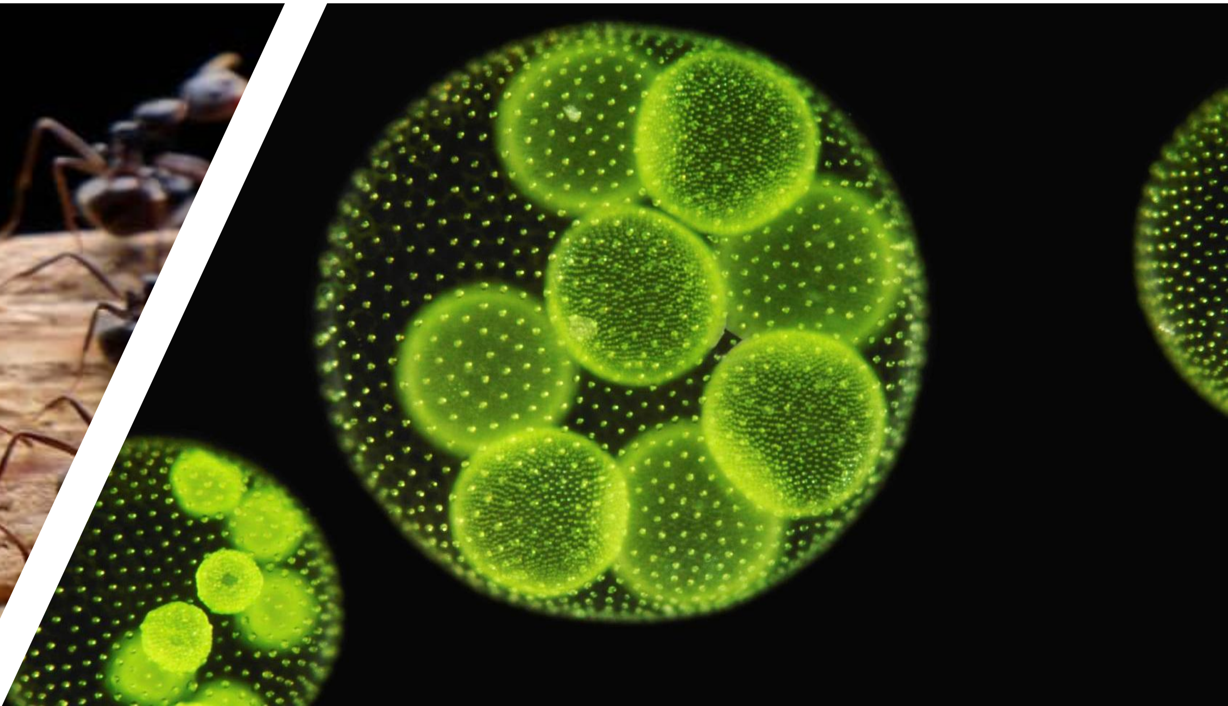
Evolutionary Game Theory II

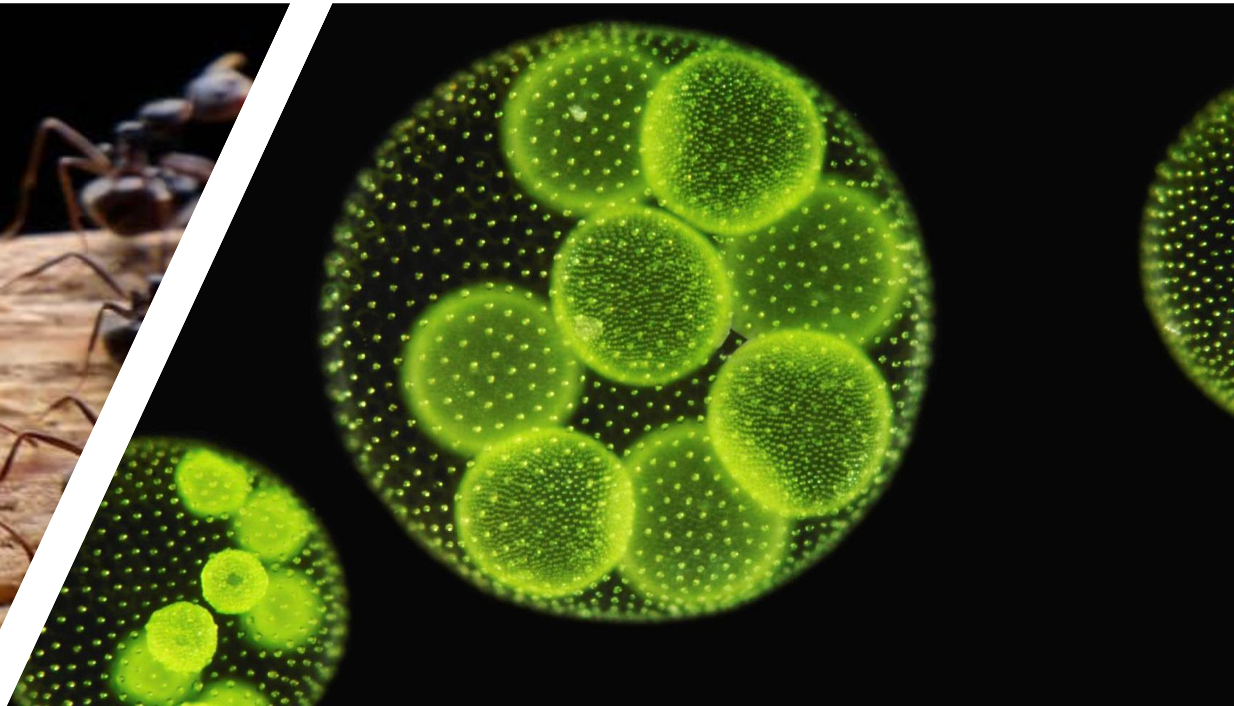
The Evolution of Cooperation

Fabrizio Mafessoni, Universita' di Trieste, Biologia Evoluzionistica, 13/03/2026



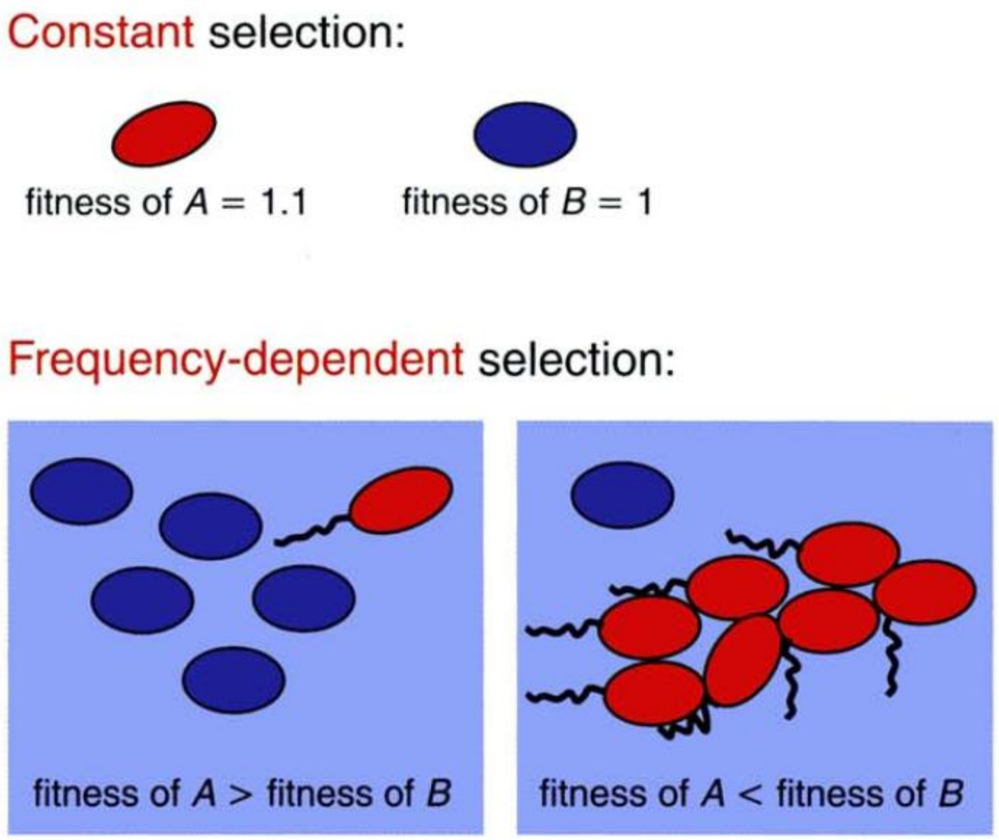



But before, the usual summary of previous episodes..



Evolutionary Game theory

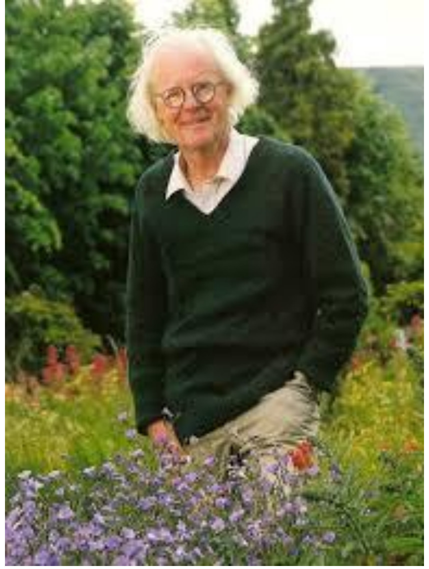
The study of ***«frequency-dependent» fitness***



Interaction between individuals can be represented as payoff matrices




	Hawk	Dove
Hawk	-1,-1	4,0
Dove	0,4	2,2



John Maynard-Smith
(1920-2004)

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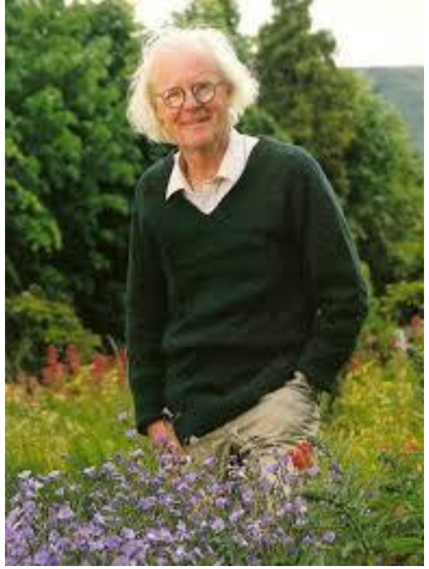

John Maynard-Smith
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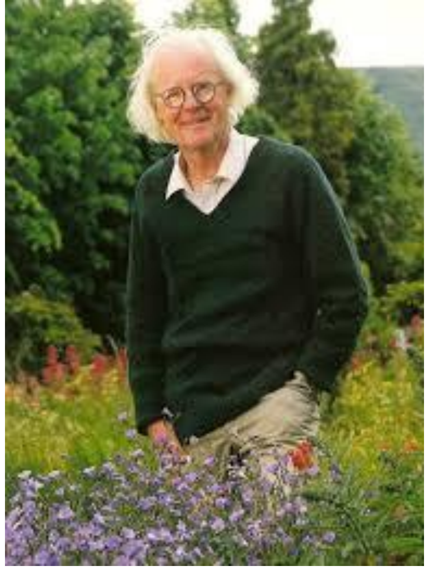
Symmetric games can be represented in two equivalent ways



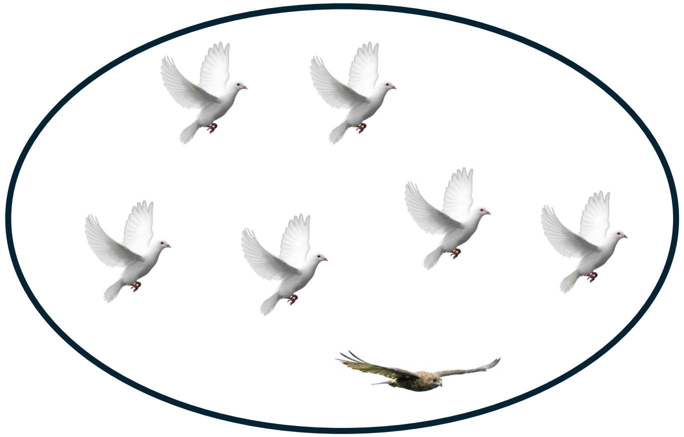
John Maynard-Smith
(1920-2004)

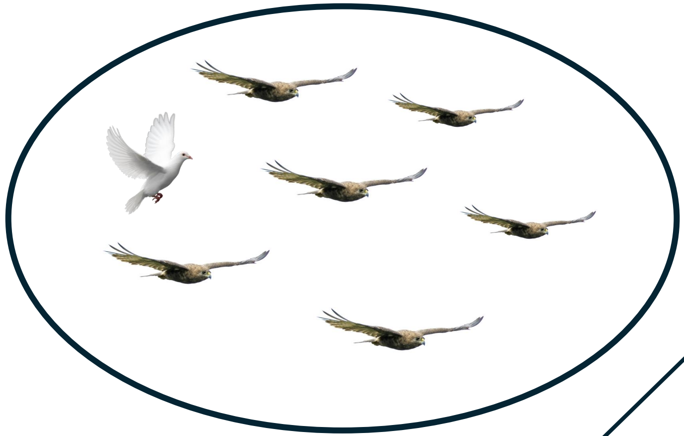


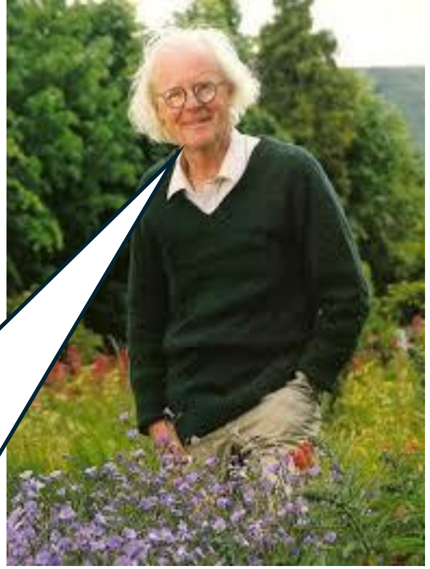

	Hawk	Dove
Hawk	-1,-1	4,0
Dove	0,4	2,2

	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)

We can infer where evolution will lead to by asking which strategy will not be "invaded" by "better" strategies

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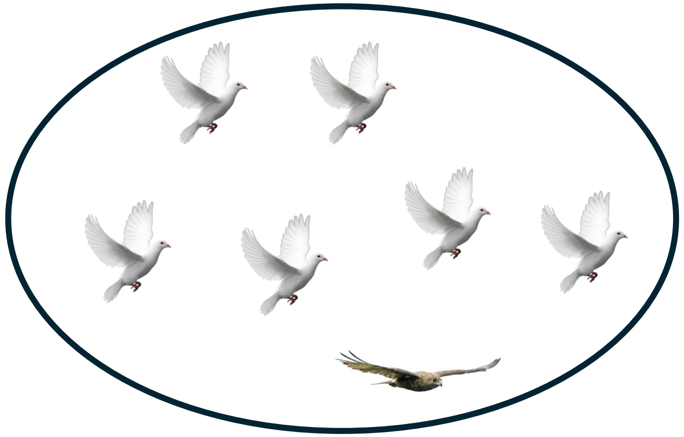

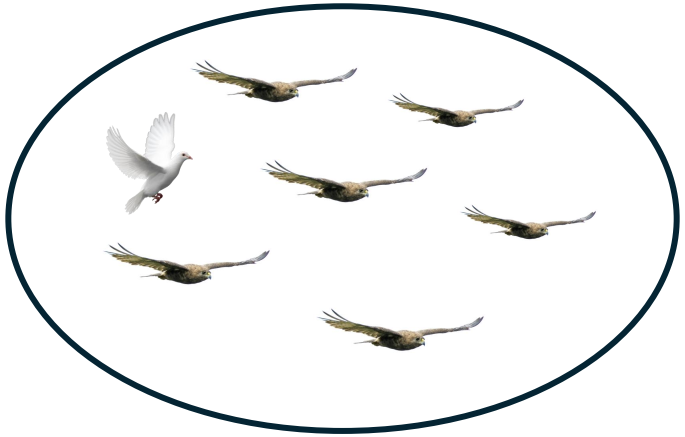

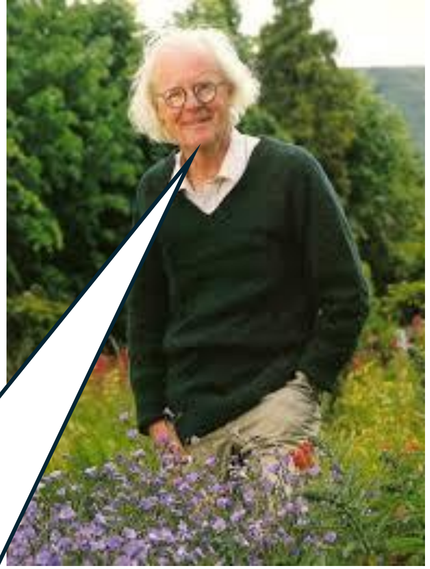

John Maynard-Smith
(1920-2004)

Both Hawks and Doves can be invaded, so they are not ESS

	Hawk	Dove
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Dove	0,4	2,2

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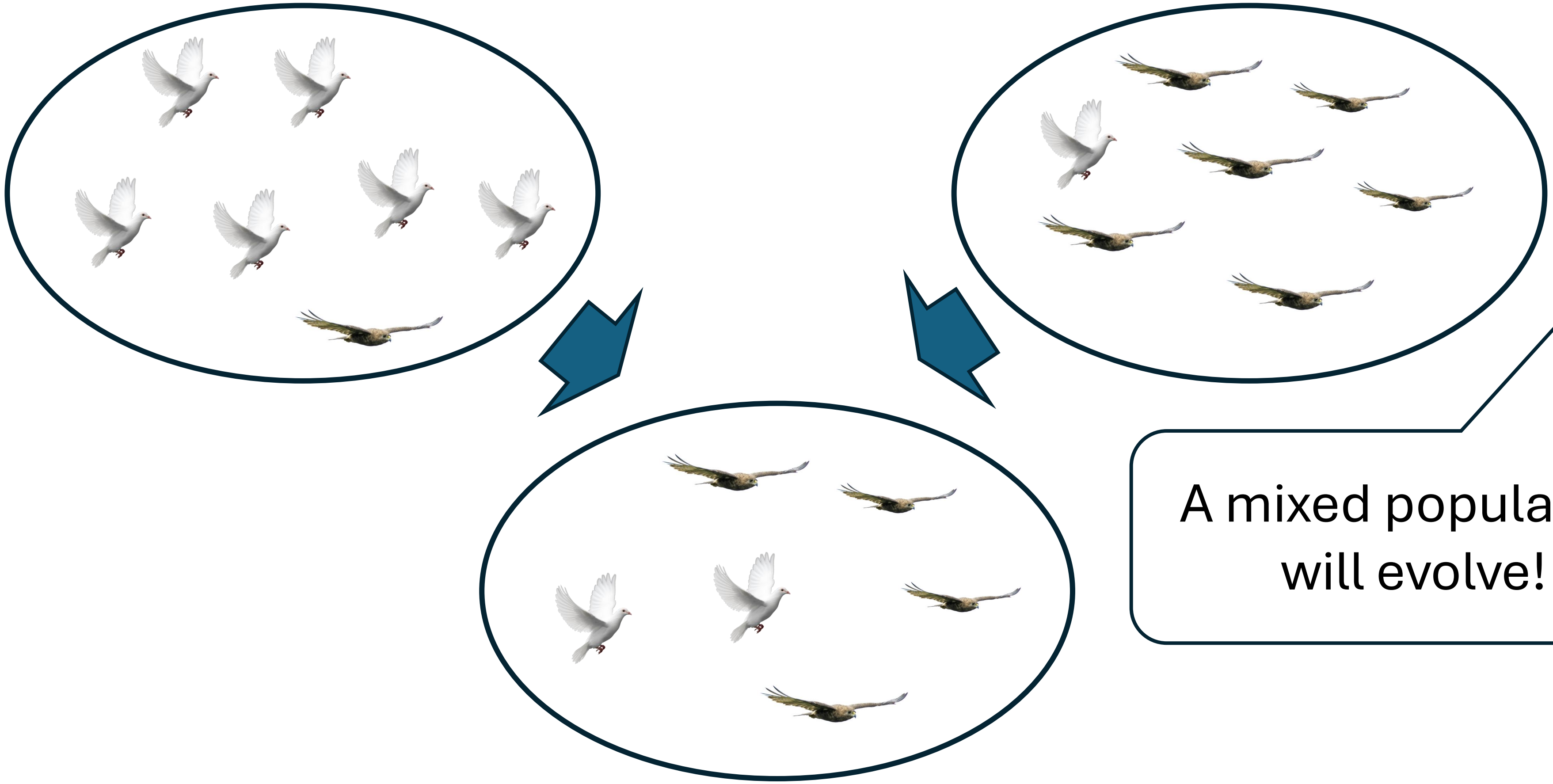

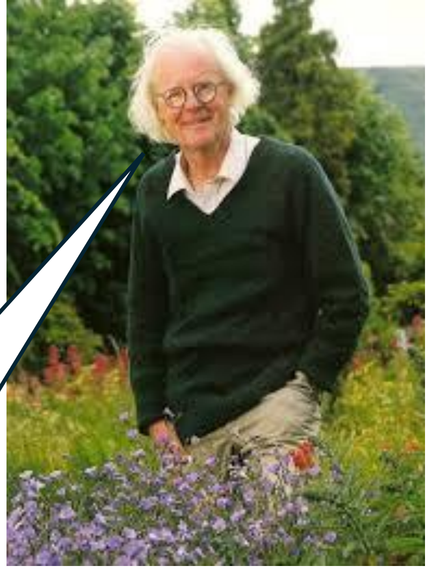

John Maynard-Smith
(1920-2004)

A mixed population
will evolve!

	Hawk	Dove
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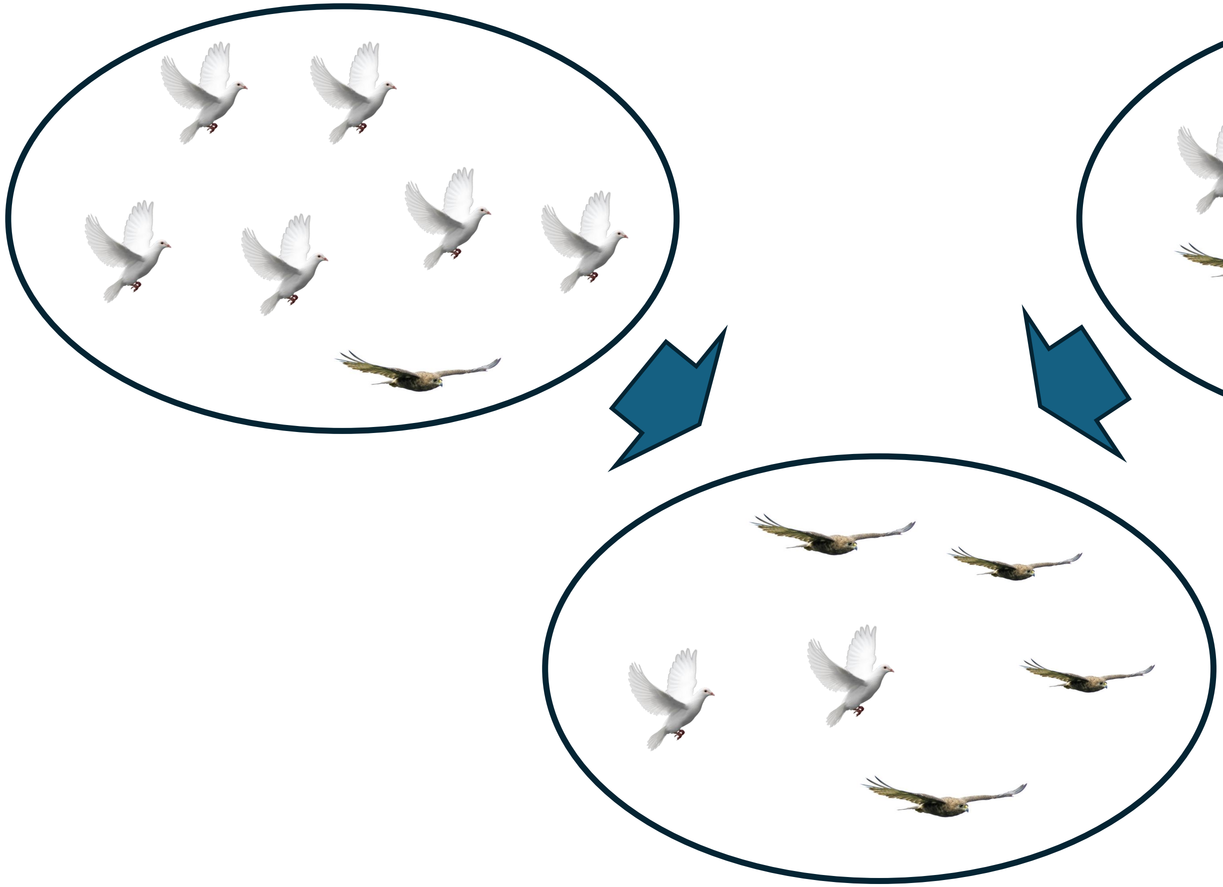

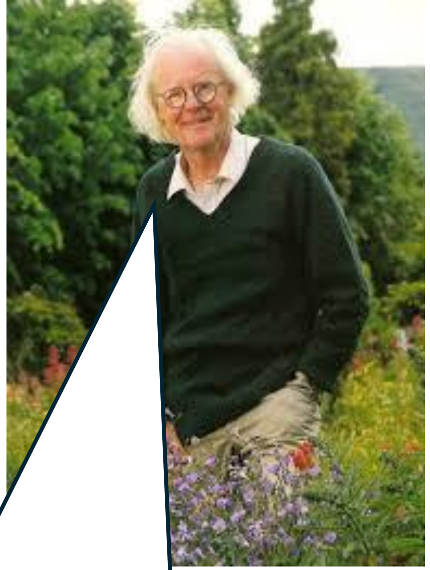

ynard-Smith
0-2004)

The ESS equilibrium is where the fitness of Hawks and Dove is the same (here 2/3 Hawks)




	Hawk	Dove
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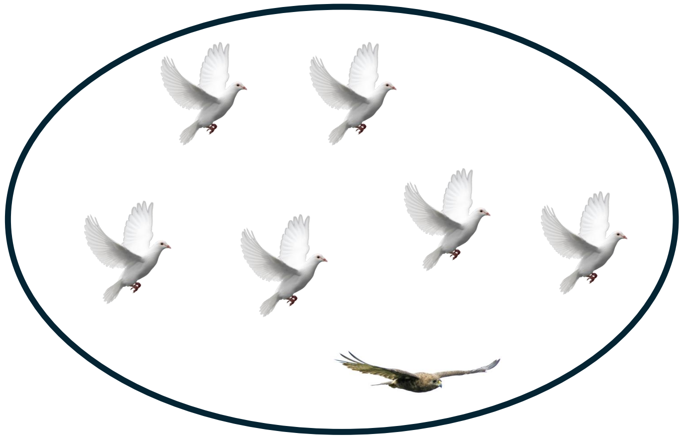
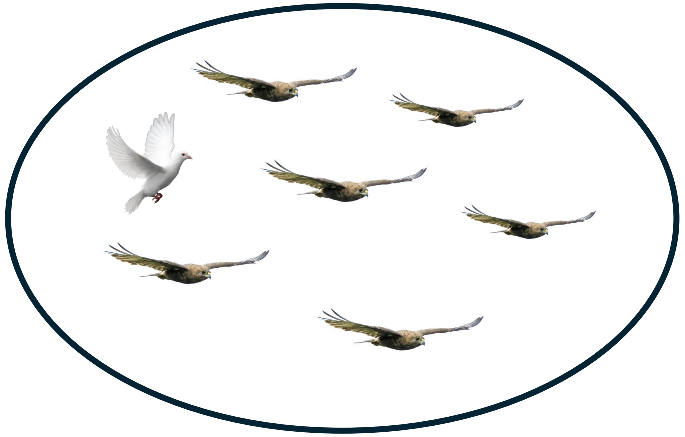
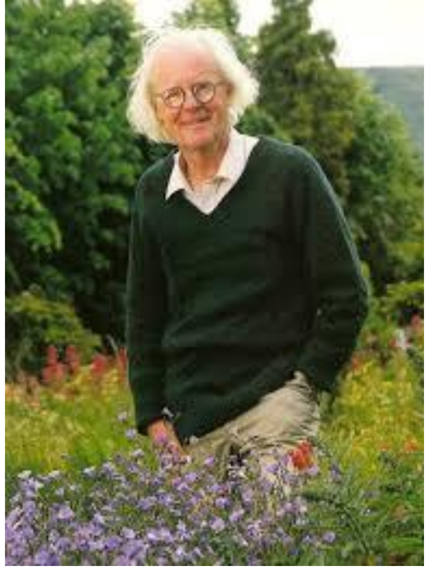
Dove	0,4	2,2

