Group formation and the evolution of microbial 'societies'

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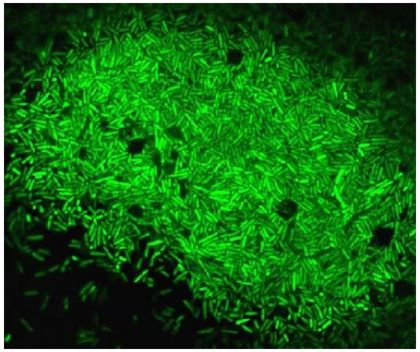
Cooperation and the Evolution of Multicellularity
KITP, January 2013

Outline

1. Cooperation in social groups
2. The evolutionary emergence of groups
3. Group formation by differential attachment
4. Group formation in space
5. Sociality and multicellularity

Sociality in microbes

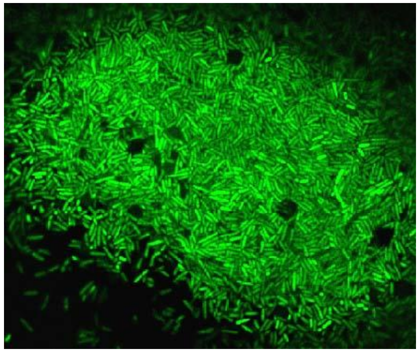
- Biofilms



http://ausubellab.mgh.harvard.edu/

Sociality in microbes

- Biofilms



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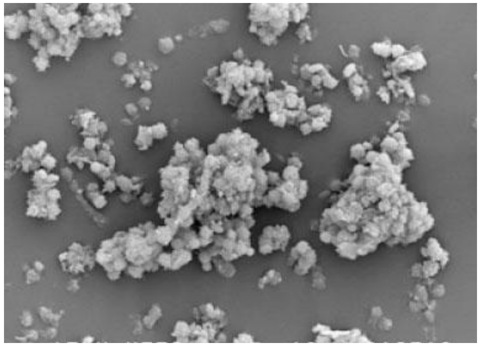
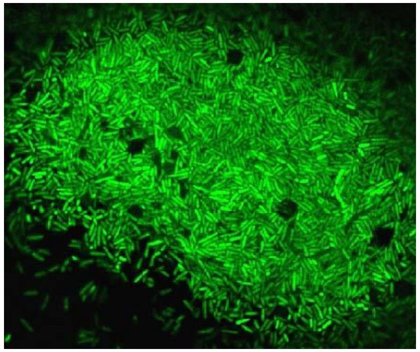
- Yeast flocculation



Smukalla & al. 2008 Cell

Sociality in microbes

- Biofilms



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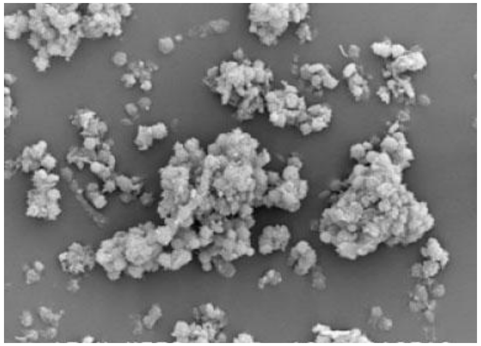
- Yeast flocculation



Smukalla & al. 2008 Cell

- 'Social' microbes: Dictyostelium and Mixobacteria

Nanjundiah & Santhe 2011 Integr Biol

Velicer & Yu 2003 Nature

Sociality

=

Being in a group

\+

Acting for the common good

(of the grooup's units)

Sociality

=

Being in a group

+

Acting for the common good
(of the group's units)

≠

Individuality at the collective level

Microbus Œconomicus

clonal reproduction
minimal cognition
Darwinian evolution

Microbus Œconomicus

clonal reproduction
minimal cognition
Darwinian evolution

How can social groups evolve?

Does group formation influence evolution?

Evolution of cooperation

“Cooperators “ versus **“cheaters”**

The tragedy of the commons

Cheaters have higher fitness

⬇

Cooperative groups are evolutionary unstable

Public Good Games

Individuals within a group have 2 possible strategies:

- Cooperators contribute to the public good at a cost c
- Cheaters do not contribute

Linear PGG: The total investment is multiplied by b and equally divided among all group members

$\Rightarrow$ Cheaters always have a higher payoff than cooperators in the same group

Public good games in equations

N	size of the group
b	contribution of cooperators to the public good
C	cost of such a contribution

Payoffs (= fitness), if k is the number of cooperators:

$$P_c = \frac{kb}{N} - c$$

$$P_d = \frac{kb}{N}$$

Tragedy of the commons: $P_d > P_c$

Public good games in equations

N	size of the group
b	contribution of cooperators to the public good
C	cost of such a contribution

Payoffs (= fitness), if k is the number of cooperators:

$$P_c = \frac{kb}{N} - c = \underbrace{\boxed{\frac{b}{N} - c}}_{\text{due to self}} + \underbrace{\boxed{\frac{(k-1)b}{N}}}_{\text{due to others}}$$

$$P_d = \frac{kb}{N}$$

Tragedy of the commons: $P_d > P_c$

The evolution of cooperation

- Kinship
- Limited dispersal
- Optional participation
- Reciprocity
- Punishment
- Green Beards
- …

SA West, AS Griffin, A Gardner, SP Diggle
Social evolution theory for microorganisms
Nature Rev Microbiology 2006

Indirect/direct fitness increase

The evolution of cooperation

- Kinship
- Limited dispersal
- Optional participation
- Reciprocity
- Punishment
- Green Beards
- ...

JA Flechter and M Doebeli
A simple and general explanation for the evolution of altruism
Proc. R. Soc. B 2009

'Interaction environment'

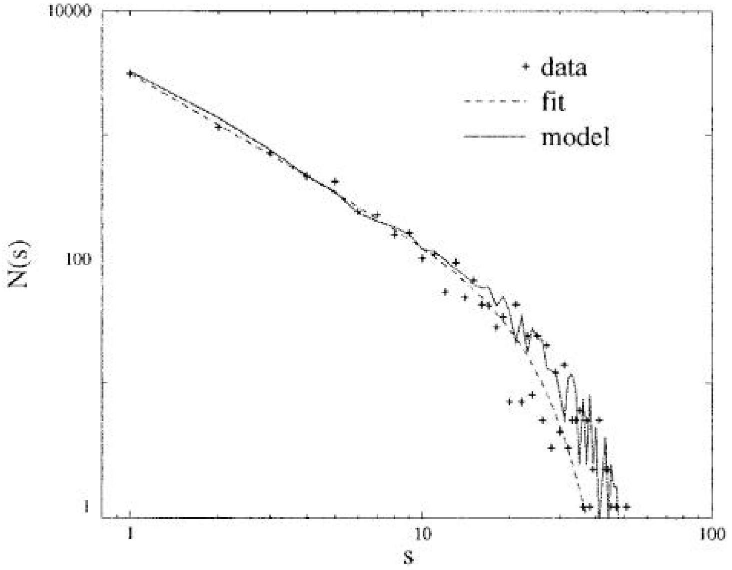
$$P_c = \frac{b}{N} - c + \frac{e_c b}{N}$$

average number e_c and e_d of cooperators met by one cooperator/defector

$$P_d = \frac{e_d b}{N}$$

⇒ Fixed group size framework

Groups of organisms



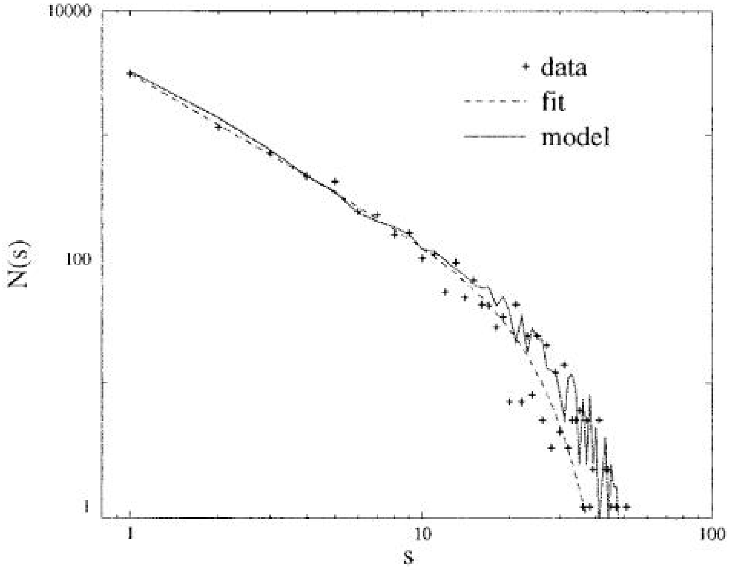
Power law group size distributions


Proc. Natl. Acad. Sci. USA
Vol. 96, pp. 4472–4477, April 1999
Ecology, Physics

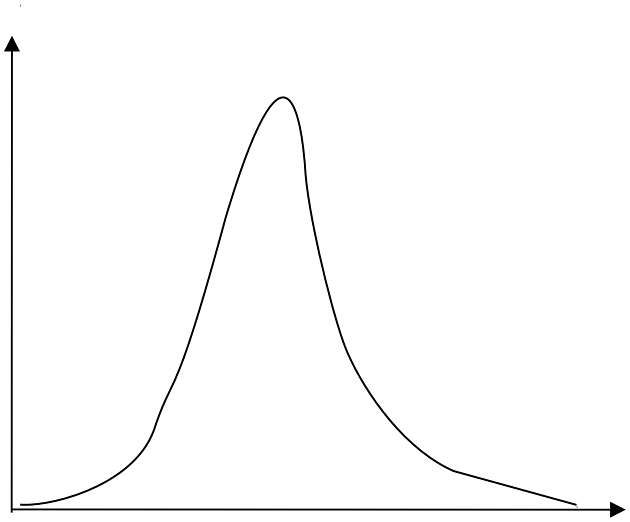
Scaling in animal group-size distributions

