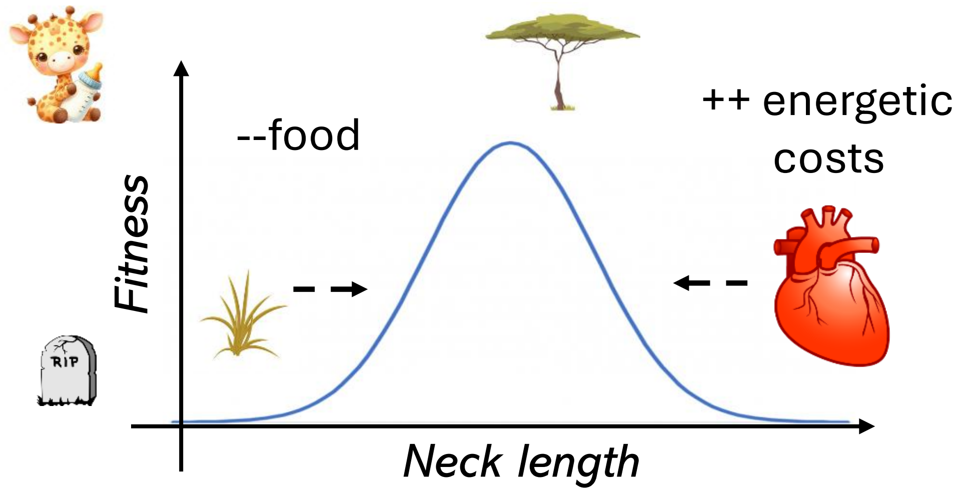
Evolutionary Game Theory

Part I: The evolution of cooperation

Fabrizio Mafessoni, Universita’ di Trieste, Corso di Biologia Evoluzionistica 2025/2026

Evolutionary fitness

Fitness represents an organism's ability to survive, reproduce, and pass its genes to the next generation relative to others in its population



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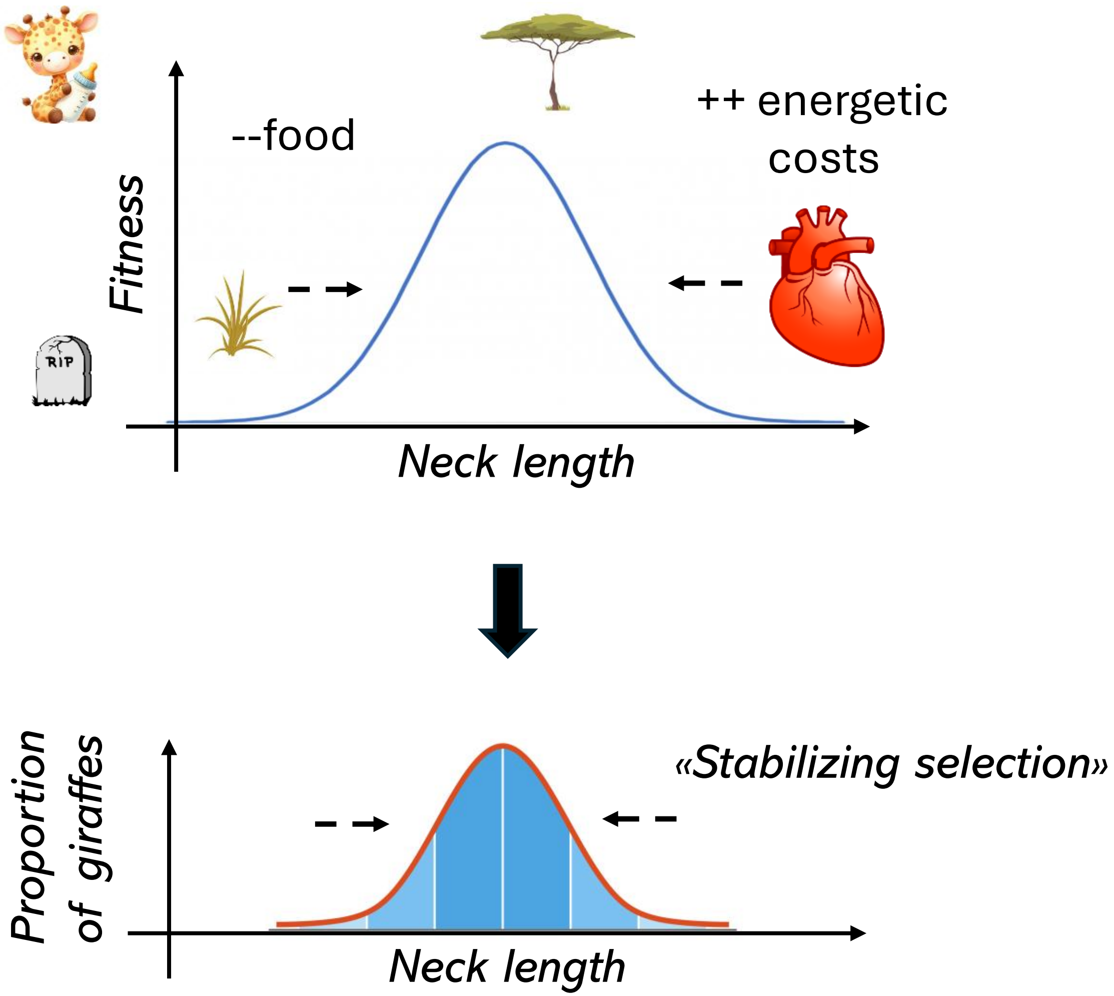
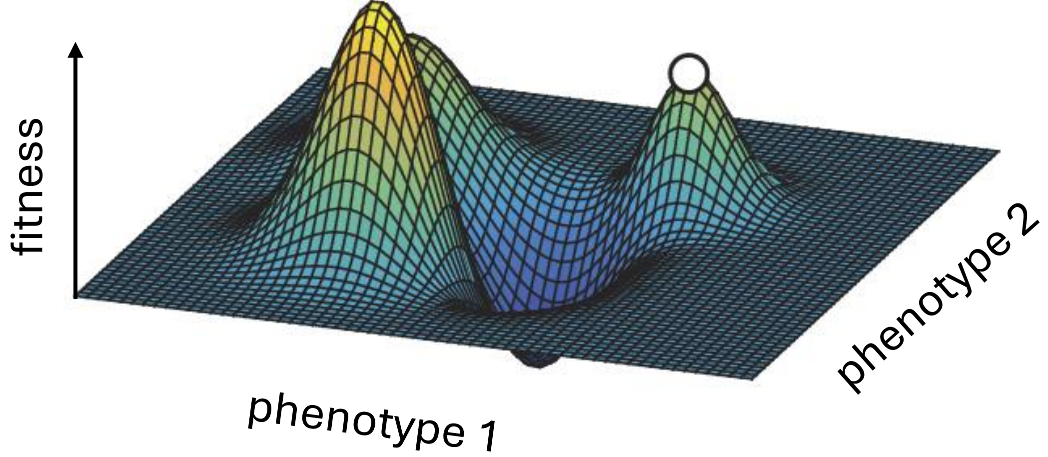
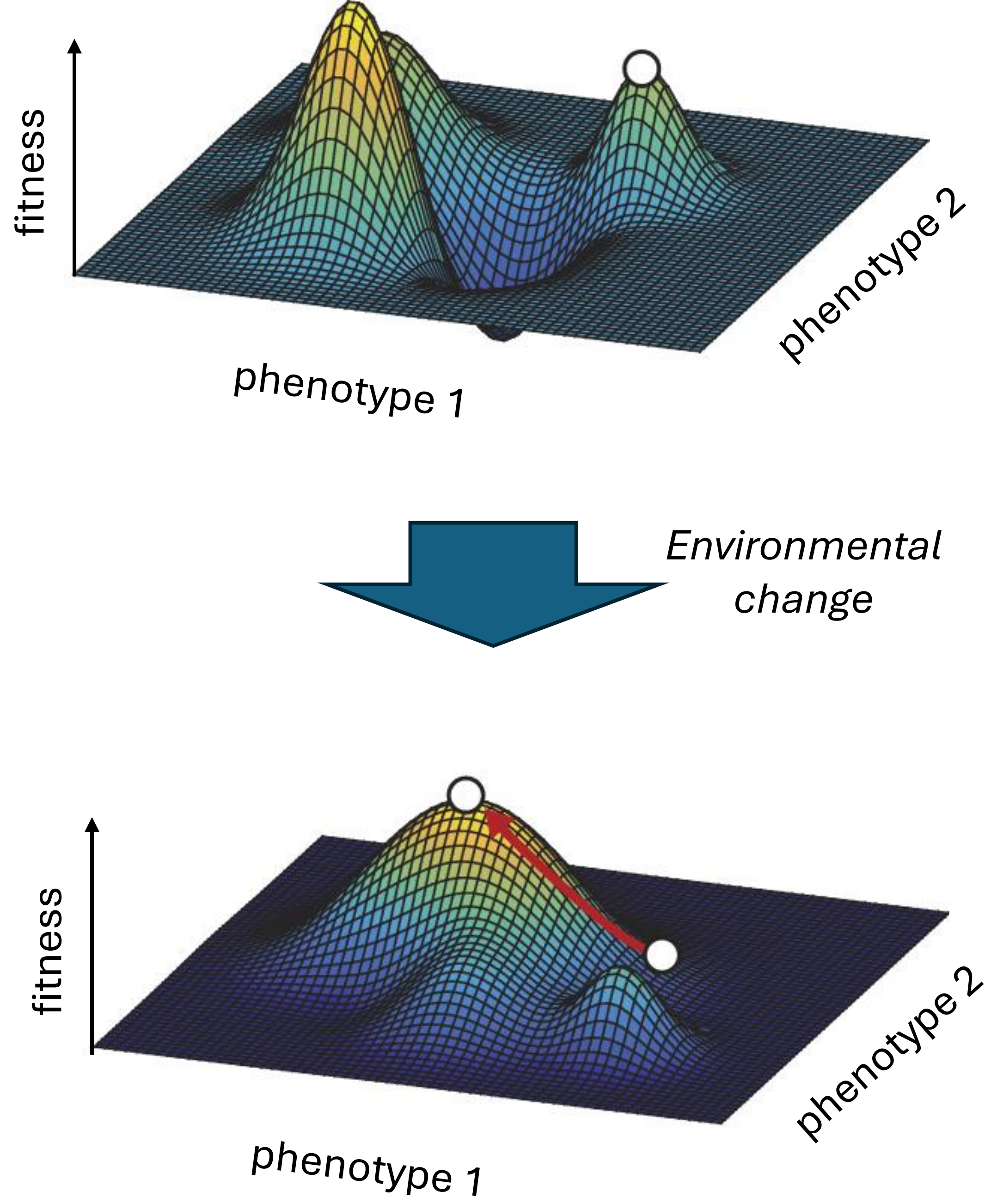


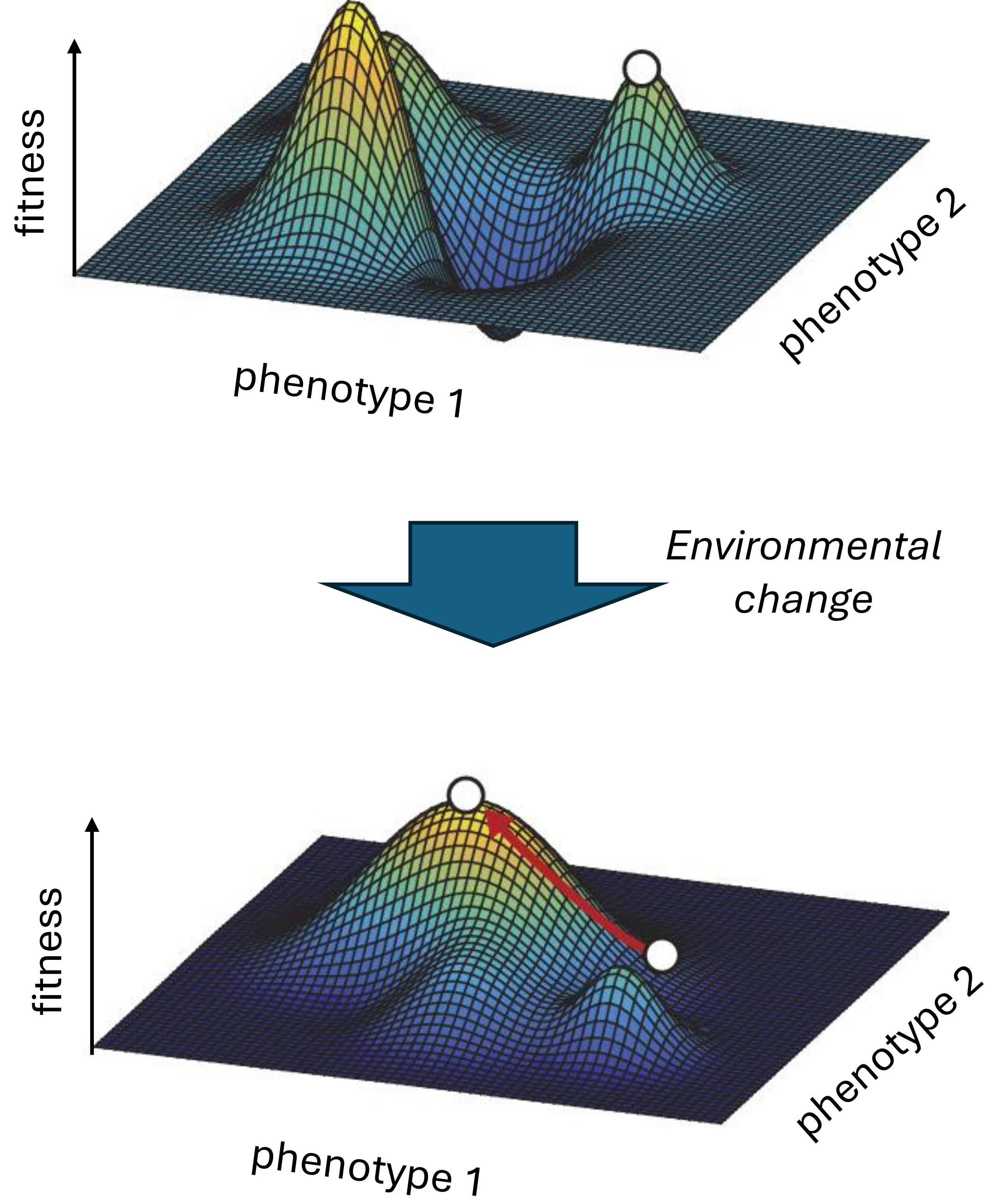
*Fitness can be represented in a **«fitness landscape»***



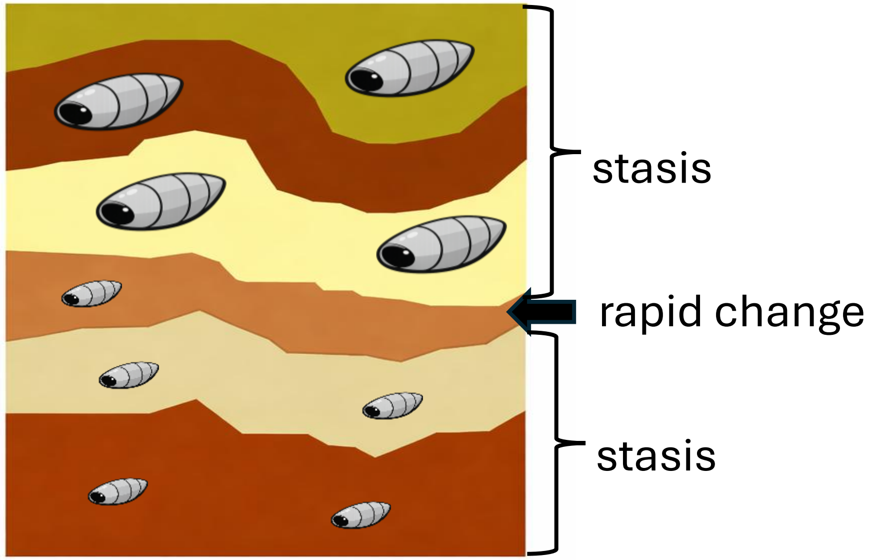
*Environmental changes can modify the «**fitness landscape**»*



Environmental changes can modify the ***«fitness landscape»***

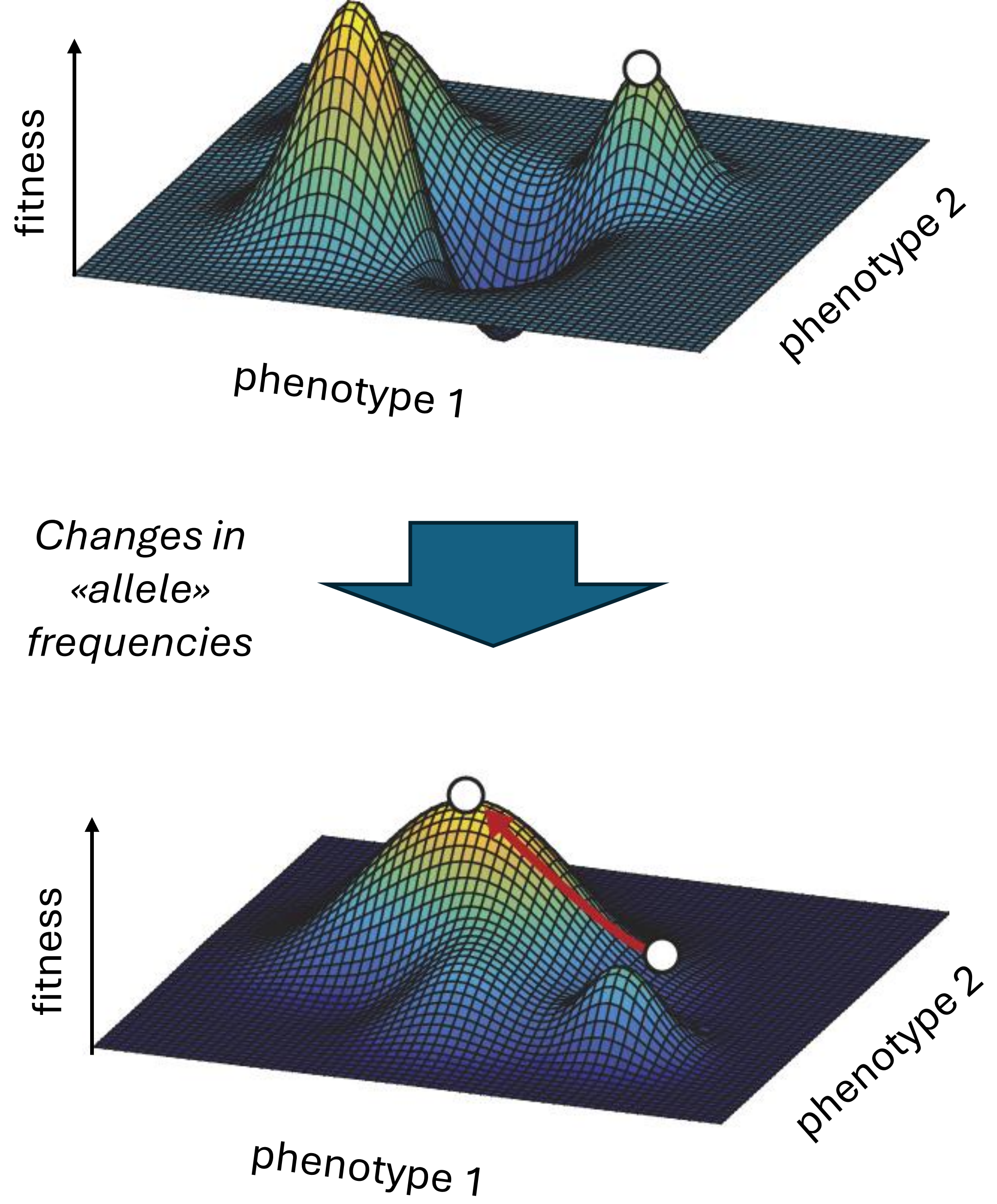


Punctuated equilibria



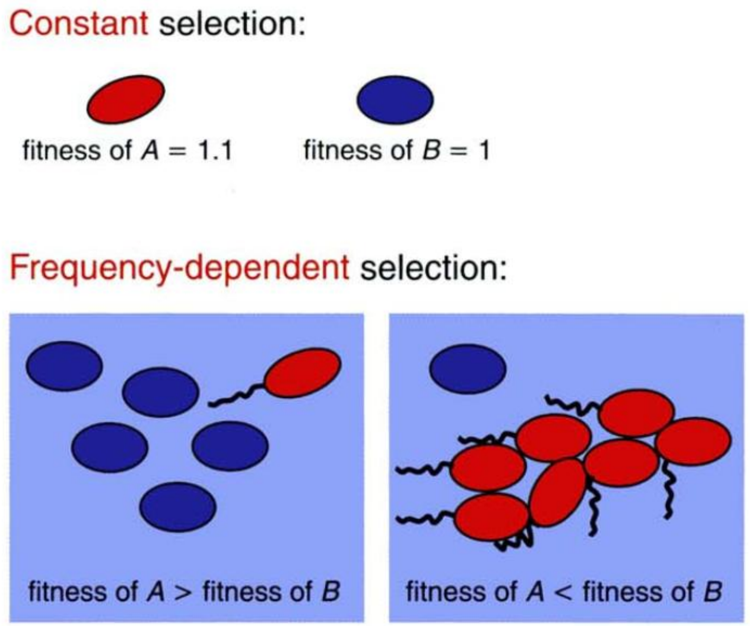
Even evolution itself can modify the fitness landscape

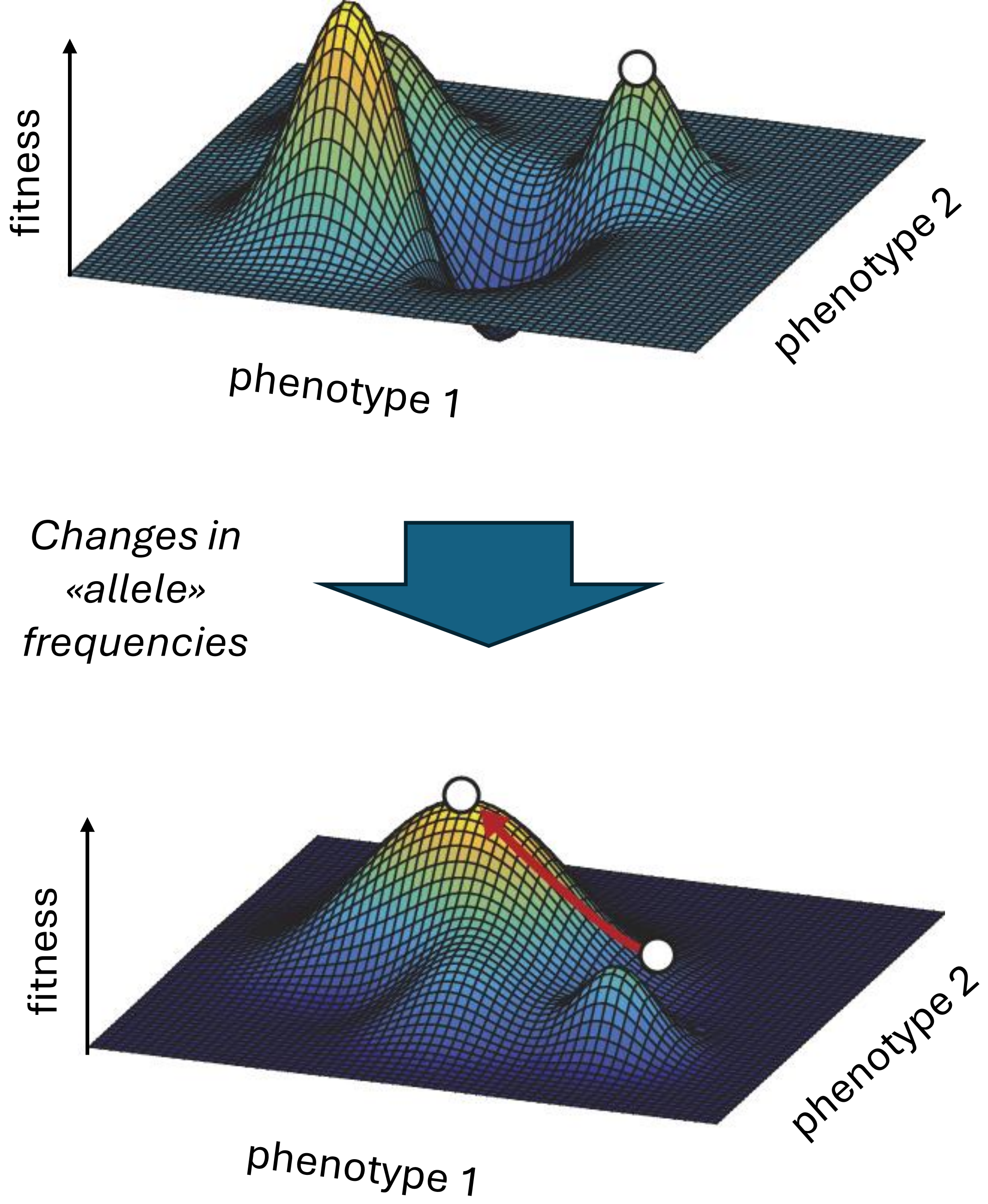
*Fitness can be **«frequency-dependent»!***



