Chromodynamics of cooperation in finite populations

- Red queens with green beards -

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Motivation

- The green beard effect
  - An arbitrary visible trait
  - Recognition of the trait in others
  - Special behavior towards others with the trait

The Prisoner's Dilemma

Your action

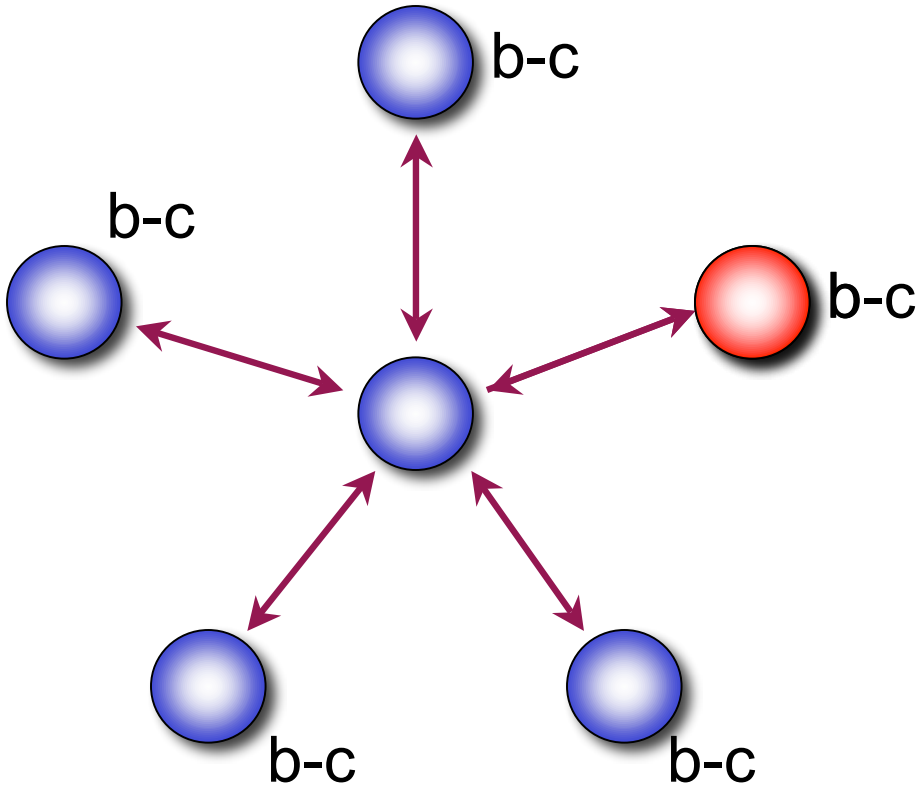
My action

	C	D
C	$b-c$	$-c$
D	b	0

My payoff

Rapoport & Chammah, Prisoner's Dilemma (1965)

