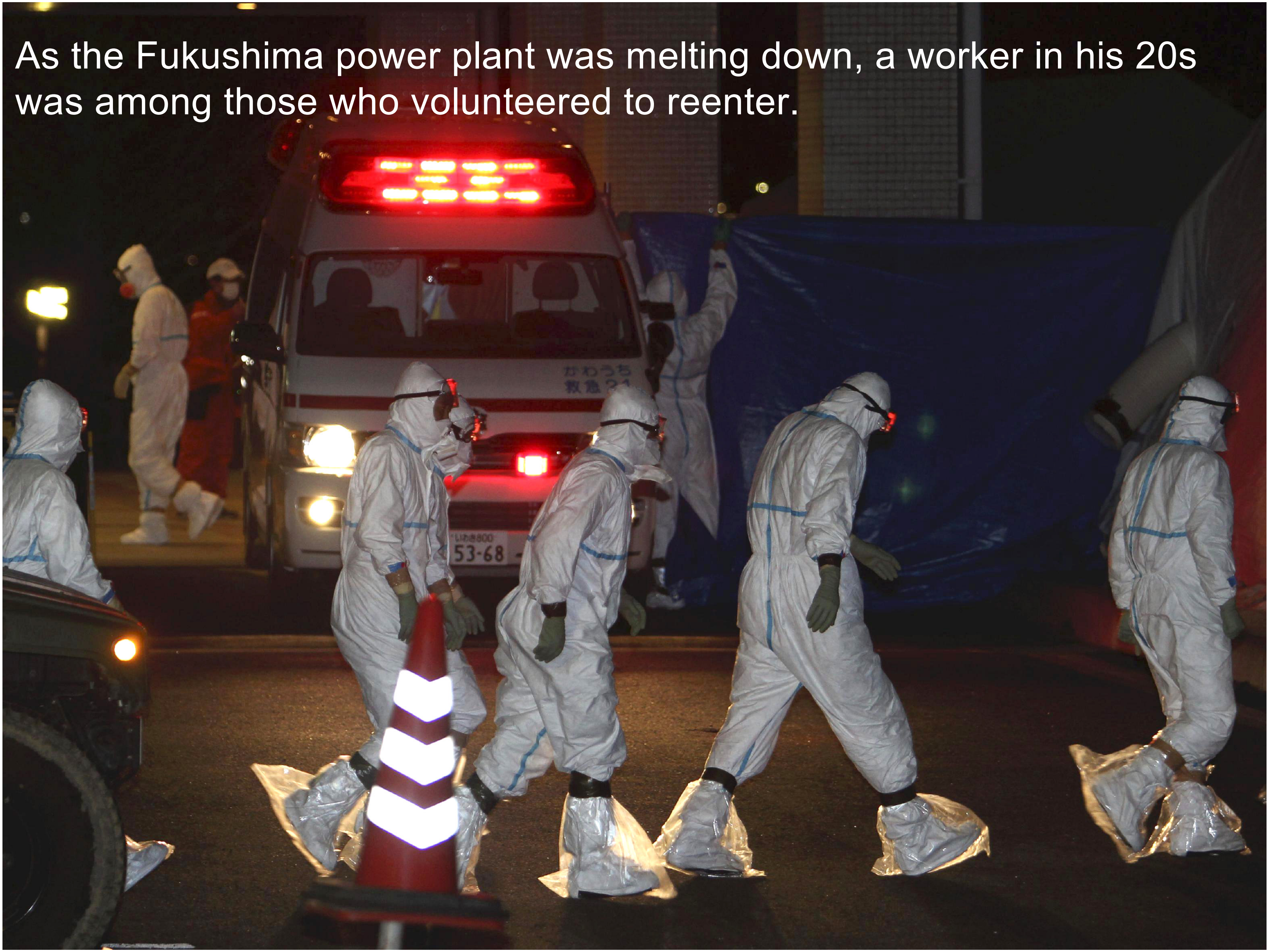
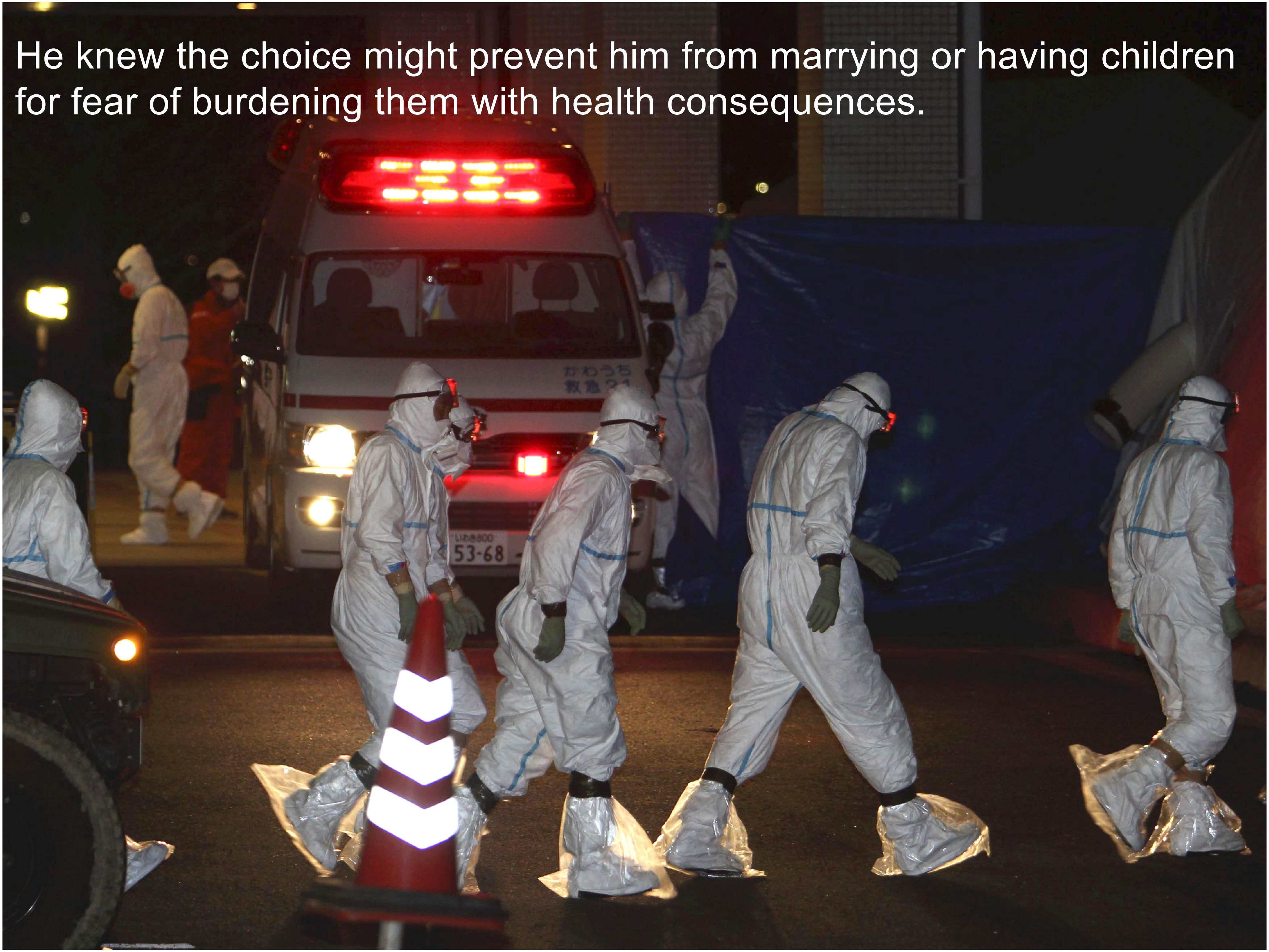
Evolution of cooperation