We can interpret this «mixed populations» as mixed strategies







John Maynard-Smith
(1920-2004)

Pure strategies: always either  or 

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

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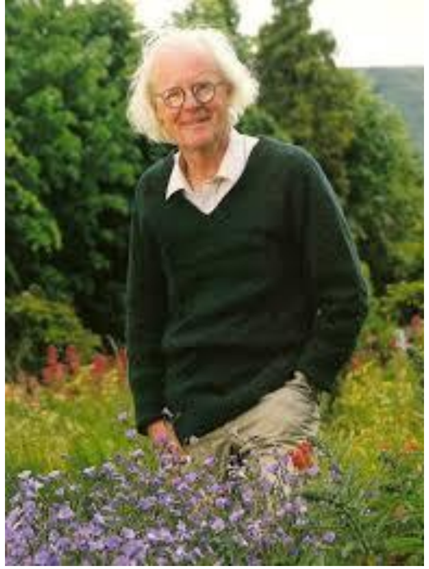
Nash Equilibria and Evolutionarily Stable Strategies (**ESS**) share similar intuitions



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(1920-2004)

Nash Equilibrium

	Hawk	Dove
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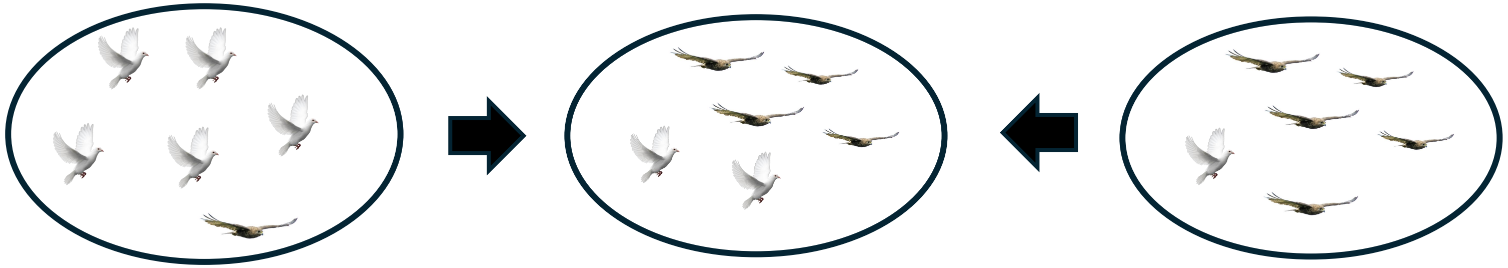
2/3  1/3 

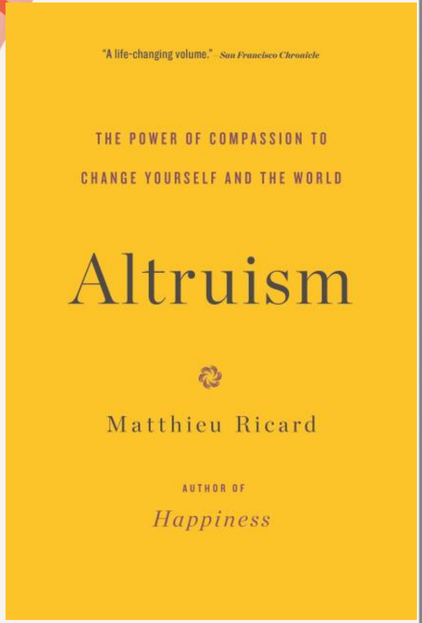
Point where no player can improve their outcome by changing strategy alone.
"If there are 2/3 Hawks, I get the same if I play Hawk or Dove!"

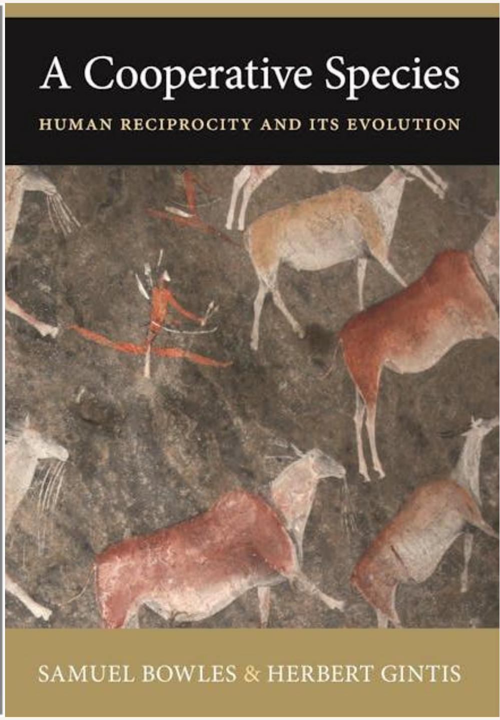
ESS



Point where a rare mutant with a different strategy cannot invade the population.
This (formally) requires that:
- 1) Either at the ESS the mutant has lower fitness than the "resident" population (it cannot invade the population)
- 2) If it has the same fitness, than its fitness must decrease as it becomes common (it can be invaded once resident)

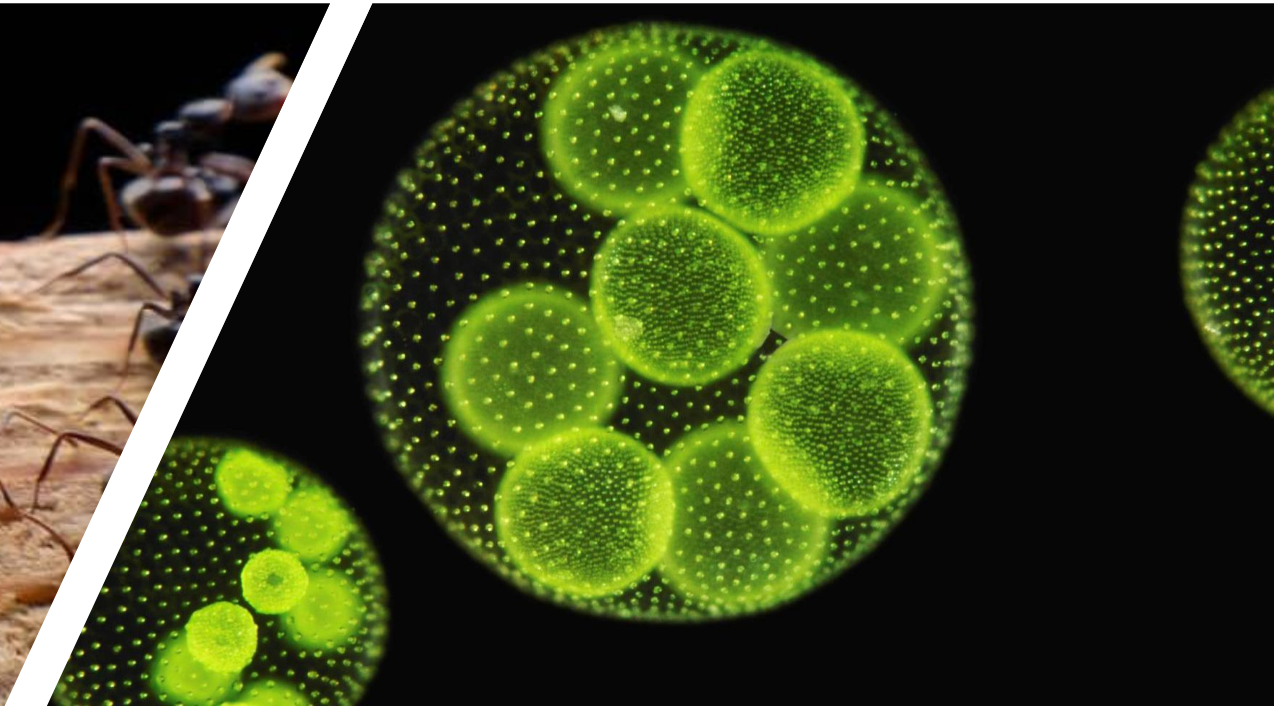
The evolution of cooperation





The evolution of cooperation

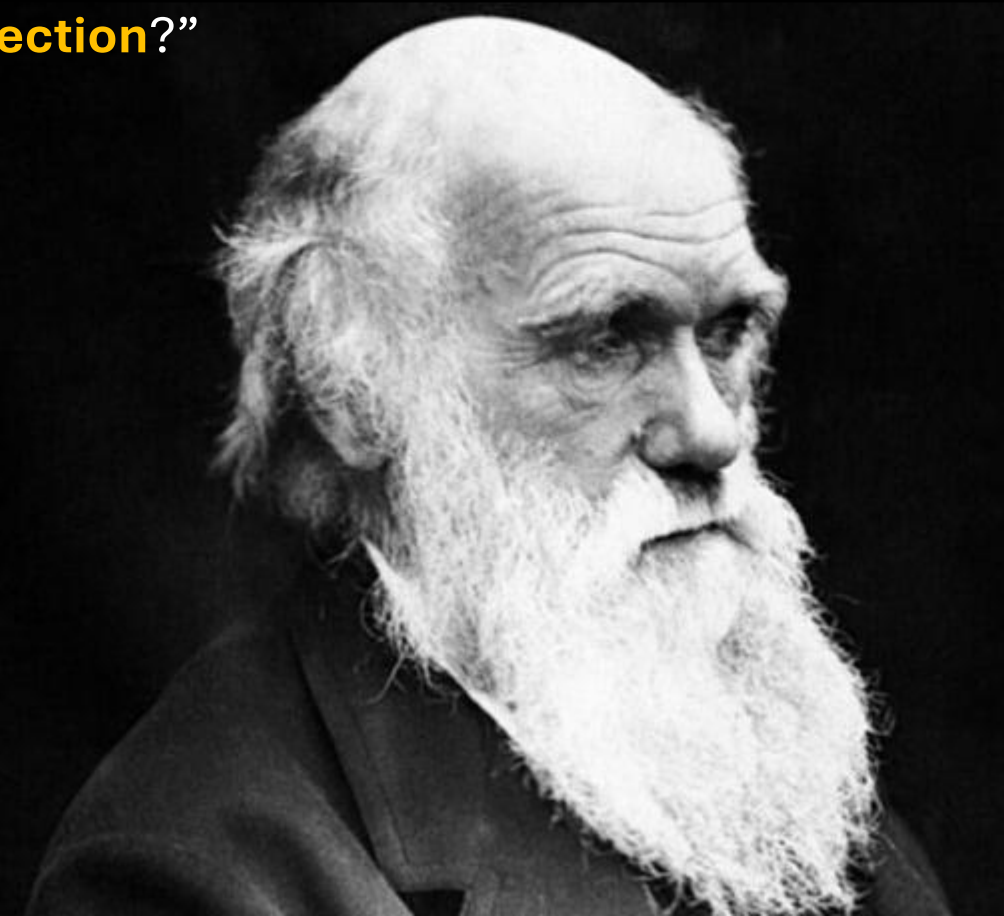


From the «On the Origin of Species»:

“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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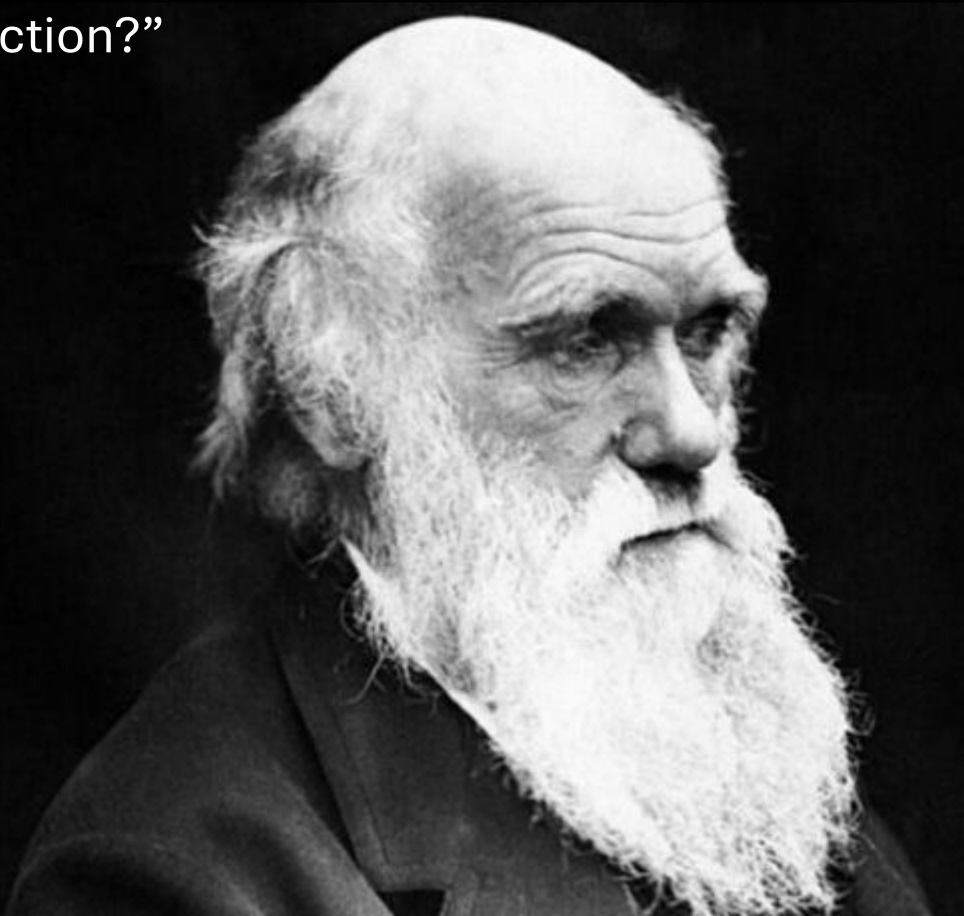
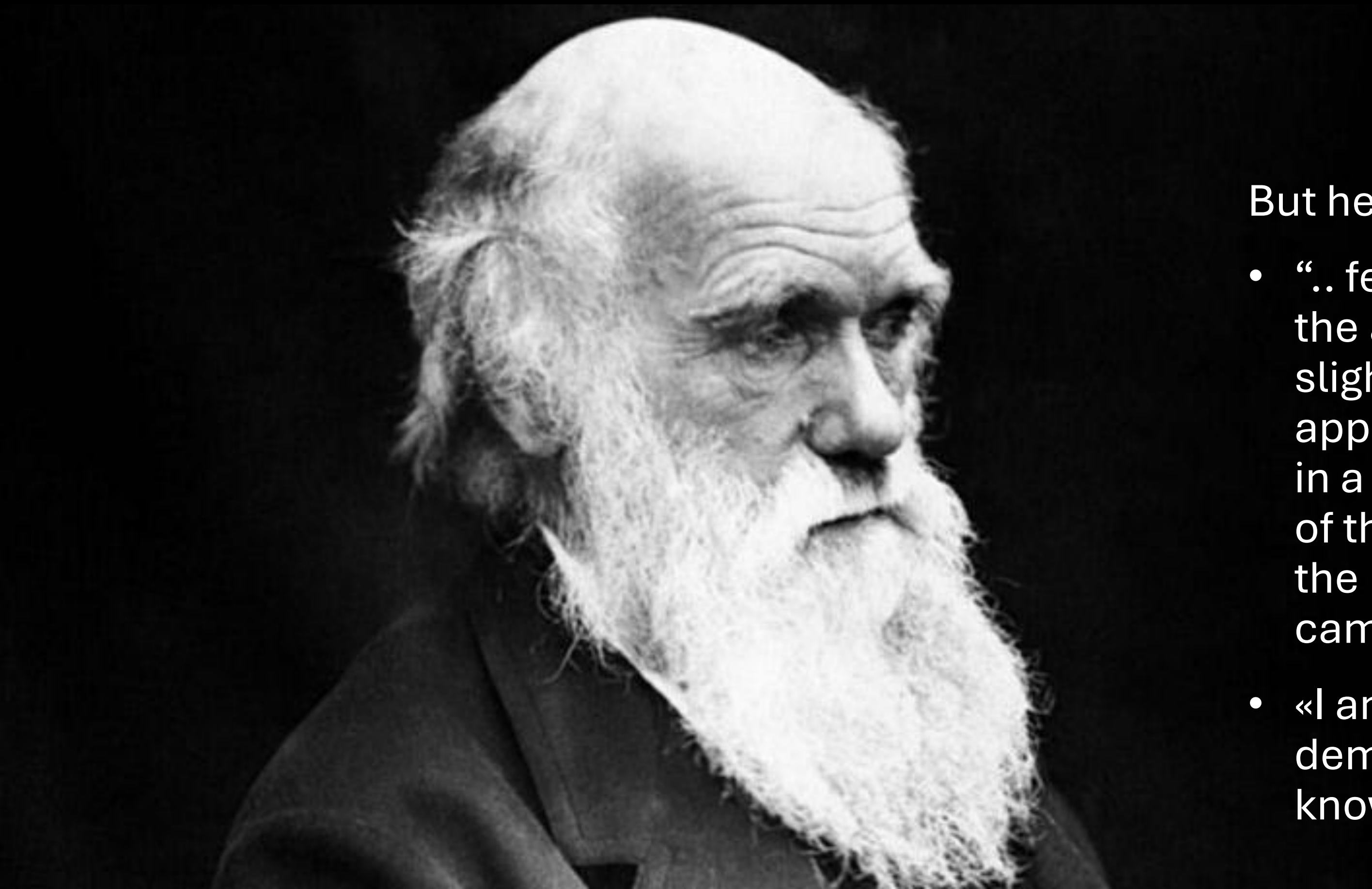


“Hence I can see no real difficulty in any character having become correlated with the sterile condition of certain members of insect-communities: the difficulty lies in understanding how such correlated modifications of structure could have been slowly accumulated by natural selection. This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that **selection may be applied to the family, as well as to the individual**, and may thus gain…”



But he also 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.”

Eusociality

- **Reproductive division of labor:** queens reproduce, workers usually do not
- **Cooperative brood care:** individuals help raise offspring that are not their own
- **Overlapping generations:** parents and offspring coexist and interact

Ants, bees, wasps, and termites show eusociality, but ants are the most extreme case as workers are **completely sterile** and functions almost as a superorganism.

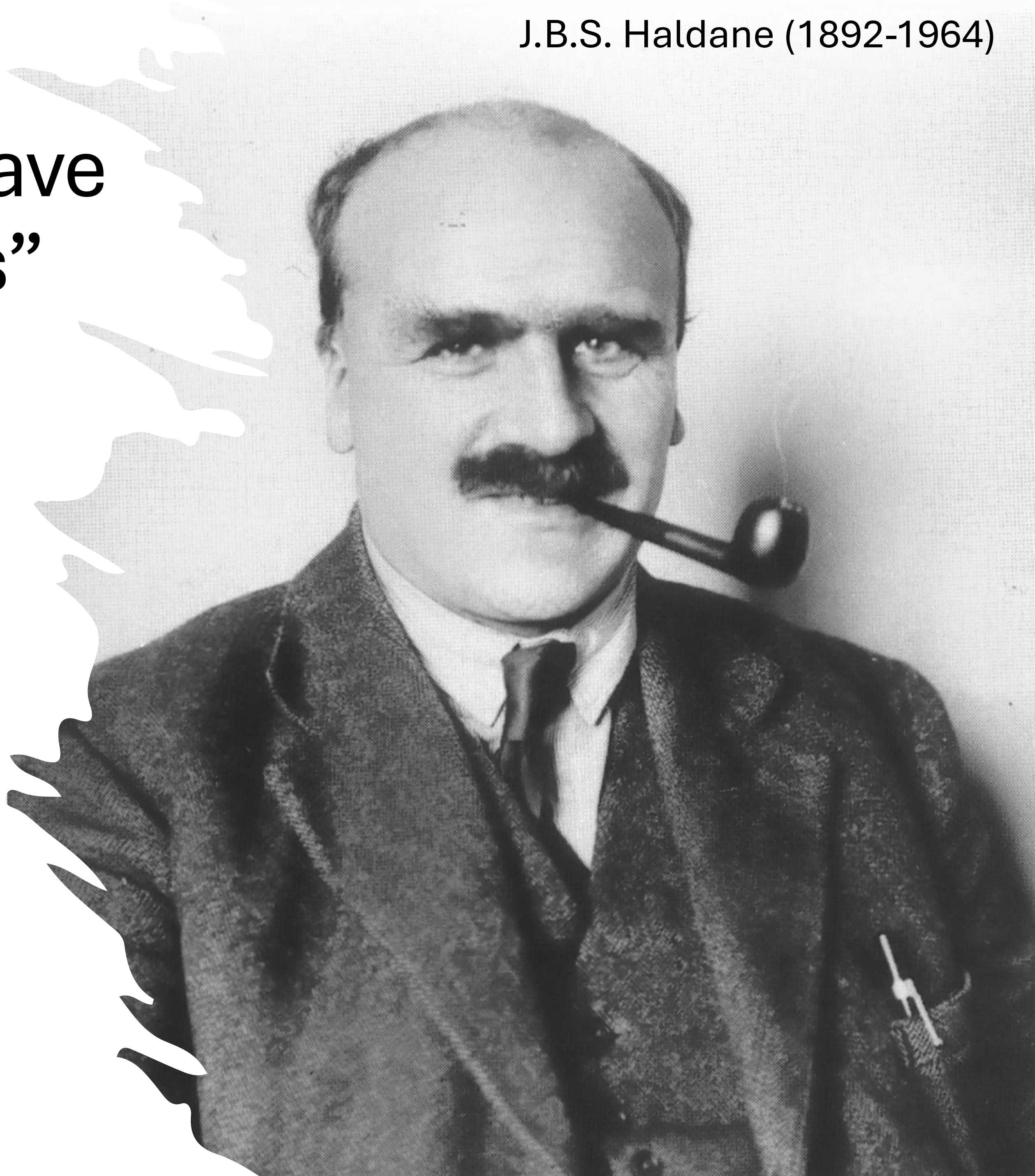
In order hymenoptera, haplodiploid sex determination:

- Diploid females (2n), from fertilized eggs
- Haploid males (1n), from unfertilized eggs

J.B.S. Haldane (1892-1964)

“I will jump into the river to save two brothers or eight cousins”

JBS Haldane, sometimes in the 50s, in a pub.



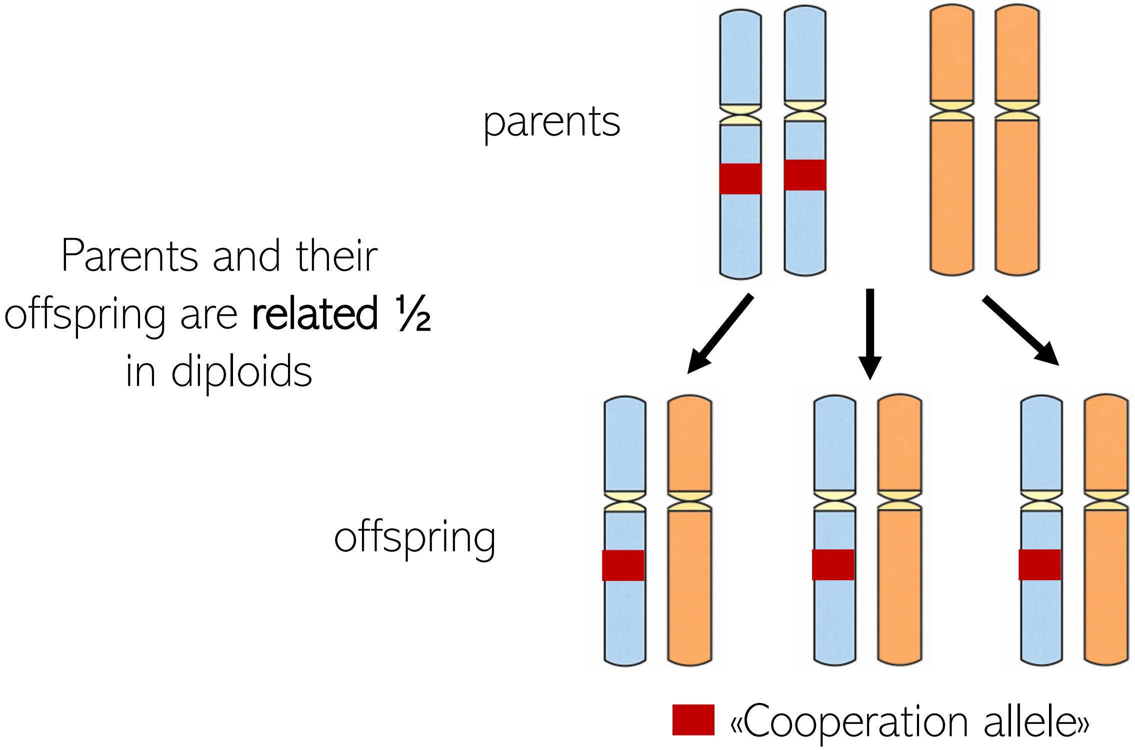
Hamilton's rule and kin-selection (1964)

Natural selection favors altruism when:

$$r\,b > c$$

where ***c*** is the **cost** of cooperation, ***b*** the **benefit** given and ***r*** is the **relatedeness** coefficient.

Bill Hamilton
(1936-2000)



Hamilton’s rule and kin-selection (1964)

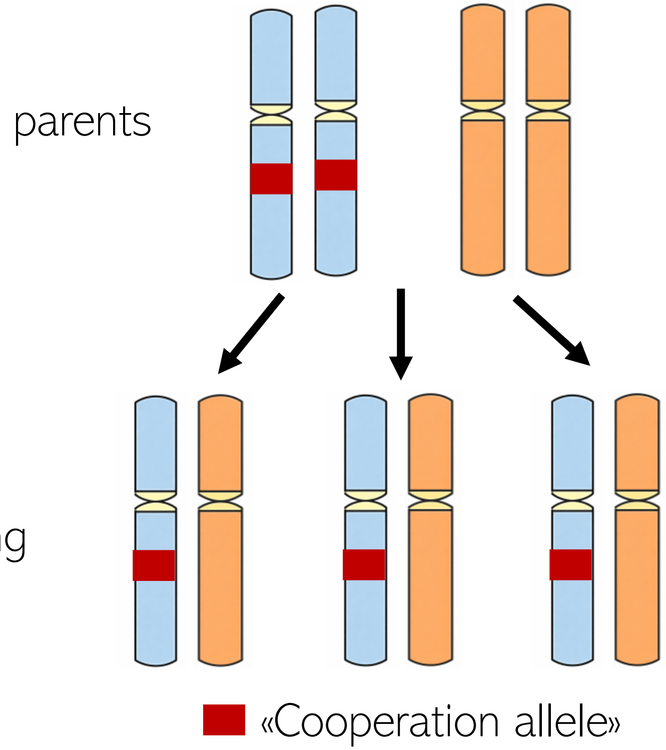
Natural selection favors altruism when:

$$r\,b > c$$

where ***c*** is the **cost** of cooperation, ***b*** the **benefit** given and ***r*** is the **relatedeness** coefficient.

In other words, the more related two individuals are, the more kin selection favors altruism as helping another individual translates into helping the spread of the «cooperative allele»

Bill Hamilton
(1936-2000)



A mother helping 3 of his offspring is helping 3/2 of herself (actually her cooperative allele)!