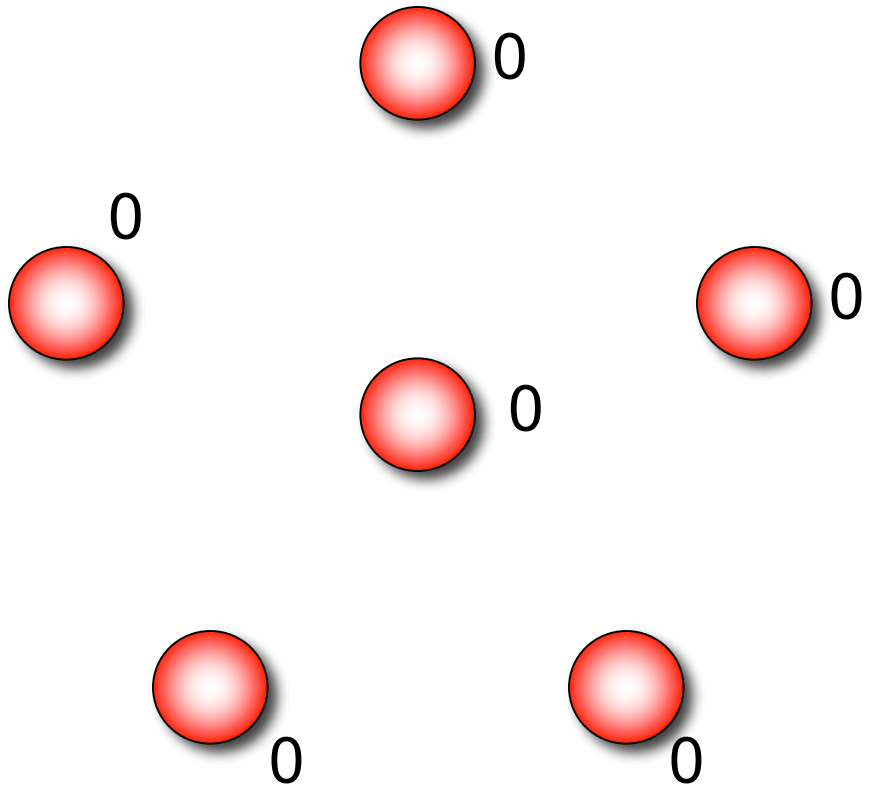
Defection pays



Defector has
the highest payoff

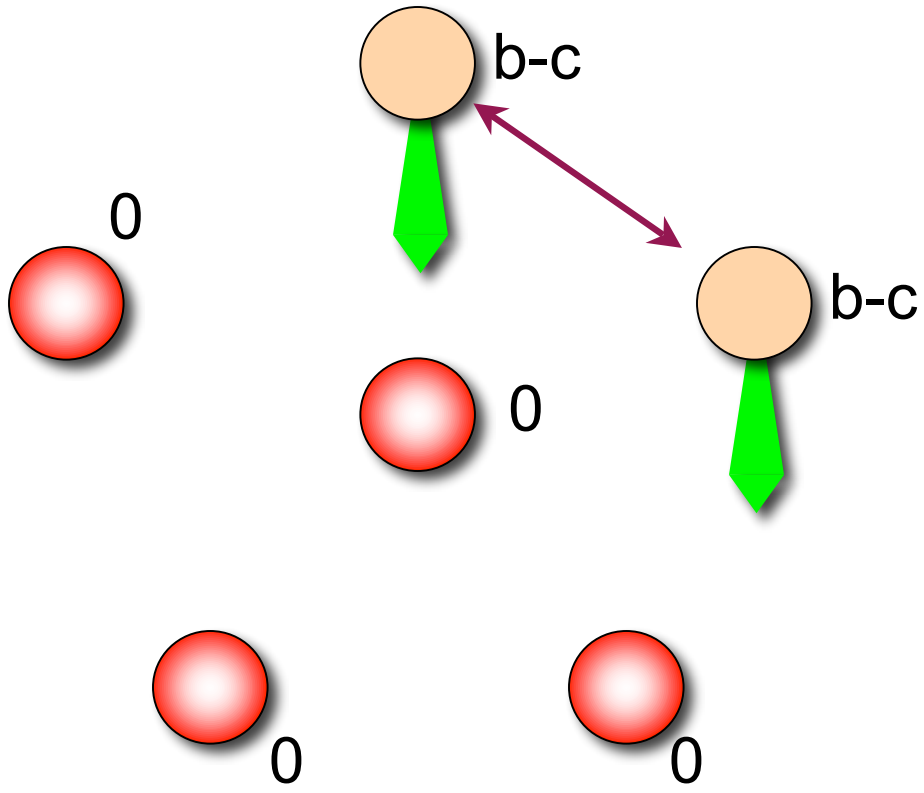
	C	D
C	$b-c$	$-c$
D	b	0

Defectors take over



How can cooperation be established again?

Green beards



Signals help to establish cooperation

Hamilton, JTB 7:1 (1964)

Green beards in biology

NATURE | VOL 394 | 6 AUGUST 1998

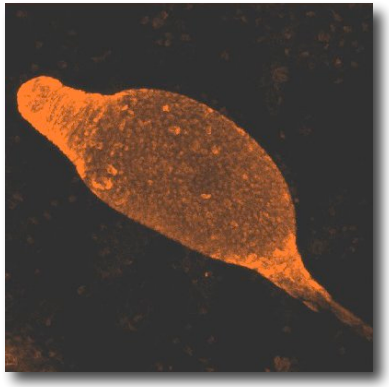
Selfish genes: a green beard in the red fire ant