ERIC BONABEAU*†, LAURENT DAGORN‡, AND PIERRE FRÉON§

Groups of organisms



Power law group size distributions



'Typical' group size

Proc. Natl. Acad. Sci. USA
Vol. 96, pp. 4472–4477, April 1999
Ecology, Physics

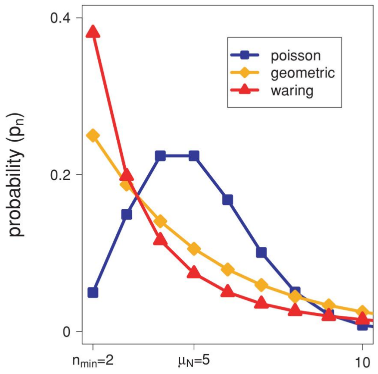
Scaling in animal group-size distributions

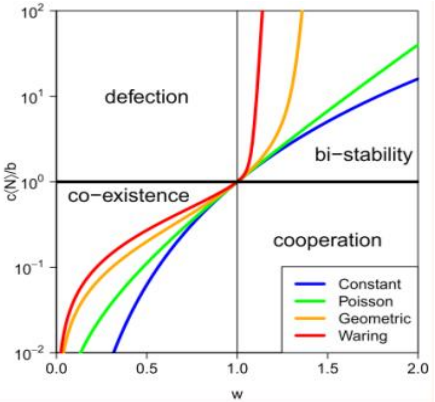
Eric Bonabeau*†, Laurent Dagorn‡, and Pierre Fréon§

Models with variable group size

GROUP-SIZE DIVERSITY IN PUBLIC GOODS GAMES

Jorge Peña EVOLUTION *2011*

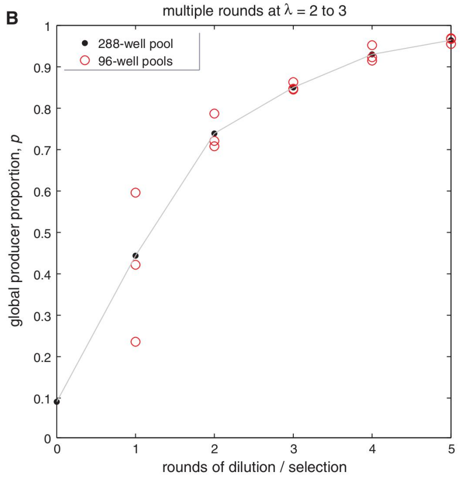




Simpson's Paradox in a Synthetic Microbial System

John S. Chuang,* Olivier Rivoire, Stanislas Leibler

9 JANUARY 2009 VOL 323 **SCIENCE**



Volunteering as Red Queen Mechanism for Cooperation in Public Goods Games

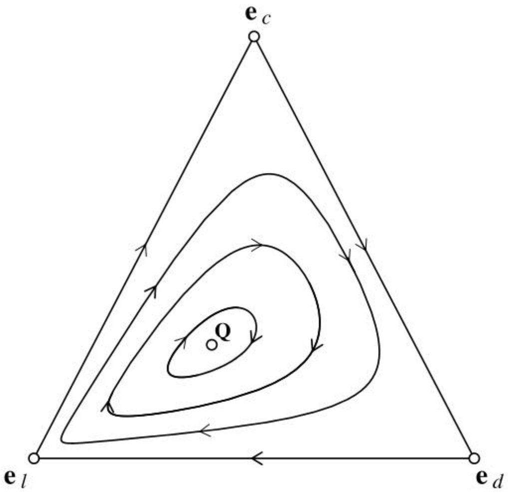
Christoph Hauert,[1,2] Silvia De Monte,[1,3] Josef Hofbauer,[1] Karl Sigmund[1,4]*

SCIENCE VOL 296 10 MAY 2002

Evolutionary games and population dynamics: maintenance of cooperation in public goods games

Christoph Hauert[1,*], Miranda Holmes[2,†] and Michael Doebeli[2]

Proc. R. Soc. B (2006) **273**, 2565–2570

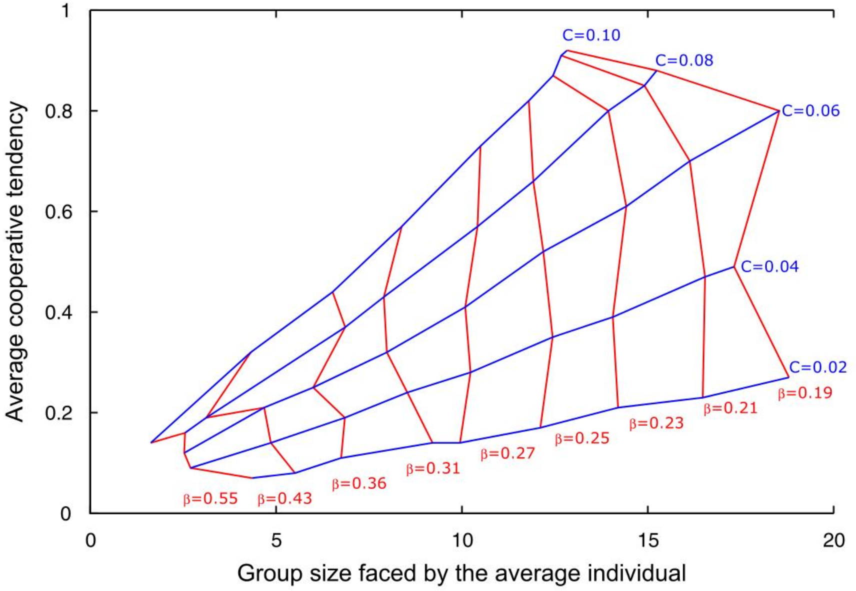


Models with evolvable group size

It takes grouping and cooperation to get sociality

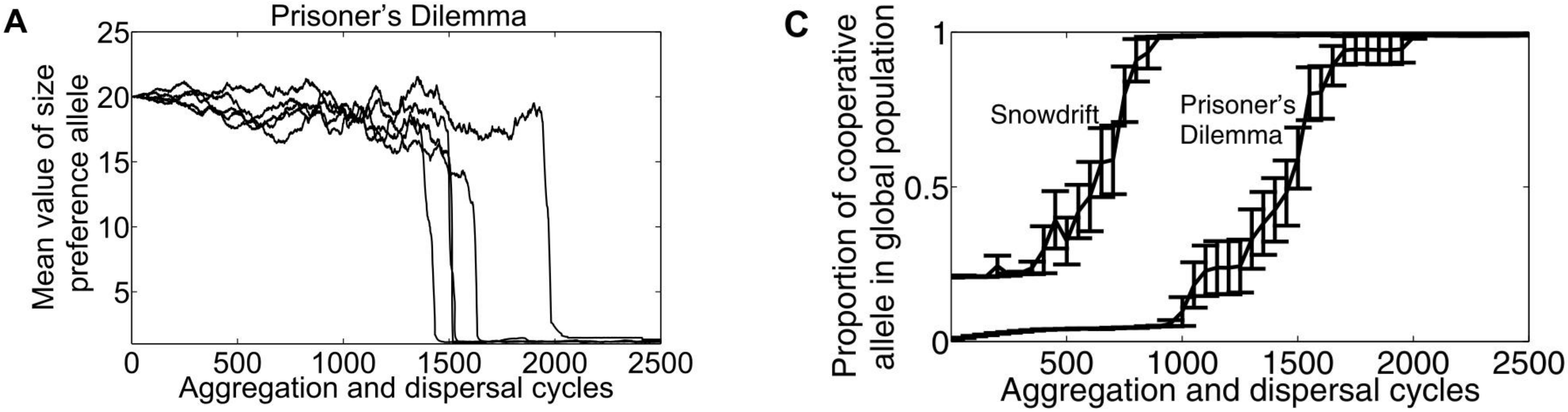
Matthijs van Veelen[a,*], Julián García[a,b], Leticia Avilés[c]