Evolutionary Game Theory

*The study of **«frequency-dependent» fitness***





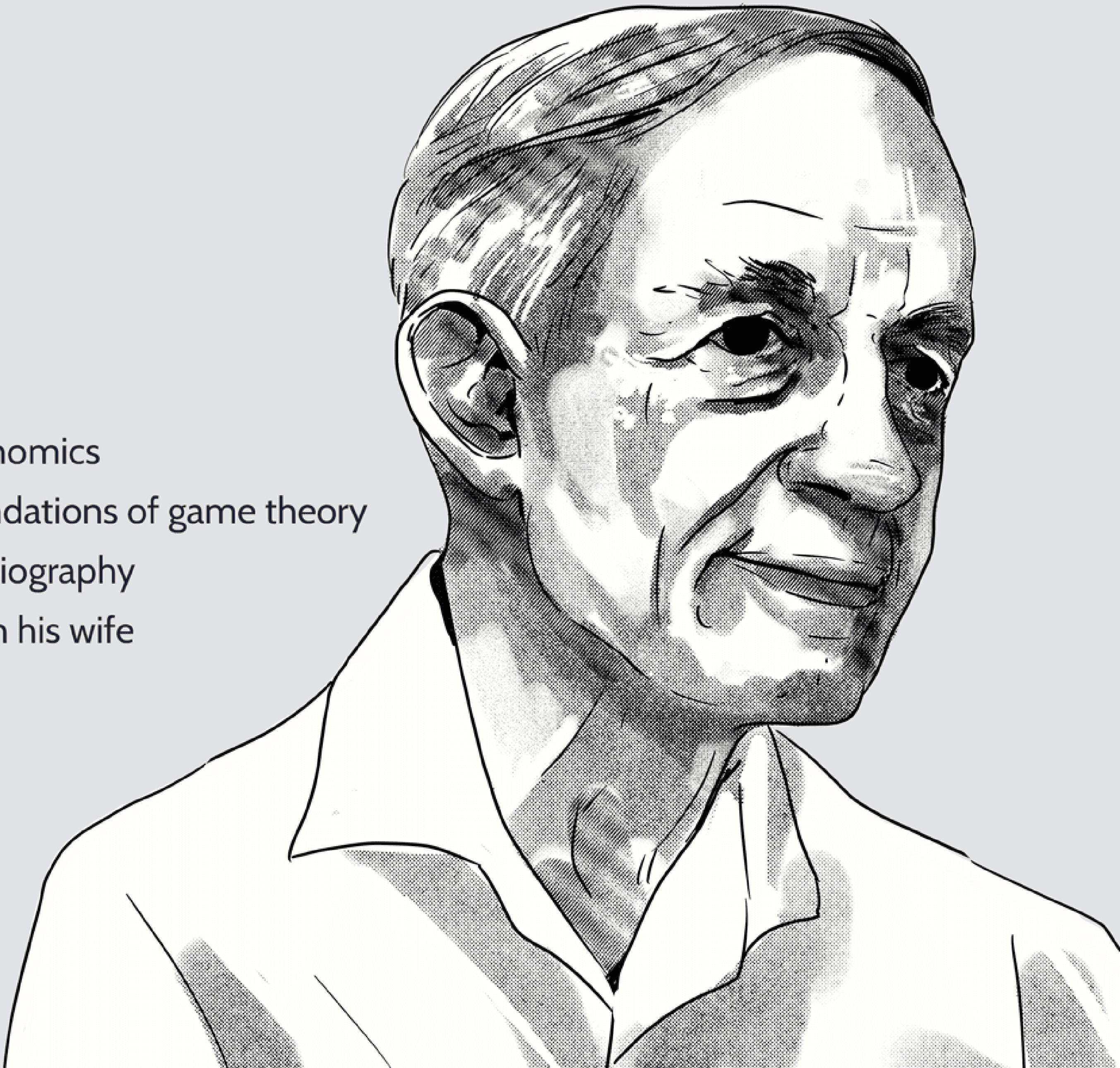
John F. Nash, Jr.

Born: June 13, 1928

Died: May 23, 2015

Mathematician

- 1994 Nobel Prize Recipient in Economics
- Developed the mathematical foundations of game theory
- *A Beautiful Life*, a film based on a biography by Sylvia Nasar, chronicles life with his wife and struggles with mental illness



Investopedia

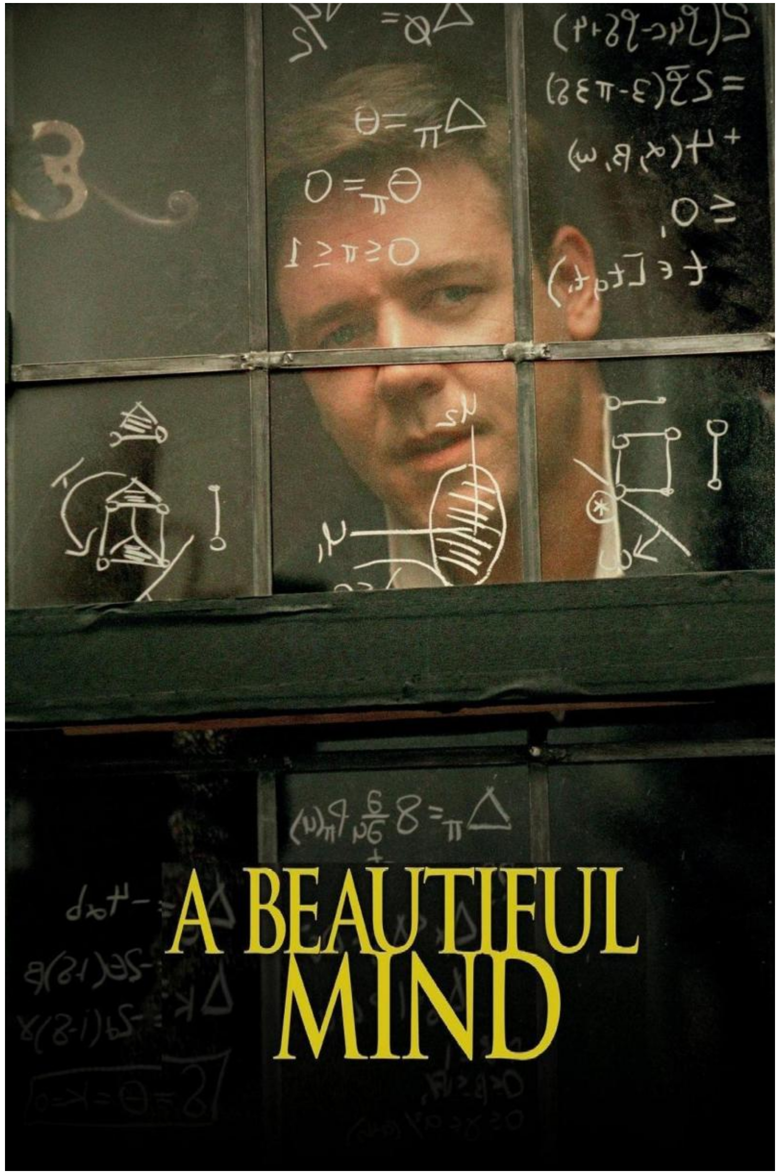

A BEAUTIFUL MIND
HE SAW THE WORLD IN A WAY NO ONE COULD HAVE IMAGINED.

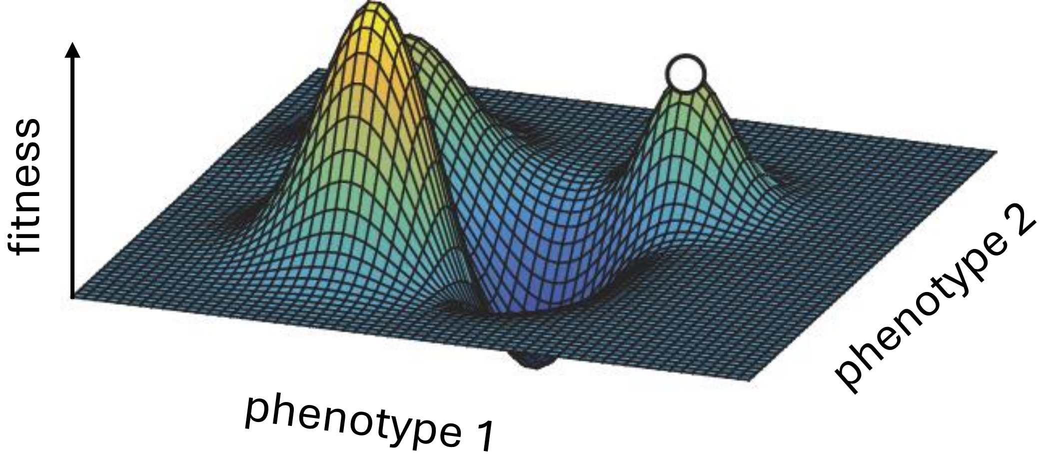
Nash equilibrium

- In many strategic situations, there exists a set of strategies where **no player can improve their outcome by changing strategy alone**.
- That point is called a **Nash equilibrium**.

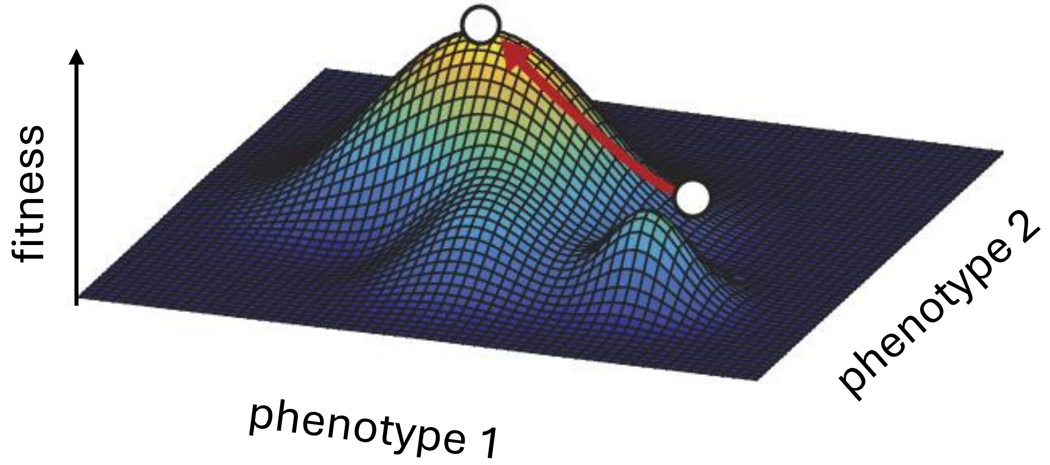
Evolutionary Game Theory

*The study of **«frequency-dependent» fitness***



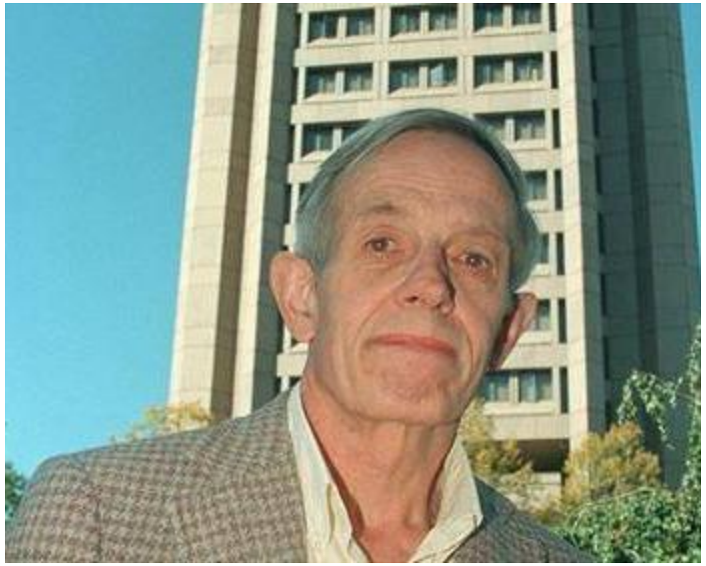


Changes in «allele» frequencies

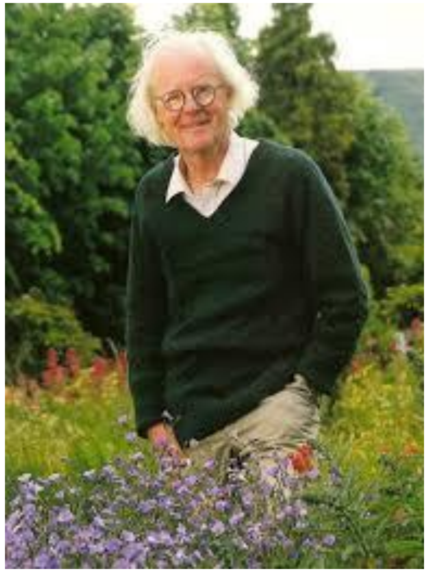


Evolutionary Game Theory

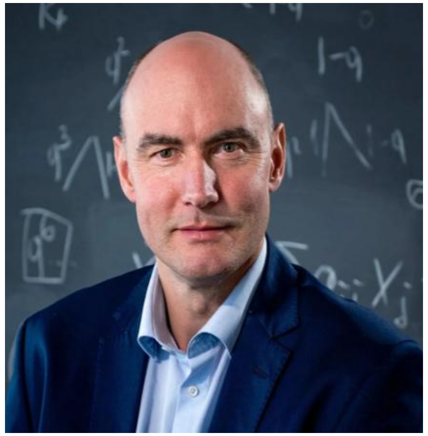
John Nash



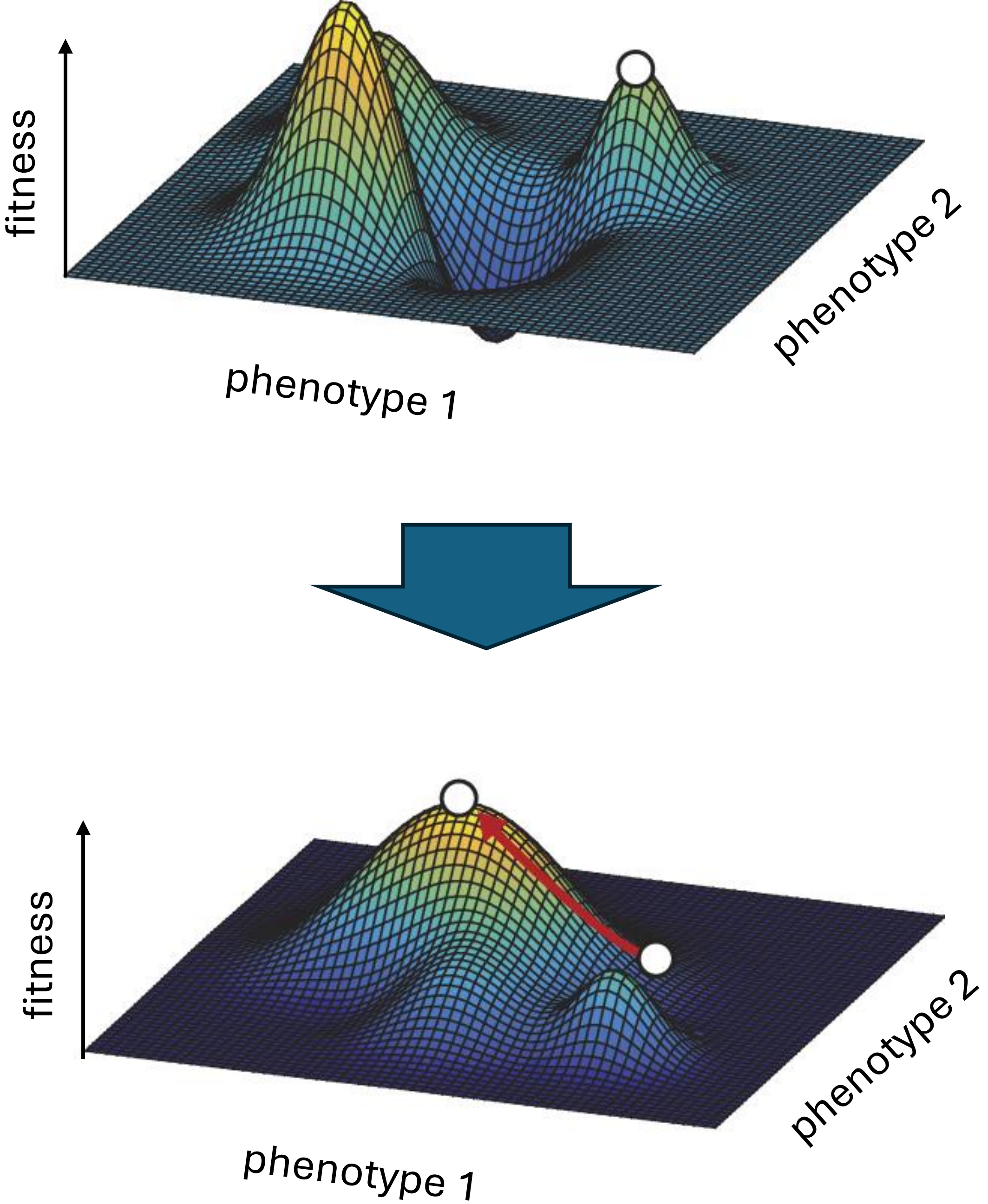
John Maynard-Smith



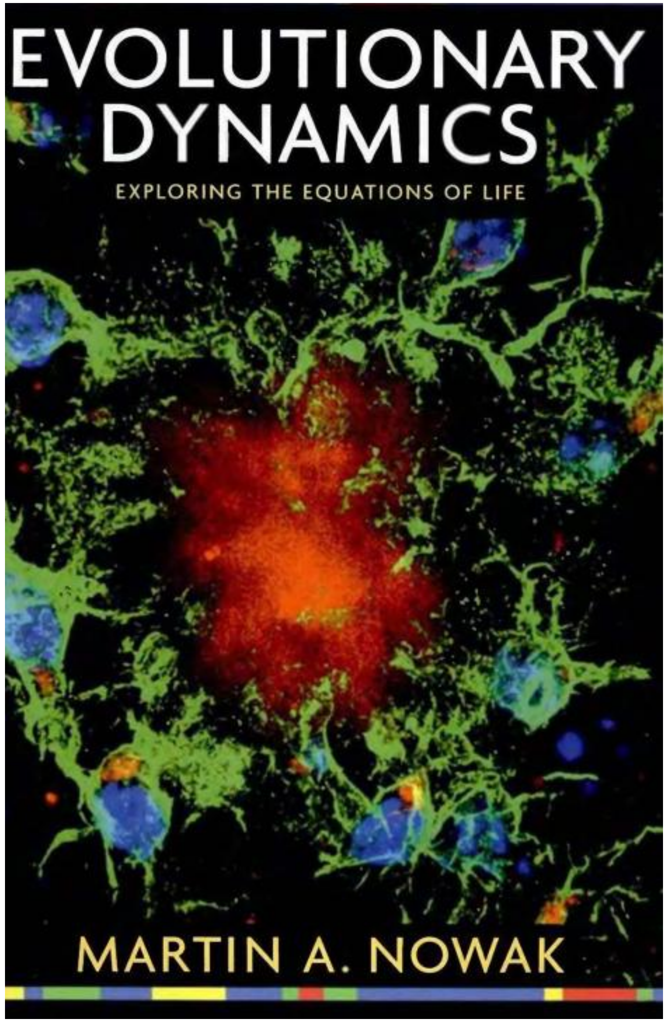
George Price



Martin Nowak



Evolutionary Game Theory



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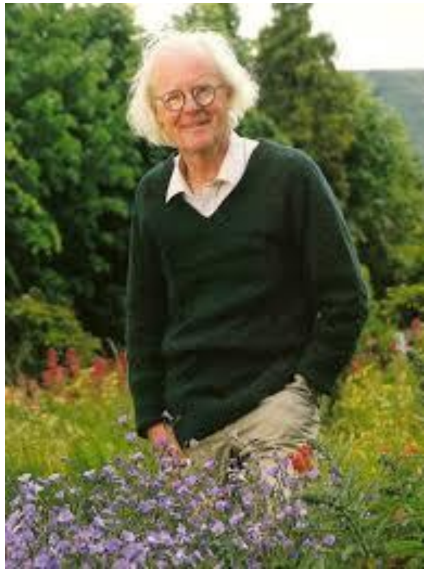