Laurent Keller* & Kenneth G. Ross†

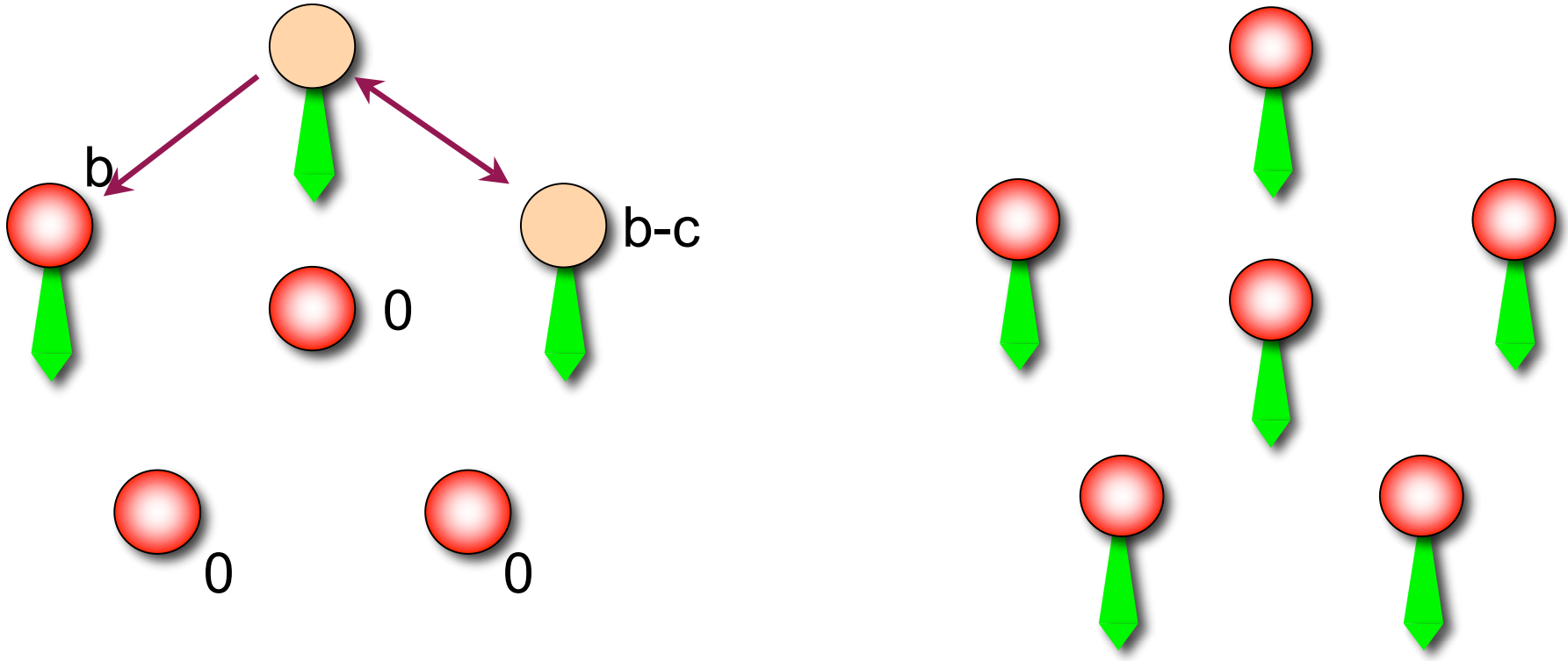
SCIENCE VOL 299 3 JANUARY 2003

Single-Gene Greenbeard Effects in the Social Amoeba *Dictyostelium discoideum*

David C. Queller,[1]* Eleonora Ponte,[2] Salvatore Bozzaro,[2] Joan E. Strassmann[1]