Journal of Theoretical Biology 264 (2010) 1240–1253



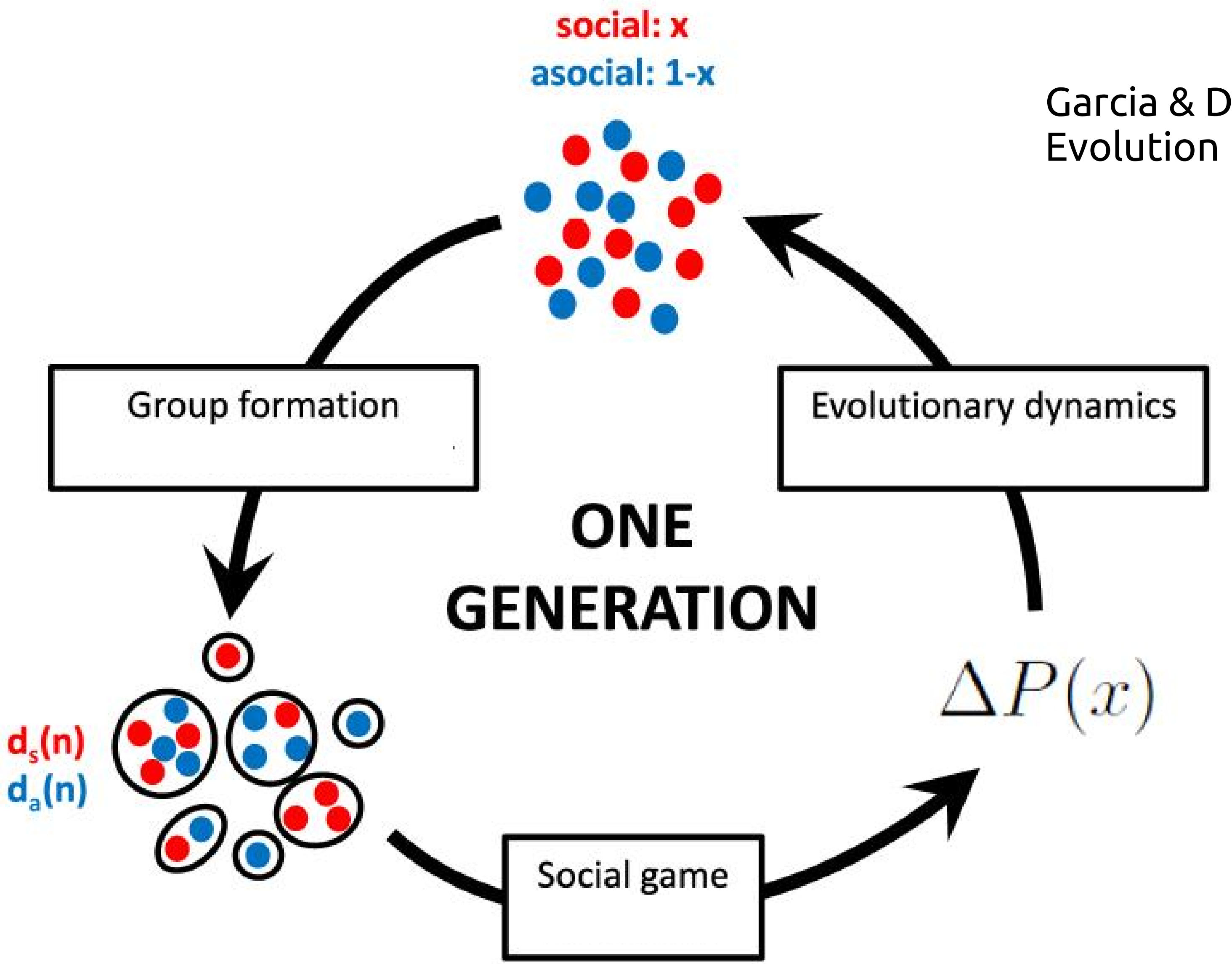
THE CONCURRENT EVOLUTION OF COOPERATION AND THE POPULATION STRUCTURES THAT SUPPORT IT

Simon T. Powers,[1,2] Alexandra S. Penn,[3] and Richard A. Watson[4] **EVOLUTION** *JUNE 2011*



Expliciting group formation in a life cycle

Garcia & De Monte
Evolution (2012)



social: x
asocial: $1-x$

Group formation

$d_s(n)$
$d_a(n)$

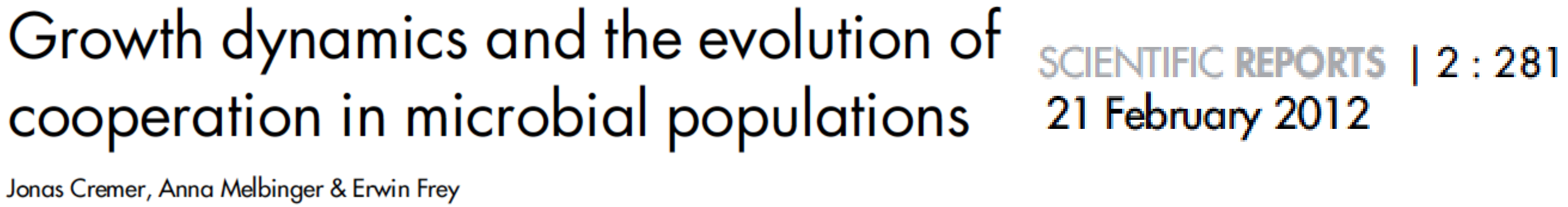
ONE
GENERATION

Social game

$\Delta P(x)$

Evolutionary dynamics

See also:



Growth dynamics and the evolution of cooperation in microbial populations

Jonas Cremer, Anna Melbinger & Erwin Frey

SCIENTIFIC REPORTS | 2 : 281
21 February 2012

Hypotheses

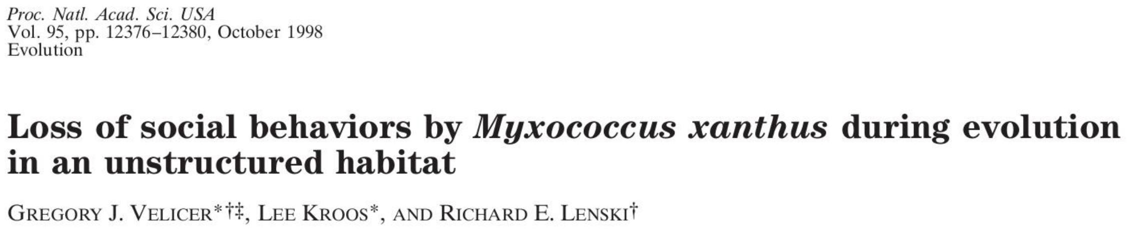
Social trait encoded by a single gene:

- Costly (reduces individual fitness)
- Increases the propensity to form groups
- Increases the coherence of the group, hence the fitness of its components

Example:

Extracellular fibrils excreted by mixobacteria increase collective gliding at a fitness cost.

Collective motility is usually associated to sociality.



Proc. Natl. Acad. Sci. USA
Vol. 95, pp. 12376–12380, October 1998
Evolution

Loss of social behaviors by *Myxococcus xanthus* during evolution in an unstructured habitat

Gregory J. Velicer[*†‡], Lee Kroos[*], and Richard E. Lenski[†]

Evolutionary dynamics

The replicator equation

$$\frac{dx}{dt} = x\,(1-x)\,\Delta P(x)$$

payoff difference = relative fitness

Evolutionary dynamics

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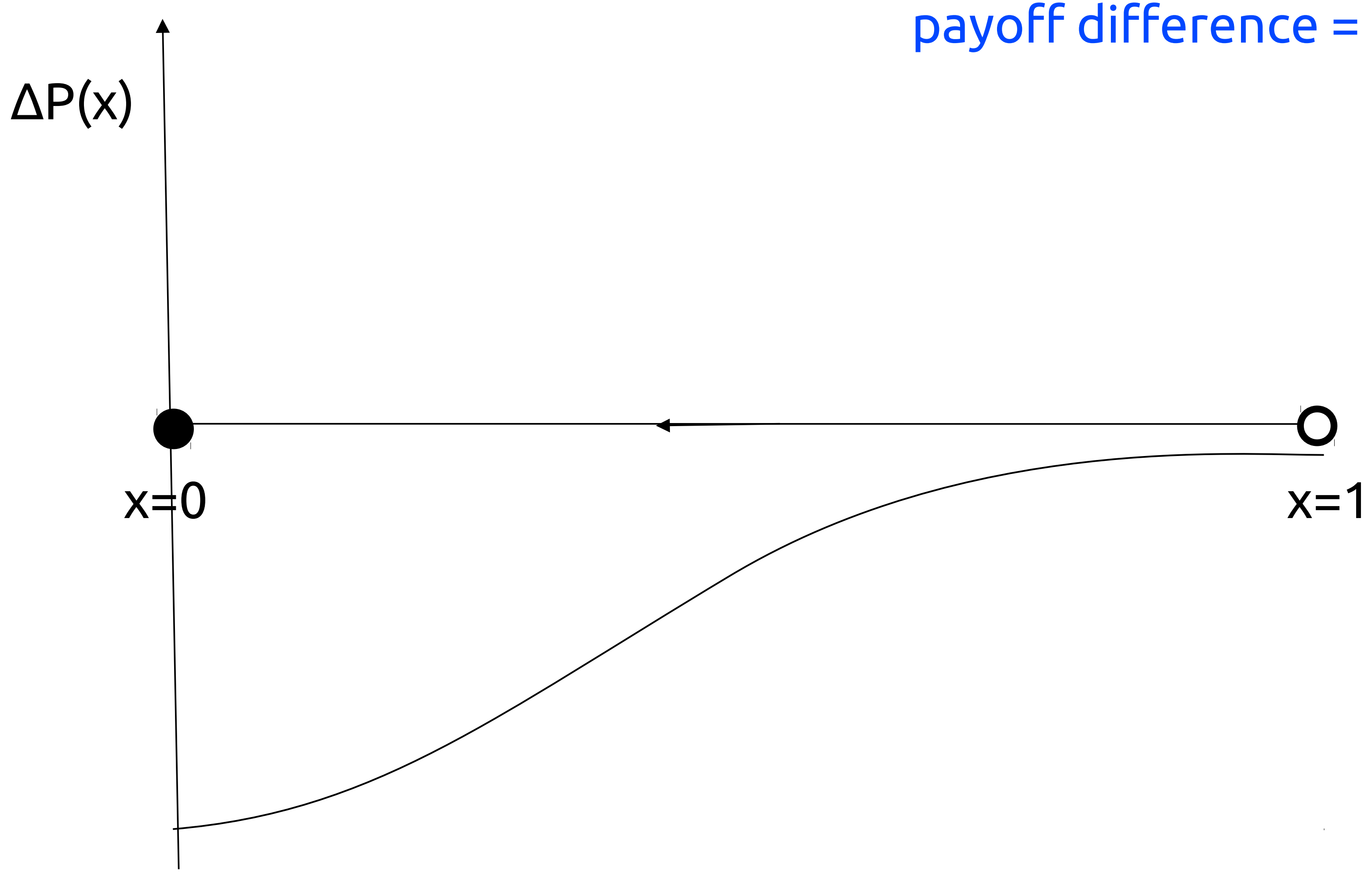