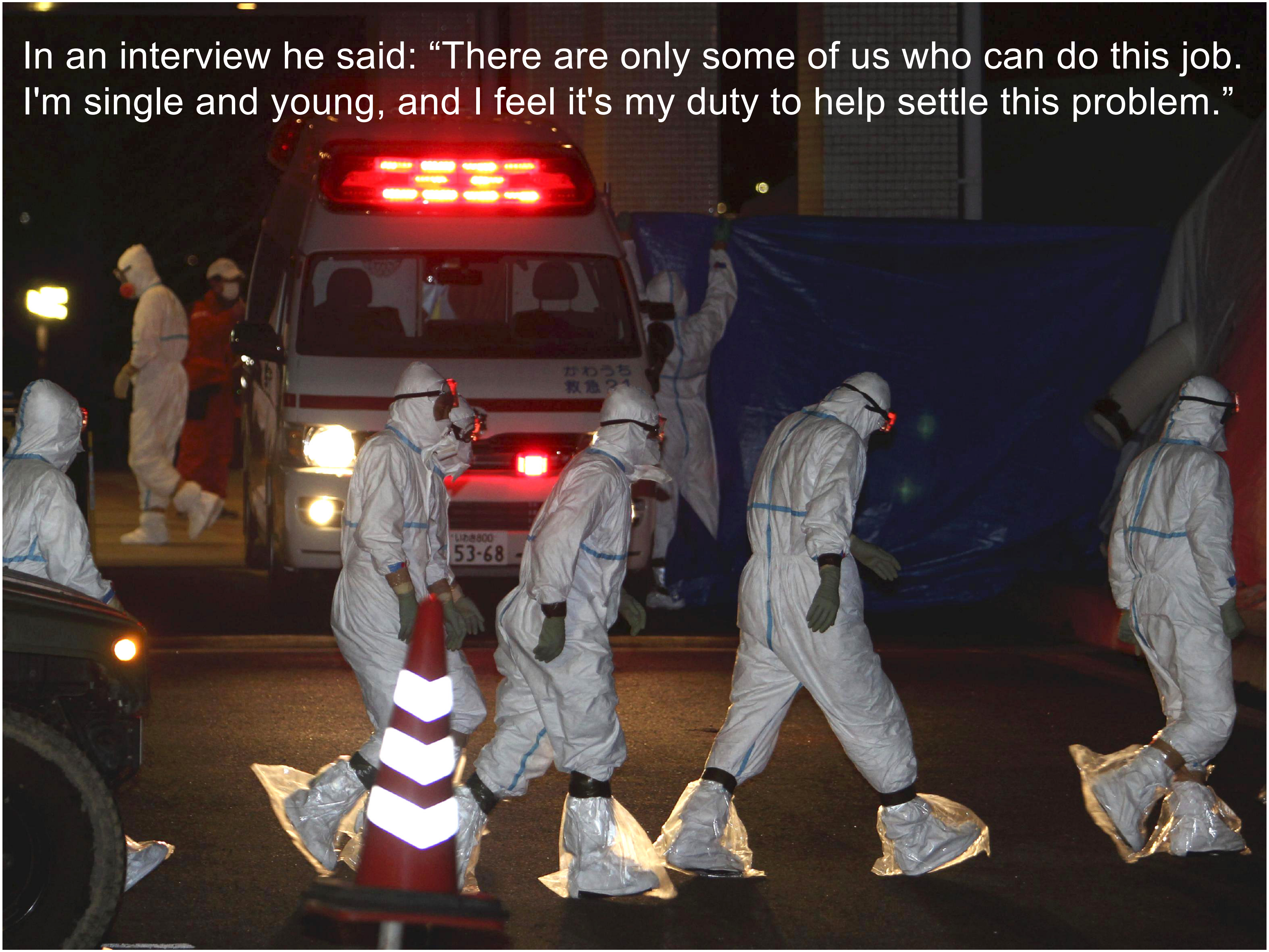
Martin Nowak, Math 242



As the Fukushima power plant was melting down, a worker in his 20s was among those who volunteered to reenter.


He knew the choice might prevent him from marrying or having children for fear of burdening them with health consequences.
53-68

In an interview he said: “There are only some of us who can do this job. I'm single and young, and I feel it's my duty to help settle this problem.”



Wesley Autrey,
the New York Subway Hero

What is cooperation?

Donor
pays a cost, *c*

Recipient
gets a benefit, *b*

Cost and benefit are measured in terms of fitness.
Reproduction can be genetic or cultural.

Prisoner's Dilemma

	I cooperate	I defect
you cooperate	$b - c$	$- c$
you defect	b	0

you get

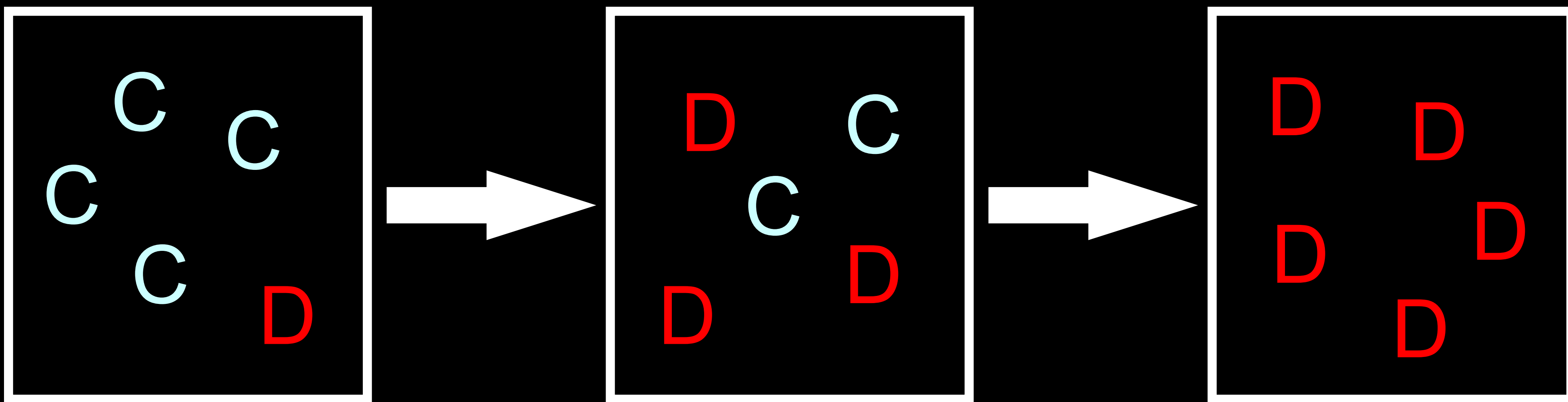
$b > c > 0$

What is the dilemma ?

Two *rational* players defect and end up with a low payoff, 0.

Two *irrational* players might cooperate and receive a higher payoff, $b - c$.

Natural selection chooses defection



In any mixed population, defectors have a higher payoff than cooperators.

Natural selection needs help to favor cooperators over defectors.

Five mechanisms for the evolution of cooperation:

Direct reciprocity
Indirect reciprocity
Spatial selection
Group selection
Kin selection

Direct reciprocity

‘I help you, you help me.’

Repeated Prisoner's Dilemma

Player 1 : C D C D C C C ….

Player 2 : D C D D C C C ….

The Folk theorem

Repeated Prisoner's Dilemma

Player 1 : C D C D C C C ….

Player 2 : D C D D C C C ….

What is a good strategy for playing this game?

Robert Axelrod

Tit-for-tat

- I start with cooperation.
- If you cooperate, then I will cooperate.
- If you defect, then I will defect.

Anatol Rapaport

Tit-for-tat is unforgiving

Errors destroy cooperation

Tit-for-tat : CCCCDCDCDCDDDDDD….

Tit-for-tat : CCCDCDCDCDDDDDDD….

Let natural selection design a strategy

Random

Let natural selection design a strategy

Always defect

↑

Random

Let natural selection design a strategy

Tit-for-tat

↑

Always defect

↑

Random

Let natural selection design a strategy

Tit-for-tat → Generous Tit-for-tat

↑

Always defect

↑

Random

Generous Tit-for-tat

- I start with cooperation.
- If you cooperate, then I will cooperate.
- If you defect, then I will cooperate with a certain probability $(q = 1 - c / b)$.