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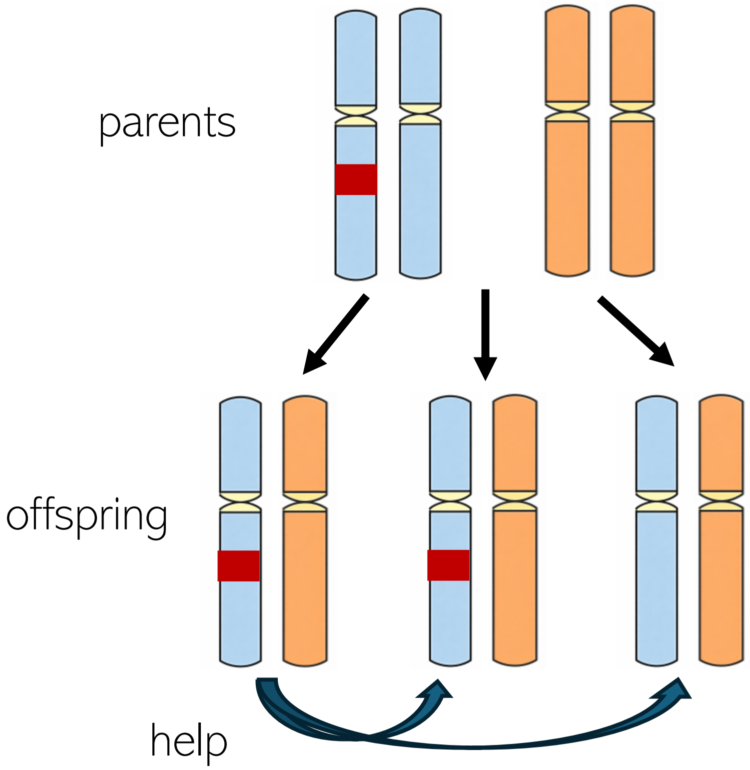
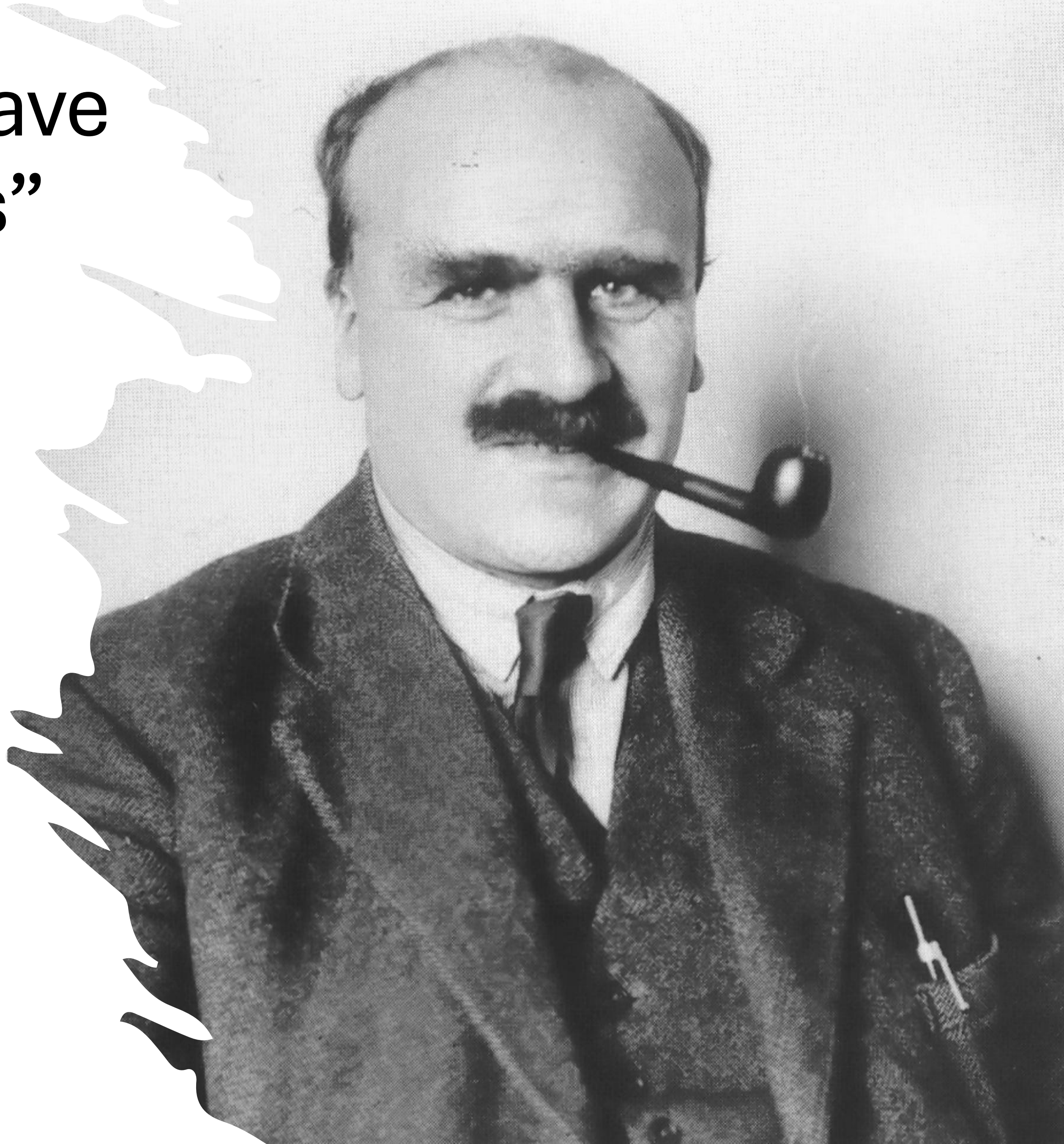
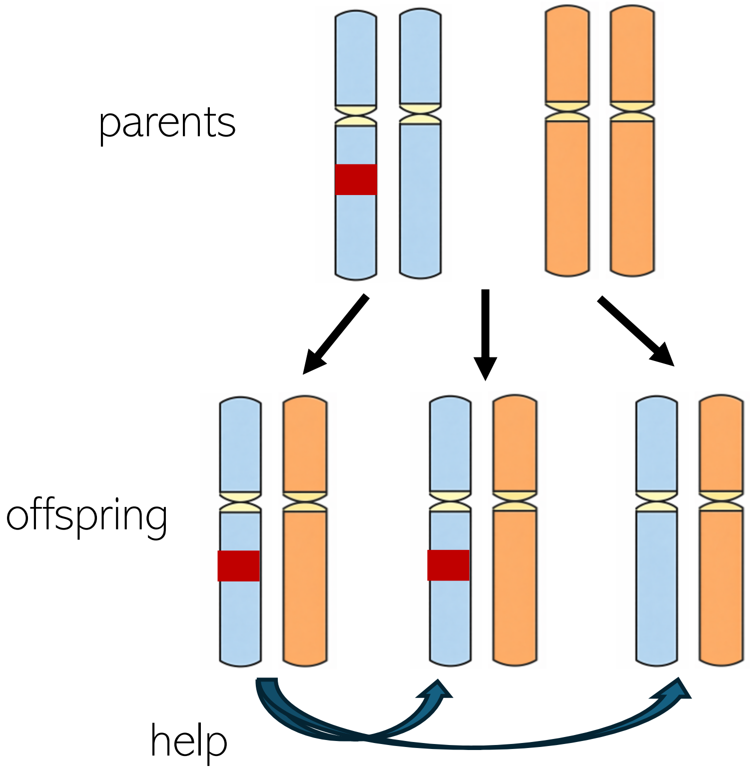




ocean full of sharks

"I will jump into the ~~river~~ to save two brothers or eight cousins"

JBS Haldane, sometimes in the 50s, in a pub.

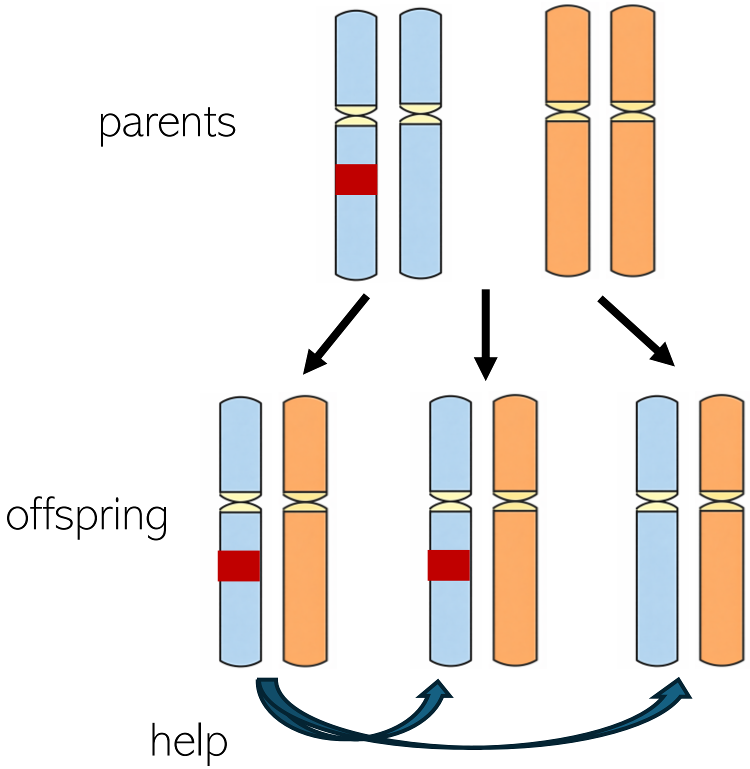


“I will jump into the ~~river~~ ocean full of sharks to save two brothers or eight cousins”

JBS Haldane, sometimes in the 50s, in a pub.

He already has fitness as if he already had three children (including his mom)

Let’s call this «**inclusive fitness**»



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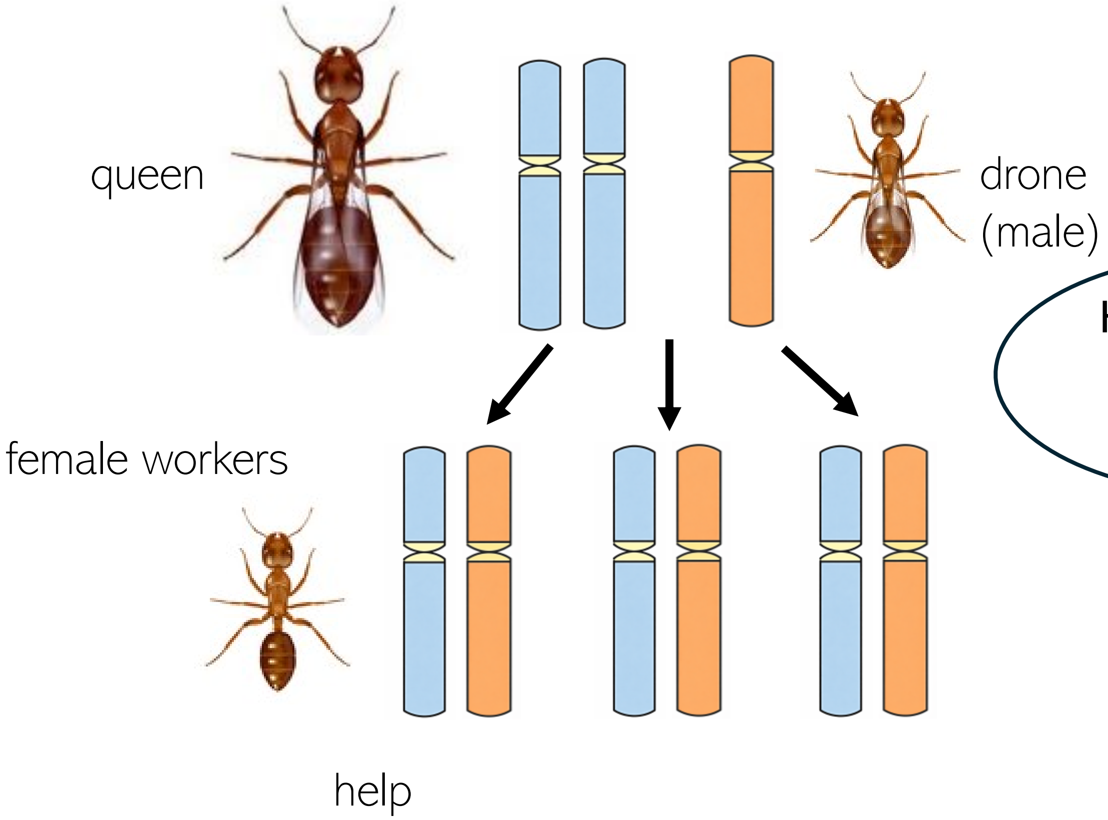
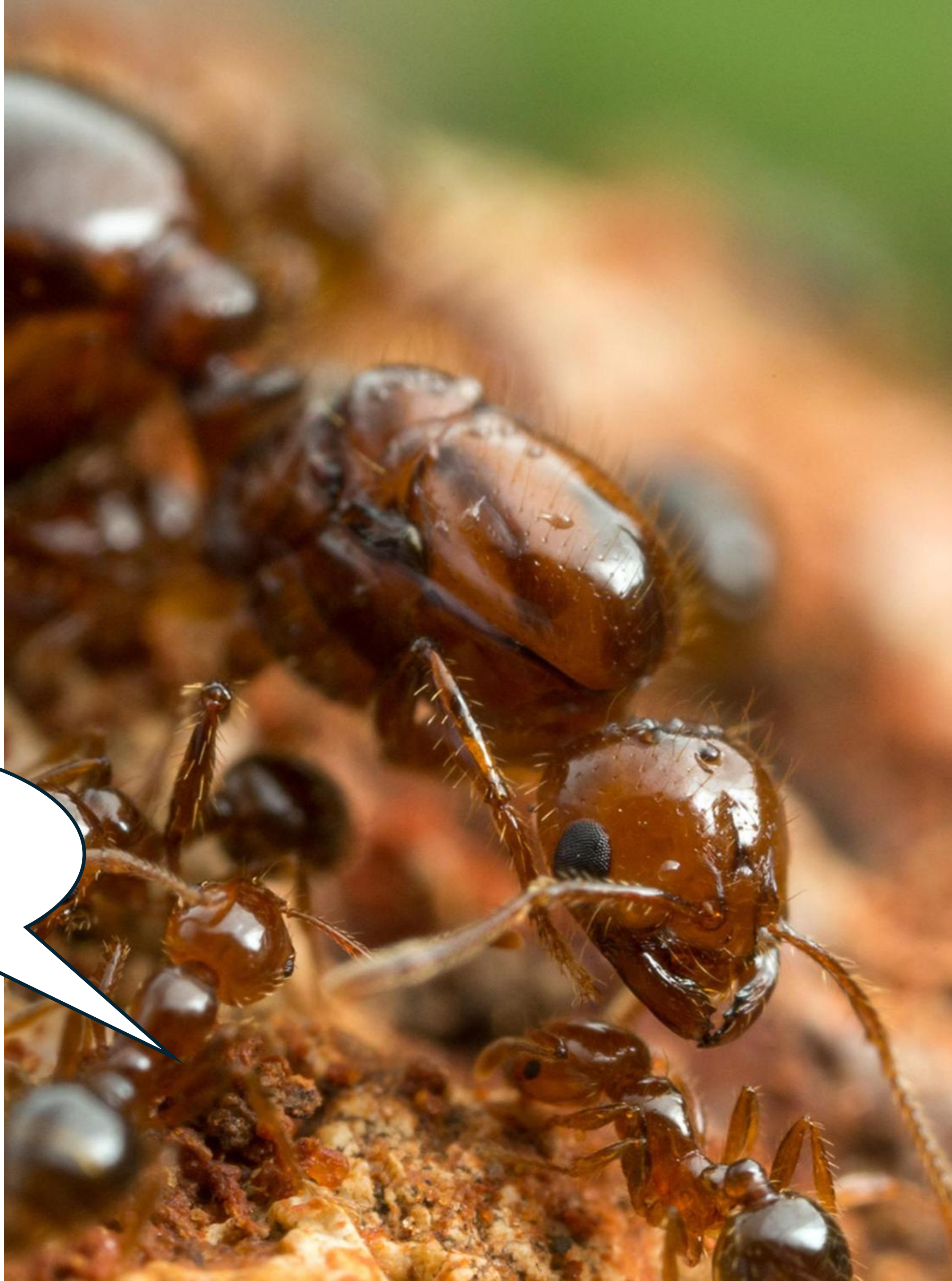
Australian teen swam hours to shore to get help for mother and siblings swept out to sea

FEB 3, 2026

“I will not reproduce to make my overly-related queen/mother make more babies”

An ant

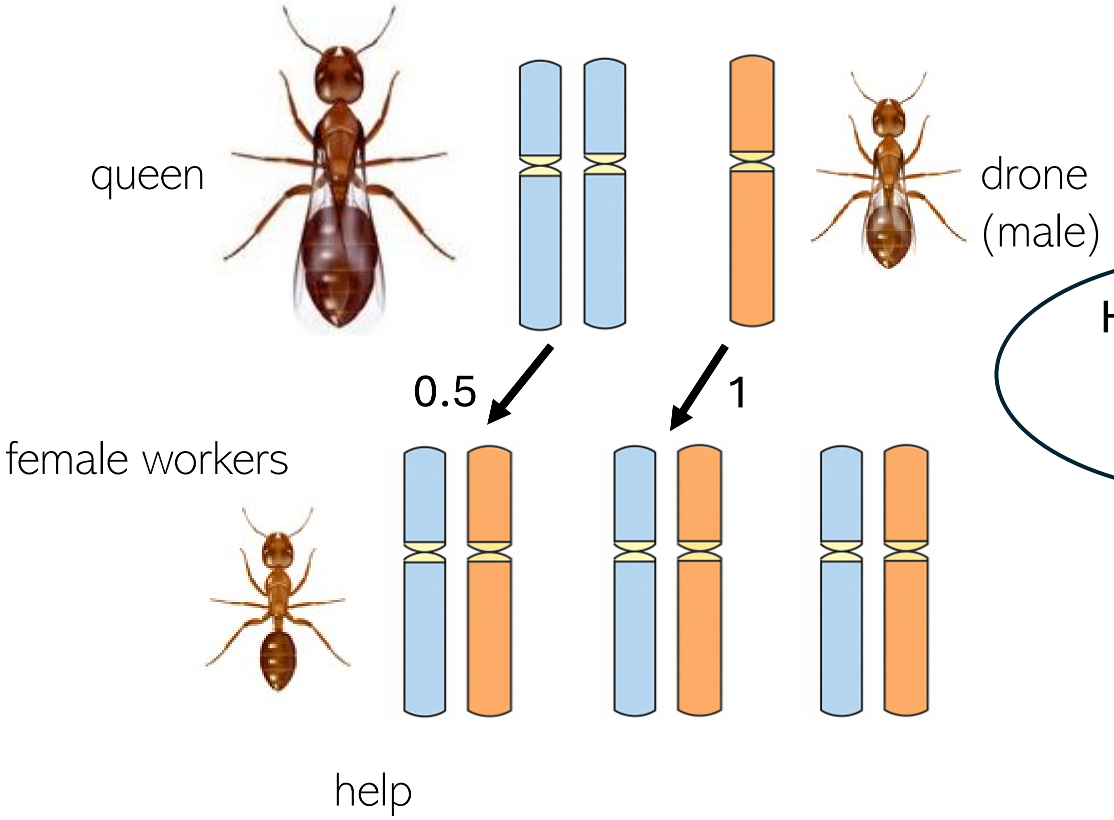


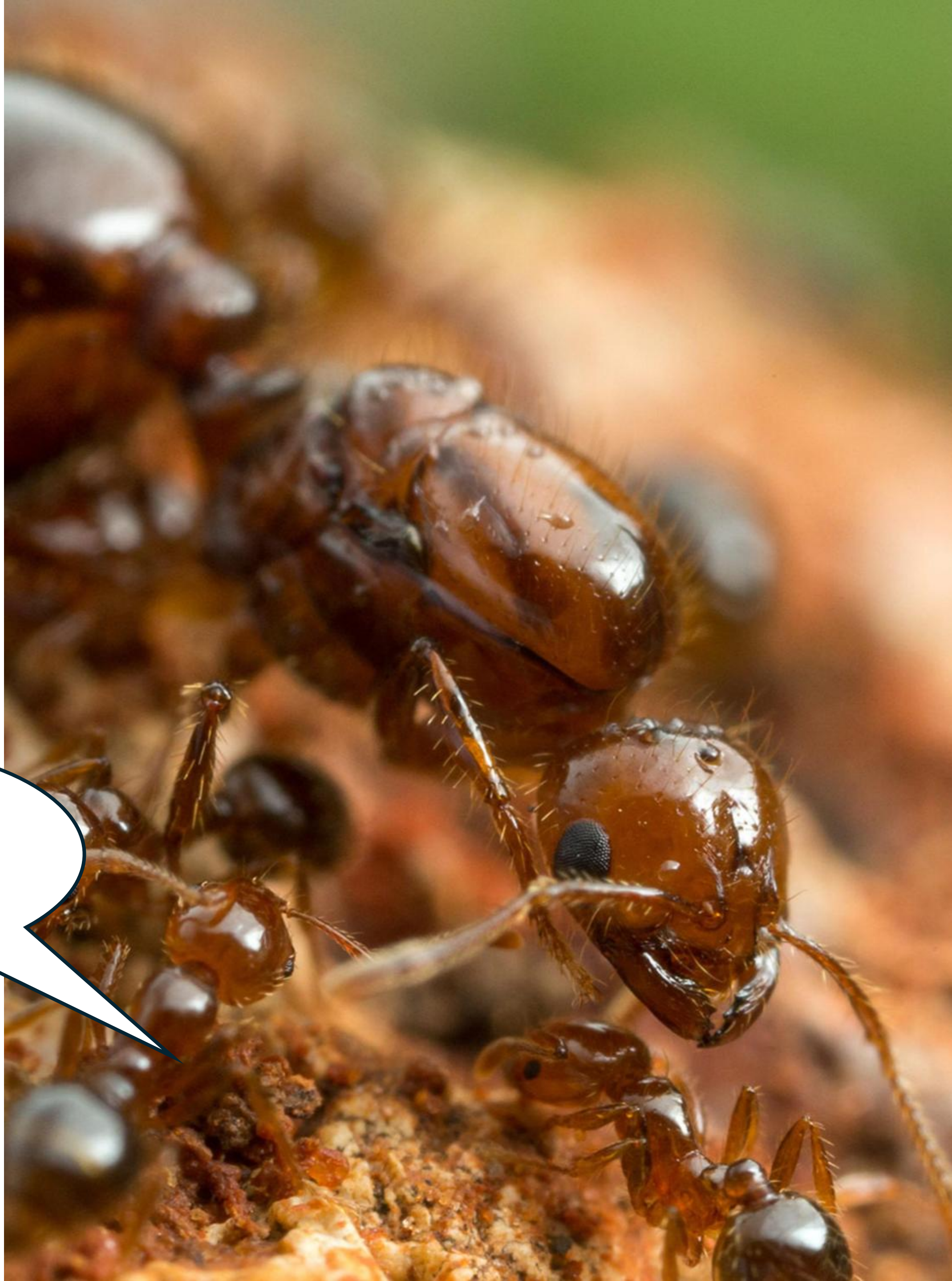


“I will not reproduce to make my overly-related queen/mother make more babies”

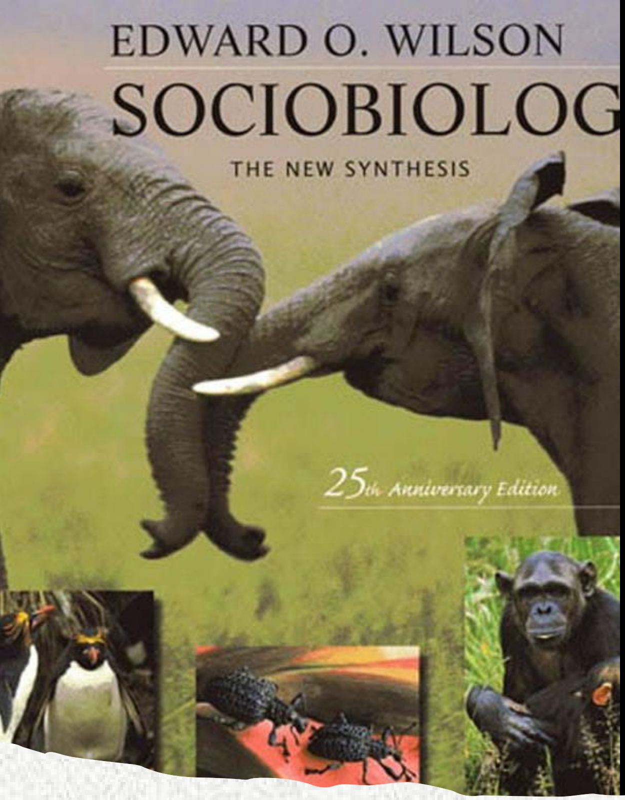
An ant

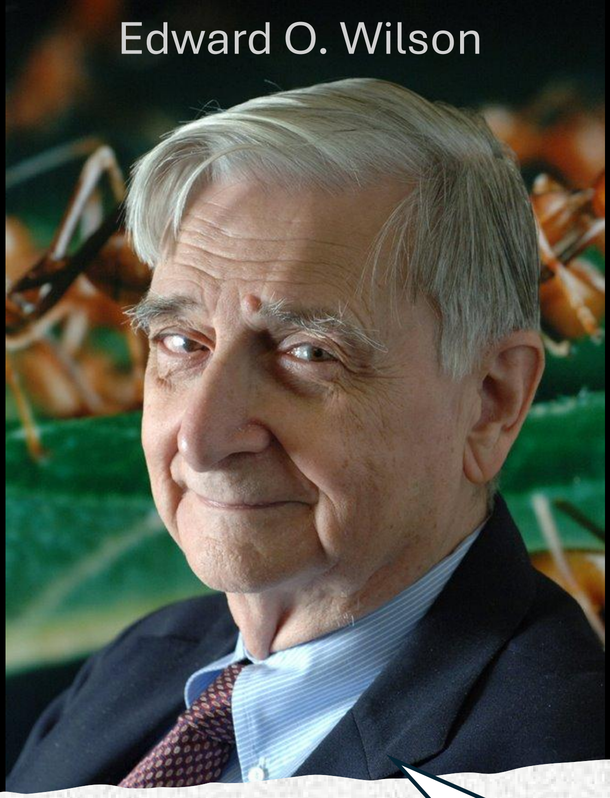
r between siblings= ½*0.5+ ½*01=0.75

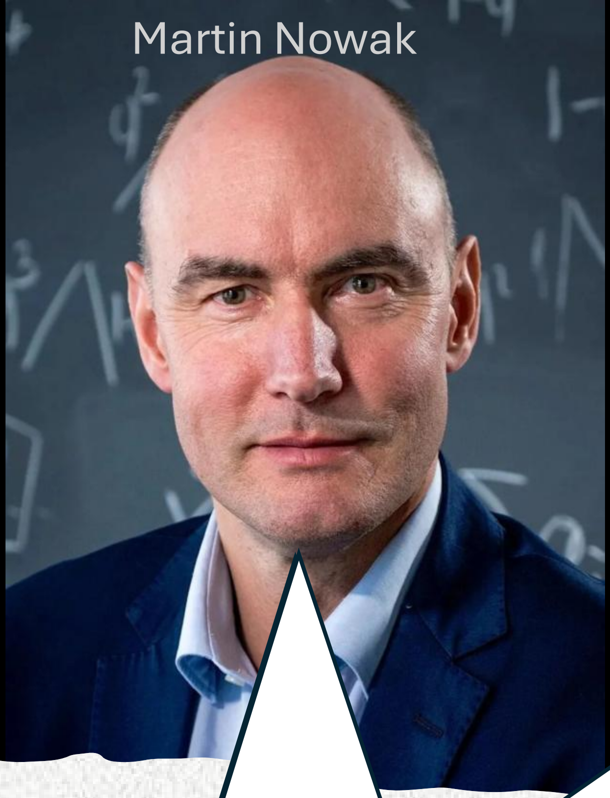


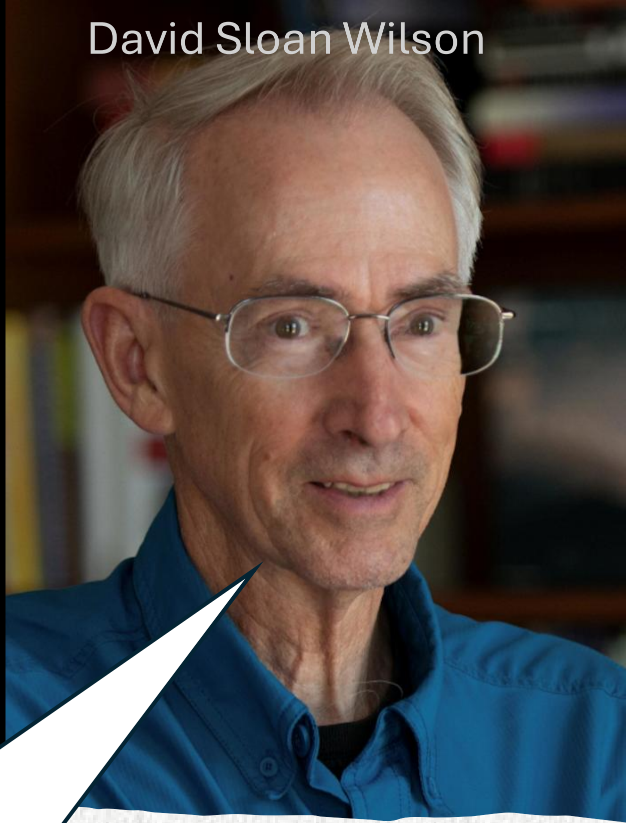



EDWARD O. WILSON
SOCIOBIOLOG
THE NEW SYNTHESIS
25th Anniversary Edition
Edward O. Wilson
Martin Nowak
David Sloan Wilson
This is too reductionist!
Antonella Tramacere, Roma Tre