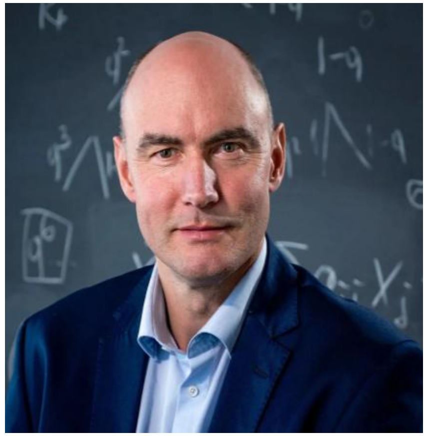

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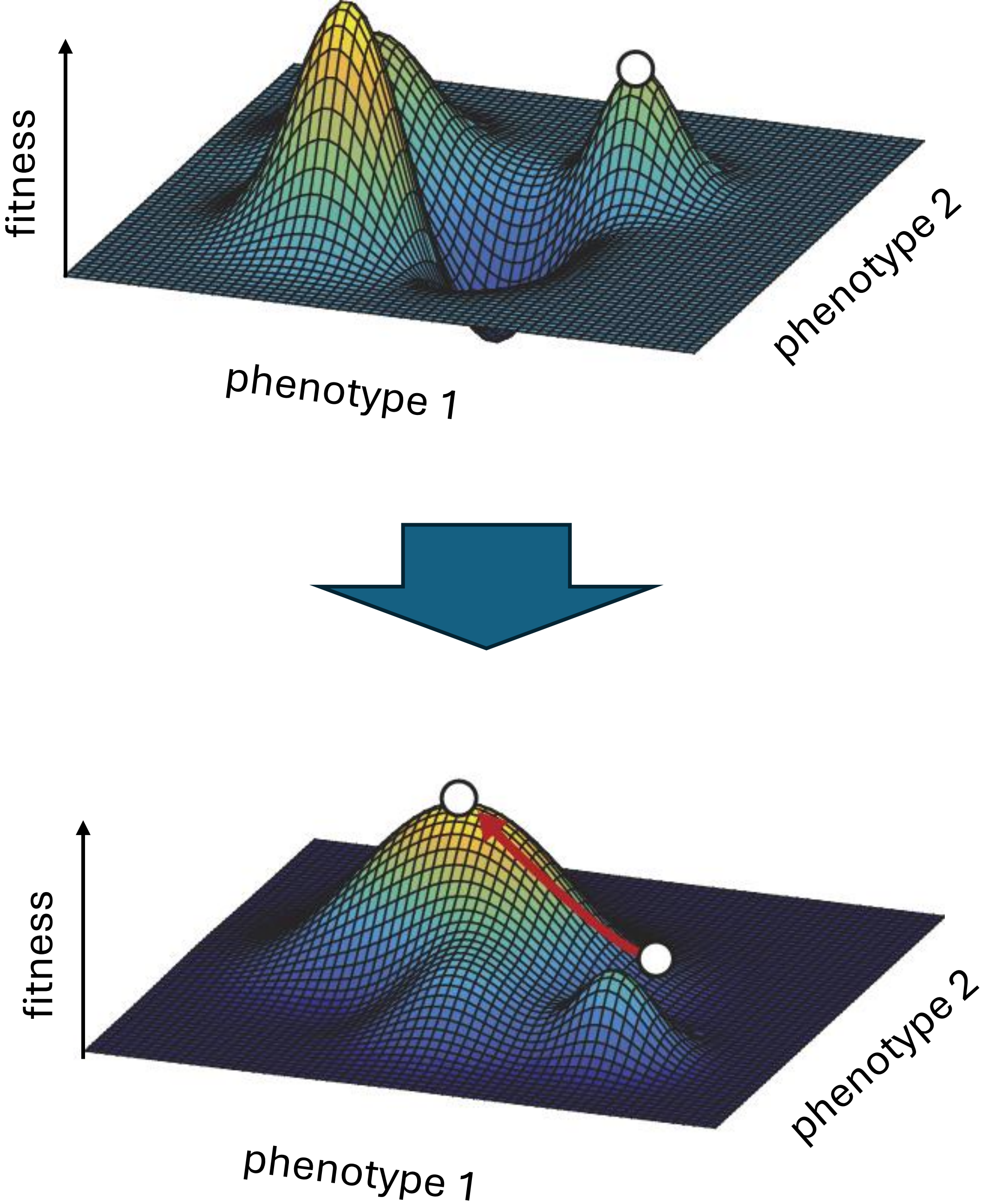
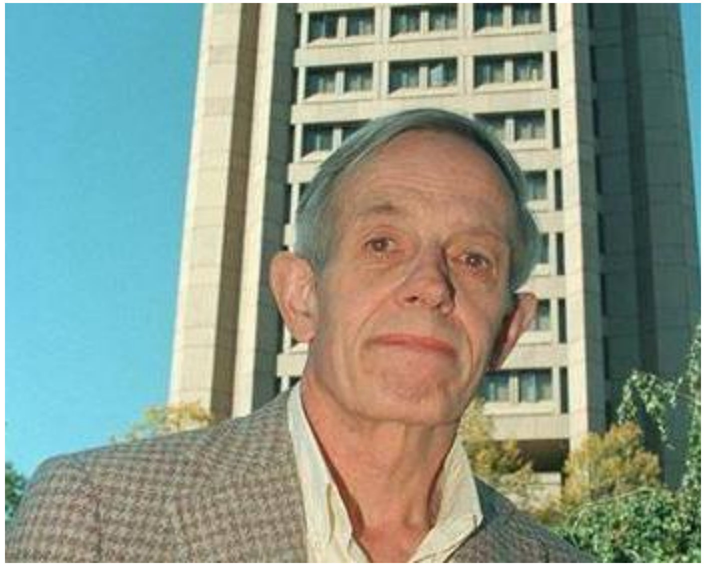


moodle

The evolution of cooperation

John Nash



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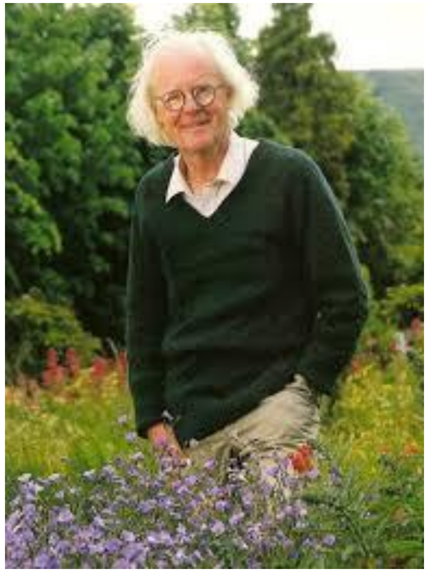
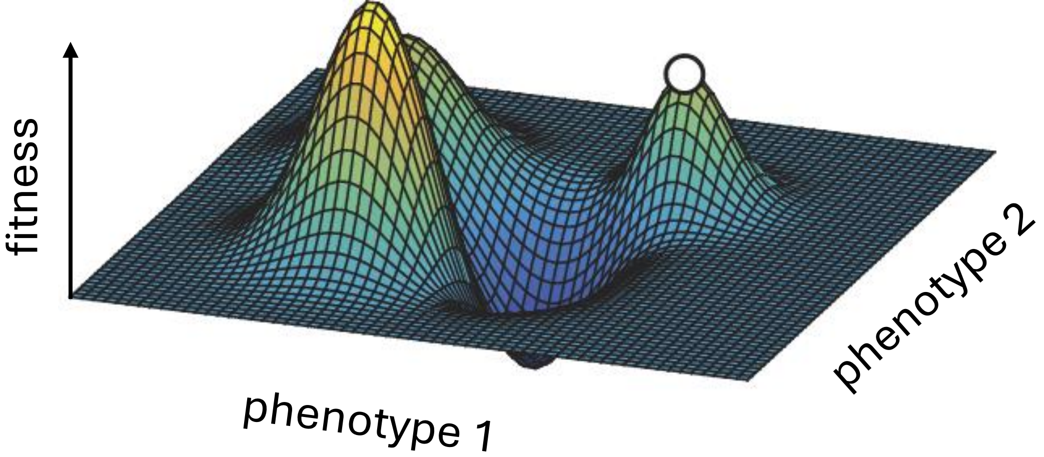
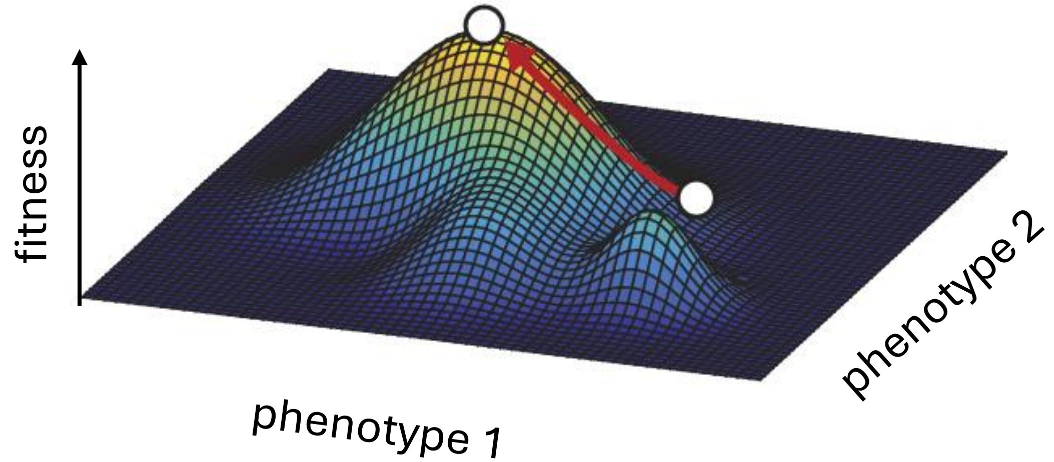


George Price

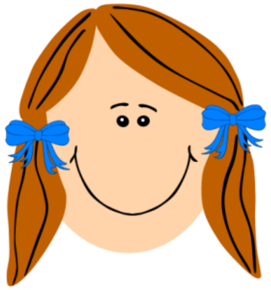
Bill Hamilton





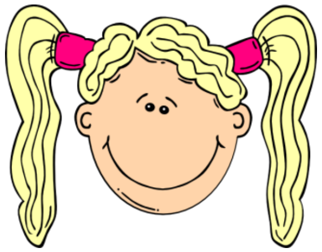
What is a game? The payoff-matrix

Right player (Bibi)



	Strategy A	Strategy B
Strategy A	5	1
Strategy B	3	2

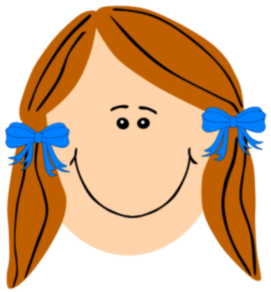
Left player (Alice)



Payoffs obtained by the left player (Alice) for each combination of strategies

What is a game? The payoff-matrix

Right player (Bibi)



	Strategy A	**Strategy B**
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Strategy B	3	2

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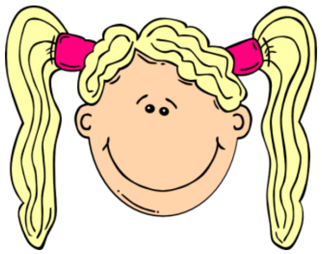
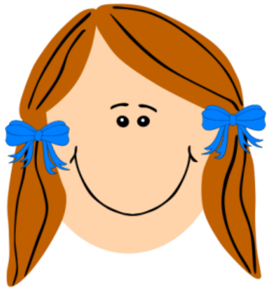


What payoff do I get if I play A and Bibi plays B?

What is a game? The payoff-matrix

Right player (Bibi)



Left player (Alice)

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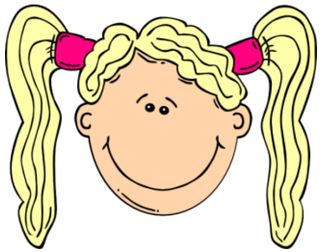
Strategy A	5	1
Strategy B	3	2



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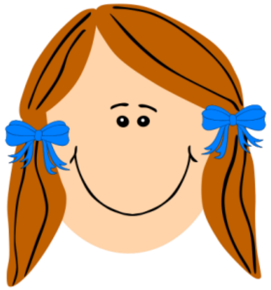

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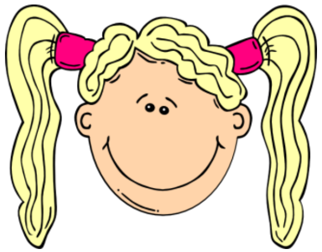
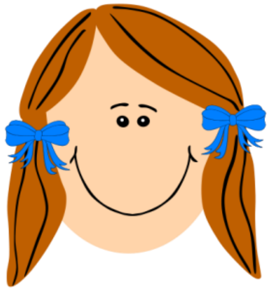


And if we both play B?

What is a game? The payoff-matrix

Right player (Bibi)



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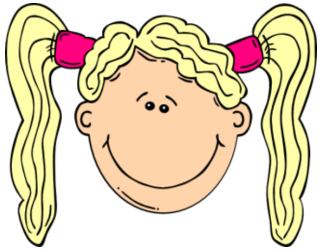

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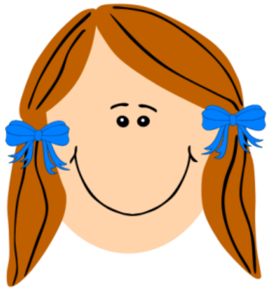

Left player (Alice)

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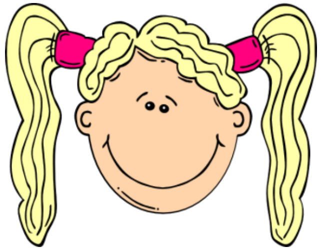
Strategy B	3	2



Last, and if I play B and she plays A?

What is a game? The payoff-matrix

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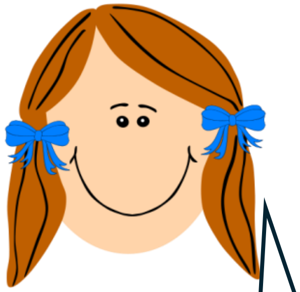
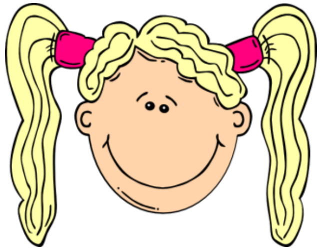


	Strategy A	Strategy B
Strategy A	5	1
Strategy B	3	2

Left player (Alice)

And what do I get in this case?



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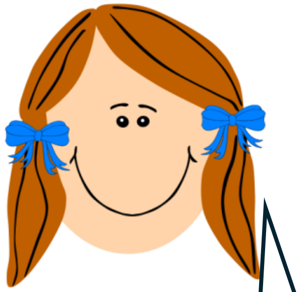

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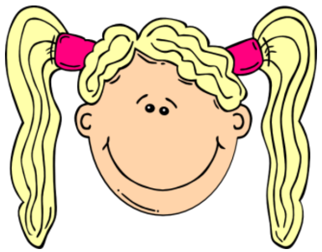
Left player (Alice)

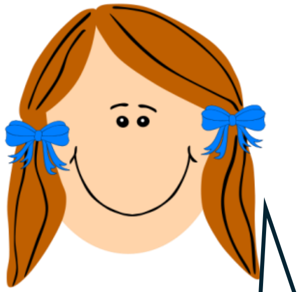


And what do I get in this case?

Last, and if I play B and she plays A?

Sometimes you might see payoff matrices written like this too

..perhaps it is clearer but redundant when players are symmetric

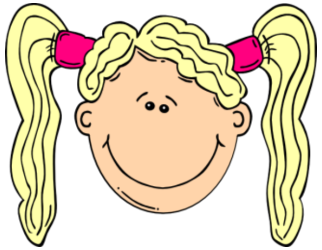


Right player (Bibi)

Left player (Alice)

	Strategy A	**Strategy B**
Strategy A	5,5	1,3
Strategy B	3,1	2,2

And what do I get in this case?



Last, and if I play B and she plays A?

The evolution of aggressiveness


01565647 © Klein & Hubert / naturepl.com

«The game of (red) deers» or «The game of testosterone»

	Fight	**Back down**
Fight	-1	4
Back down	0	2

«The game of (red) deers» or «The game of testosterone»

	Fight	Back down
Fight	-1 risk 	4 
Back down	0 	2 

«The game of (red) deers» or «The game of testosterone»

- Ten rounds of game.
- At each round each of you will choose a random partner
- Write down the payoffs!
- Winner gets special mention and chocolate. Loser does not reproduce.

	Fight	**Back down**
Fight	-1 risk 	4 
Back down	0 	2 

Results of the «testosterone game»

- How much did you score?

Results of the «testosterone game»

- How much did you score?

- What strategy did you use in the first round?

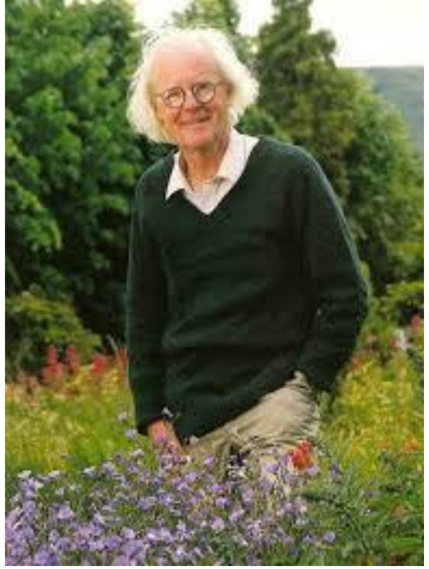
Results of the «testosterone game»

- How much did you score?

- What strategy did you use in the first round?

- What strategy did you use at the end?

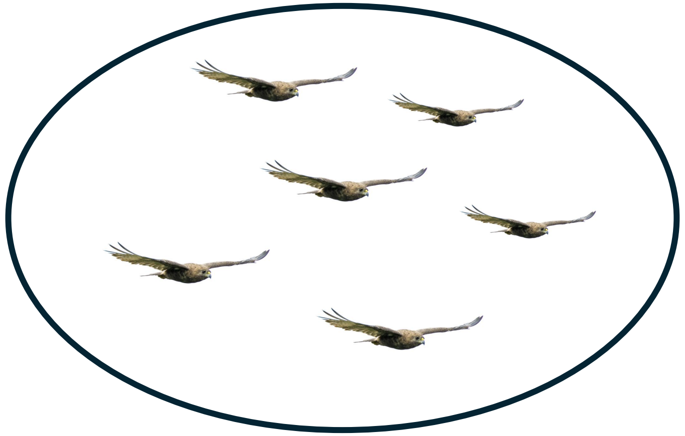
The game we just played is famous as «Hawks vs Doves»



John Maynard-Smith
(1920-2004)

	Hawk	**Dove**
Hawk	-1	4
Dove	0	2

What happens if everybody fights/is a Hawk?



If we play  then we get: **?**

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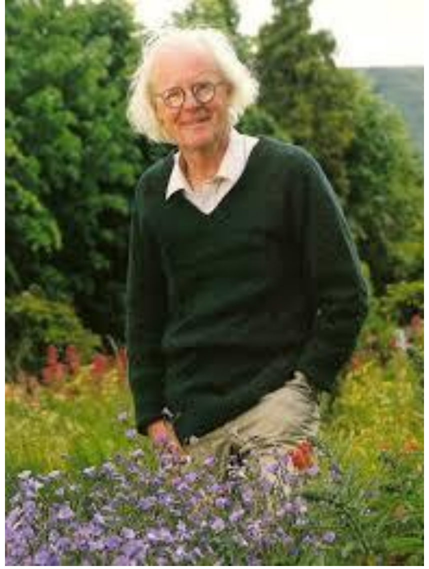

John Maynard-Smith
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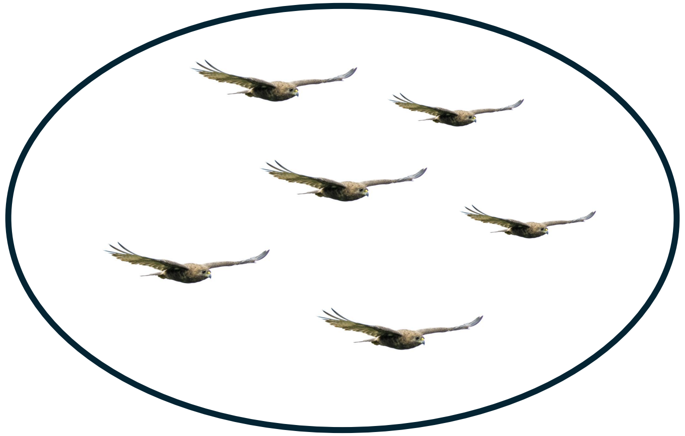
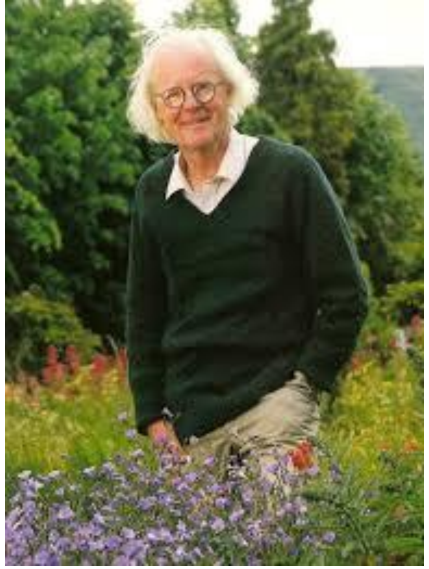


If we play  then we get: **-1**

If we play  then we get: **0**

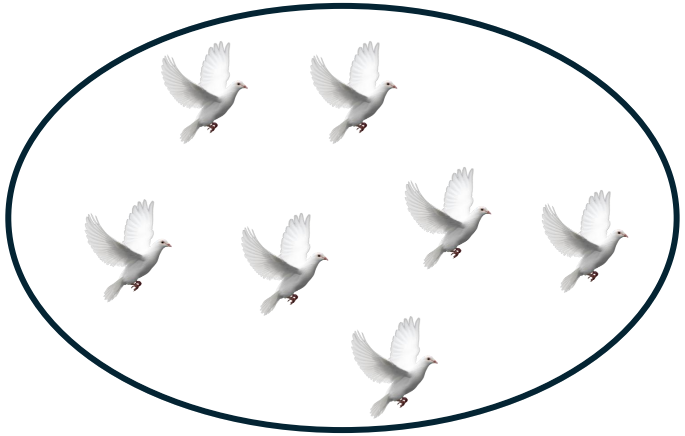
Better being a **dove**!



John Maynard-Smith
(1920-2004)

	Hawk	**Dove**
Hawk	-1	4
Dove	0	2

What happens if everybody is a dove?



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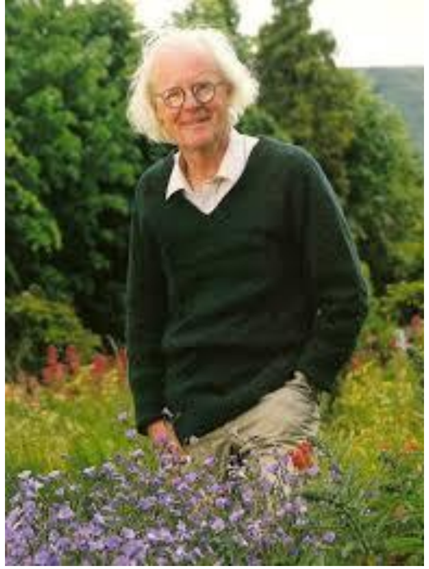

John Maynard-Smith
(1920-2004)




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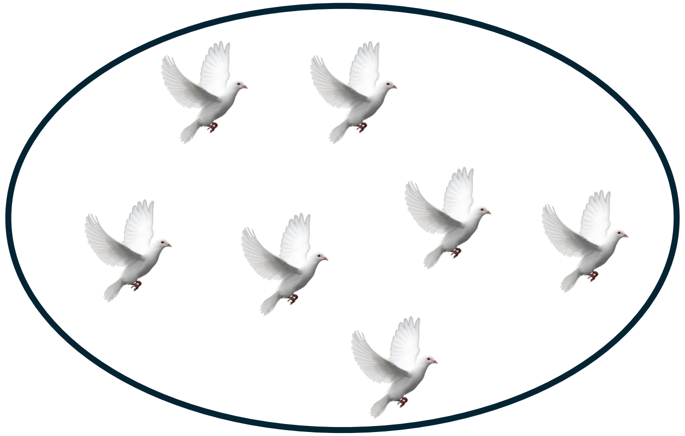
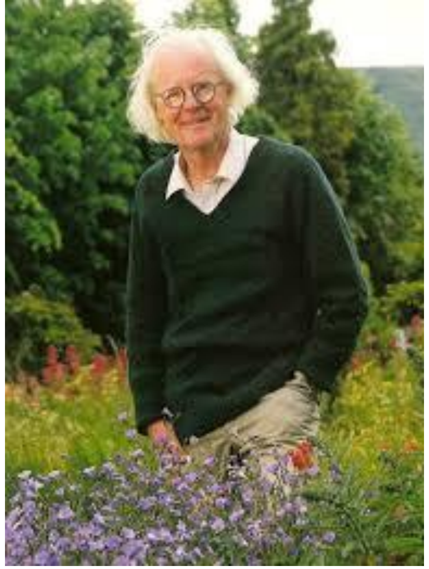
What happens if everybody is a dove?