Evolution of forgiveness

Let natural selection design a strategy

Tit-for-tat → Generous Tit-for-tat

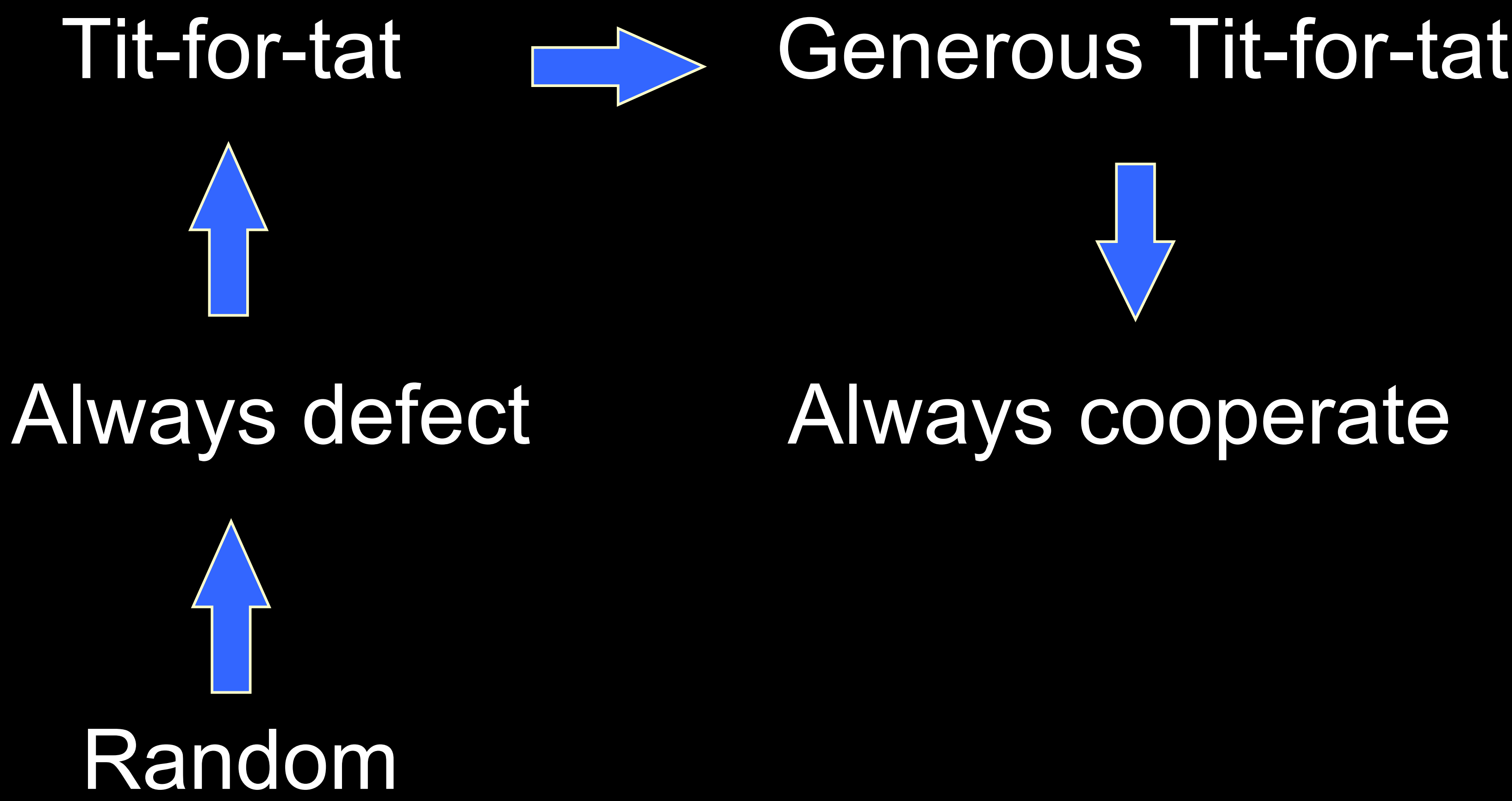
↑

Always defect

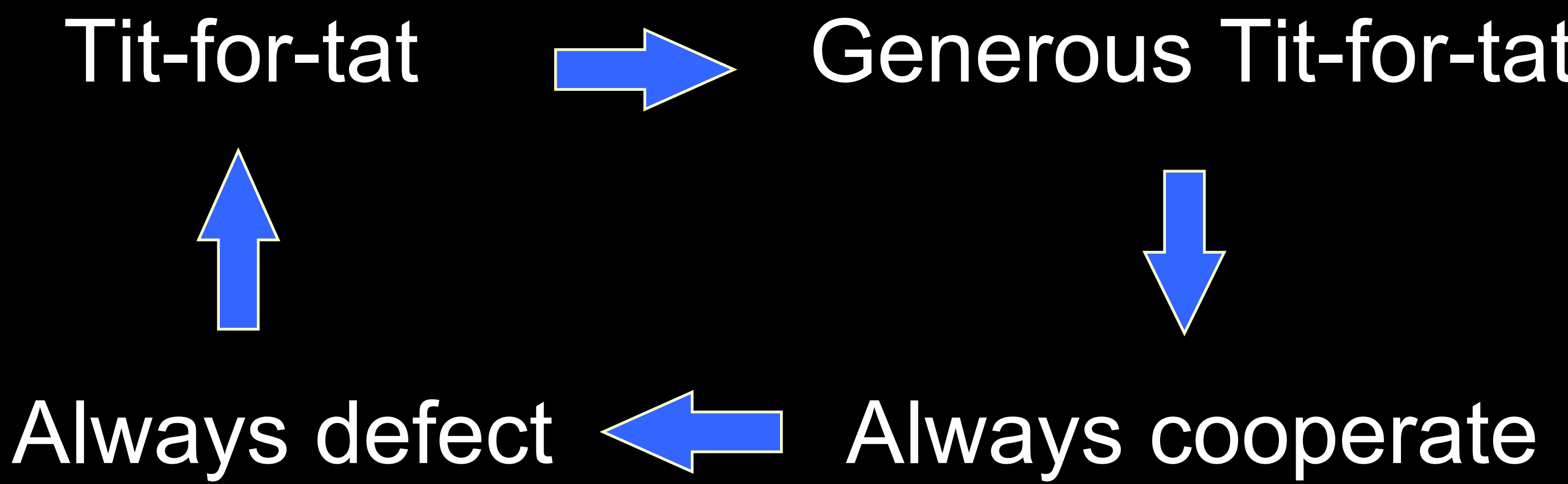
↑

Random

Let natural selection design a strategy

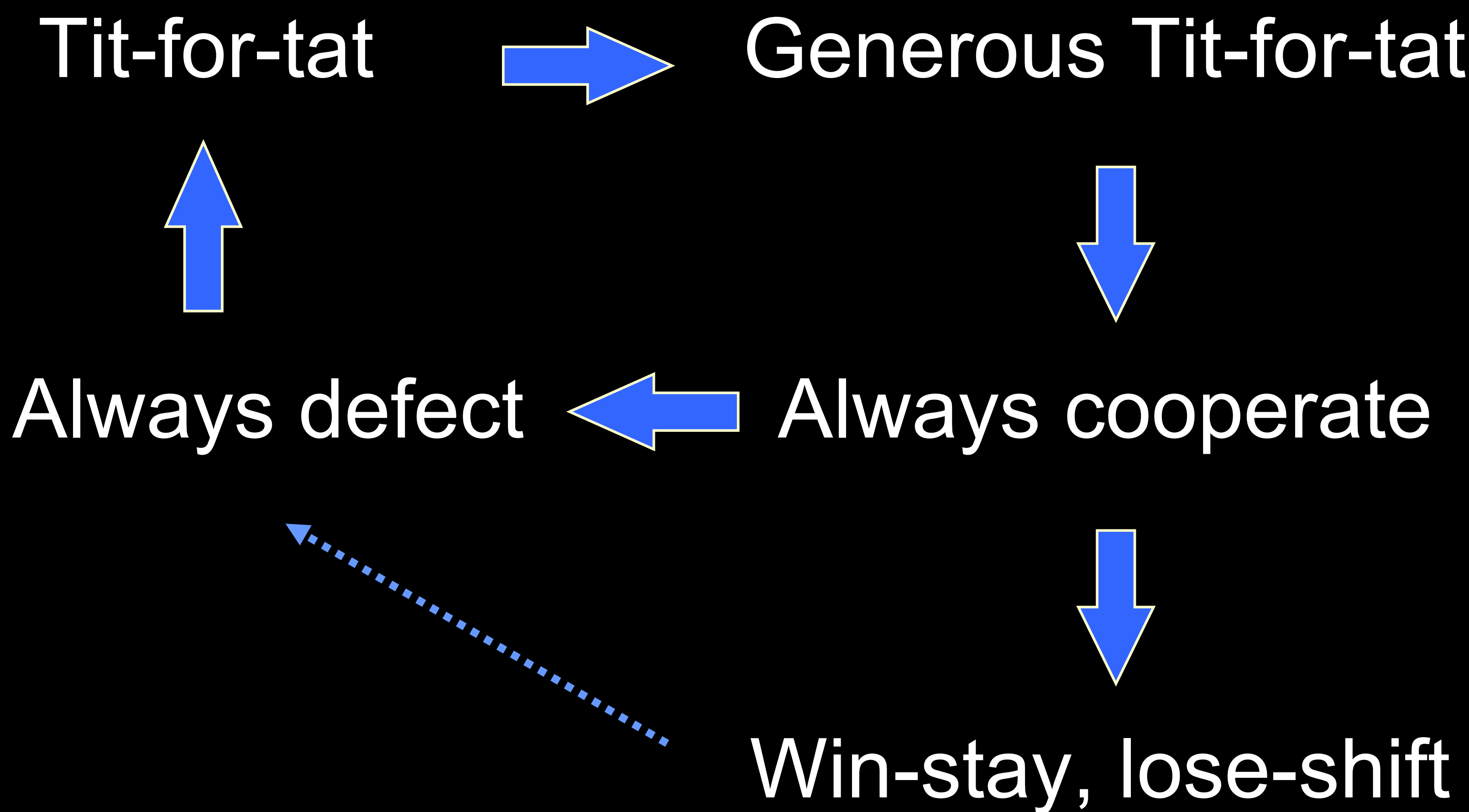


Let natural selection design a strategy



War and peace

Let natural selection design a strategy



Win-stay, lose-shift

- If I am doing well (payoff *b* or *b*-*c*) then I will repeat my move.
- If I am doing badly (payoff 0 or -*c*) then I will change my move.

