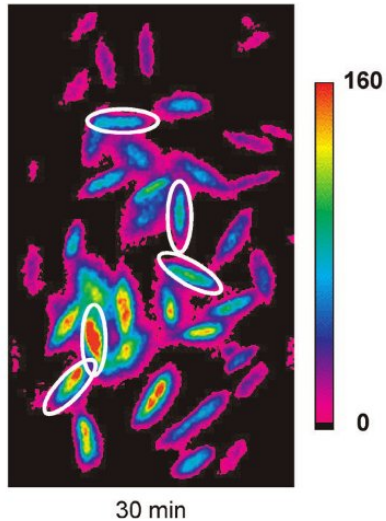


Group size evolution and the emergence of sociality

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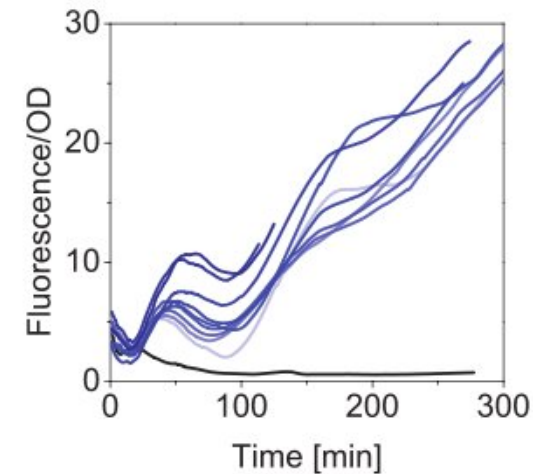
Sociality in microbes



Bacteria: extracellular nutrient scavenging

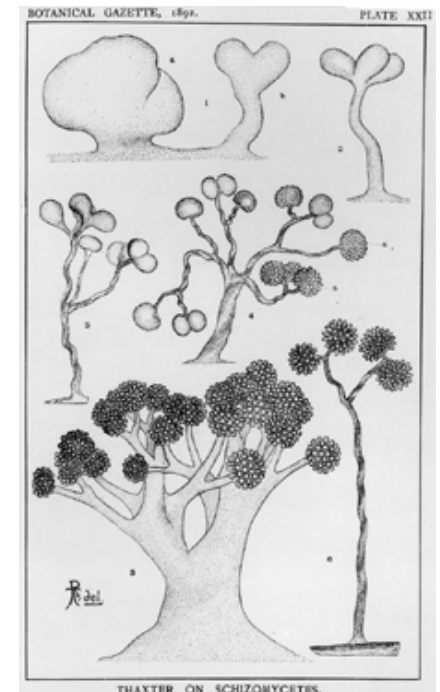
Diatoms: 'collective suicide'

Dyctyostelium and Myxobacteria: multicellular life stage



Common features

- ➡ existence of a subpopulation of public good producers or cooperators
- ➡ regulation of cell density or colony size



Group size and the evolution of cooperation

Most models consider that social groups have a fixed size.

The average fitness of cooperators can be modulated by:

- kinship

- green beards

- assortative mating

- spatial extension/metapopulations

- duration of the interaction or of the public good

- ...

In general, cooperation evolves in small groups.

Group size dynamics and evolution

Some models for the evolution of cooperation have dynamically varying group sizes as a consequence of:

demography (Hauert et al. 2006)

facultative participation (Hauert et al. 2002)

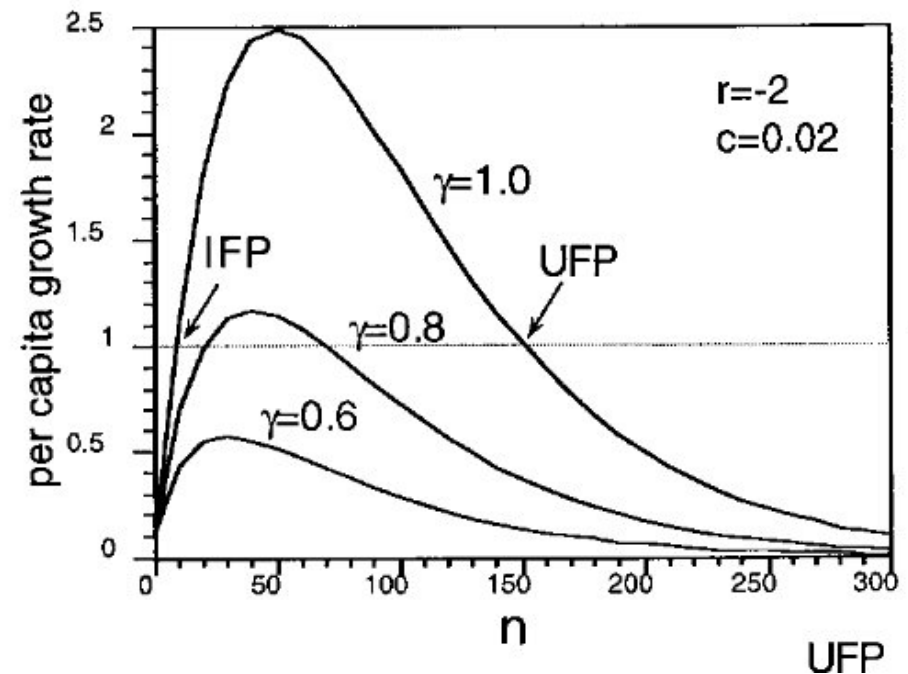
time-dependent forcing (Chuang et al. 2008)

Models for group size evolution

based on a priori assumptions on nonlinear group size effect on fitness

(Aviles 1999, 2002, van Veelen et al. 2010)

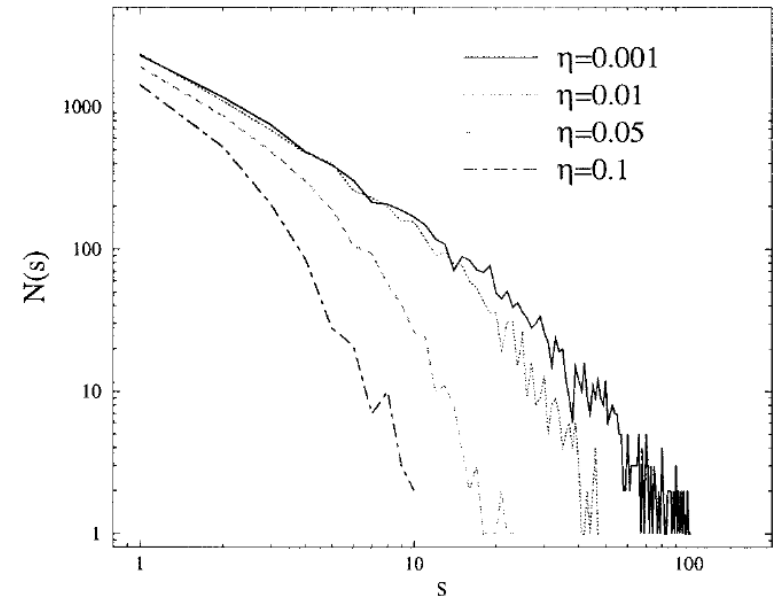
⇒ explicit aggregation process



Aggregation

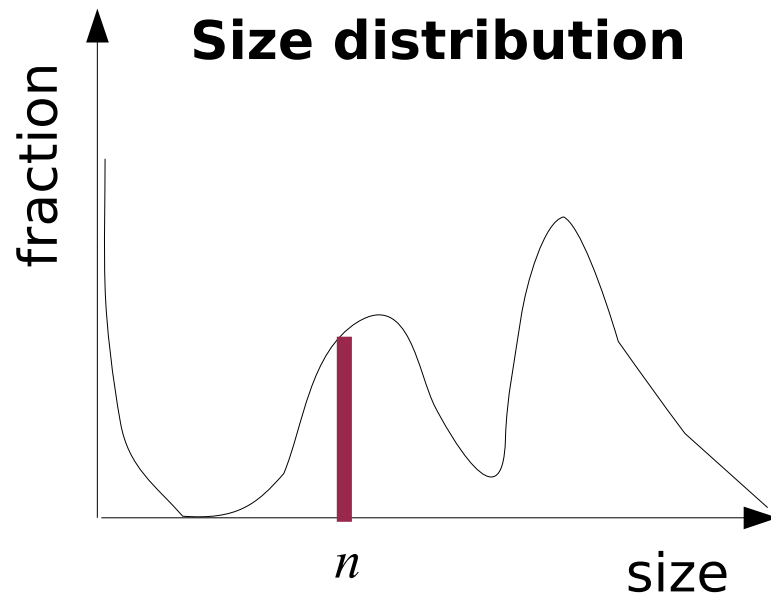


exemple



Random group formation
by attachment leads to
scale-free size distributions
(Bonabeau et al., 1999)