If we play  then we get: **4**

If we play  then we get: **2**

Better being a **hawk**!



John Maynard-Smith
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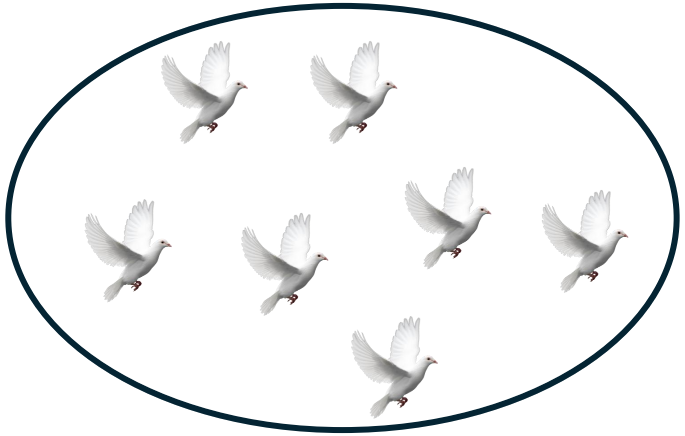

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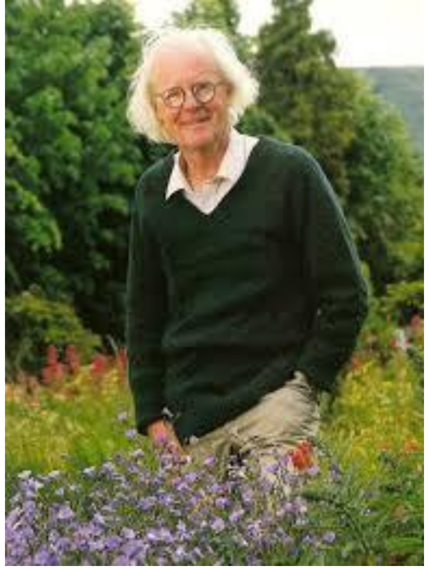


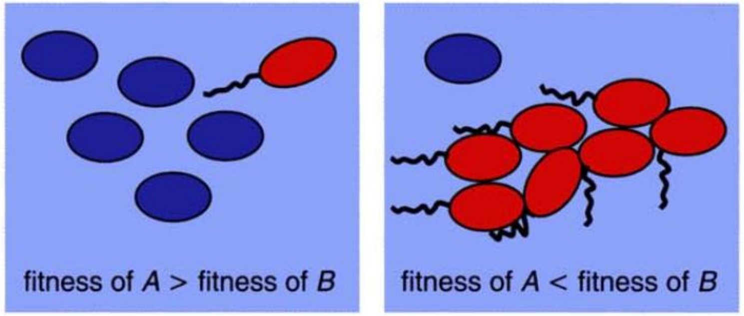
John Maynard-Smith
(1920-2004)

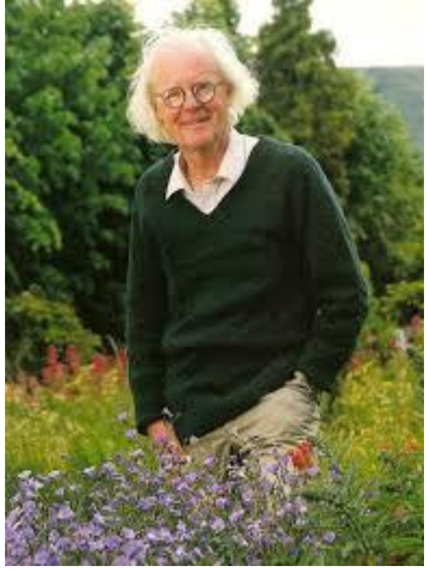
	Hawk	**Dove**
Hawk	-1	4
Dove	0	2

It is not always best to be aggressive or shy! It depends on who is around!

Constant selection:

Frequency-dependent selection:



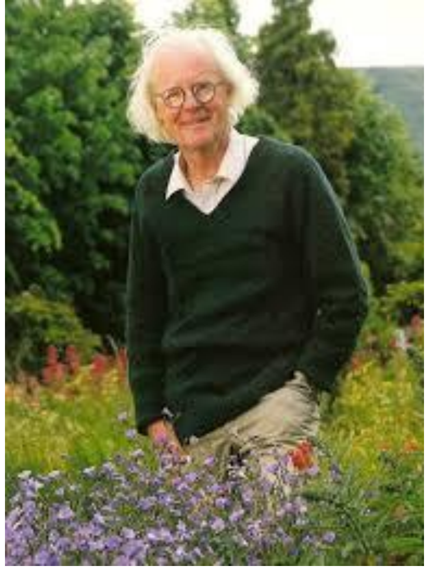


John Maynard-Smith
(1920-2004)




	Hawk	Dove
Hawk	-1	4
Dove	0	2

So what strategy should one choose?



John Maynard-Smith
(1920-2004)




	Hawk	Dove
Hawk	-1	4
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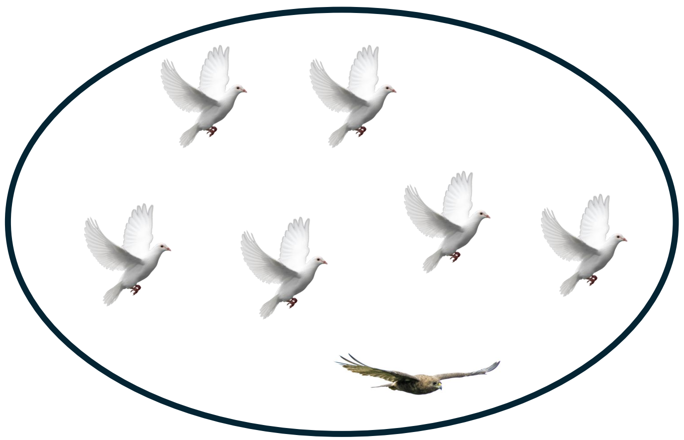
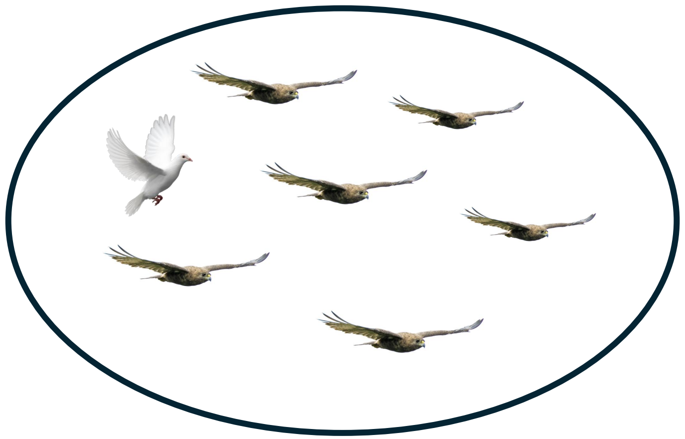
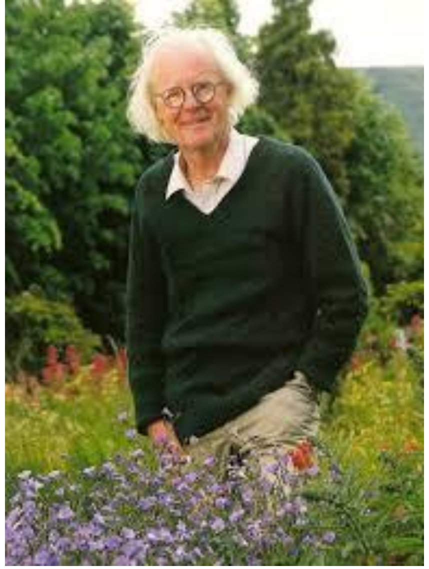
Mixed strategies







John Maynard-Smith
(1920-2004)

Since a «Hawk» mutant will always spread/invade a population of Doves and a «Dove» mutant will always spread/invade a population of Hawks let's explore **«Mixed strategies»** in which an individual play Hawk with a probability p (Dove with probability 1-p)

Pure strategies: always  or 

Mixed strategies: *p*  and *1-p* 

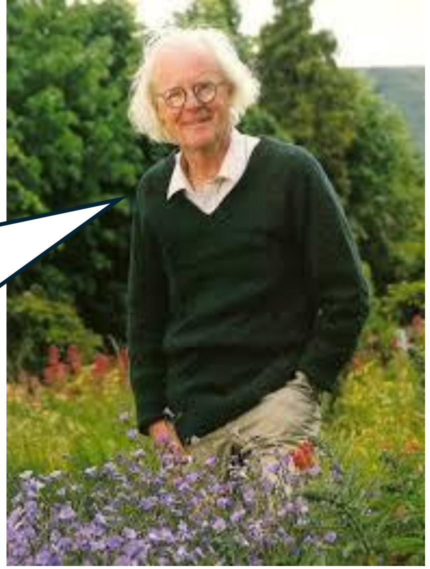
 

	Hawk	Dove
Hawk	-1	4
Dove	0	2

Mixed strategies

What other famous game do you know where mixed strategies are convenient?



John Maynard-Smith (1920-2004)

Pure strategies: always  or 

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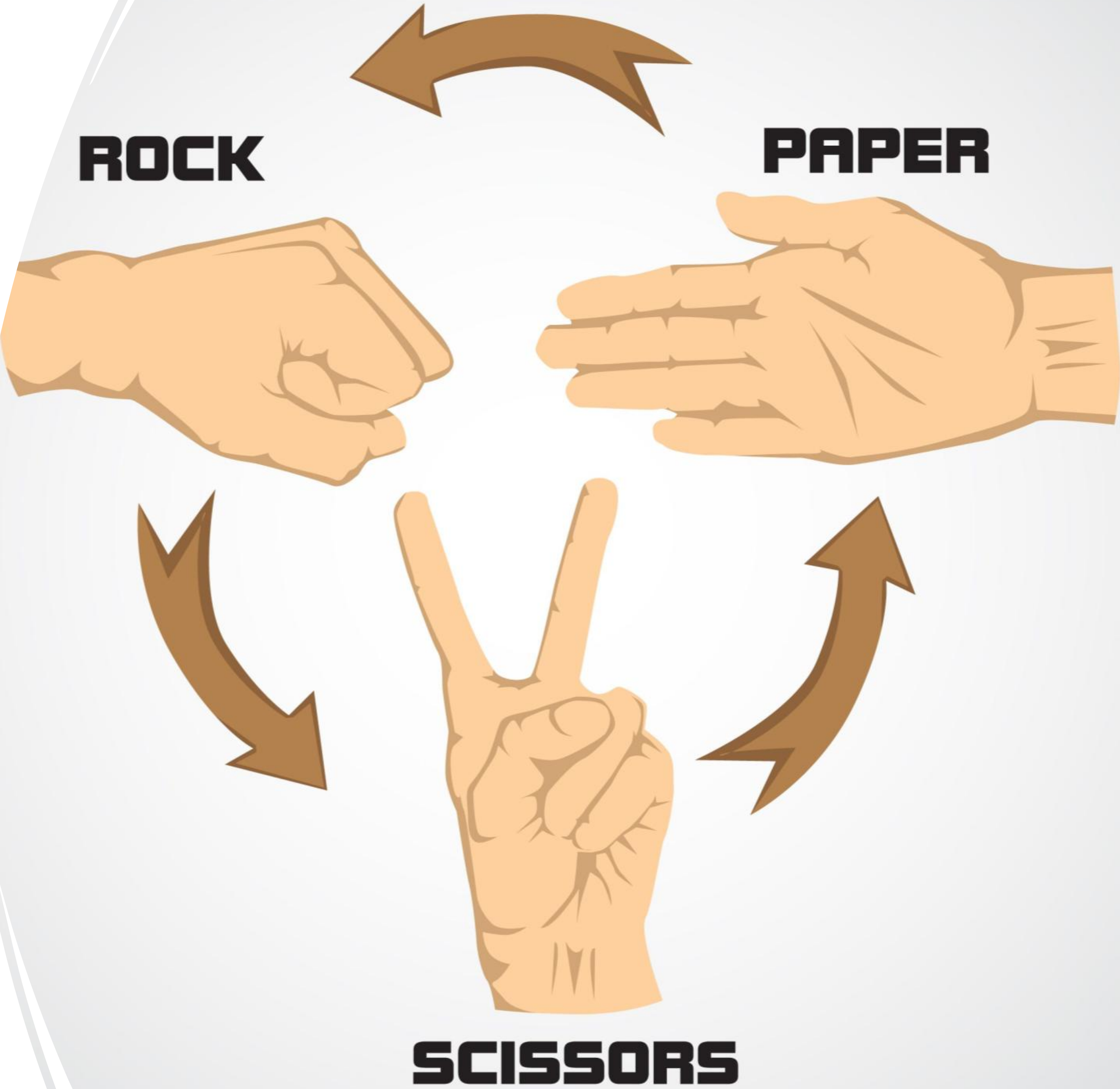
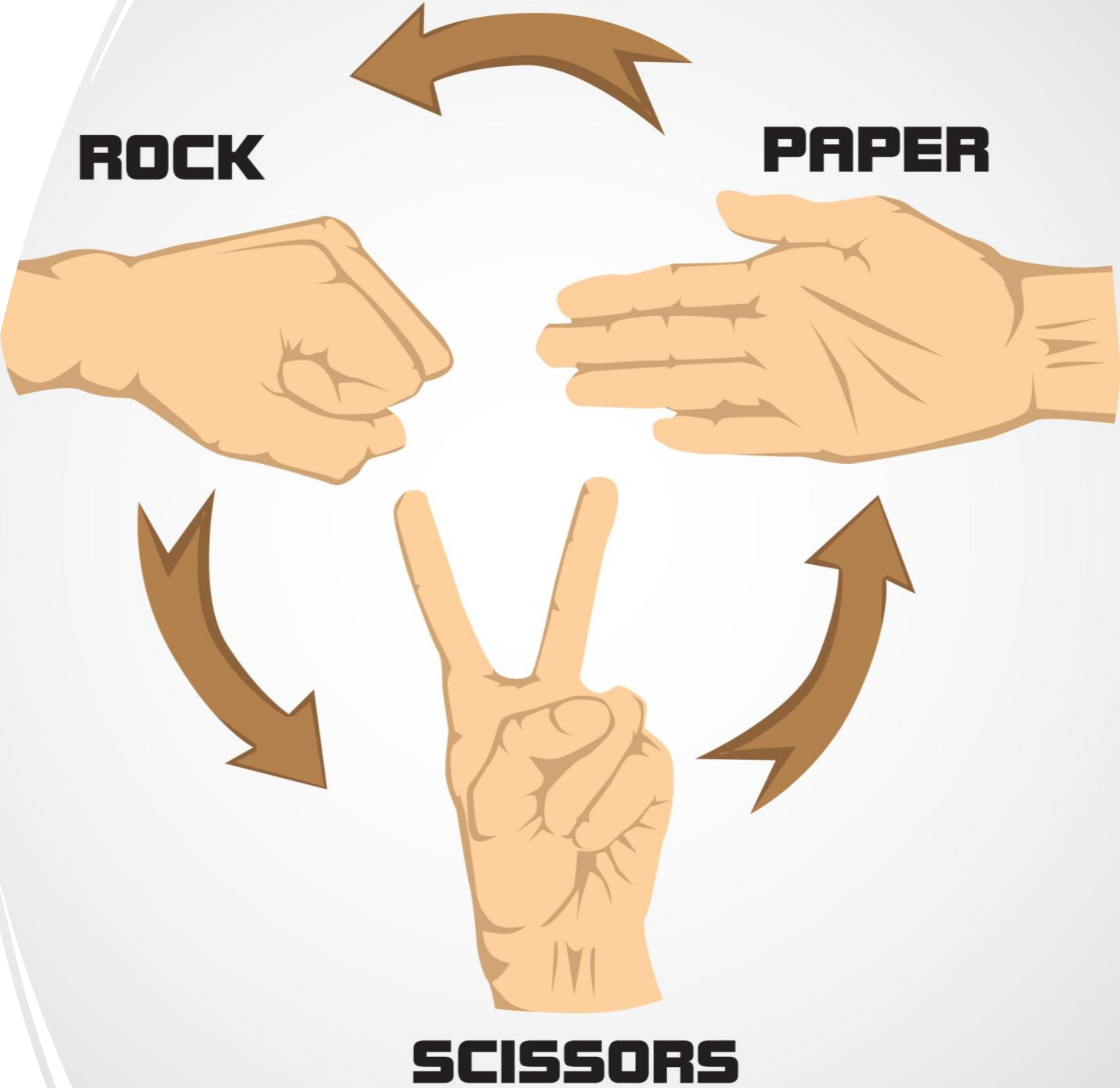
What is the payoff matrix?



What is the payoff matrix?

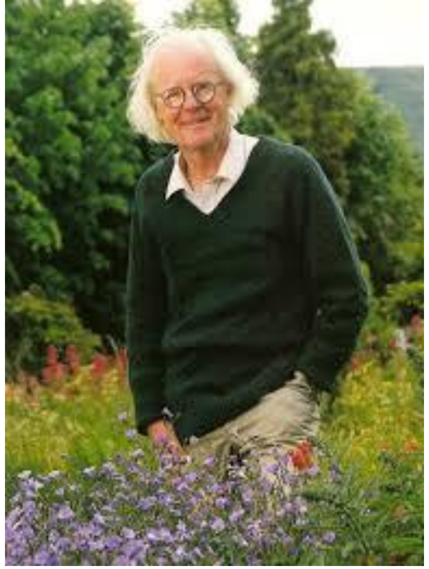
Gains of Player 1		Player 2 chooses...		
				
Player 1 chooses...		0	-1	1
		1	0	-1
		-1	1	0



Let’s look at how the fitness (*W*) of Hawks and Doves change with the frequencies of Hawks (*p*)

$W_H =$?

$W_D =$?



John Maynard-Smith (1920-2004)

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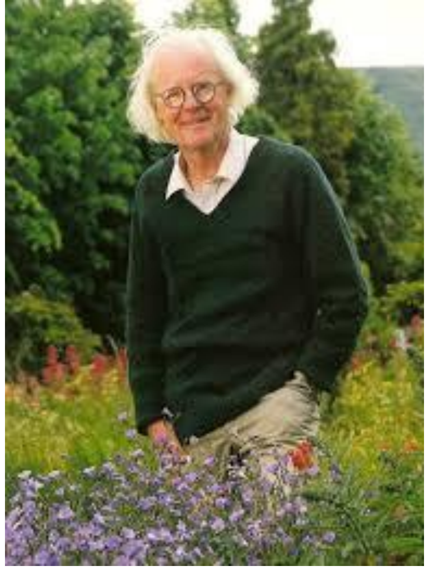

John Maynard-Smith
(1920-2004)

$$W_H = (-1)*p + 4*(1-p) = 4-5p$$

$$W_D = 0*p + 2*(1-p) = 2-2p$$

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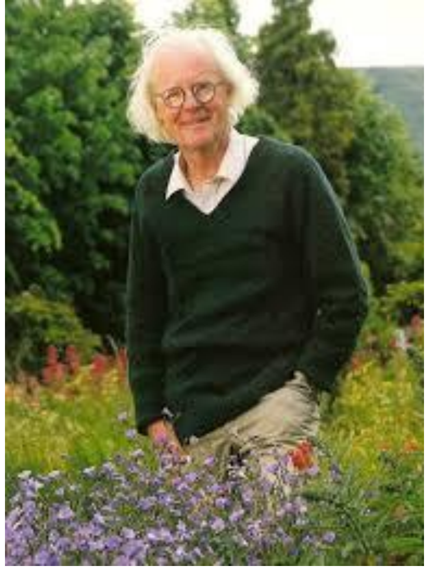

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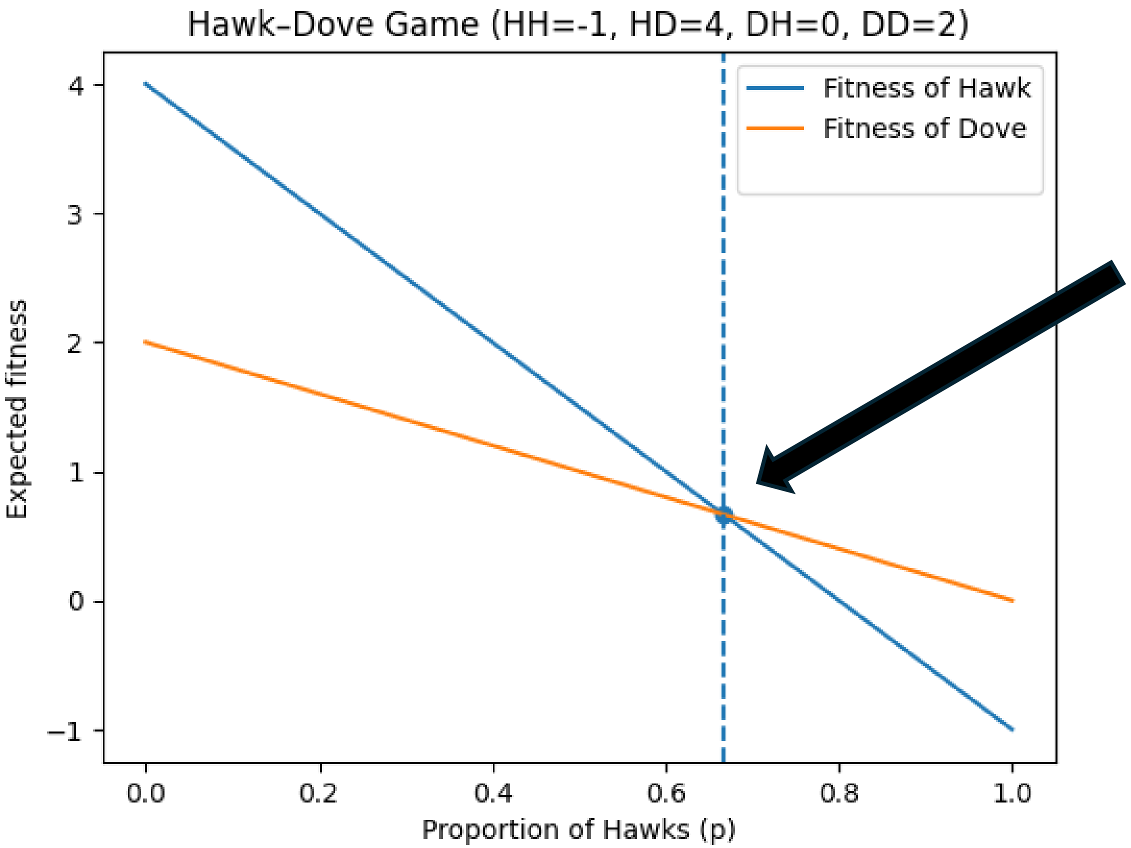

What is this point?