If b/c<2 then a stochastic variant of WSLS does well (where you return to C after DD only with a certain probability).

Direct reciprocity

… allows the evolution of cooperation if

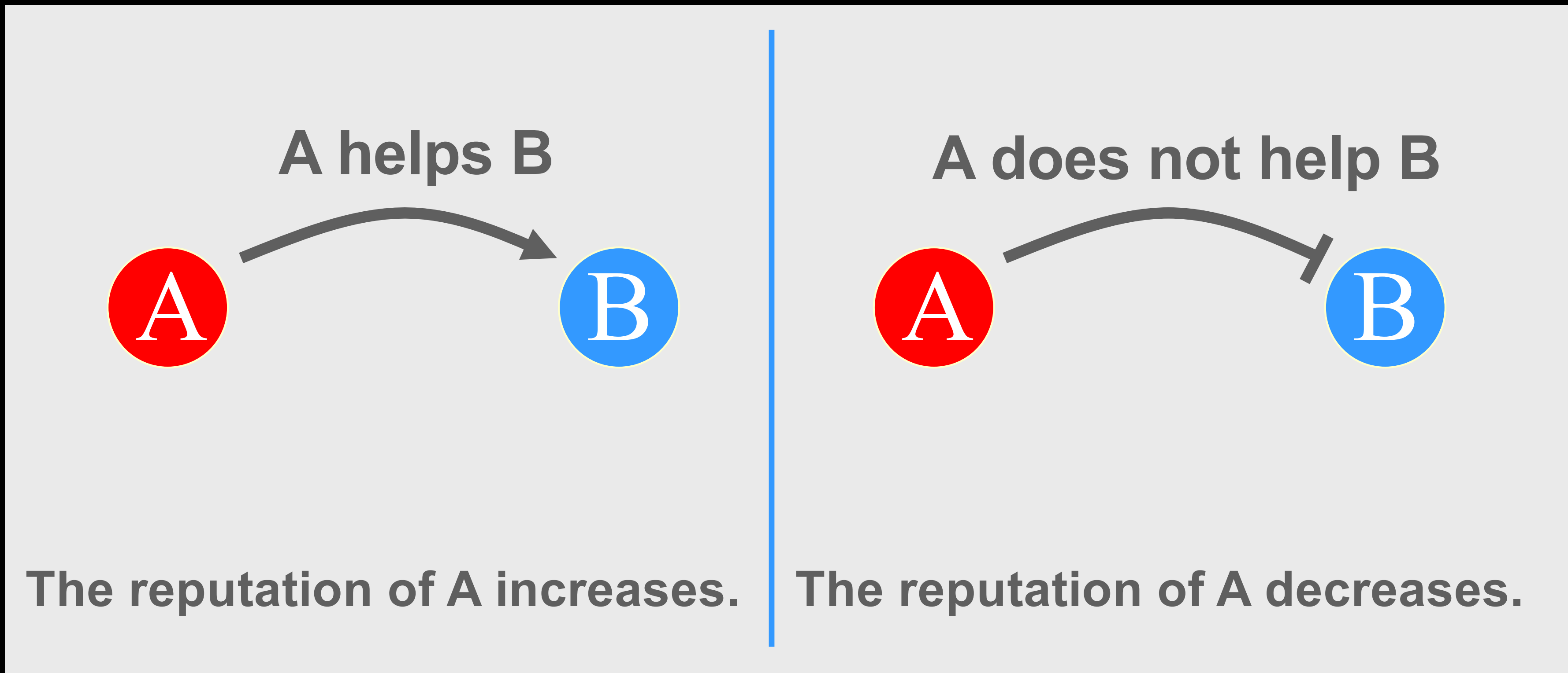
$w > c / b$

b…benefit
c…cost
w…probability of another round

Indirect reciprocity

‘I help you.
Somebody helps me.’

Indirect reciprocity works via reputation



	donor	recipient	donor's reputation
cooperate	-c	+b	+1
defect	0	0	-1

Nowak & Sigmund, Nature 1998

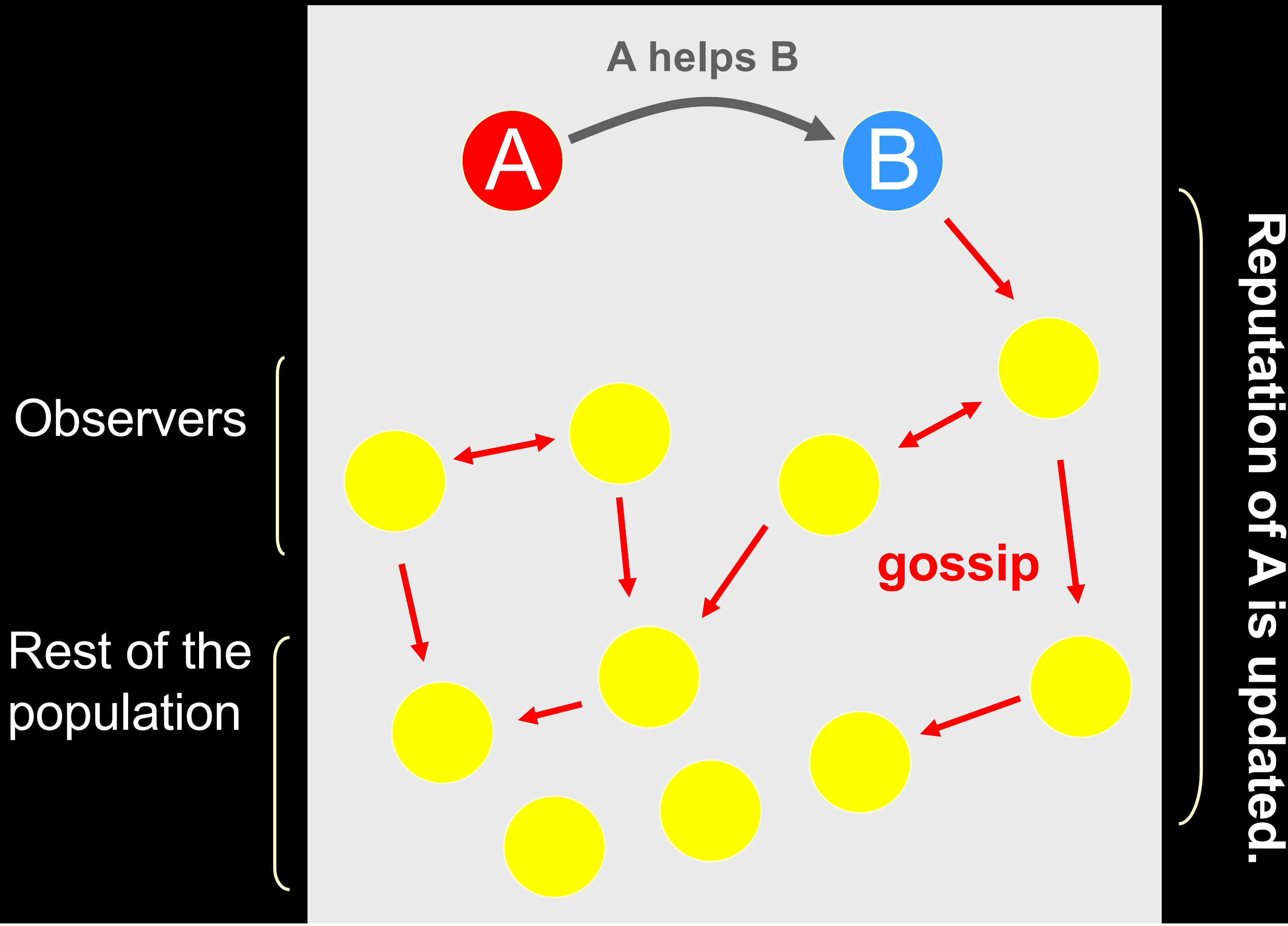
Experimental confirmation:

People help those who help others.