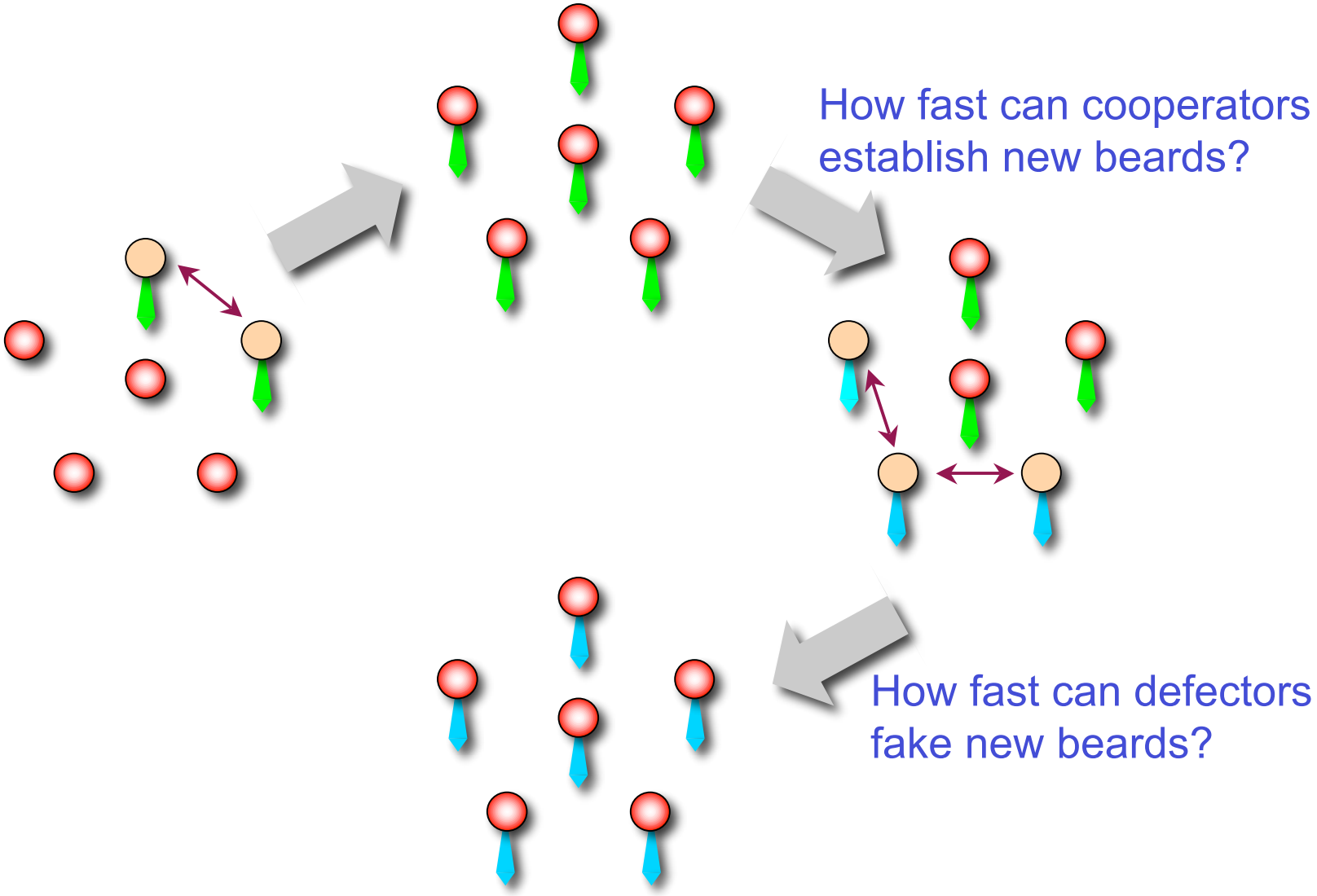
Invasion of fake beards



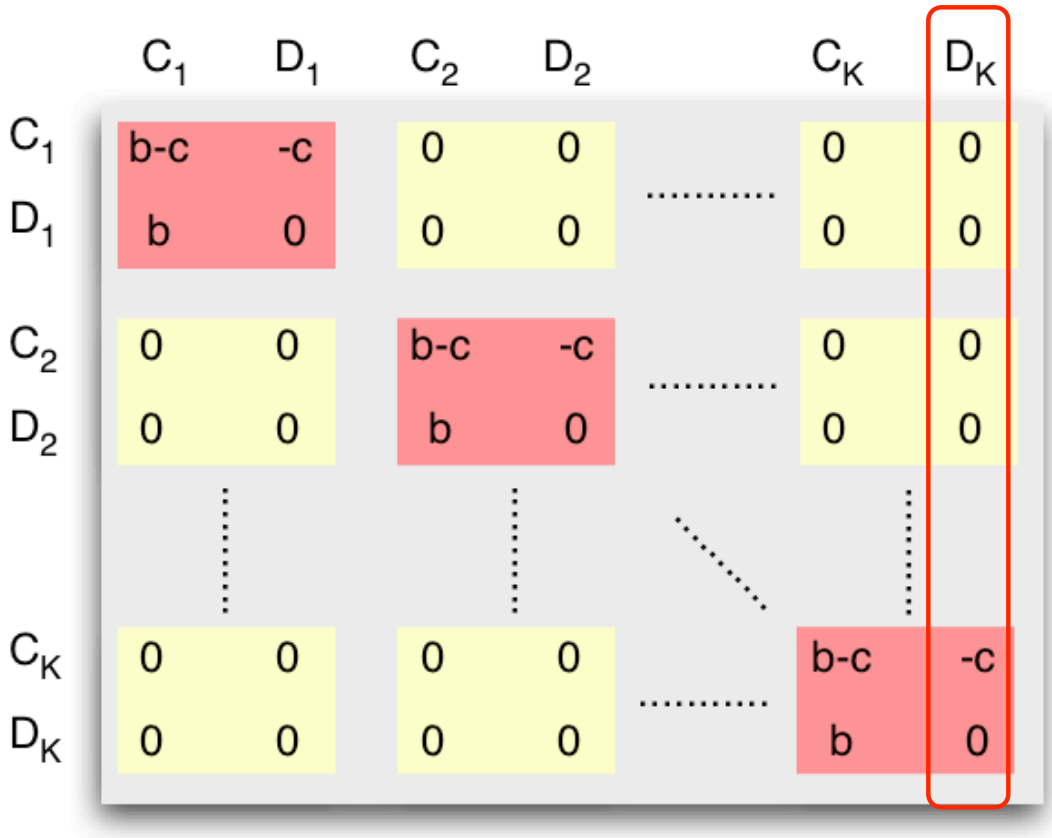
... a green beard works “for a limited time only”...

Dawkins, The Selfish Gene (1976)

Red queens with green beards



Payoff matrix



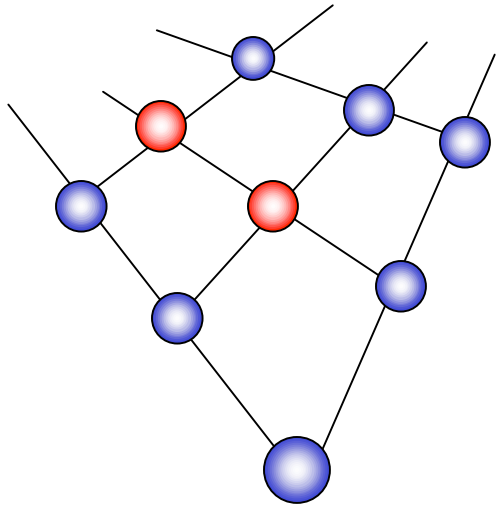
	C_1	D_1	C_2	D_2	.....	C_K	D_K
C_1	b-c	-c	0	0	.....	0	0
D_1	b	0	0	0	.....	0	0
C_2	0	0	b-c	-c	.....	0	0
D_2	0	0	b	0	.....	0	0
⋮	⋮	⋮	⋮	⋮	⋱	⋮	
C_K	0	0	0	0	.....	b-c	-c
D_K	0	0	0	0	.....	b	0

- K Nash equilibria, but no strict one
- In which states does the system spend most time? C or D?