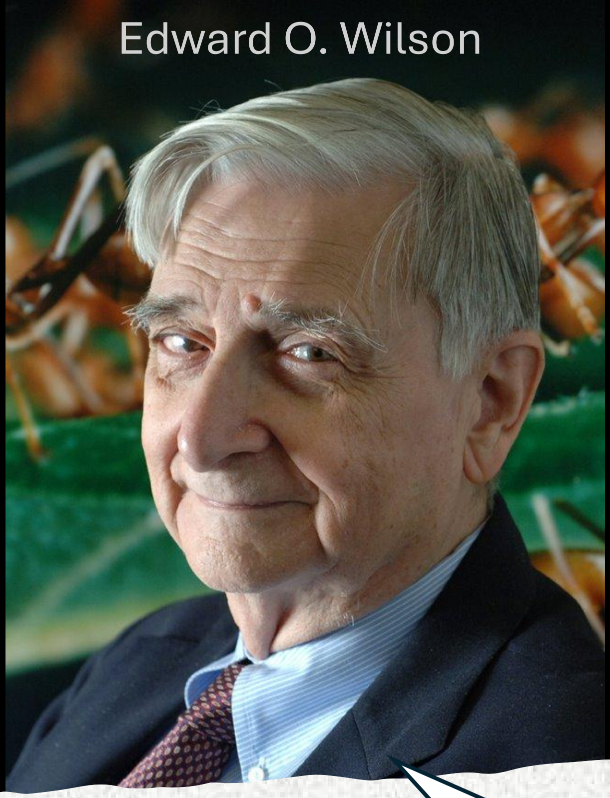


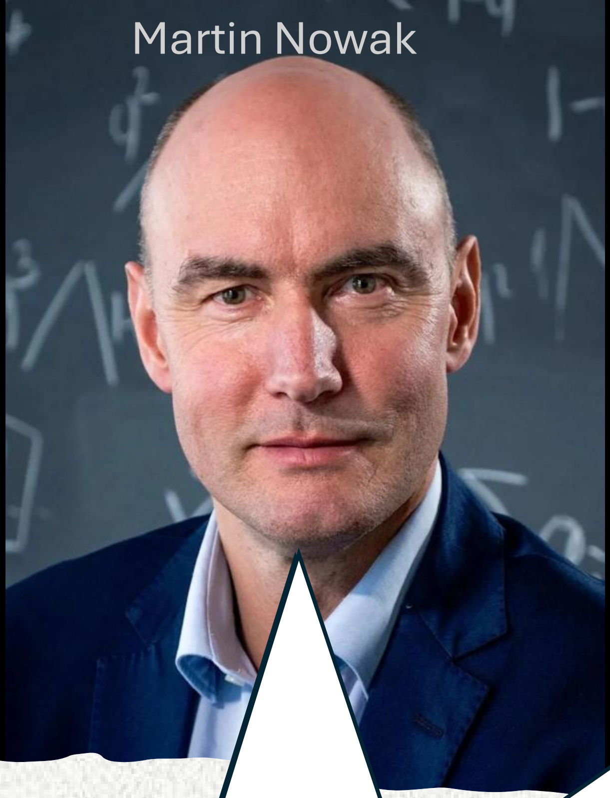


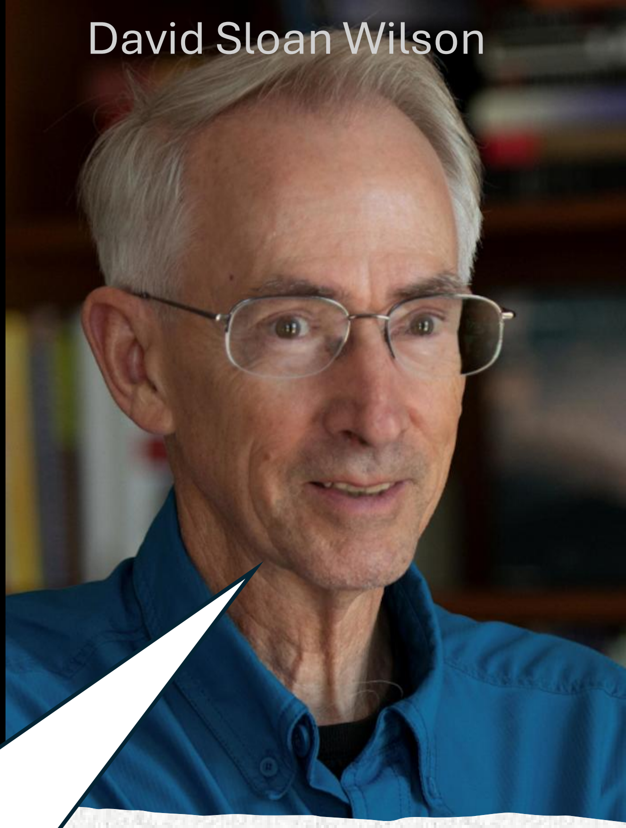
Actually I care more that it is not mathematically rigorous*..

*And if you care, inclusive fitness is also «dynamically insufficient». We'll see a little bit what it means next time


A solitary wasp from the Sphecidae family

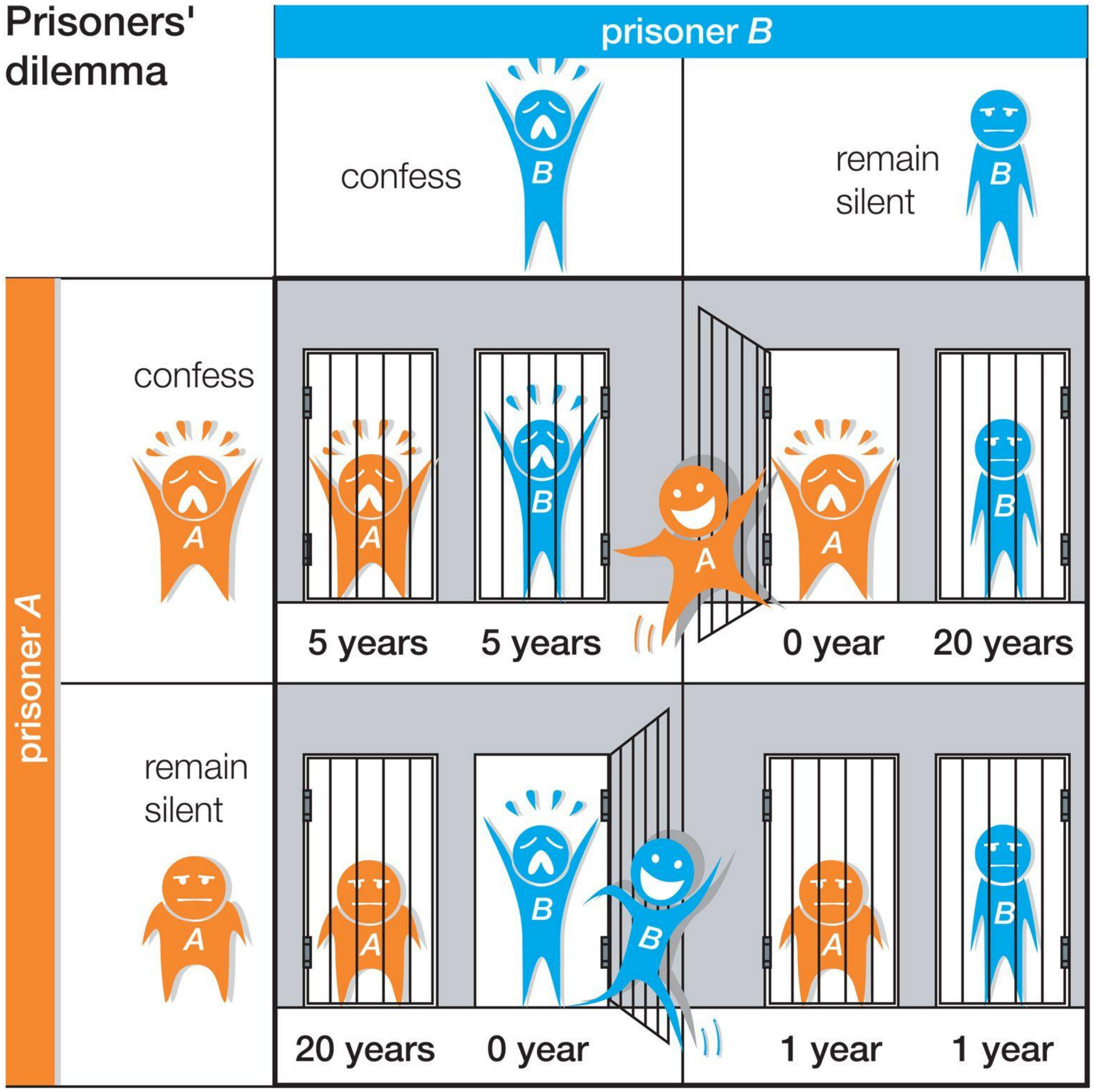

Edward O. Wilson


Martin Nowak

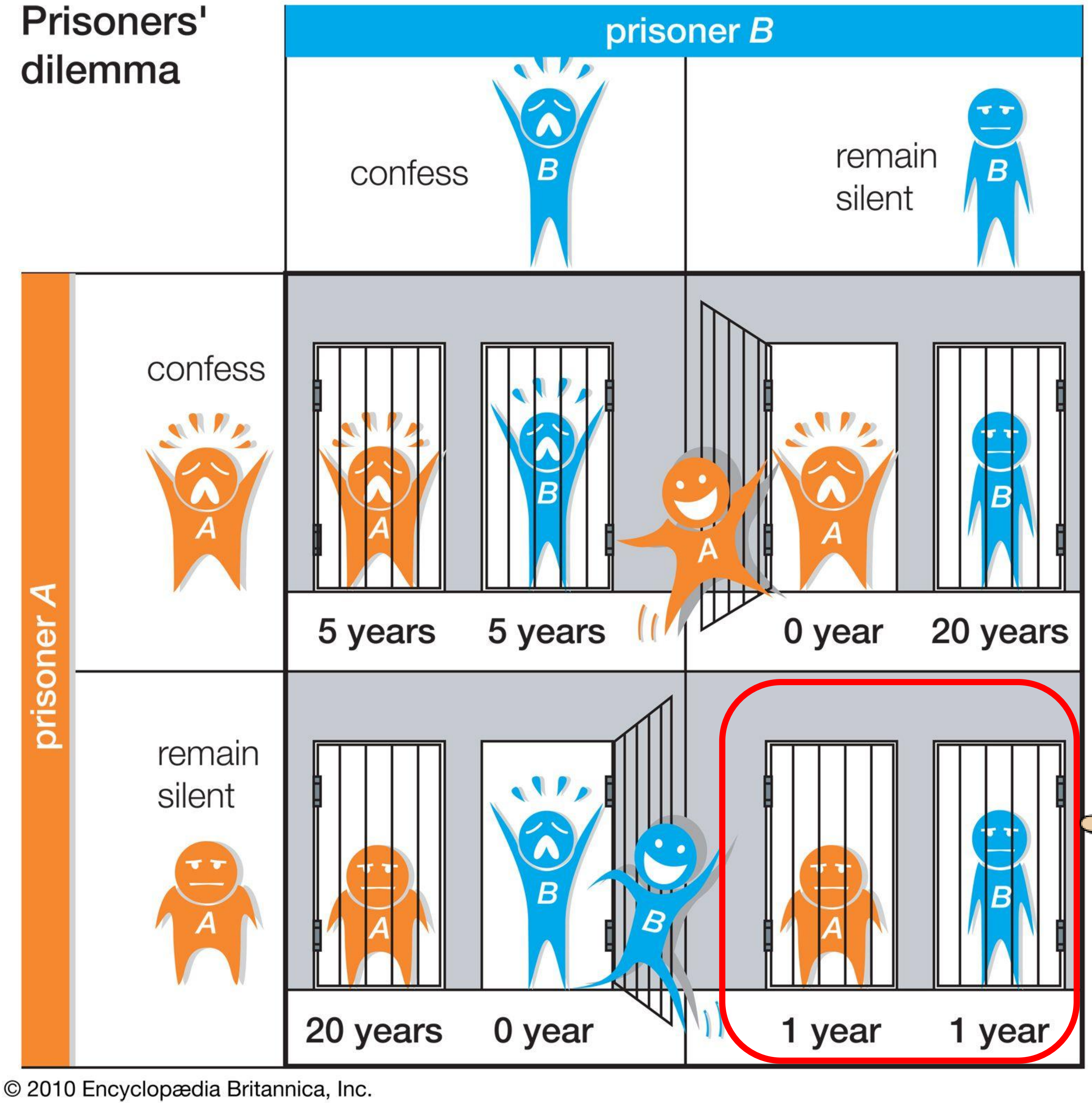

David Sloan Wilson

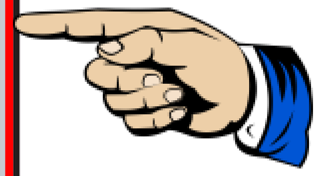
And I care more that almost all hymenoptera are haplodiploid, but **most are not eusocial**!
That among ants and bees there's **cheaters** too!
And there are many **non-haplodiploid eusocial** animals!


Heterocephalus glaber



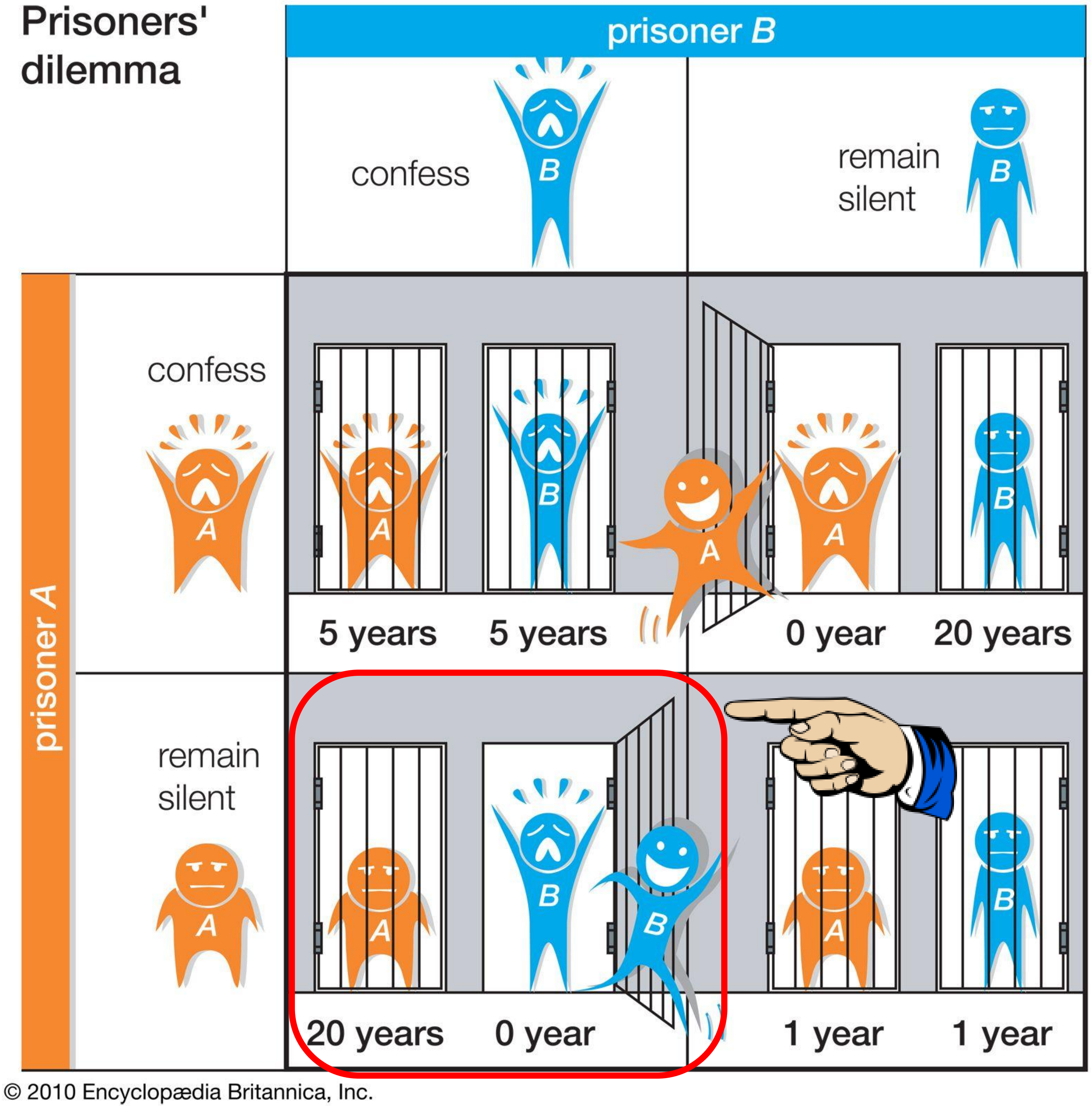
Two prisoners agree before being caught not to snitch. They can either cooperate with each other (remain silenct) or defect (confess).





Two prisoners agree before being caught not to snitch. They can either cooperate with each other (remain silenct) or defect (confess).

- *If nobody confess and stick to the plan, remaining silent (cooperation among each other), the police has little proofs, so they get 1 year each.*



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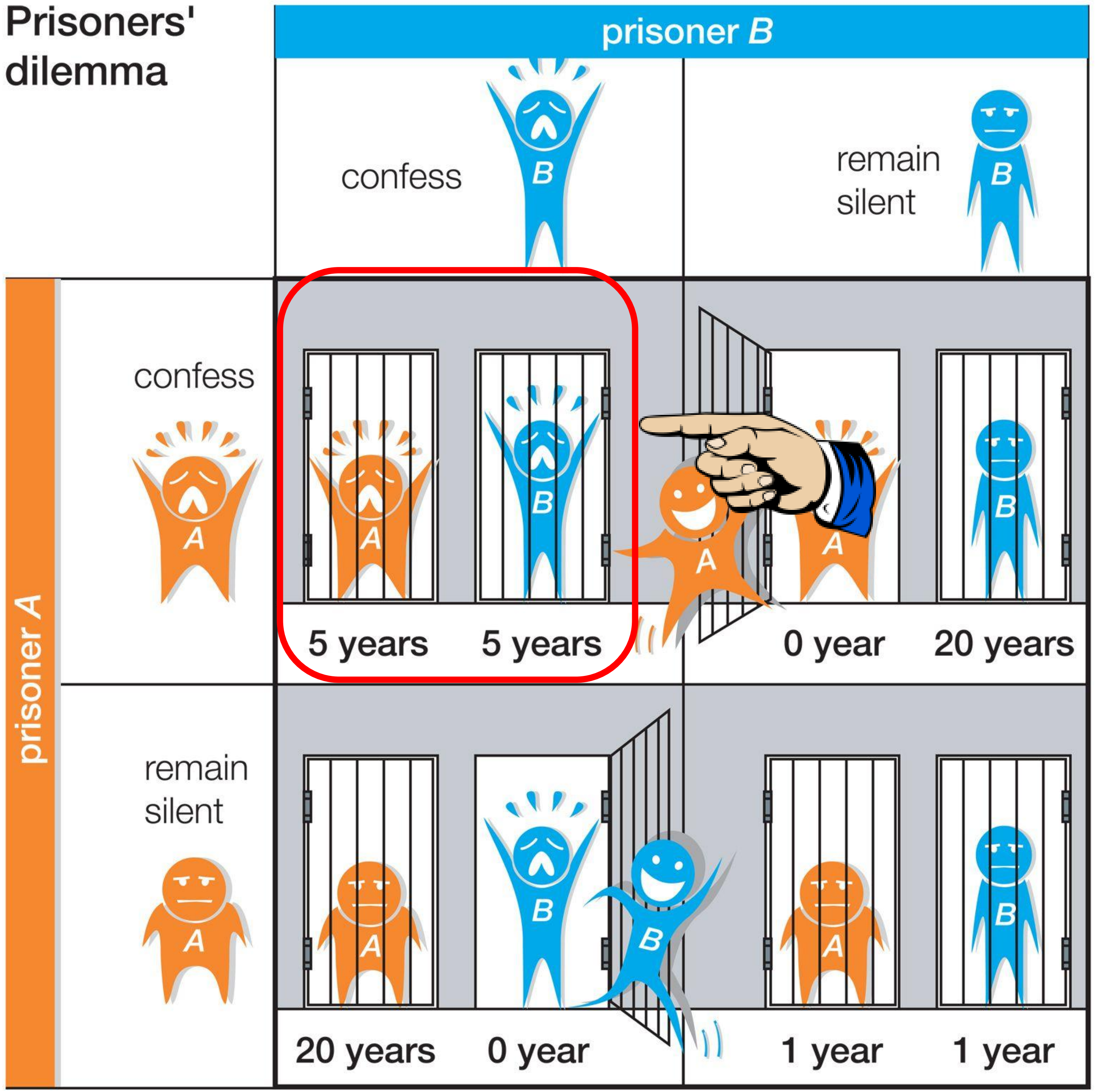
- *However if one cooperate but the other is a snitch and confess, he gets 20 years and the other 0 years as discount.*



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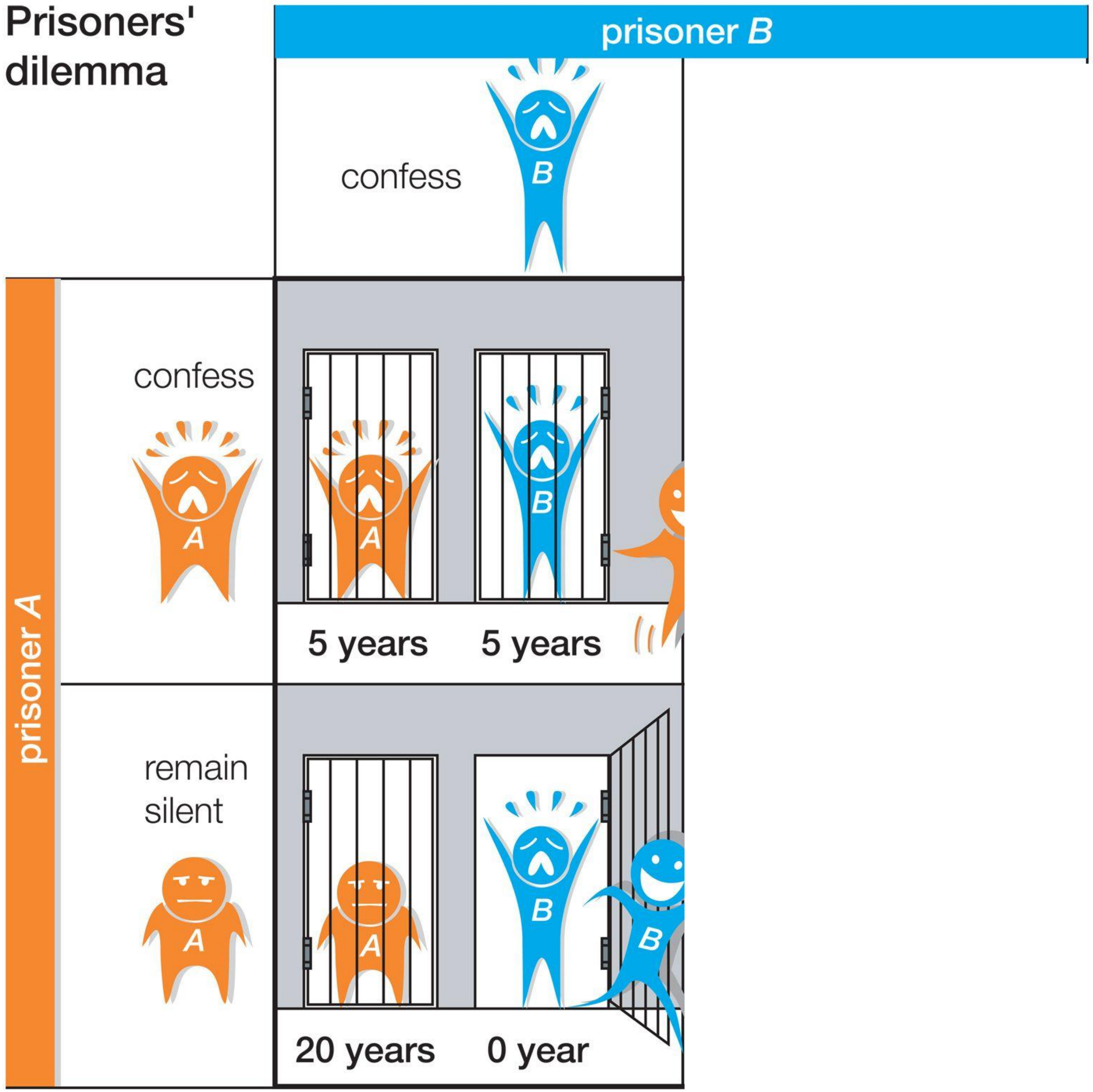
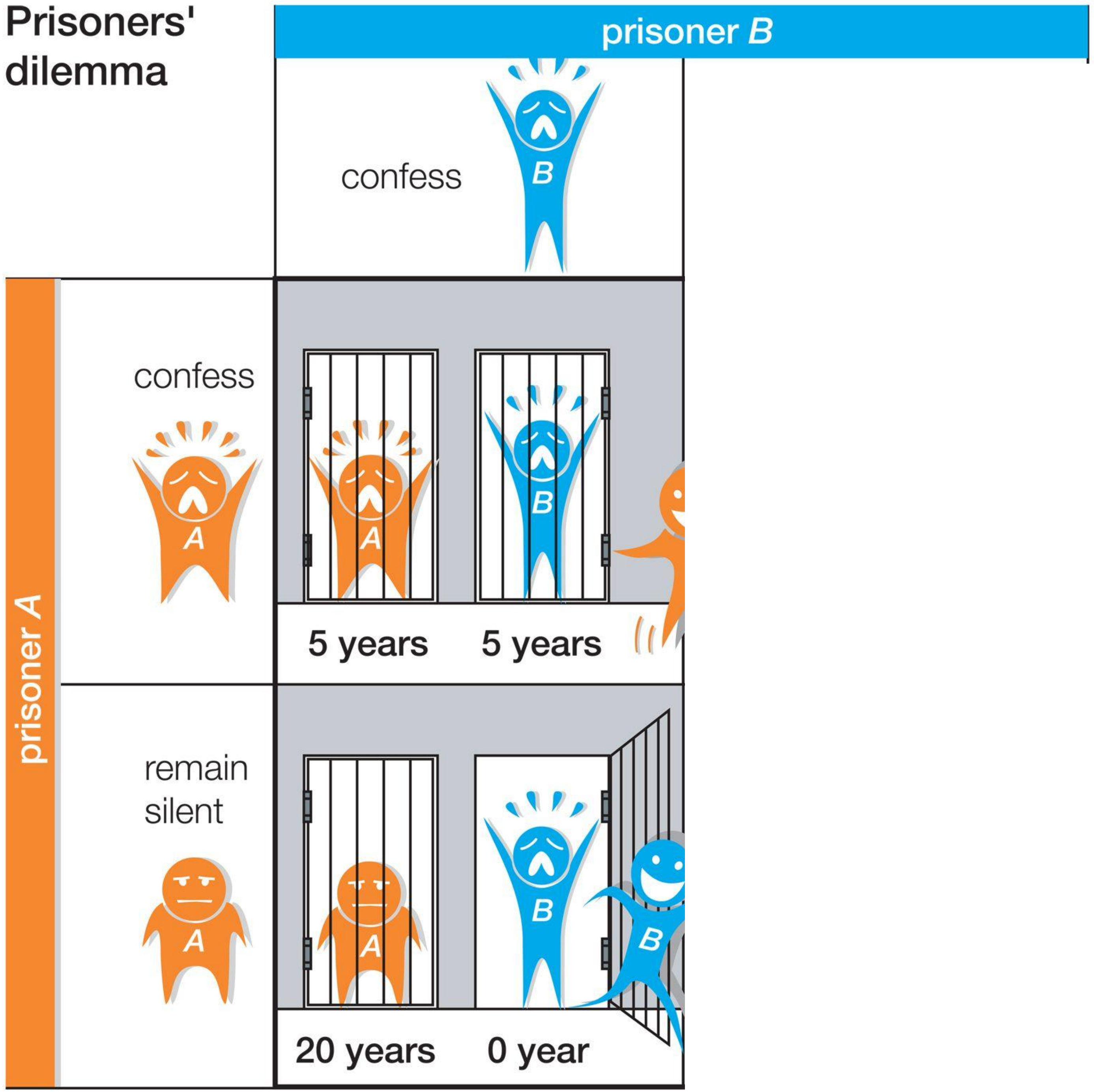
- If nobody confess and stick to the plan, remaining silent (cooperation among each other), the police has little proofs, so they get 1 year each.
- However if one cooperate but the other is a snitch and confess, he gets 20 years and the other 0 years as discount.
- If they both confess, they only get 5 years each. Not great, but better for A than if prisoner A remained silent



