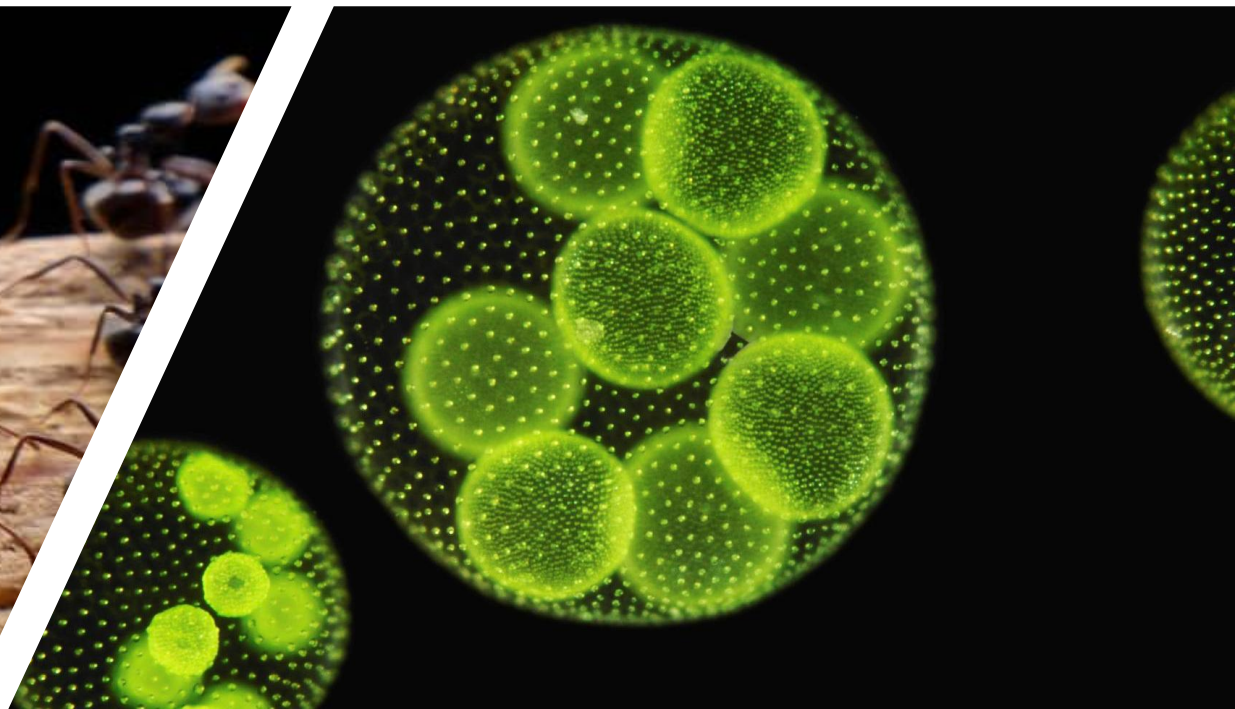




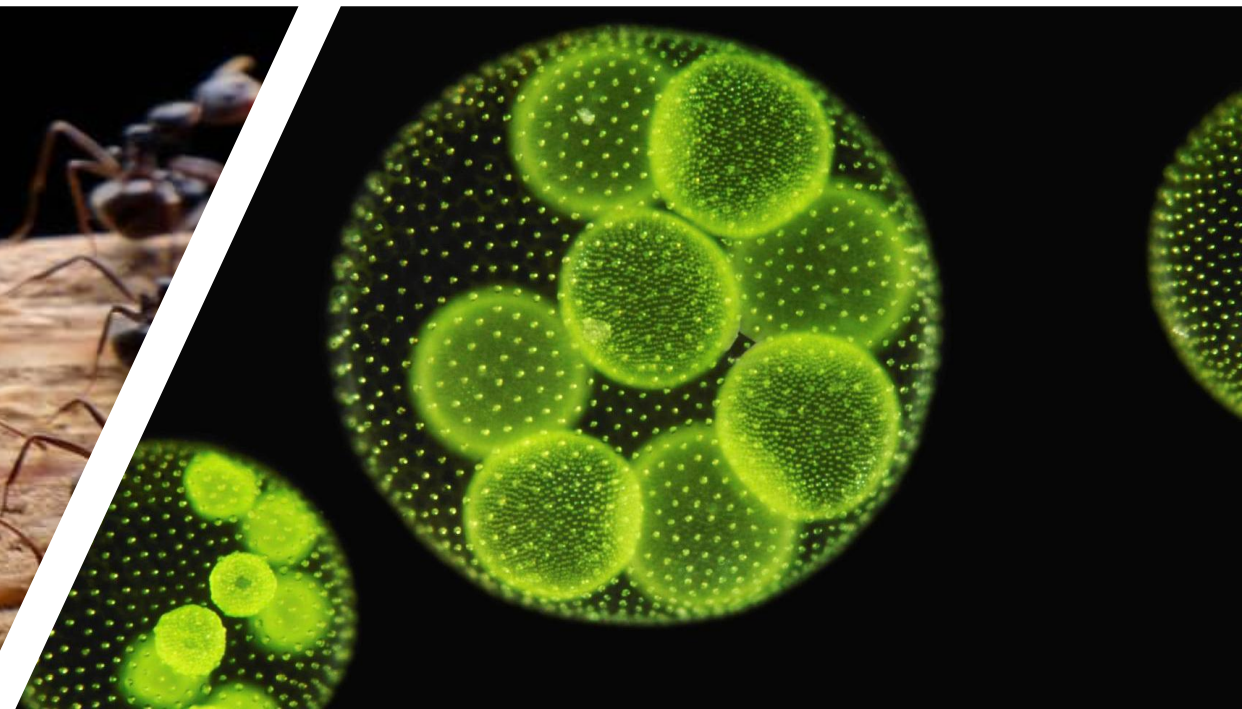
Evolutionary Game Theory II

The Evolution of Cooperation





But before, the usual summary of previous episodes..



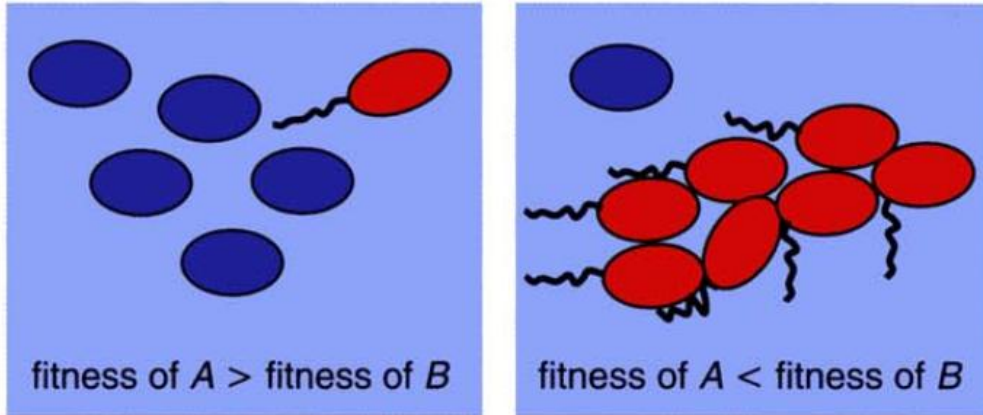
Evolutionary Game theory

The study of «frequency-dependent» fitness

Constant selection:

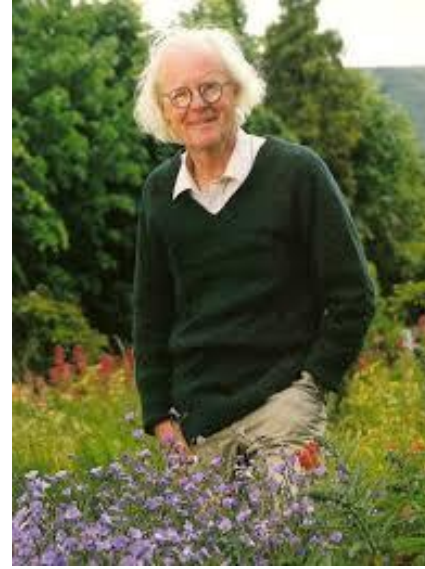


Frequency-dependent selection:



Interaction between individuals can be represented as payoff matrices

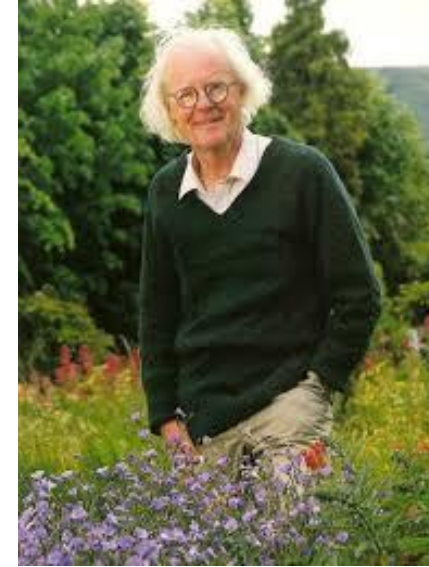
| | Hawk | Dove |
|------|-------|------|
| Hawk | -1,-1 | 4,0 |
| Dove | 0,4 | 2,2 |



John Maynard-Smith
(1920-2004)

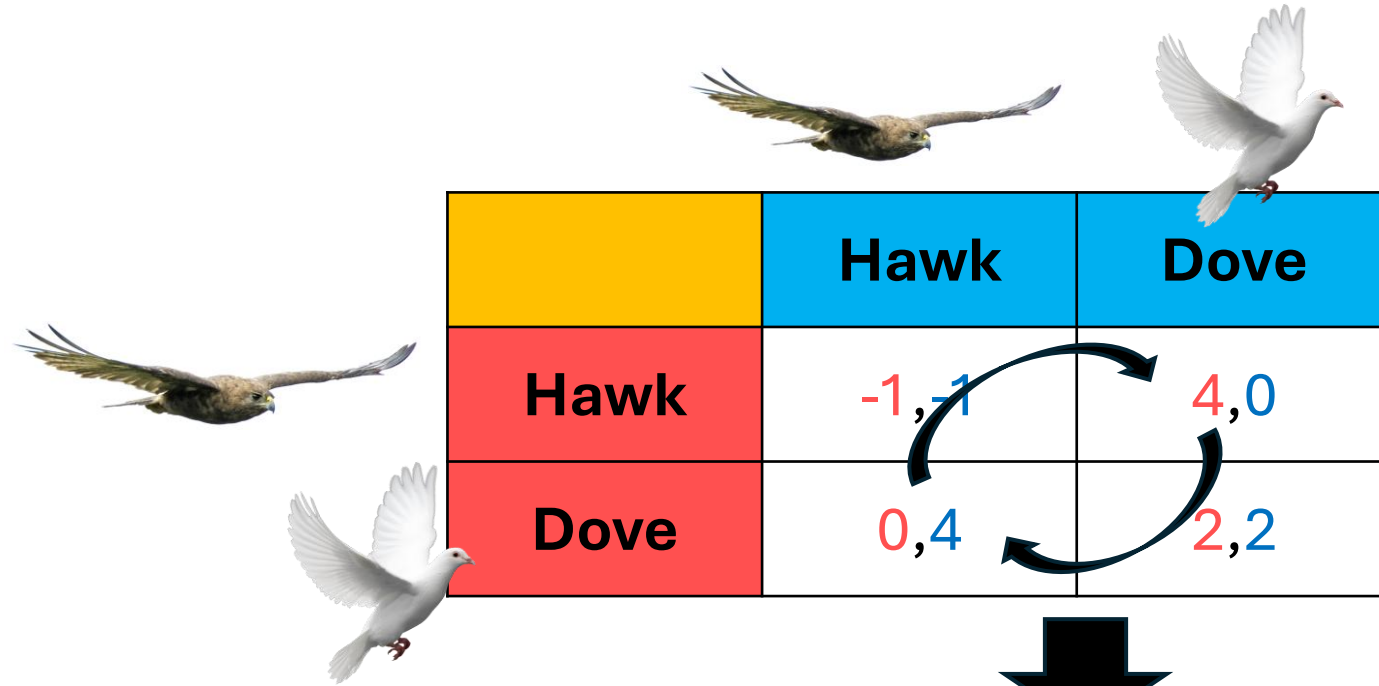
Interaction between individuals can be represented as payoff matrices

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




John Maynard-Smith
(1920-2004)

Symmetric games can be represented in two equivalent ways



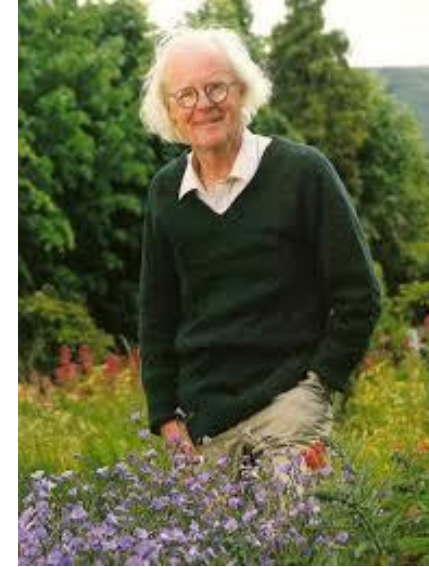
| | Hawk | Dove |
|------|--------|------|
| Hawk | -1, -1 | 4, 0 |
| Dove | 0, 4 | 2, 2 |

A diagram showing a hawk and a dove. The hawk is on the left, and the dove is on the right. A large black arrow points from the top-left cell (-1, -1) to the top-right cell (4, 0), and another large black arrow points from the bottom-left cell (0, 4) to the bottom-right cell (2, 2).



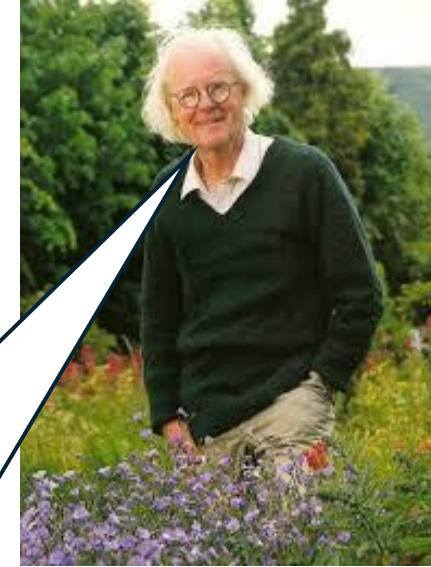
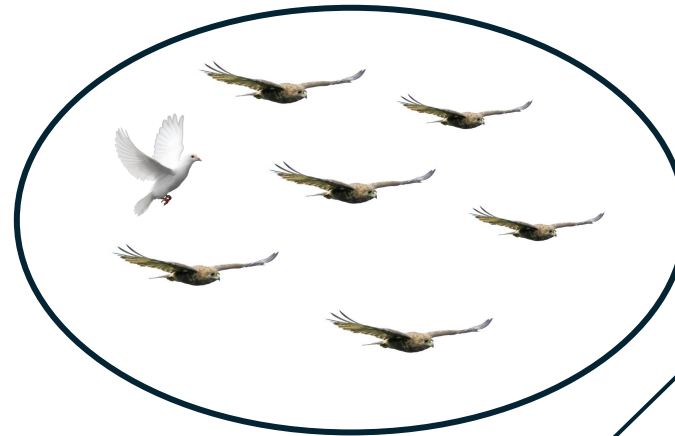
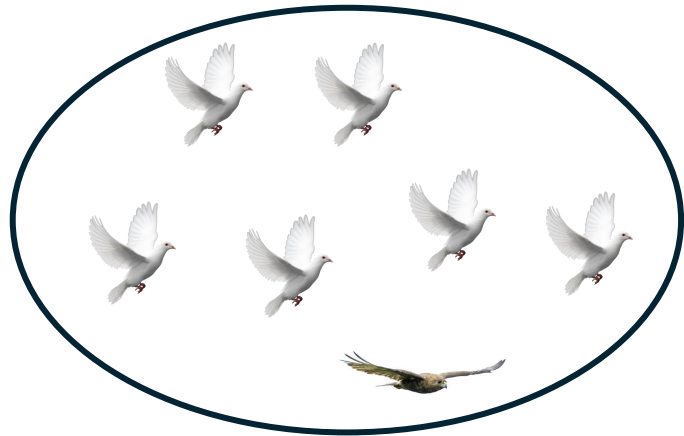
| | Hawk | Dove |
|------|------|------|
| Hawk | -1 | 4 |
| Dove | 0 | 2 |

A diagram showing a hawk and a dove. The hawk is on the left, and the dove is on the right. A large black arrow points from the top table to this table.



John Maynard-Smith
(1920-2004)

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



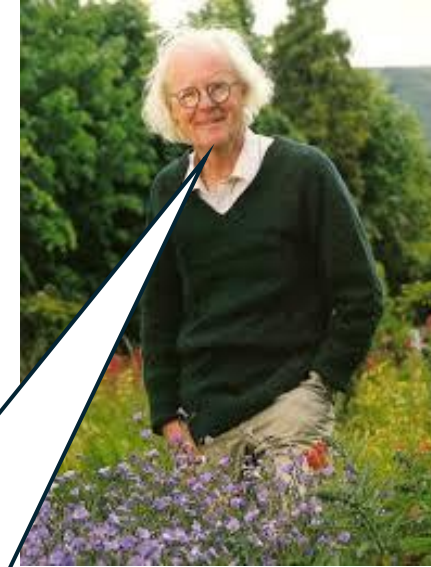
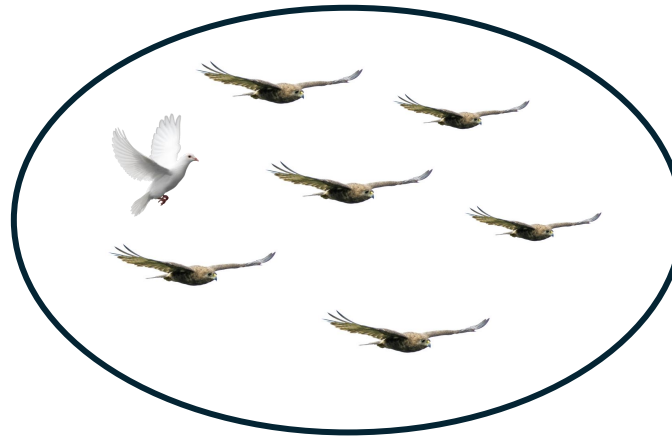
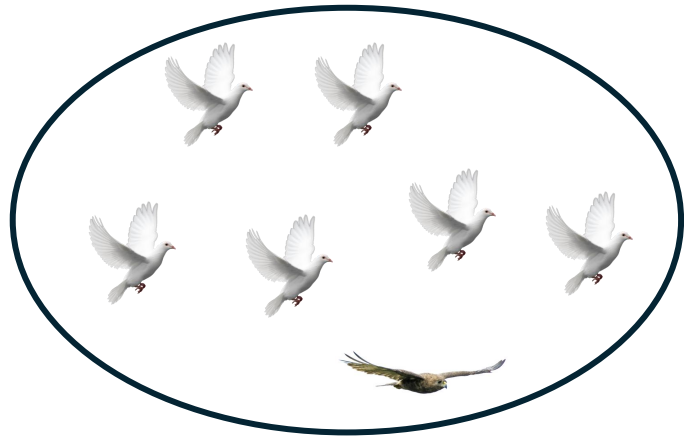
John Maynard-Smith
(1920-2004)

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

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

The table is a 2x2 matrix with 'Hawk' and 'Dove' as both rows and columns. The top-left cell (Hawk vs Hawk) has a red background and contains '-1,-1'. The top-right cell (Hawk vs Dove) has a blue background and contains '4,0'. The bottom-left cell (Dove vs Hawk) has a red background and contains '0,4'. The bottom-right cell (Dove vs Dove) has a blue background and contains '2,2'. Above the table, a hawk is flying above the 'Hawk' column and a dove is flying above the 'Dove' column. To the left of the table, a hawk is flying above the 'Hawk' row and a dove is flying above the 'Dove' row.