Evolutionary dynamics

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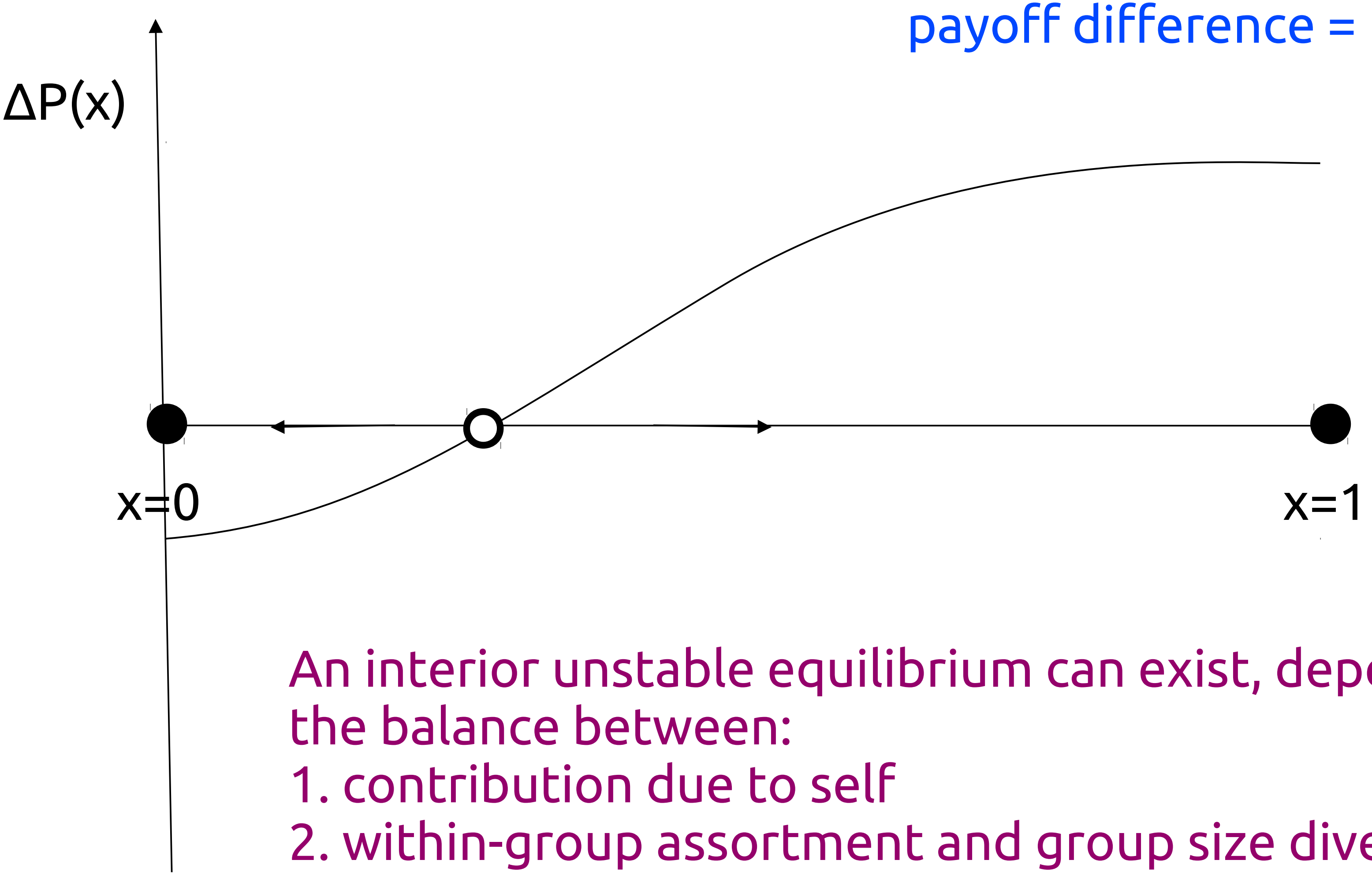


An interior unstable equilibrium can exist, depending on the balance between:

1. contribution due to self
2. within-group assortment and group size diversity

Payoffs computation

Payoffs in a group of fixed size n:

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

$$P_a(n) = \frac{e_a(n)\,b}{n}$$

Payoffs computation

Payoffs in a group of fixed size n:

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

$$P_a(n) = \frac{e_a(n)\, b}{n}$$

$$\Delta P(x) = -c + \sum_{n \geq 2} \frac{b\, d_s(n)}{n} + \sum_{n \geq 2} \frac{b}{n} \left[d_s(n) e_s(n) - d_a(n) e_a(n) \right]$$

due to self

due to the interaction environment

e_i	within-group assortment
d_i	group size diversity

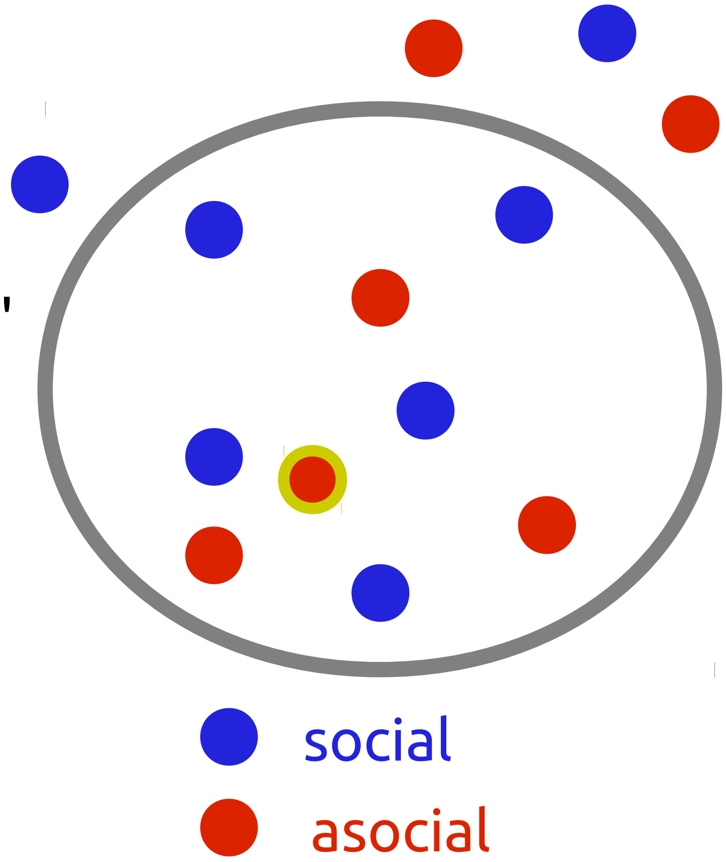
A model for group formation by differential attachment

1. T individuals are randomly chosen

2. one individual is assigned the status 'recruiter'

3. other individuals interact once with the recruiter, and stick to him with probability dependent on the strategies of recruiter and focal player :

$$\pi_{aa} \leq \pi_{as} = \pi_{sa} \leq \pi_{ss}$$



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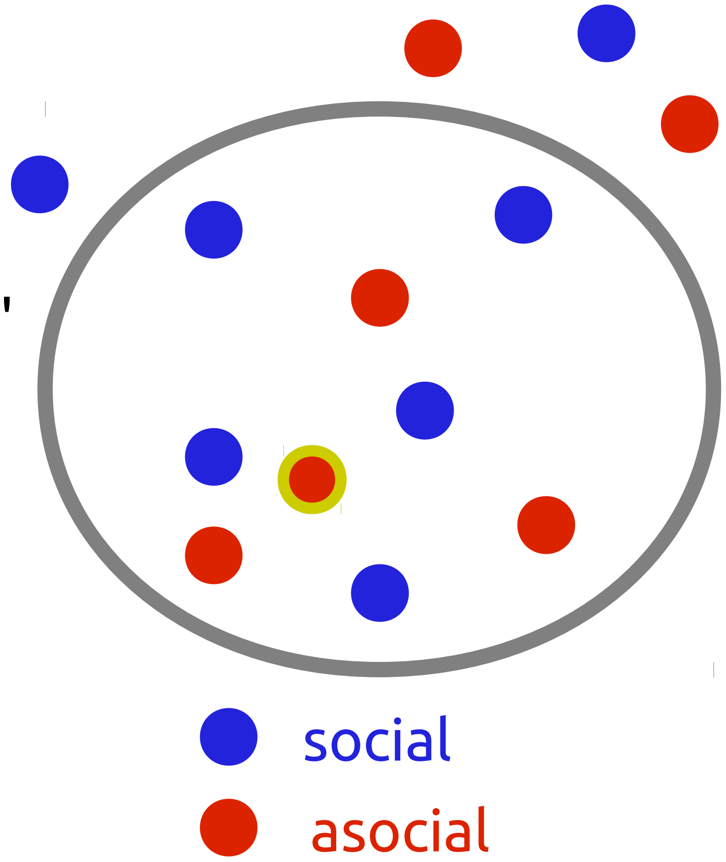