	Hawk	Dove
Hawk	-1	4
Dove	0	2

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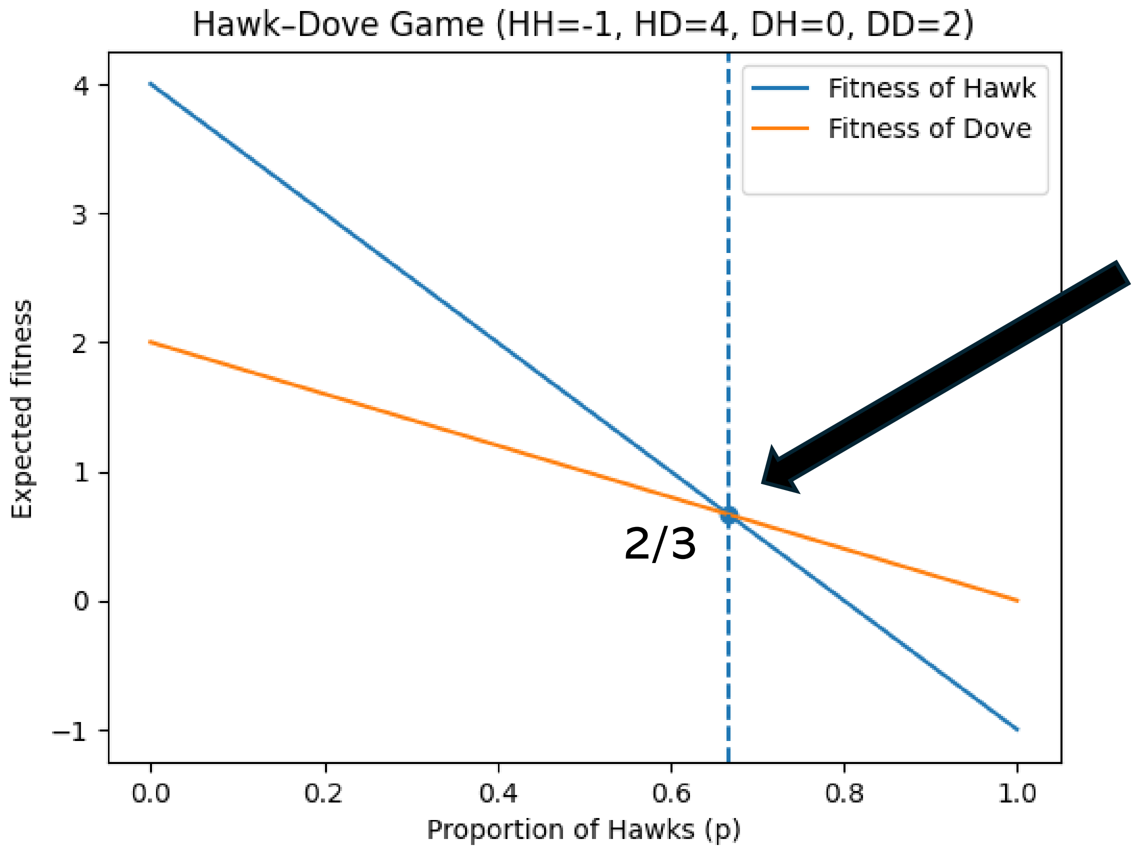
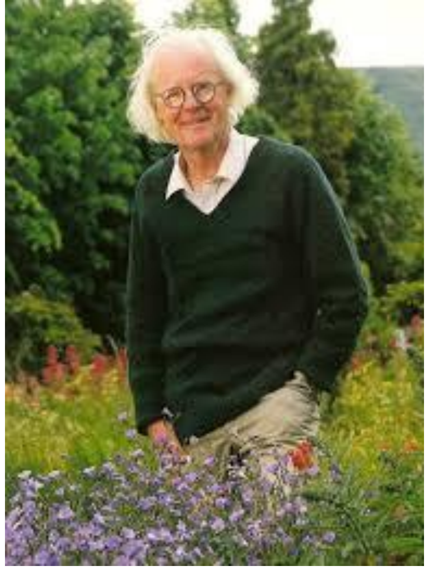




John Maynard-Smith (1920-2004)

What is this point?

$W_H = W_D$

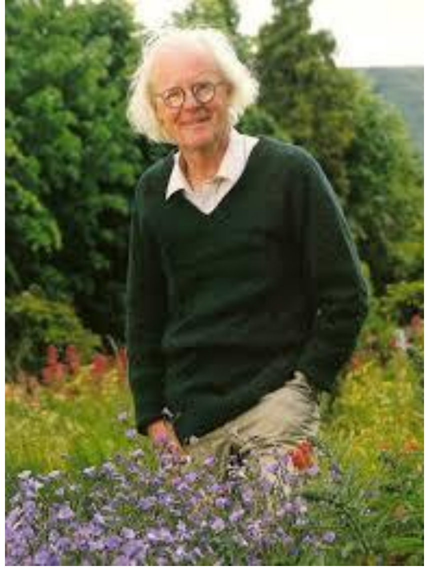
$4-5p = 2-2p$

$p^* = 2/3$



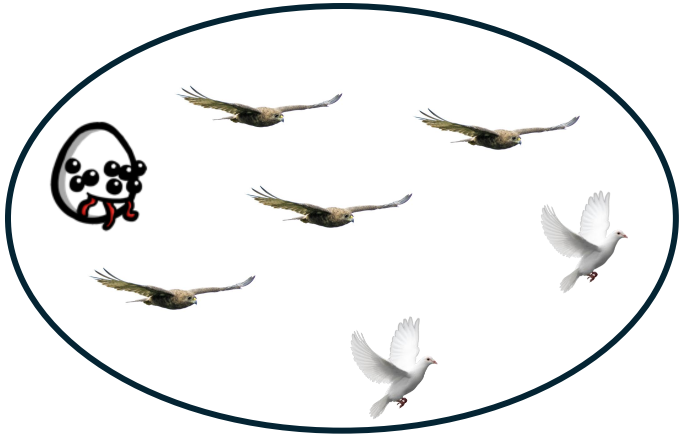

	Hawk	Dove
Hawk	-1	4
Dove	0	2

An **Evolutionarily Stable Strategy (ESS)** is a strategy that, if adopted by almost all individuals, cannot be invaded by a rare alternative strategy.



John Maynard-Smith
(1920-2004)

Let's think in our case of a **rare mutant** playing ***q*** times Hawk in a population with 2/3 Hawks and 1/3 Doves.



The **fitness of the mutant** will be

$E(q,p)=q*W_H+ (1-q)*W_D$

Mutant 

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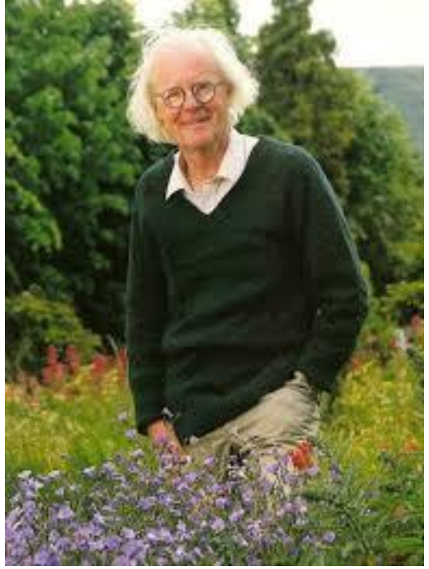

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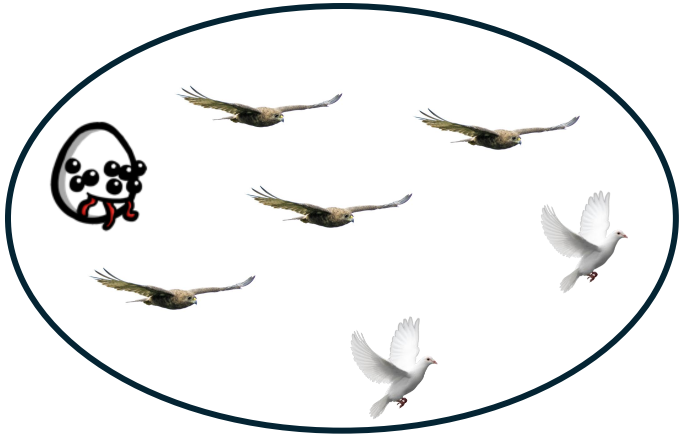
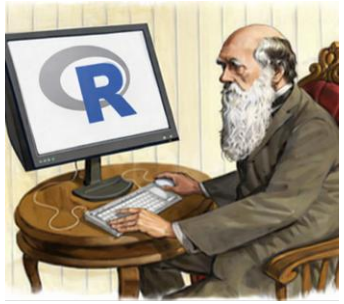


The **fitness of the mutant** will be

$E(q,p)=q*W_H+(1-q)*W_D$

Mutant 

```
p <- 2/3
W_H <- p*(-1) + (1-p)*4        #fitness Hawks
W_D <- p*0 + (1-p)*2           #fitness Doves
W_q <- q*W_H + (1-q)*W_D       #fitness mutant
```



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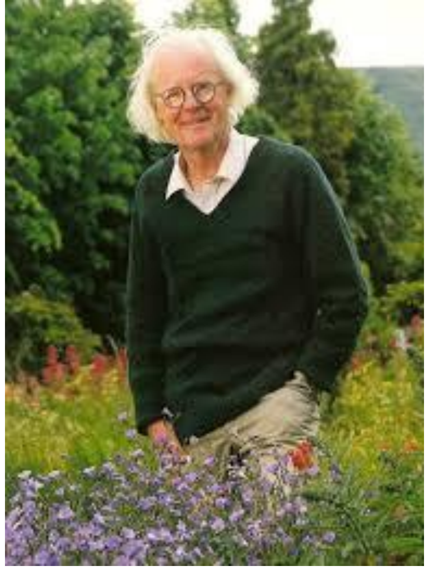

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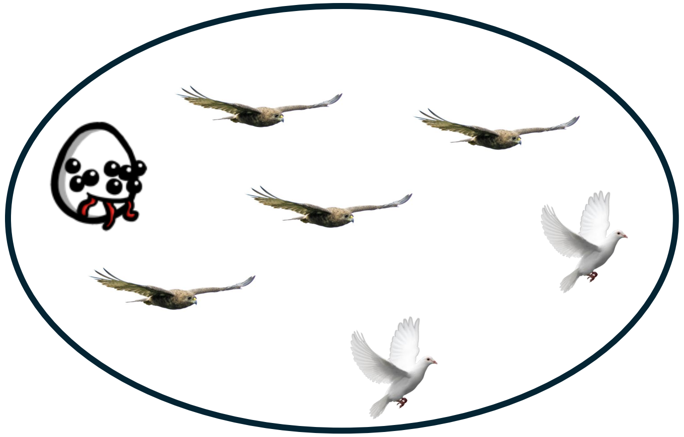

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Mutant

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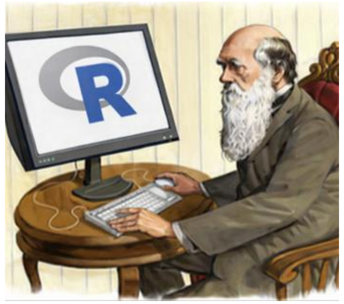
W_D <- p*0 + (1-p)*2           #fitness Doves
W_q <- q*W_H + (1-q)*W_D       #fitness mutant
plot(q, W_q, type="l", lwd=2,
     xlab="Probability mutant plays Hawk (q)",
     ylab="Expected fitness",
     main="Fitness of mutant strategy vs ESS population")
abline(h=W_H, lty=2)
```



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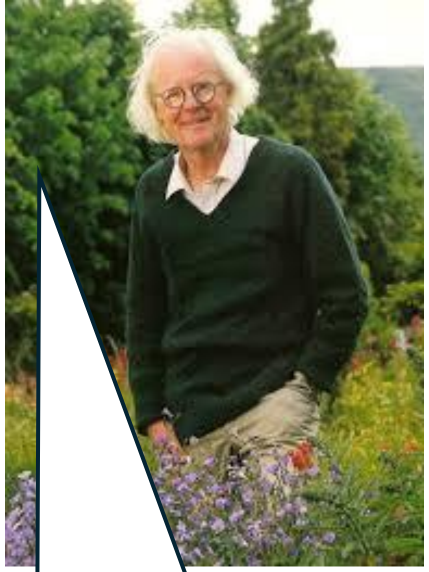

Jo nard-Smith
2004)

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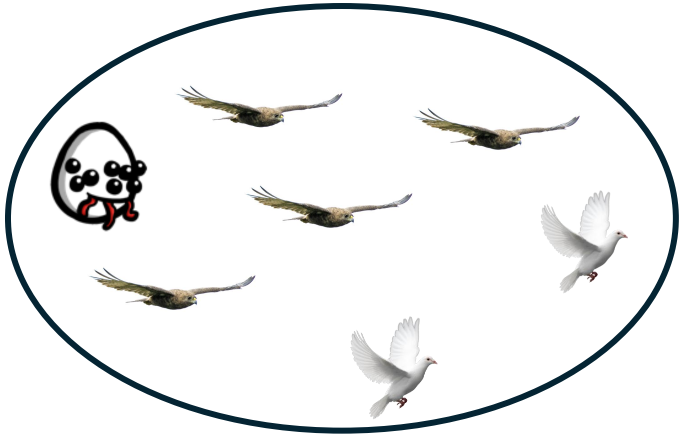
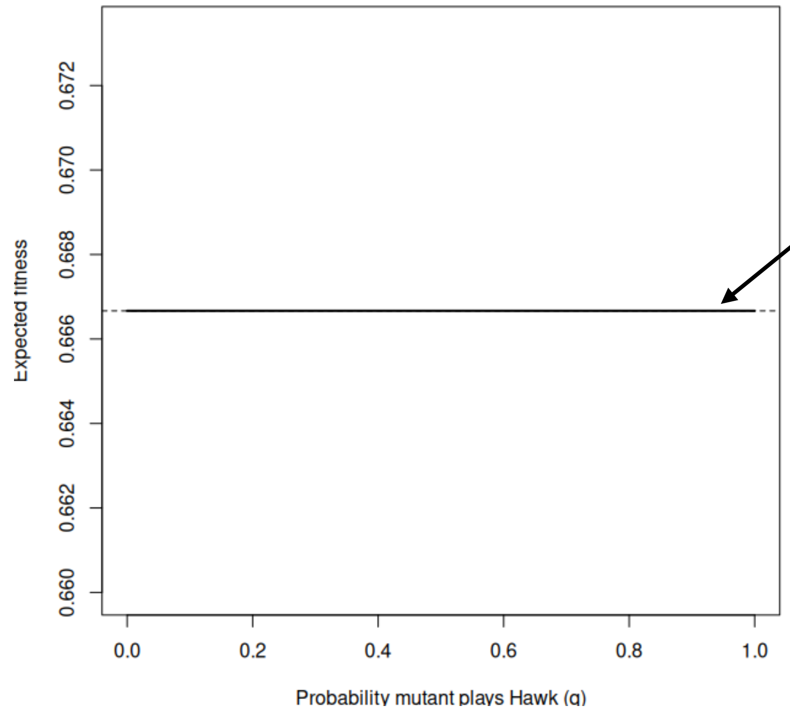


Mutant 

The **fitness of the mutant** will be
$E(q,p) = q^*W_H + (1-q)^*W_D$



Any rare mutant will not get a higher fitness in the population at the ESS. At most the same!

First condition for an ESS:
$E(p^*,p^*) \geq E(q,p^*)$

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Hawk	-1	4
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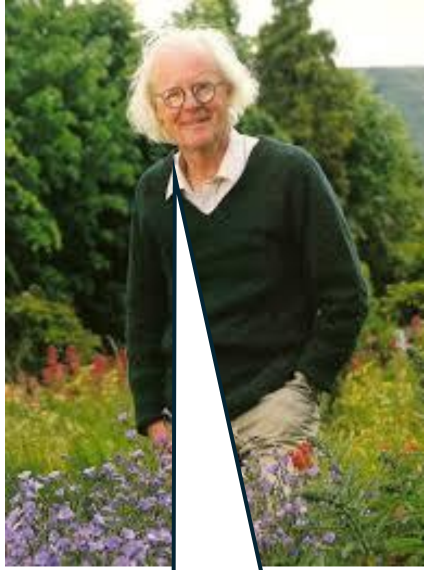
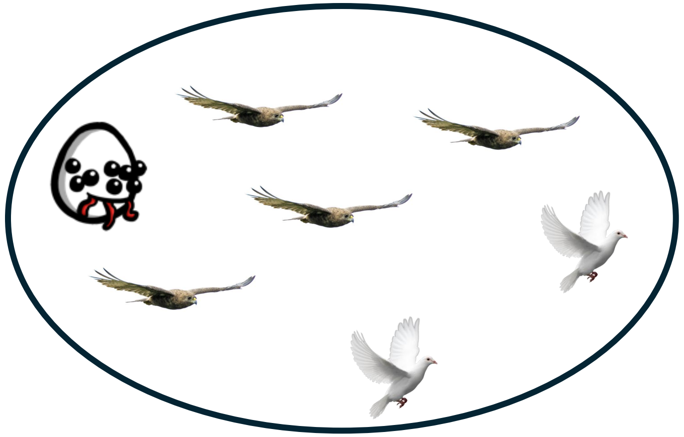


John Ma d-Smith
(192 04)

Are we sure then that $p^{*}=2/3$ is an ESS?

Let's think in our case of a **rare mutant** playing ***q*** times Hawk in a population with 2/3 Hawks and 1/3 Doves.



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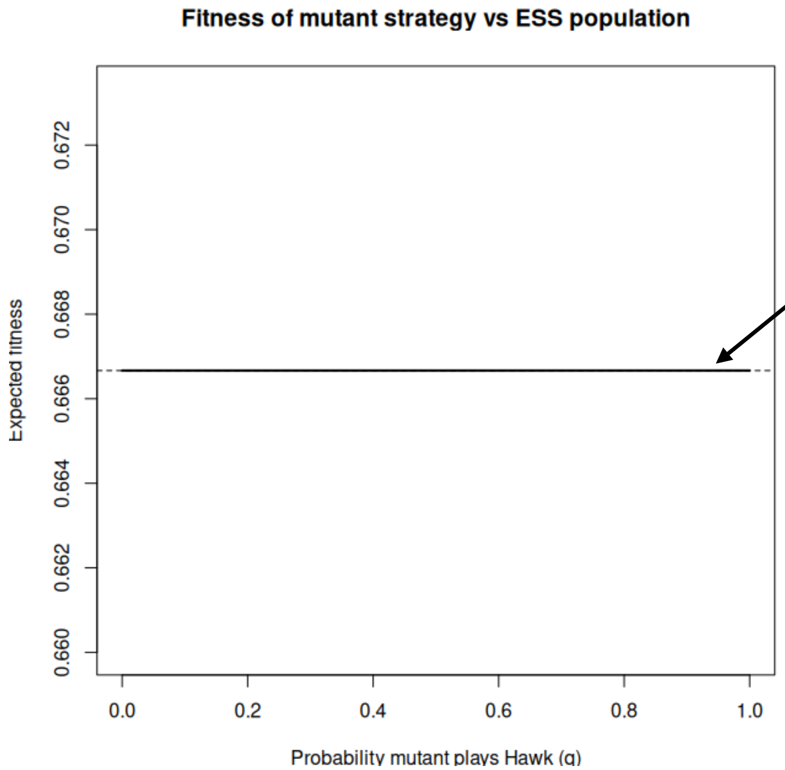

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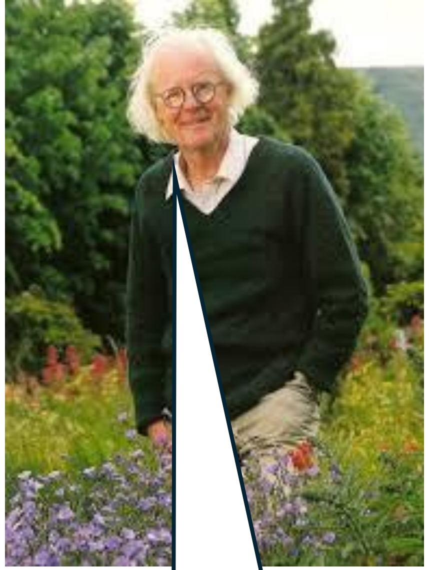
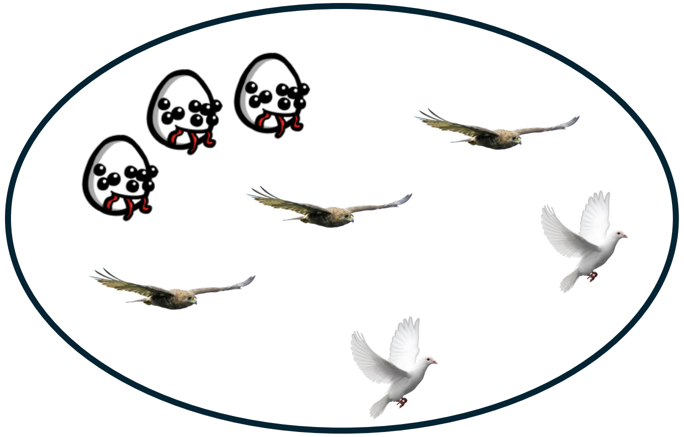


John Ma d-Smith
(192 04)

It could still initially spread in the population by chance!

Let's think in our case of a **rare mutant** playing ***q*** times Hawk in a population with 2/3 Hawks and 1/3 Doves.



Mutant

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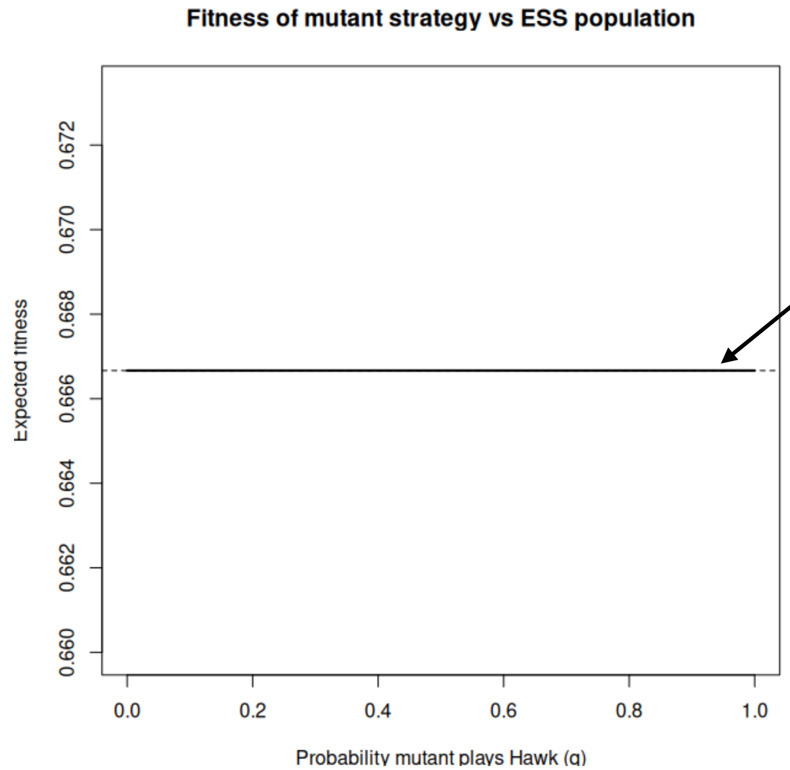

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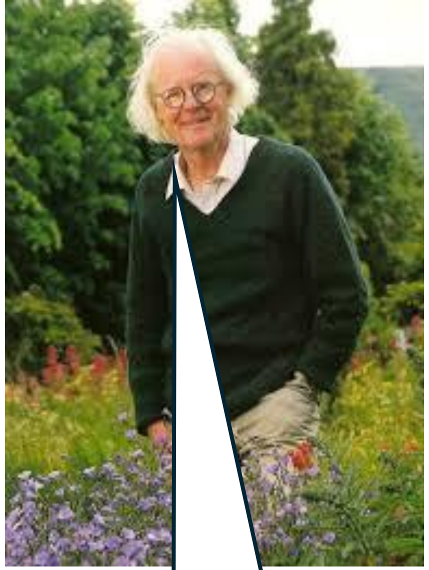
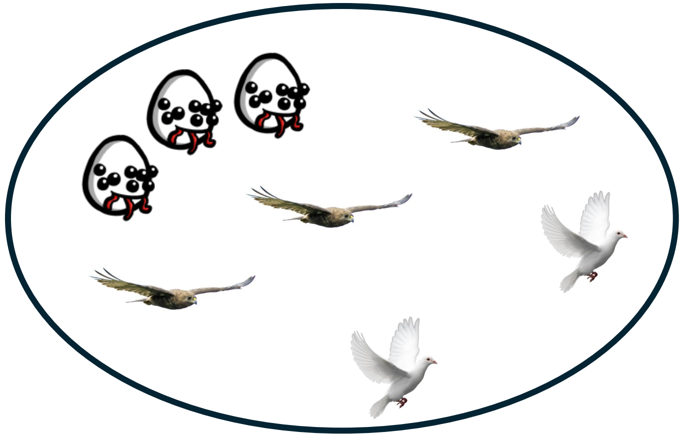


John Ma d-Smith
(192 04)

How can we verify that it doesn't?



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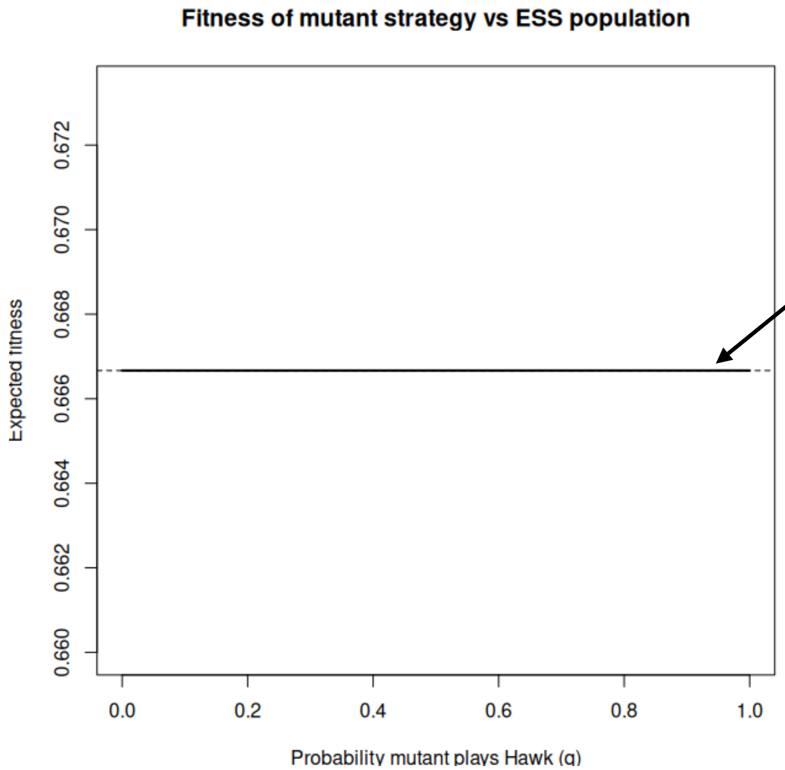

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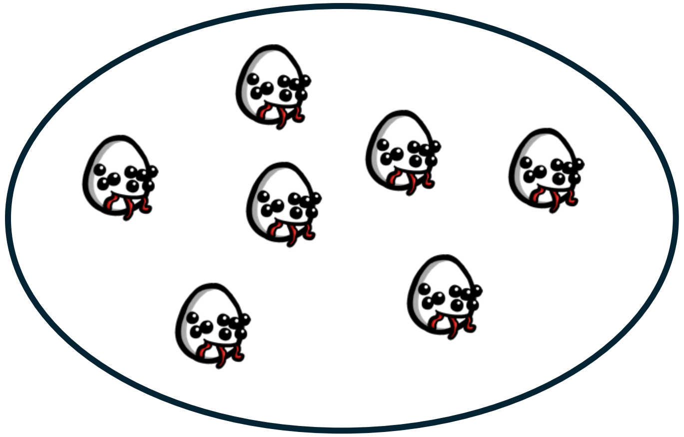
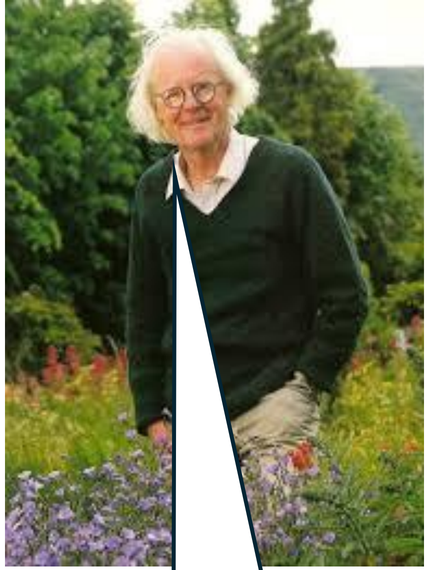
An **Evolutionarily Stable Strategy (ESS)** is a strategy that, if adopted by almost all individuals, cannot be invaded by a rare alternative strategy.

Let's calculate what happens when **almost all individuals are mutants**, and let's calculate the **fitness of the mutant** E(q,q) and that of our focal strategy **p***, E(**p***,q).



Mutant



John Ma d-Smith
(192 04)

Let's check that the mutant cannot become common!

	Hawk	Dove
Hawk	-1	4
Dove	0	2

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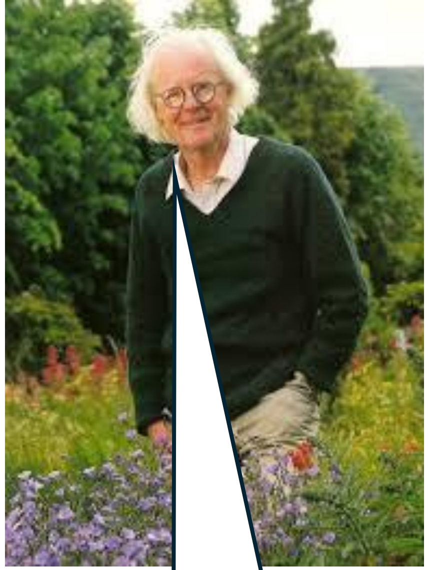

John Ma d-Smith
(192 04)

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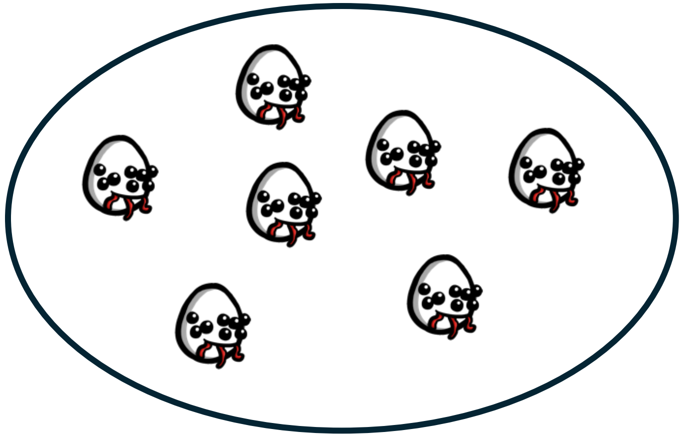
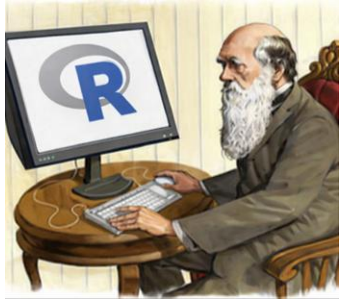
Mutant



A population of mutant is always invaded by **p***