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

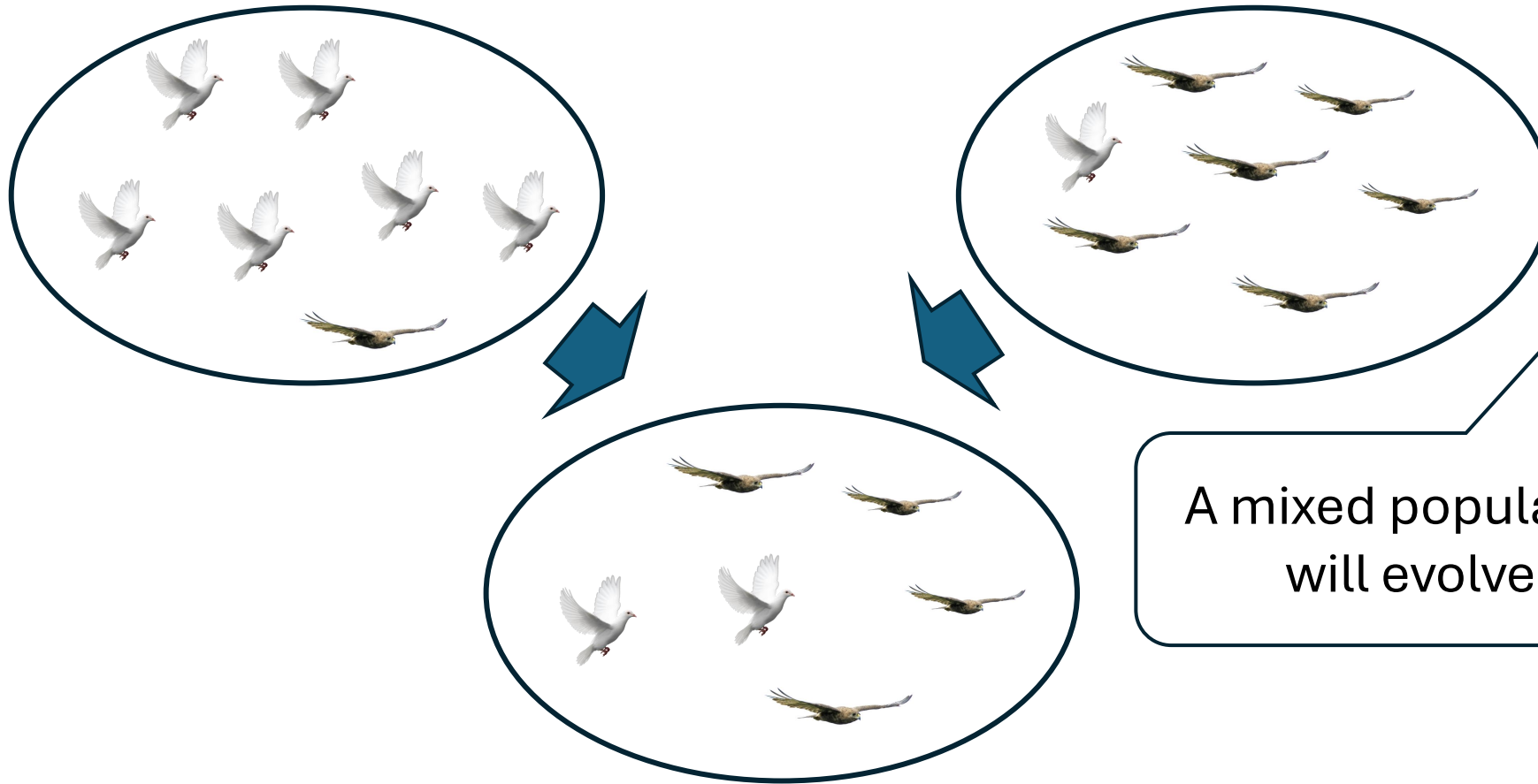


John Maynard-Smith
(1920-2004)

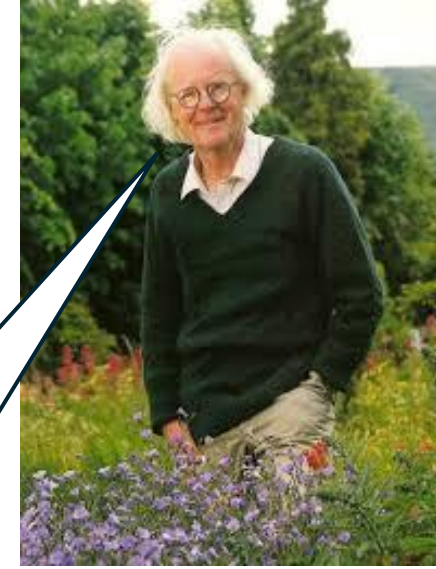
Both Hawks and Doves
can be invaded, so
they are not ESS

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

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



A mixed population will evolve!

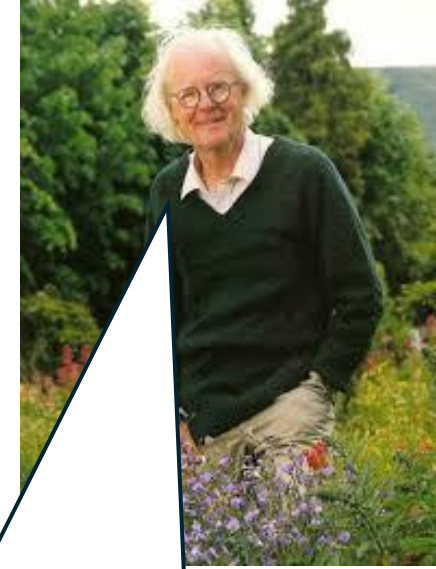
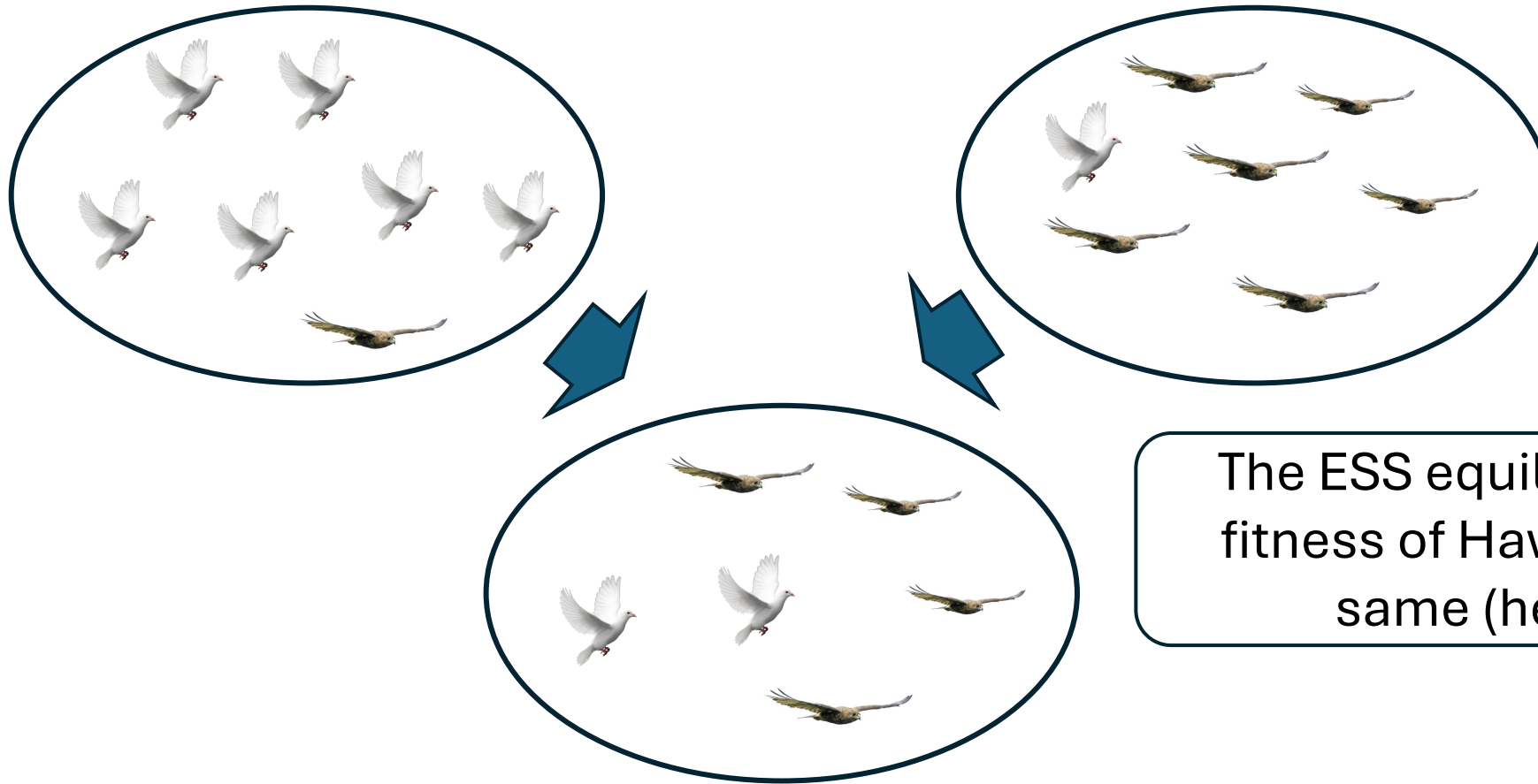


John Maynard-Smith
(1920-2004)

A payoff matrix for the Hawk-Dove game. The columns are labeled 'Hawk' and 'Dove' with corresponding bird icons. The rows are labeled 'Hawk' and 'Dove' with corresponding bird icons. The cells contain numerical payoff pairs.

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

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

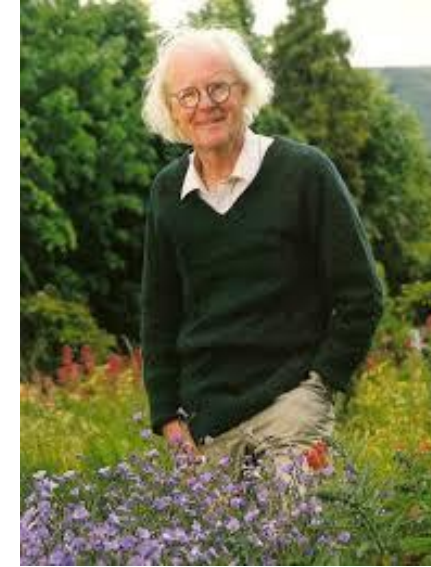
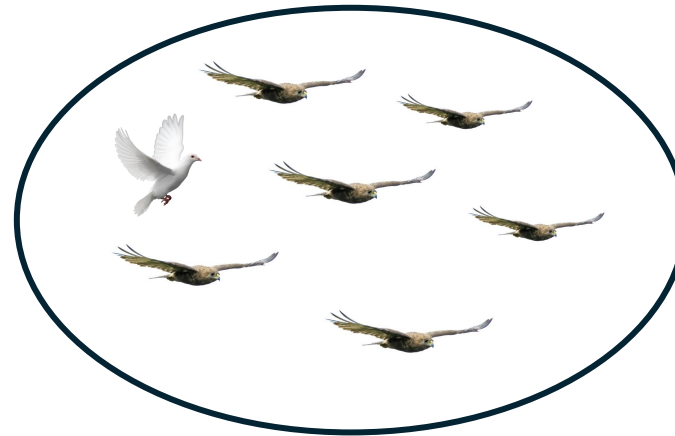


ynard-Smith
(1920-2004)

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

| | Hawk | Dove |
|------|-------|------|
| Hawk | -1,-1 | 4,0 |
| 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



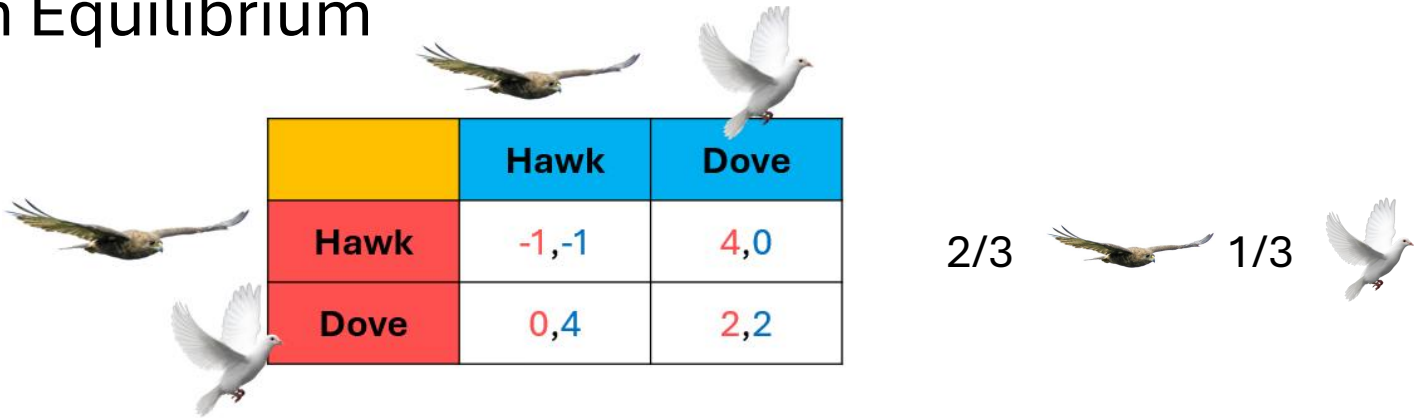
and $1-p$



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

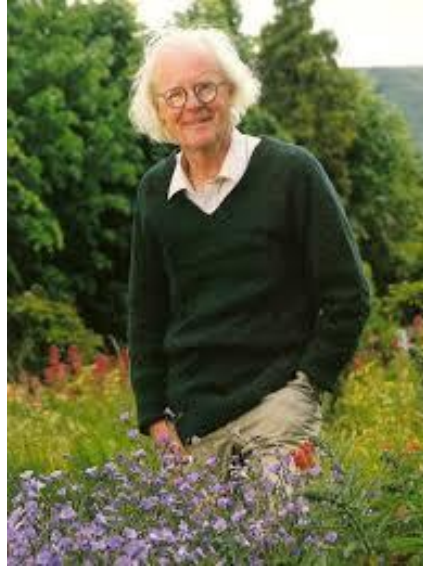
Nash Equilibria and Evolutionarily Stable Strategies (ESS) share similar intuitions

Nash Equilibrium



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!”



John Maynard-Smith (1920-2004)

ESS

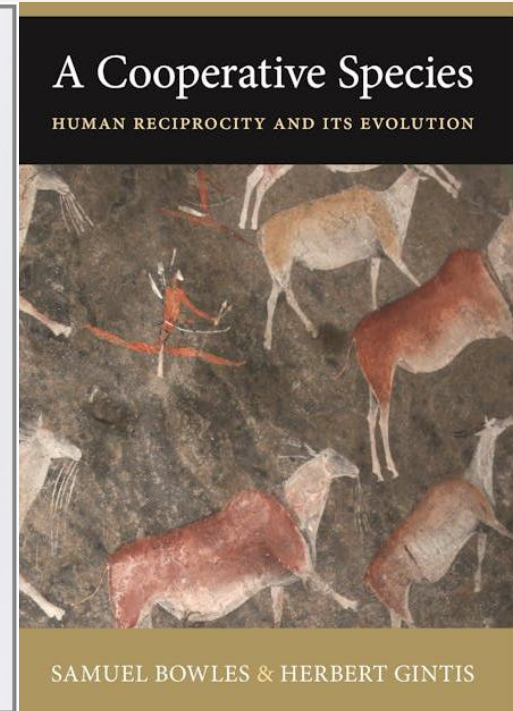
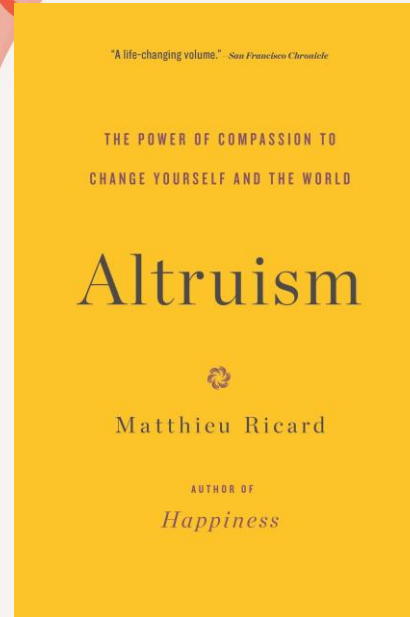


Point where a rare mutant with a different strategy cannot invade the population.

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)

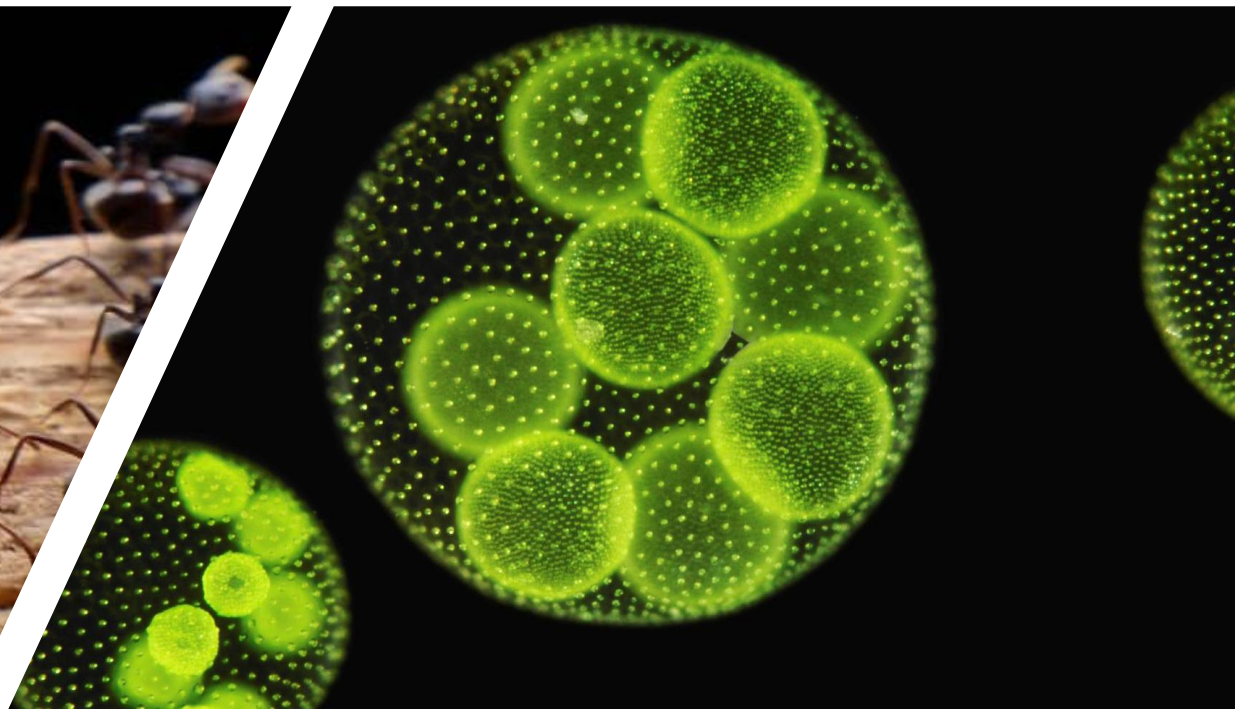
The evolution of cooperation





The evolution of cooperation

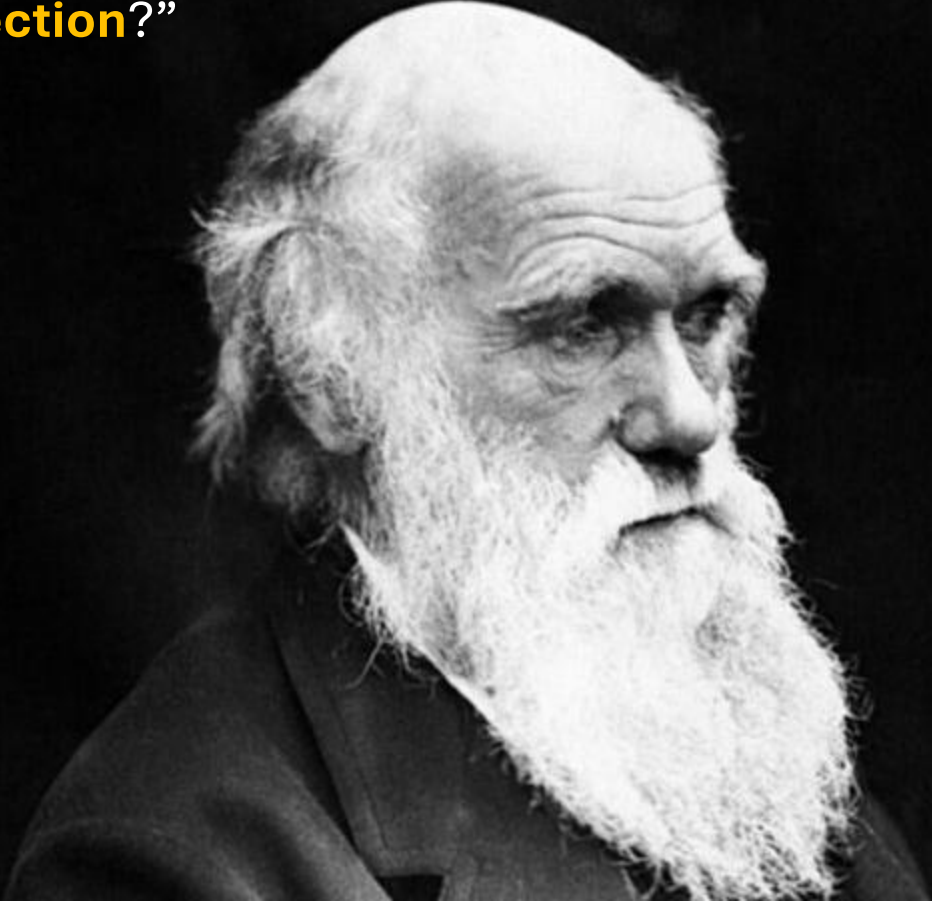




From the «On the Origin of Species»:

“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.**”