Helpful people have a higher payoff in the end.

Wedekind & Milinski, Science 2000

Gossip spreads reputation

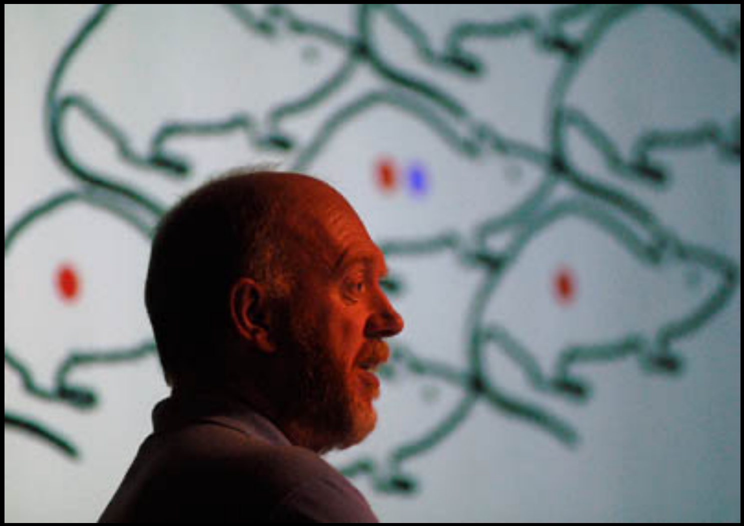


Games of indirect reciprocity are cognitively demanding; individuals need to monitor the social network of a group.

=> evolution of social intelligence

Individuals must be able to talk to each other about others.

=> evolution of human language



David Haig:

“For direct reciprocity you need a face.

For indirect reciprocity you need a name.”