```
# payoffs of pure strategies against q
EHq <- -1*q + 4*(1-q)
EDq <- 2*(1-q)
# resident payoff vs mutant
E_pq <- p*EHq + (1-p)*EDq
# mutant payoff vs itself
E_qq <- q*EHq + (1-q)*EDq
```



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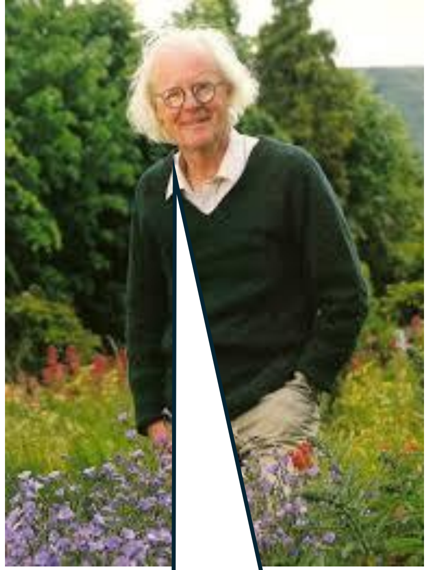

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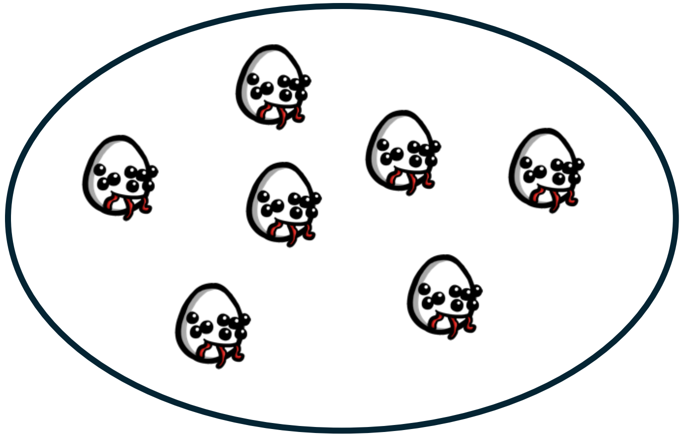

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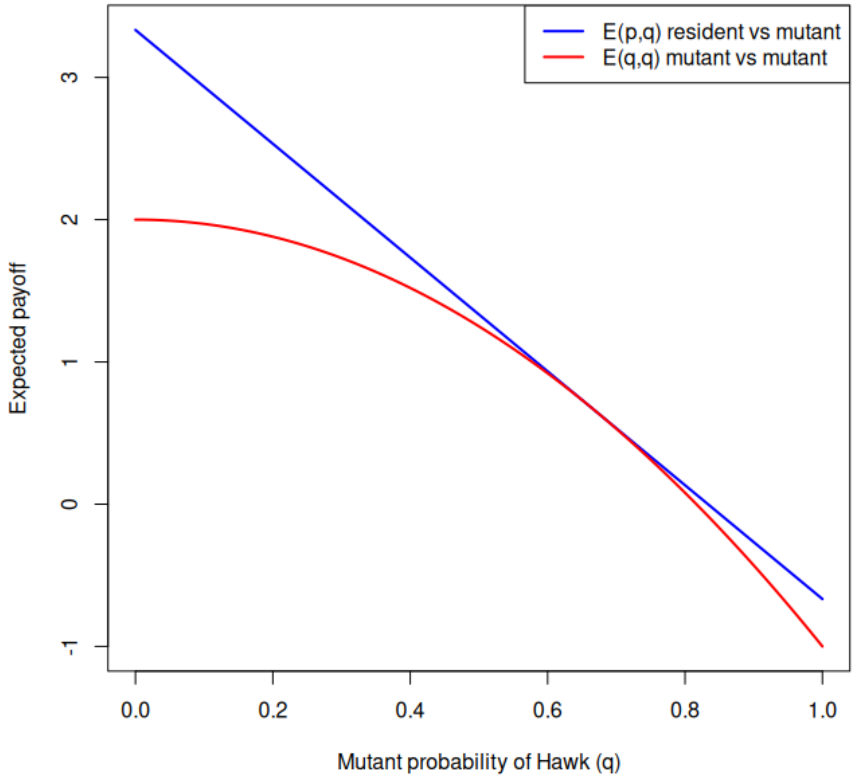

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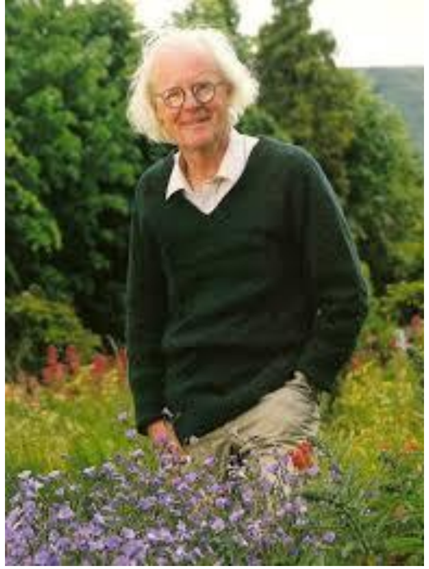
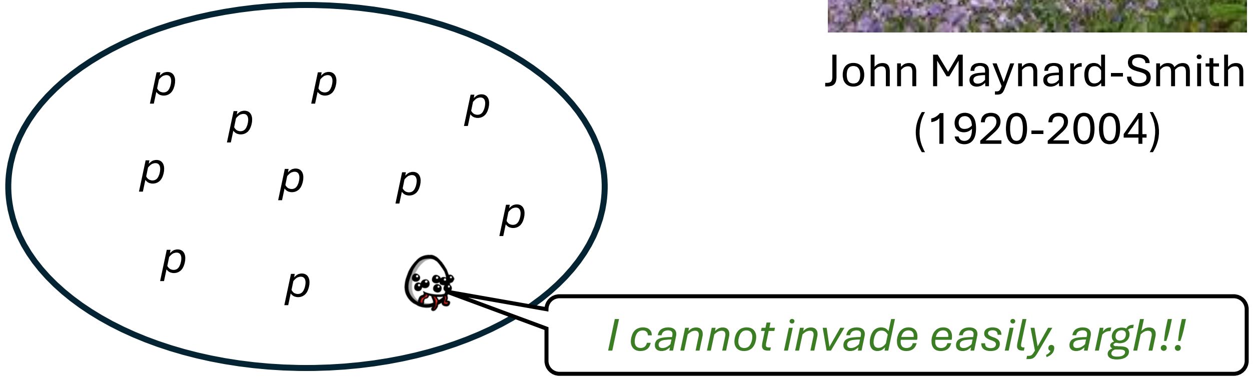


John Maynard-Smith
(1920-2004)

A strategy p is an ESS if for every alternative strategy q if:

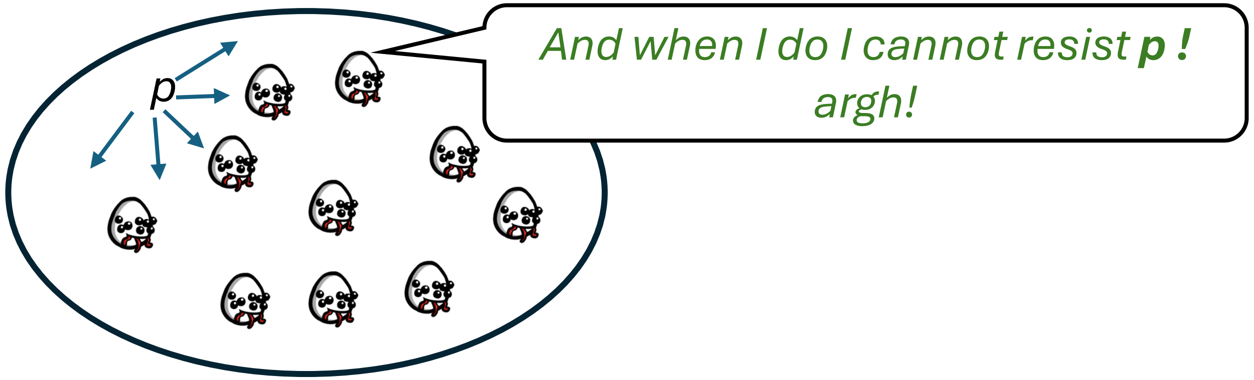
First condition:

$$E(p,p) \geq E(q,p)$$



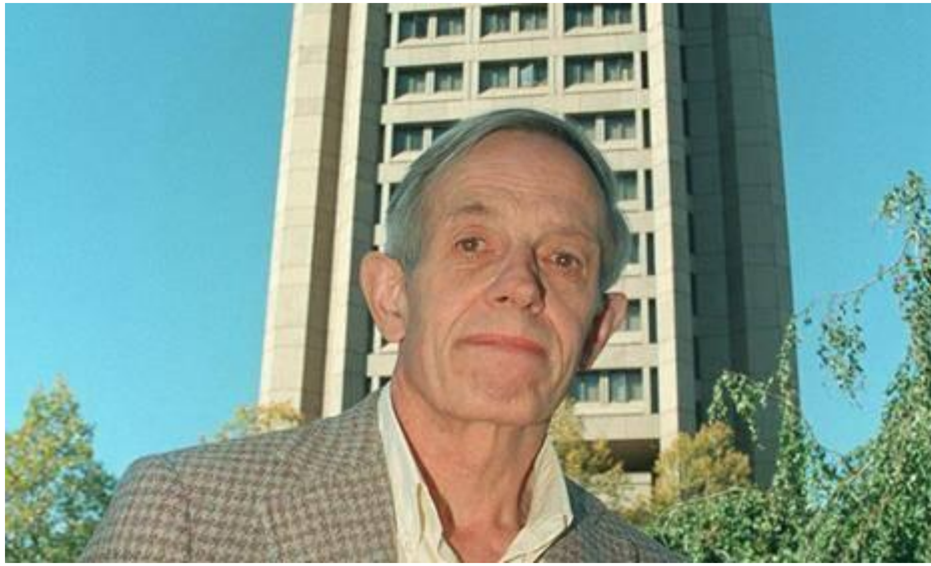
Second condition (if equality holds):

$$E(p,q) > E(q,q)$$



Nash equilibrium

- In many strategic situations, there exists a set of strategies where **no player can improve their outcome by changing strategy alone**.
- That point is called a **Nash equilibrium**.
- Every ESS is a **Nash equilibrium**, but not every Nash equilibrium is evolutionarily stable.
- The second condition is what ensures **evolutionary stability**.



$E(p,p) \geq E(q,p)$

$E(p,q) > E(q,q)$

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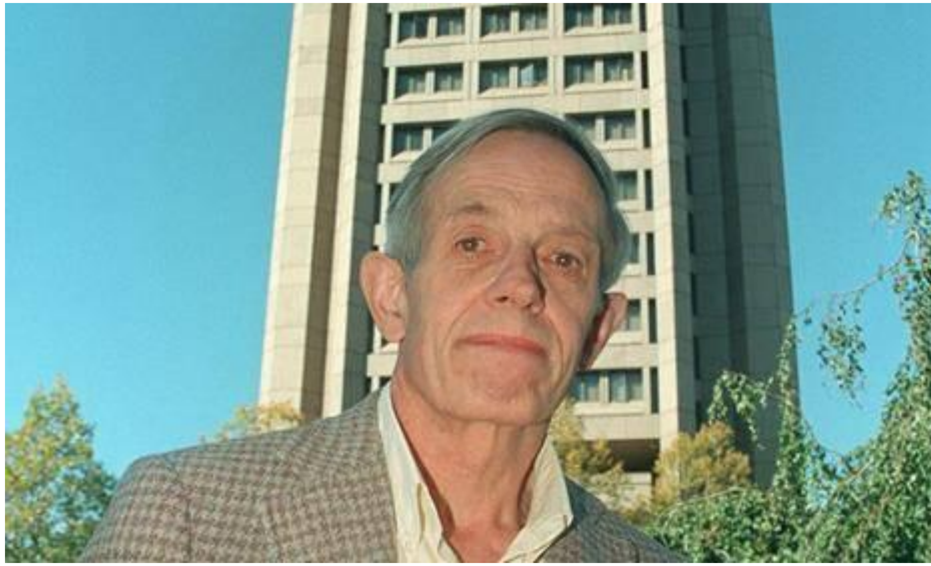
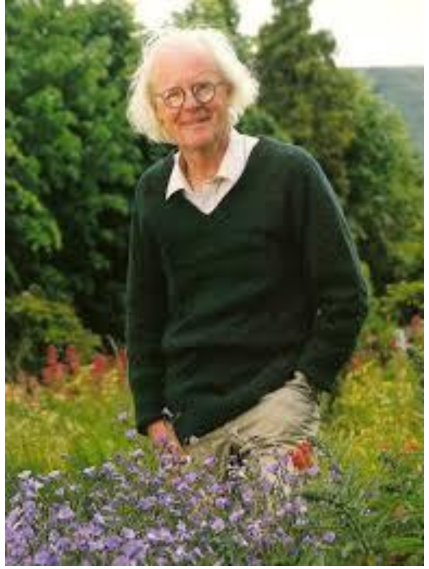


Nash equlibrium:
$E(p,p) \geq E(q,p)$

Evolutionary Stable Strategy (ESS):
1° Condition: $E(p,p) \geq E(q,p)$
2° Condition: if $E(p,p) = E(q,p)$, then
$E(p,q) > E(q,q)$

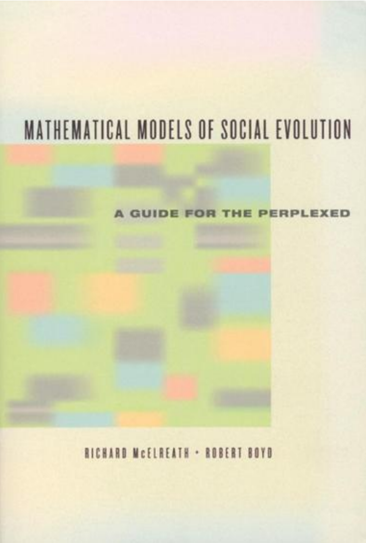
Hawk and Doves in Maynard Smith's formulation



John Maynard-Smith
(1920-2004)

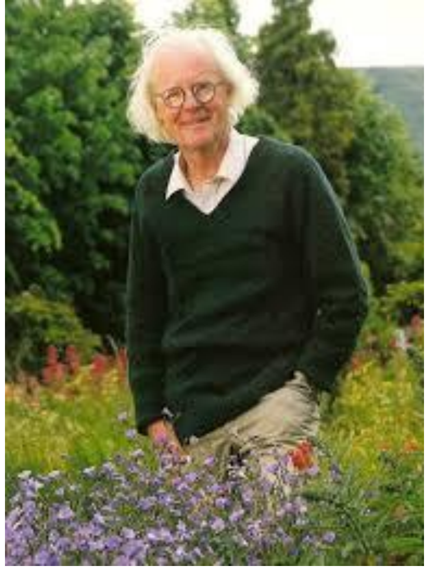
	Hawk	Dove
Hawk	$\frac{1}{2}v - \frac{1}{2}c$	v
Dove	0	$\frac{1}{2}v$

v is the prize of winning
c is the cost of fights/injuries



rmcelreath/VLEGT: Verty short course on evolutionary game theory

Hawk and Doves in Maynard Smith's formulation

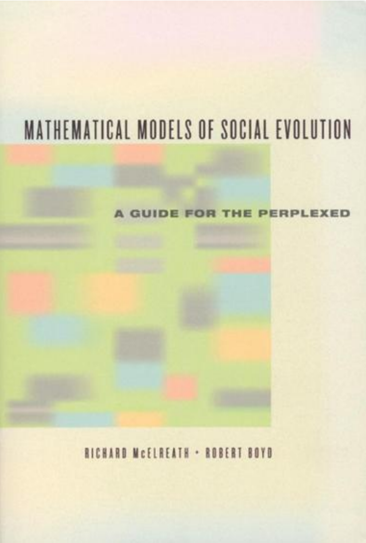


John Maynard-Smith
(1920-2004)

	Hawk	Dove
Hawk	$\frac{1}{2}v - \frac{1}{2}c$	v
Dove	0	$\frac{1}{2}v$

v is the prize of winning
c is the cost of fights/injuries