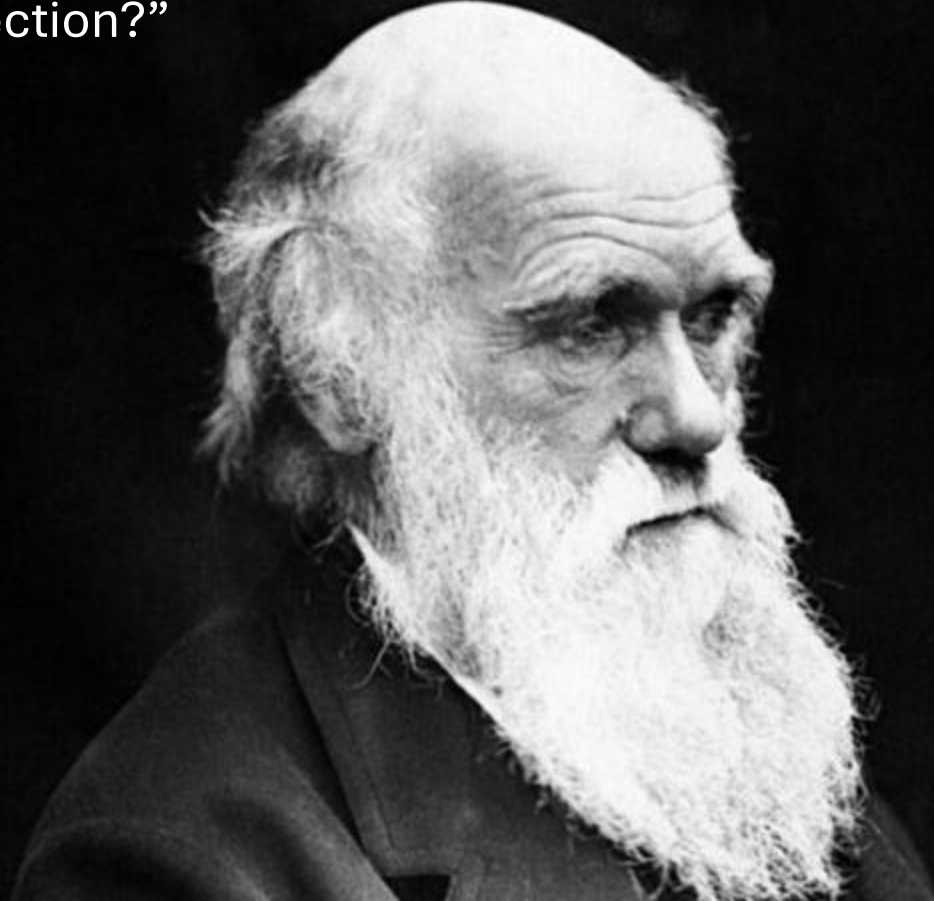
“But with the working ant we have an insect differing greatly from its parents, yet absolutely sterile; so that it could never have transmitted successively acquired modifications of structure or instinct to its progeny. It may well be asked **how is it possible to reconcile his case with the theory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



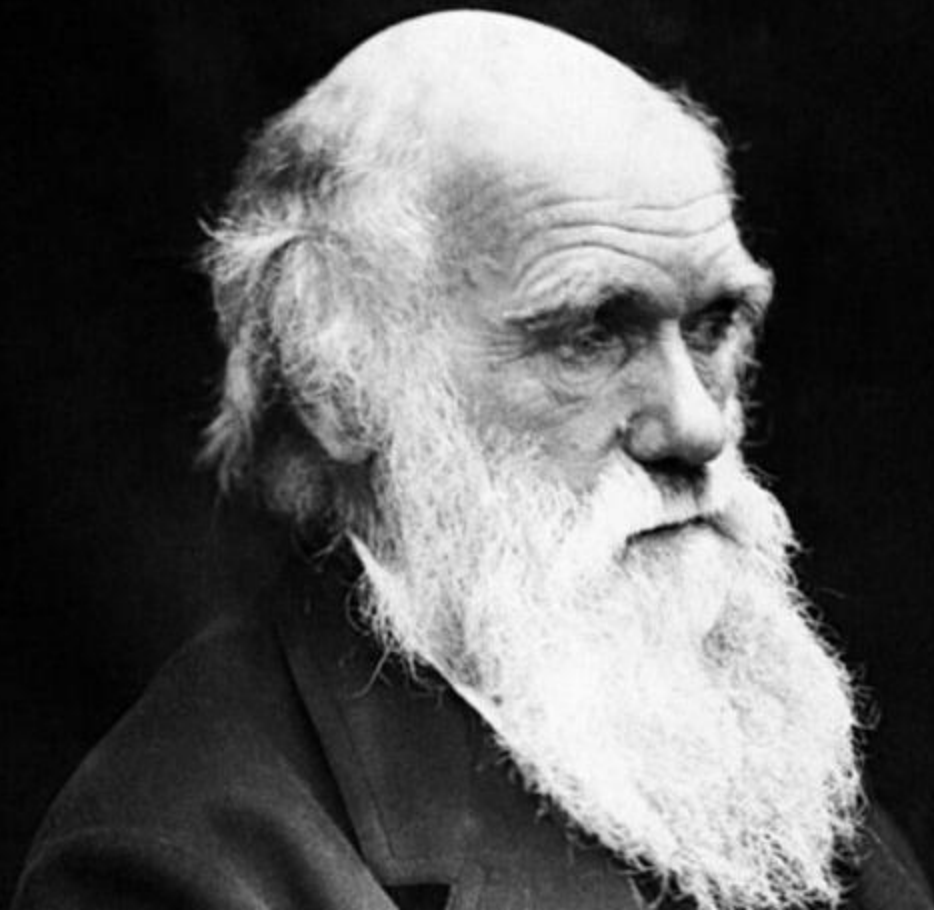
From the «On the Origin of Species»:

“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?”



“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

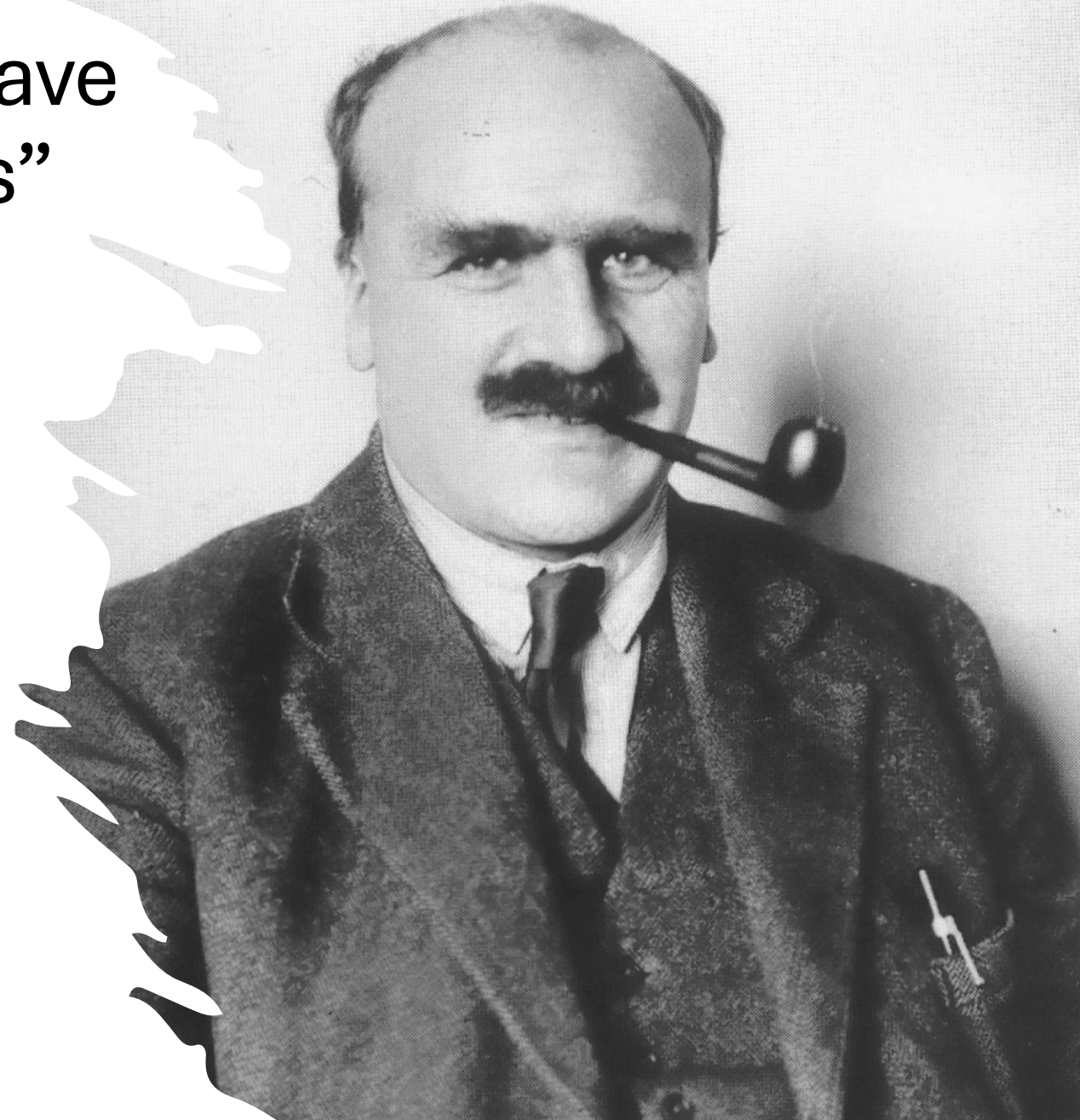
Ants, bees, wasps, and termites show eusociality, but ants are the most extreme case as workers are **completely sterile** and function almost as a superorganism.

In order Hymenoptera, haplodiploid sex determination:

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

“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:

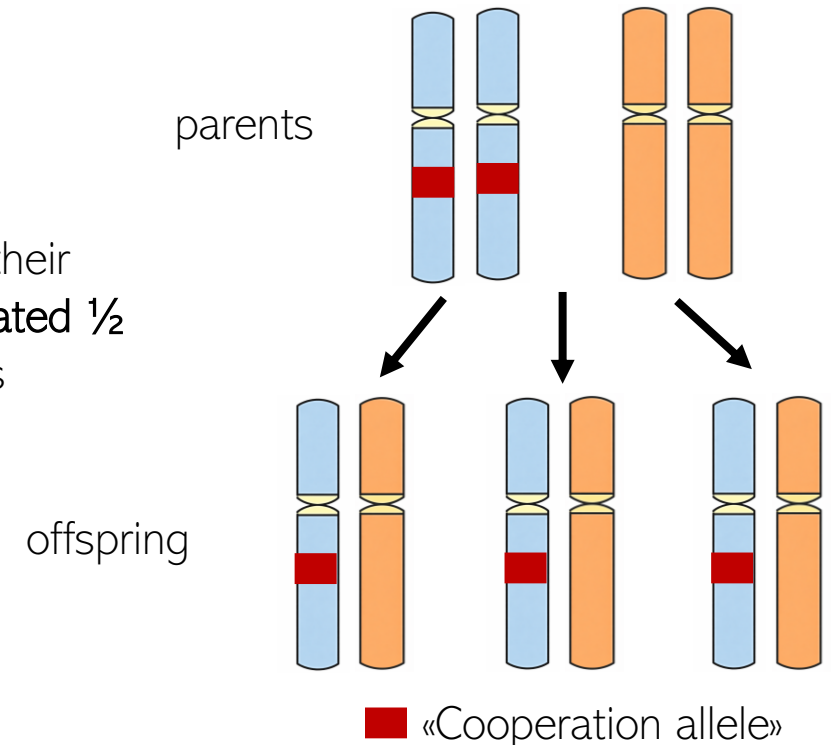
$$r > b/c$$

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



Bill Hamilton
(1936-2000)

Parents and their
offspring are **related** $\frac{1}{2}$
in diploids



Hamilton's rule and kin-selection (1964)

Natural selection favors altruism when:

$$r > b/c$$

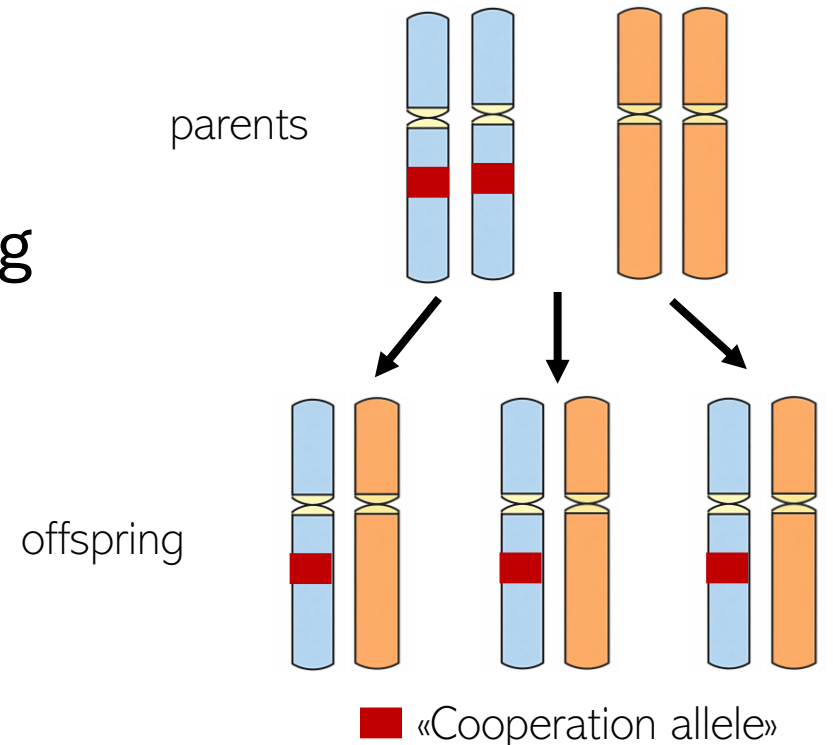
where **c** is the **cost** of cooperation, **b** the **benefit** given and **r** is the **relatedness** coefficient.

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»

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

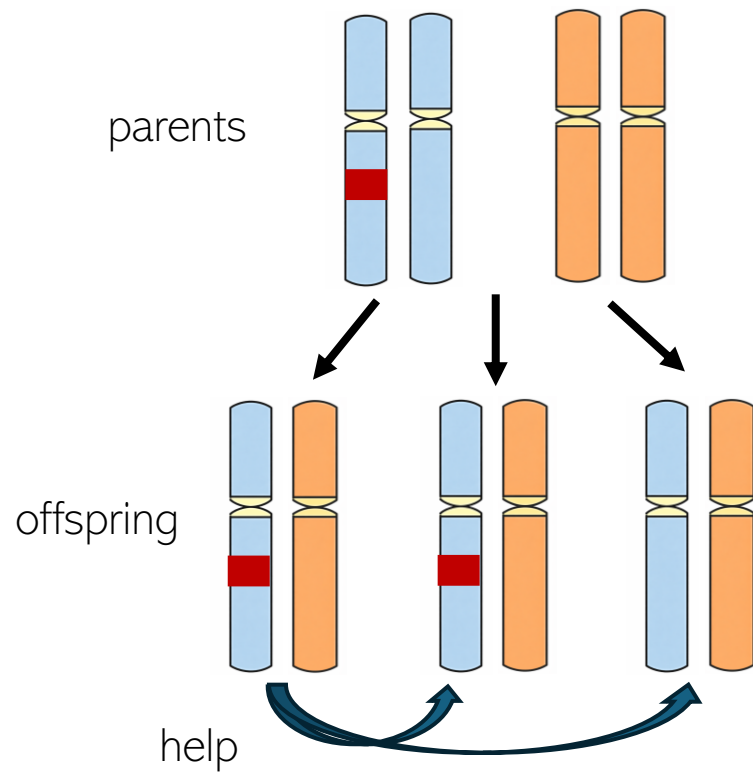
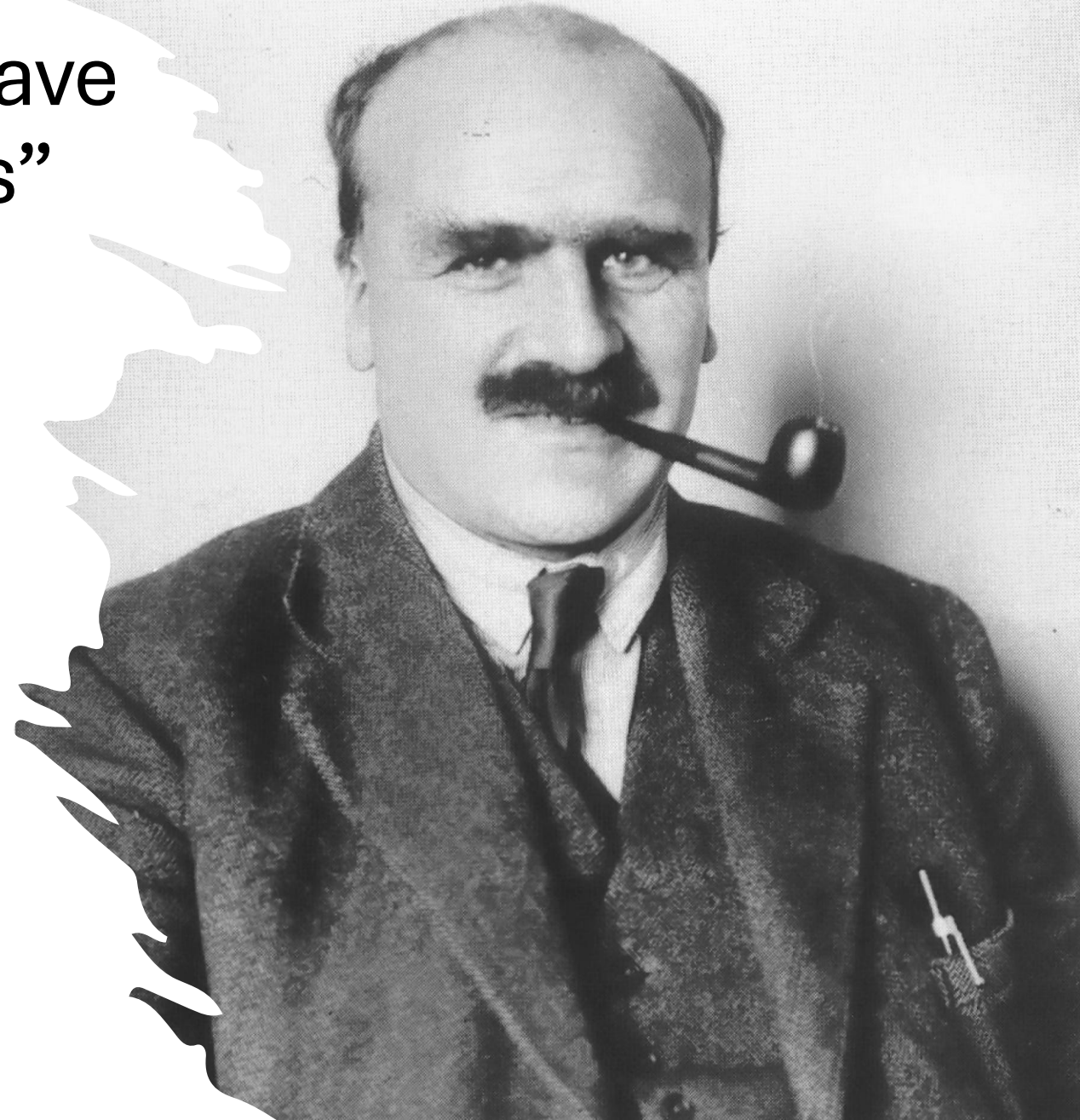


Bill Hamilton
(1936-2000)



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

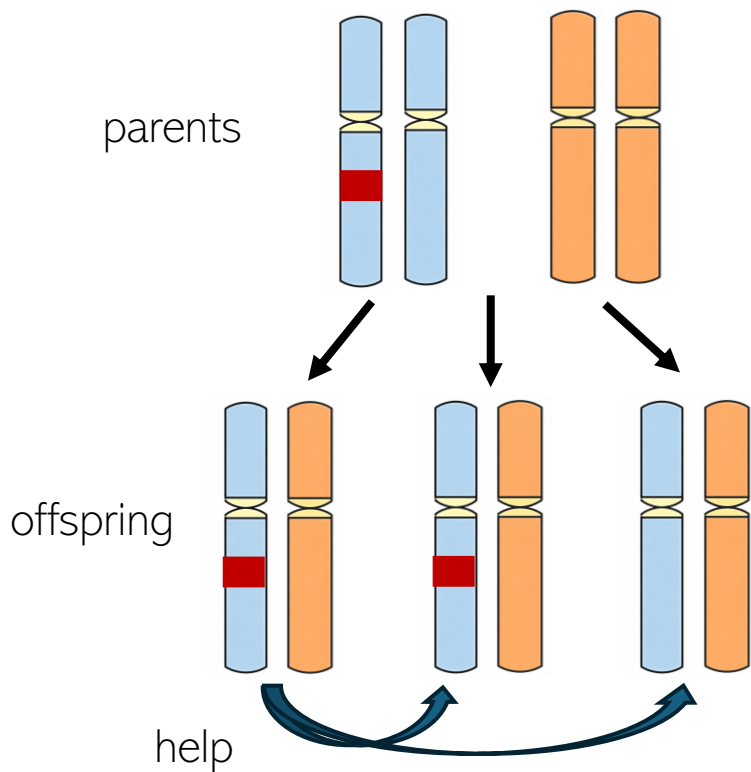
JBS Haldane, sometimes in the 50s, in a pub.



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.



WORLD > AUSTRALIA • 2 MIN READ


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

FEB 3, 2026



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.