All in all

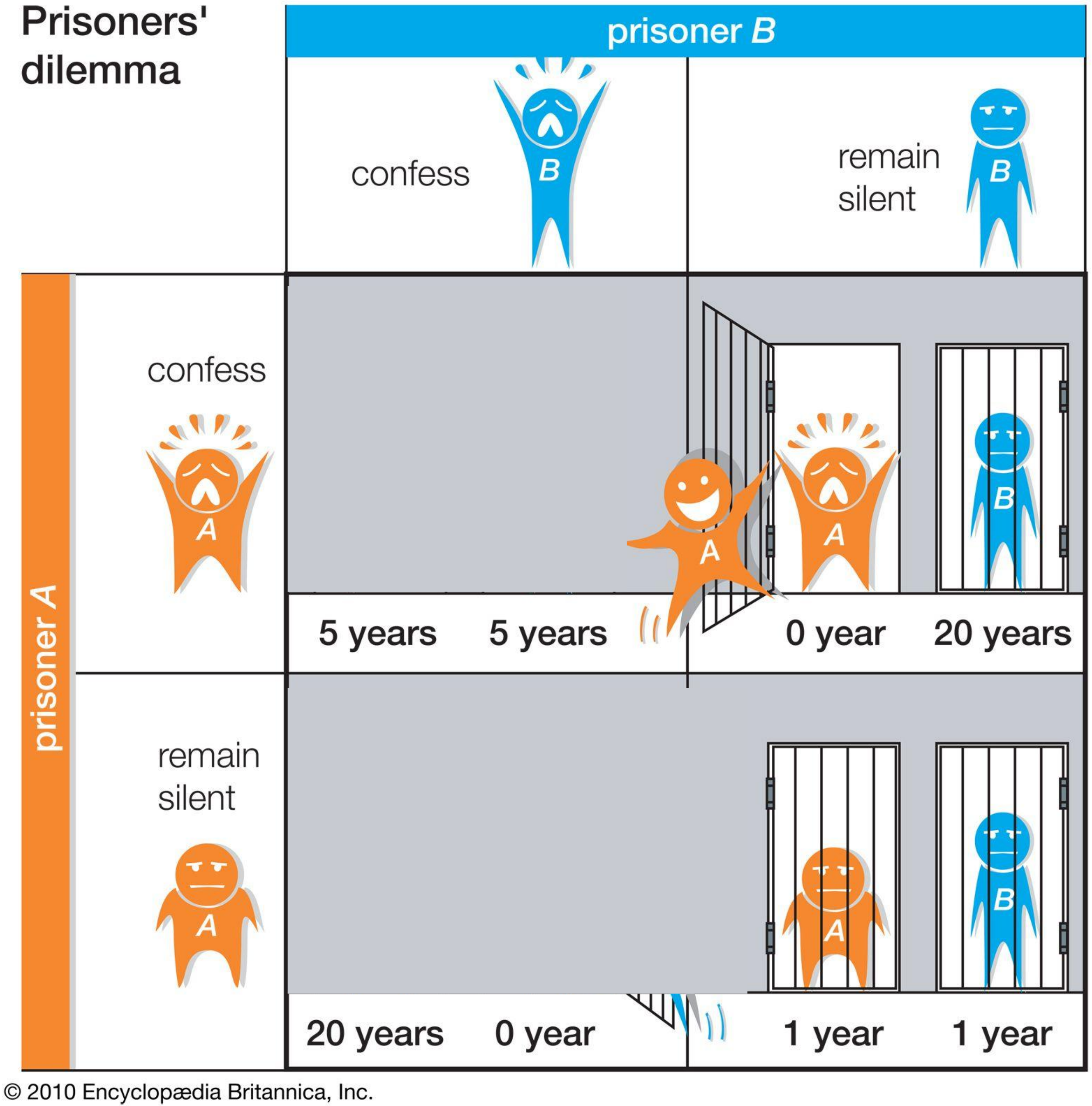
If Prisoner's B confesses (defects), what's convenient for A to do?



All in all

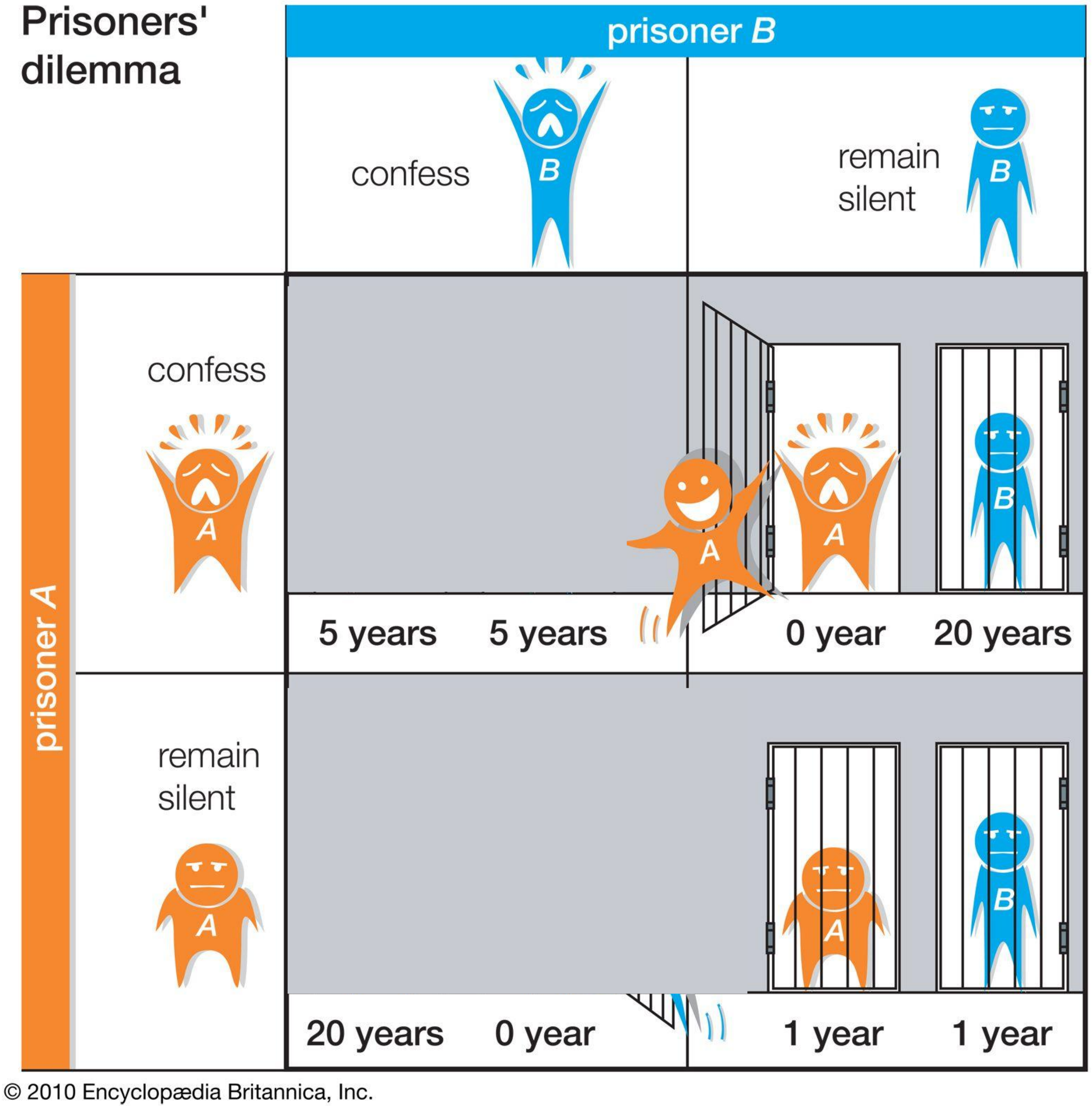
If Prisoner's B confesses (defects), what's convenient for A to do?

*Prisoner A should confess/**defect** too!*



All in all

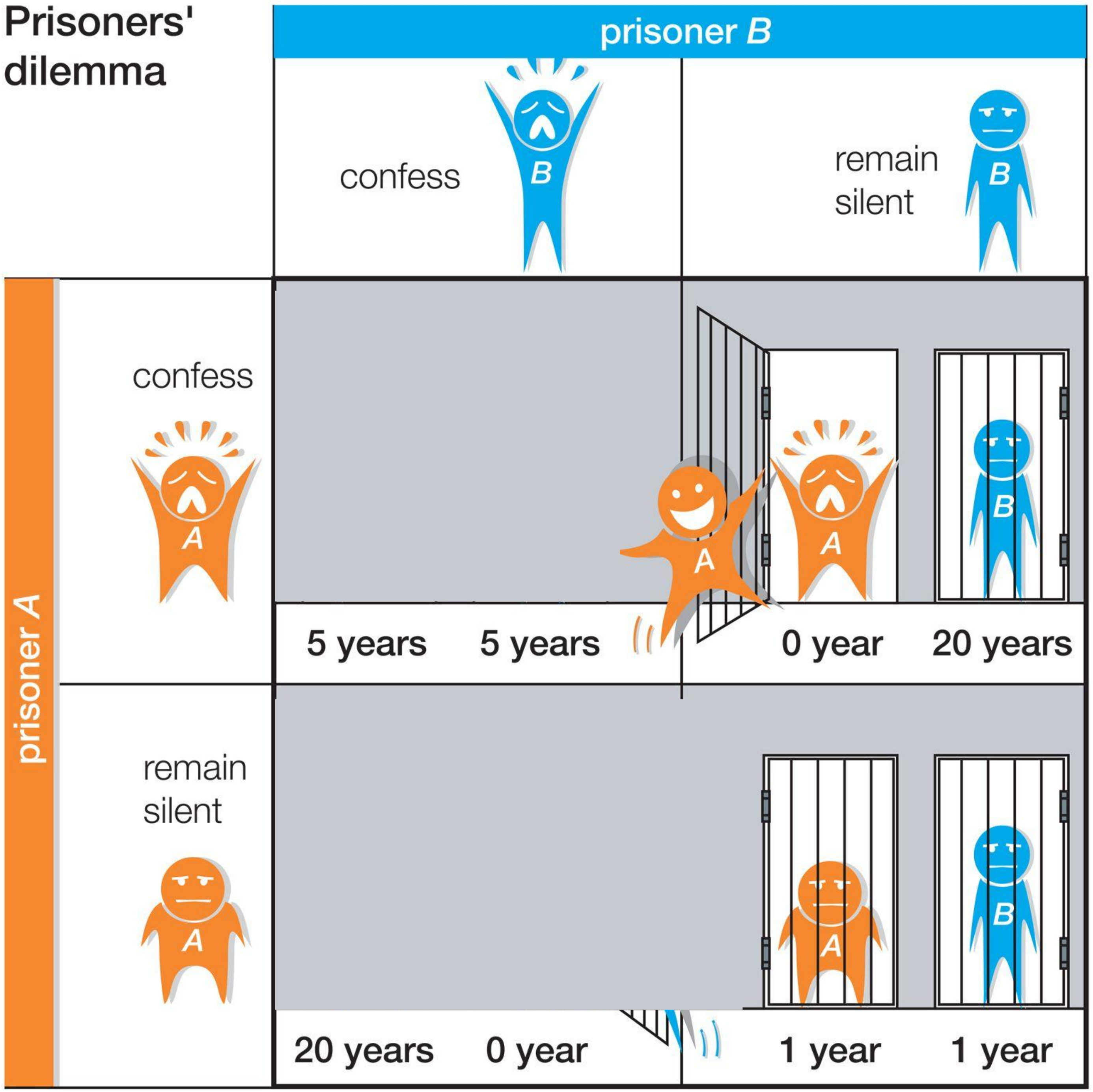
If Prisoner's B remains silent (cooperates), what's convenient for A to do?



All in all

If Prisoner's B remains silent (cooperates), what's convenient for A to do?

Prisoner B should still confess/**defect**!



A prisoner should always defect! Never cooperate!

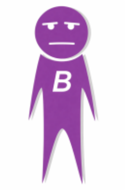
If Prisoner's B confesses (defects), what's convenient for A to do?

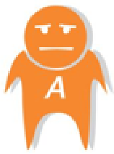
Prisoner A should confess/**defect** too!

If Prisoner's B remains silent (cooperates), what's convenient for A to do?

Prisoner B should still confess/**defect**!

The Prisoner's dilemma is a «strict» social dilemma where it is always convenient to defect





	C (cooperate)	D (Defect)
C (Cooperate)	b-c,b-c	-c,b
D (Defect)	b,-c	0,0

b=benefit provided by the cooperator
c=cost of cooperation

The Prisoner's dilemma is a «strict» social dilemma where it is always convenient to defect

	C (cooperate)	D (Defect)
C (Cooperate)	b-c	-c
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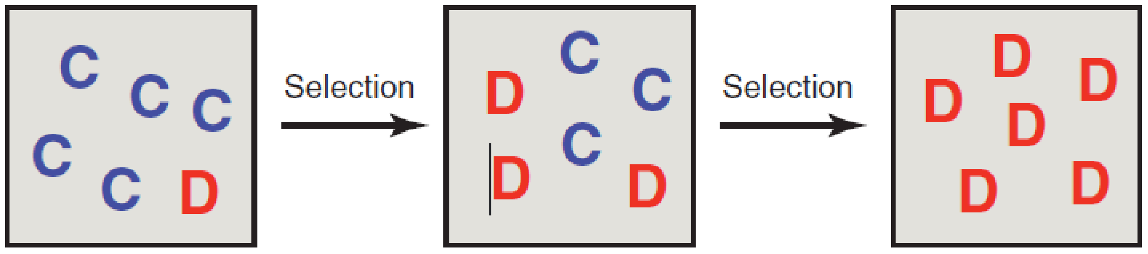

	C (cooperate)	D (Defect)
C (Cooperate)	b-c	-c
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b=benefit provided by the cooperator
c=cost of cooperation

The Prisoner's dilemma is a «strict» social dilemma where it is always convenient to defect

	C (cooperate)	D (Defect)
C (Cooperate)	b-c	-c
D (Defect)	b	0

b=benefit provided by the cooperator
c=cost of cooperation

When would you expect cooperation to evolve in this case (other than kin-selection)?




	C (cooperate)	D (Defect)
C (Cooperate)	b-c	-c
D (Defect)	b	0

Prisoner's dilemma is the most challenging social dilemma for cooperation

	C (cooperate)	D (Defect)
C (Cooperate)	b-c	-c
D (Defect)	b	0

Long ago, in 1978..

- ..Robert Axelrod organized a tournament among game theorists, all implementing their best computer program to compete among each other on the repeated (or iterated) Prisoner's Dilemma.
- Let's see what you come up with!

	C (cooperate)	D (Defect)
C (Cooperate)	3	0
D (Defect)	5	1

Now let's play it!

- Choose a strategy and write it down: for example «always defect», «random», «CDCDCD», etc.
- Do not reveal it!
- Pair-up.
- Play for 10 iterations with the same opponent.
- Record the payoffs.
- The top 4 strategies will get chocolate, who gets the least will be eaten alive by baby spiders

	C (cooperate)	D (Defect)
C (Cooperate)	3	0
D (Defect)	5	1

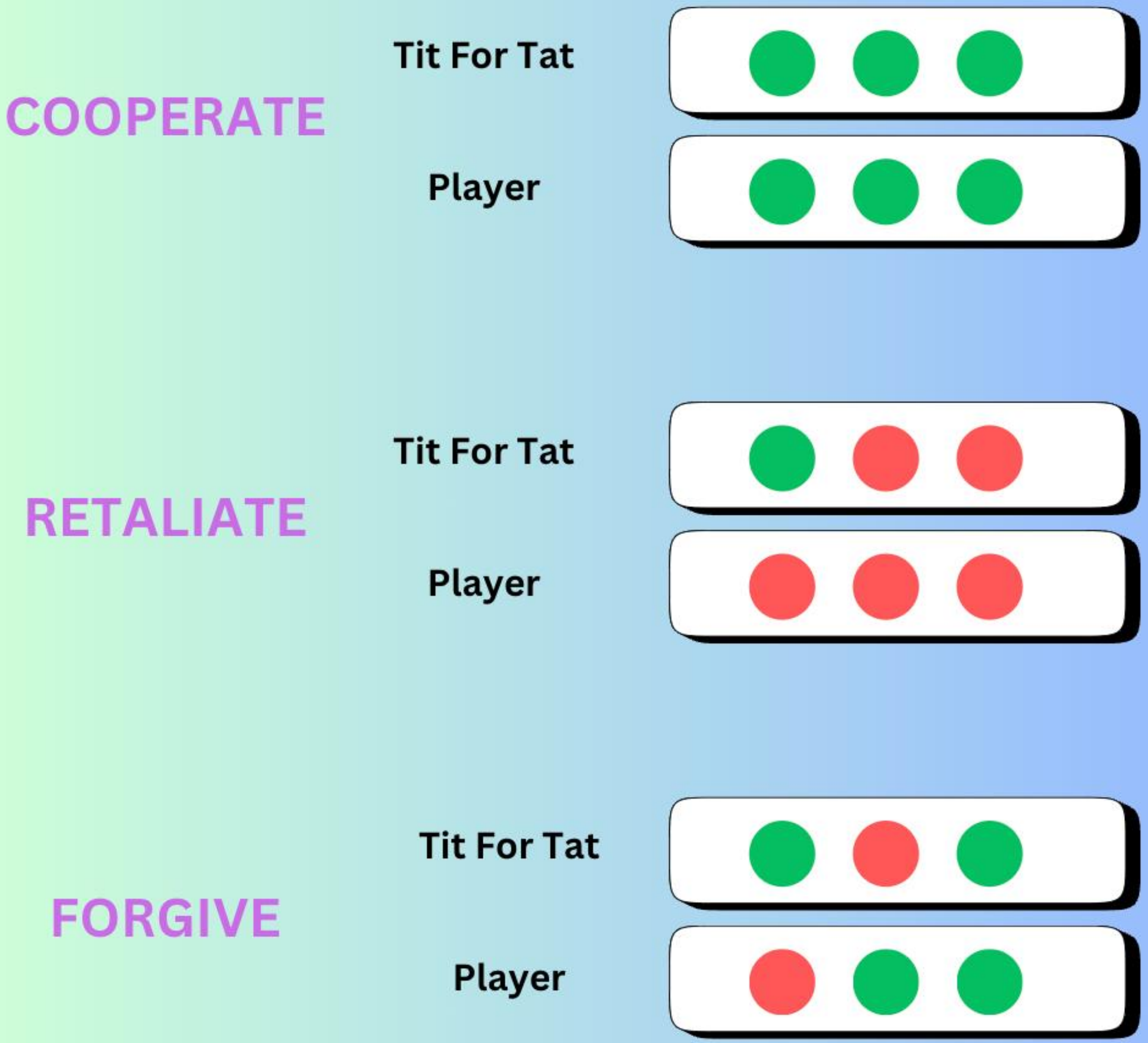

Who scored the highest payoff?
What strategies did you choose?
What worked and what didn’t?

In 1978 the winner was Tit-for-tat!

Effective Choice in the Prisoner's Dilemma

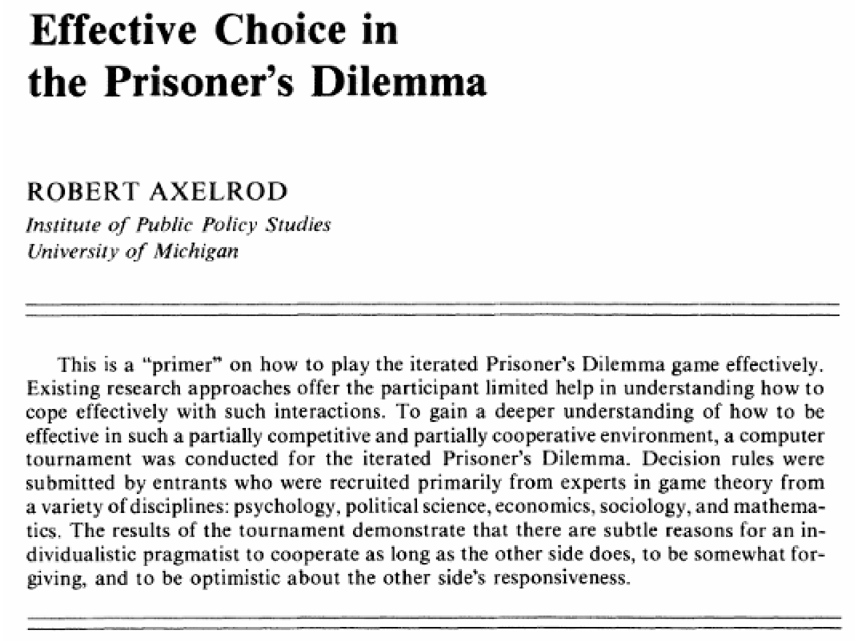
ROBERT AXELROD
Institute of Public Policy Studies
University of Michigan

This is a "primer" on how to play the iterated Prisoner's Dilemma game effectively. Existing research approaches offer the participant limited help in understanding how to cope effectively with such interactions. To gain a deeper understanding of how to be effective in such a partially competitive and partially cooperative environment, a computer tournament was conducted for the iterated Prisoner's Dilemma. Decision rules were submitted by entrants who were recruited primarily from experts in game theory from a variety of disciplines: psychology, political science, economics, sociology, and mathematics. The results of the tournament demonstrate that there are subtle reasons for an individualistic pragmatist to cooperate as long as the other side does, to be somewhat forgiving, and to be optimistic about the other side's responsiveness.



"The Evolution of Reciprocal Altruism" (1971), Trivers

Does Tit-for-Tat have any problem?



