

EVOLUTION & ADAPTATION (*EEB214S*) 2012

# Lecture 11: Cooperation and conflict

why animals are nice to each other?



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## Why would you alarm call?

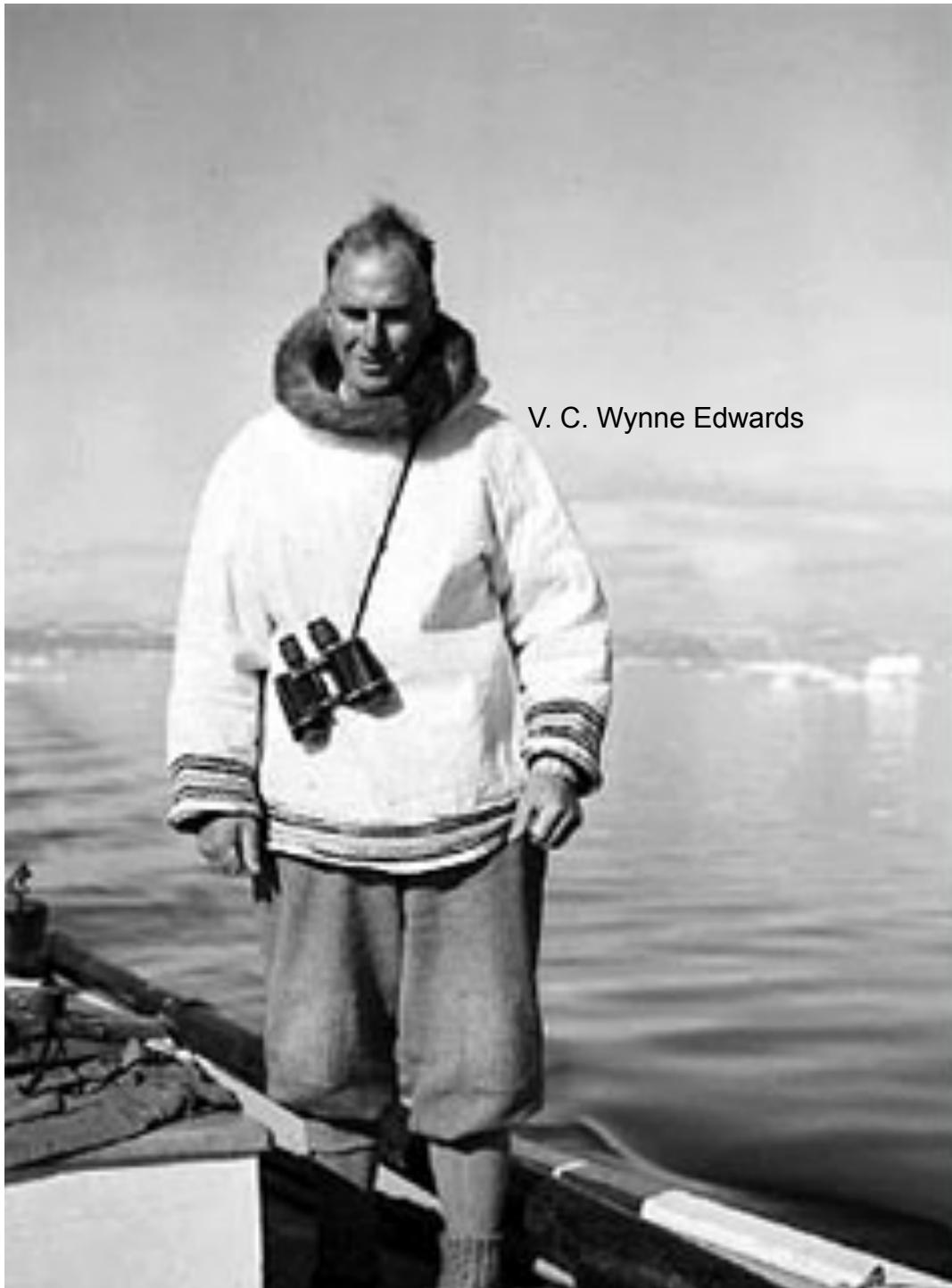
Belding's ground squirrels  
(North America)

Caller is 2x as  
likely to be  
caught!

# Why are ground squirrels behaving altruistically?

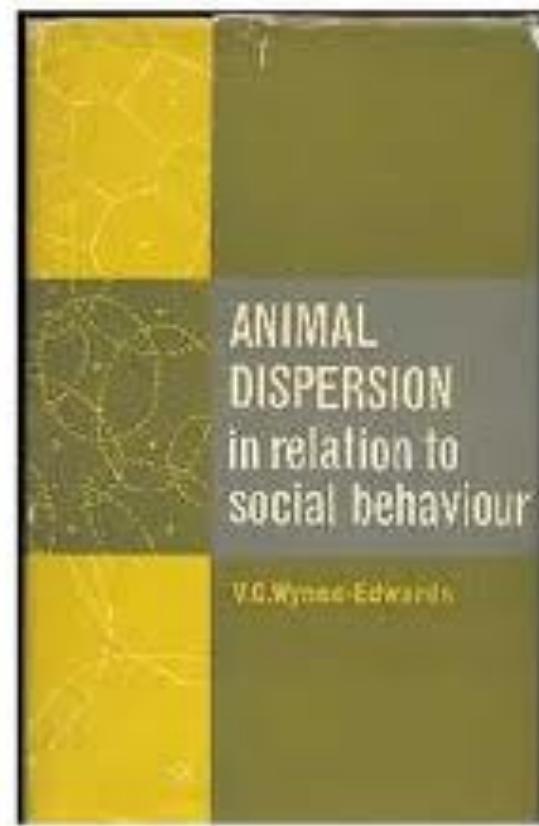
Although alarm calling reduces its own relative chances of successful reproduction, it enhances the relative chance of others in its group to survive and reproduce successfully.

Could selection be acting on the group?



V. C. Wynne Edwards

## Group Selection



# V. C. Wynne Edwards



His logic goes like this:

seldom in nature do we see animal populations actually outstripping their resources  
nor do we see a huge amount of disease and death (which could be the  
mechanisms of controlling numbers)



therefore animal populations must be self regulating

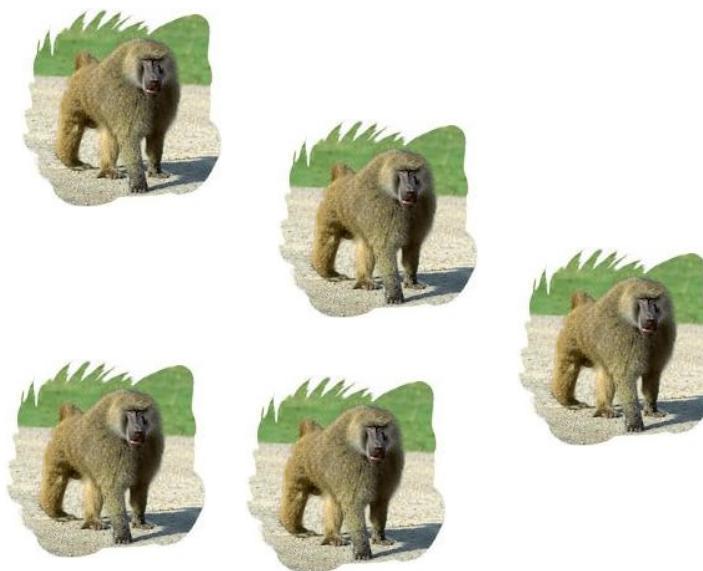


# How do animals self-regulate the numbers in their populations?

V. C. Wynne Edwards two central ideas are:

- Only dominant males mate, while lower males don't, self-limiting the size of the population
- Animals on territories breed while those without territories (and therefore resources) don't

Let's imagine what would happen to a cheater under this explanation of altruism...