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

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

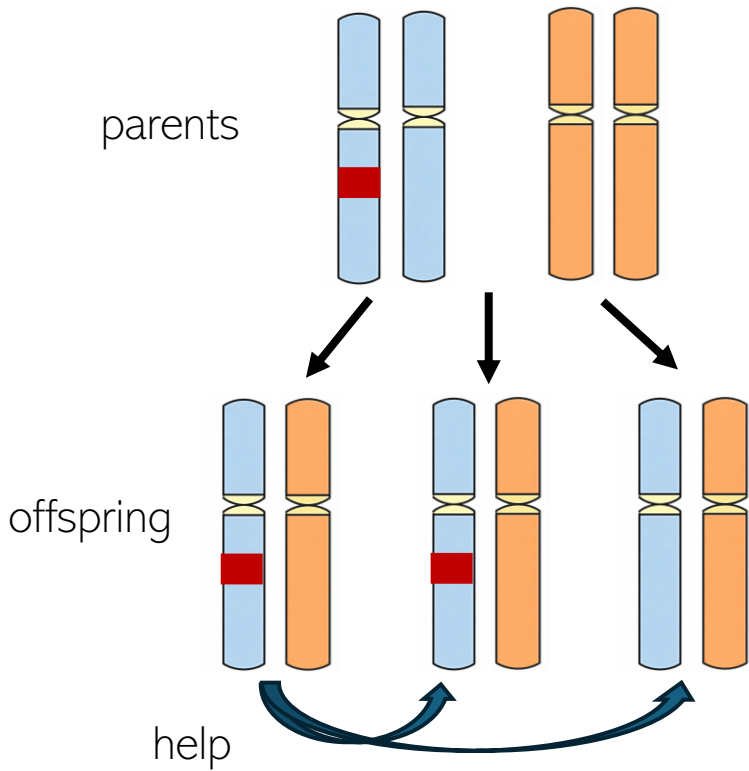
Bill Hamilton
reviewed in 1999

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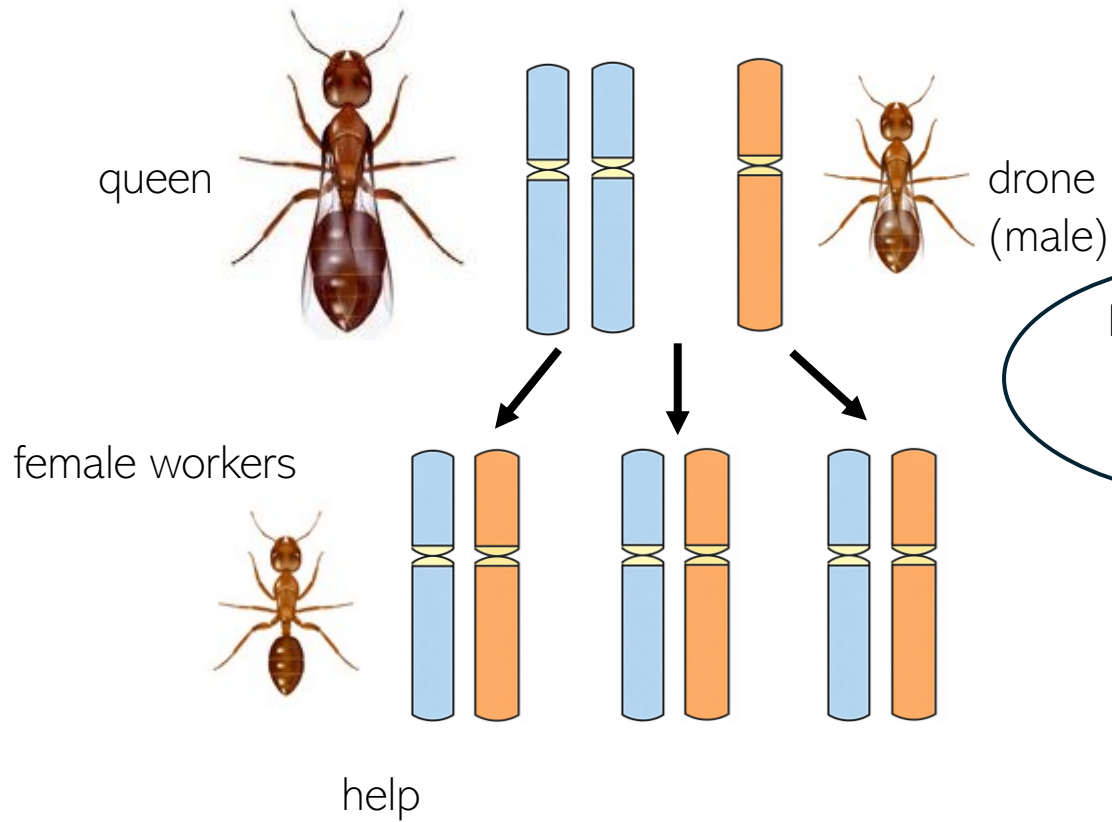
Australian teen swam hours to shore to get help for mother and siblings swept out to sea

FEB 3, 2026



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

An ant



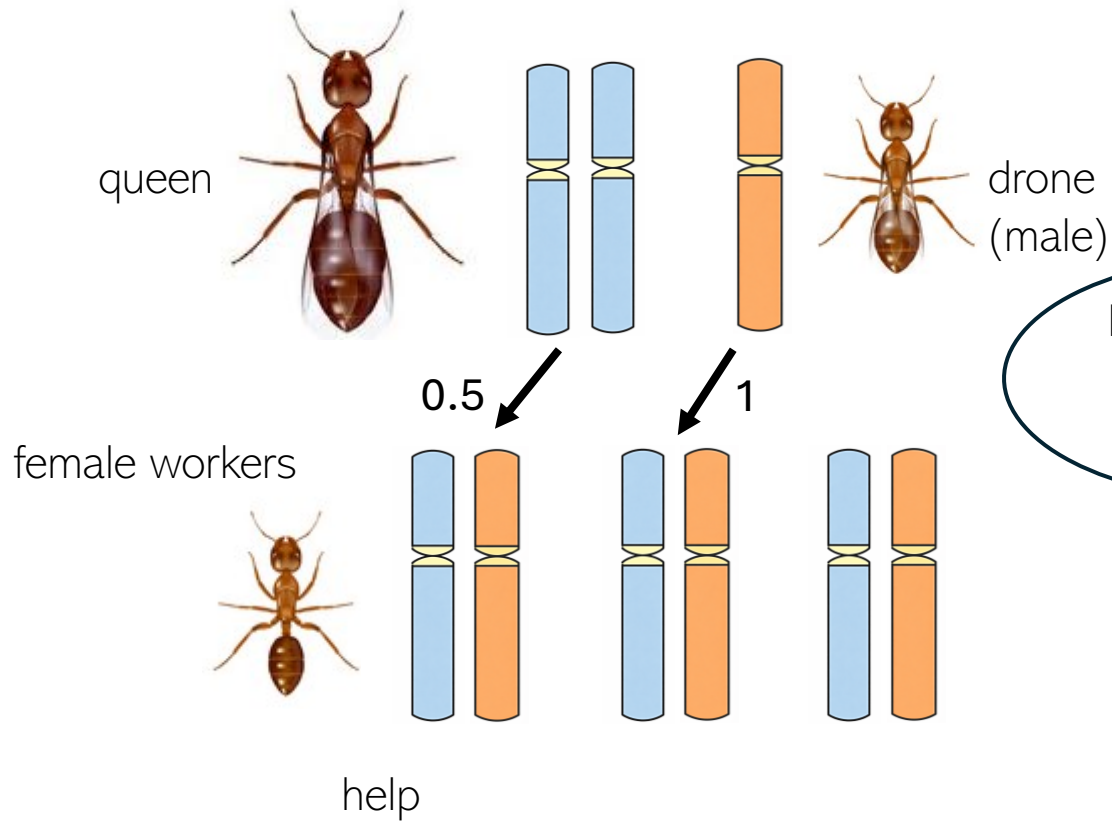
How much are we related to each other?



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

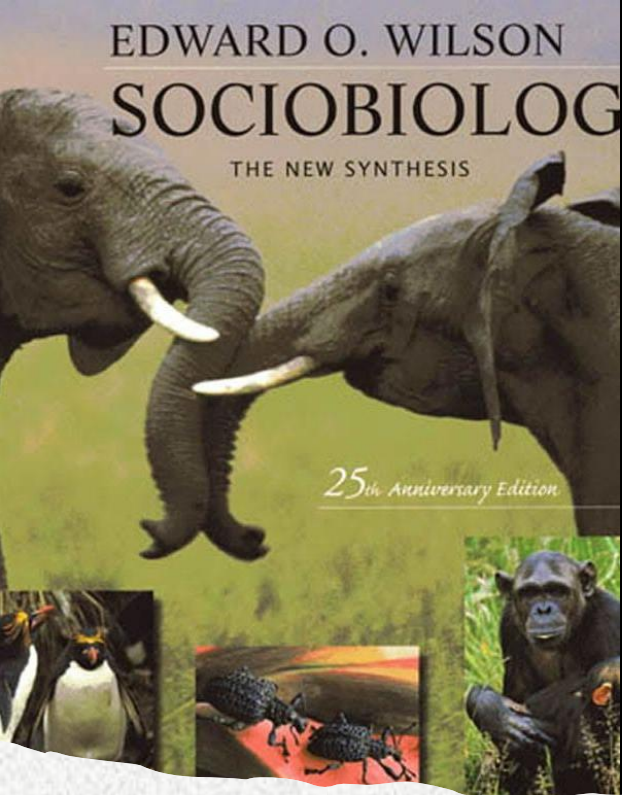
An ant

$$r \text{ between siblings} = \frac{1}{2} * 0.5 + \frac{1}{2} * 0.1 = 0.75$$



How much are we related to each other?

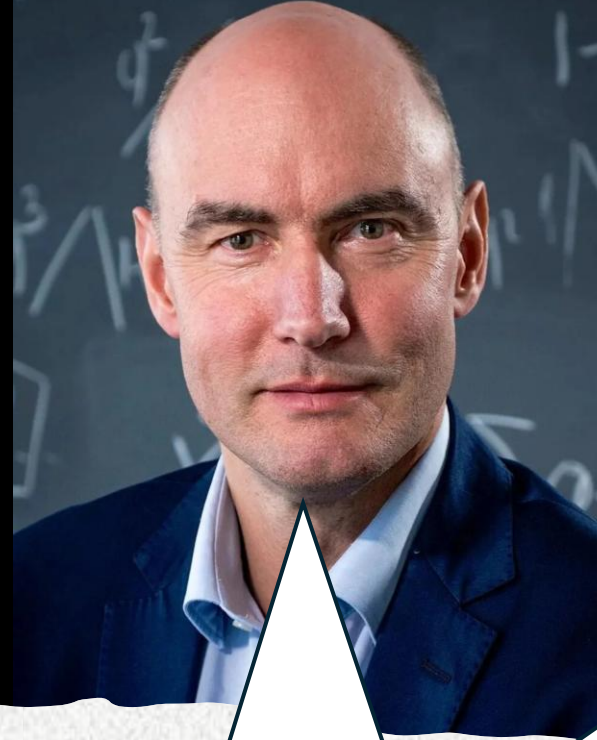




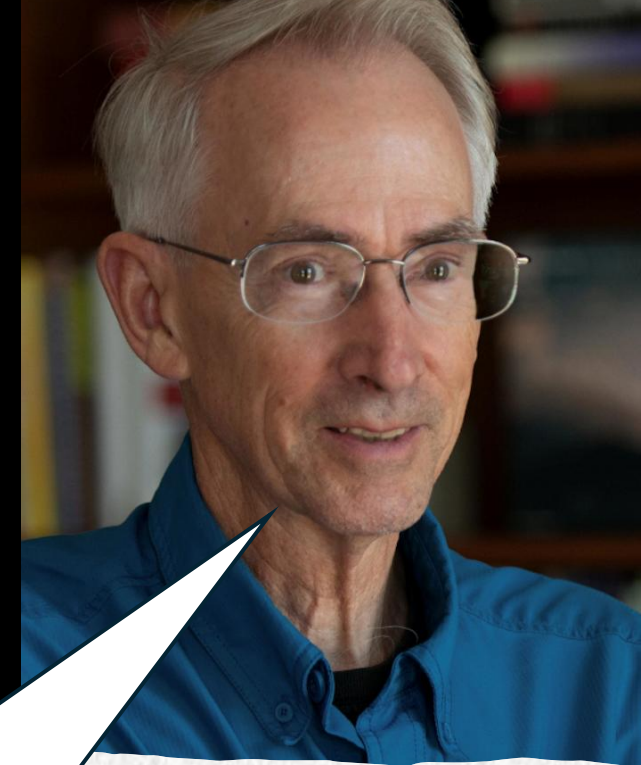
Edward O. Wilson



Martin Nowak

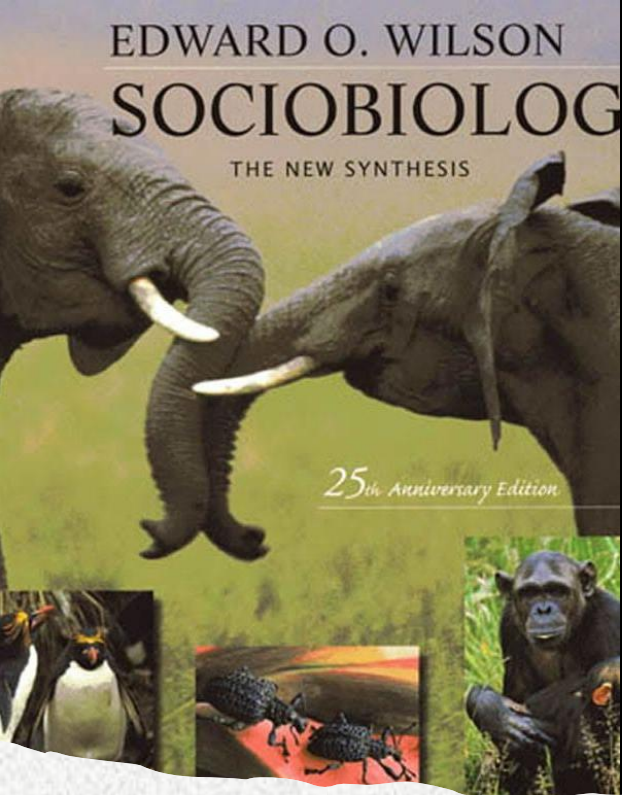


David Sloan Wilson



Antonella Tramacere, Roma Tre

This is too reductionist!



EDWARD O. WILSON

SOCIOBIOLOGY

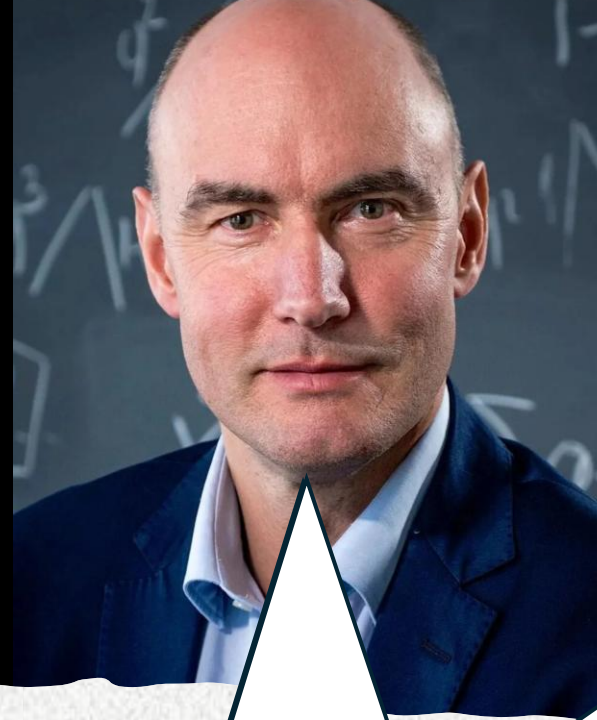
THE NEW SYNTHESIS

25th Anniversary Edition

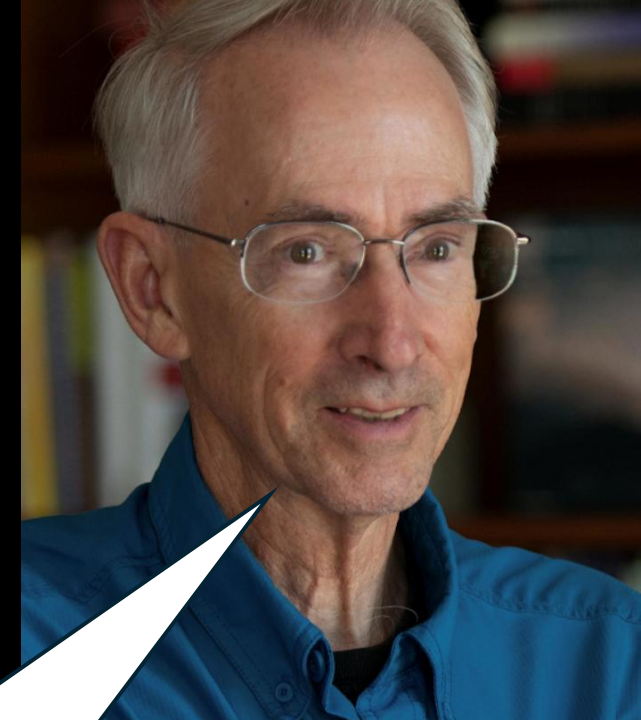
Edward O. Wilson



Martin Nowak



David Sloan Wilson

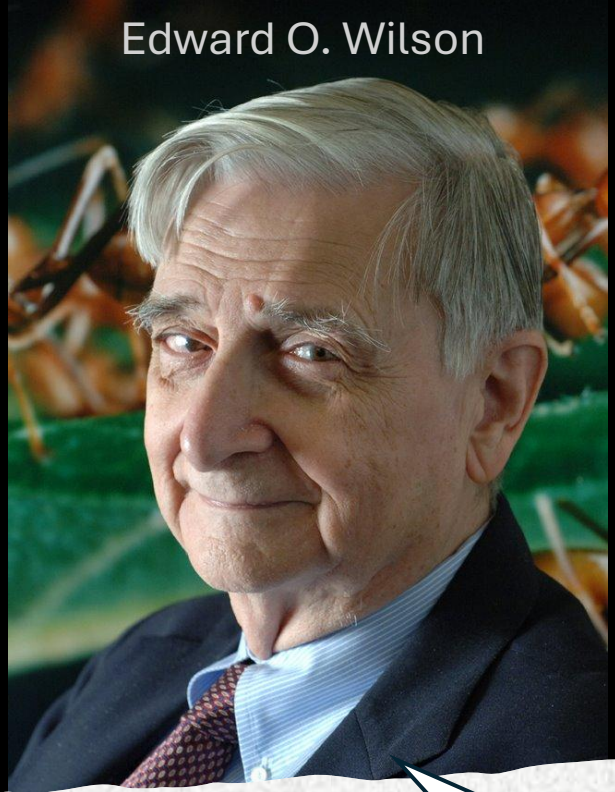


Actually I care more that it is not
mathematically rigorous*..

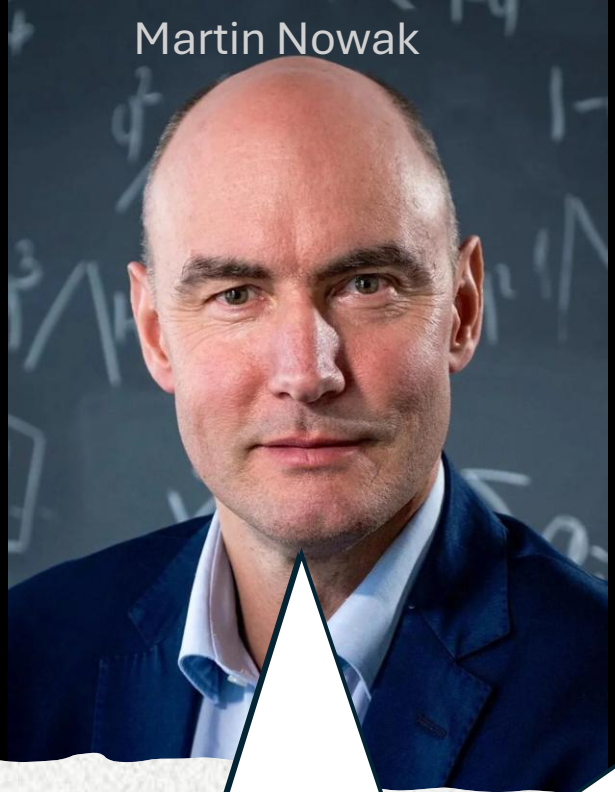
*And if you care, inclusive fitness is also «dynamically insufficient». We'll see a little bit what it means next time



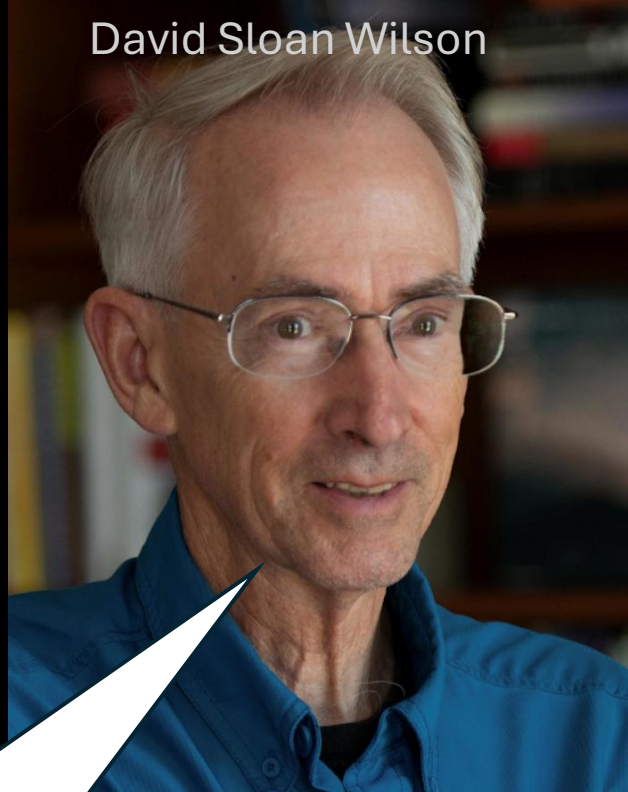
A solitary wasp from the Sphecidae family