1. T individuals are randomly chosen

2. one individual is assigned the status 'recruiter'

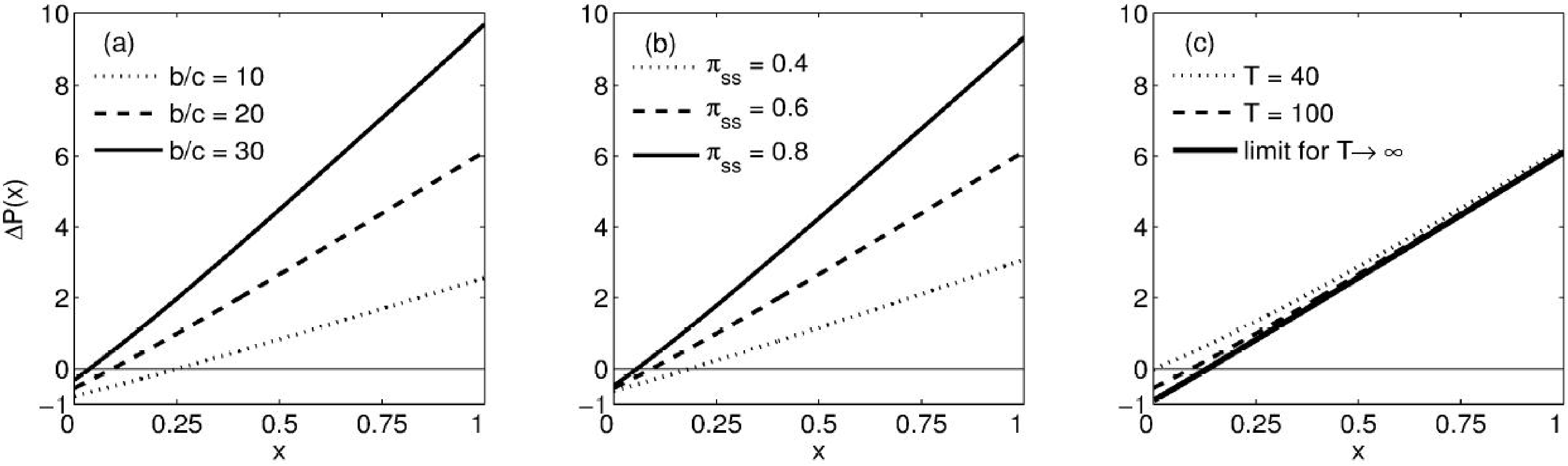
3. other individuals interact once with the recruiter, and stick to him with probability dependent on the strategies of recruiter and focal player :

$$\pi_{aa} \leq \pi_{as} = \pi_{sa} \leq \pi_{ss}$$

No a priori assortment if $\pi_{as}^{2} = \pi_{aa}\,\pi_{ss}$

➡ The fraction of social coplayers is the same for social and asocial players

Payoff of social vs asocial strategy

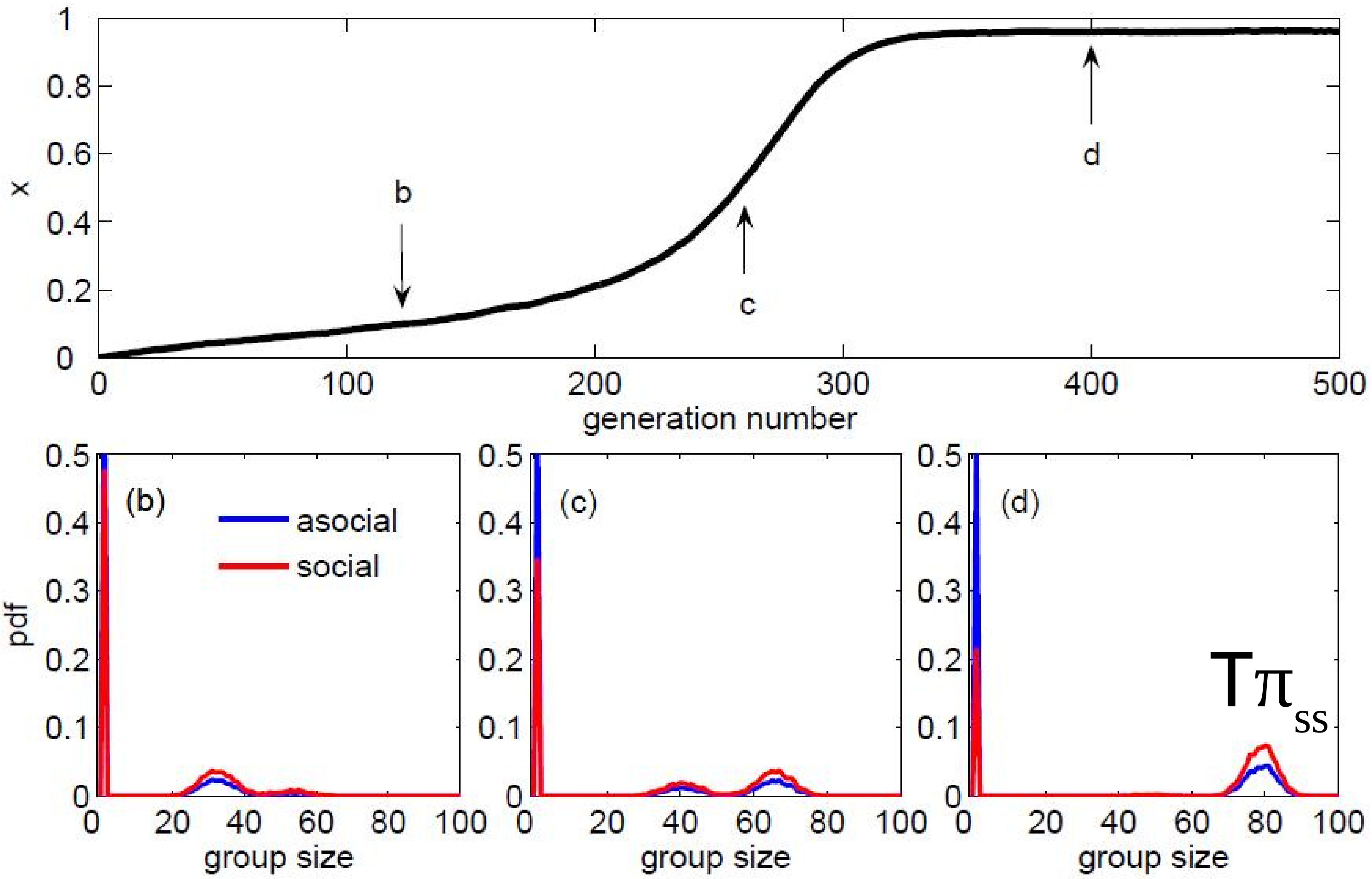


A threshold frequency exists above which sociality evolves

This threshold is below 1 for any maximal group size

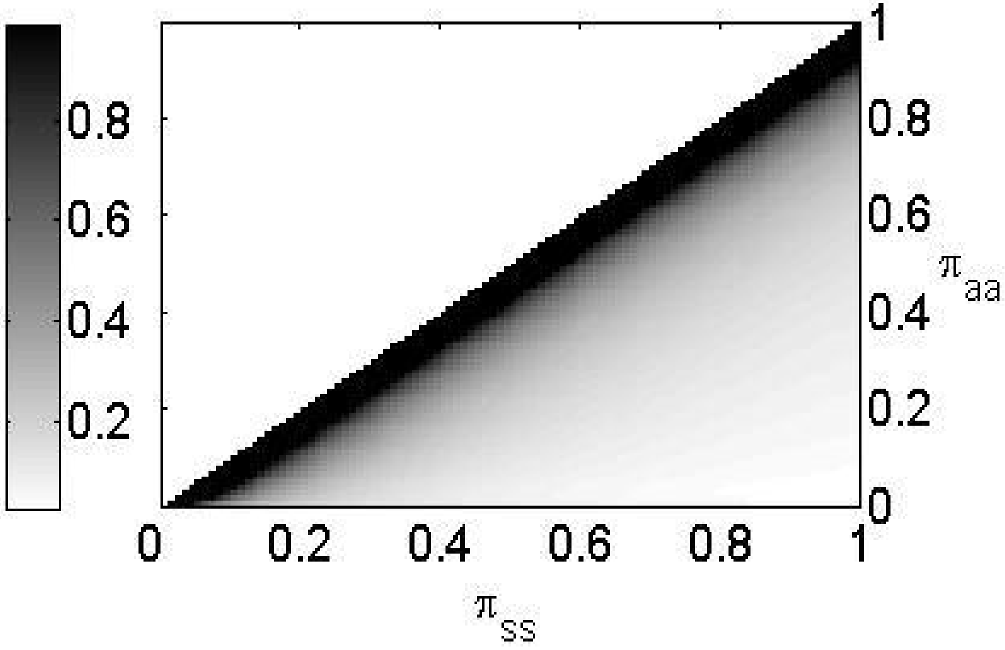
➡ Sociality can evolve also when max group size is large