Who wins in an evolutionary sense in this situation?



# Wynne Edwards definition of group selection = **wrong**

- **Altruistic behaviour** is a behaviour that reduces its owners fitness while increasing the fitness of another
- **Selfish behaviour** is the opposite, gain for the giver at the expense of others

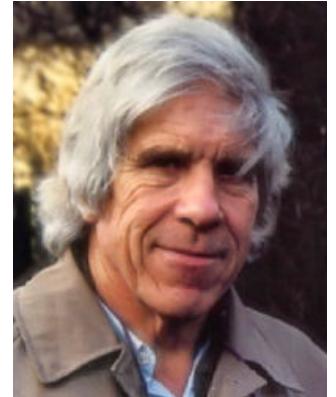
What are the alternatives for why altruistic behaviour persists?



George Price



W. D. Hamilton



## Inclusive fitness

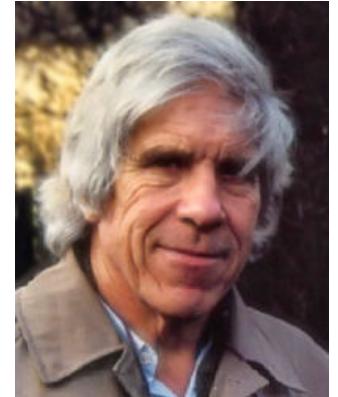
They proposed that an individual's total fitness can be viewed as the sum of its **direct fitness**, which is the number of viable offspring that it produces, and its **indirect fitness**, which is the incremental effect that the individual's behaviour has on the (direct) fitness of its genetic relatives.

Direct fitness + indirect fitness = inclusive fitness



George Price

W. D. Hamilton



## Hamilton's rule

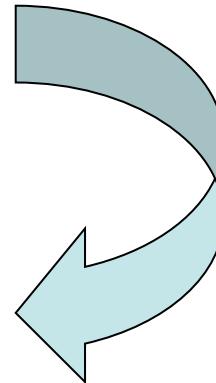
an allele X for helping a relative increase in frequency whenever

$$rb - c > 0$$

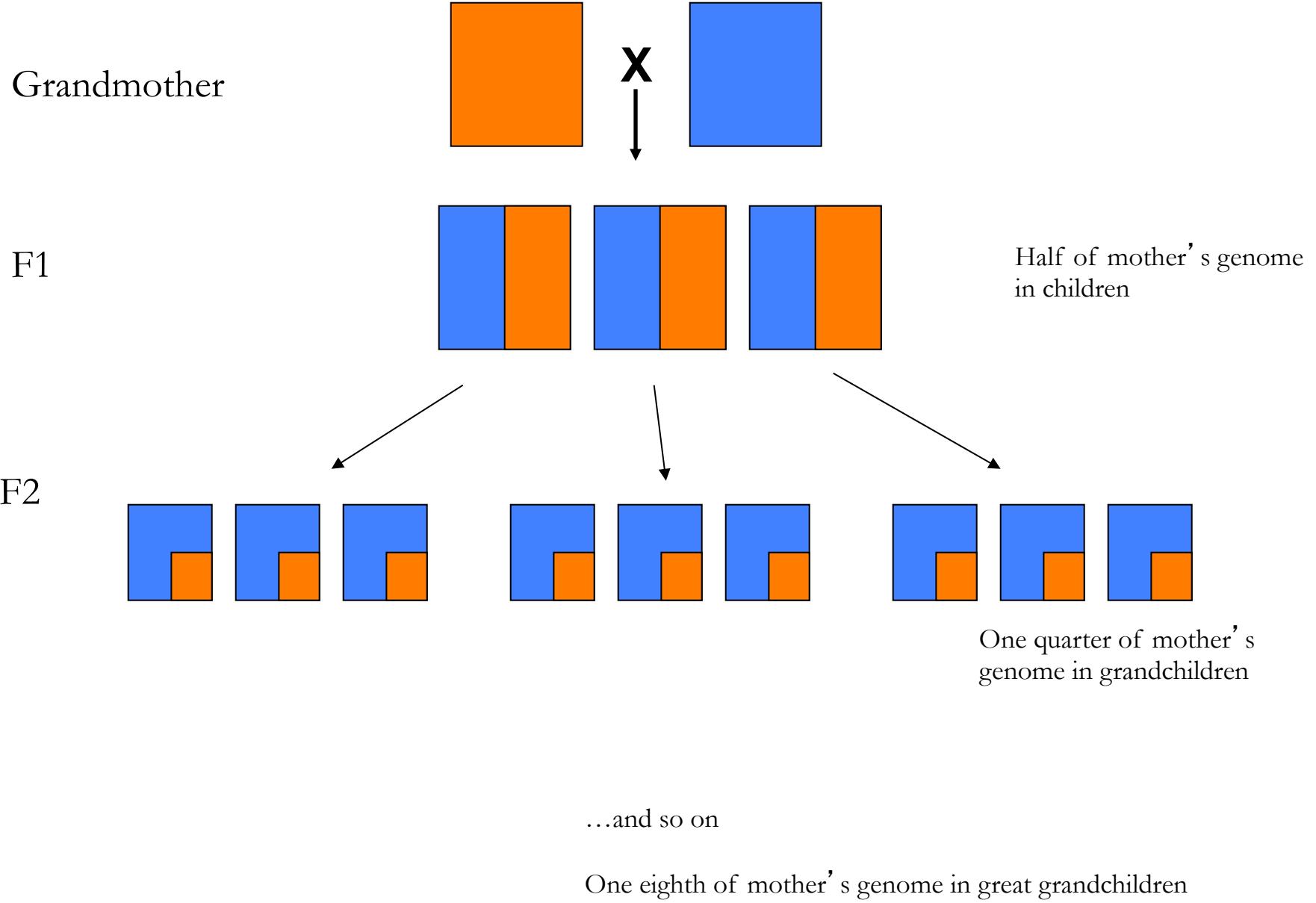
where b is the benefit that the genetic relative receives from traits associated with allele X, c is cost accrued to the individual expressing the trait, and r is the coefficient of relatedness

The extent to which natural selection favours assisting one's family members depends on how related individuals are, and how high or low the associated costs and benefits of helping are

# Coefficient of relatedness



How much genetic material does father/mother share with offspring?



JBS Haldane:

When asked whether a man should lay down his life for his brother.

He replied: "For two brothers," he said, "or four cousins."

Inclusive fitness theory has played a prominent role in understanding the transition from solitary to group living





Kim Taylor / naturepl.com



...showed how it could explain the behaviour of ants and bees, whose curious pattern of reproduction means that females are more closely related to their sisters than to their offspring.



Eusociality is often characterised by...



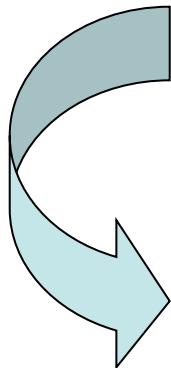
- Reproductive division of labour - only a fraction of the population is reproducing
- Cooperative rearing - individuals, not just the parents, rear young
- Overlapping generations - members of different generations live and work together.