Aggregation + evolution



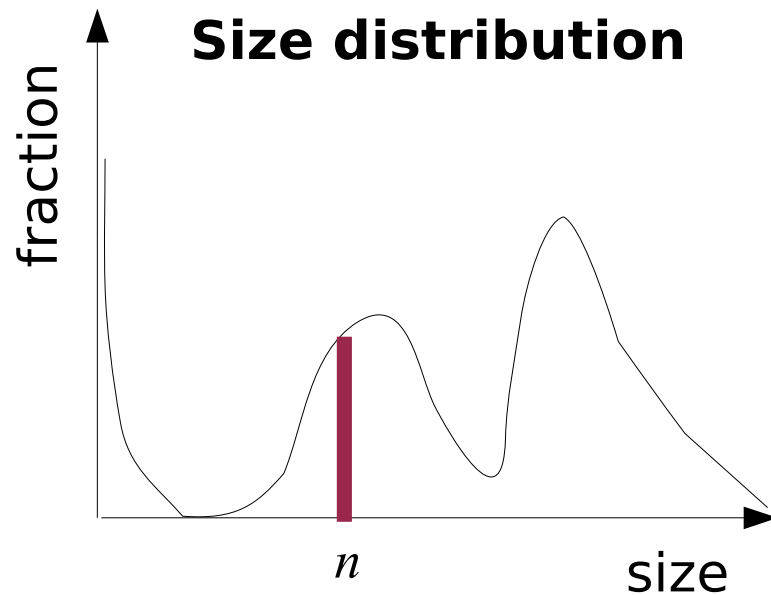
Replicator equations for a social game

Public goods game

payoff of a social player in a group of n players, m of which are social

$$P_s(n, m) = b \frac{m}{n} - c$$

Aggregation + evolution



Replicator equations for a social game

Public goods game

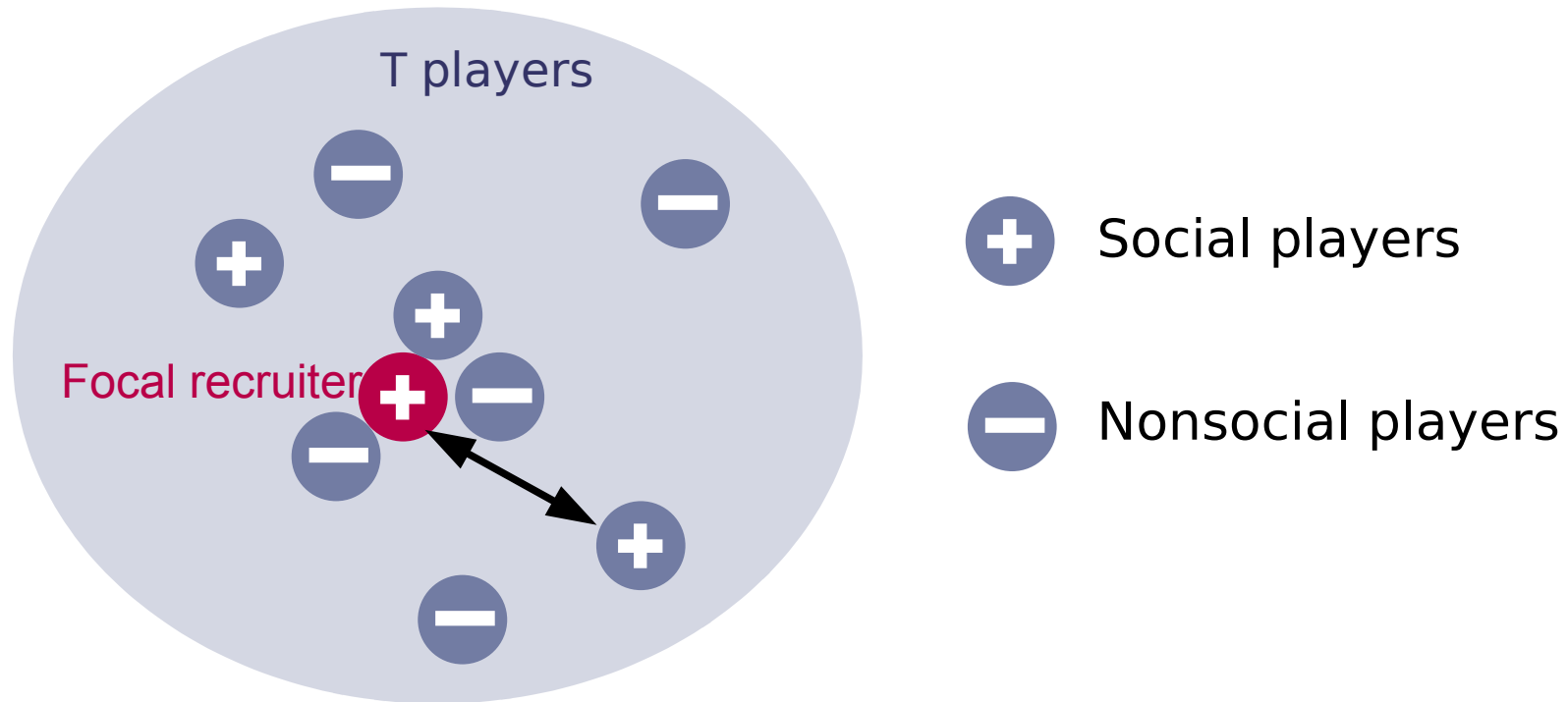
payoff of a social player in a group of n players, m of which are social

$$P_s(n, m) = b \frac{m}{n} - c$$

What is the role of group size inhomogeneities?

How can the aggregation process affect the evolution of sociality?

