invaded by a gentle gene
  - Vice-versa is also true.

The Game of Chicken

- Look at mixed strategies!

- Mixed NE?

	a	b
a	0,0	2,1
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The Game of Chicken

- Look at mixed strategies!
- Mixed NE?
  - $\{({}^{2}/_{3}, {}^{1}/_{3}),({}^{2}/_{3}, {}^{1}/_{3})\}$
- Symmetric NE?

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The Game of Chicken

- Look at mixed strategies!
- Mixed NE?
  - $\{(^2/_3, {}^1/_3),(^2/_3, {}^1/_3)\}$
- Symmetric NE?
  - Yes!

	a	b
a	0,0	2,1
b	1,2	0,0

- It seems that there is an equilibrium in which 2/3 of the genes are aggressive and 1/3 are non-aggressive.

New Definition: ESS

- In a symmetric 2 player game, the mixed strategy $\hat{p}$ is ES (in mixed strategies) if:

A) $(\hat{p}, \hat{p})$ is a symmetric Nash Equilibrium

$$u(\hat{p}, \hat{p}) \geq u(p', \hat{p}) \quad \forall p'$$

and

B) if $u(\hat{p}, \hat{p}) = u(p', \hat{p})$ then

$$u(\hat{p}, p') > u(p', p')$$

Warning!

- By definition of a mixed NE: Expected payoffs are equal for players

- So in this example, we need to check
  - for all p’ = possible mixed deviation

$$u(\hat{p}, p') > u(p', p') \ \forall p'$$

Warning!

- Instead of a formal proof, let's discuss an heuristic to check that this is true
  - We've got a population in which 2/3 are aggressive and 1/3 are passive
  - Suppose there is a mutation *p'* that is more aggressive than p (e.g. 90% aggressive, 10% passive)
  - Since the aggressive mutation is doing very badly against herself, it would eventually die out
  - Indeed, the mutation would obtain a payoff of 0

	a	b
a	0,0	2,1
b	1,2	0,0

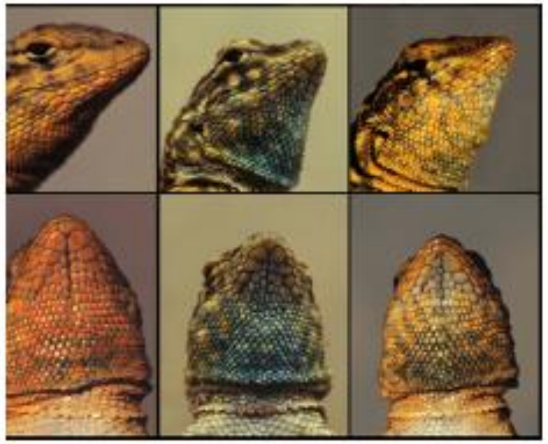
Interpretation of Mixed in Nature

- *But what does it mean to have a mixed ESS in nature?*

Interpretation of Mixed in Nature

- *But what does it mean to have a mixed ESS in nature?*
- It could mean that the gene itself is randomizing.
- It could be that there are actually two types surviving in the population.
- This is Coexistence!

Coexistence



http://bio.research.ucsc.edu/~barrylab/classes/animal_behavior/MALESS.HTM

The Hawk-Dove Game

	H	D
H	(v-c)/2, (v-c)/2	v,0
D	0, v	v/2, v/2

- We're now going to look at a more general game of aggression vs. non-aggression
- Note: we're still in the context of ***within spices competition***
  - So it's not a battle against two different animals, hawks and doves


The Hawk-Dove Game

- The idea is that there is a potential battle against an aggressive vs. a non-aggressive animal
- The prize is food, and it's value is v > 0
- There's a cost for fighting, which is c > 0

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The Hawk-Dove Game

- The idea is that there is a potential battle against an aggressive vs. a non-aggressive animal
- The prize is food, and it's value is $v > 0$
- There's a cost for fighting, which is $c > 0$
- We're going to analyze ES strategies (ESS)
- We're going to be able to understand what happens to the ESS mix as we change the values of prize and costs

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The Hawk-Dove Game

	H	D
H	(v-c)/2, (v-c)/2	v,0
D	0, v	v/2, v/2

- Can we have a ES population of doves?
- Is *(D,D)* a NE?
  - No, hence "D" is not ESS
  - Indeed, a mutation of hawks against doves would be profitable in that it would obtain a payoff of v

The Hawk-Dove Game

	H	D
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The Hawk-Dove Game

	H	D
H	(v-c)/2, (v-c)/2	v,0
D	0, v	v/2, v/2

- Can we have a ES population of Hawks?
- Is *(H,H)* a NE?
- It is a symmetric NE if $(v-c)/2 \geq 0$

The Hawk-Dove Game

	H	D
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D	0, v	v/2, v/2

- Can we have a ES population of Hawks?
- Is *(H,H)* a NE?
- It is a symmetric NE if $(v-c)/2 \geq 0$

- **Case 1:** $v>c$ ➔ *(H,H)* is a ***strict*** NE ➔ "*H*" is ESS

The Hawk-Dove Game

	H	D
H	(v-c)/2, (v-c)/2	v,0
D	0, v	v/2, v/2

- **Case 2:** v=c ➔ (v-c)/2 = 0 ➔ *u(H,H)* = *u(D,H)*
  - Need to check how H performs against a mutation of D
  - Is *u(H,D)* = *v* larger than *u(D,D)* = *v/2?*

➔ H is ESS if $v \geq c$

The Hawk-Dove Game

	H	D
H	(v-c)/2, (v-c)/2	v,0
D	0, v	v/2, v/2
	$\hat{p}$	$1-\hat{p}$

- What if $c > v$?
  - We know "H" is not ESS and "D" is not ESS
  - What about a mixed strategy?
- **Step 1**: we need to find a symmetric mixed NE

The Hawk-Dove Game

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D	0, v	v/2, v/2
	$\hat{p}$	$1-\hat{p}$

$$\left.\begin{aligned} u(H,\hat{p}) &= \hat{p}\left(\frac{v-c}{2}\right) + (1-\hat{p})v \\ u(D,\hat{p}) &= \hat{p}0 + (1-\hat{p})\frac{v}{2} \end{aligned}\right\} \Rightarrow \hat{p} = \frac{v}{c}$$

$$\Rightarrow \left(\frac{v}{c}, 1-\frac{v}{c}\right)$$

The Hawk-Dove Game

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D	0, v	v/2, v/2
	$\hat{p}$	$1-\hat{p}$

- The mixed NE is not strict by definition
- We need to check: (For more information, go to slide 72!)

$$u(\hat{p}, p') > u(p', p') \ \forall p'$$

Conclusions from Hawk-Dove Game

- In case v < c we have an evolutionarily stable state in which we have v/c hawks
  1. As v ↗ we will have more hawks in ESS
  2. As c ↗ we will have more doves in ESS

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- In case v < c we have an evolutionarily stable state in which we have v/c hawks
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- What are the payoffs?

- Let's take the D perspective

$$E\left[u(D,\hat{p})\right] = E\left[u(H,\hat{p})\right] = 0\frac{v}{c} + \left(1 - \frac{v}{c}\right)\frac{v}{2}$$

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Practical Evolutionary Games

- Packages in R: EvolutionaryGames
- https://cran.r-project.org/web/packages/EvolutionaryGames/vignettes/UsingEvolutionaryGames.html

- Packages in Python: egttools
- https://pypi.org/project/egttools/
- https://github.com/topics/evolutionary-game-theory