In Hymenopterans (ants, bees and wasps) eusociality is thought to have evolved at least nine separate times. **Why?**



What gives you higher inclusive fitness, helping your mum raise your sisters or raising your own offspring?



Sister to sister are related by 0.75

Female to offspring are related by 0.5

Sister to brother by 0.25

Females brood, while males don't

# Haplodiploidy alone doesn't explain everything



Kim Taylor / naturepl.com



## Helpers at the nest





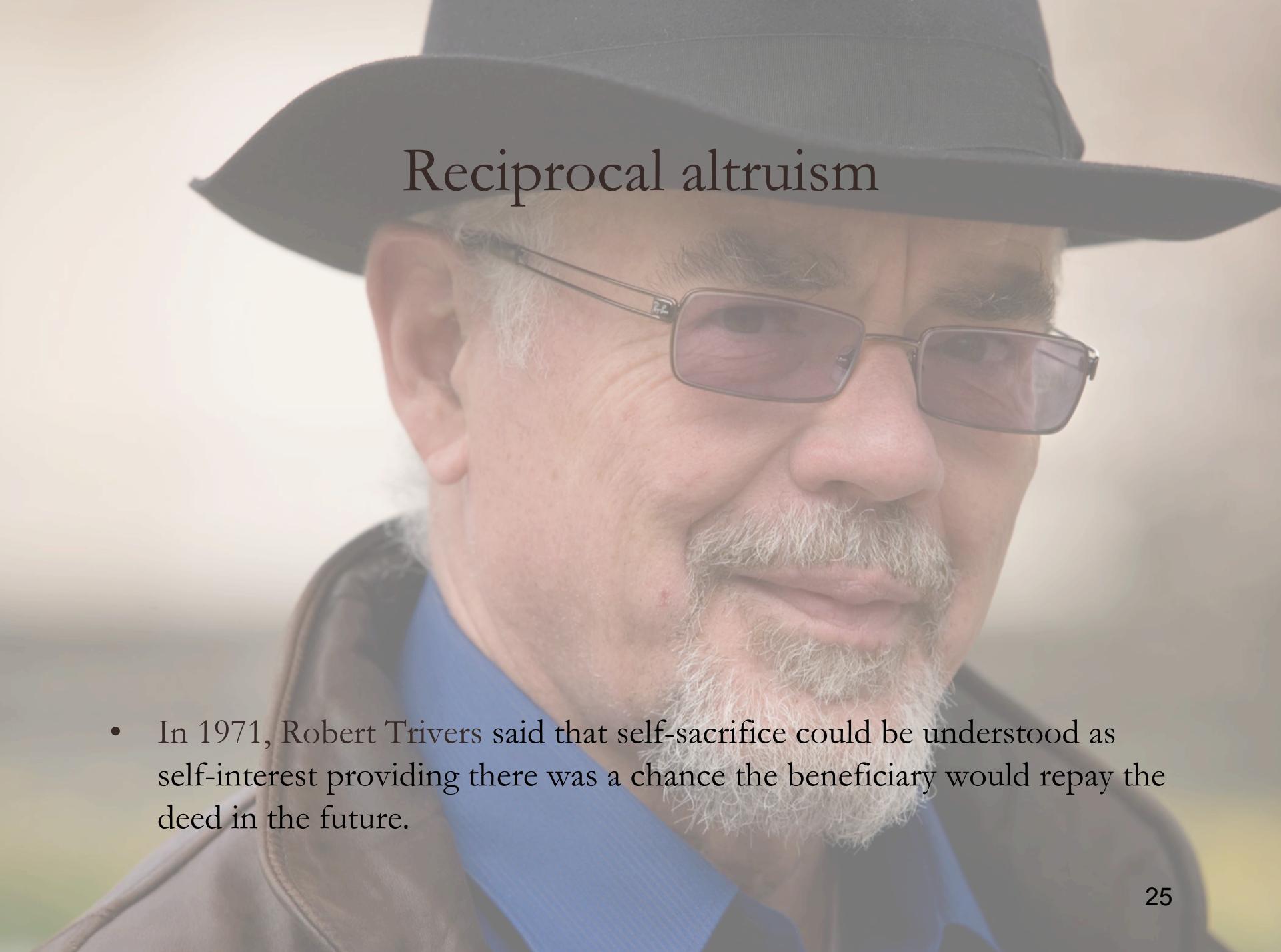
## Long-tailed tits



- In February–March, all members of the winter flock will pair and attempt to nest
- Pairs whose nests fail have three choices: try again, abandon nesting for the season or abandon nesting for the season and help at a neighbouring nest.
- It has been shown that failed pairs split and help at the nests of relatives (recognition being established vocally)
- The helped nests have greater success due to higher provisioning rates and better nest defence



But there is cooperation in many species which do not have these patterns of relatedness; also between animals which are not closely related, nor even members of the same species.



# Reciprocal altruism

- In 1971, Robert Trivers said that self-sacrifice could be understood as self-interest providing there was a chance the beneficiary would repay the deed in the future.