Aggregation by differential attachment



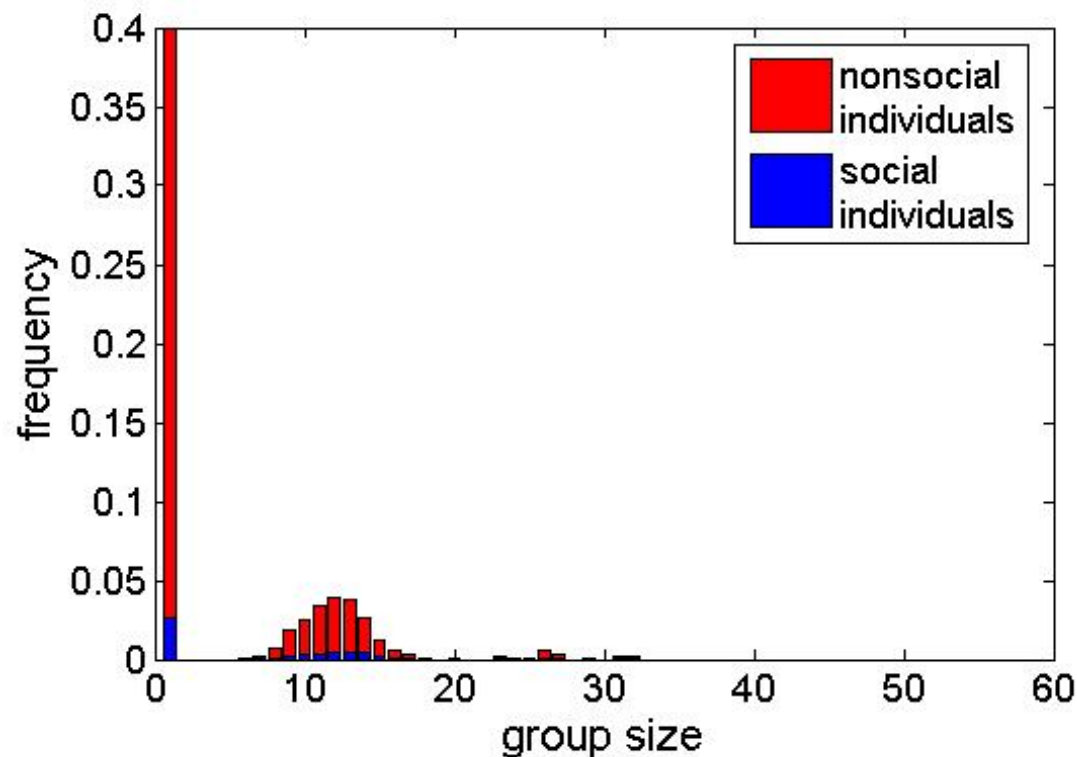
Aggregation rules

Social players have higher attachment probability than nonsocial ones ($p^+ > p^-$), and they pay a cost c .

The focal recruiter has the opportunity of meeting T other players in the aggregation stage, and it remains bound to them with a probability depending on p^+ and p^- .

Evolution of frequencies

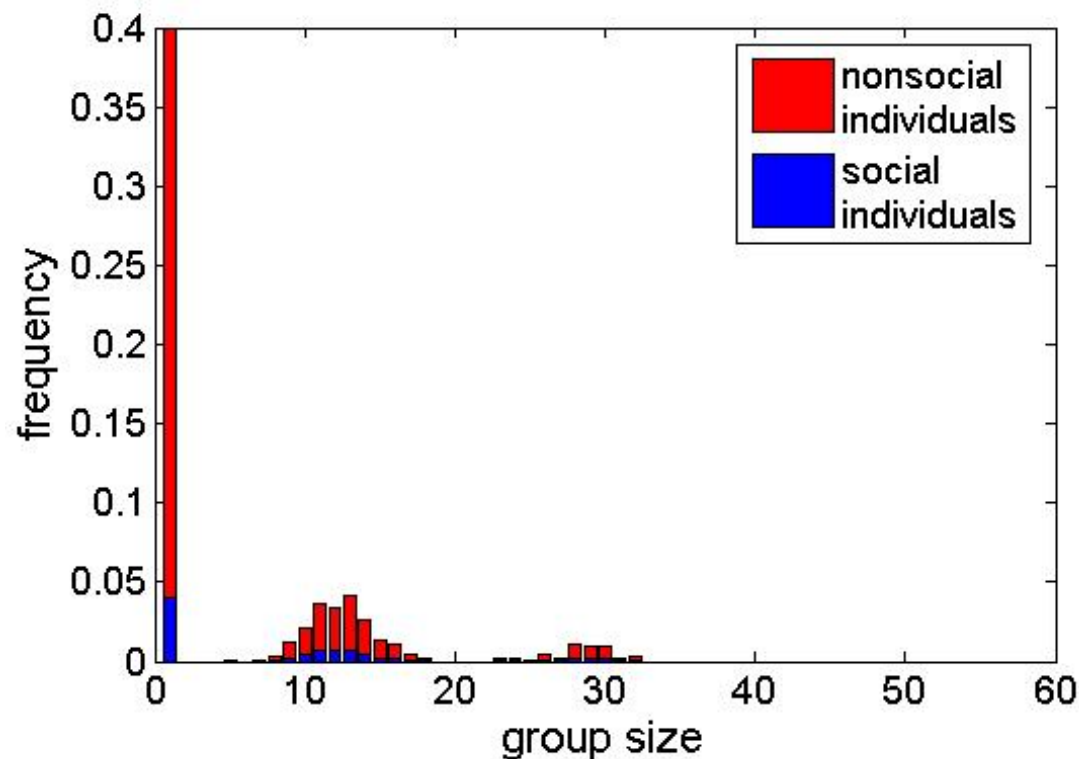
A one-round public goods game is played within each group, and all individuals reproduce according to their payoff.



As a consequence, the group size distribution evolves with time.