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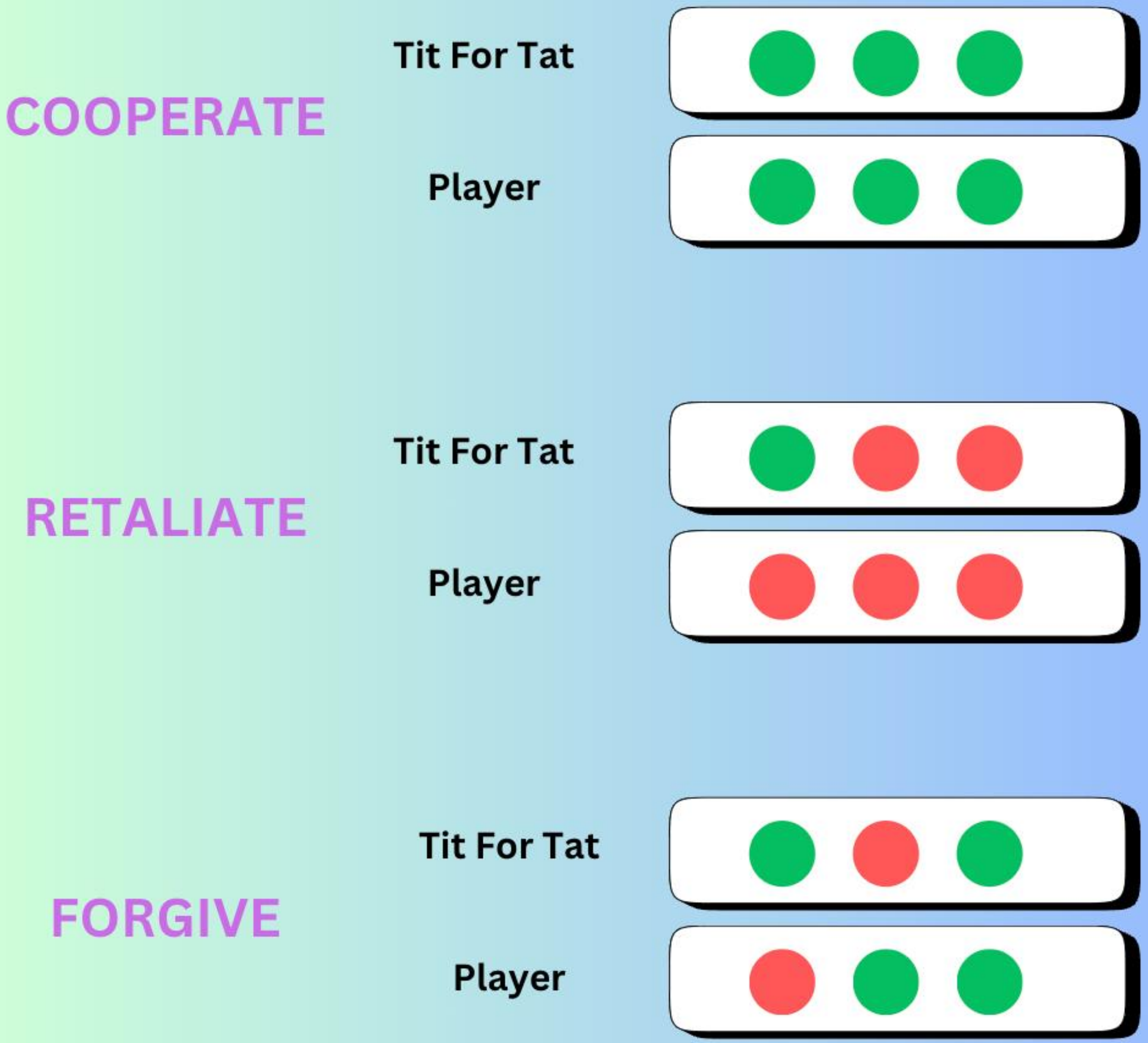


Tit-for-tat is not forgiving enough

Tit-for-tat cannot correct mistakes

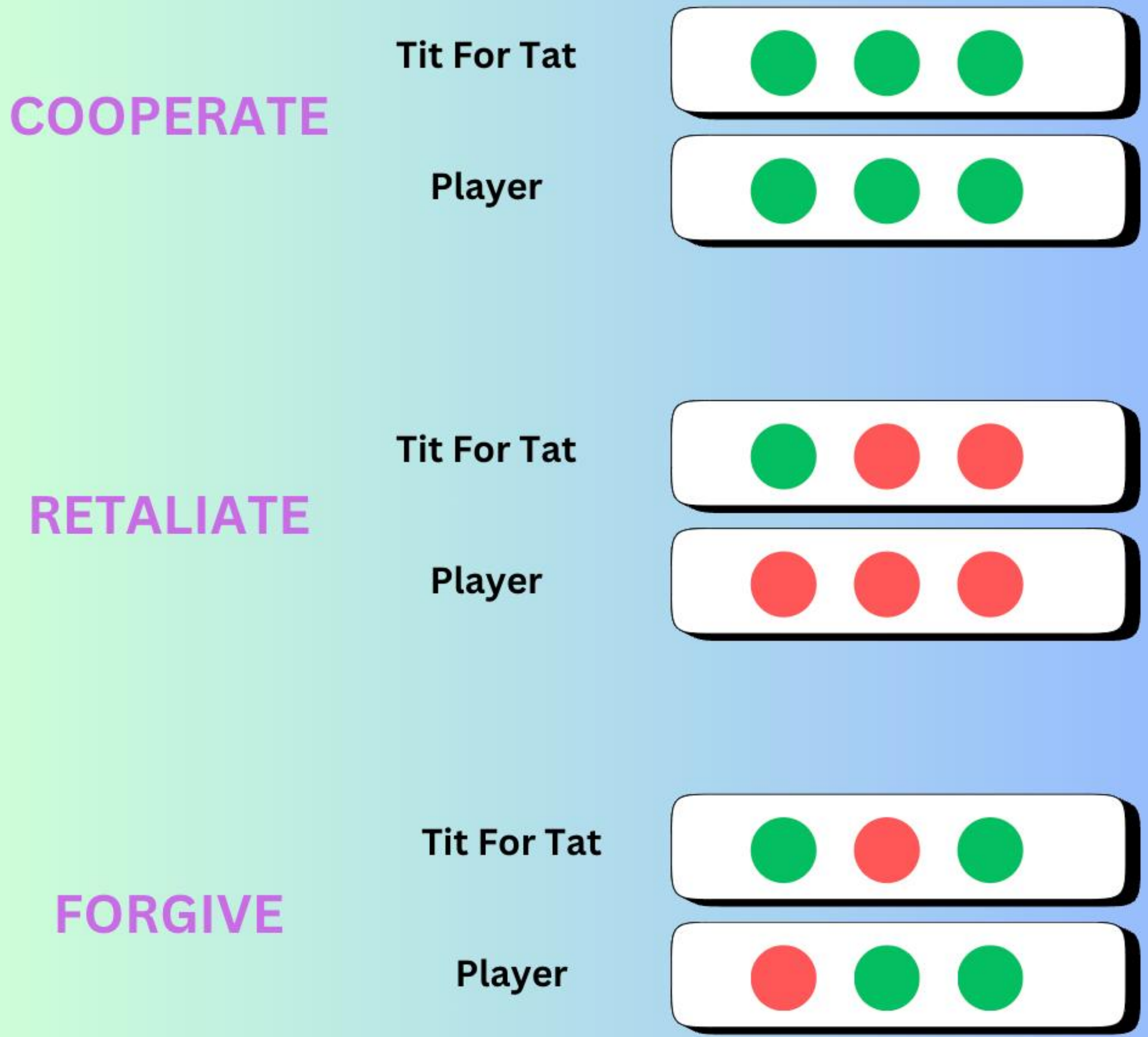
TFT: C C C D* C D C D D D . . .

TFT: C C C C D C D D* D D . . .

Generous tit-for-tat can correct mistakes

GTFT: C C C D* C D C C C C . . .

GTFT: C C C C D C C C C C . . .





Blood sharing in vampire bats (Desmodus rotundus)

- They feed at night, but if they fail to feed, they can **starve within ~2–3 days**
- Successful bats regurgitate blood to unsuccessful roost mate
- Individuals preferentially donate to bats that previously donated to them.

Reciprocal grooming in primates

- Reciprocal grooming tends to be balanced over time
- In many species **up to 20% of the day** can be spent grooming.
- **Often exchanged for something else (used as "social currency"):**
  - coalition support in fights
  - tolerance around food
  - infant access
  - mating opportunities
  - alliance formation
- Benefits?
- Costs?.

Reciprocal grooming in primates

Costs:

- time
- attention (less vigilance)
- opportunity costs (not feeding)

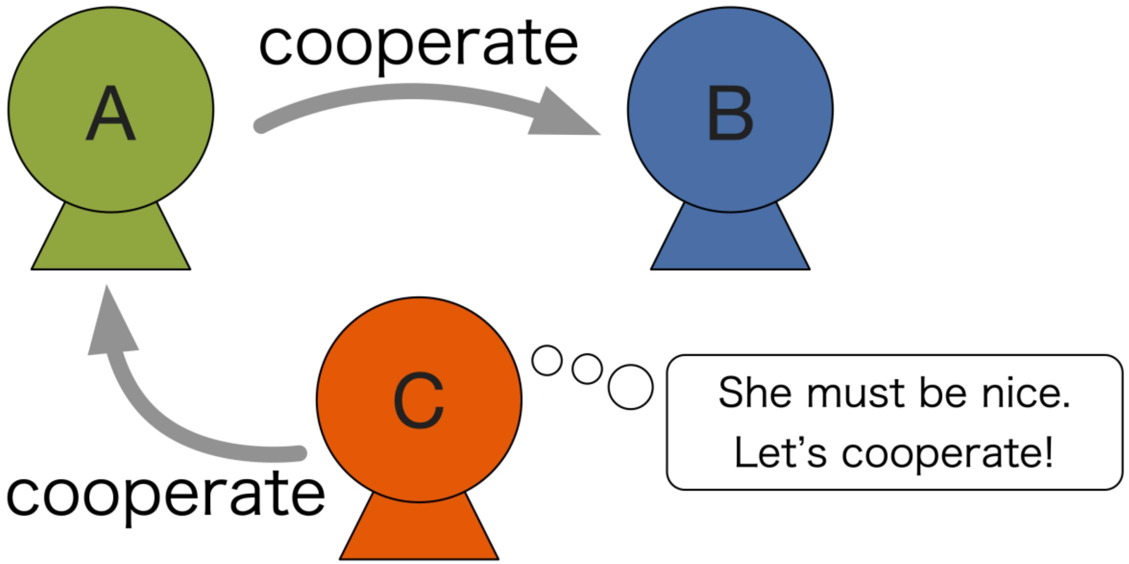
Benefits:

- parasite removal
- relaxation

What do you notice? What could happen in such contexts?

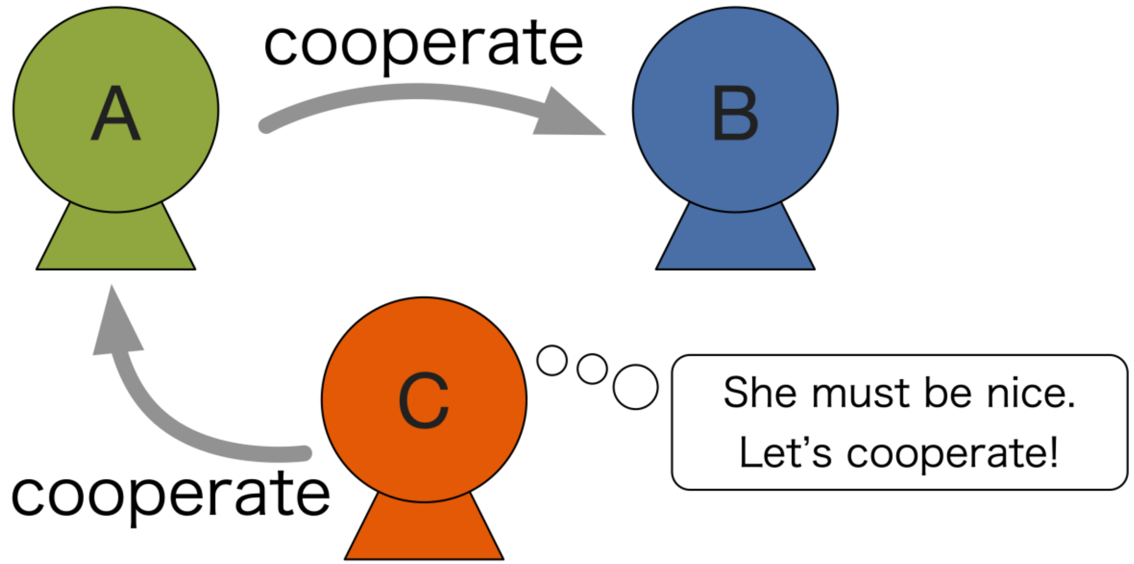
What do you notice? What could happen in such contexts?

Indirect reciprocity (Reputation-based)



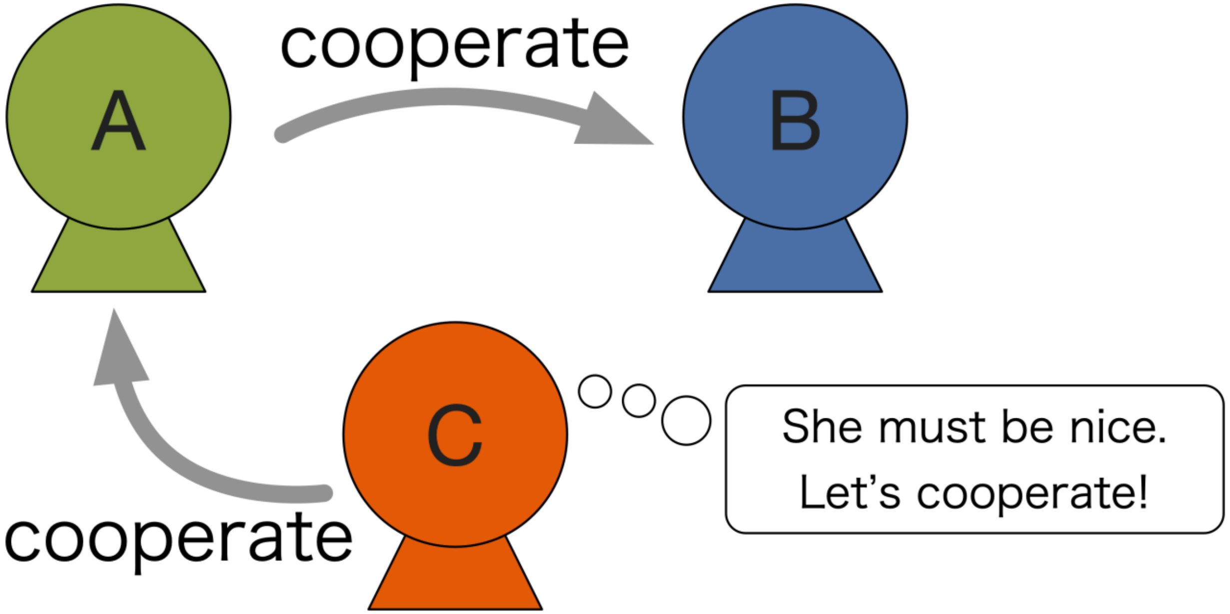
Indirect reciprocity (Reputation-based)

Actually in this case it is probably not what the observer is thinking. There is not a lot of evidence that most primates are do indirect-reciprocity: it is cognitively complex and they are more likely influenced by dominance hierarchies and do simpler “direct reciprocity”, only in complex networks




CS660605
YO! CHECK IT OUT EVERYONE! I'M GIVING MONEY TO THE NEEDY ANONYMOUSLY! FOLLOW ME! #SECRETGIVER!
CARTOONSTOCK
CARTOON COLLECTIONS COMPANY
SODA
STOVER


@reallygreatsite
10 Essential Steps to Plan a Memorable Charity Gala


A
cooperate
B
C
She must be nice.
Let's cooperate!
cooperate


VOLUNTEER


2016
DATE: January 2016
$100,000.00
PAY TO THE ORDER OF Puppy Jake
One Hundred Thousand
DOLLARS
TRUMP
DonaldTrumpforVets.com
MAKE AMERICA GREAT AGAIN!

biology
letters

Biol. Lett. (2006) **2**, 412–414
doi:10.1098/rsbl.2006.0509
Published online 27 June 2006

Cues of being watched enhance cooperation in a real-world setting

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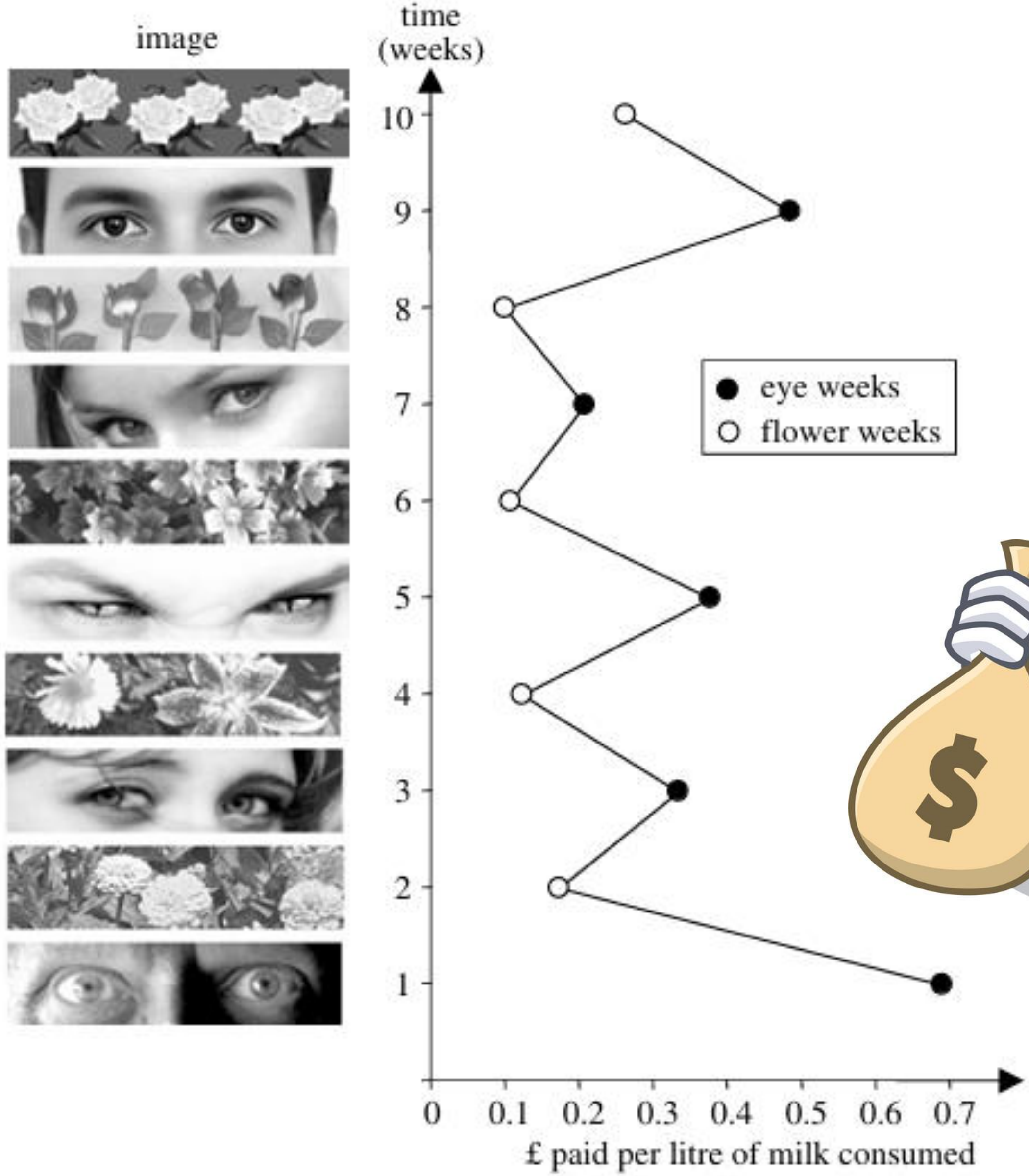
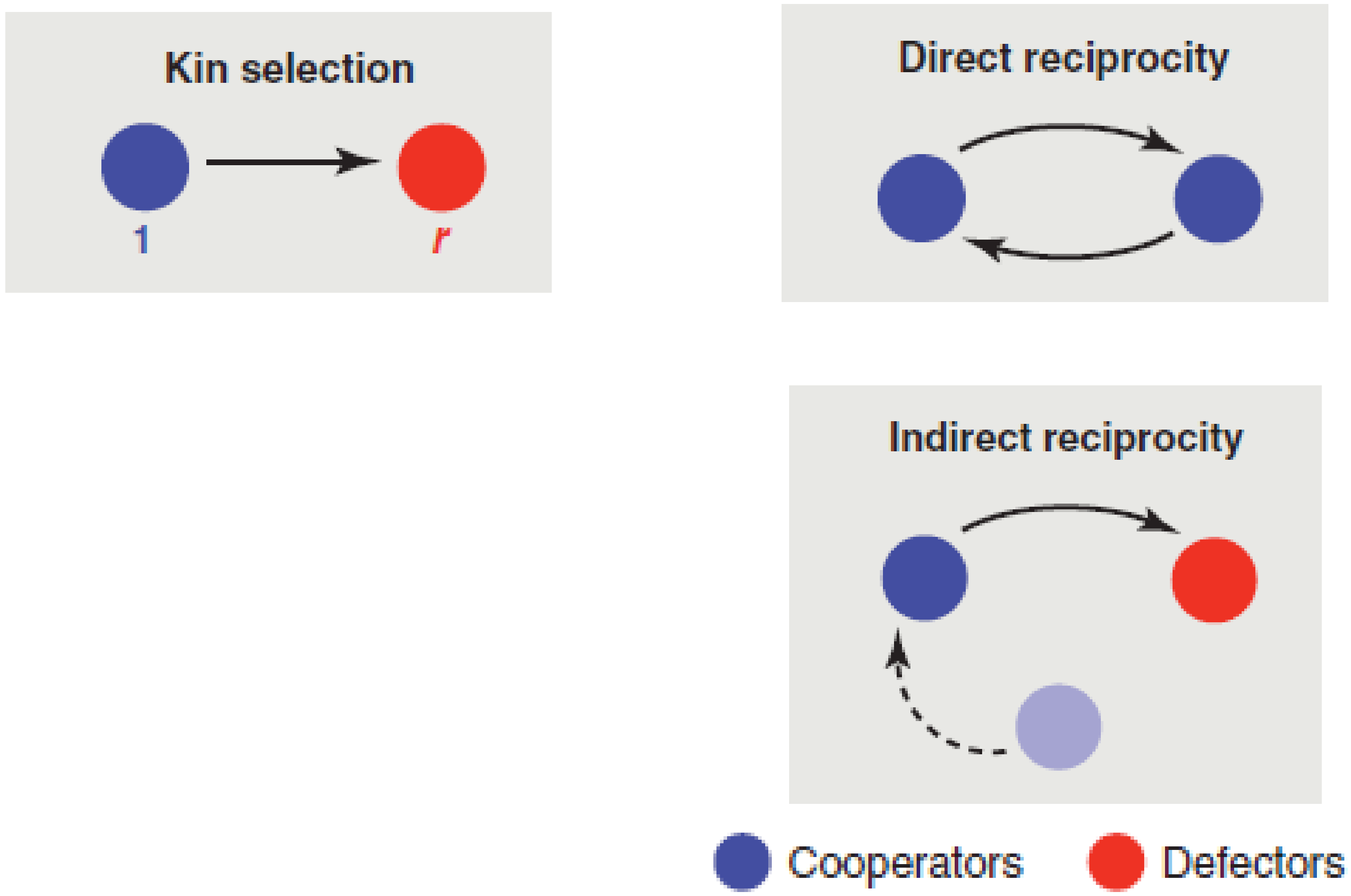
**Author for correspondence* (*melissa.bateson@ncl.ac.uk*).

We examined the effect of an image of a pair of eyes on contributions to an honesty box used to collect money for drinks in a university coffee room. People paid nearly three times as much for their drinks when eyes were displayed rather than a control image. This finding provides the first evidence from a naturalistic setting of the importance of cues of being watched, and hence reputational concerns, on human cooperative behaviour.



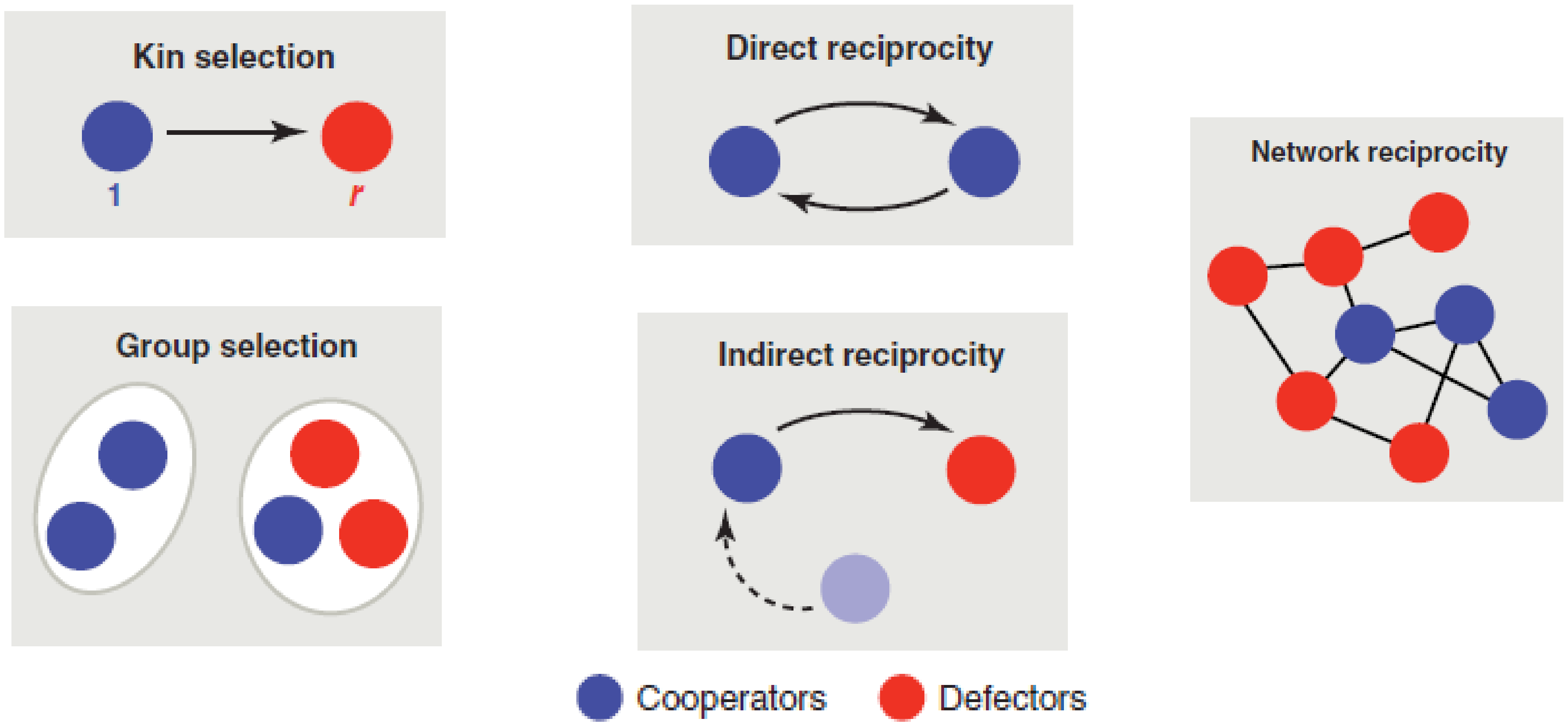

SOCIAL NORMS
LAW
%$#

Can you imagine other mechanisms promoting the evolution of cooperation?