Edward O. Wilson



Martin Nowak



David Sloan Wilson

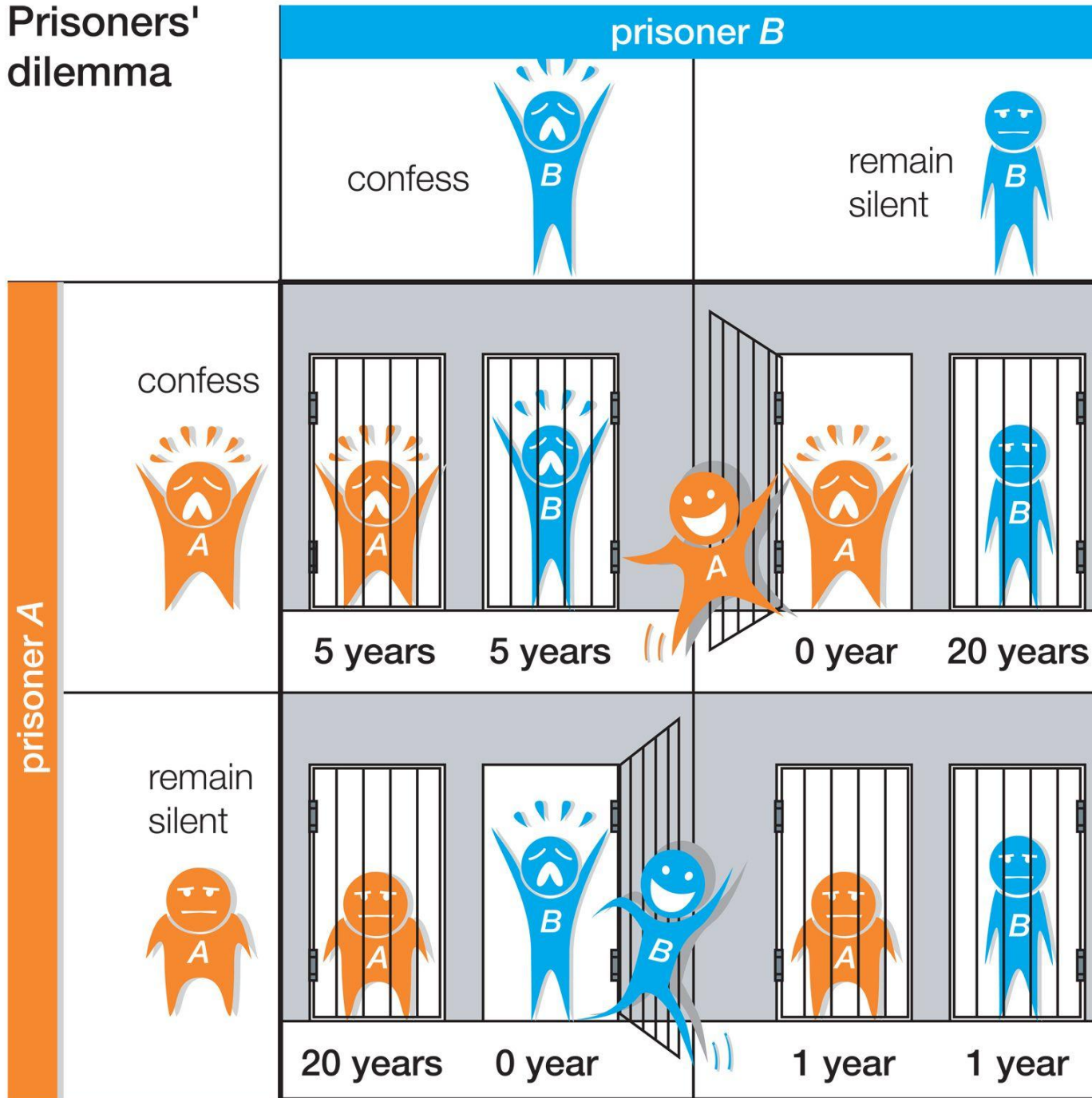


Heterocephalus glaber

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!

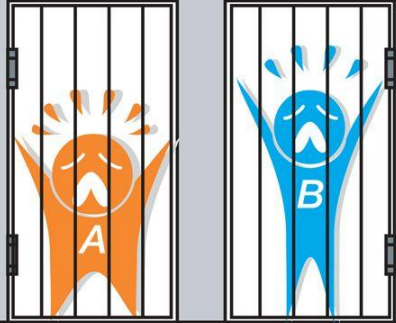
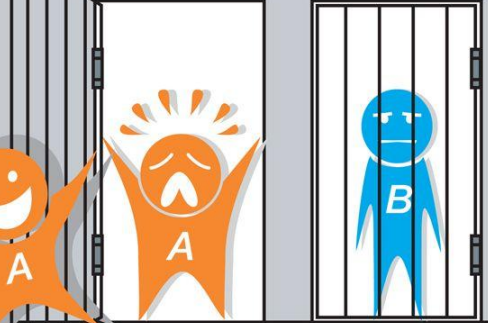
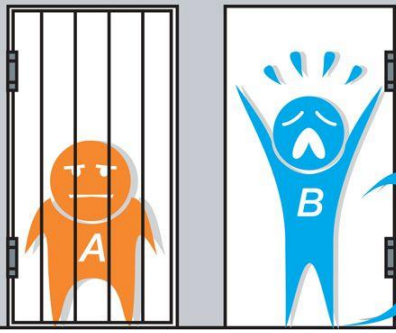
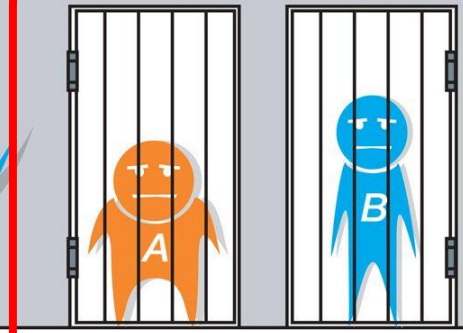


Prisoners' dilemma



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

Prisoners' dilemma

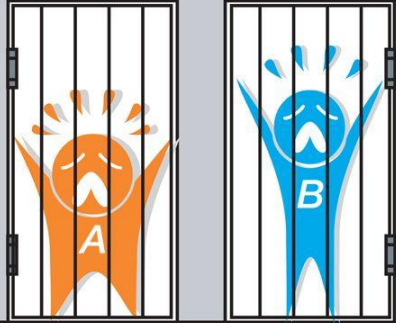
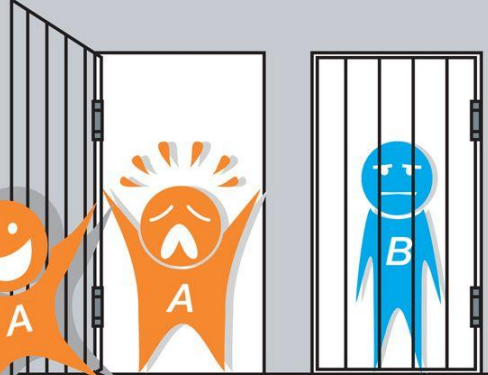
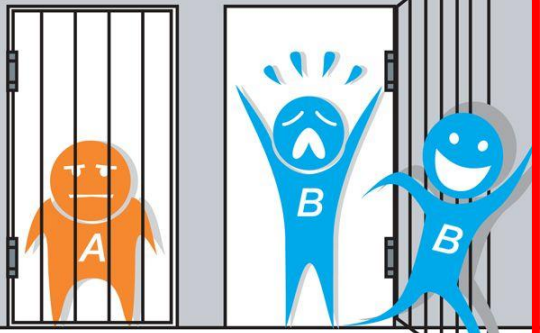

| | | prisoner B | | | |
|------------|---------------|--|---|---------------|--|
| | | confess | | remain silent | |
| prisoner A | confess |  5 years 5 years |  0 year 20 years | | |
| | remain silent |  20 years 0 year |  1 year 1 year | | |

Two prisoners agree before being caught not to snitch. They can either cooperate with each other (remain silent) 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.*



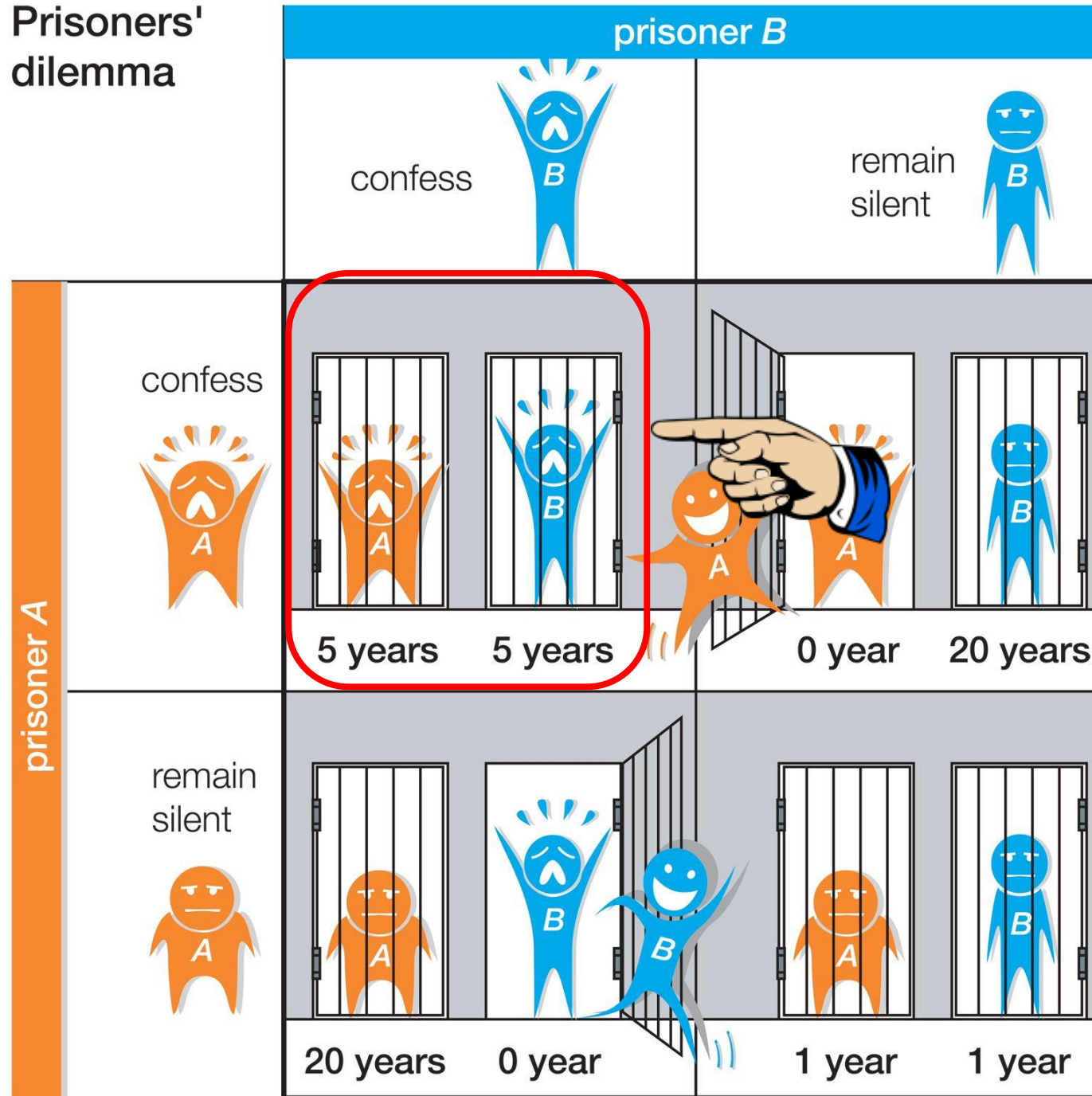
Prisoners' dilemma

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|------------|---------------|---|---|---------------|--|
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| prisoner A | confess |  5 years 5 years |  0 year 20 years | | |
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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.*

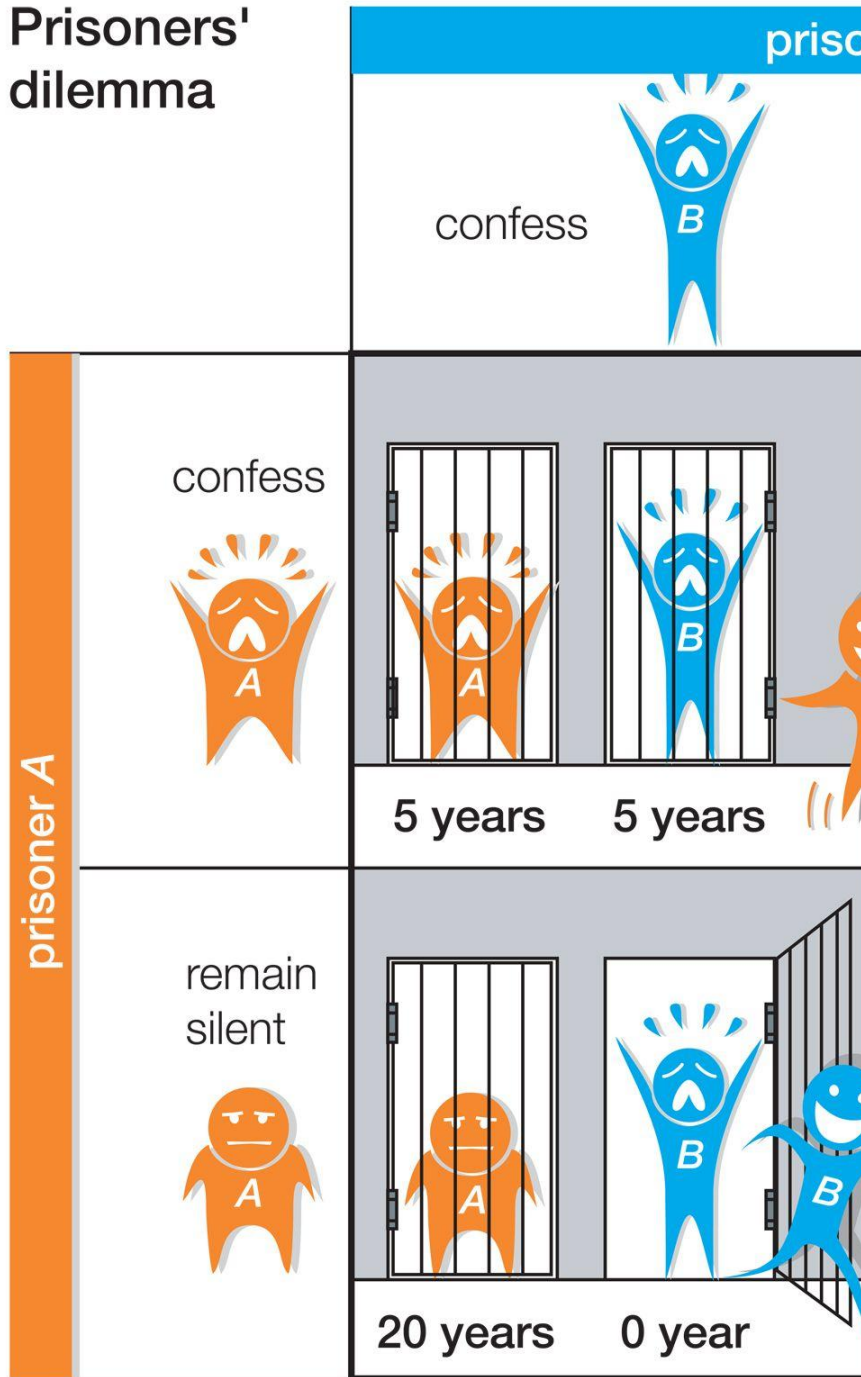
Prisoners' dilemma



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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*

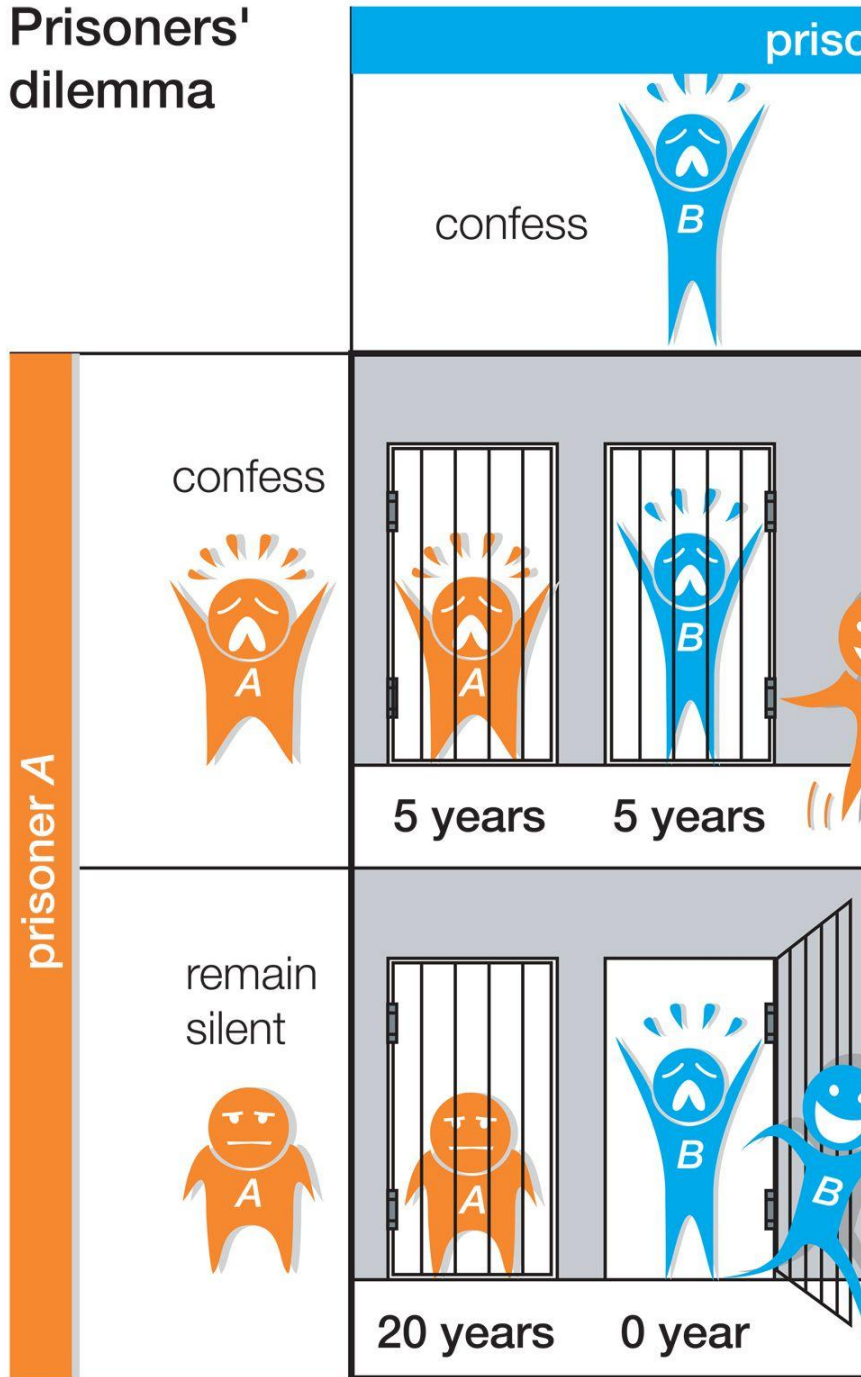
Prisoners' dilemma



All in all

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

Prisoners' dilemma




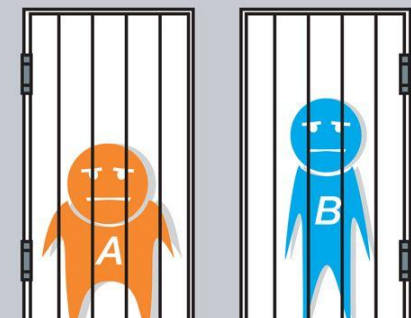


All in all

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

Prisoner A should confess/defect too!



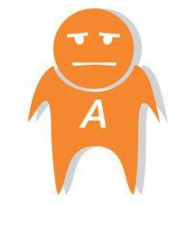

Prisoners' dilemma

| | | prisoner B | |
|------------|---------------|---|--|
| | | confess | remain silent |
| prisoner A | confess |  5 years 5 years |  0 year 20 years |
| | remain silent |  20 years 0 year |  1 year 1 year |

All in all

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

Prisoners' dilemma

| | | prisoner B | |
|------------|---------------|---|---|
| | | confess | remain silent |
| prisoner A | confess |  5 years 5 years |  0 year 20 years |
| | remain silent |  20 years 0 year |  1 year 1 year |

All in all

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

Prisoner B should still confess/defect!