Traulsen & Nowak, PLoS One 3:e270 (2007).

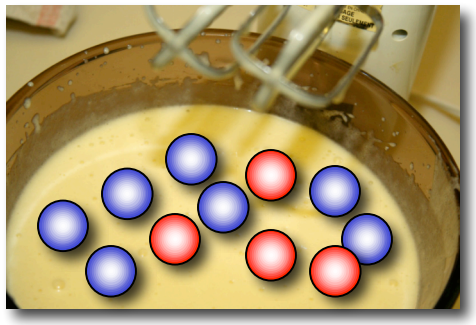
A mathematical model

- Structured population



Other mechanisms for the evolution of cooperation (kin selection, spatial reciprocity)

- Single, well mixed population

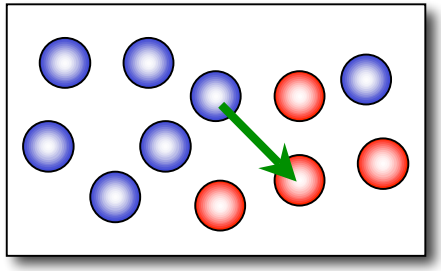


A mathematical model

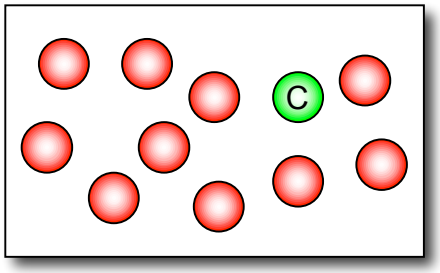
- How many individuals?

- How many beards?

- Transmission of successful strategies?



- Invention of new strategies?



A mathematical model

- How many individuals? $N < \infty$
- How many beards? K
- Transmission of successful strategies?

  Birth-death process with weak selection
- Invention of new strategies?