A rule for indirect reciprocity

$$q > c / b$$

q … probability to know someone's reputation

c … cost of cooperation

b … benefit of cooperation

Spatial selection

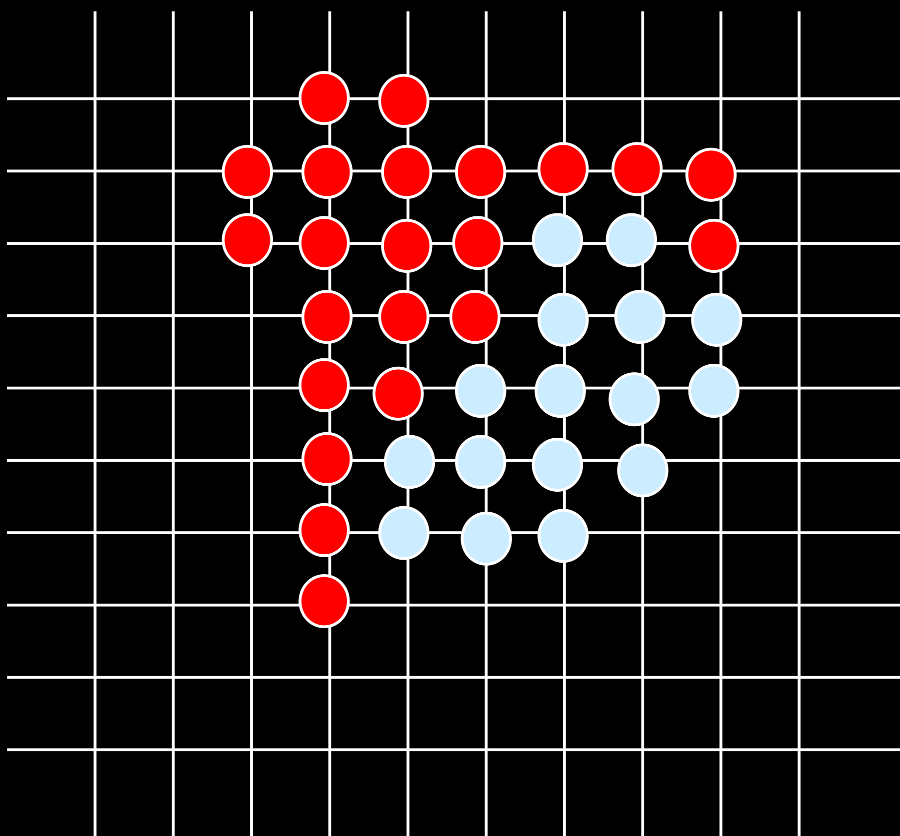
Spatial games

Games on graphs

Games in phenotype space

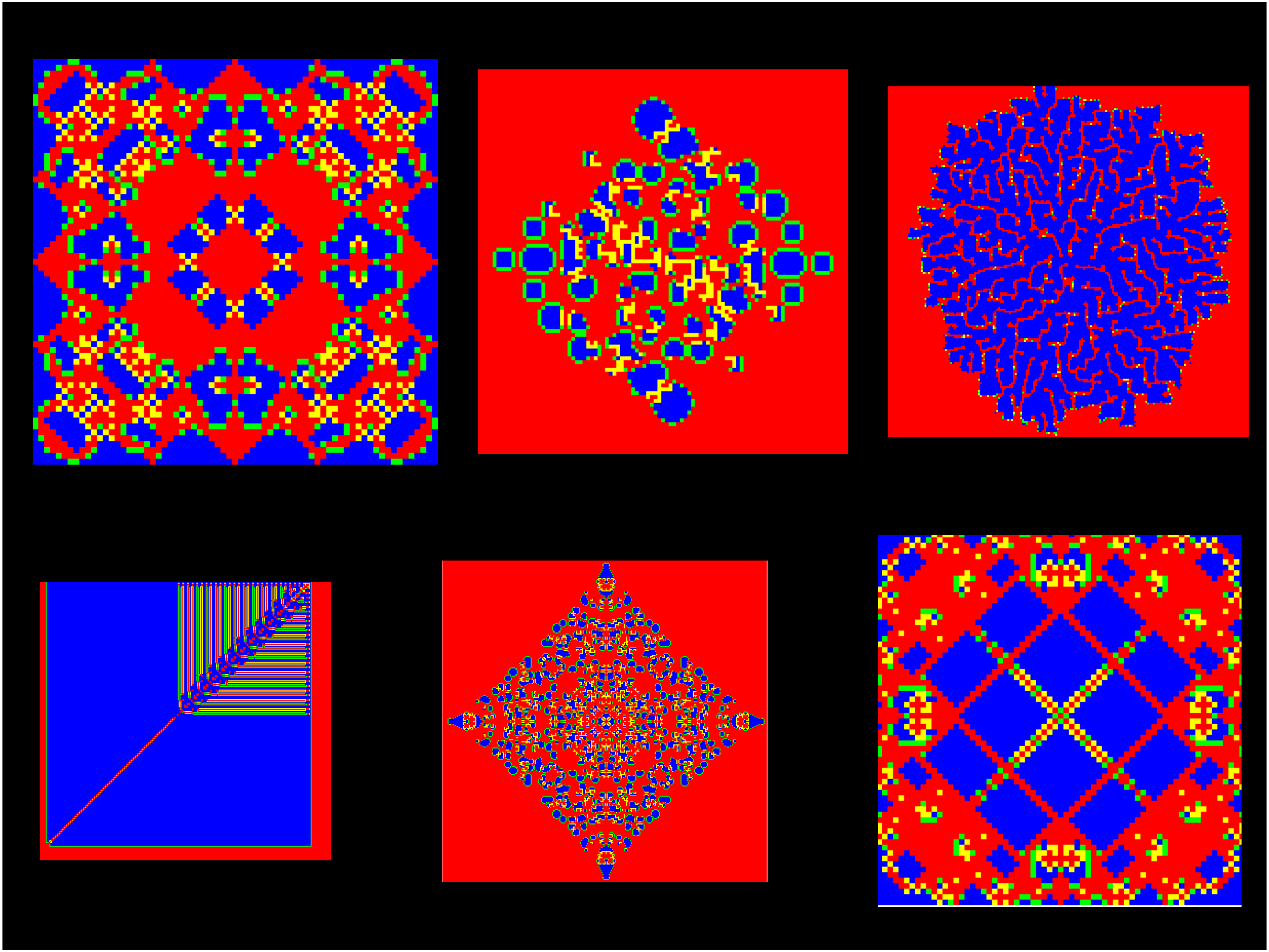
Games on sets

Spatial games

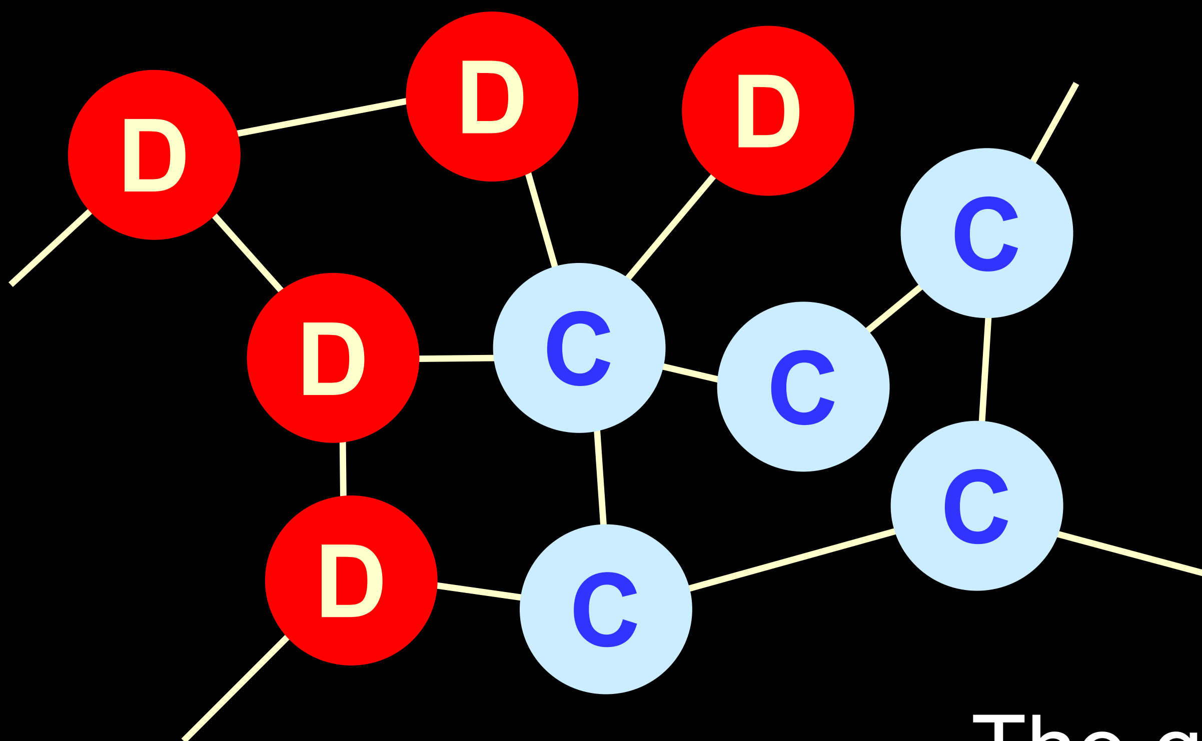


Cooperators
Defectors

Nowak & May, Nature 1992



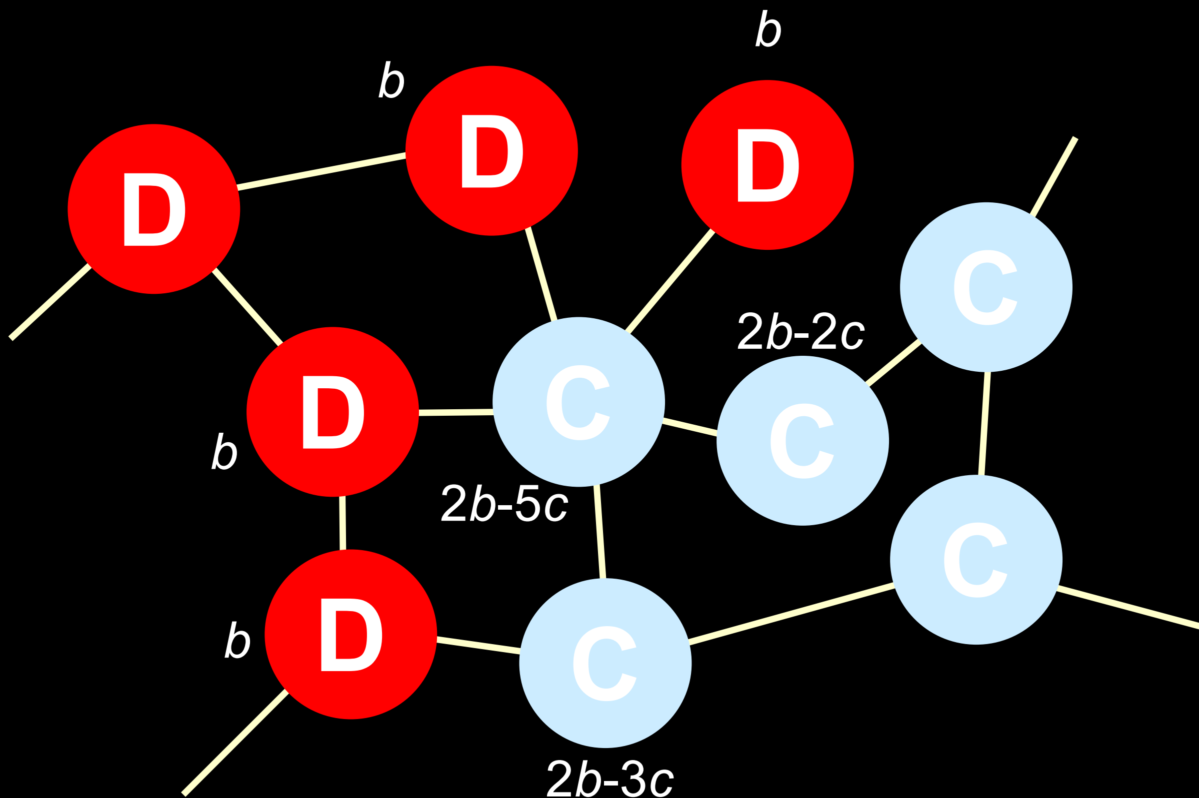
Games on graphs



Cooperators
Defectors

The graph describes
a spatial structure
or a social network.

'Evolutionary graph theory' (Lieberman et al, Nature 2005)



Cooperators pay a cost *c*
for each neighbor to receive benefit *b*.

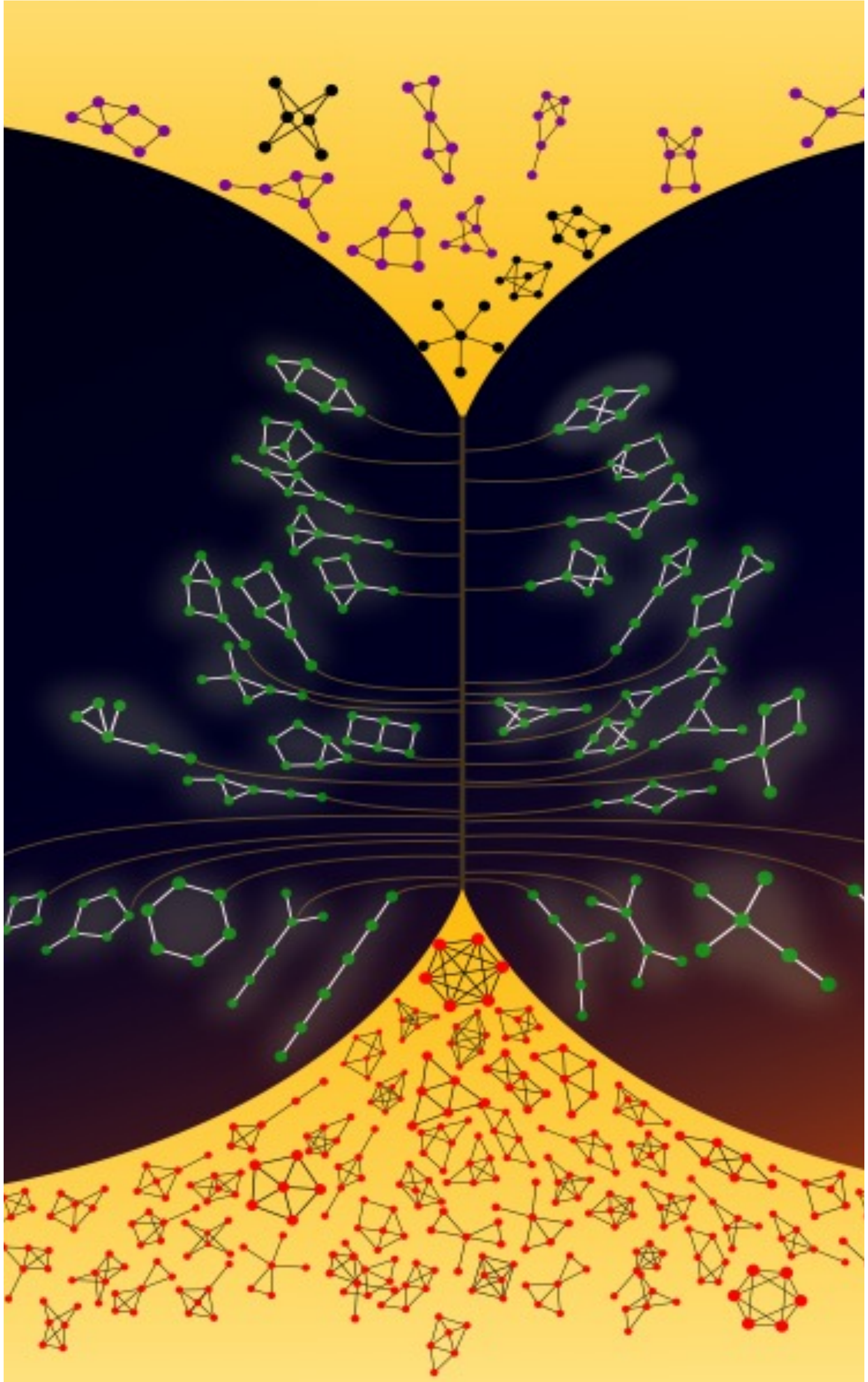
Spatial selection on graphs favors cooperation if