Fives rules for the evolution of cooperation

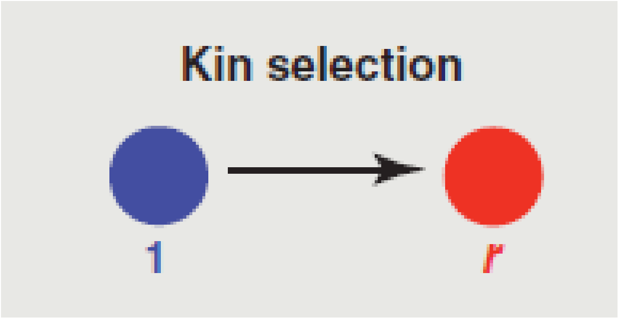
Martin Nowak, 2006, Nature

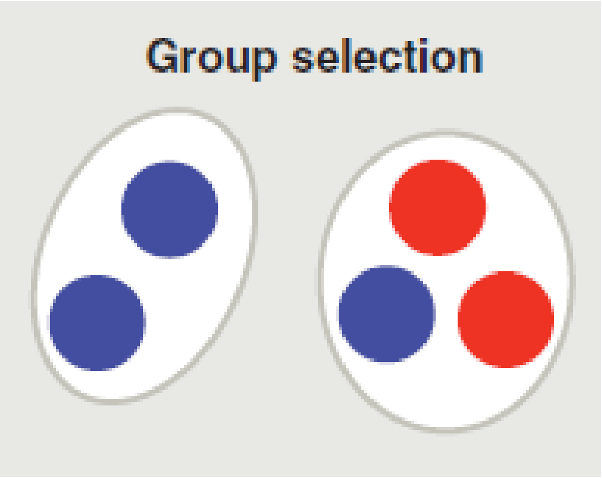


Fives rules for the evolution of cooperation

Martin Nowak, 2006, Nature

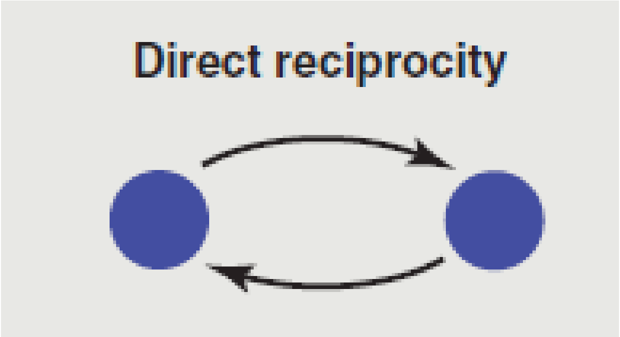
Related individuals



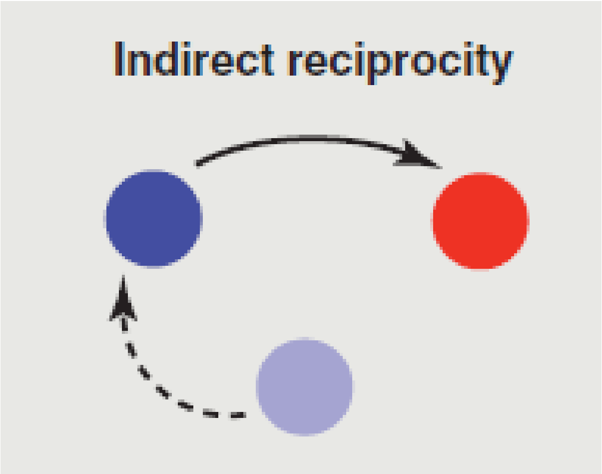


Individuals in groups

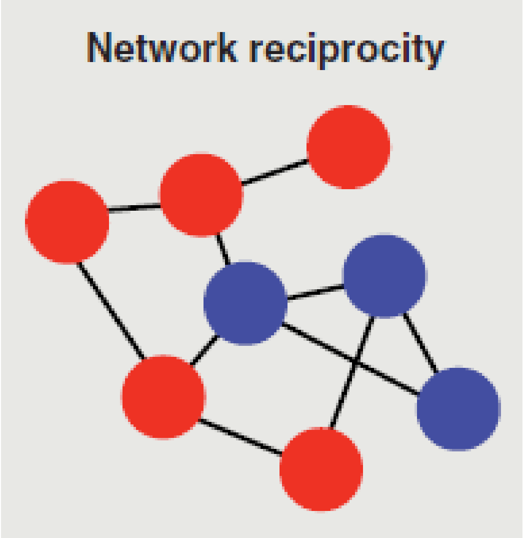
Repeated interactions



Reputation

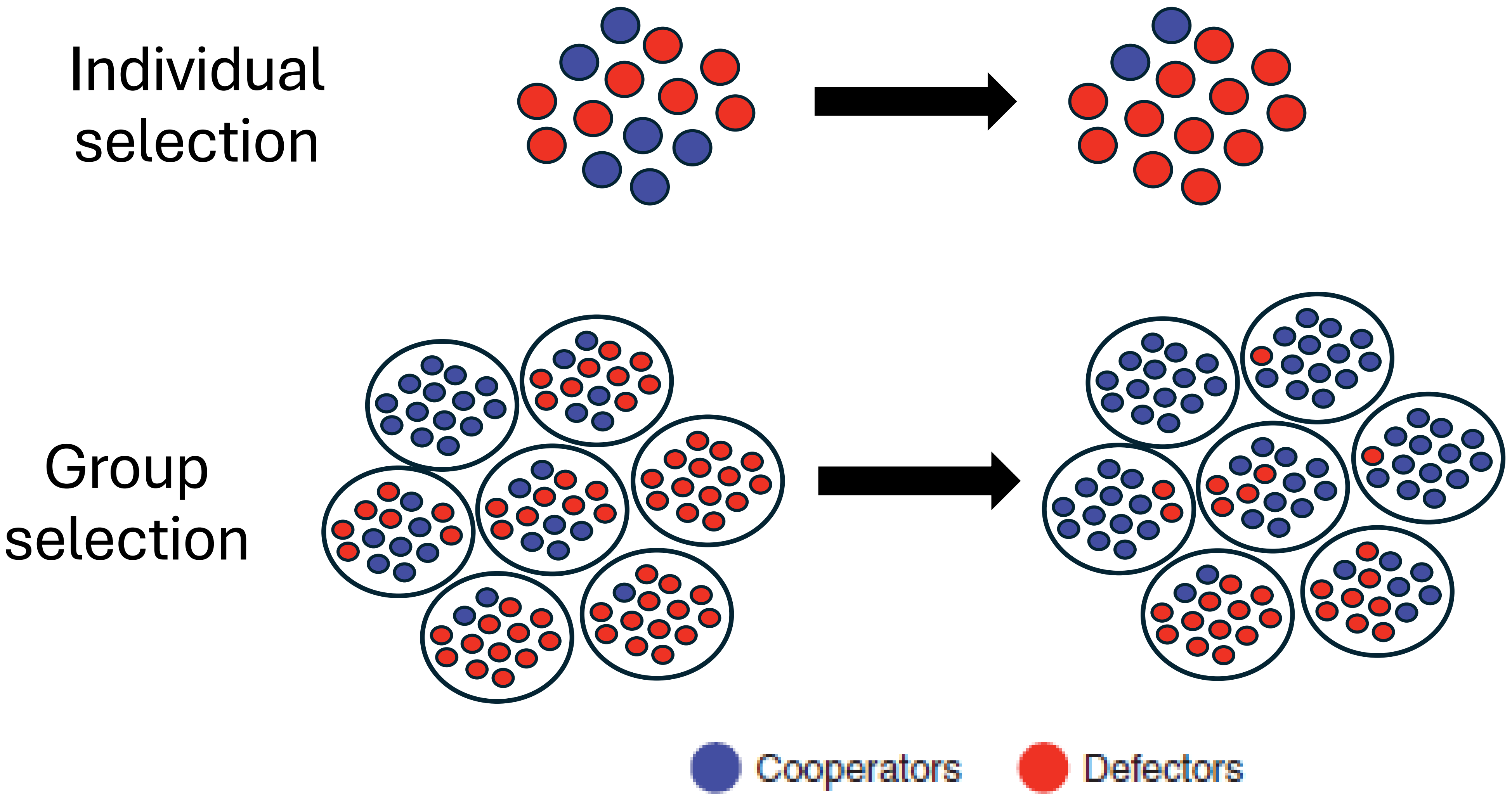


Cooperators Defectors



Interactions in space

Competition among groups favours cooperation



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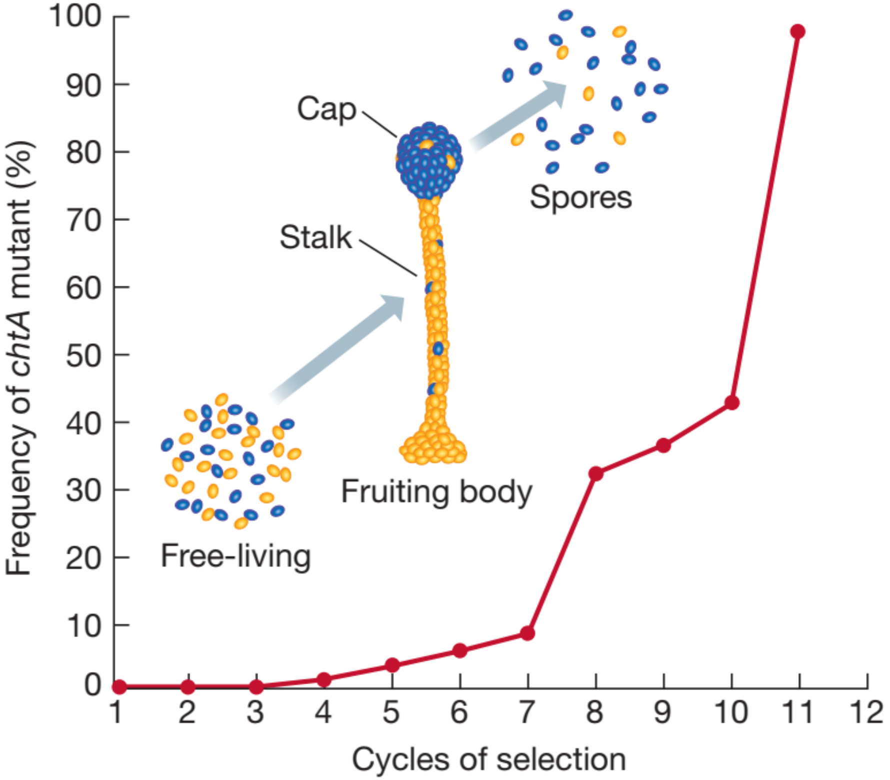
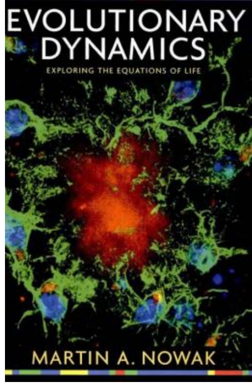


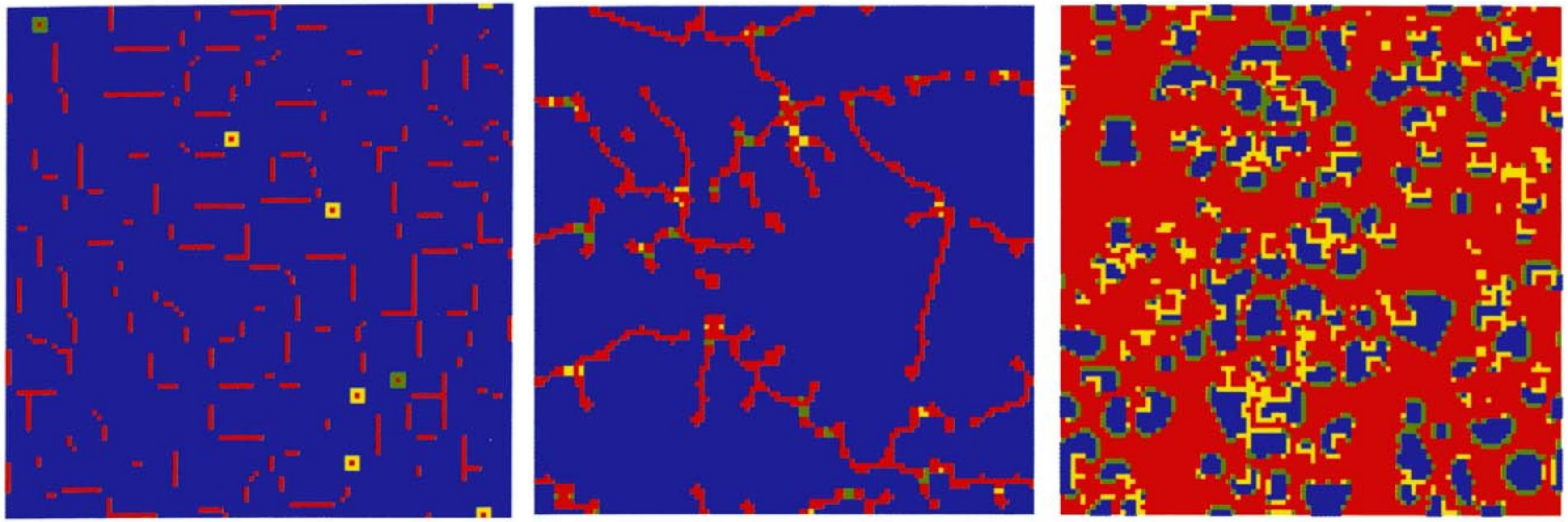
FIGURE 12.1 In the slime mold *Dictyostelium discoideum*, cells with a mutation at the *chtA* locus are cheaters that behave selfishly. In a mixture of wild-type cells (in yellow) and cells with the *chtA* mutation (blue), the mutant cells become concentrated in the cap and so are more likely to form the reproductive spores. Over the course of 11 growth and development cycles, the frequency of the selfish mutant increased in laboratory culture. (After [19].)

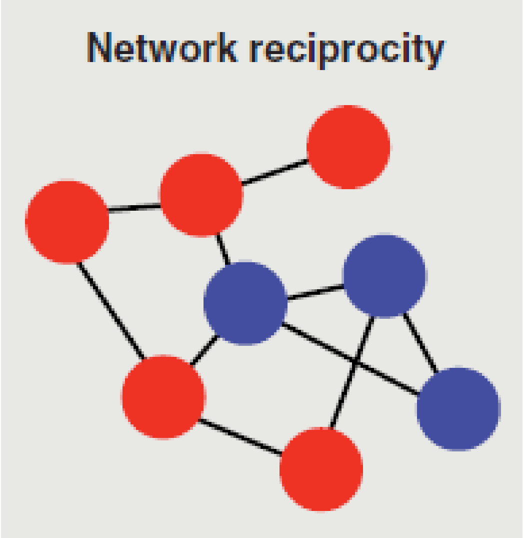
Spatial games on lattices (grids)



More cooperators

More defectors, but cooperators resist in «bubbles»

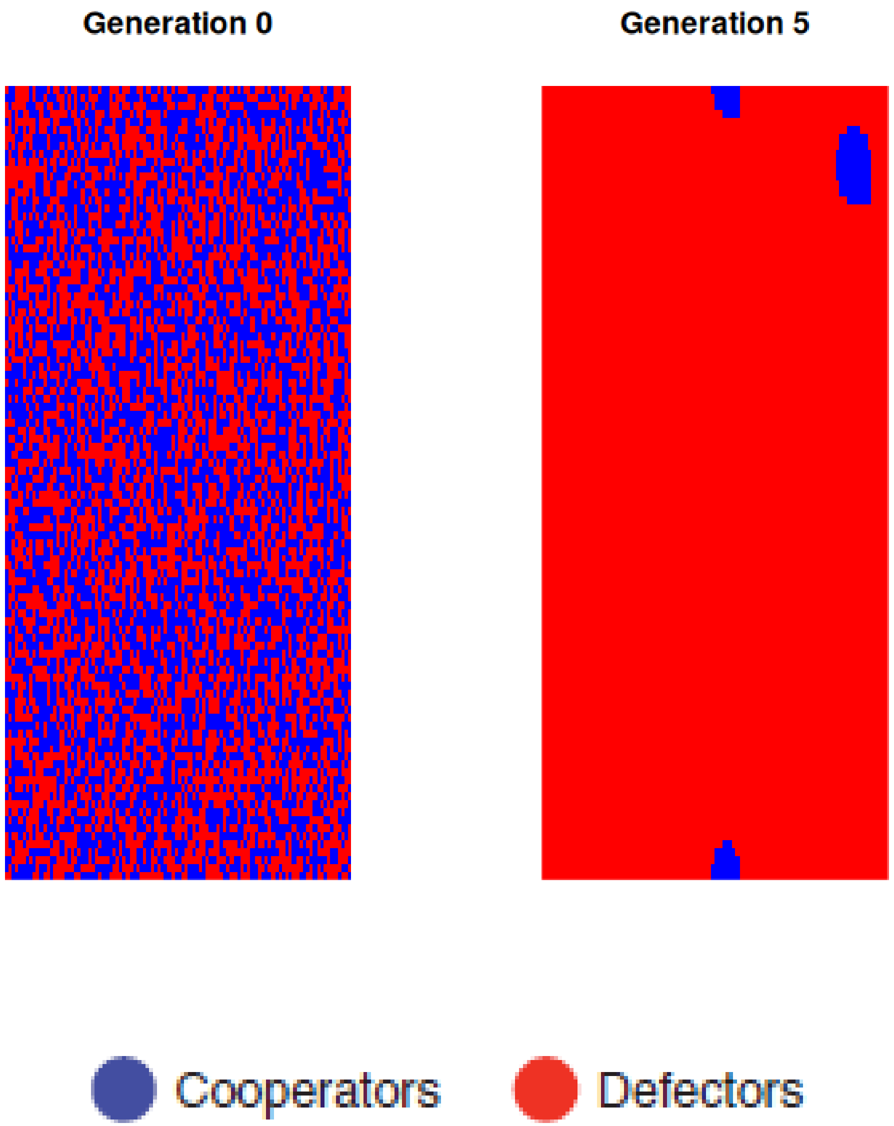


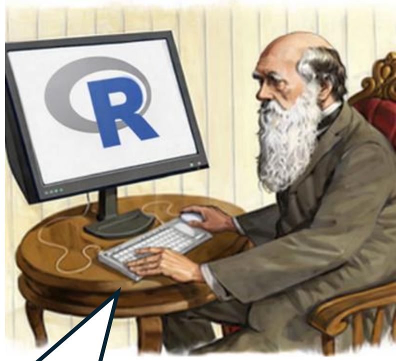


Interactions in space

increasing b-c in payoff matrix

Spatial games on lattices (grids)

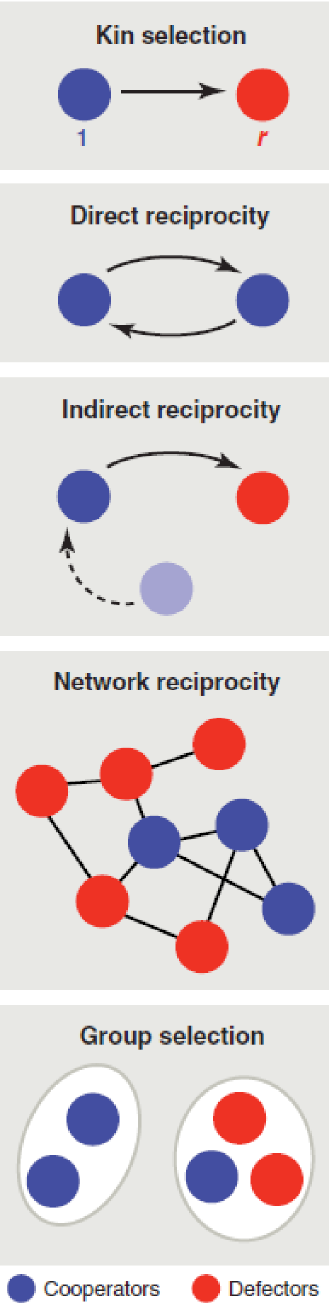




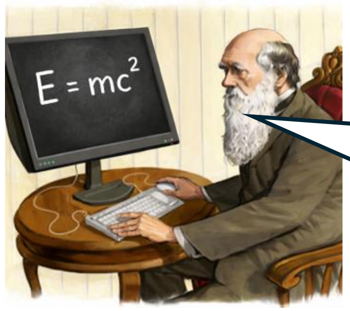
If you want to try the simulations yourself you can find the R code to generate this on Moodle

Fives rules for the evolution of cooperation

		Payoff matrix C	Payoff matrix D	ESS	
Kin selection	C	$(b-c)(1+r)$	$br-c$	$\frac{b}{c} > \frac{1}{r}$	*r*…genetic relatedness
	D	$b-rc$	0		
Direct reciprocity	C	$(b-c)/(1-w)$	$-c$	$\frac{b}{c} > \frac{1}{w}$	*w*…probability of next round
	D	b	0		
Indirect reciprocity	C	$b-c$	$-c(1-q)$	$\frac{b}{c} > \frac{1}{q}$	*q*…social acquaintanceship
	D	$b(1-q)$	0		
Network reciprocity	C	$b-c$	$H-c$	$\frac{b}{c} > k$	*k*…number of neighbors
	D	$b-H$	0		
Group selection	C	$(b-c)(m+n)$	$(b-c)m-cn$	$\frac{b}{c} > 1+\frac{n}{m}$	*n*…group size *m*…number of groups
	D	bn	0		

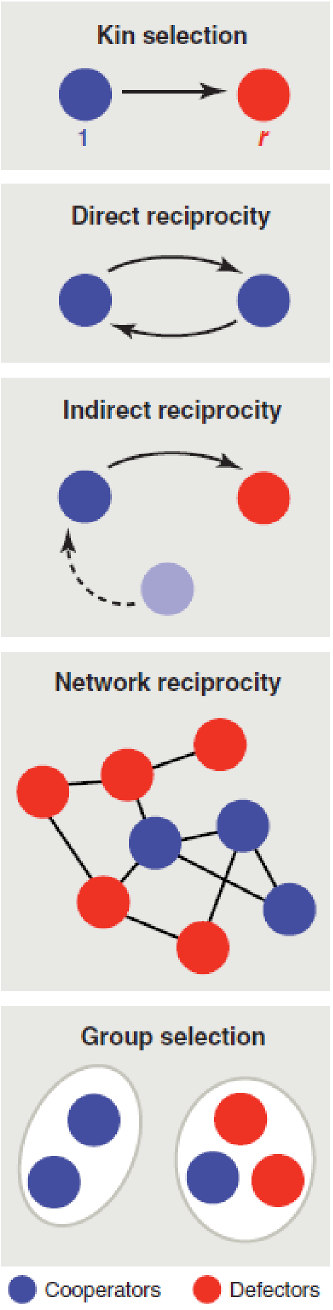


Fives rules for the evolution of cooperation



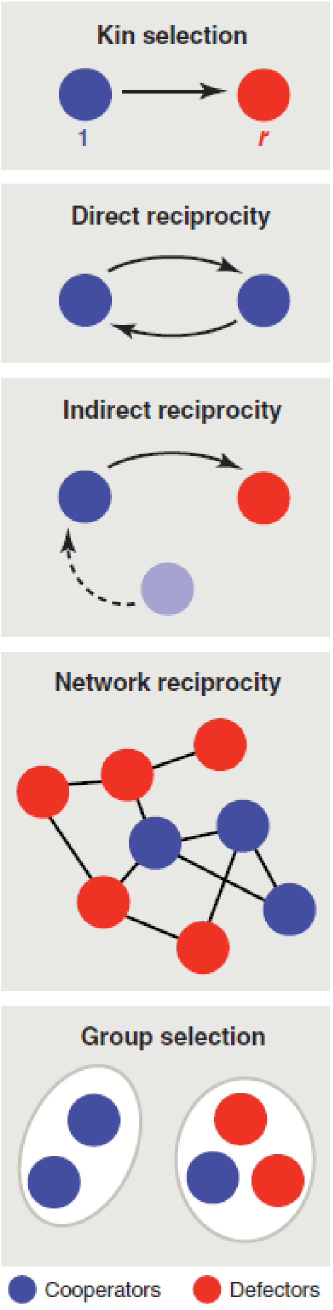
Try to derive Hamilton's rule using Game Theory and the same approach we used for Hawks and Doves!

Kin selection	C	$(b-c)(1+r)$	$br-c$	$\frac{b}{c} > \frac{1}{r}$	r…genetic relatedness
	D	$b-rc$	0		
Direct reciprocity	C	$(b-c)/(1-w)$	$-c$	$\frac{b}{c} > \frac{1}{w}$	w…probability of next round
	D	b	0		
Indirect reciprocity	C	$b-c$	$-c(1-q)$	$\frac{b}{c} > \frac{1}{q}$	q…social acquaintanceship
	D	$b(1-q)$	0		
Network reciprocity	C	$b-c$	$H-c$	$\frac{b}{c} > k$	k…number of neighbors
	D	$b-H$	0		
Group selection	C	$(b-c)(m+n)$	$(b-c)m-cn$	$\frac{b}{c} > 1+\frac{n}{m}$	n…group size; m…number of groups
	D	bn	0		



Are they really five?

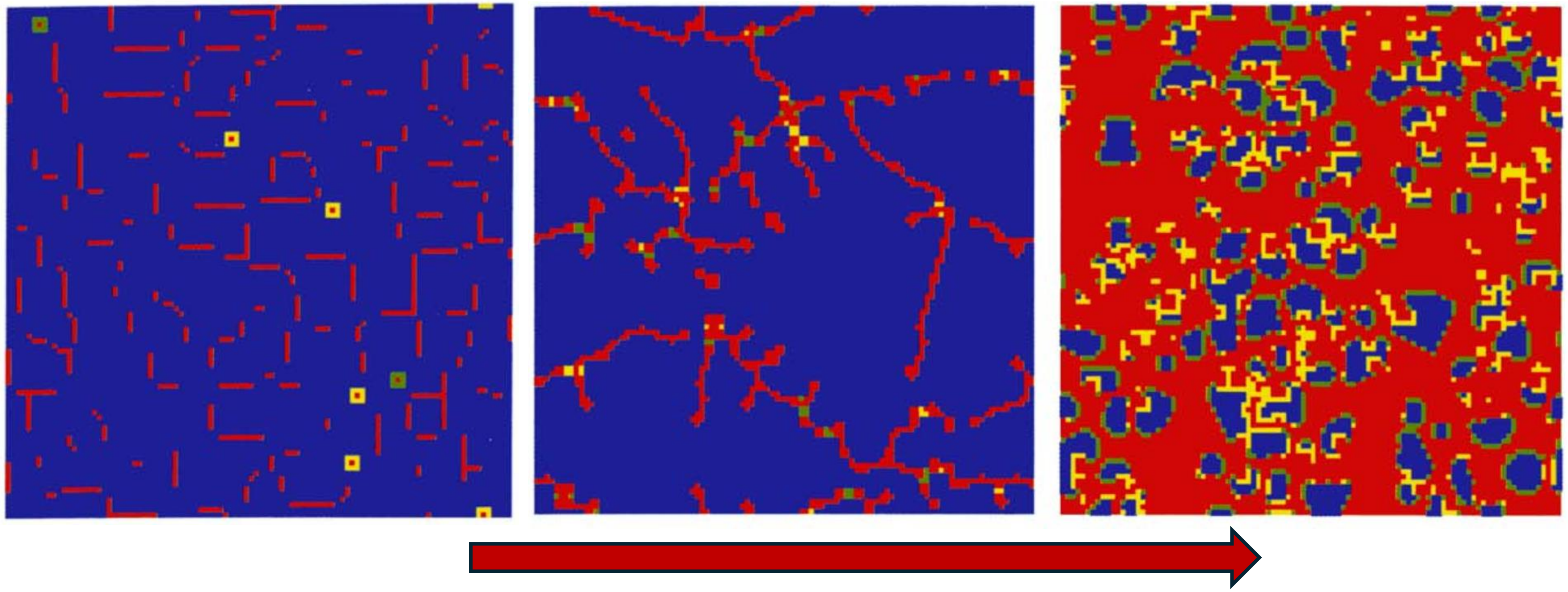
		Payoff matrix: C	Payoff matrix: D	ESS	
Kin selection	C	$(b-c)(1+r)$	$br-c$	$\frac{b}{c} > \frac{1}{r}$	*r*…genetic relatedness
	D	$b-rc$	0		
Direct reciprocity	C	$(b-c)/(1-w)$	$-c$	$\frac{b}{c} > \frac{1}{w}$	*w*…probability of next round
	D	b	0		
Indirect reciprocity	C	$b-c$	$-c(1-q)$	$\frac{b}{c} > \frac{1}{q}$	*q*…social acquaintanceship
	D	$b(1-q)$	0		
Network reciprocity	C	$b-c$	$H-c$	$\frac{b}{c} > k$	*k*…number of neighbors
	D	$b-H$	0		
Group selection	C	$(b-c)(m+n)$	$(b-c)m-cn$	$\frac{b}{c} > 1+\frac{n}{m}$	*n*…group size
	D	bn	0		*m*…number of groups



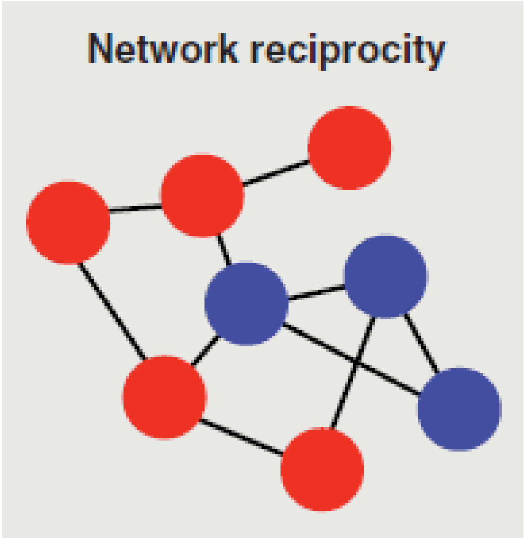
Are they really five?