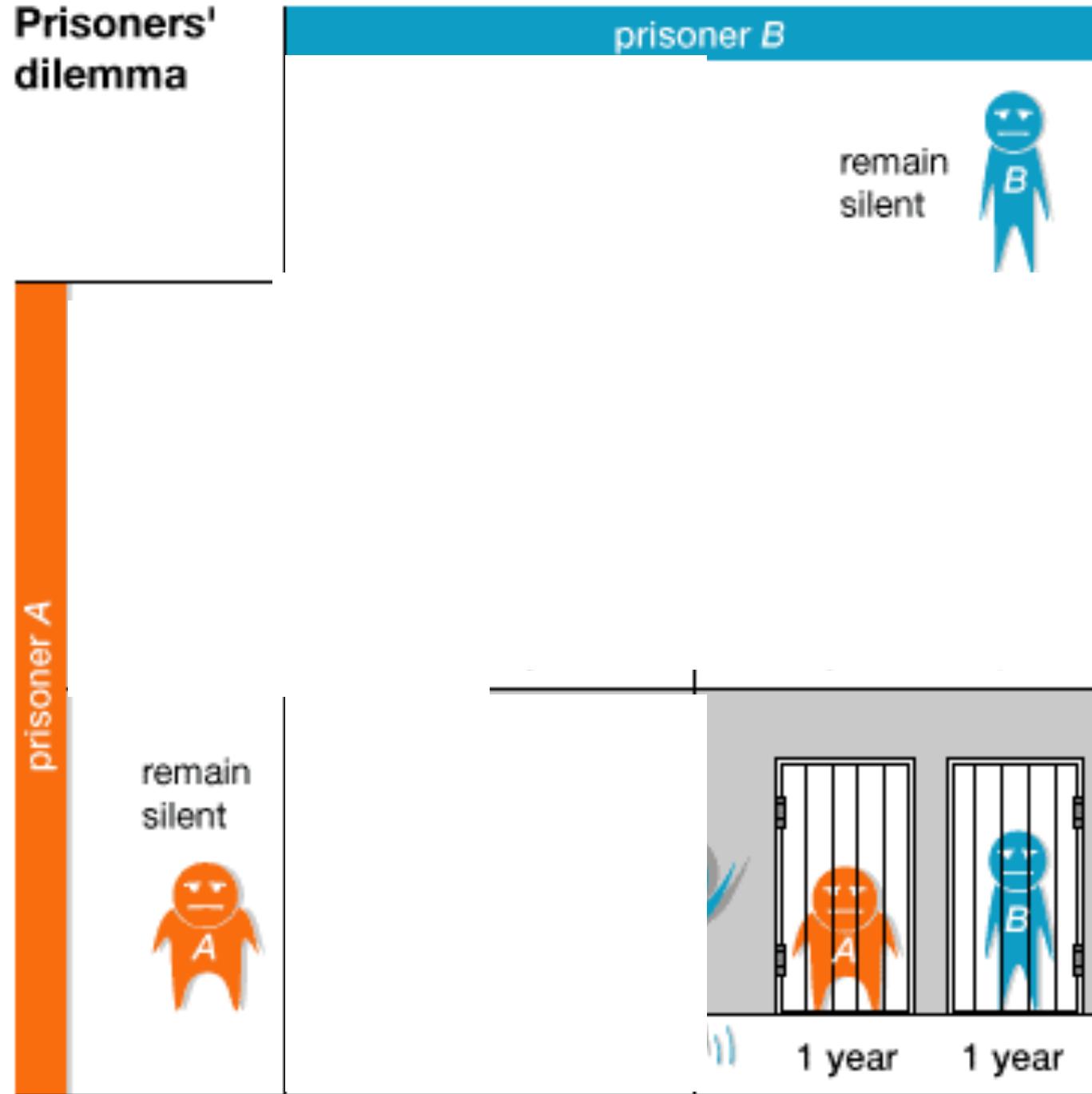
# The Prisoners' Dilemma

Imagine a scenario where we have two criminal suspects, brought in and interrogated separately and asked:

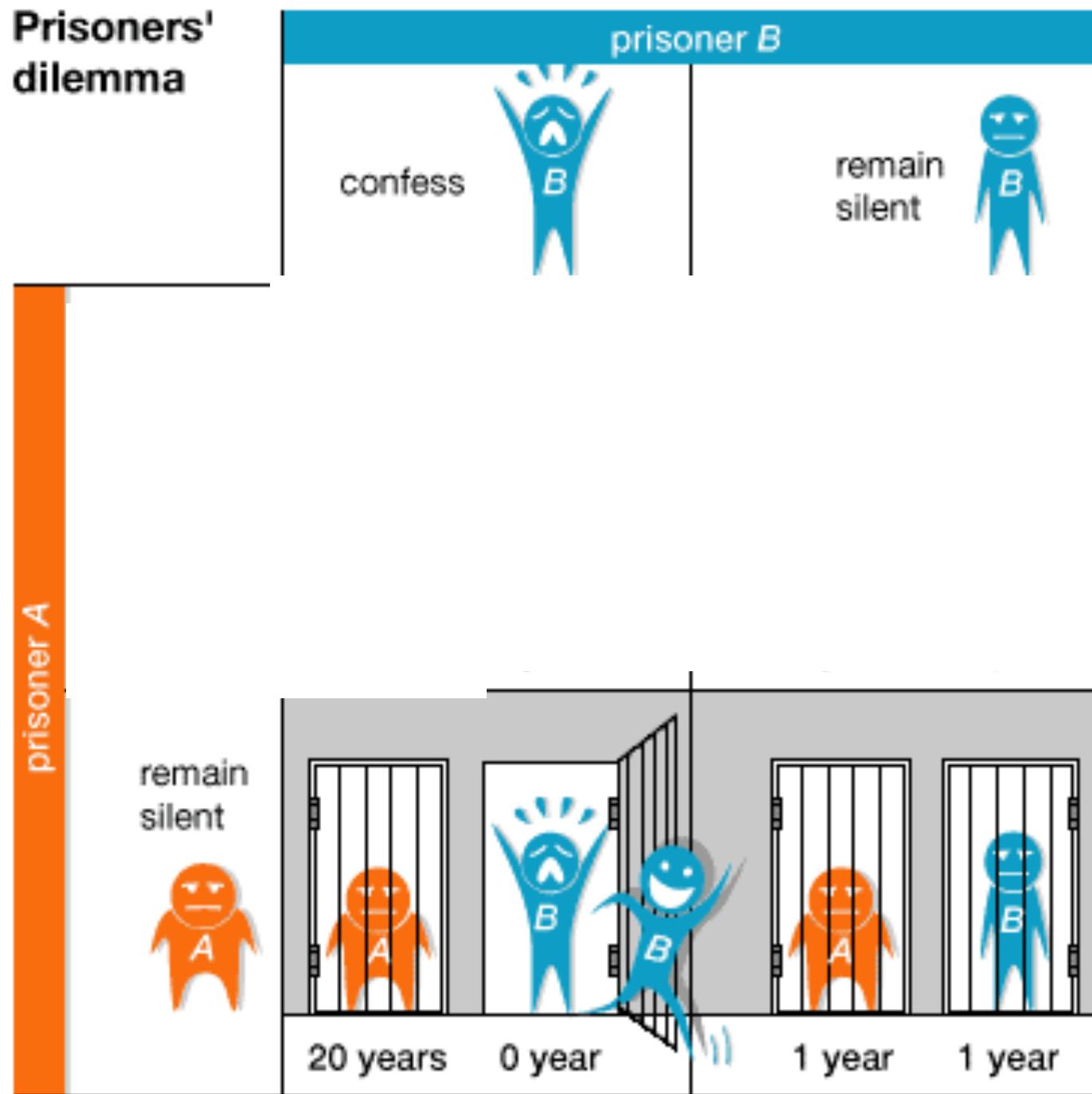
“If you testify against the other guy, you’ll walk away a free man and the other guy will go to prison for 20 years”