  1. A new beard with a random strategy appears with probability $u \ll 1$

Selection / learning mechanisms

- Moran process

$$T_{i,i+1} = \frac{i(1-w+w\pi_A)}{1-w+w(i\pi_A+(N-i)\pi_B} \frac{N-i}{N}$$

- ”Fermi”-process

$$T_{i,i+1} = \frac{N-i}{N} \frac{i}{N} \frac{1}{1+e^{-\beta(\pi_A-\pi_B)}}$$

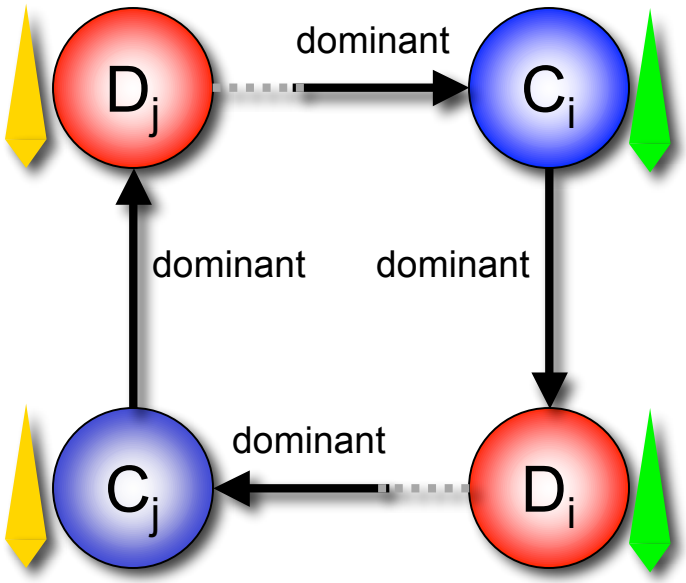
- …

Same fixation probability for weak selection

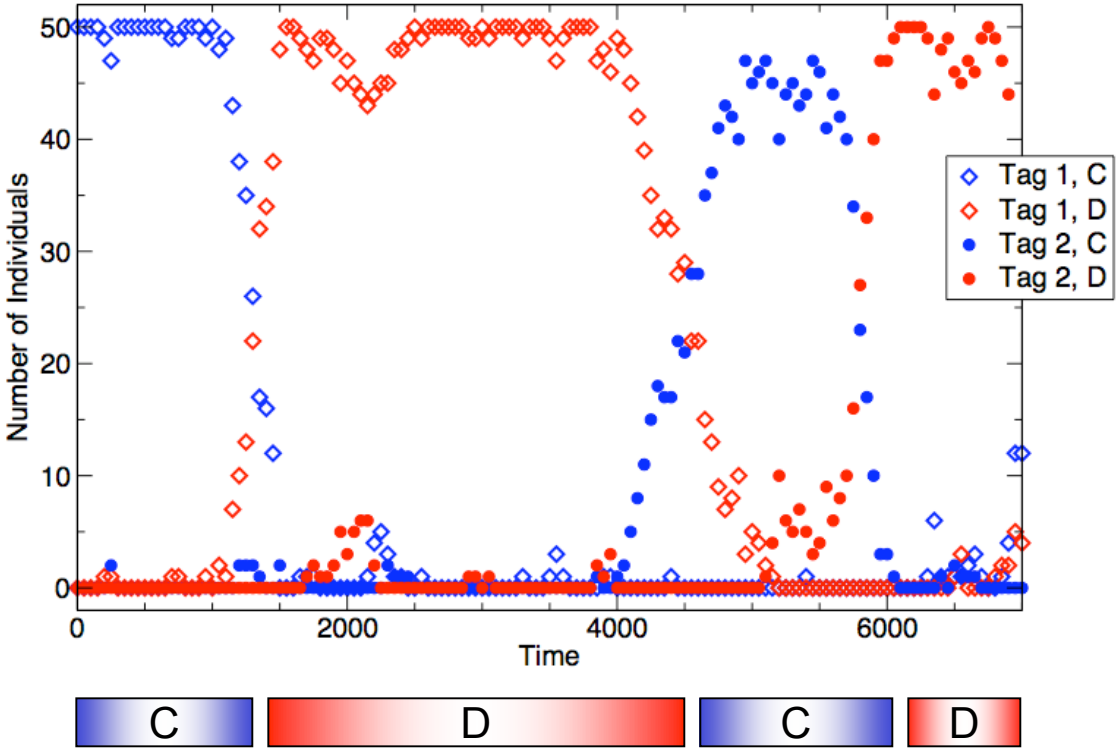
$$\phi \approx \frac{1}{N} + w \ldots$$

Nowak, Sasaki, Taylor & Fudenberg, Nature 428:646 (2004); Blume, Games and Econ. Behav. 5:387 (1993); Traulsen, Pacheco & Nowak, PRE 74:021905 (2006)

Simulation

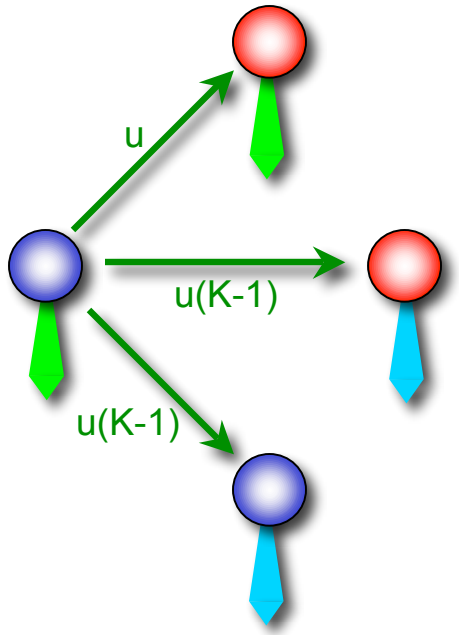


"Tides of cooperation"

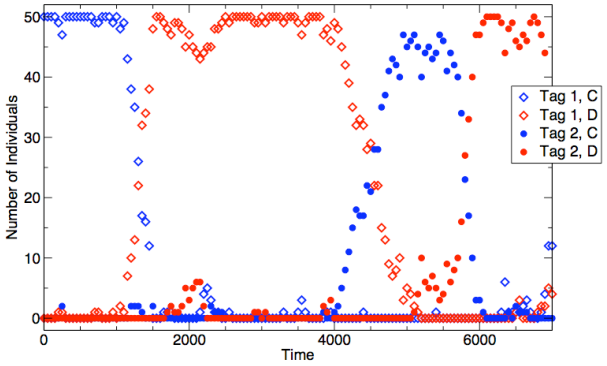


When are the tides on the cooperator side?

	C_1	D_1	C_2	D_2	.....	C_K	D_K
C_1	b-c	-c	0	0	.....	0	0
D_1	b	0	0	0	.....	0	0
C_2	0	0	b-c	-c	.....	0	0
D_2	0	0	b	0	.....	0	0
⋮	⋮	⋮	⋮	⋮	⋱	⋮	⋮
C_K	0	0	0	0	.....	b-c	-c
D_K	0	0	0	0	.....	b	0



- Small mutation rate u<<1



A condition for cooperation

- Calculate fixation probabilities

$$\phi_{A\to B} = \left(\sum_{i=0}^{N-1} \prod_{j=1}^{i} \frac{T^-(j)}{T^+(j)} \right)^{-1}$$