When are Hawks and Doves evolutionary stable?



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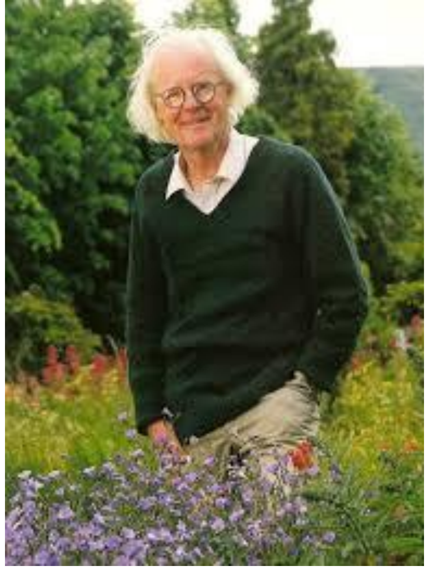

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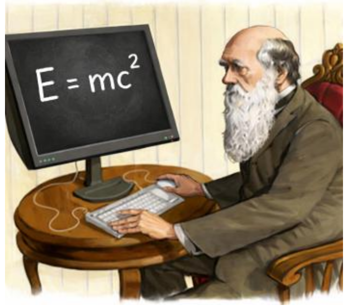
Evolutionary stability of Pure Strategies

$$\underbrace{\frac{v-c}{2}}_{\text{Hawk-vs-Hawk}} > \underbrace{0}_{\text{Dove-vs-Hawk}}$$

Hawks are evolutionarily stable if $v > c$
or “the value of the resource exceeds the cost of injury”



$$\underbrace{\frac{v}{2}}_{\text{Dove-vs-Dove}} > \underbrace{v}_{\text{Hawk-vs-Dove}}$$

Doves are evolutionarily stable if $v < 0$
which is never

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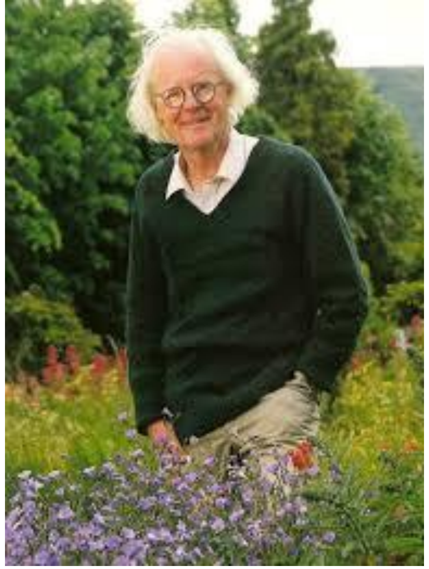

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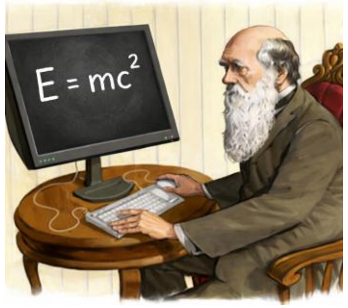

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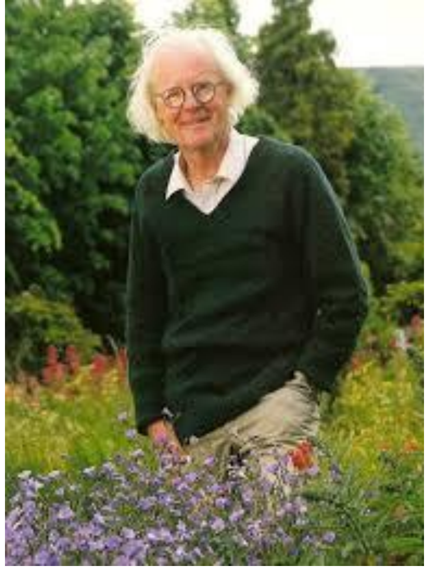

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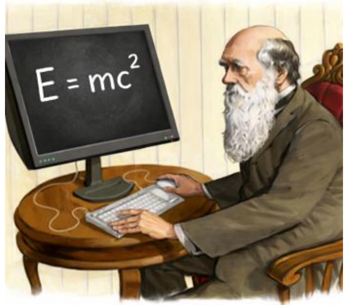
Evolutionary stability of mixed strategies

$$p\frac{v-c}{2} + (1-p)v$$

Average fitness of Hawks

$$p(0) + (1-p)\frac{v}{2}$$

Average fitness of Doves



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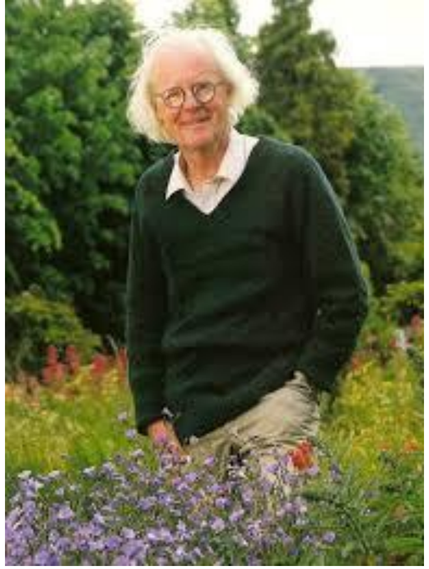

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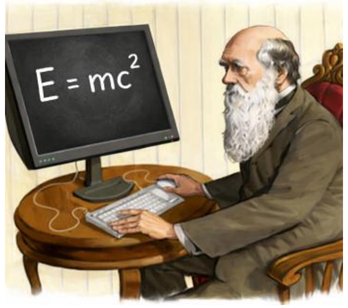
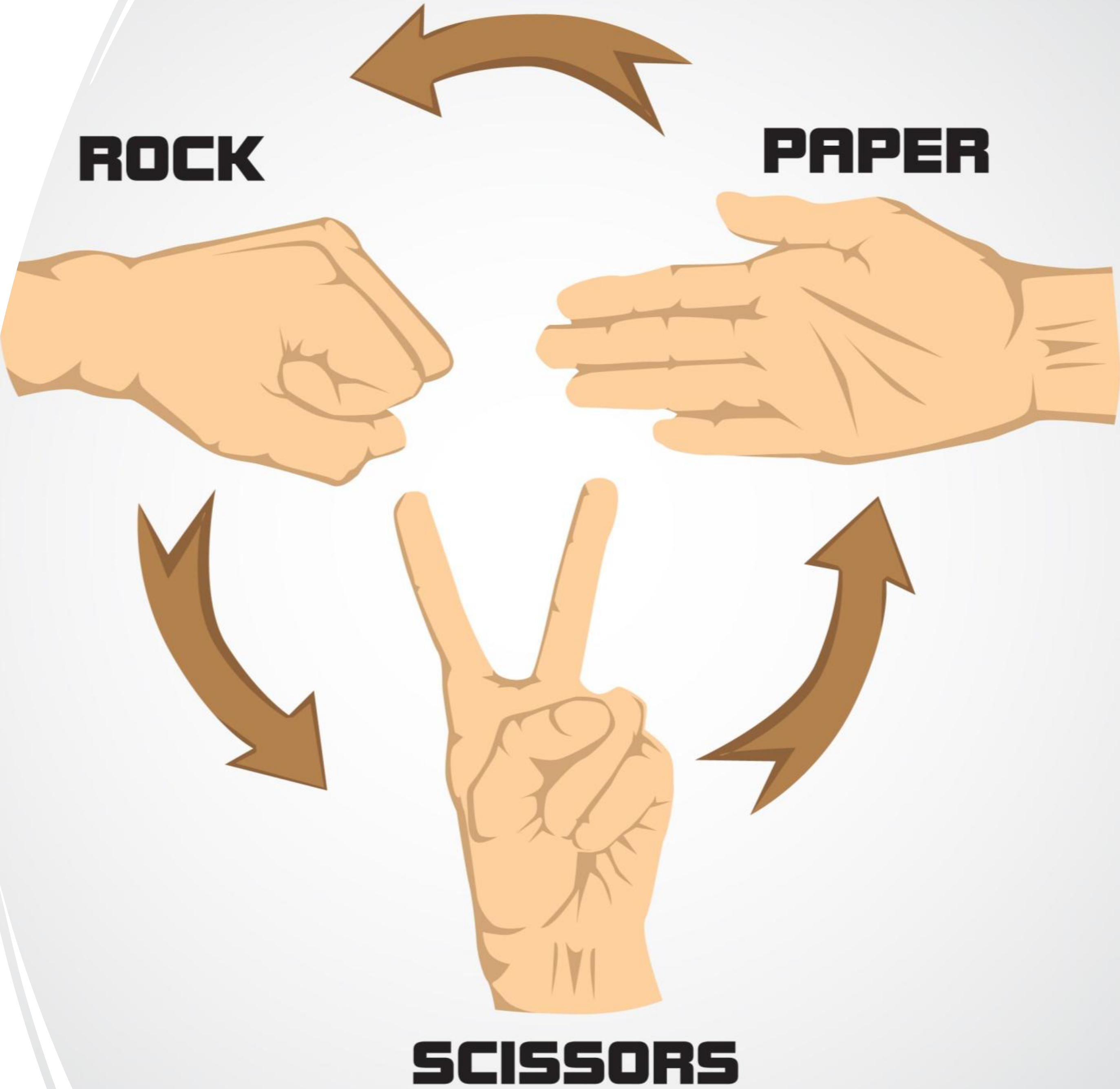


$$\underbrace{p\frac{v-c}{2} + (1-p)v}_{\text{Hawk fitness}} > \underbrace{p(0) + (1-p)\frac{v}{2}}_{\text{Dove fitness}} \Rightarrow p < v/c$$

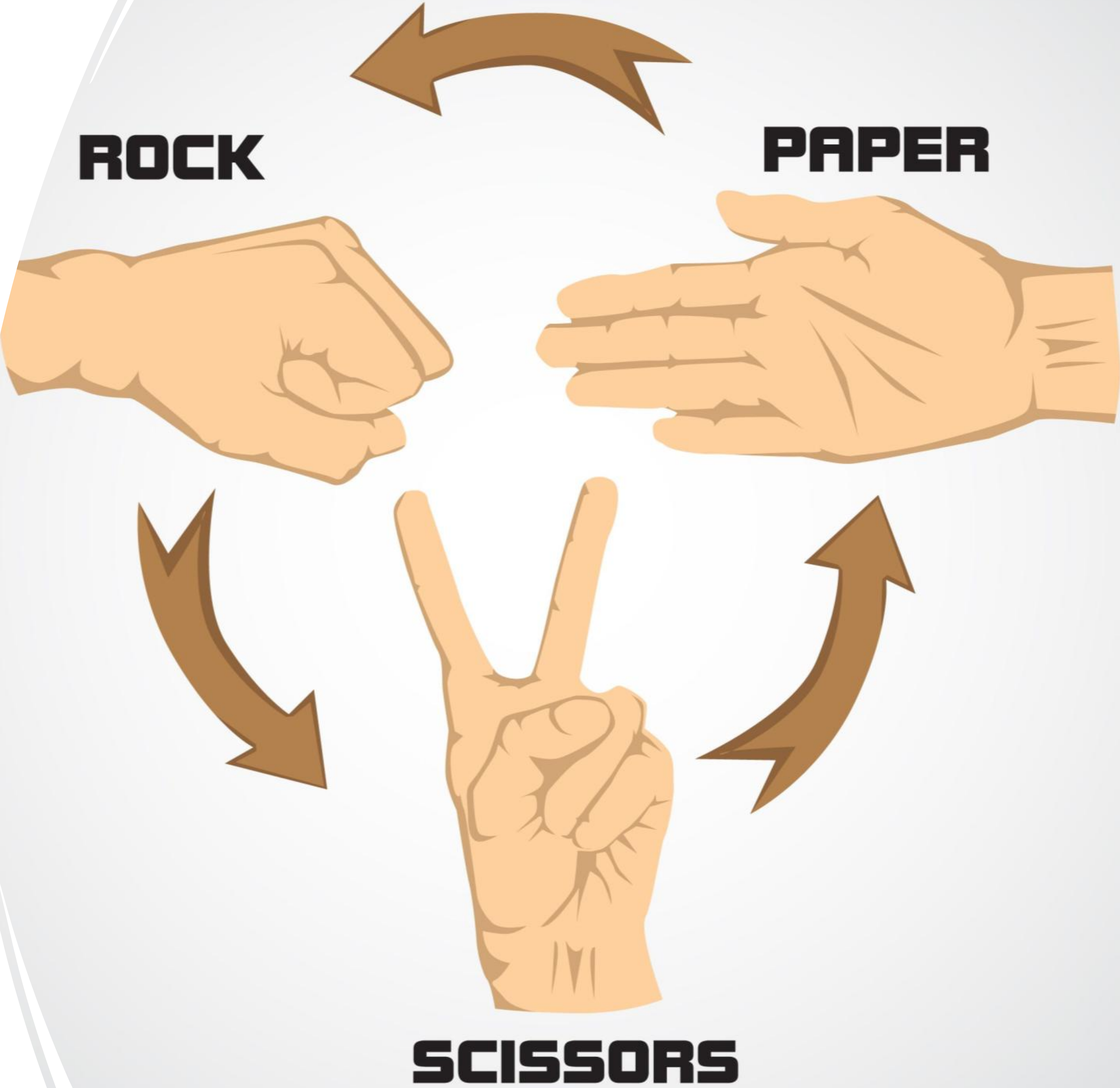
Hawks increase when they are less than the ratio v/c, which is the ESS

What is the payoff matrix?



What is the payoff matrix?

Gains of Player 1		Player 2 chooses...		
				
Player 1 chooses...		0	-1	1
		1	0	-1
		-1	1	0



What is the Evolutionary Stable Strategy (ESS)?

Gains of Player 1		Player 2 chooses...		
Player 1 chooses...		0	-1	1
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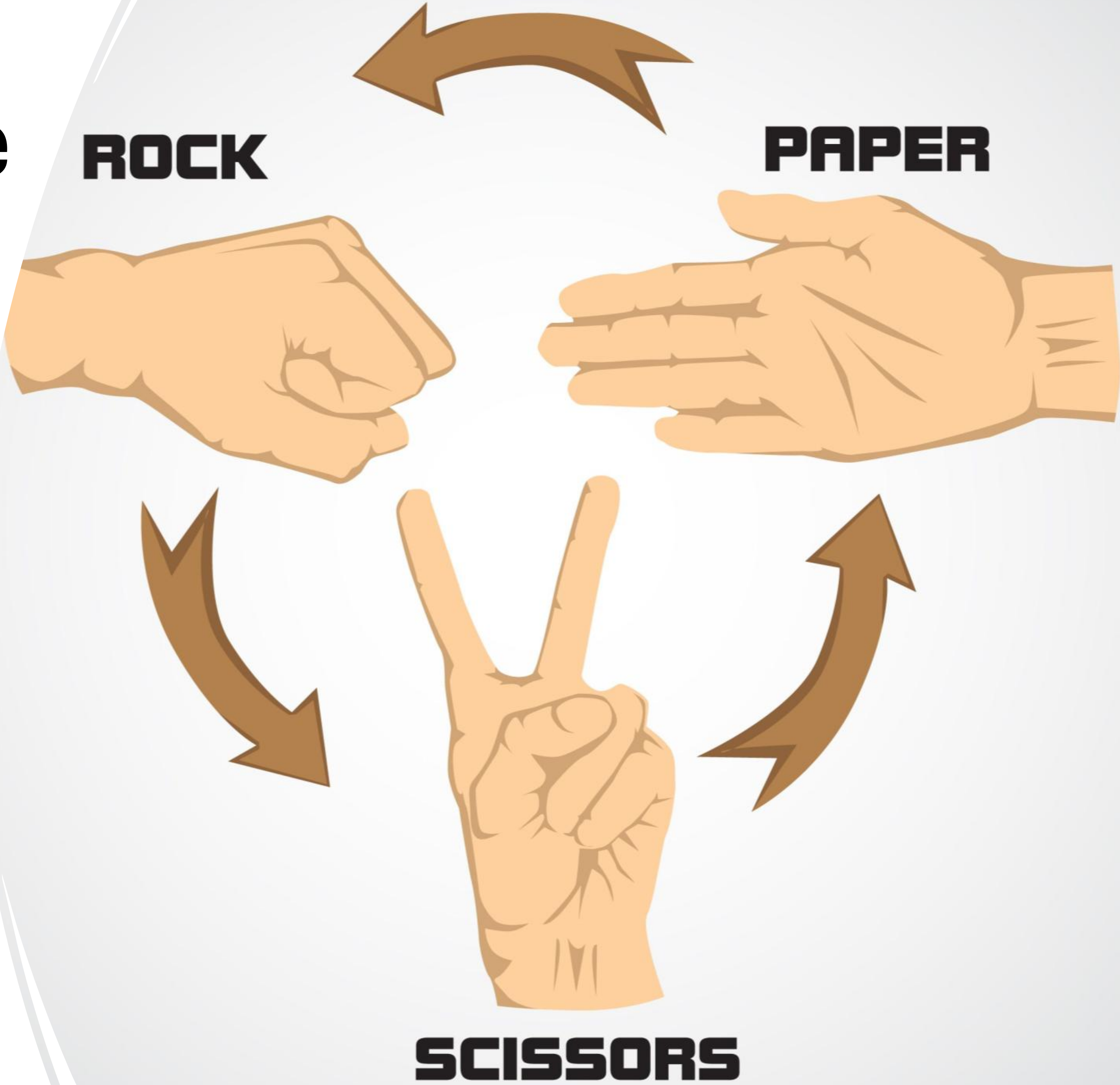
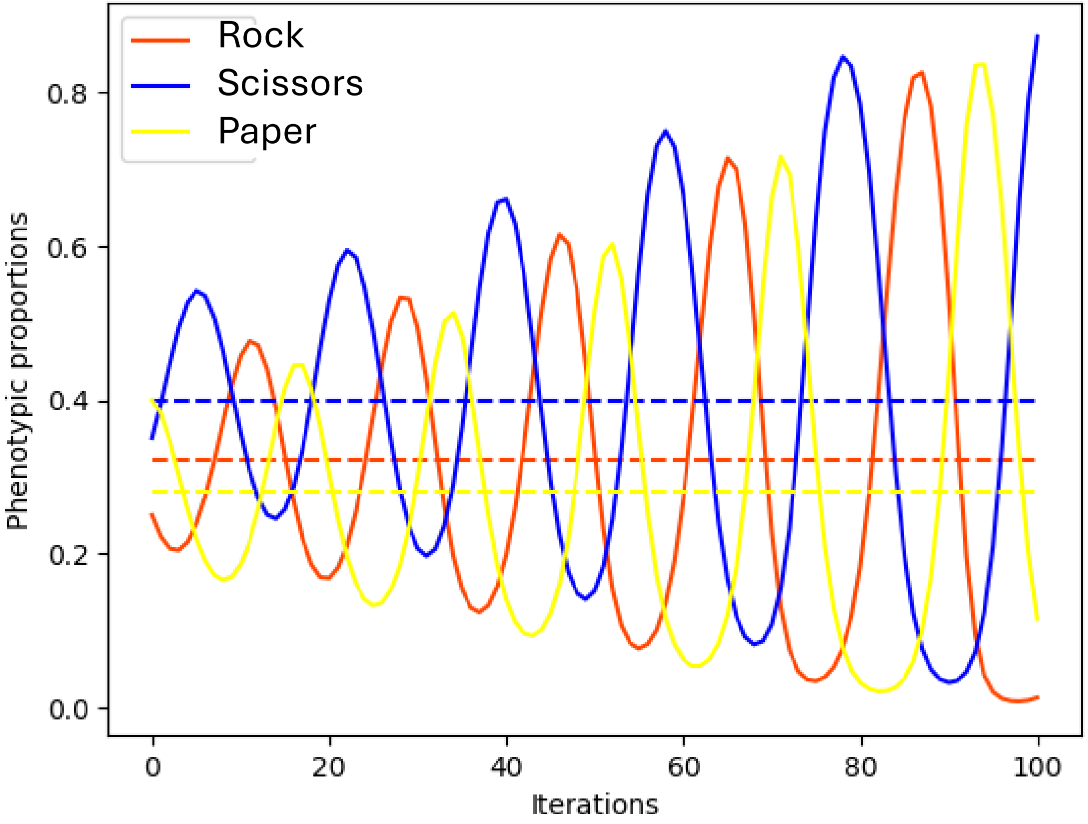
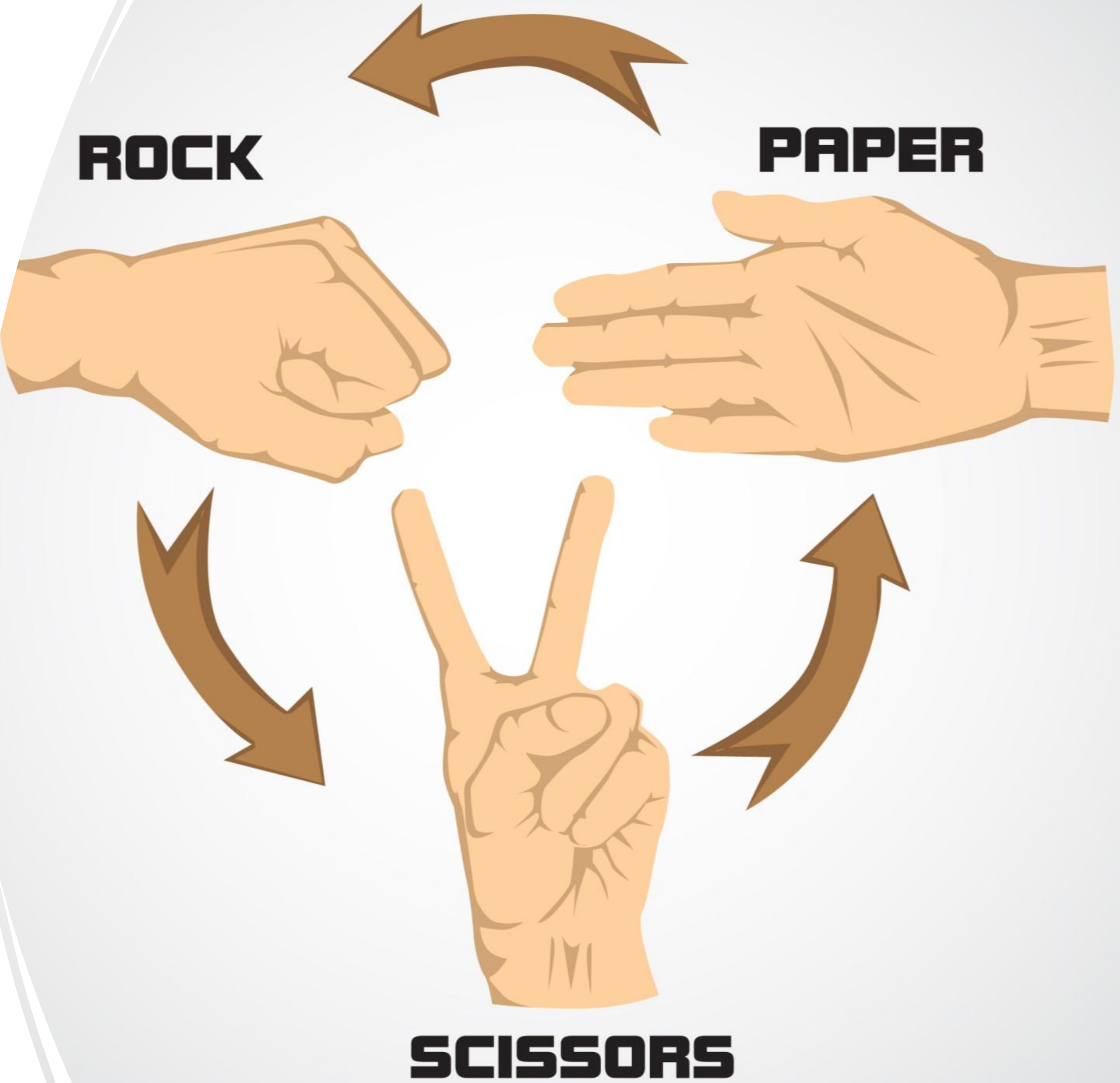


Perturbations from the EES can lead to cyclic dynamics

Cargnellutti-Rossato et al, 2023