Evolutionary dynamics of group size distribution

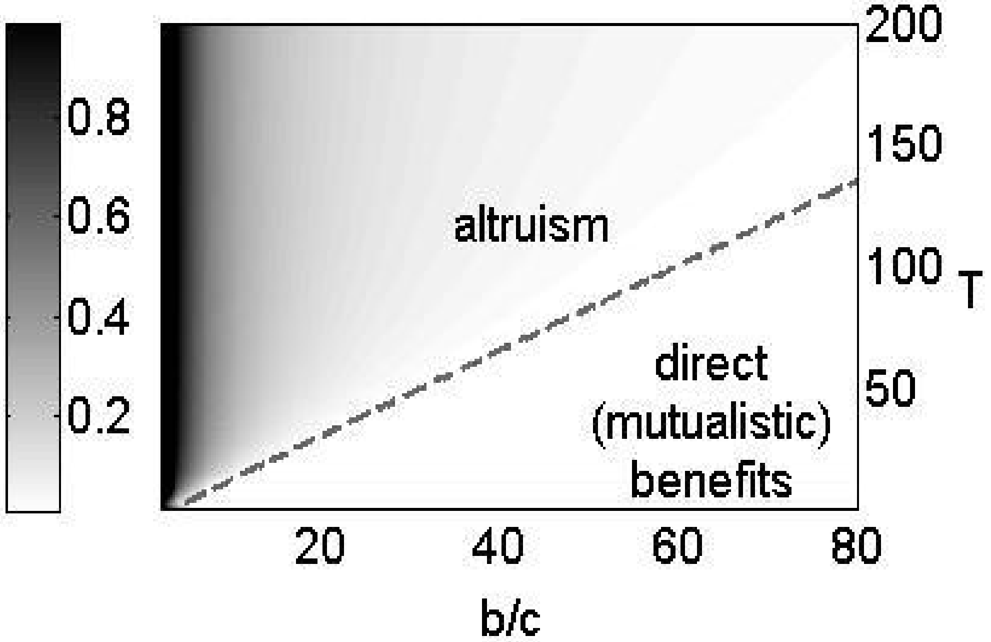


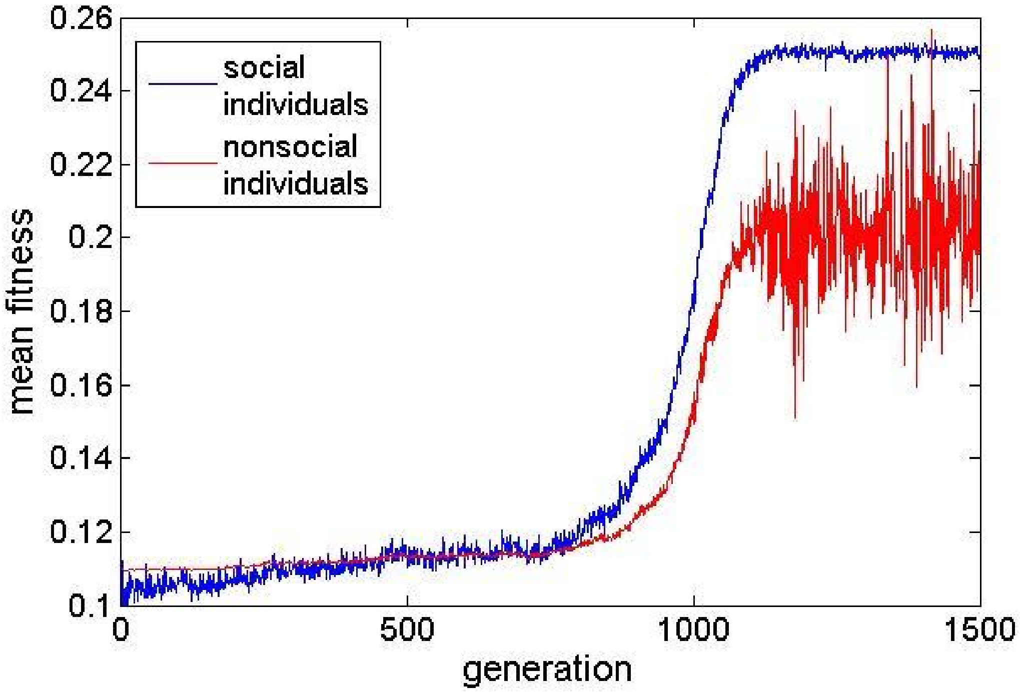
- no bias towards small group sizes
- evolutionary issue independent on game parameters

Parameter dependence



Threshold frequency above which sociality invades





Mutations, switches and finite-size fluctuations can lead the system over the threshold

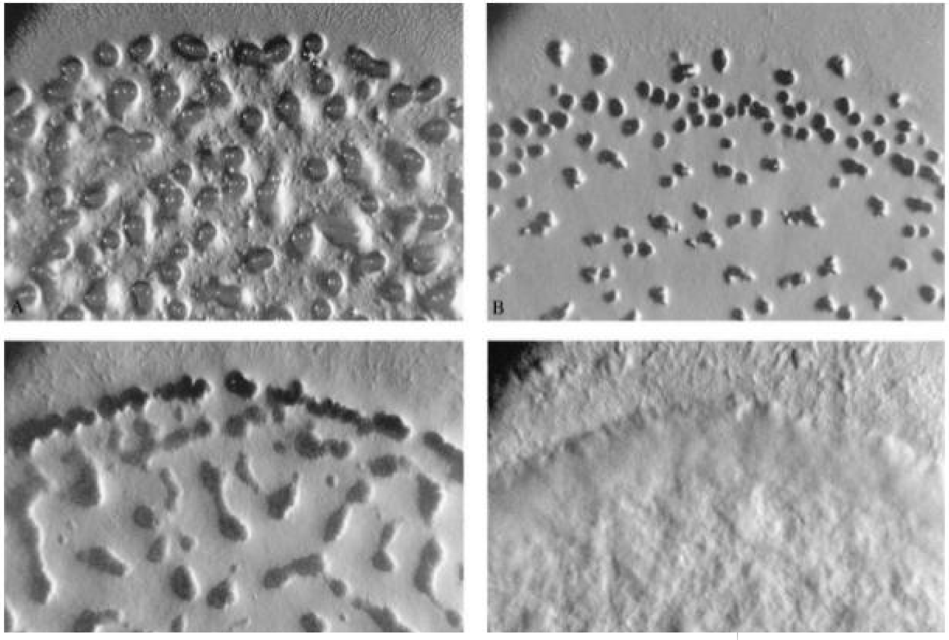
Summary

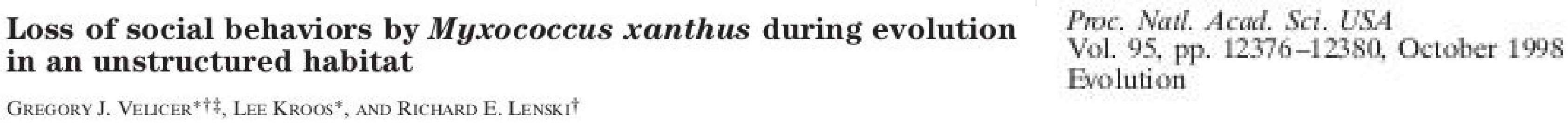
Sociality can evolve under 'blind' interactions (no kin recognition) and in the absence of genetic relatedness, if:

- the sociality gene plays a role both in group formation and in group performance
- sociality is costly
- sociality implies a higher probability to attach to other individuals (irrespective of their behaviour)

➡ By quantitative differences in attachment probability, socials are in larger groups (on average) than asocials

Relation to microbes





Loss of social behaviors by *Myxococcus xanthus* during evolution in an unstructured habitat

Gregory J. Velicer[*,†,‡], Lee Kroos[*], and Richard E. Lenski[†]

Proc. Natl. Acad. Sci. USA
Vol. 95, pp. 12376–12380, October 1998
Evolution

Possibility for large group sizes to emerge

Differential attachment is sufficient to create assortment

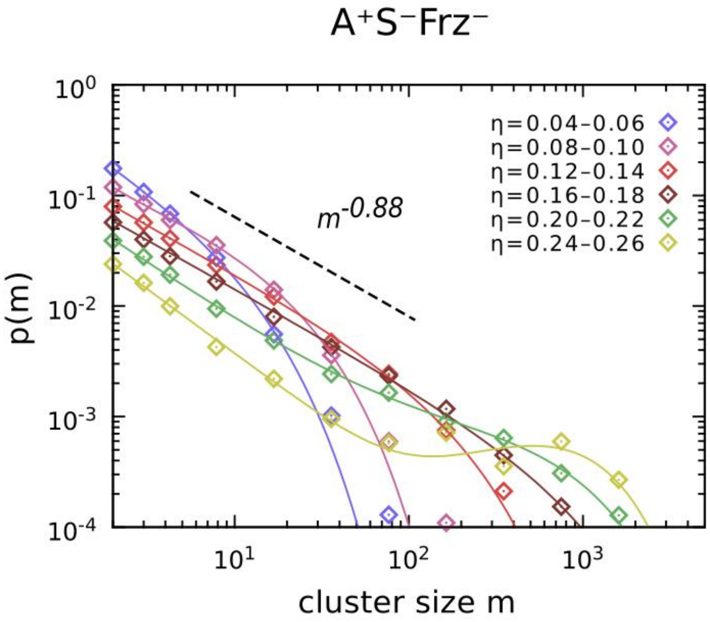
Role of lonely individuals (more often asocials)