Prisoners' dilemma

| | | prisoner B | |
|------------|---------------|---------------------------|---------------------------|
| | | confess | remain silent |
| prisoner A | confess | <p>5 years 5 years</p> | <p>0 year 20 years</p> |
| | remain silent | <p>20 years 0 year</p> | <p>1 year 1 year</p> |

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

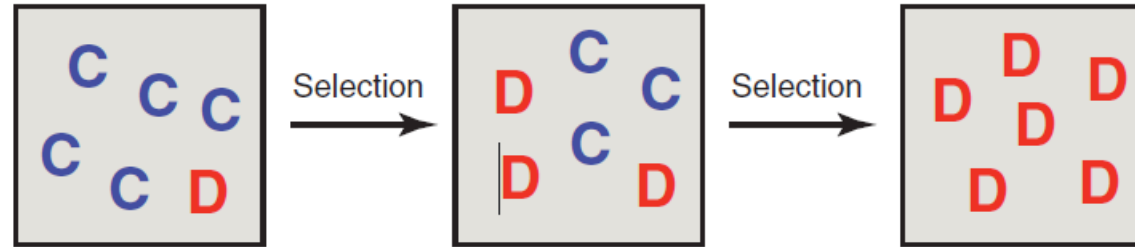
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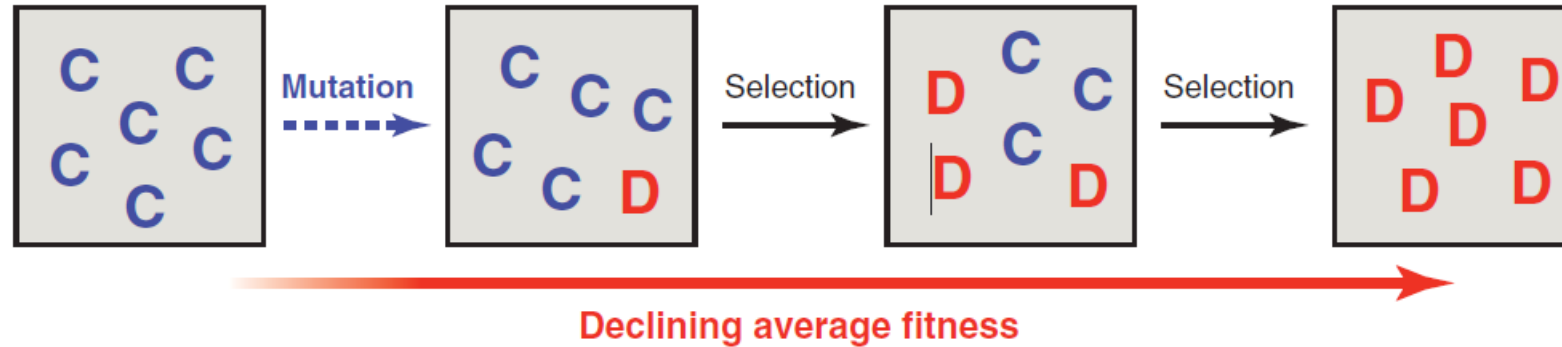
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The Prisoner's dilemma is a «strict» social dilemma where it is always convenient to defect



| | 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) | 5 | 0 |
| D (Defect) | 3 | 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) | 5 | 0 |
| D (Defect) | 3 | 1 |



Who scored the highest payoff?

What strategies did you choose?

What worked and what didn't?





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



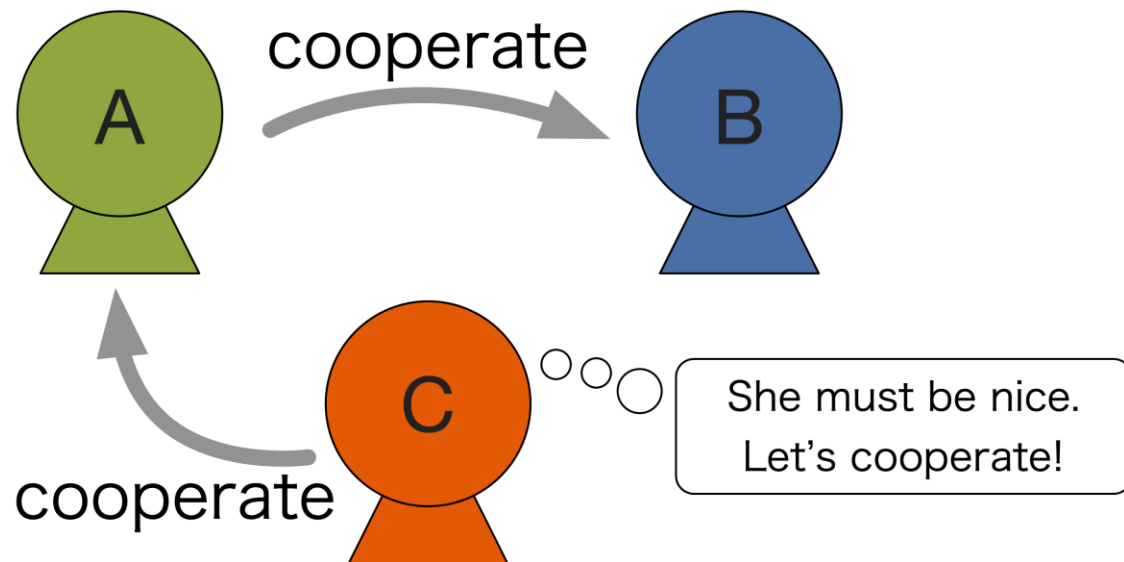
What do you notice? What could happen in such contexts?



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



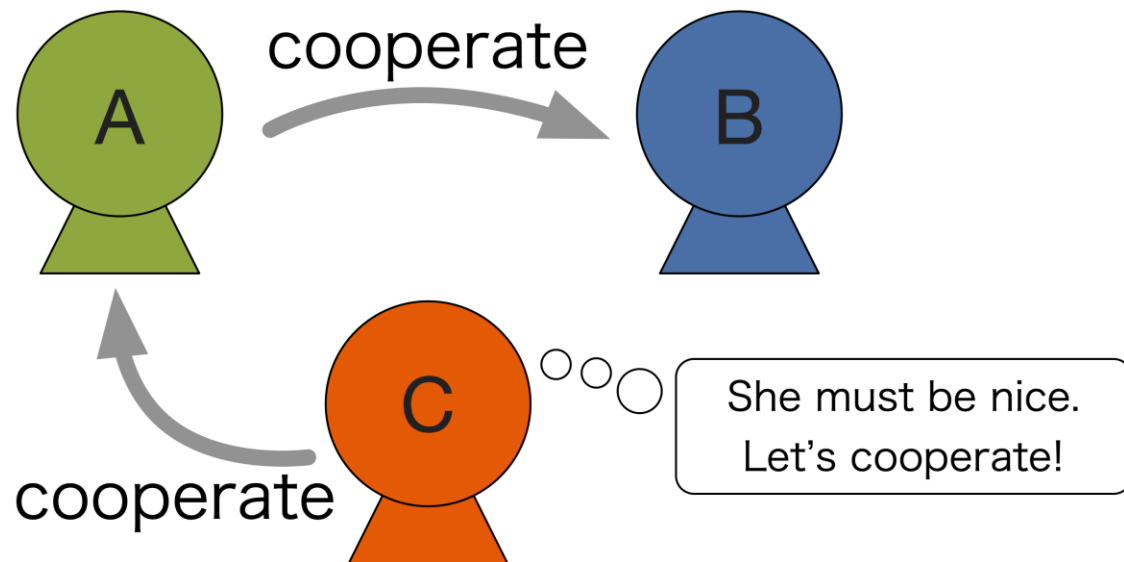
Indirect reciprocity (Reputation-based)





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 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



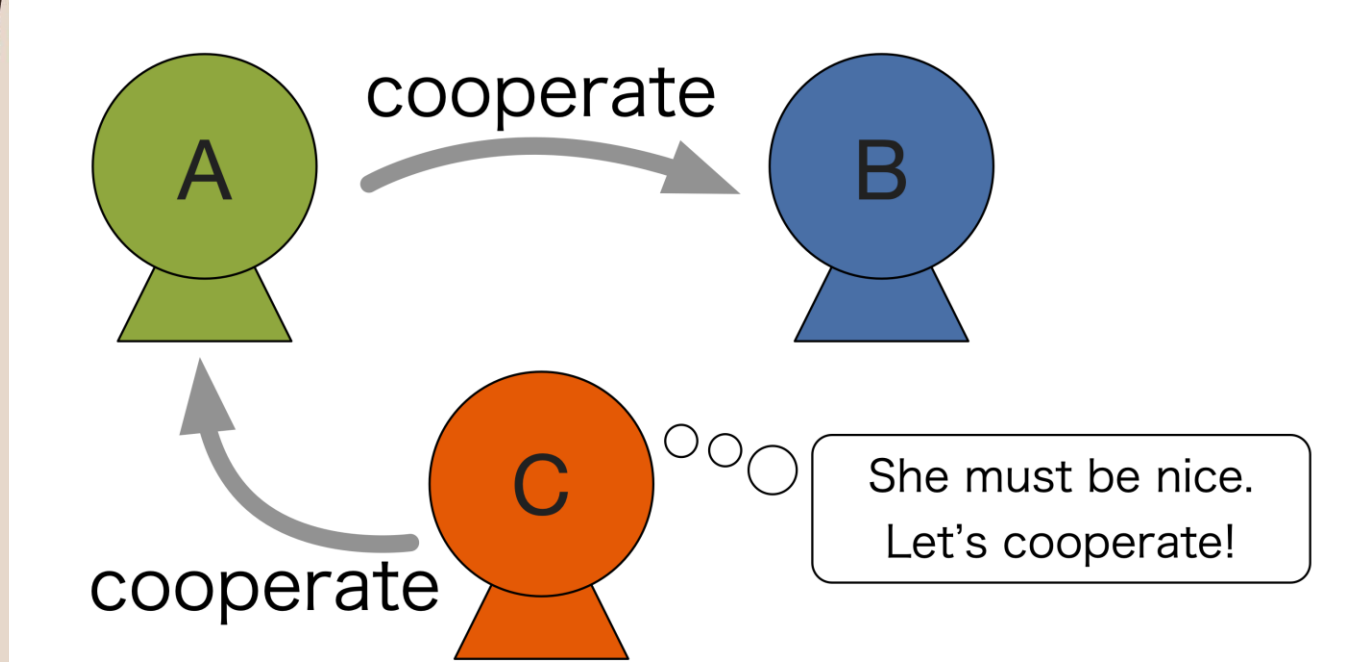
CS660605

Yo! CHECK IT OUT EVERYONE!
I'M GIVING MONEY TO THE
NEEDY ANONYMOUSLY! FOLLOW
ME! #SECRETGIVER!





10 Essential Steps to Plan a Memorable Charity Gala



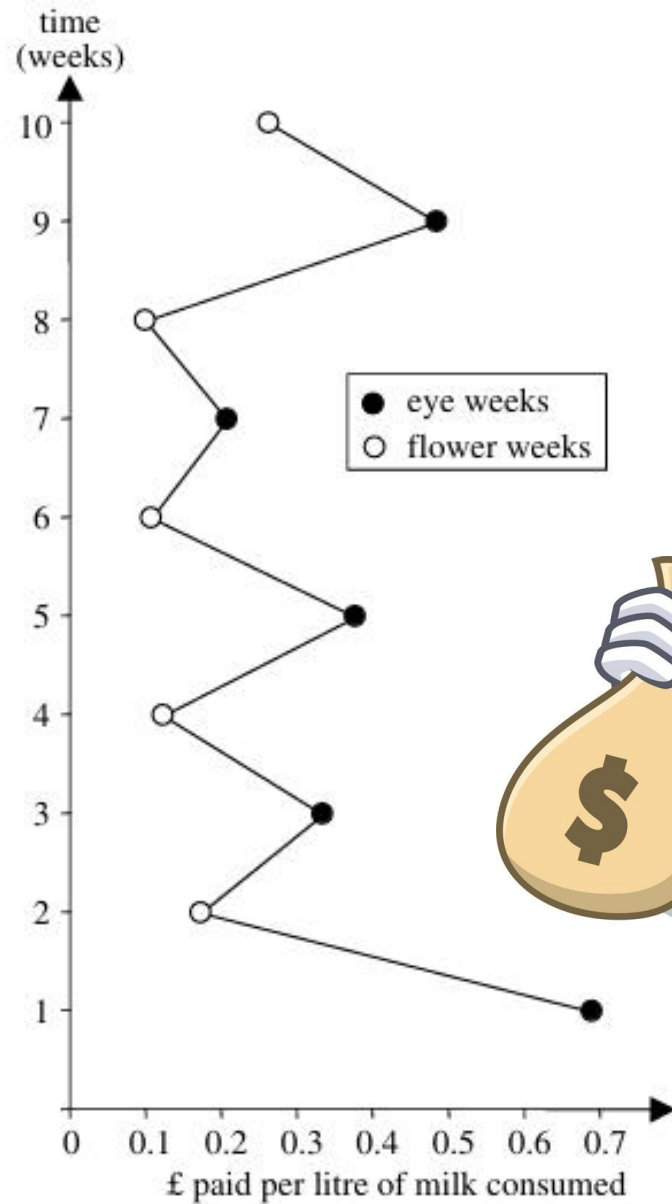
Cues of being watched enhance cooperation in a real-world setting

Melissa Bateson*, Daniel Nettle
and Gilbert Roberts

Evolution and Behaviour Research Group, School of Biology and Psychology, University of Newcastle upon Tyne, Henry Wellcome Building for Neuroecology, Framlington Place, Newcastle upon Tyne NE2 4HH, UK

*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.

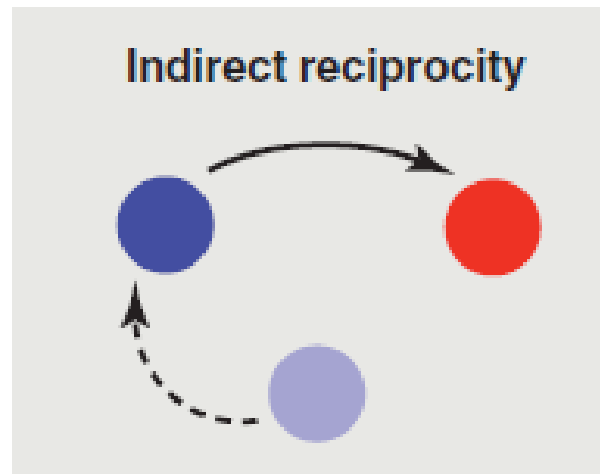
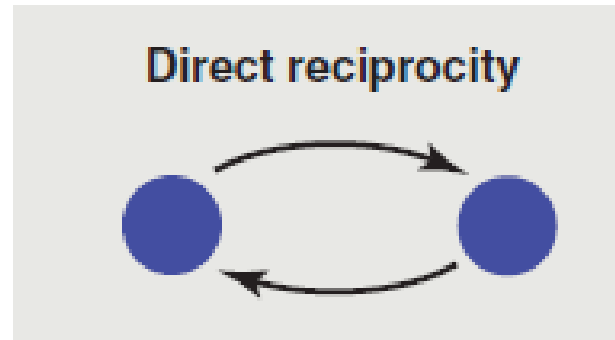
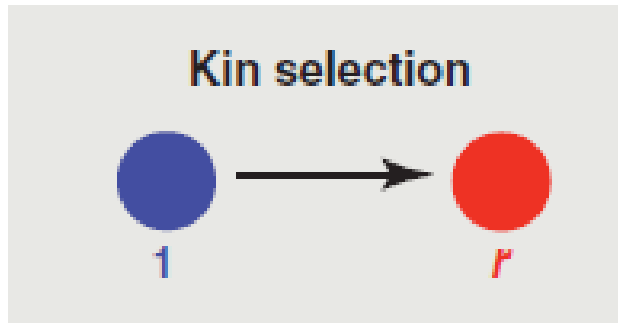




SOCIAL NORMS



Can you imagine other mechanisms promoting the evolution of cooperation?



● Cooperators ● Defectors

Fives rules for the evolution of cooperation

Martin Nowak, 2006, Nature

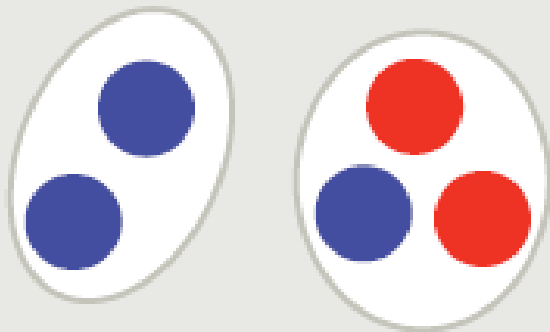
Kin selection



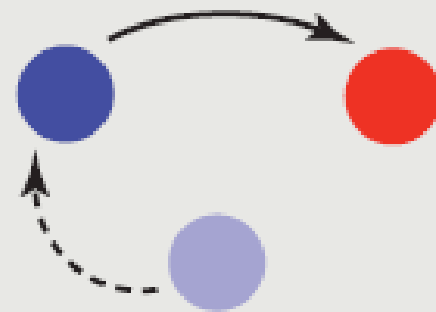
Direct reciprocity



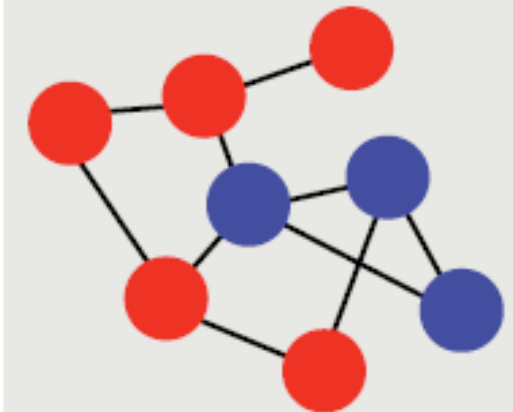
Group selection



Indirect reciprocity



Network reciprocity

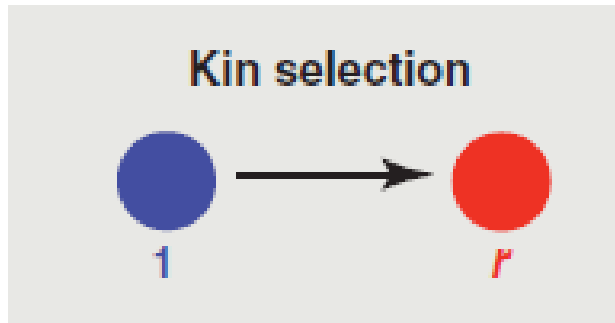


● Cooperators ● Defectors

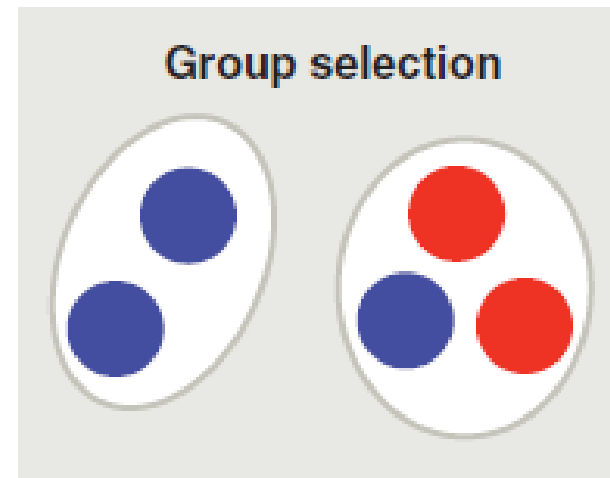
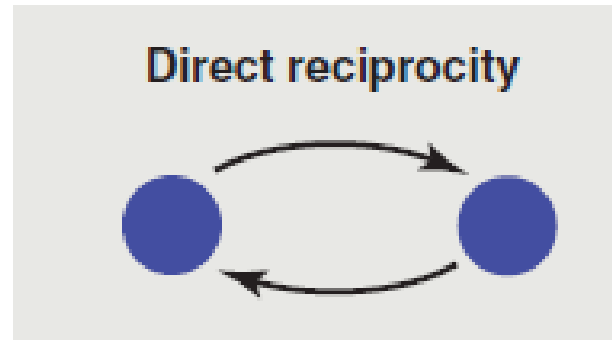
Fives rules for the evolution of cooperation

Martin Nowak, 2006, Nature

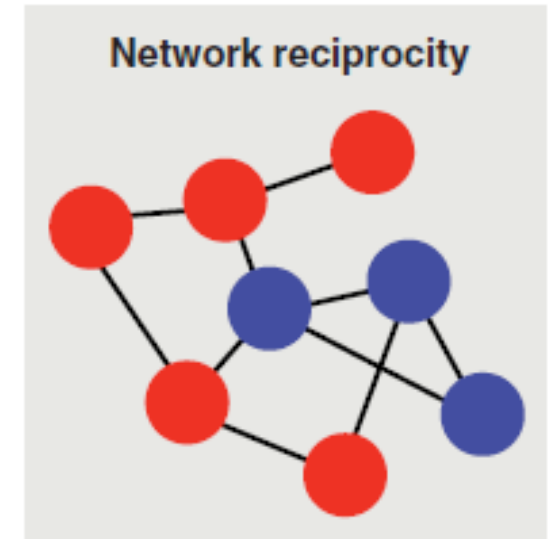
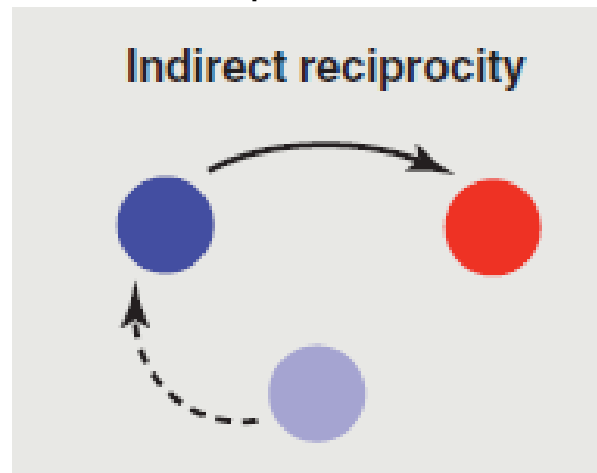
Related individuals