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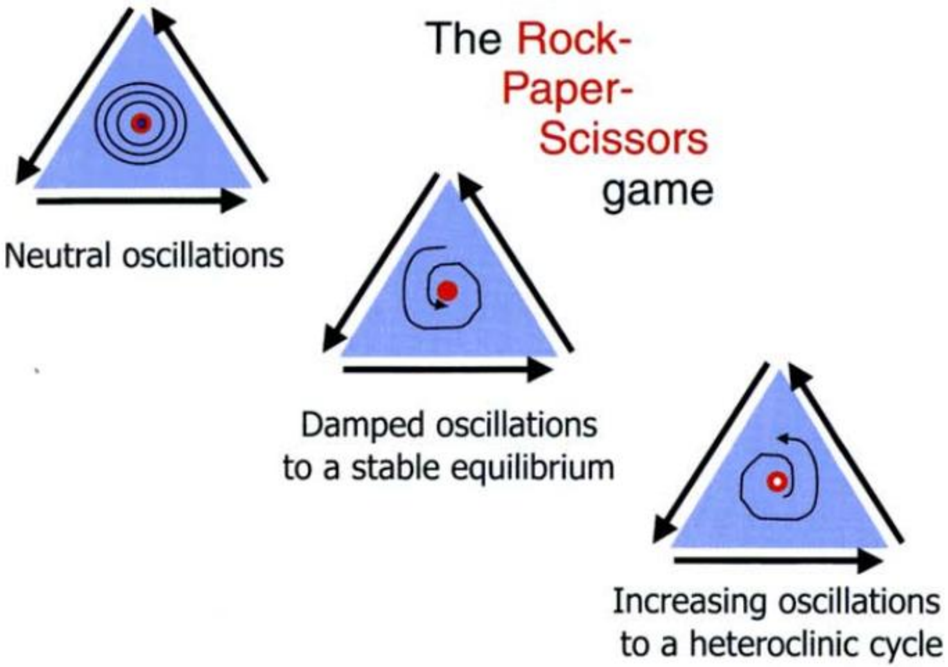
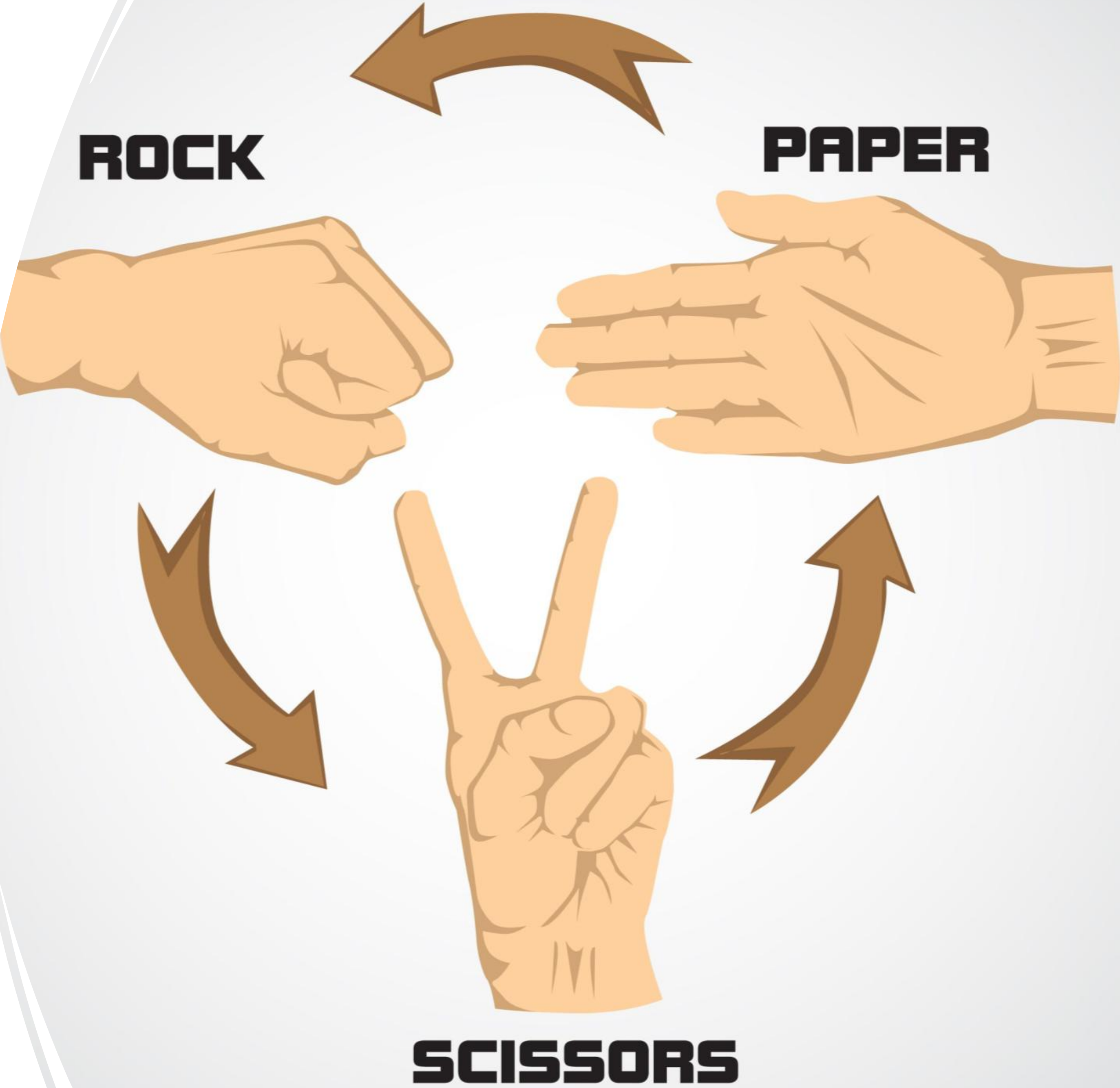
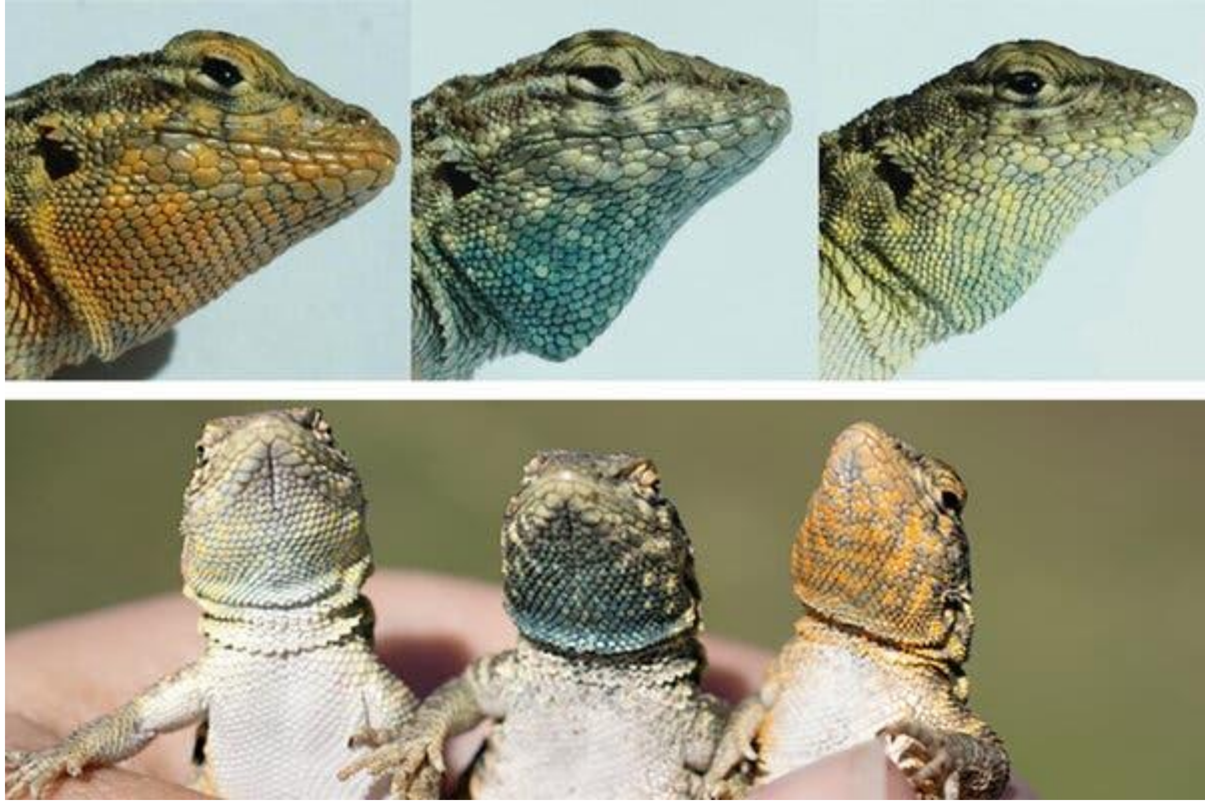
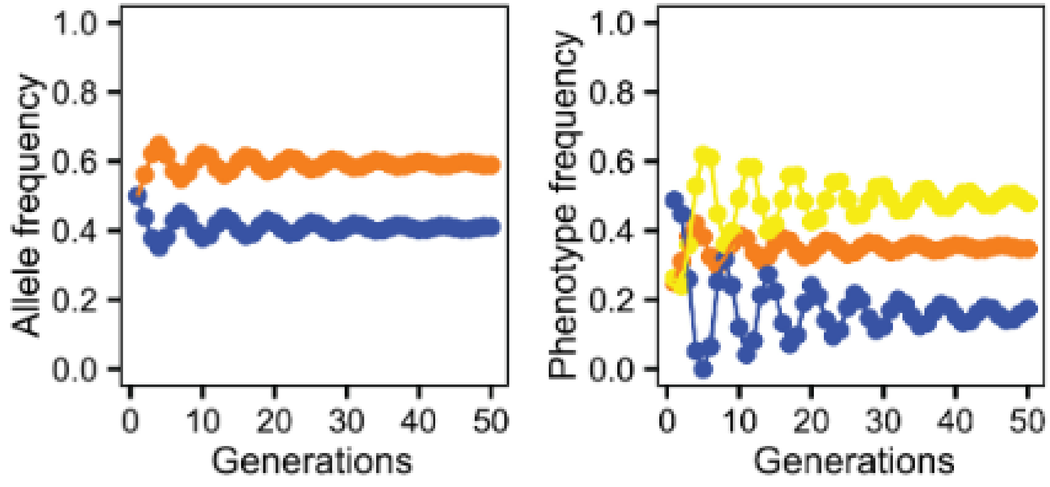




Orange males are larger and more aggressive, controlling larger territories
and mating with multiple females.
Blue males have smaller territories and focus on one female, ensuring th
eir offspring are their own.
Yellow males, known as "sneakers," mimic female markings and mate wit
hout establishing a territory, increasing their chances of mating with other
males.



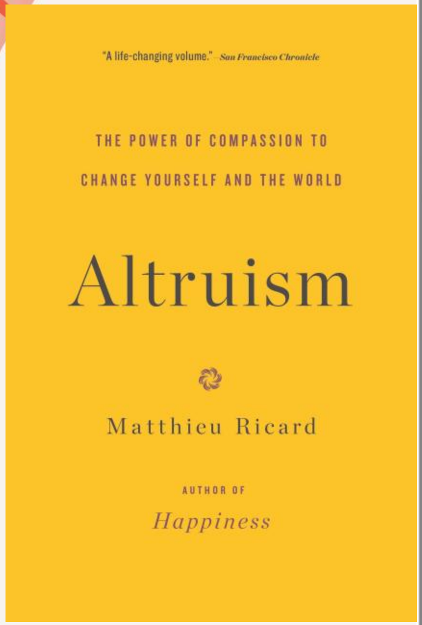
Uta stansburiana

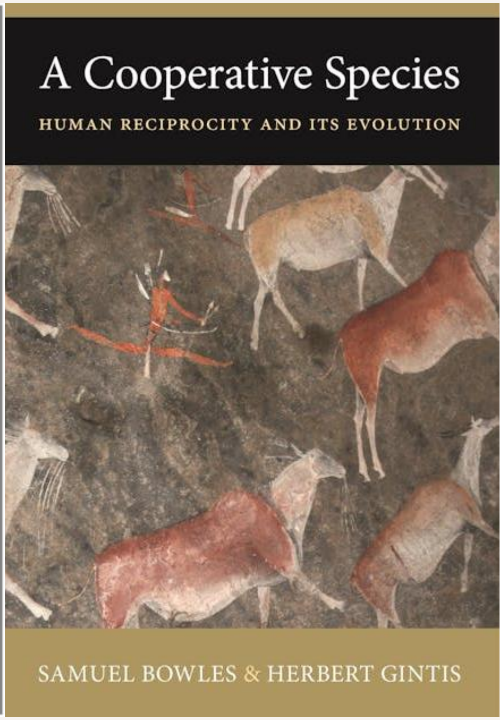


[This Diminutive Reptile Plays Rock-Paper-Scissors - The New York Times]

[Corl et al.,2026, Science]

The evolution of cooperation





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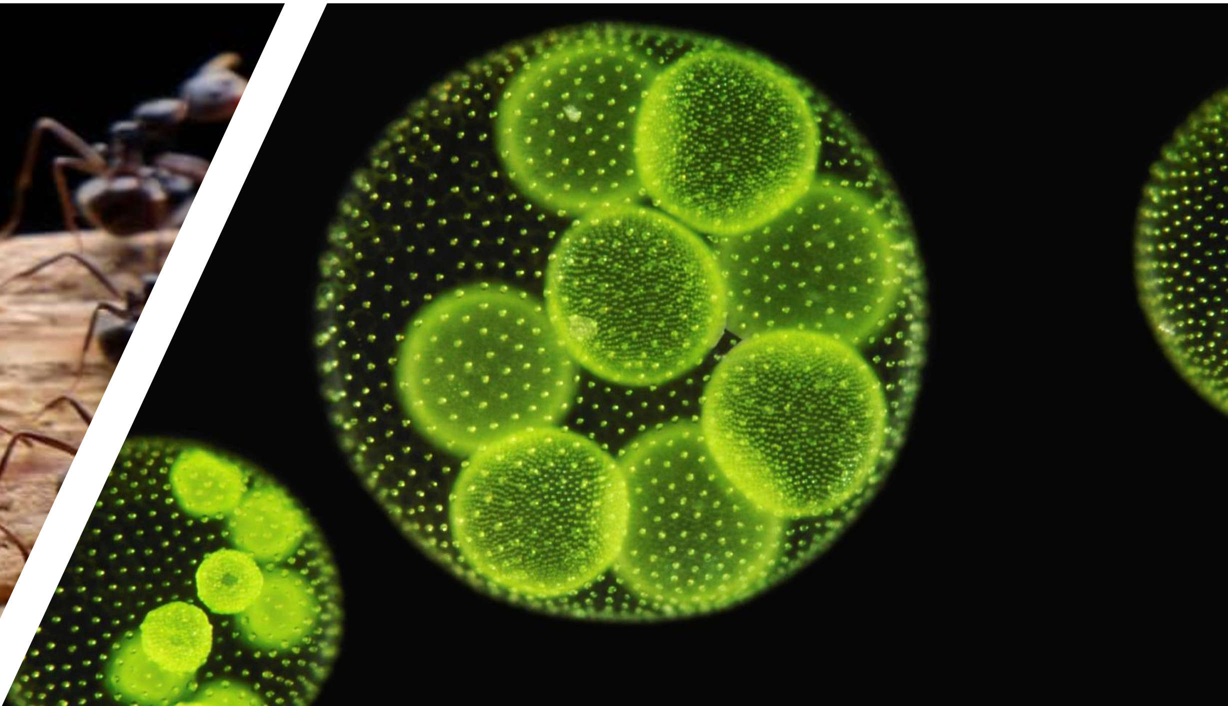
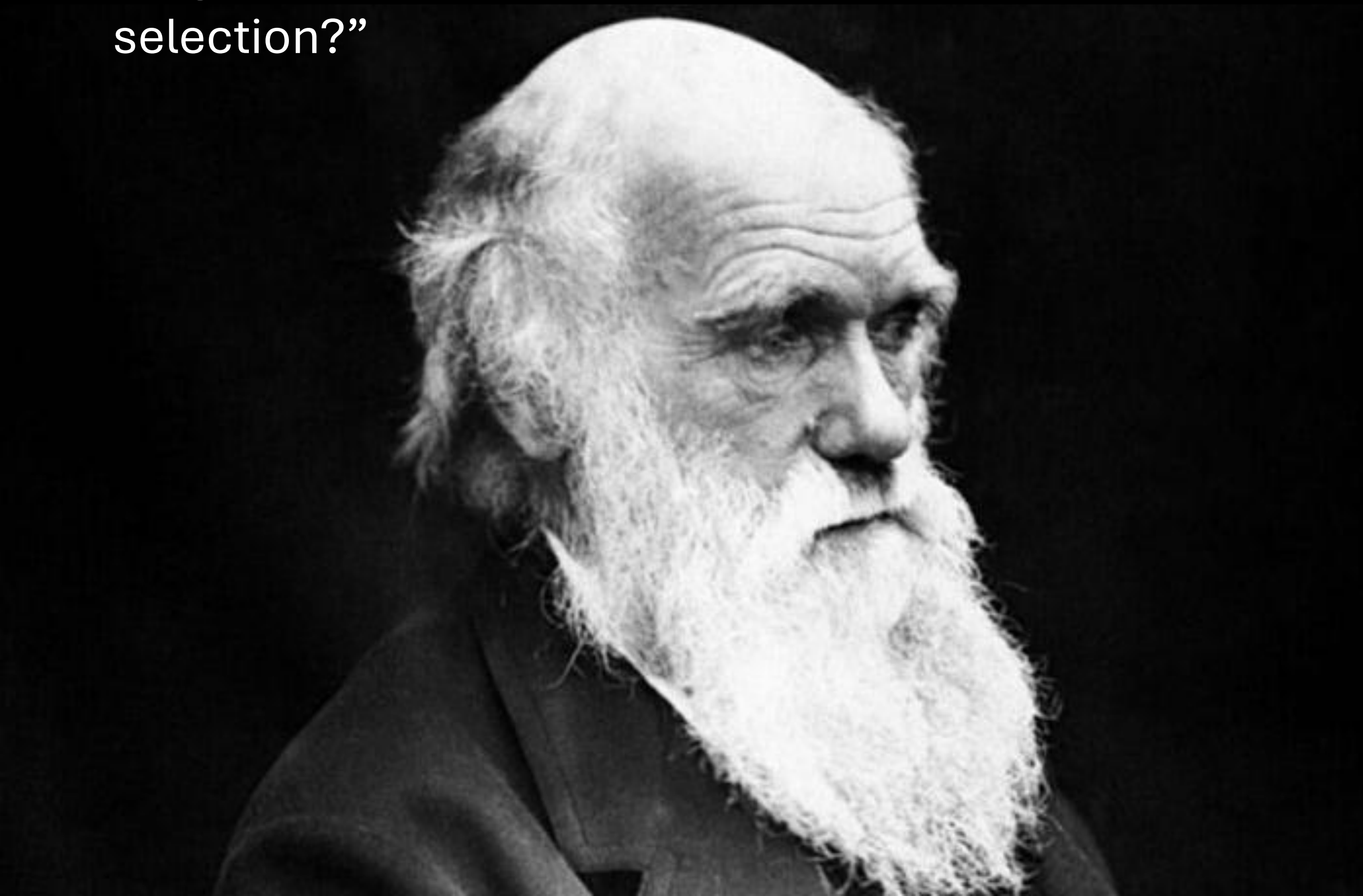


From the «On the Origin of Species»:

“It will indeed be thought that I have an overweening confidence in the principle of natural selection, when I do not admit that such wonderful and well established facts at once annihilate my theory.”

“But with the working ant we have an insect differing greatly from its parents, yet absolutely sterile; so that it could never have transmitted successively acquired modifications of structure or instinct to its progeny. It may well be asked how is it possible to reconcile his case with the theory of natural selection?”



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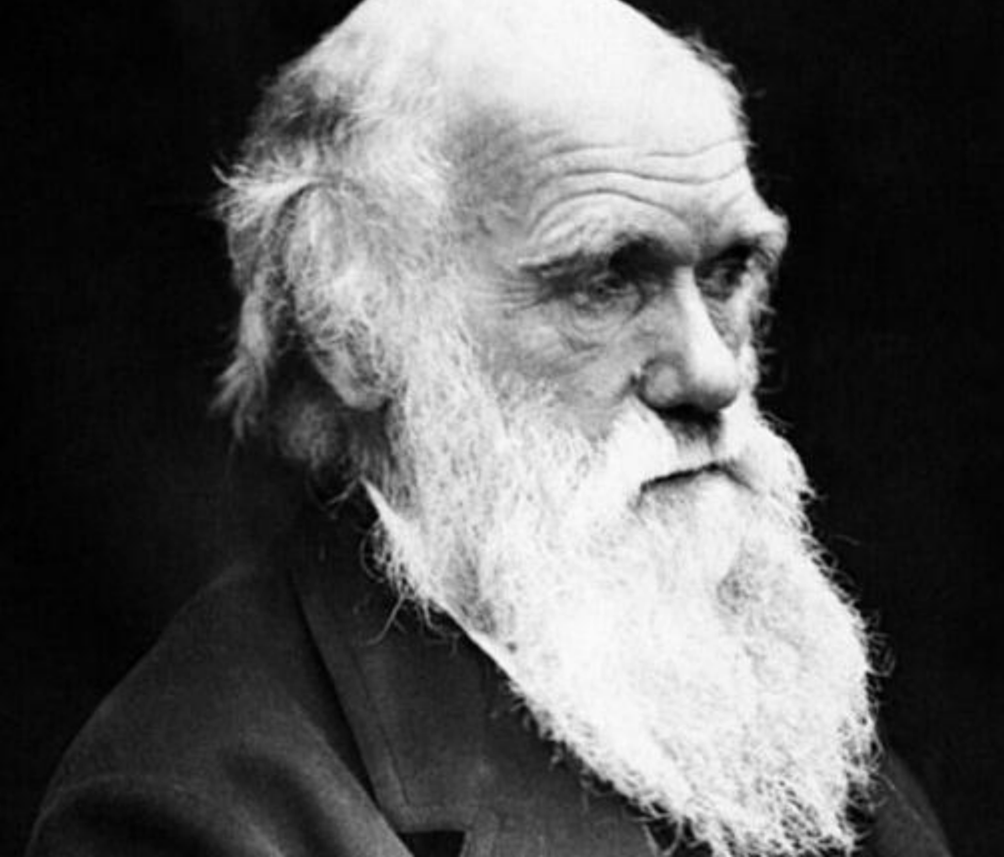

But also he used it against Lamarck:

- ".. females,—in this case, we may safely conclude from the analogy of ordinary variations, that each successive, slight, profitable modification did not probably at first appear in all the individual neuters in the same nest, but in a few alone; and that by the long-continued selection of the fertile parents which produced most neuters with the profitable modification, all the neuters ultimately came to have the desired character."
- «I am surprised that no one has advanced this demonstrative case of neuter insects, against the well-known doctrine of Lamarck."