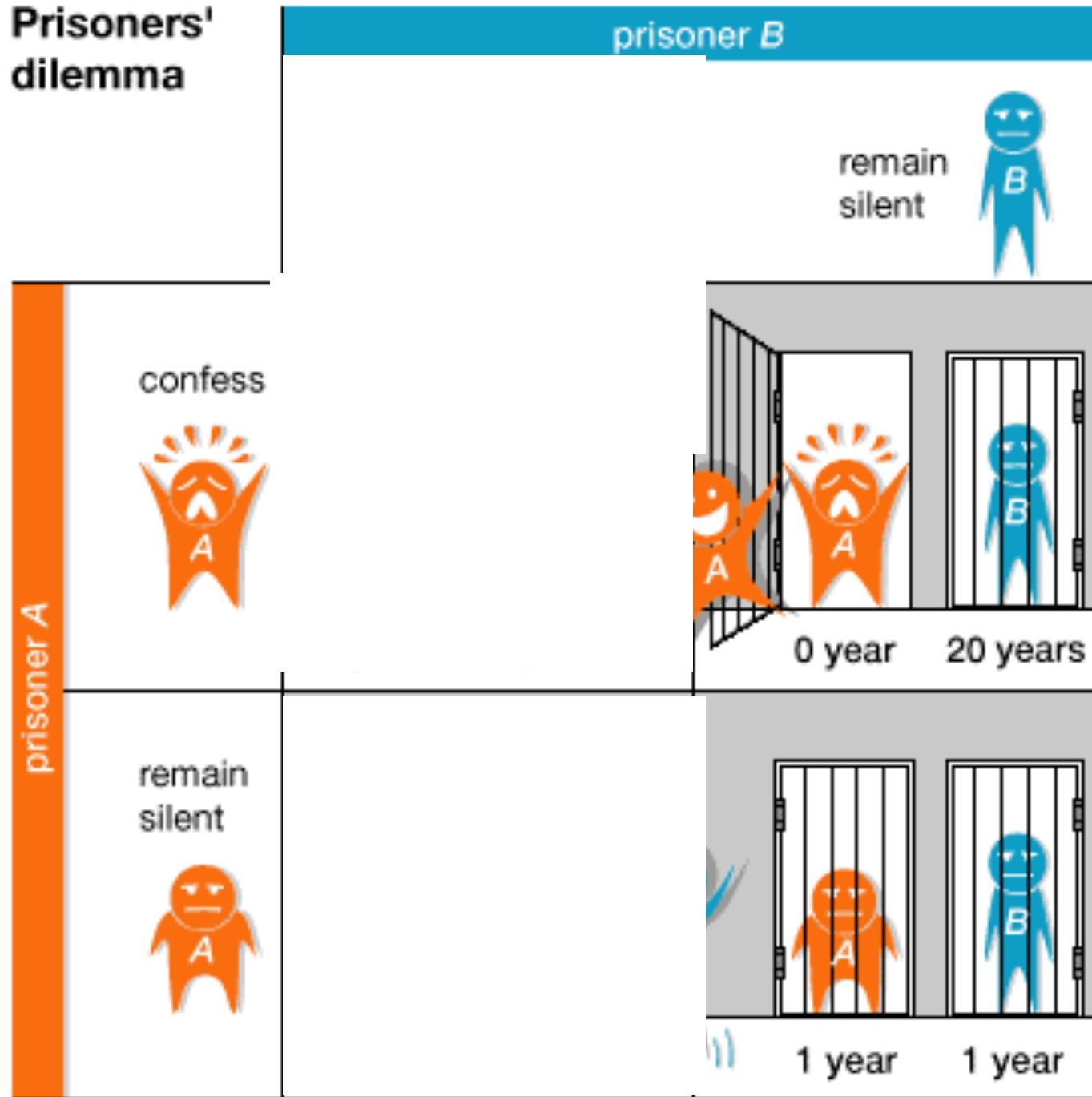
## Prisoners' dilemma



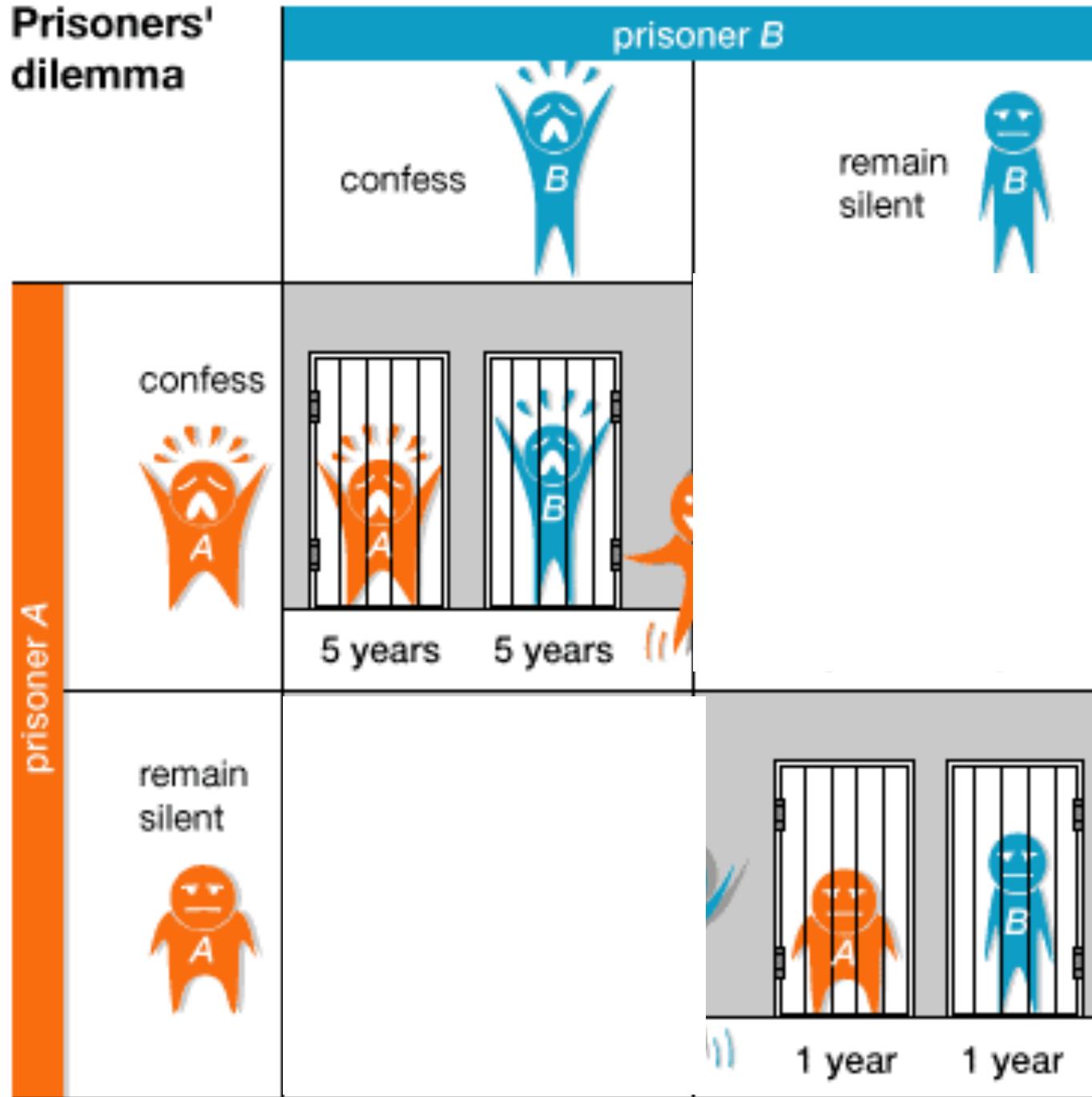
## Prisoners' dilemma



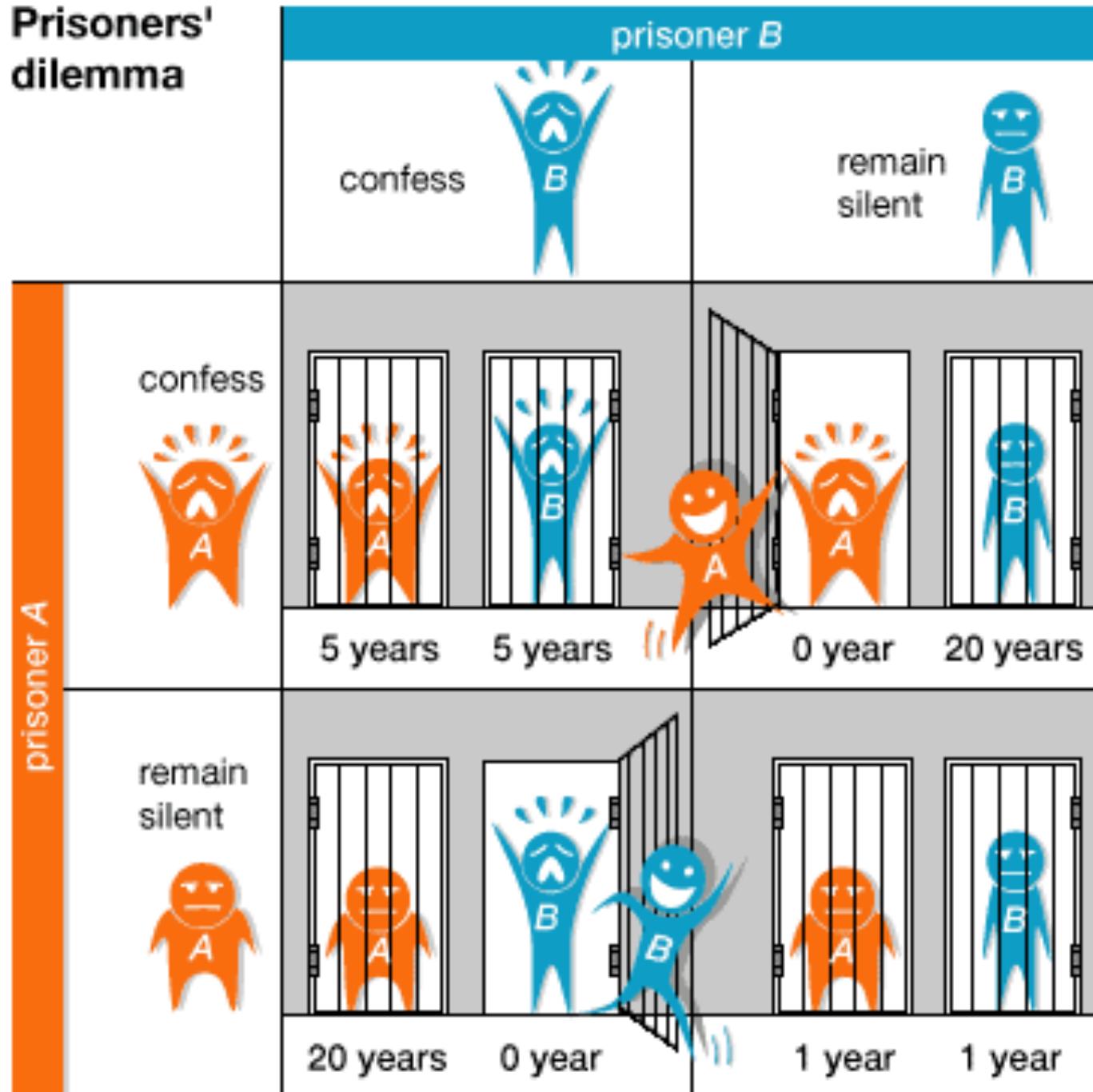
## Prisoners' dilemma



## Prisoners' dilemma



## Prisoners' dilemma



# What should the prisoner do?

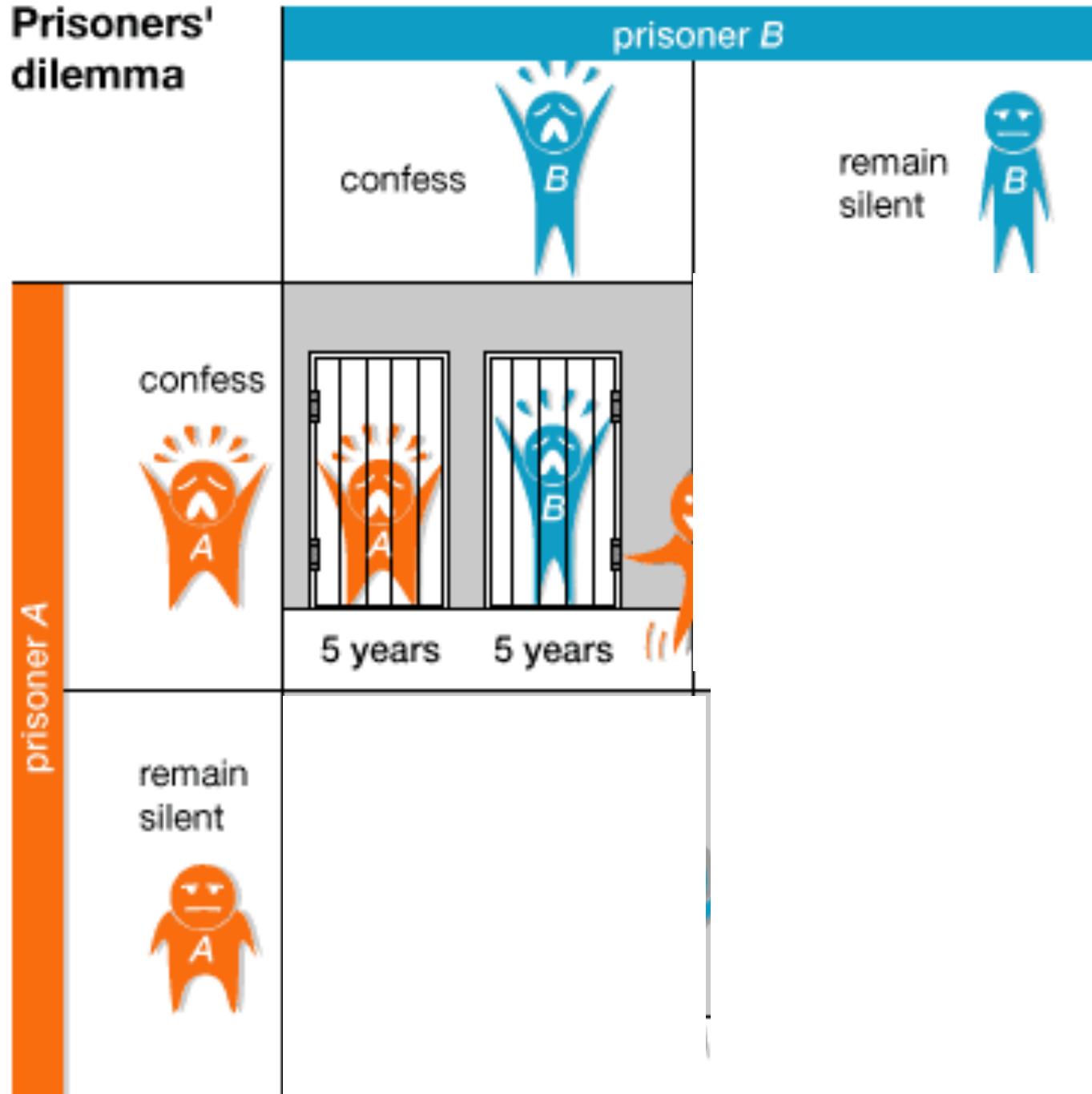
Anyone seen ‘A Beautiful Mind’?

- For your interest...a pair of strategies in which neither player can benefit by unilaterally changing his strategy is known as a **Nash equilibrium**.
- Note that an individual serves a shorter sentence if he agrees to testify, *irrespective* of what the other suspect decides to do.



What happens most often when this game  
is played?