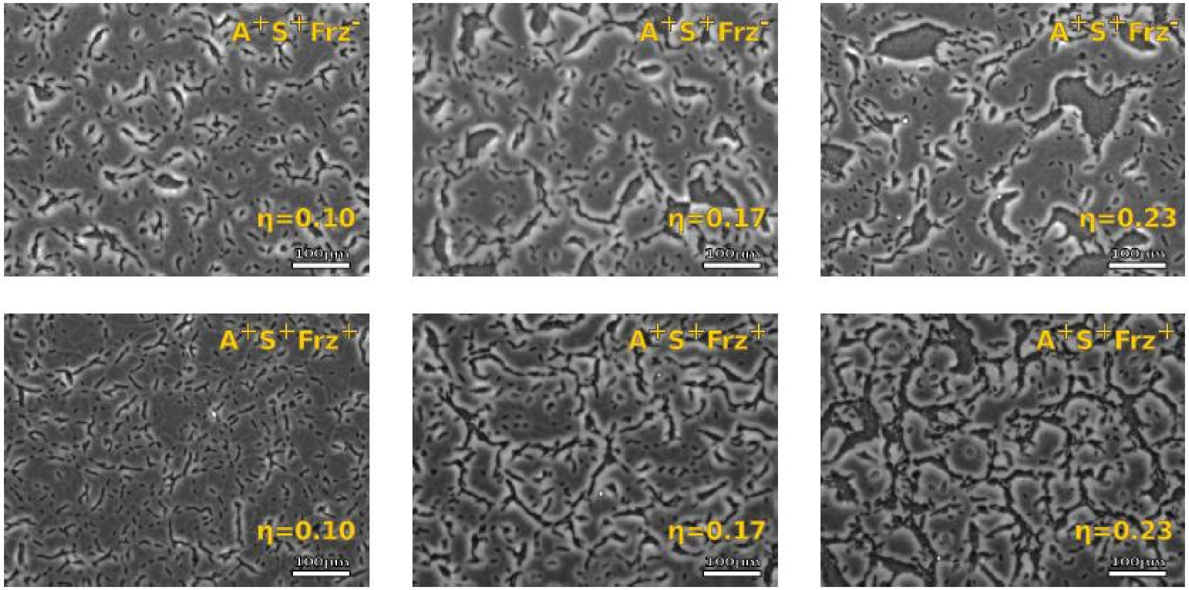
What physical properties shape microbial groups?

PRL **108,** 098102 (2012) PHYSICAL REVIEW LETTERS week ending 2 MARCH 2012

Collective Motion and Nonequilibrium Cluster Formation in Colonies of Gliding Bacteria

Fernando Peruani,[1,2] Jörn Starruß,[3] Vladimir Jakovljevic,[4] Lotte Søgaard-Andersen,[4] Andreas Deutsch,[3] and Markus Bär[5]





Pattern-formation mechanisms in motility mutants of Myxococcus xanthu

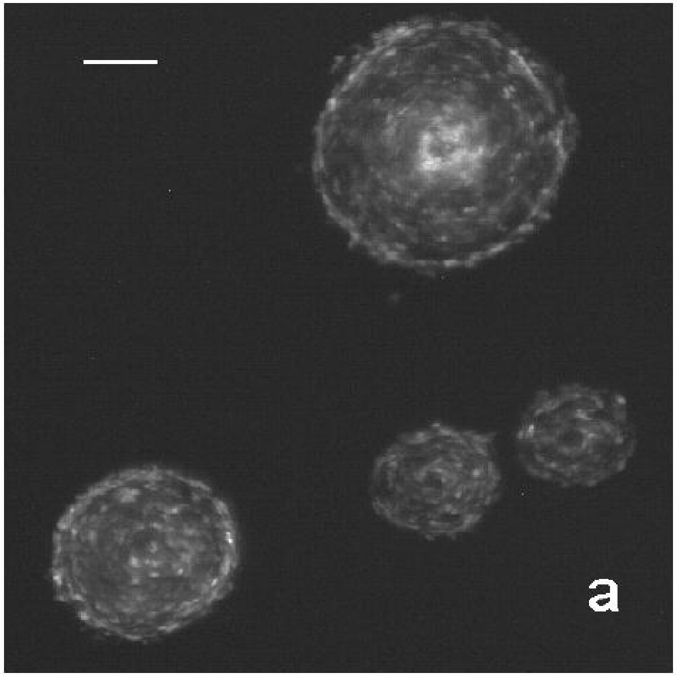
J. Starruss et al., Interface Focus (2012)

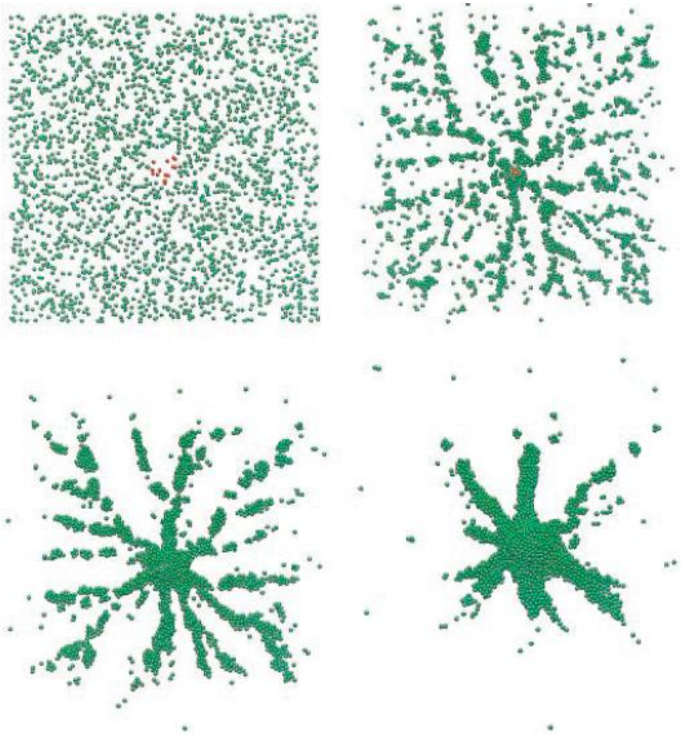
What physical properties shape microbial groups?

VOLUME 83, NUMBER 6 PHYSICAL REVIEW LETTERS 9 AUGUST 1999

Self-organized Vortex State in Two-Dimensional *Dictyostelium* Dynamics

Wouter-Jan Rappel, Alastair Nicol, Armand Sarkissian, and Herbert Levine





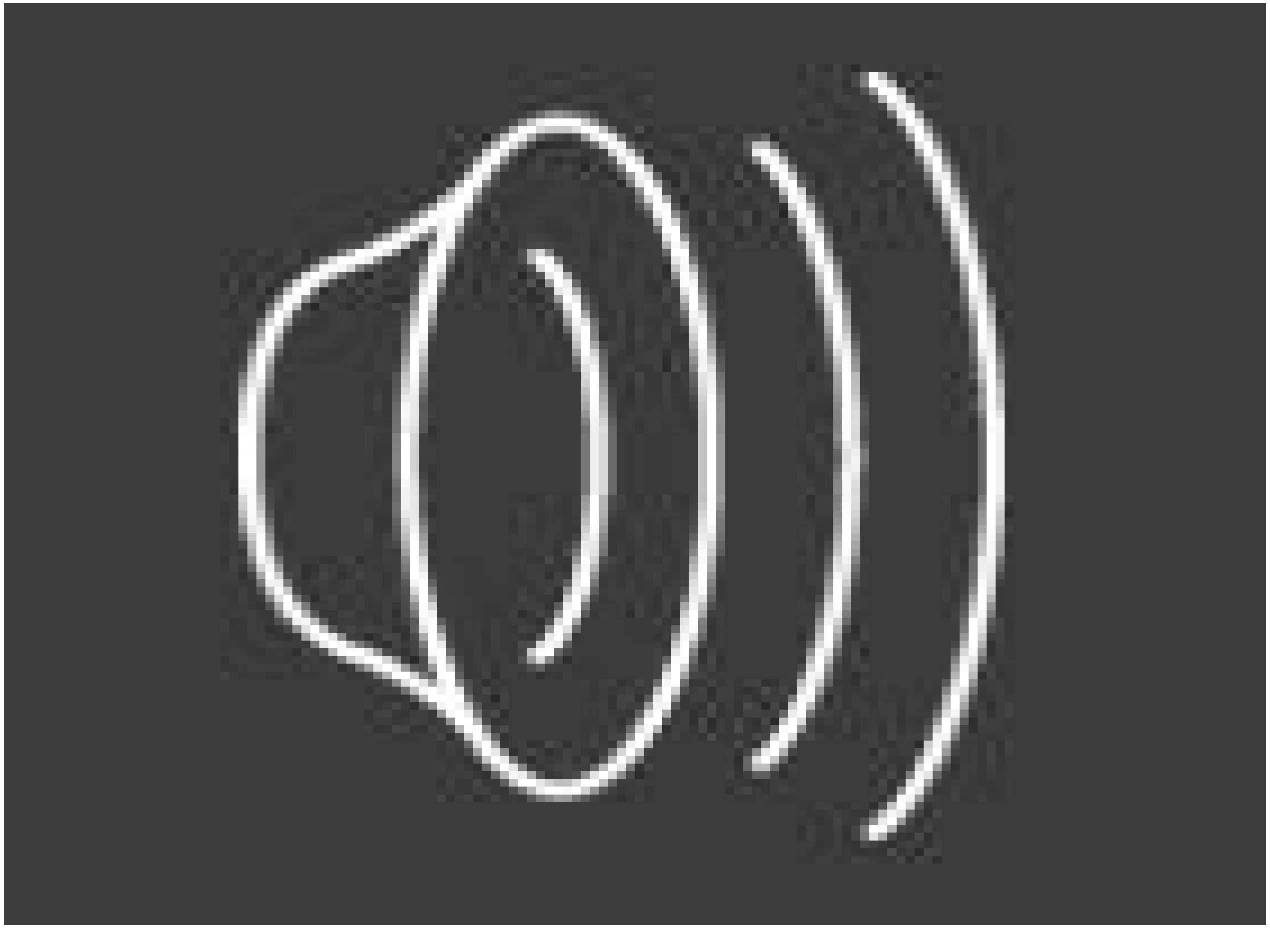
A model for individual and collective cell movement in *Dictyostelium discoideum*