Repeated interactions



Reputation



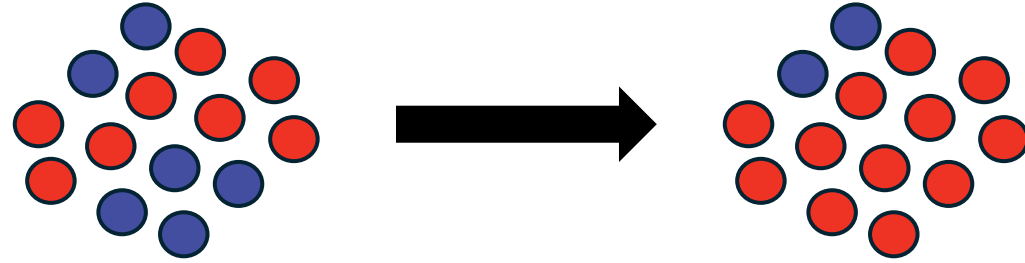
Individuals in groups

Interactions in space

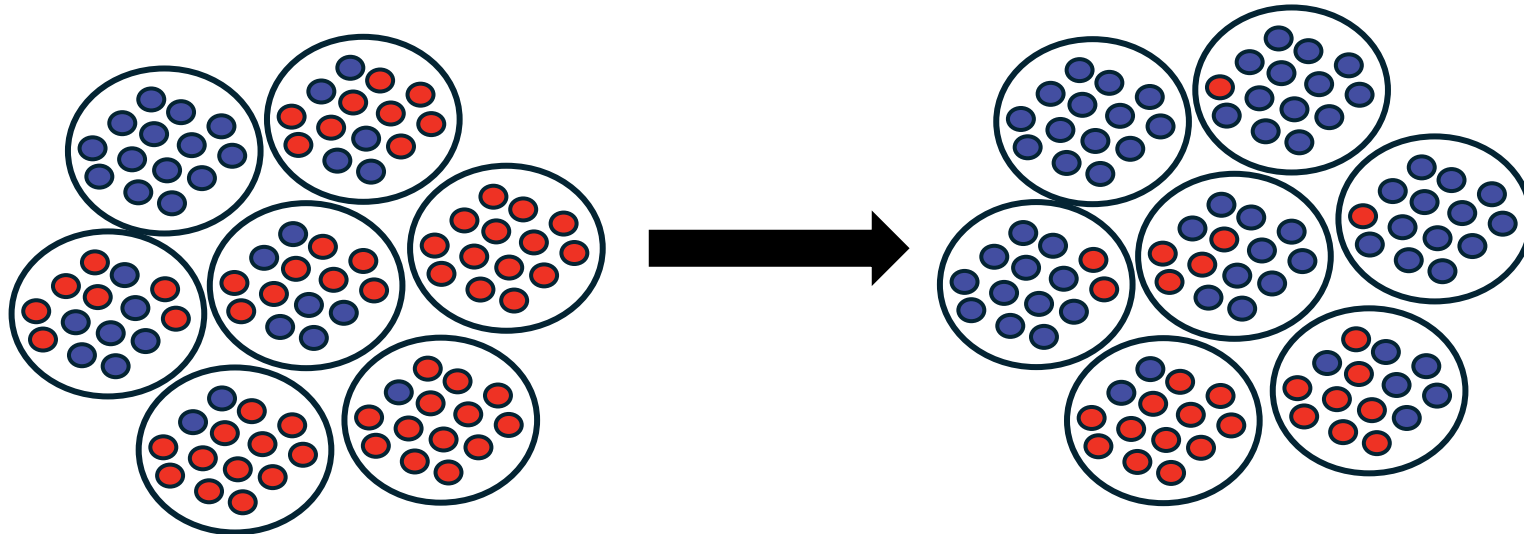
● Cooperators ● Defectors

Competition among groups favours cooperation

Individual
selection



Group
selection



 Cooperators  Defectors

Competition among groups favours cooperation

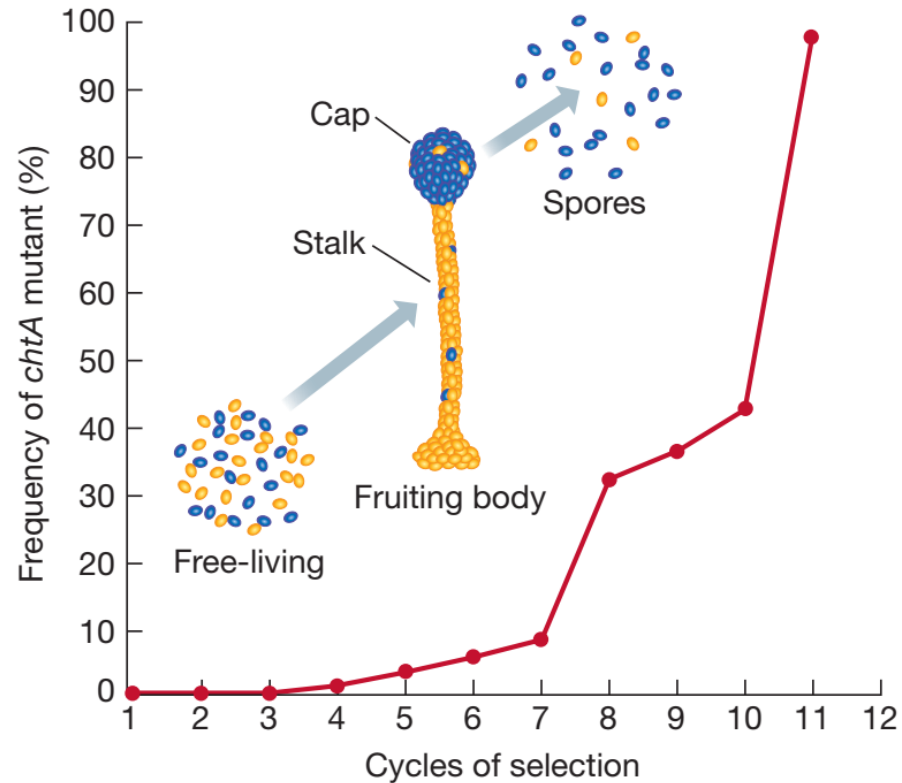
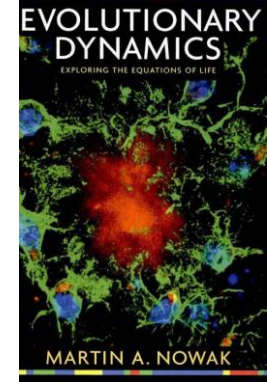


FIGURE 12.1 In the slime mold *Dictyostelium discoideum*, cells with a mutation at the *chtA* locus are cheaters that behave selfishly. In a mixture of wild-type cells (in yellow) and cells with the *chtA* mutation (blue), the mutant cells become concentrated in the cap and so are more likely to form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

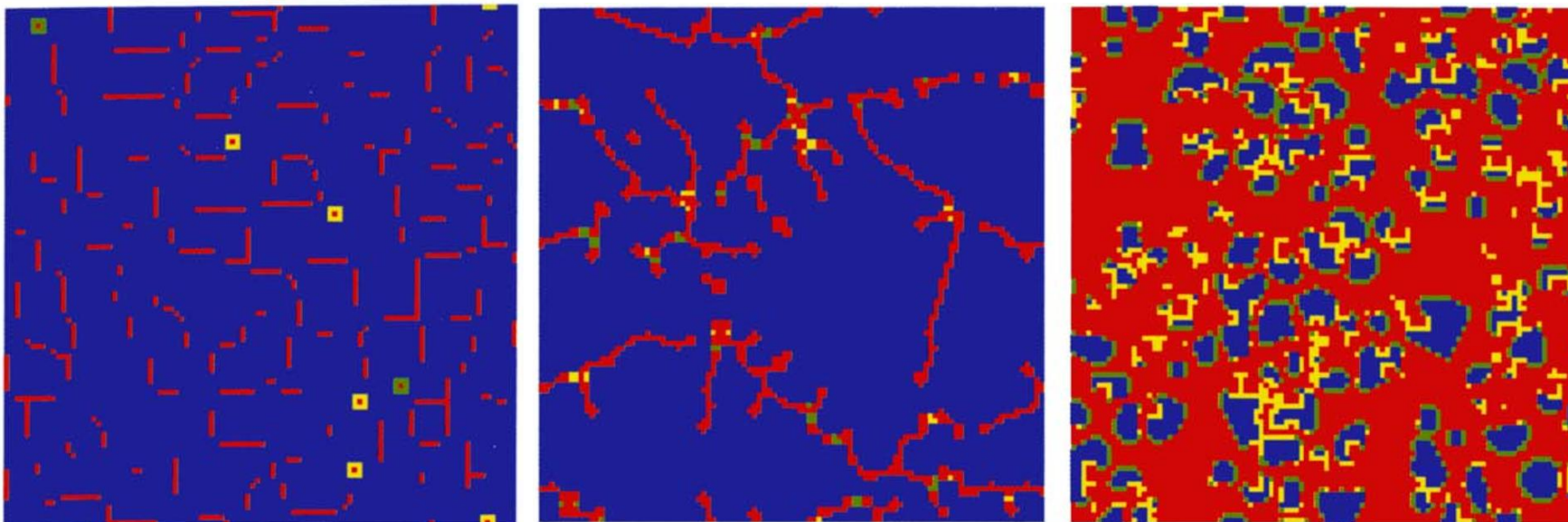


Spatial games on lattices (grids)



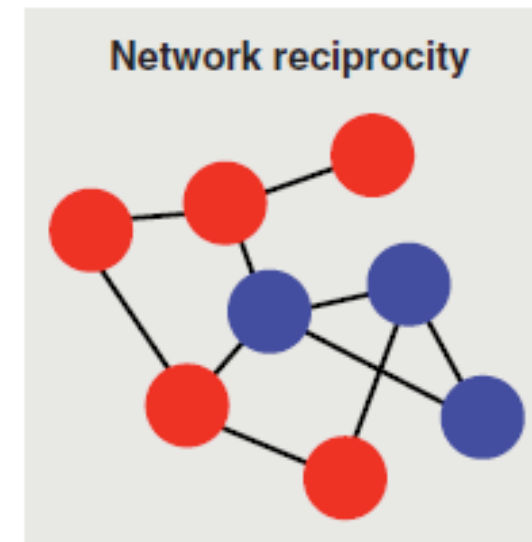
More cooperators

More defectors, but cooperators resist in «bubbles»



increasing $b-c$ in payoff matrix

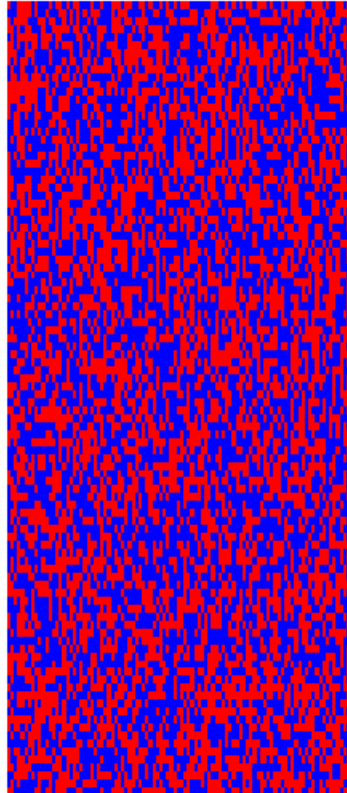
● Cooperators ● Defectors



Interactions in space

Spatial games on lattices (grids)

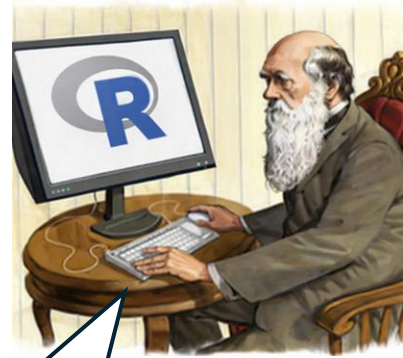
Generation 0



Generation 5



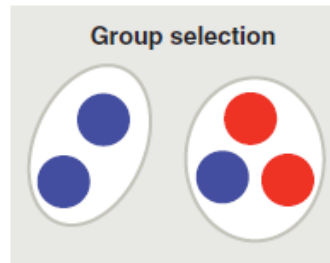
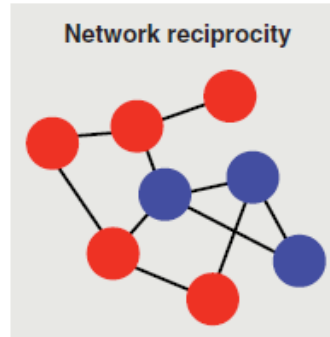
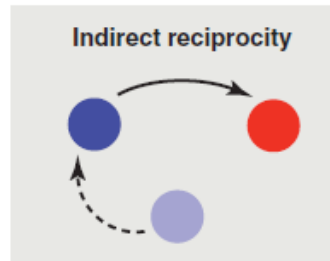
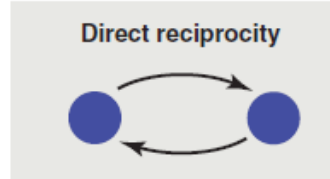
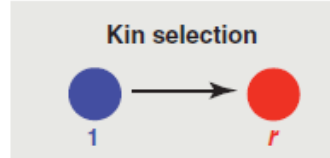
● Cooperators ● Defectors



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

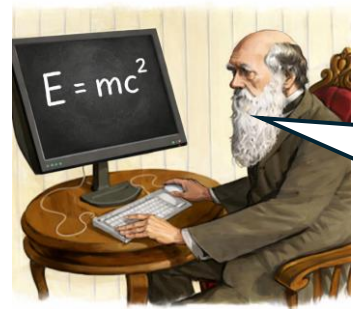
Fives rules for the evolution of cooperation

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



● Cooperators ● Defectors

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

| | | | |
|----------|--------------|--------|-----------------------------|
| <i>C</i> | $(b-c)(1+r)$ | $br-c$ | $\frac{b}{c} > \frac{1}{r}$ |
| <i>D</i> | $b-rc$ | 0 | |

r...genetic relatedness

Direct reciprocity

| | | | |
|----------|---------------|------|-----------------------------|
| <i>C</i> | $(b-c)/(1-w)$ | $-c$ | $\frac{b}{c} > \frac{1}{w}$ |
| <i>D</i> | b | 0 | |

w...probability of next round

Indirect reciprocity

| | | | |
|----------|----------|-----------|-----------------------------|
| <i>C</i> | $b-c$ | $-c(1-q)$ | $\frac{b}{c} > \frac{1}{q}$ |
| <i>D</i> | $b(1-q)$ | 0 | |

q...social acquaintanceship

Network reciprocity

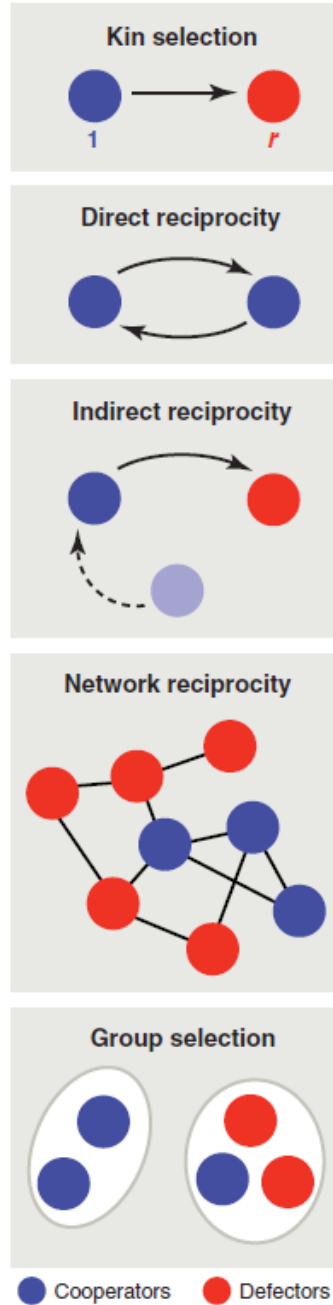
| | | | |
|----------|-------|-------|-------------------|
| <i>C</i> | $b-c$ | $H-c$ | $\frac{b}{c} > k$ |
| <i>D</i> | $b-H$ | 0 | |

k...number of neighbors

Group selection

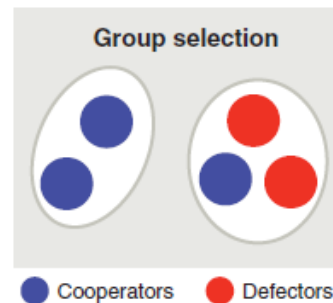
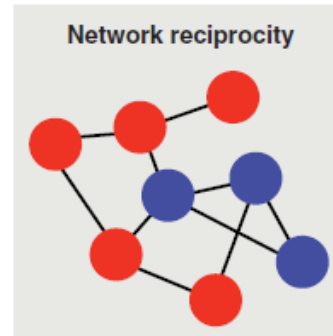
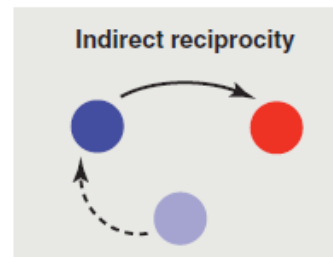
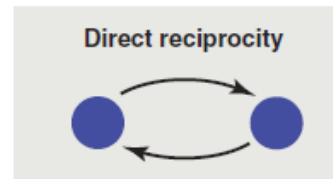
| | | | |
|----------|--------------|-------------|---------------------------------|
| <i>C</i> | $(b-c)(m+n)$ | $(b-c)m-cn$ | $\frac{b}{c} > 1 + \frac{n}{m}$ |
| <i>D</i> | bn | 0 | |

n...group size
m...number of groups



Are they really five?

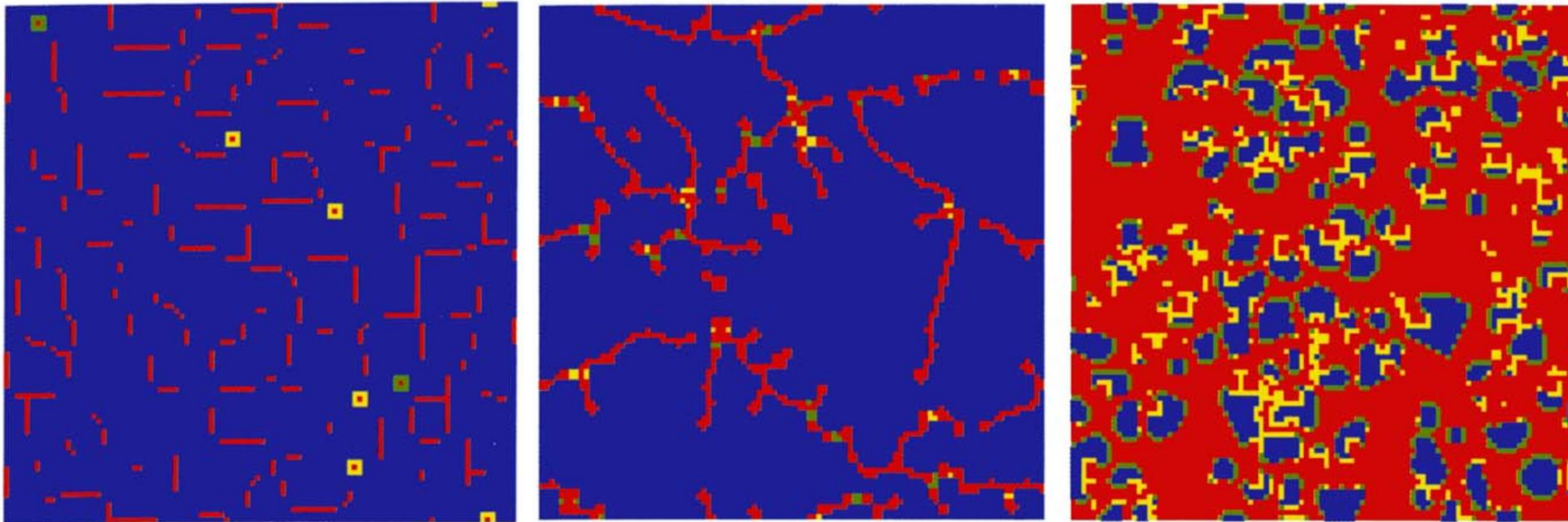
| | | Payoff matrix | | ESS | |
|-----------------------------|----------|---------------|-------------|---------------------------------|--|
| | | <i>C</i> | <i>D</i> | | |
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| | <i>D</i> | bn | 0 | | |



Are they really five?