## Prisoners' dilemma

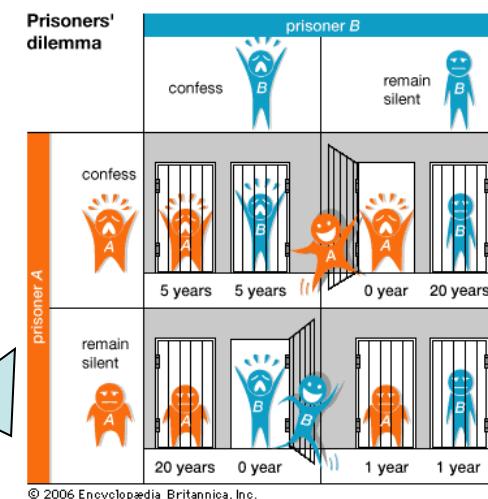
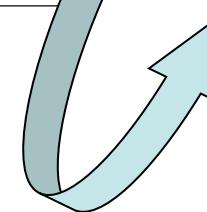
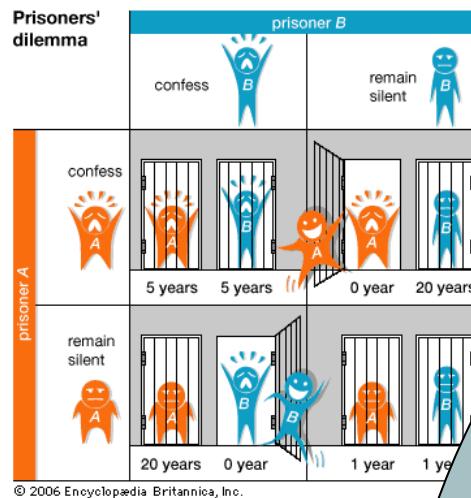
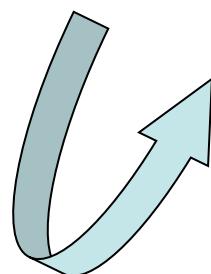
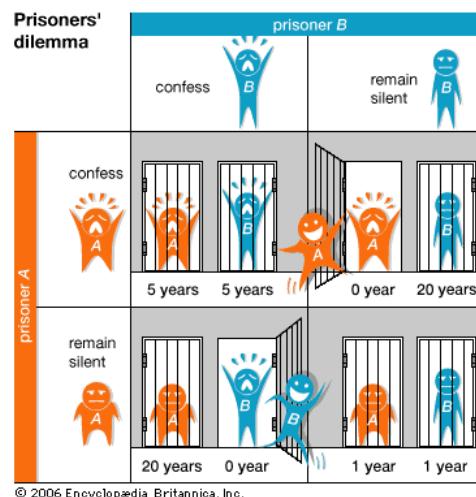


# Prisoners' dilemma worked out:

- Both cooperate, each prisoner receives 1 year ( $R$ , the reward for mutual cooperation)
- If both defect, each prisoner receives 5 years ( $P$ , is the punishment for mutual defection)
- If prisoner A testifies, but B cooperates, prisoner A gets 0 years ( $T$  is the temptation to testify), and B gets 20 years ( $S$ , suckers payoff)
- **As long as  $T > R > P > S$ , then no one will choose the cooperate.**

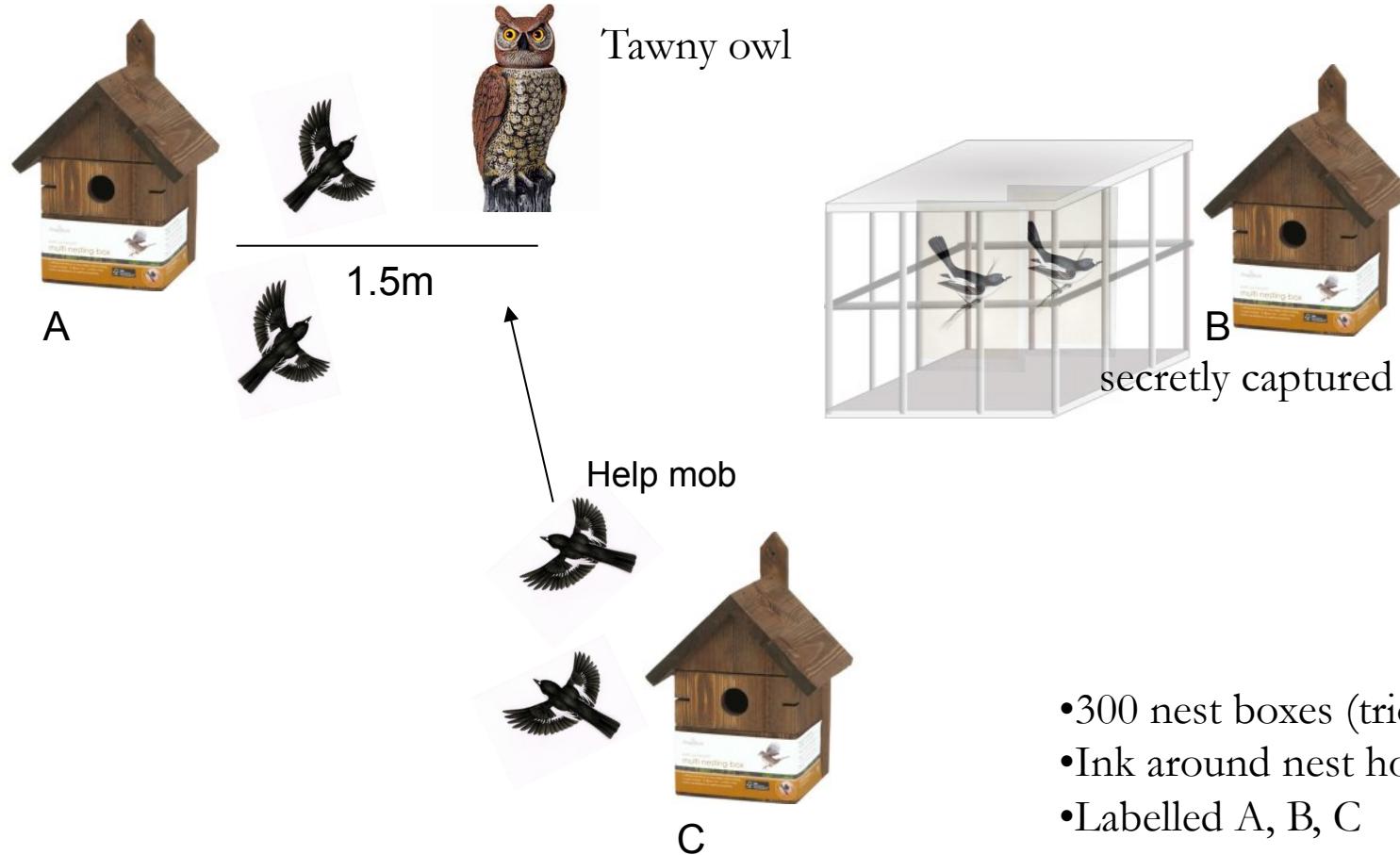
# But what if the game is played repeatedly?

- It seems when it is uncertain how many times the game will be played, individual players are more likely to cooperate in the hope that they will encourage cooperation in return - tit-for-tat model of cooperative behaviour.