Evolution of frequencies

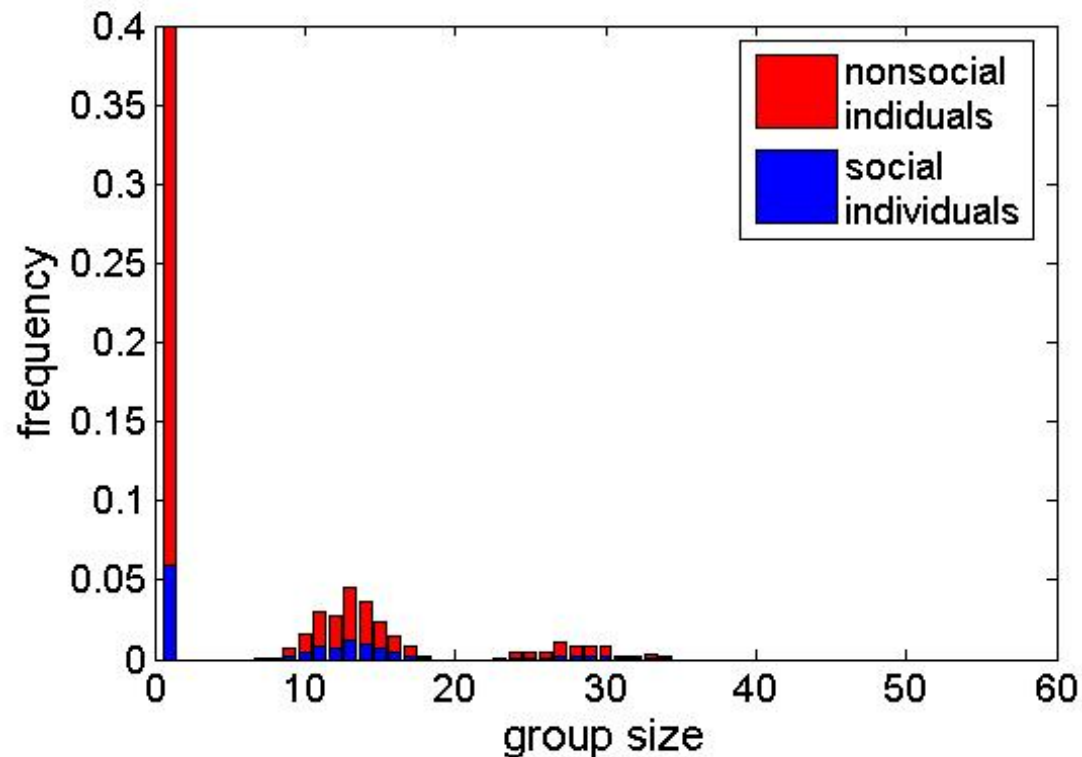
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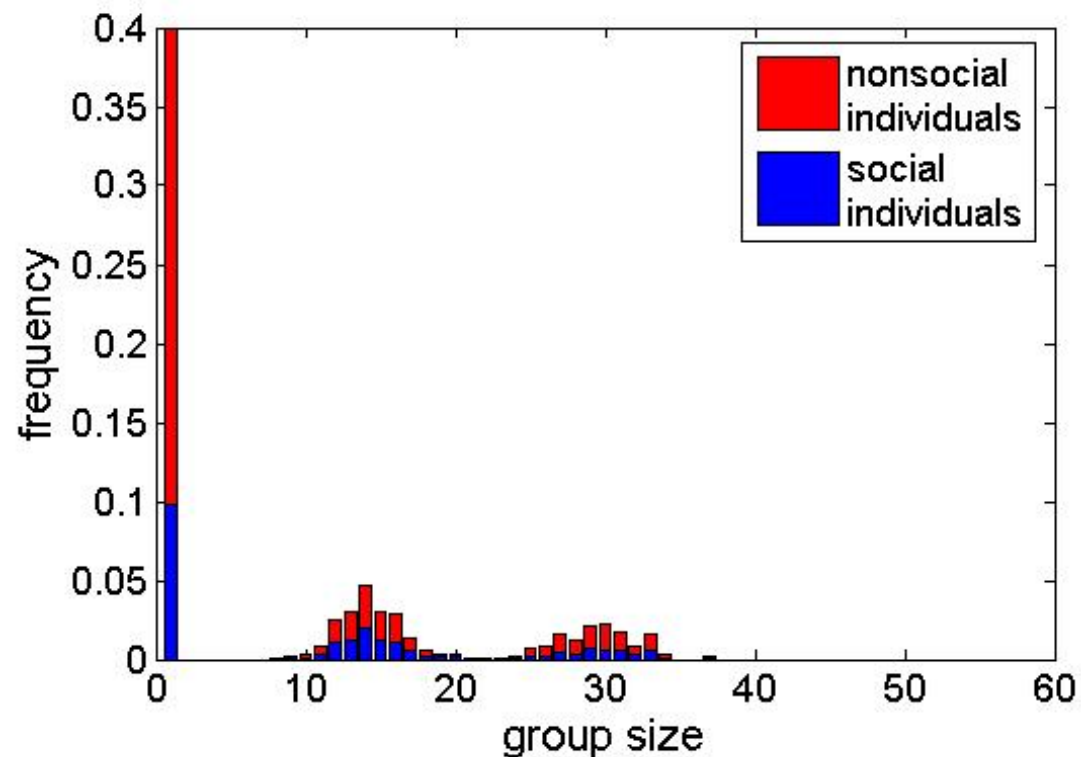
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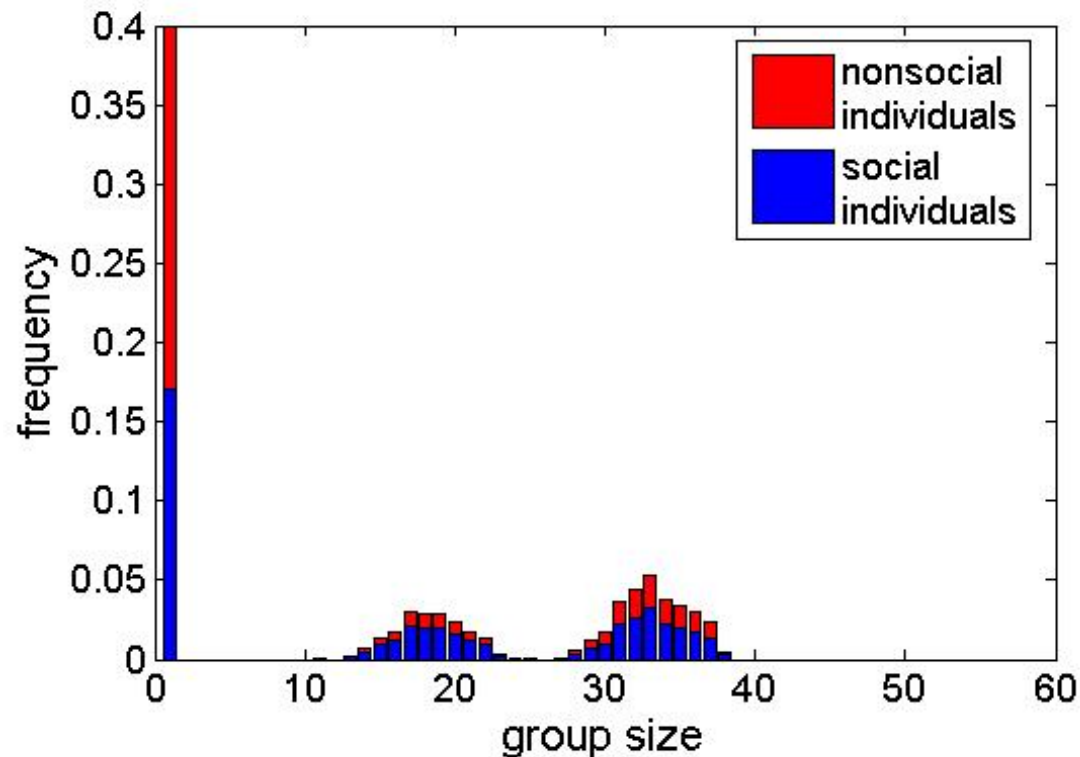
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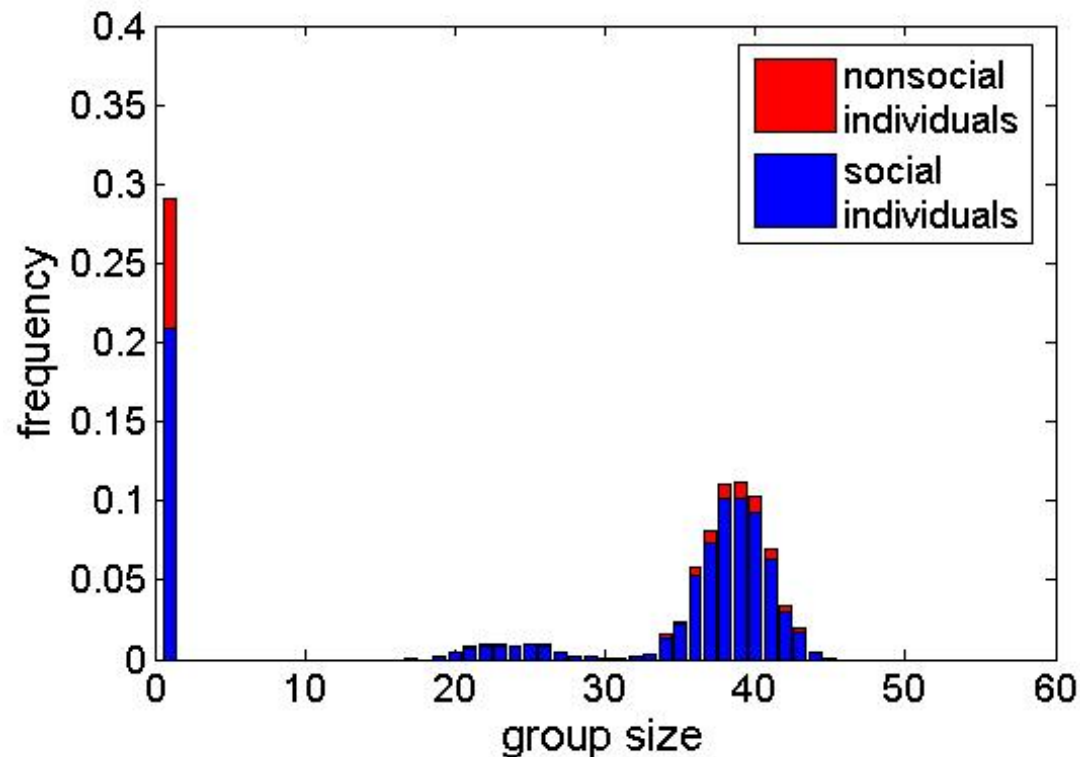
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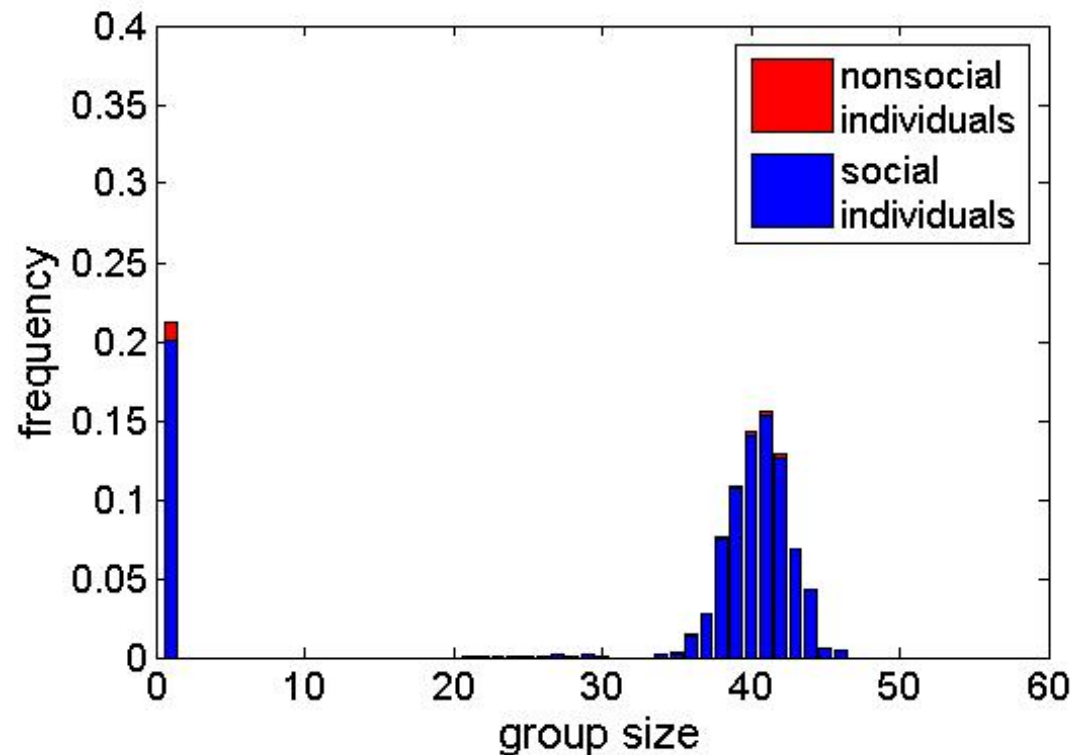
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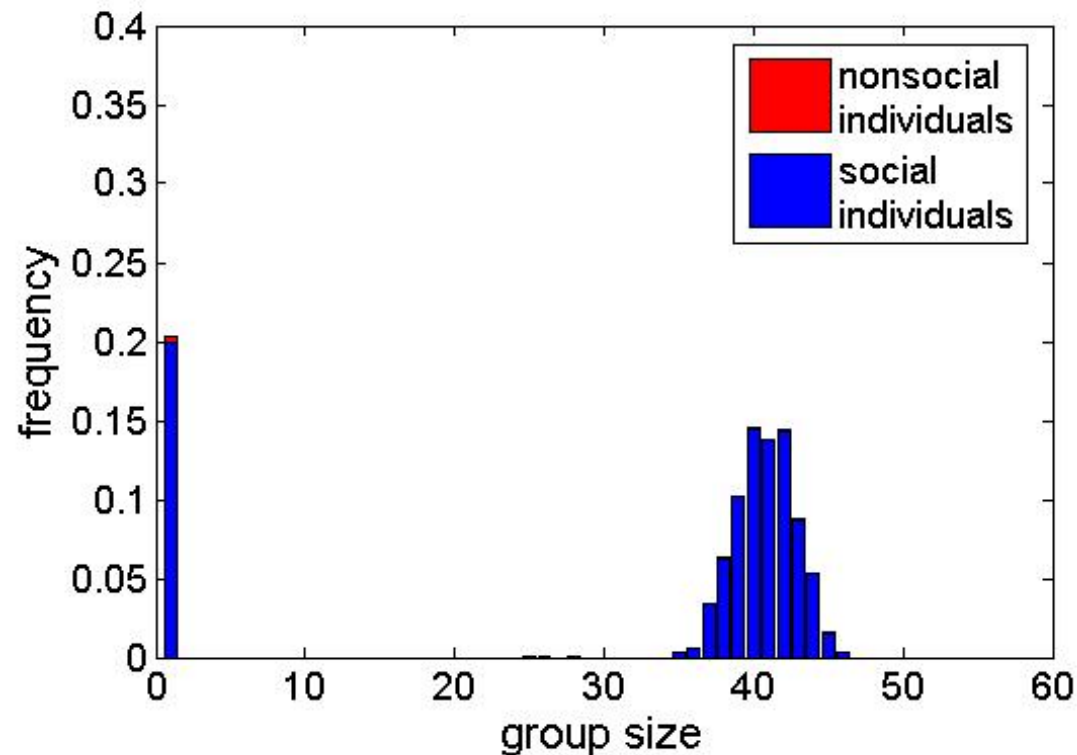
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Evolution of frequencies