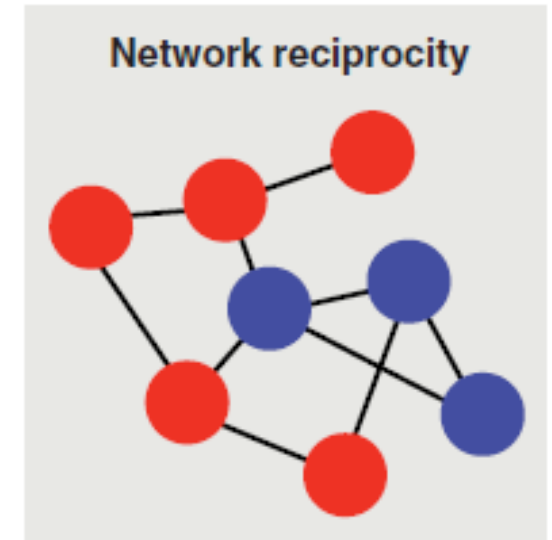
More cooperators

More defectors, but
cooperators resist in
«bubbles»

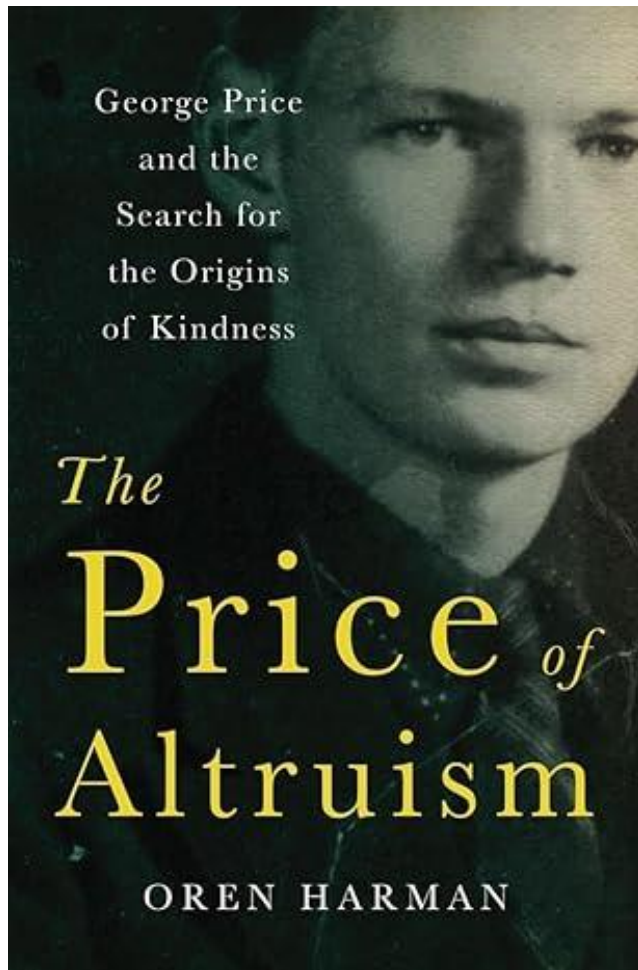


increasing $b-c$ in payoff matrix

● Cooperators ● Defectors



Interactions in space



George R. Price
(1922-1974)

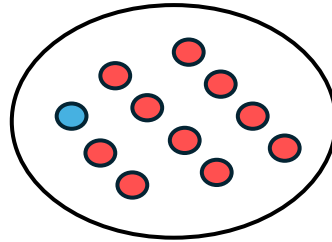


Price equation: it all boils down to «positive assortment» between individuals

evolutionary
change in
altruism

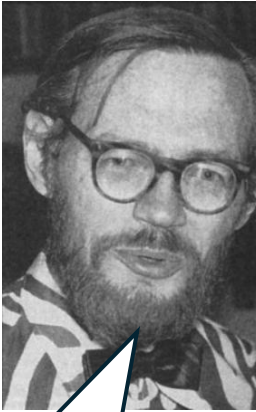
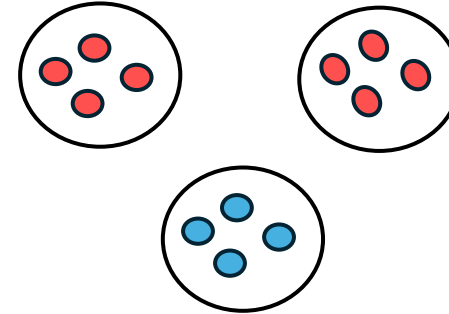
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effect of selection
within groups



+

effect of selection
between groups



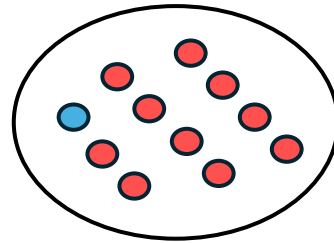
By «group» we mean anything that creates a correlation between the fitness of two cooperative individuals: kinship, space, groups, repeated interactions, etc.

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

evolutionary
change in
altruism

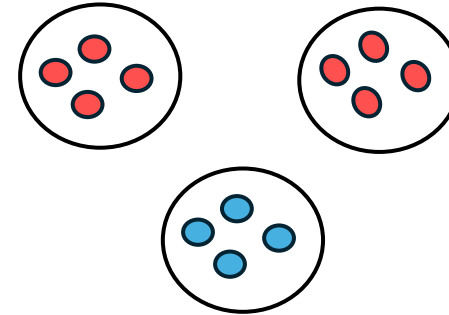
=

effect of selection
within groups



+

effect of selection
between groups



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

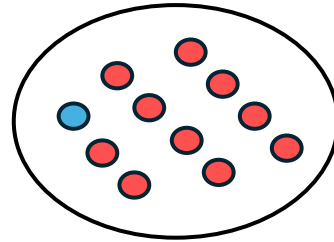
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change in
altruism

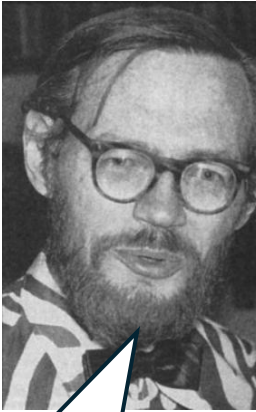
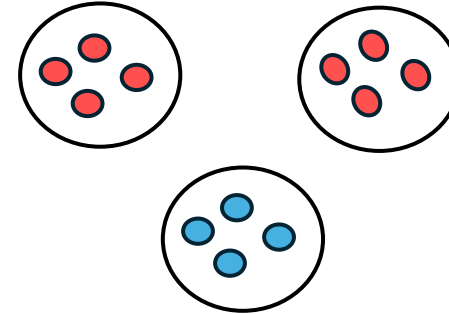
=

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

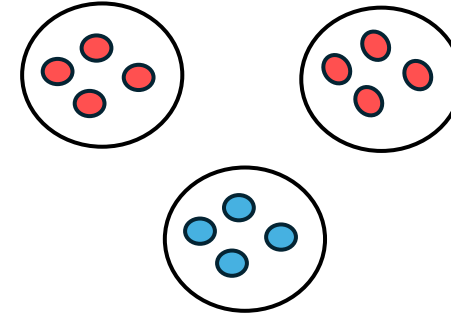
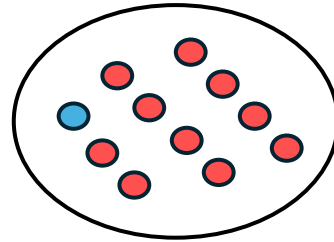
evolutionary
change in
altruism

=

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

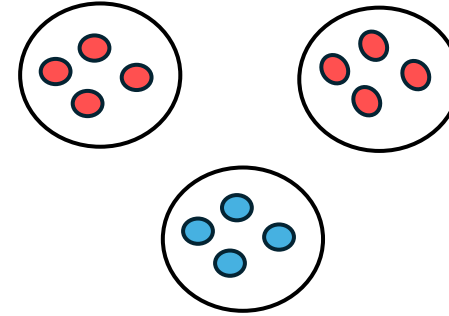
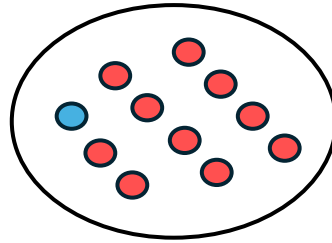
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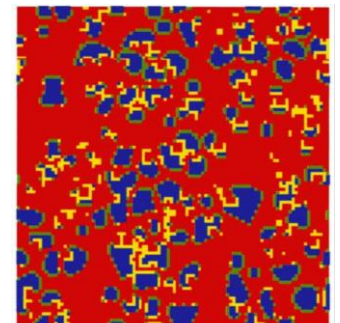
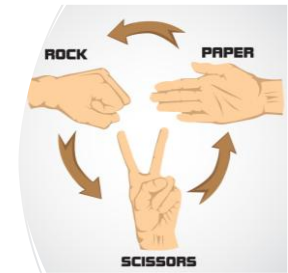
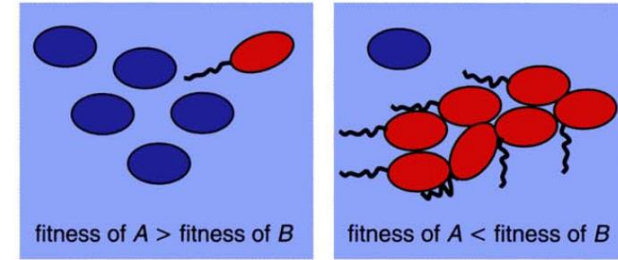
Cooperators meet
less often defectors

“groups” of
cooperators are
favoured

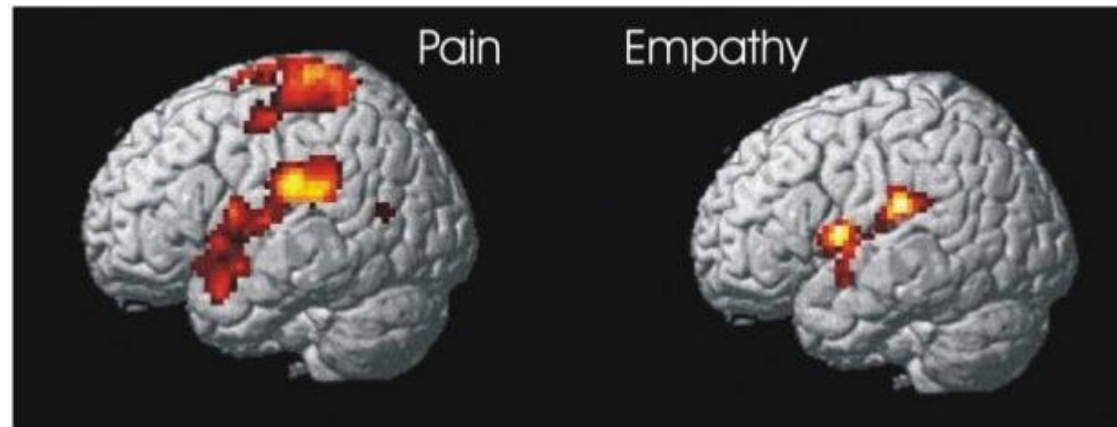


Conclusions

- 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



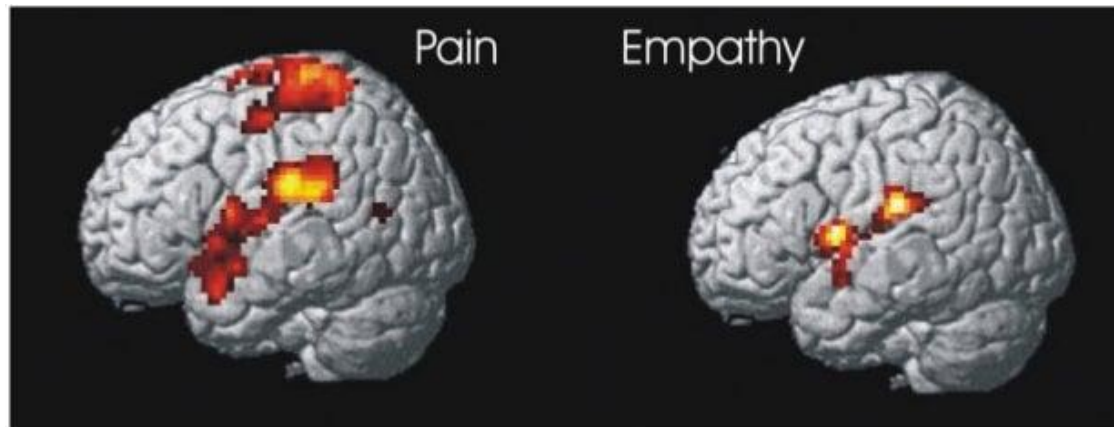
But what if some aspects of helping behavior evolves not because of positive assortment but because of evolutionary trade-offs?

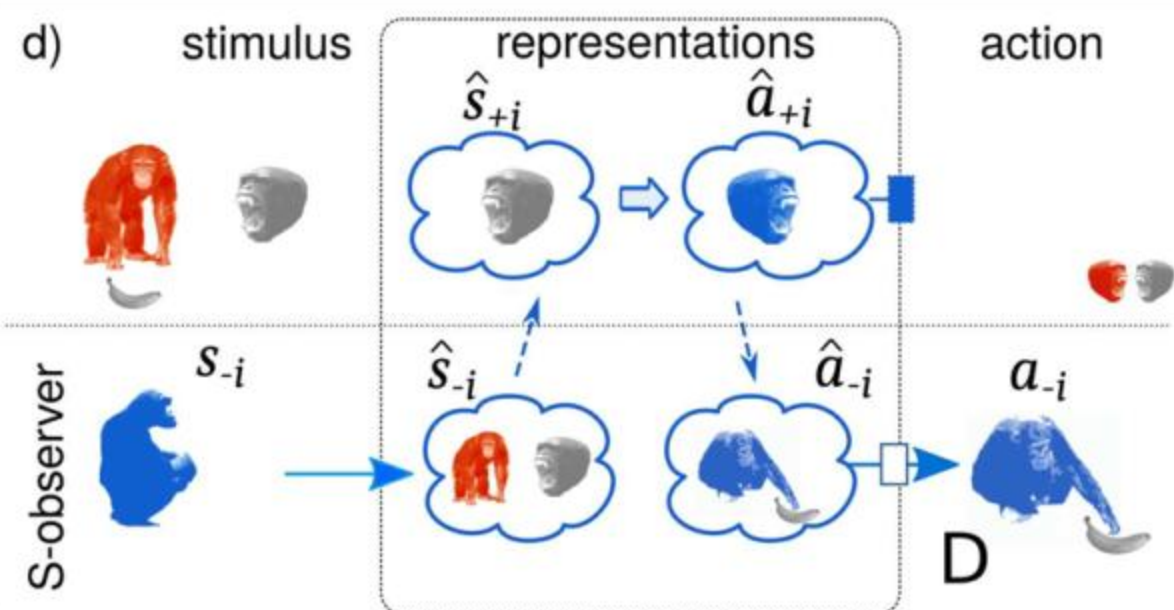
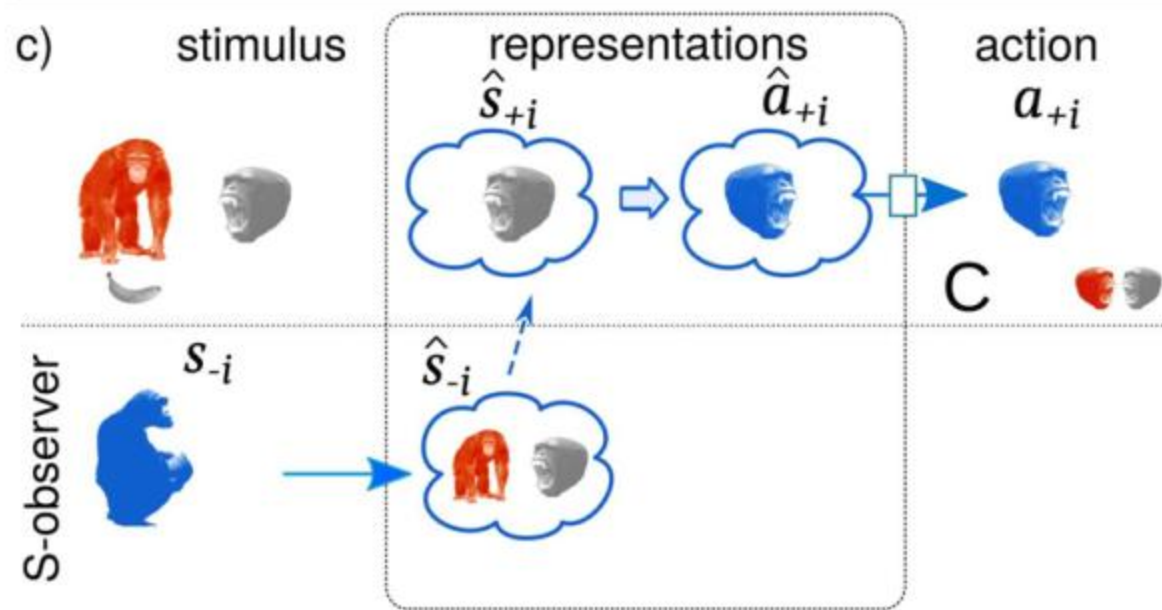
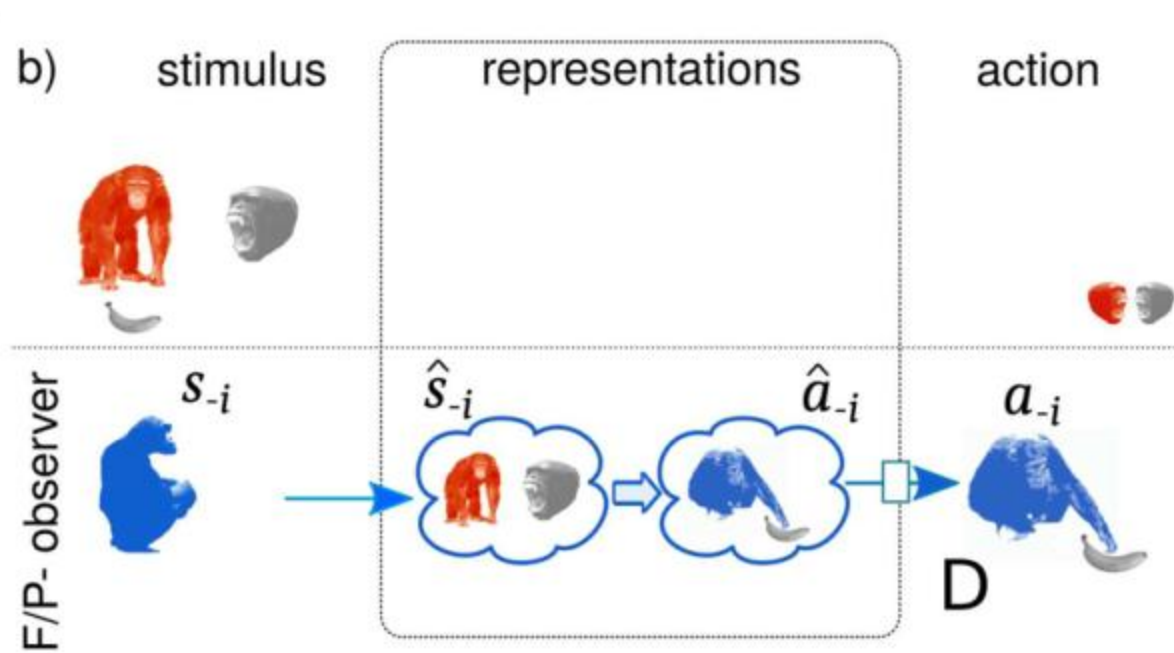
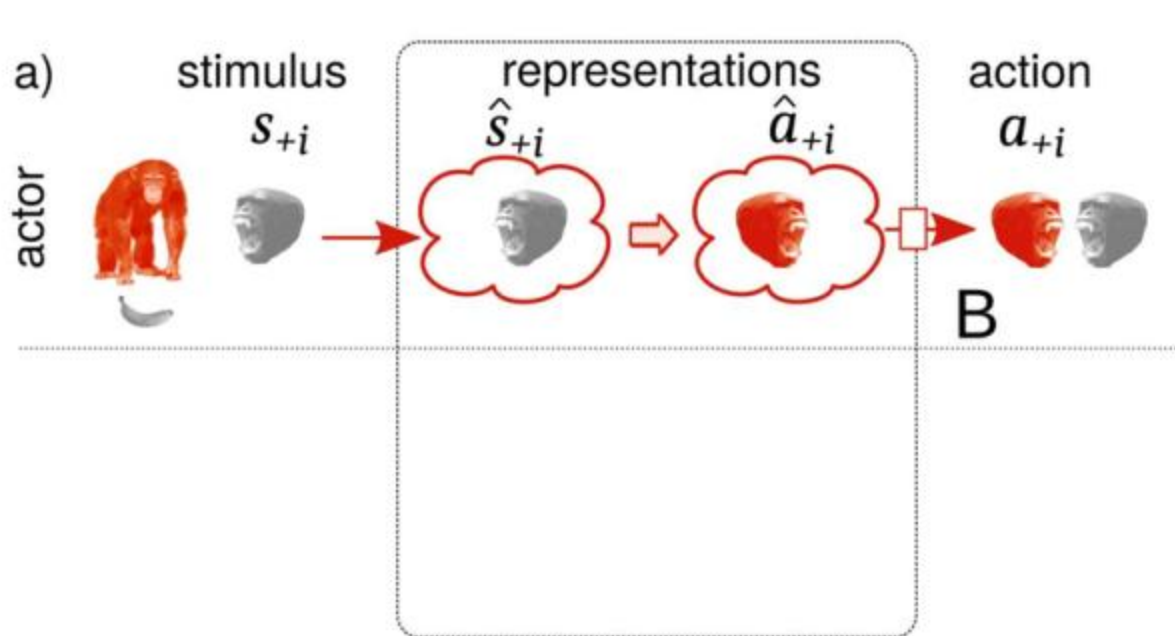


The complexity of understanding others as the evolutionary origin of empathy and emotional contagion

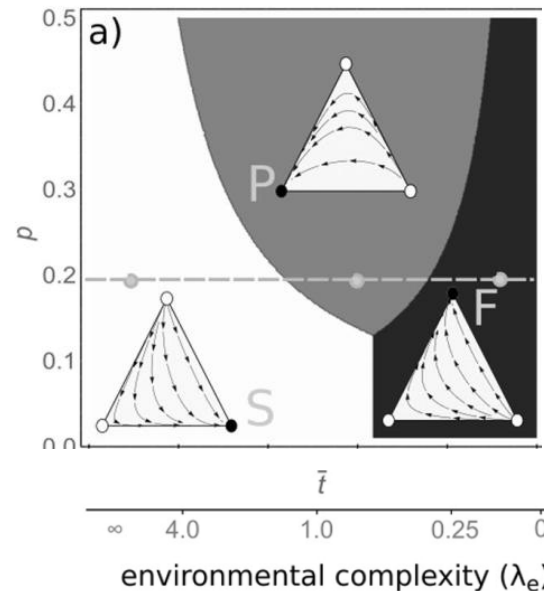
Fabrizio Mafessoni¹ & Michael Lachmann²

- 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, reciprocal interactions)
- Why would this evolve? When would this lead to cooperation?





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)

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