- Assume weak selection

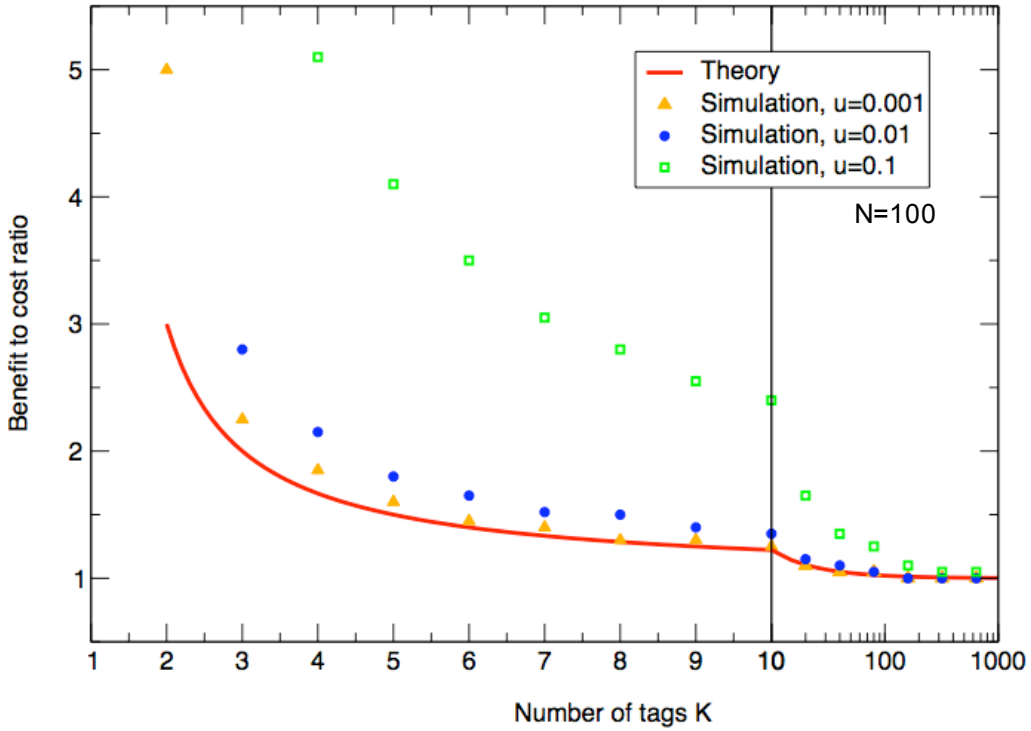
- Stationary distribution

$$P_C \approx \frac{1}{2} + Nw\left(b - c - \frac{b+c}{K}\right)$$

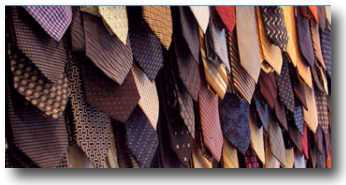
$$\frac{b}{c} > \frac{K+1}{K-1}$$

Wild & Traulsen, JTB 247:382 (2007)

Dominance of cooperators

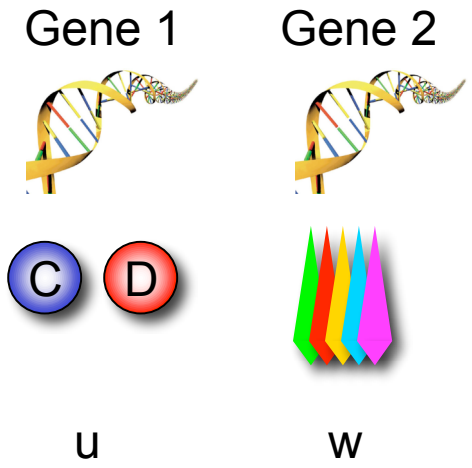


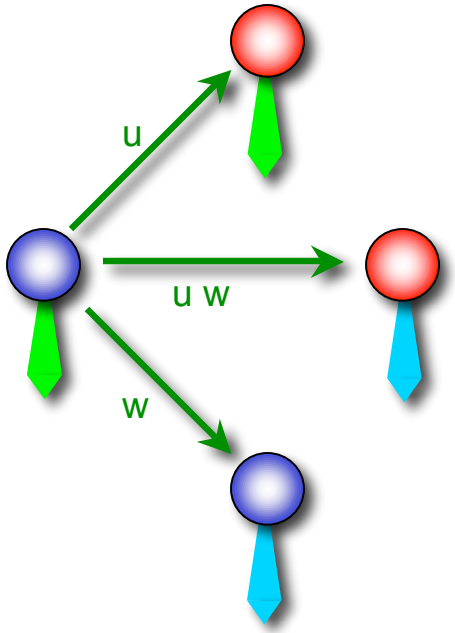
$$\frac{b}{c} > \frac{K+1}{K-1}$$



Traulsen & Nowak, PLoS One 3:e270 (2007).