More cooperators

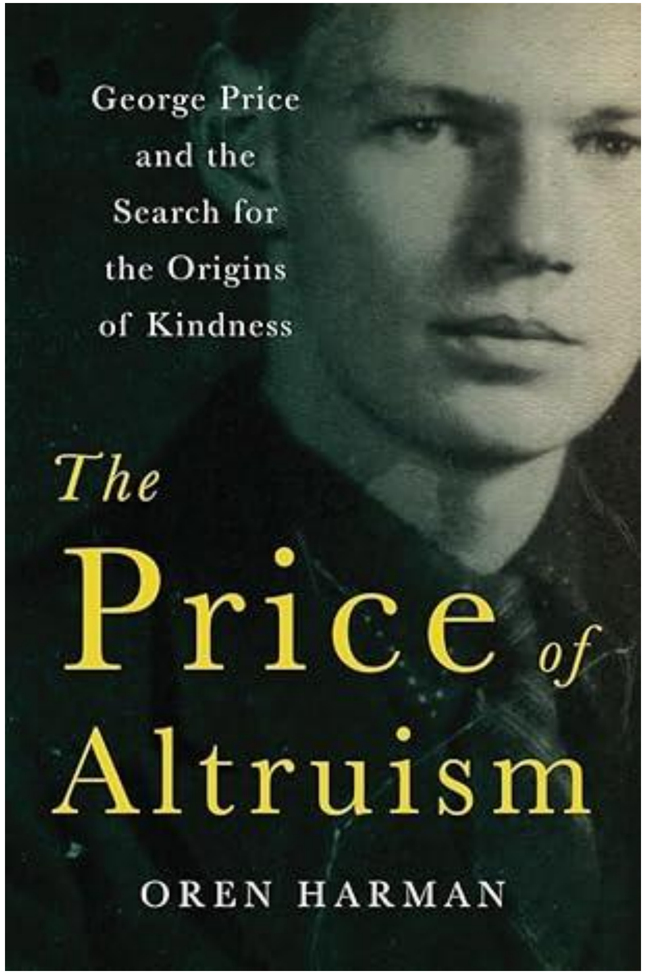
More defectors, but cooperators resist in «bubbles»

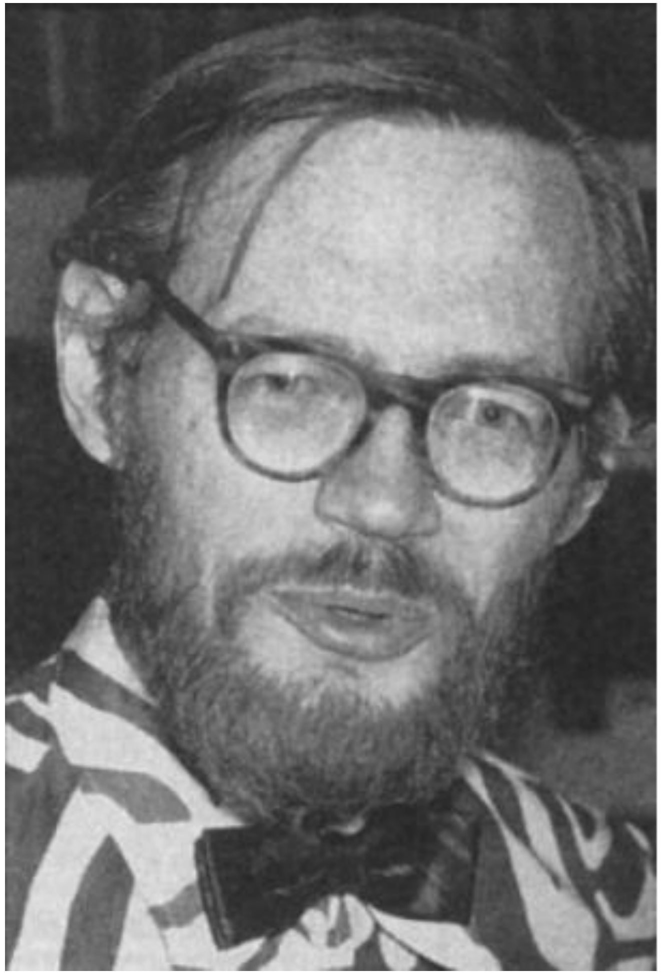


increasing b-c in payoff matrix



Interactions in space

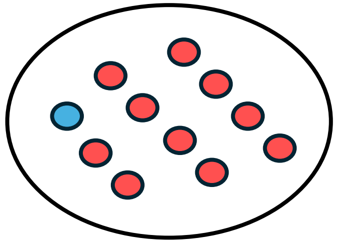


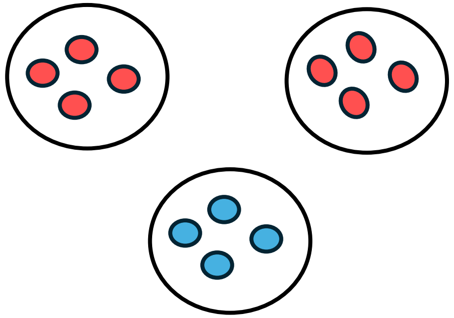


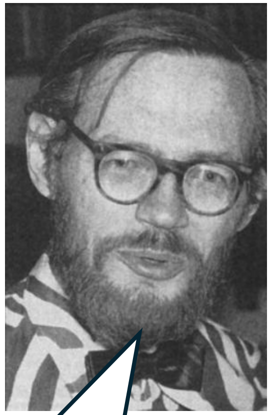
George R. Price
(1922-1974)

Price equation: it all boils down to «positive assortment» between individuals

evolutionary change in altruism = effect of selection within groups + effect of selection between groups



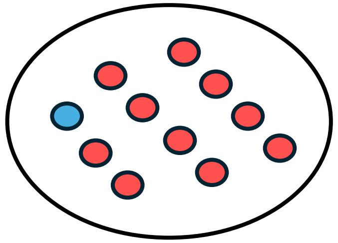


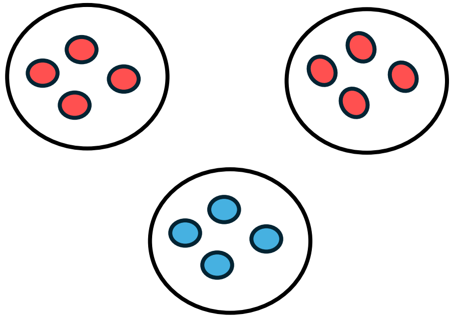


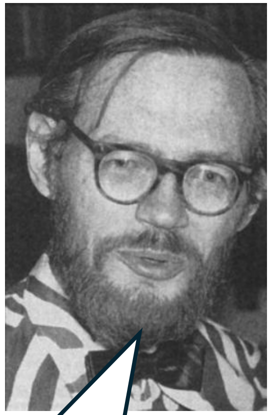
By «group» we mean anything that creates a correlation between the fitness of two cooperative individuals: kinship, space, groups, repeated interactions, etc.

Price equation: it all boils down to «positive assortment» between individuals

evolutionary change in altruism = effect of selection within groups + effect of selection between groups





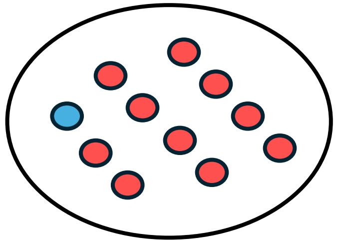


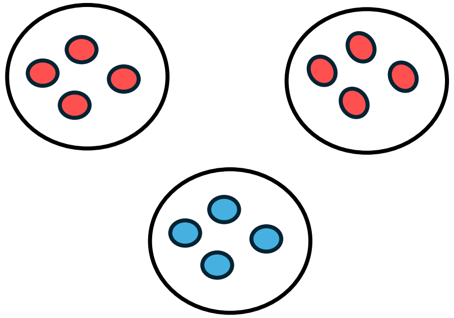
«**Positive assortment**» is probably a better term than the simplistic «groups»!

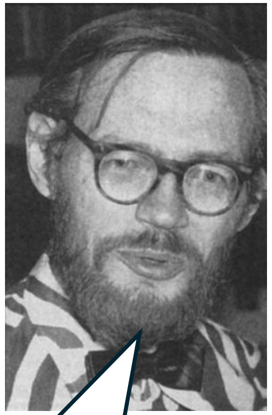
By «group» we mean anything that creates a correlation between the fitness of two cooperative individuals: kinship, space, groups, repeated interactions, etc.

Price equation: it all boils down to «positive assortment» between individuals

evolutionary change in altruism = effect of selection within groups + effect of selection between groups





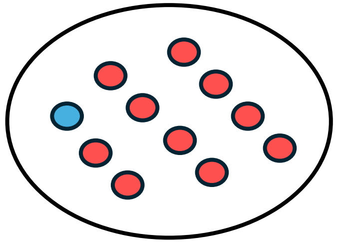


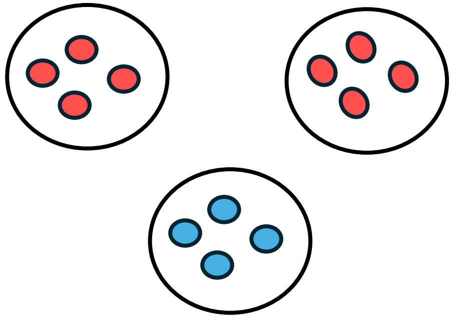
«**Positive assortment**» is probably a better term than the simplistic «groups»!

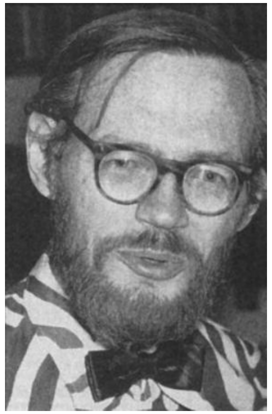
By «group» we mean anything that creates a correlation between the fitness of two cooperative individuals: kinship, space, groups, repeated interactions, etc.

Altruism can evolve whenever altruists interact disproportionately with other altruists

evolutionary change in altruism = effect of selection within groups + effect of selection between groups

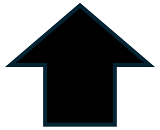


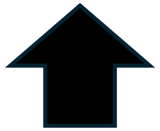




Whenever cooperators interact more often with other cooperators

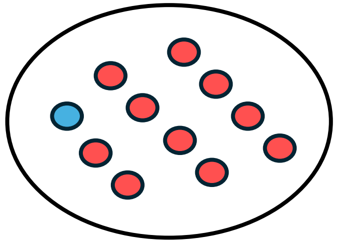
Positive assortment

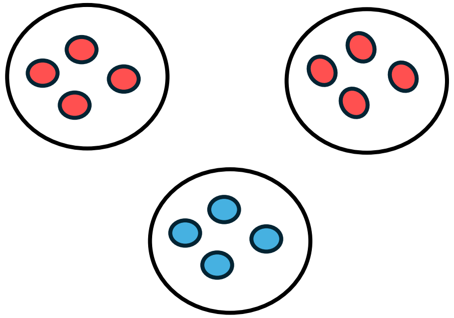


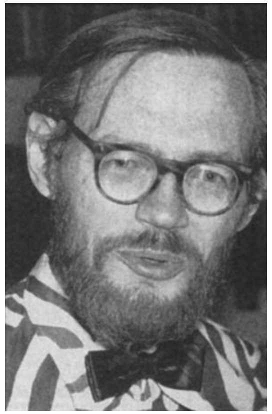


More like “one rule for cooperation”: positive assortment

evolutionary change in altruism = effect of selection within groups + effect of selection between groups







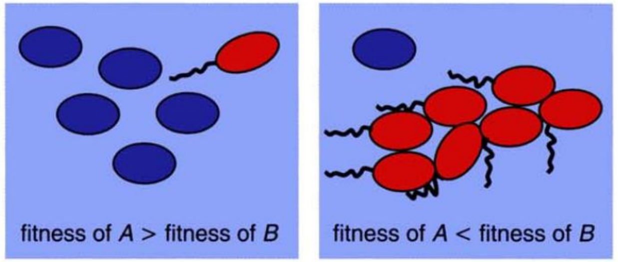
Whenever cooperators interact more often with other cooperators

Positive assortment ↑ ↓ ↑

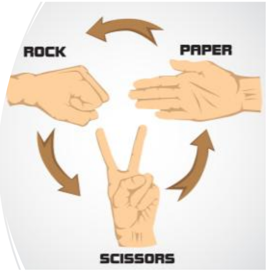
Cooperators meet less often defectors

“groups” of cooperators are favoured

Conclusions

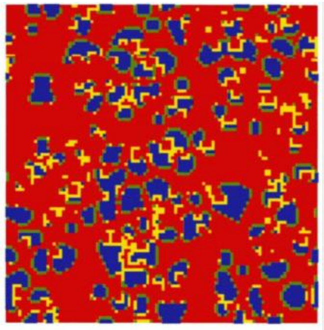


- Selection is usually frequency-dependent, since individuals interact



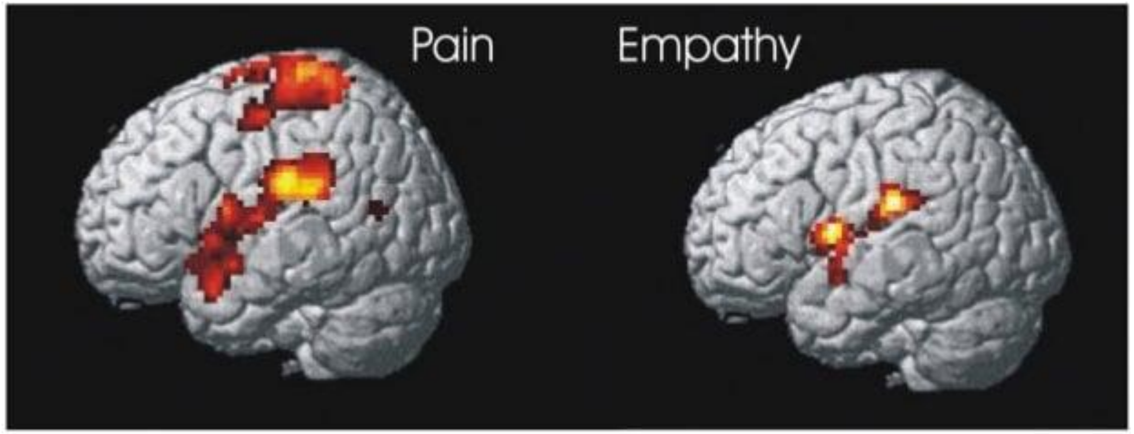
- Frequency-dependent fitness can be modeled using game theory
- Evolutionarily Stable Strategies are strategies that once evolved are hard to replace (they cannot be invaded by mutants with better strategies)

- Cooperation evolves when some form of positive assortment (kinship, space, groups, repeated interactions, information, etc.) promotes the interaction of cooperators with other cooperators



OK, positive assortment! But we saw that sometimes evolution is constrained by evolutionary trade-offs!

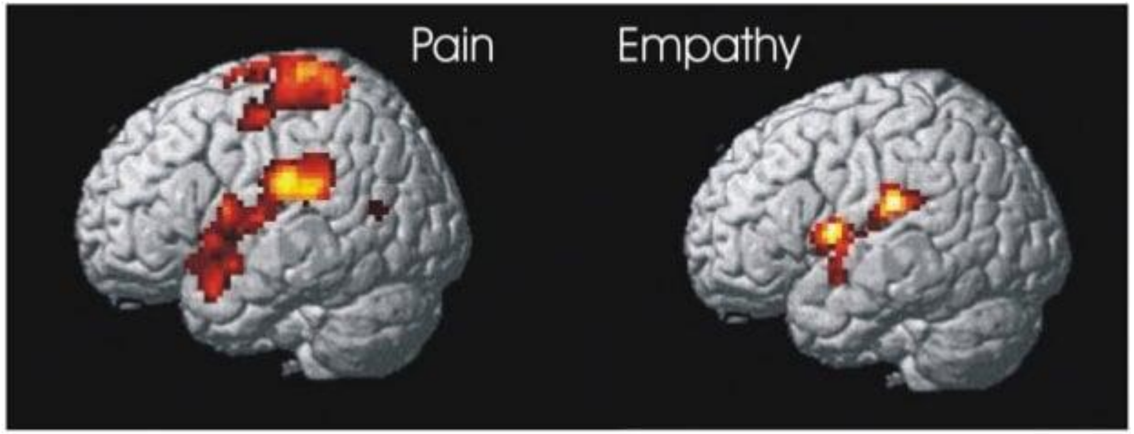
What if some aspects of helping behavior evolve not because of positive assortment but because of evolutionary trade-offs?

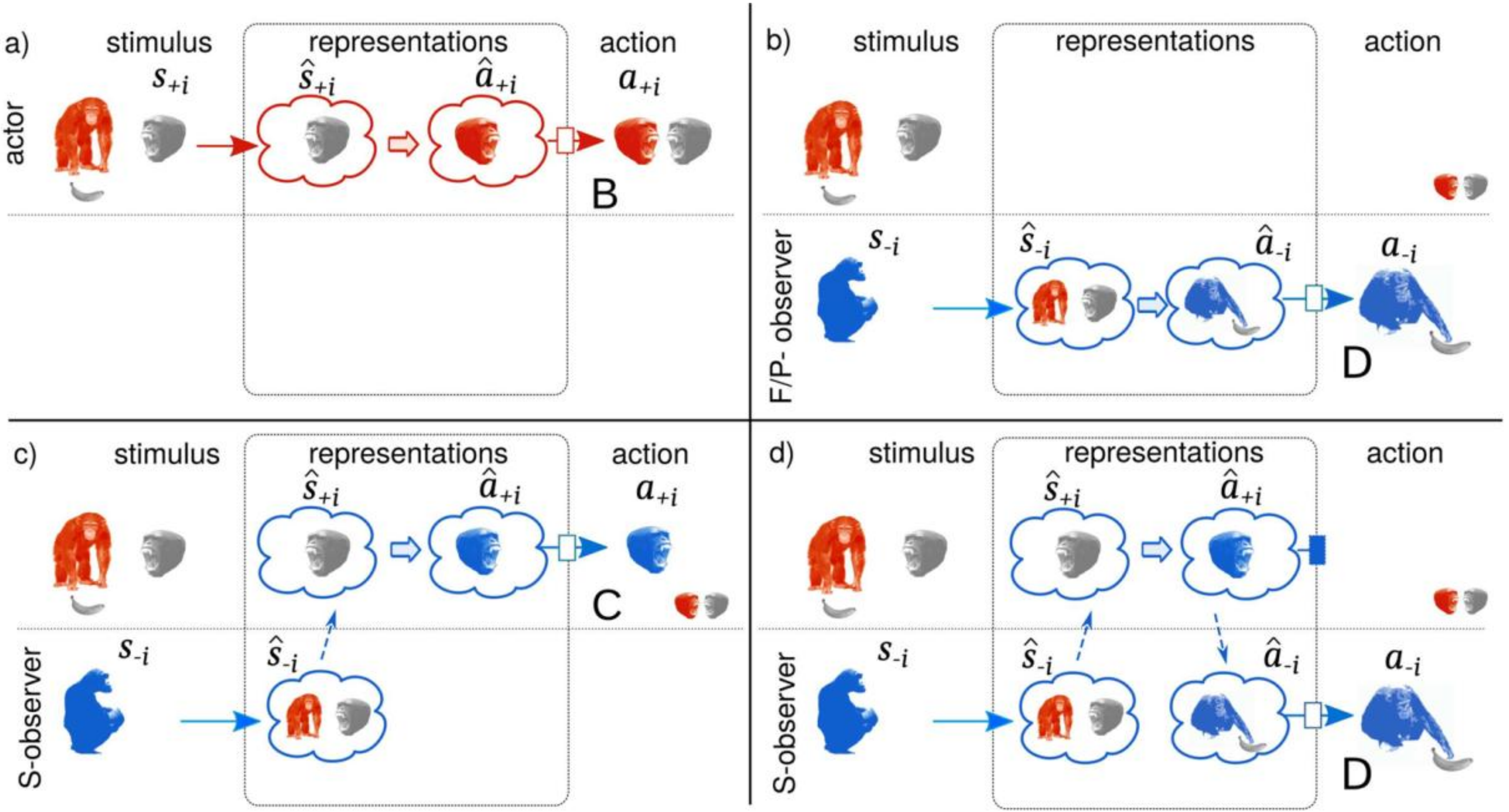


The complexity of understanding others as the evolutionary origin of empathy and emotional contagion

Fabrizio Mafessoni[1] & Michael Lachmann[2]

- When one perceives pain (or does a specific action) or observes somebody receiving that pain (or doing that action) similar brain regions are activated (empathy and mirror neurons).
- This phenomenon and emotional contagion is stronger in contexts where cooperation is favored (related individuals, recriprocal interactions)
- Why would this evolve? When would this lead to cooperation?

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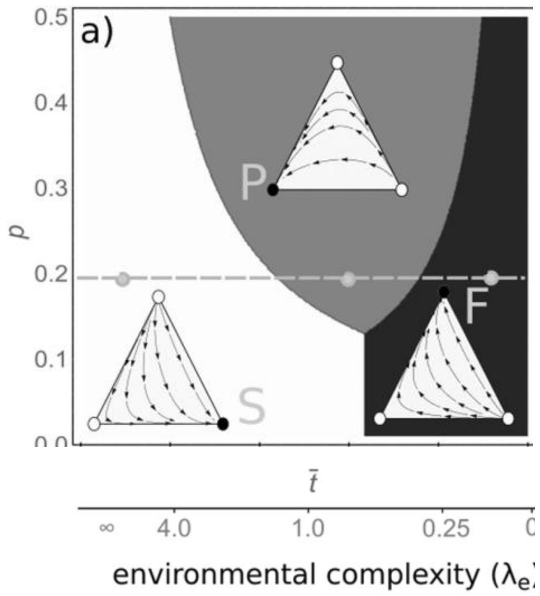
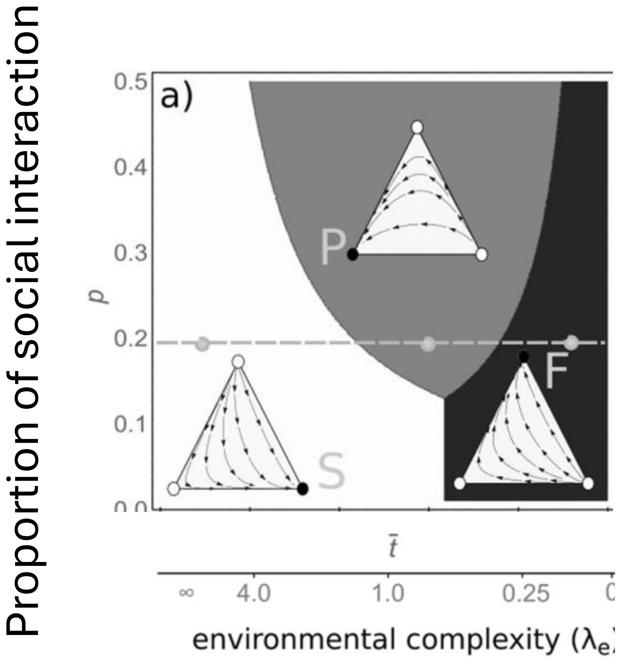
Simulative/empathetic strategies evolve in more complex environments



- What if «empathy» and «mirror neurons» are strategies to simulate other's behavior (S)?
- When do they perform better than strategies relying exclusively on learning (P) or instinctual strategies (F)?

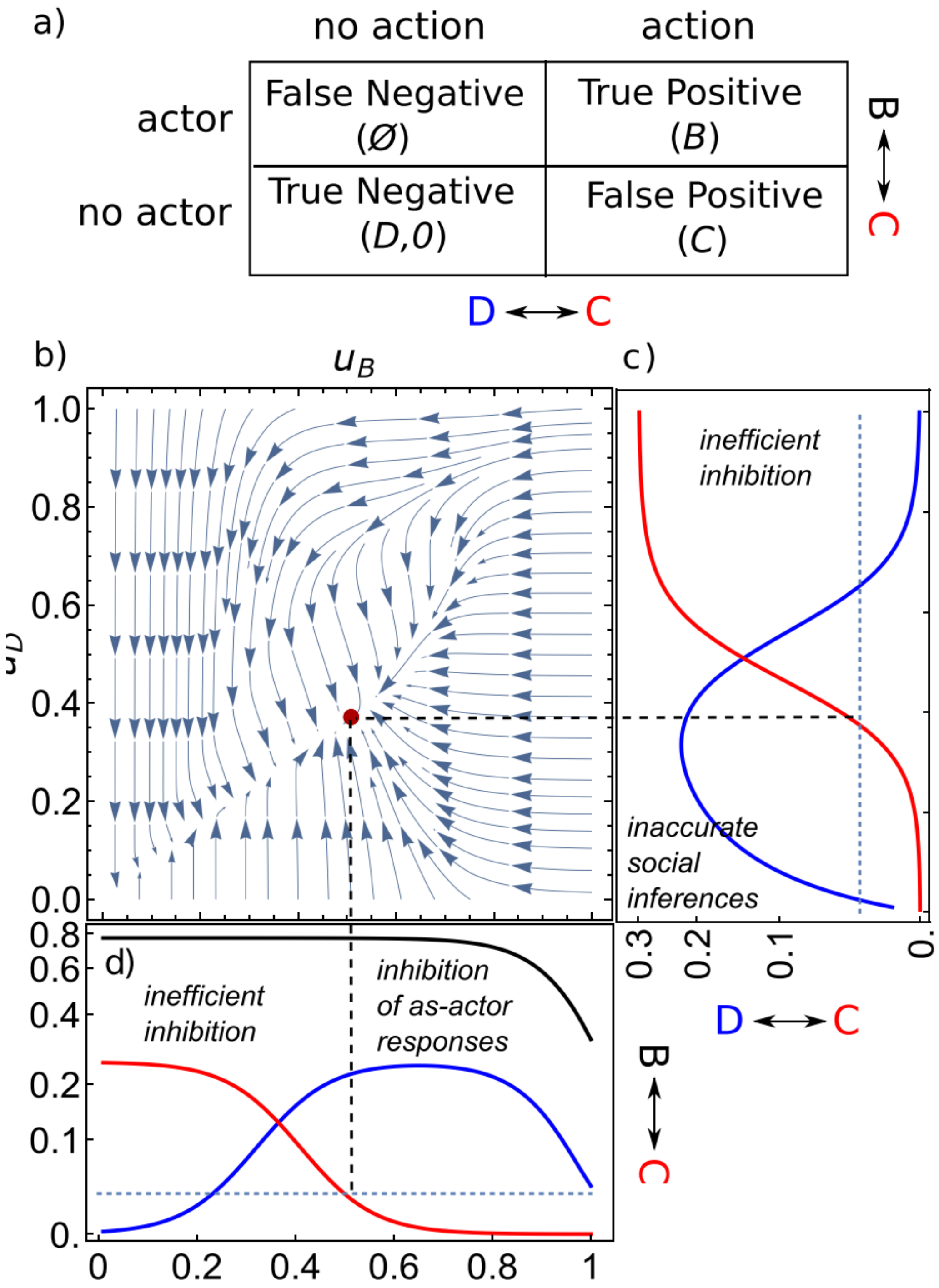
Simulative/empathetic strategies evolve in more complex environments



- What if «empathy» and «mirror neurons» are strategies to simulate other's behavior (S)?
- When do they perform better than strategies relying exclusively on learning (P) or instinctual strategies (F)?

- F (no learning) dominates in simple/stable environments (ants)!
- S evolves in complex environments (primates?)
- When social interactions abound, learning alone is sufficient to predict others (P).

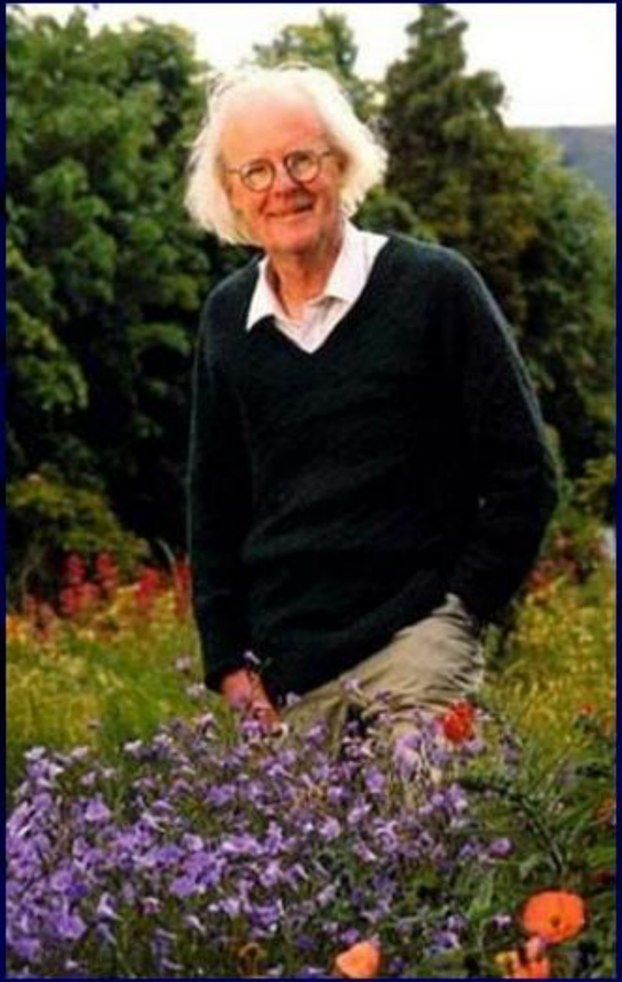
Evolutionary trade-offs can lead to evolution of cemotional contagion and true altruism



Conclusions

- Not only positive-assortment, but also evolutionary trade-offs can also lead to cooperative behavior

John Maynard Smith (1920-2004)



- Educated in Eaton
- The influence of J.B.S. Haldane
- Aeroplane engineer
- Sequence space
- Evolution of sex
- Game theory
- Animal signalling
- Balsan, Kyoto, Crafoord prizes