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As a consequence, the group size distribution evolves with time.

Evolutionary consequences of group size distribution in public goods games

Payoff difference between social (cooperators) and nonsocial (defectors)

$$\Delta P(x) = \sum_{n=2}^{+\infty} \frac{b}{n} \left[(n-1) \frac{(d_s - d_{ns})x}{(d_s - d_{ns})x + d_{ns}} + 1 \right] d_s - c$$


$$d_s = d_s(n, x)$$

Distribution of group sizes that a social individual encounters

$$d_{ns} = d_{ns}(n, x)$$

Distribution of group sizes that a nonsocial individual encounters

Evolutionary consequences of group size distribution in public goods games

Payoff difference between social (cooperators) and nonsocial (defectors)

$$\Delta P(x) = \sum_{n=2}^{+\infty} \frac{b}{n} \left[\underbrace{(n-1) \frac{(d_s - d_{ns})x}{(d_s - d_{ns})x + d_{ns}} + 1}_{\text{benefit term depending on the distributions and nonvanishing for large group sizes}} \right] d_s - c$$

benefit term depending on the distributions and nonvanishing for large group sizes

Evolutionary consequences of group size distribution in public goods games

Payoff difference between social (cooperators) and nonsocial (defectors)

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Condition for the evolution of sociality $\Delta P(x) > 0$

$$\frac{b}{c} > \frac{1}{\sum_{n=2}^{+\infty} \left[\frac{n-1}{n} \frac{(d_s - d_{ns}) x}{(d_s - d_{ns}) x + d_{ns}} + \frac{1}{n} \right] d_s}$$

Evolutionary consequences of group size distribution in public goods games

Payoff difference between social (cooperators) and nonsocial (defectors)

$$\Delta P(x) = \sum_{n=2}^{+\infty} \frac{b}{n} \left[(n-1) \frac{(d_s - d_{ns})x}{(d_s - d_{ns})x + d_{ns}} + 1 \right] d_s - c$$

Simpson's paradox:

- ⇒ Within any group, the payoff difference between social and asocial players is -c.
- ⇒ When averaged over the population, with groups of different size and composition, this payoff difference can be positive.