Independent genes

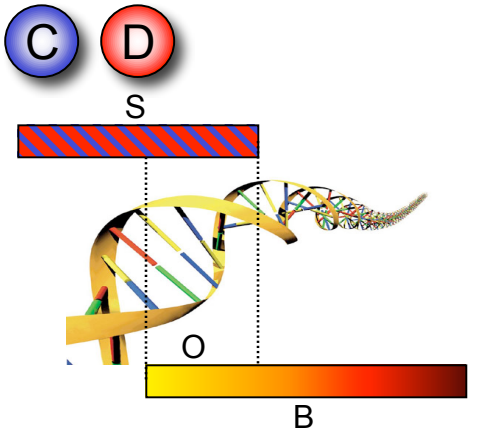




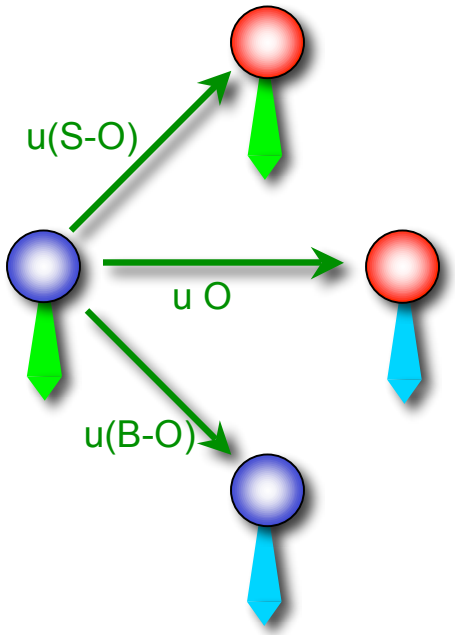
$$\frac{b}{c} > \frac{2}{w} \to \infty$$

Pleiotropic genes

Strategy



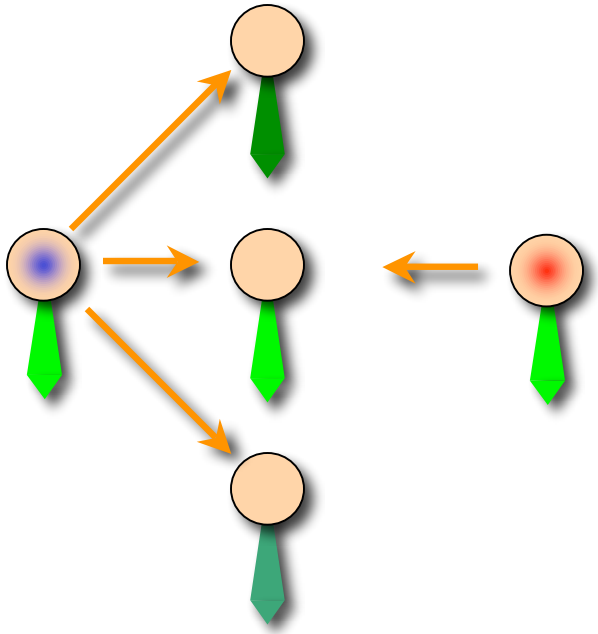
Beard color



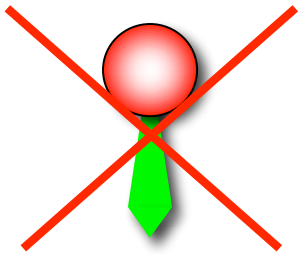
$$\frac{b}{c} > \frac{2S}{O} - 1$$

Comparison to system of Riolo et al.

- Continuous beards
- Tolerance towards others

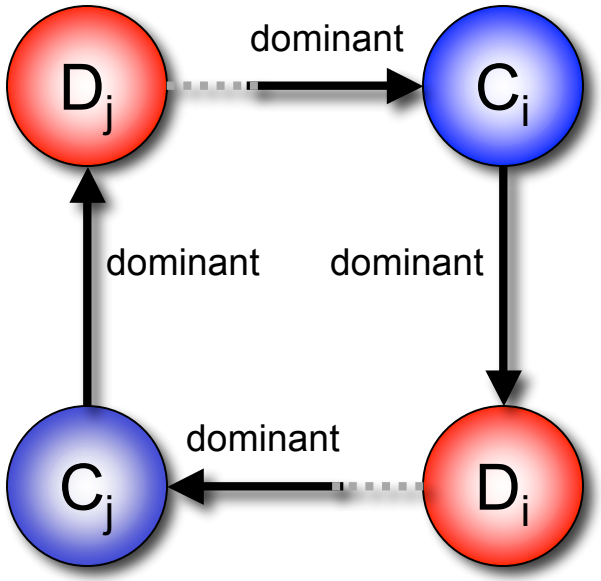


- No cheaters



Riolo, Cohen & Axelrod, Nature 414:441 (2001); Traulsen & Schuster, PRE 68:046129 (2003)

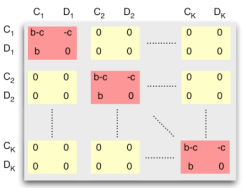
Summary: Mutation rates determine outcome



- **Single-gene:** greenbeard corresponds to “cooperation without defectors”

- **Two genes:** Cooperators can only dominate if genes for strategy and beard are linked

- **Strategy model:** Cooperation based on beards is likely



Acknowledgements

- Collaborators
  - Martin A. Nowak (Harvard)
  - ...many others

- Financial Support
  - Deutsche Akademie der Naturforscher Leopoldina (Halle/Saale)
  - Program for Evolutionary Dynamics, Harvard
  - MPI for Evolutionary Biology, Plön

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