$$b / c > k$$

k…(average) number of neighbors

weak selection

Ohtsuki et al, Nature 2006



LETTER

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Evolutionary dynamics on any population structure

Benjamin Allen[1,2,3], Gabor Lippner[3,4], Yu-Ting Chen[2,3,5], Babak Fotouhi[2,6], Naghmeh Momeni[2,7], Shing-Tung Yau[3,8] & Martin A. Nowak[2,8,9]

Evolution occurs in populations of reproducing individuals. The structure of a population can affect which traits evolve[1,2]. Understanding evolutionary game dynamics in structured populations remains difficult. Mathematical results are known for special structures in which all individuals have the same number of neighbours[3–8]. The general case, in which the number of neighbours can vary, has remained open. For arbitrary selection intensity, the problem is in a computational complexity class that suggests there is no efficient algorithm[9]. Whether a simple solution for weak selection exists has remained unanswered. Here we provide a solution for weak selection that applies to any graph or network. Our method relies on calculating the coalescence times[10,11] of random walks[12]. We evaluate large numbers of diverse population structures for their propensity to favour cooperation. We study how small changes in population structure—graph surgery—affect evolutionary outcomes. We find that cooperation flourishes most in societies that are based on strong pairwise ties.

Ecological and evolutionary dynamics depend on population structure[13–15]. Evolutionary graph theory[1,3,7] provides a mathematical tool for representing population structure: vertices correspond to individuals and edges indicate interactions. Graphs can describe spatially structured populations of bacteria, plants, animals[16], tissue architecture in multi-cellular organisms[17], or social networks[18,19]. Graph topology affects the rate of genetic change[20] and the balance of drift versus selection[1]. The classical setting of a well-mixed population is the complete graph.

Of particular note is the evolution of social behaviour, which can be studied using evolutionary game theory[21–23]. Evolutionary game dynamics, which are tied to ecological dynamics[22], arise whenever reproductive success is affected by interactions with others.

In evolutionary games on graphs[3–8,24,25], individuals interact with neighbours according to a game and reproduce on the basis of payoff (Fig. 1). A central question is to determine which strategies succeed on a given graph. In general, there cannot be a closed-form solution or polynomial-time algorithm for this question, unless it is unexpectedly found that P = NP (polynomial time = nondeterministic polynomial time)[9]. To make progress, one can consider weak selection, meaning that the game has only a small effect on reproductive success. Weak selection results are known for regular graphs, where each individual has the same number of neighbours[3–8]. Evolutionary games on heterogenous (non-regular) graphs have only been investigated using computer simulations[3,24,25], approximations[3,26] and special cases[25,27,28].

We consider games on any weighted graph (Fig. 1a), with edge weights w_{ij}. Individuals are of two types, A and B. The game is specified by a payoff matrix (see Methods). Each individual i plays the game with each neighbour, receiving an edge-weighted average payoff of f_i (Fig. 1b). The reproductive rate of i is $F_i = 1 + \delta f_i$, where $\delta > 0$ is the strength of selection. Weak selection means $\delta \ll 1$; neutral drift, $\delta = 0$, is a baseline.

At each time step, an individual is chosen uniformly at random to be replaced. Its neighbours compete for the vacancy proportionally to their reproductive rates (Fig. 1c). Offspring inherit the type of their parent. This update rule, called death–birth[3], also translates into social settings: a random individual resolves to update its strategy, and adopts one of its neighbours' strategies proportionally to their payoff.

Over time, the population will reach the state of all A or all B. Suppose we introduce a single A at a vertex chosen uniformly at random in a population of B individuals. The fixation probability, ρ_A, is the probability of reaching all A from this initial condition. Likewise, ρ_B is the probability of reaching all B when starting with a single B individual in a population otherwise of A. Selection favours A over B if $\rho_A > \rho_B$.

The outcome of selection depends on the spatial assortment of types, which can be studied using coalescent theory[10,11]. Ancestral lineages are represented as random walks[12]. A step from i to j occurs with probability $p_{ij} = w_{ij}/w_i$, where $w_i = \sum_k w_{ik}$ is the weighted degree of vertex i. The coalescence time τ_{ij} is the expected meeting time of independent random walks started at vertices i and j (Fig. 1d), which can be obtained by solving a system of linear equations (see Methods). We show in the Supplementary Information that, if T is the time to absorption

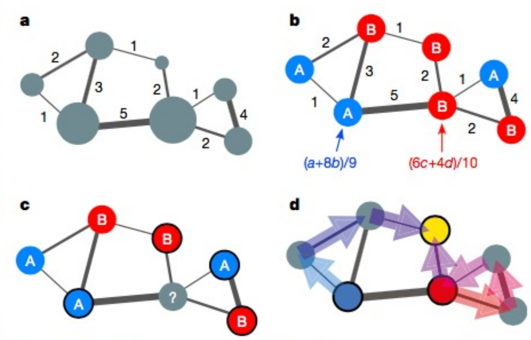

Figure 1 | Evolutionary games on weighted heterogeneous graphs. **a**, Population structure is represented by a graph with edge weights w_{ij}, which are shown next to the edges for this example. **b**, Each individual i plays a game (equation (3) in the Methods) with each neighbour, and retains the edge-weighted average payoff f_i. The reproductive rate of i is $F_i = 1 + \delta f_i$, where δ represents the strength of selection. **c**, For death–birth updating, a random individual i is selected to be replaced (indicated by a '?'); then a neighbour j is chosen with a probability proportional to $w_{ij}F_j$ to reproduce into the vacancy. **d**, The coalescence time[10–13] τ_{ij} is the expected meeting time of random walks from i and j, representing time to a common ancestor (yellow circle).