Special cases

Only one size class is present in the population

$$d_s = d_{ns} = \begin{cases} 1 & \text{if } n = N \\ 0 & \text{otherwise} \end{cases}$$

$$\Delta P(x) = \frac{b}{N} - c$$

Condition for cooperation to evolve:

$$b > N c$$

Special cases

Nonsocial individuals are excluded (green beard)

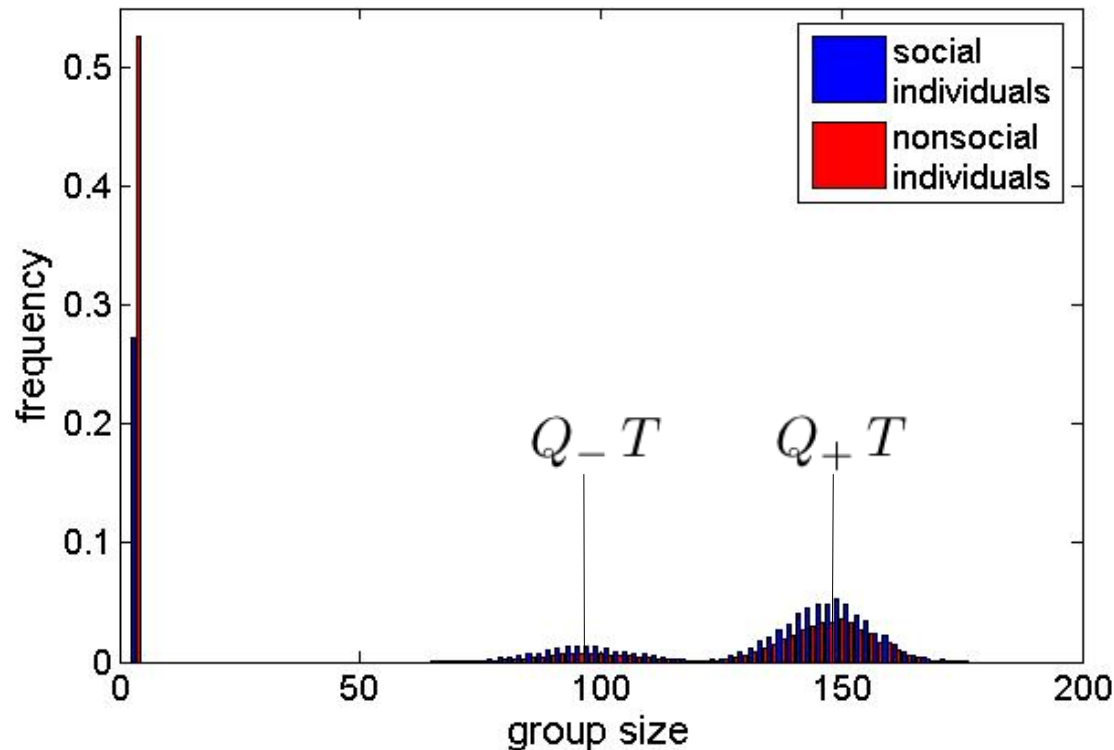
$$d_{ns} = \begin{cases} 1 & \text{if } n = 1 \\ 0 & \text{otherwise} \end{cases}$$

$$\Delta P(x) = b [1 - d_s(1, x)] - c$$

Condition for cooperation to evolve:

$$b > \frac{c}{1 - d_s(1, x)} \geq c$$

Aggregation by attachment

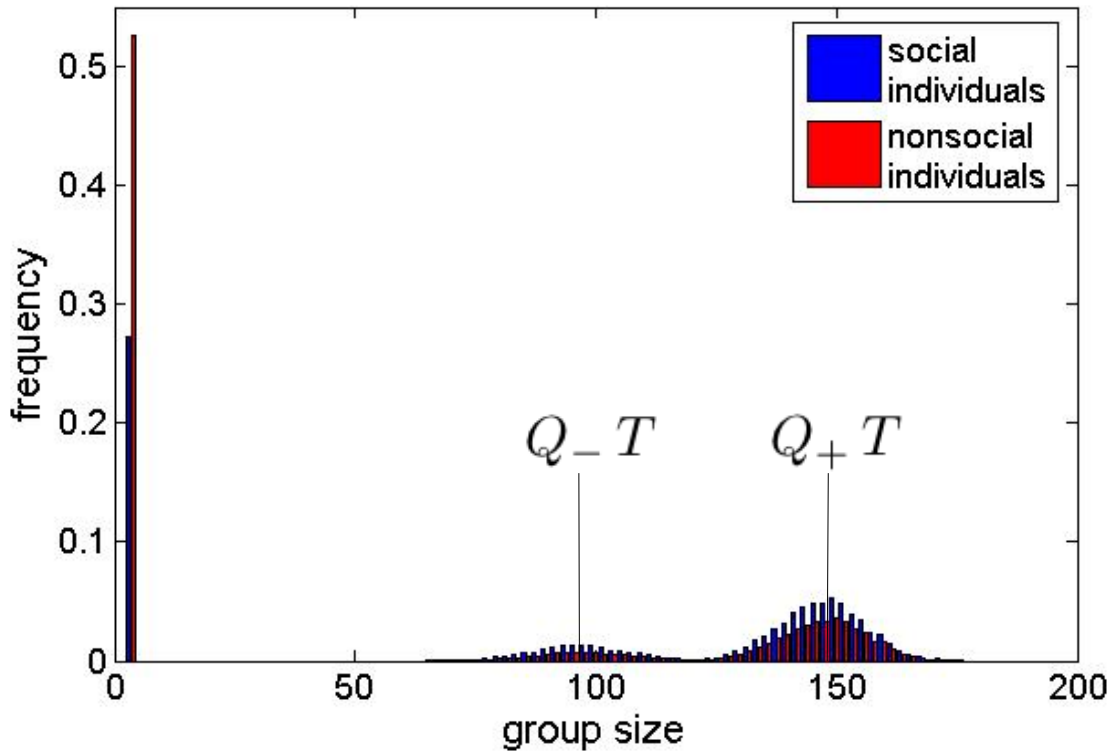


Probabilities to attach to a
social (nonsocial) recruiter

$$Q_+ = \frac{p^+ + p^-}{2} x + \frac{p^+ - p^-}{2}$$

$$Q_- = \frac{p^+ - p^-}{2} x + p^-$$

Aggregation by attachment

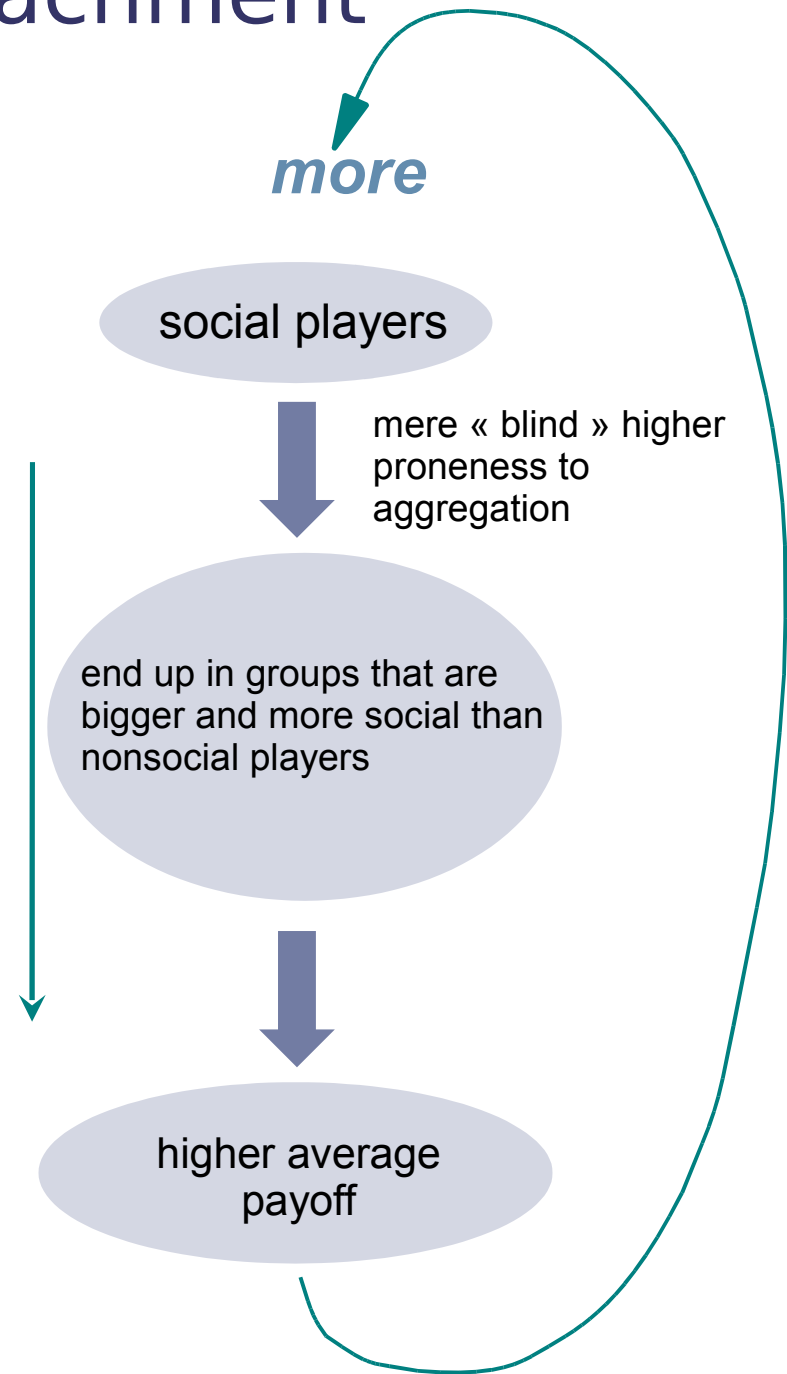


Probabilities to attach to a social (nonsocial) recruiter

$$Q_+ = \frac{p^+ + p^-}{2} x + \frac{p^+ - p^-}{2}$$

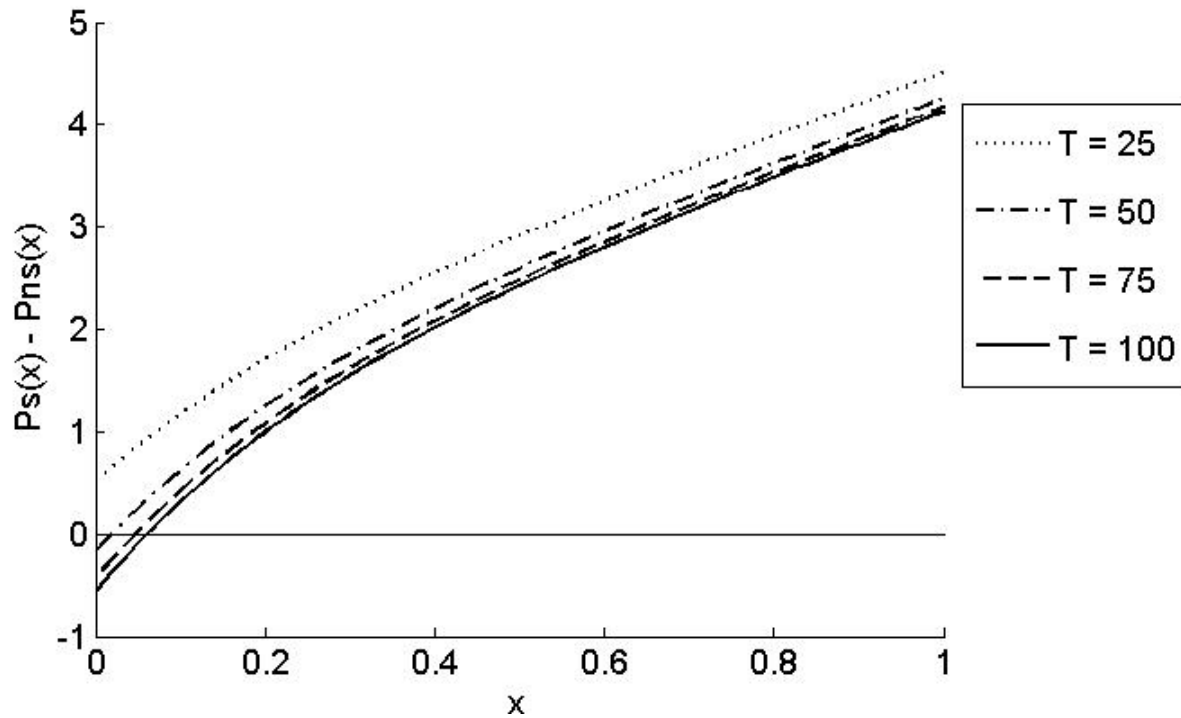
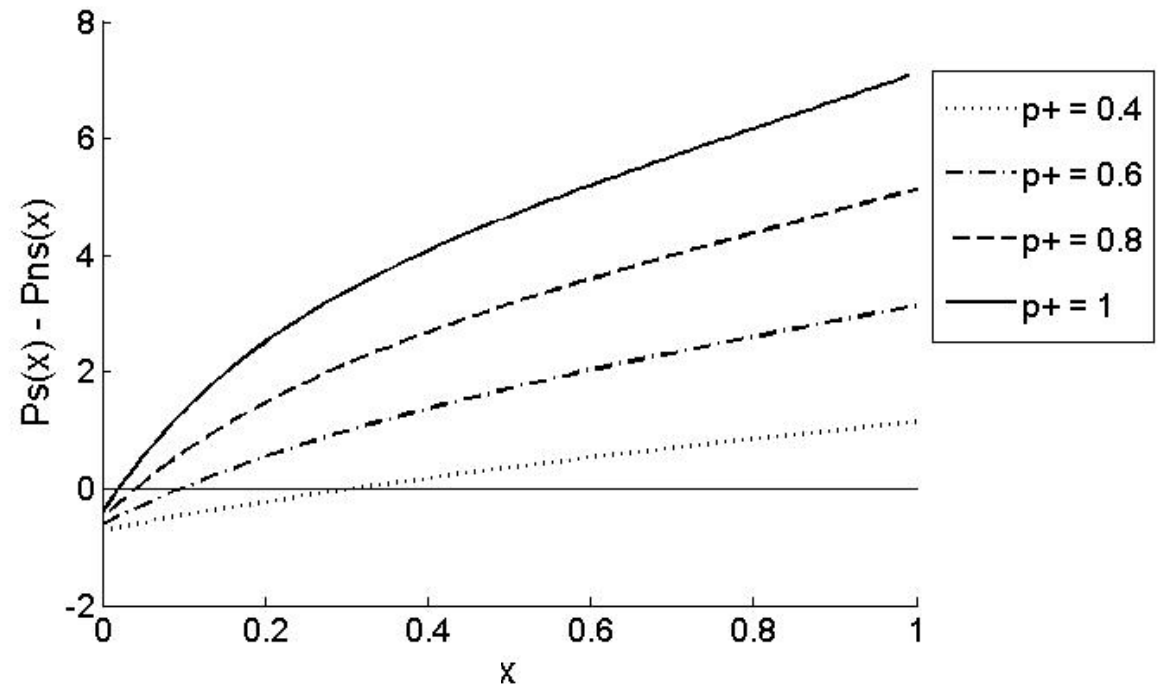
$$Q_- = \frac{p^+ - p^-}{2} x + p^-$$