# Mobbing Behaviour -

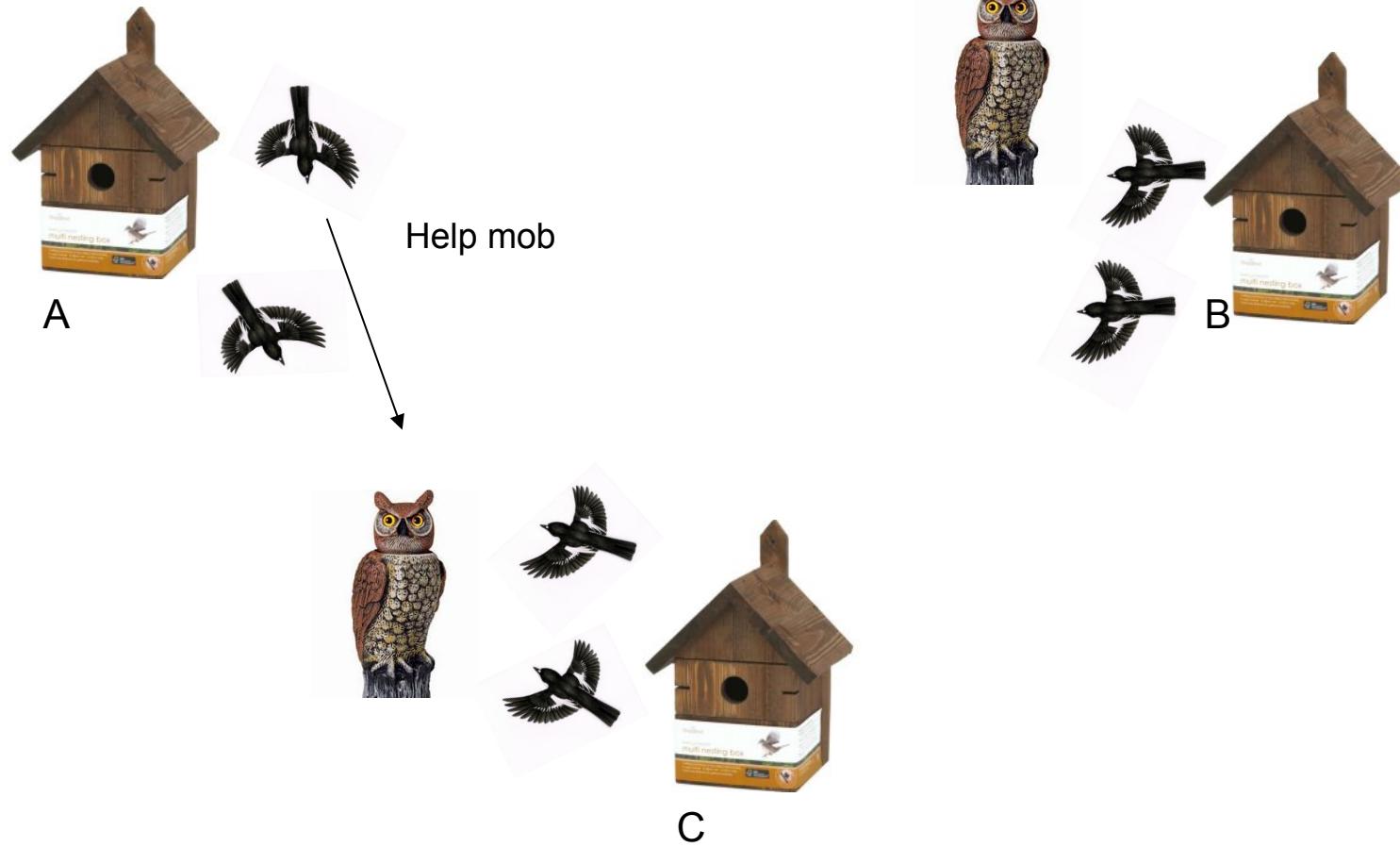
when a group of genetically unrelated but closely located individuals join together to drive away a much larger predator.



- 300 nest boxes (trios)
- Ink around nest hole
- Labelled A, B, C

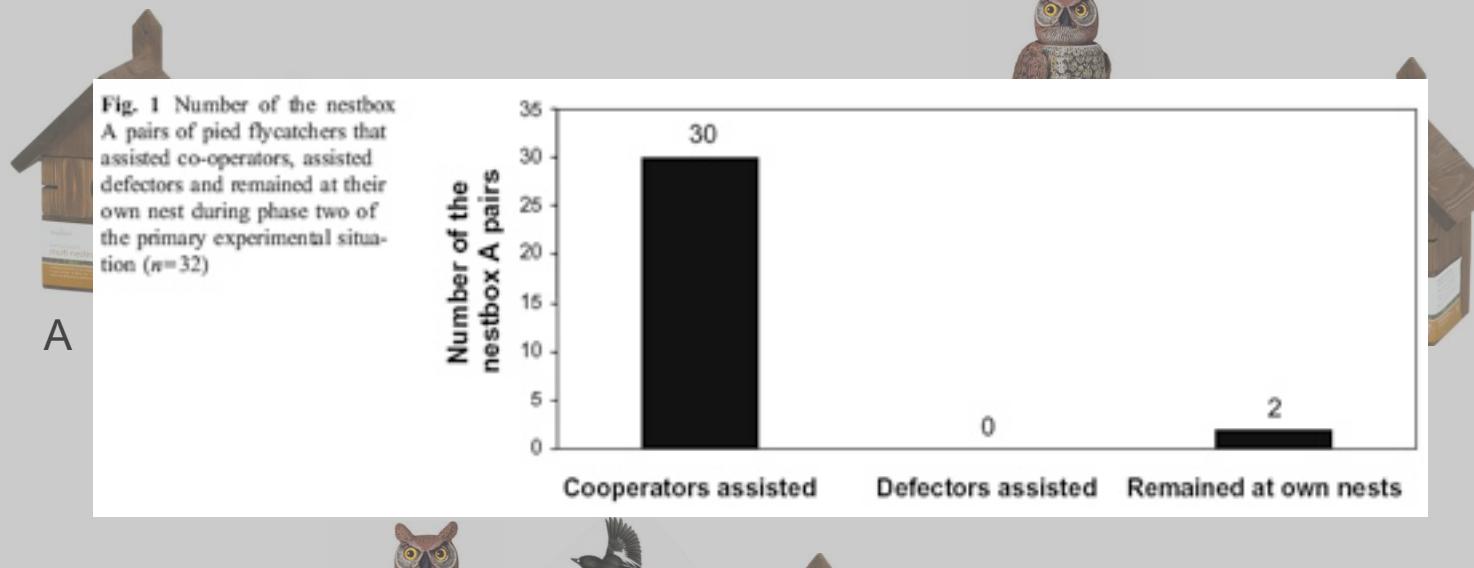
one hour later, after box B birds had been released...

**Mobbing Behaviour** - when a group of genetically unrelated but closely located individuals join together to drive away a much larger predator.



# Mobbing Behaviour

genetic  
Overwhelmingly, pair A assisted pair C and ignored pair B's pleas for help (figure 1);  
to drive away a much larger predator.



This experiment demonstrates a simple tit-for-tat behaviour where defectors are **punished** for their lack of assistance, and cooperators are **rewarded**.

But reciprocal altruism can only exist under very specific social circumstances where the animals involved interact repeatedly.



# Conflict

Conflict among nonkin (aggressive encounters)

Conflict over parental investment

Sexual conflict

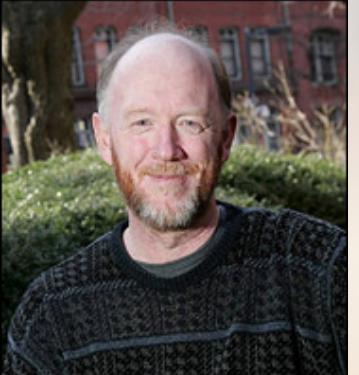
# Conflict over parental investment

- Trivers suggested that the decisions about how much to invest in a offspring are affected by how much energy the parent has available to help current offspring, and by how many offspring the parent is likely to have in the future.
- Investment in current offspring hampers investment in future offspring.
- Because offspring are related to their future siblings by 0.5 but to themselves by 1 (they contain 100% of their own genes), they therefore fight for more care at the expense of the care to their future siblings
- This creates a conflict of interest between offspring and parent.



## Begging behaviour





**Pre-eclampsia** is a medical condition in which hypertension arises in pregnancy occurs in about 6% of pregnancies

- David Haig argues, a mother and her unborn child engage in an unconscious struggle over the nutrients she will provide it.
- The fetuses raise the blood pressure of their mothers so as to drive more blood into the relatively low-pressure placenta, therefore getting more nutrients