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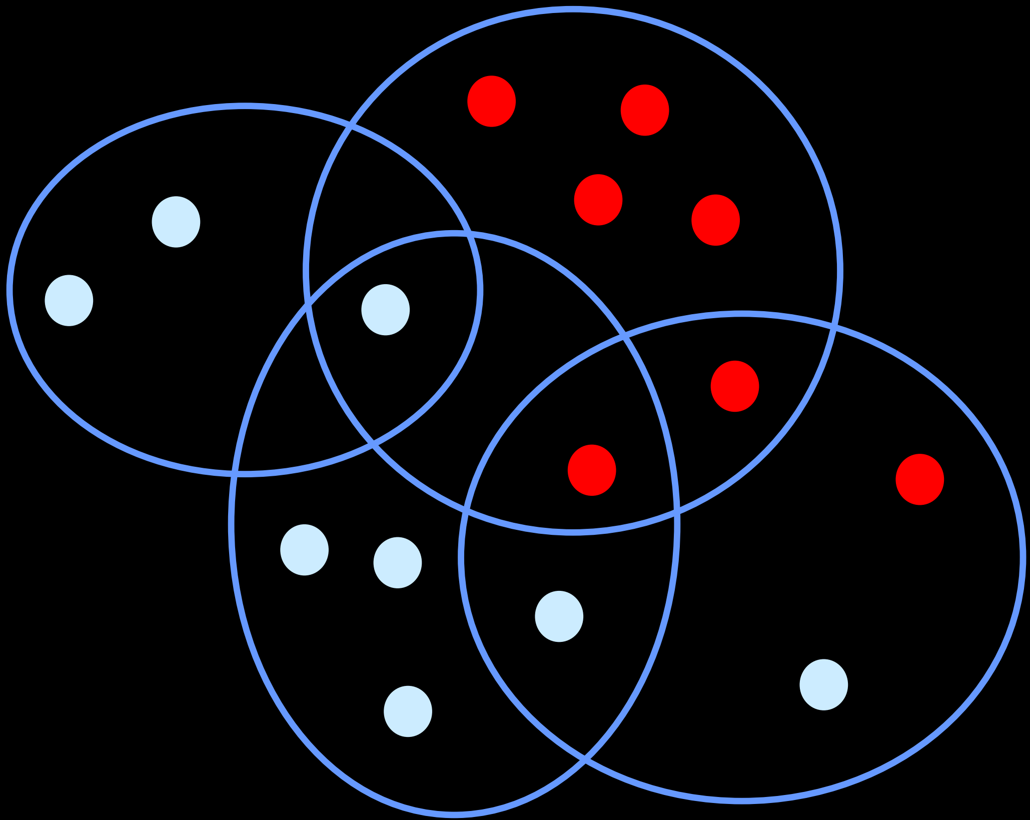
Evolutionary set theory



People belong to sets.

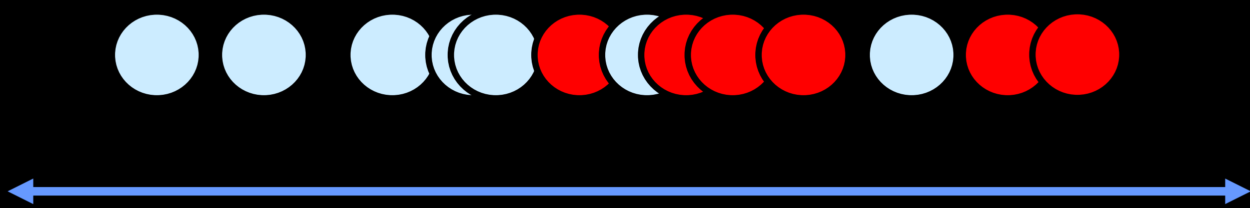
People interact with others in the same sets.

People adopt strategy and set membership of successful individuals.

Tarnita et al, PNAS 2009

Games in phenotype space

Cooperation by similarity / tag based



Phenotype space

$$\frac{b}{c} > 1 + \frac{2}{\sqrt{3}}$$

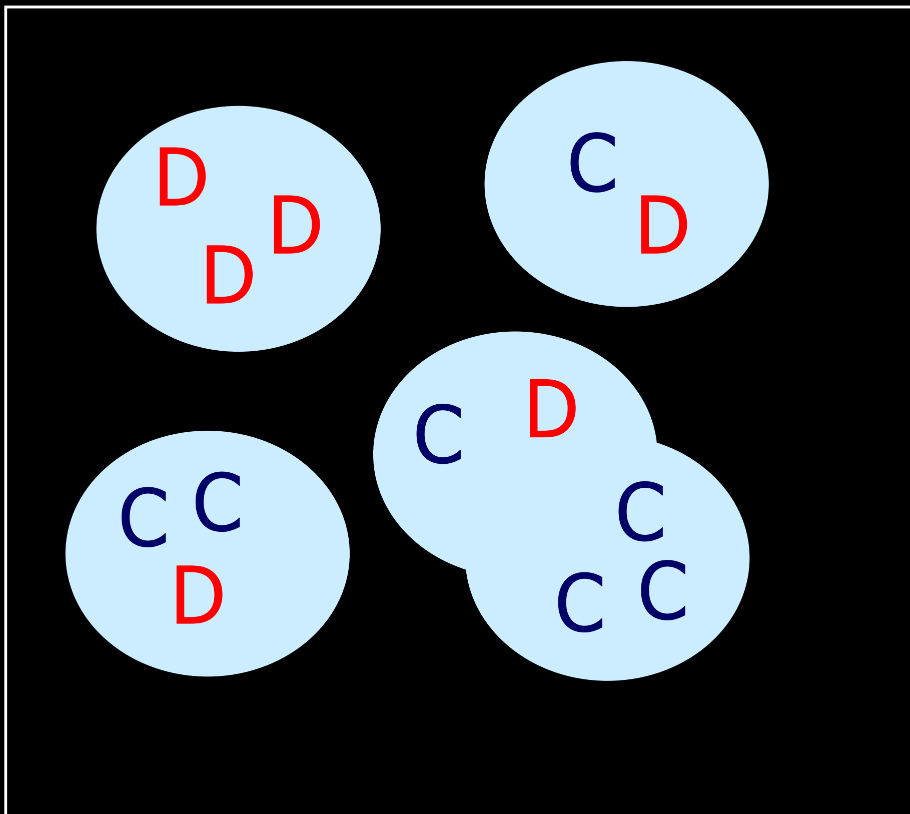
Antal et al, PNAS 2009

Group selection

‘There can be no doubt that a tribe including many members who [...] are always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over other tribes; and this would be natural selection.’

Charles Darwin, The Descent of Man, 1871

Group selection



Play the game with others in your group.

Offspring are added to the group.

Groups divide when reaching a certain size.

Groups die.

Group selection

favors cooperators if

$$b / c > 1 + n / m$$

n … group size
m … number of groups

Traulsen & Nowak, PNAS 2006

Kin selection

The interaction occurs between genetic relatives.

‘I will jump into the river to save
2 brothers or 8 cousins’

J.B.S Haldane

Five mechanisms for cooperation

Direct reciprocity : I help you, you help me.

Indirect reciprocity : I help you, somebody helps me.

Spatial selection : Neighbors help each other.

Group selection : groups of cooperators out-compete other groups.

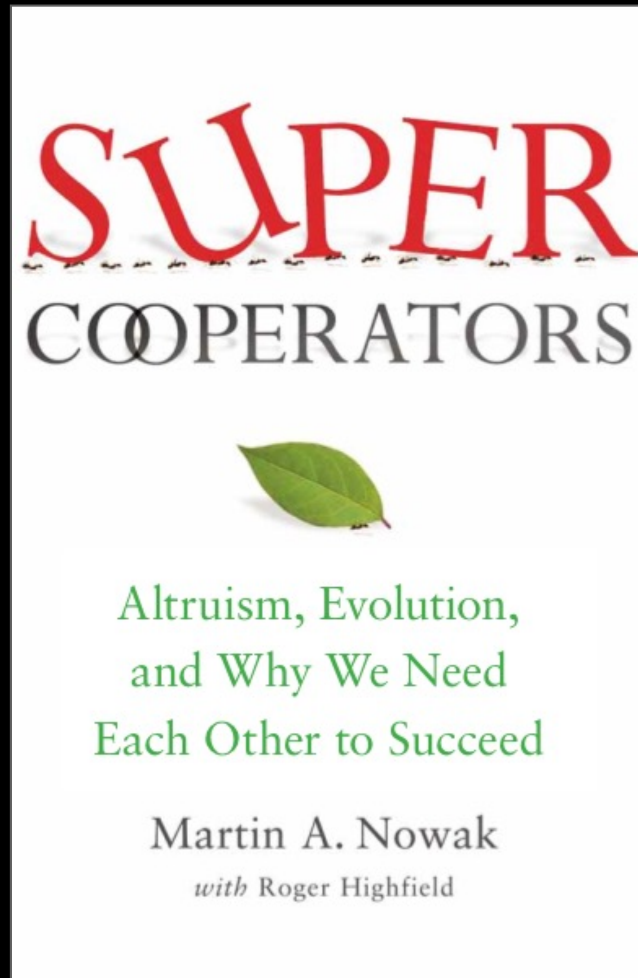
Kin selection : cooperate with genetic relatives.

Direct and indirect reciprocity
are the key components for understanding
the evolution of any pro-social behavior
in humans.

But ‘what made us human’ is
indirect reciprocity,
because it selected for social intelligence
and human language.


We must learn global cooperation
…. and cooperation with future generations.


The stability of i-life requires global cooperation
… and cooperation with future generations.


SUPER
COOPERATORS
Altruism, Evolution,
and Why We Need
Each Other to Succeed
Martin A. Nowak
with Roger Highfield