increase of groups mean size



Aggregation by attachment

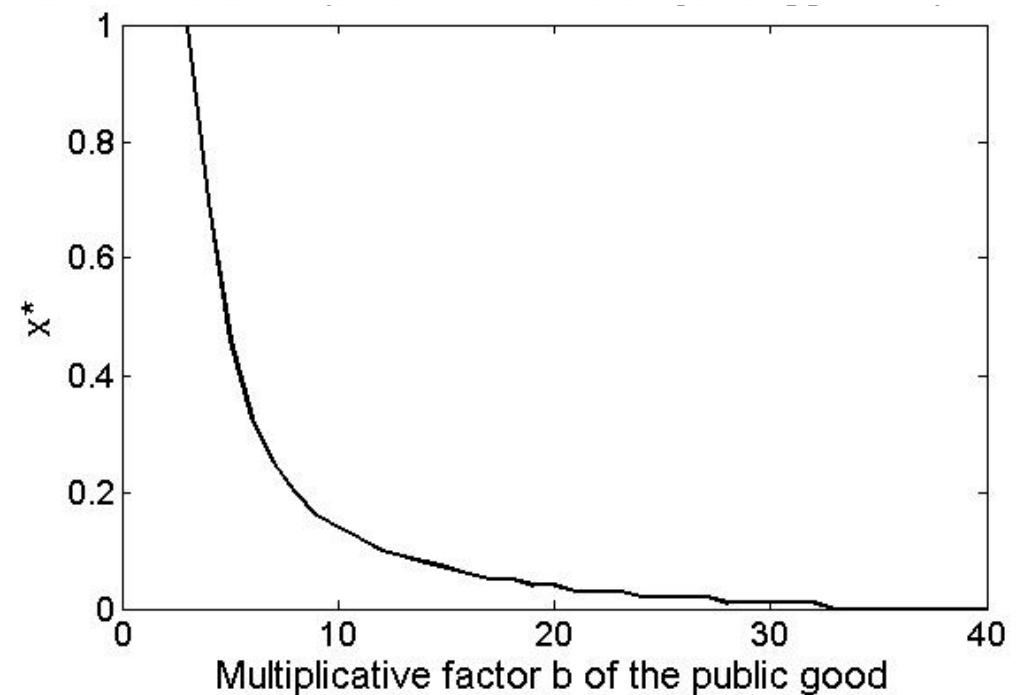
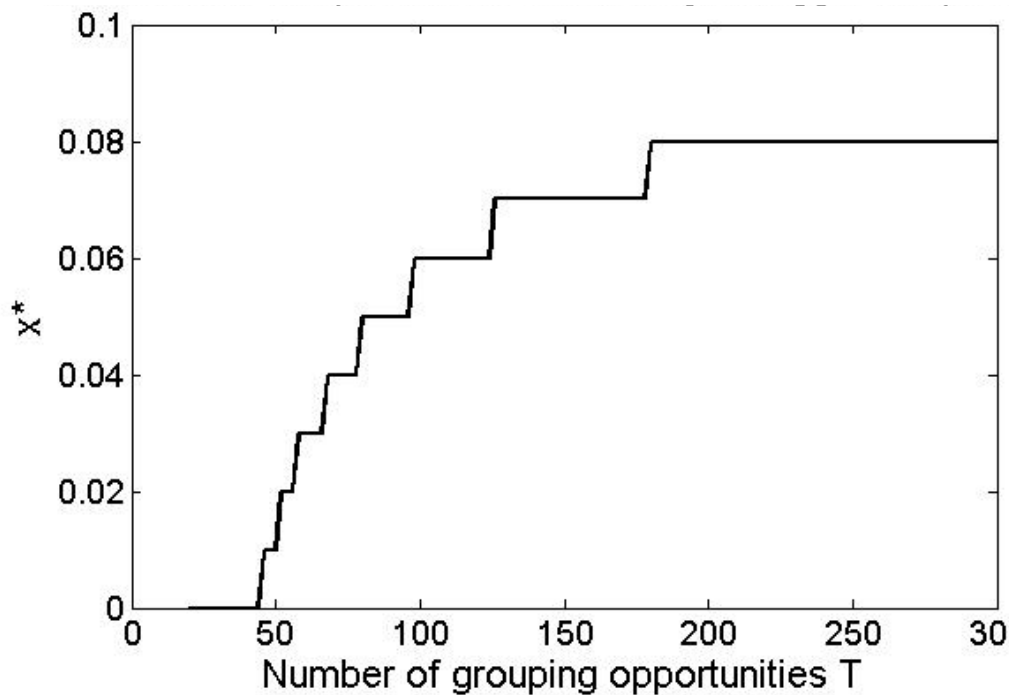
Sociality evolves more easily the larger the difference in attachment probability for social and nonsocial individuals.



The advantage of sociality is larger for smaller maximal group size

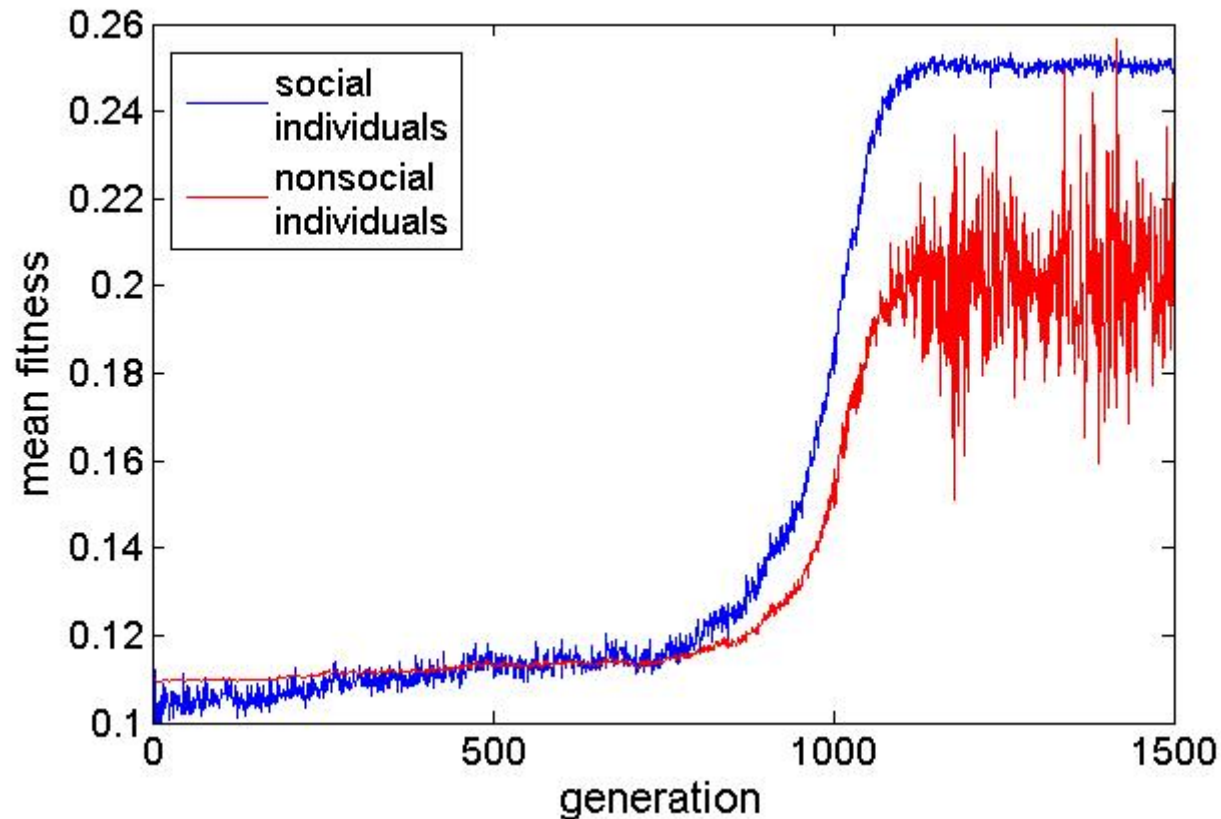
Aggregation by attachment

Cooperation can evolve if the initial fraction x^* of social individuals is above a threshold



Effect of finite-size fluctuations

In finite populations, stochastic fluctuations can lead the frequencies over the threshold and the evolution of cooperation is more likely



Conclusions

Group size inhomogeneities within a population may favour the emergence of social behaviour

In the simple case of aggregation presented here, this happens by a feedback of positive assortment onto the frequency of the social strategy via a public goods game and Darwinian selection

More complex aggregation schemes to be explored...