Eirikur Palsson* and Hans G. Othmer†‡

10448–10453 | PNAS | September 12, 2000 | vol. 97 | no. 19

Emergent population structure

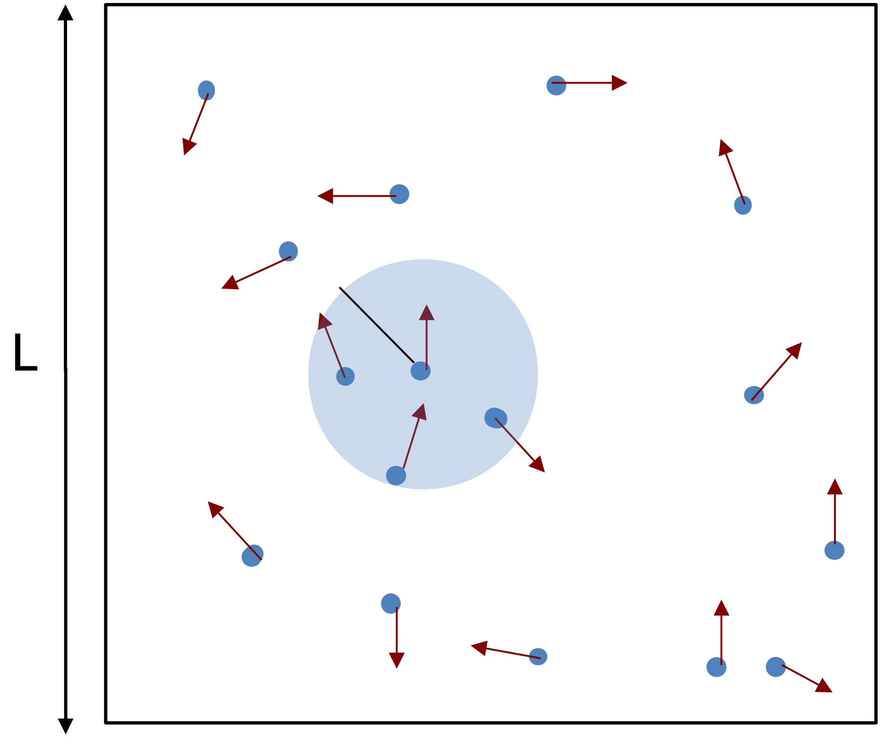
Aggregation of *Dictyostelium discoideum*



Movie by Darja Dubravcic

More 'realistic' models for group formation

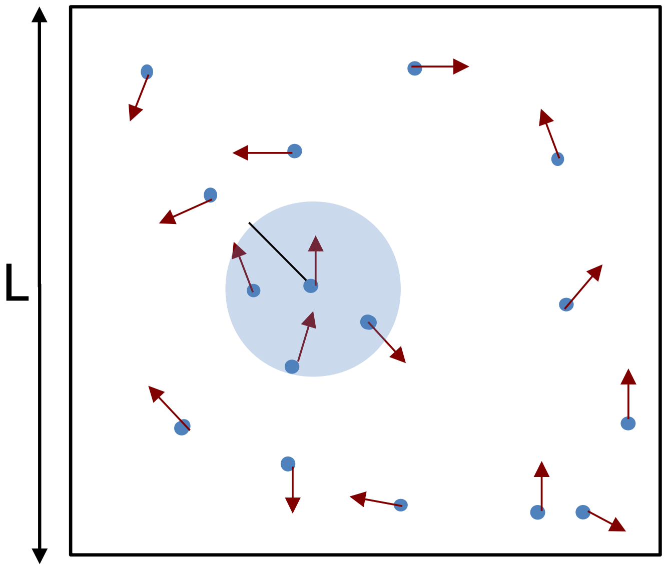
Particles interacting on a plane (boids, self-propelled particles)



density $\rho = \frac{N_{pop}}{L^2}$

More 'realistic' models for group formation

Particles interacting on a plane (boids, self-propelled particles)



density $\rho = \frac{N_{pop}}{L^2}$

$$\mathbf{x_j}^{(t+1)} = \mathbf{x_j}^{(t)} + \mathbf{v_j}^{(t+1)} \Delta t$$

$$\mathbf{v_j}^{(t+1)} = v e^{i\theta_j^{(t+1)}}$$

$$\theta_j^{(t+1)} = \arg \left\{ \mathbf{v_j}^{(t)} + \boxed{\sum_{k \neq j} \beta_{\sigma(j)\sigma(k)} \, \mathbf{f_{jk}}^{(t)}} \right\} + \boxed{\eta \, d\theta}$$

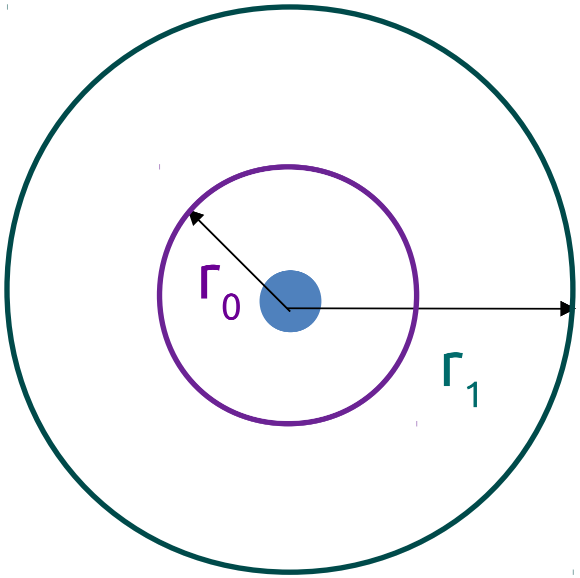
interaction

noise

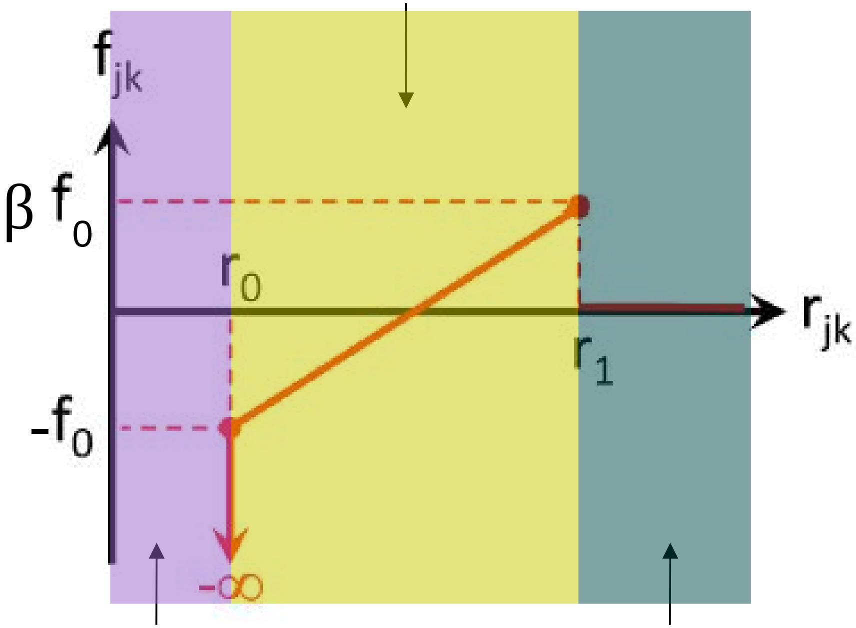
Grégoire et al. Physica D 2003
Belmonte et al. PRL 2008

Differential attachment + space

Interaction forces



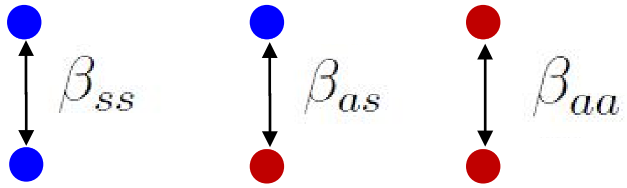
medium-range attraction



short-range repulsion

no interaction

$$\beta_{\sigma(j)\sigma(k)} = \begin{cases} \beta_{ss} & \text{if } j \text{ and } k \text{ are social} \\ \beta_{aa} & \text{if } j \text{ and } k \text{ are asocial} \\ \beta_{as} & \text{otherwise} \end{cases}$$



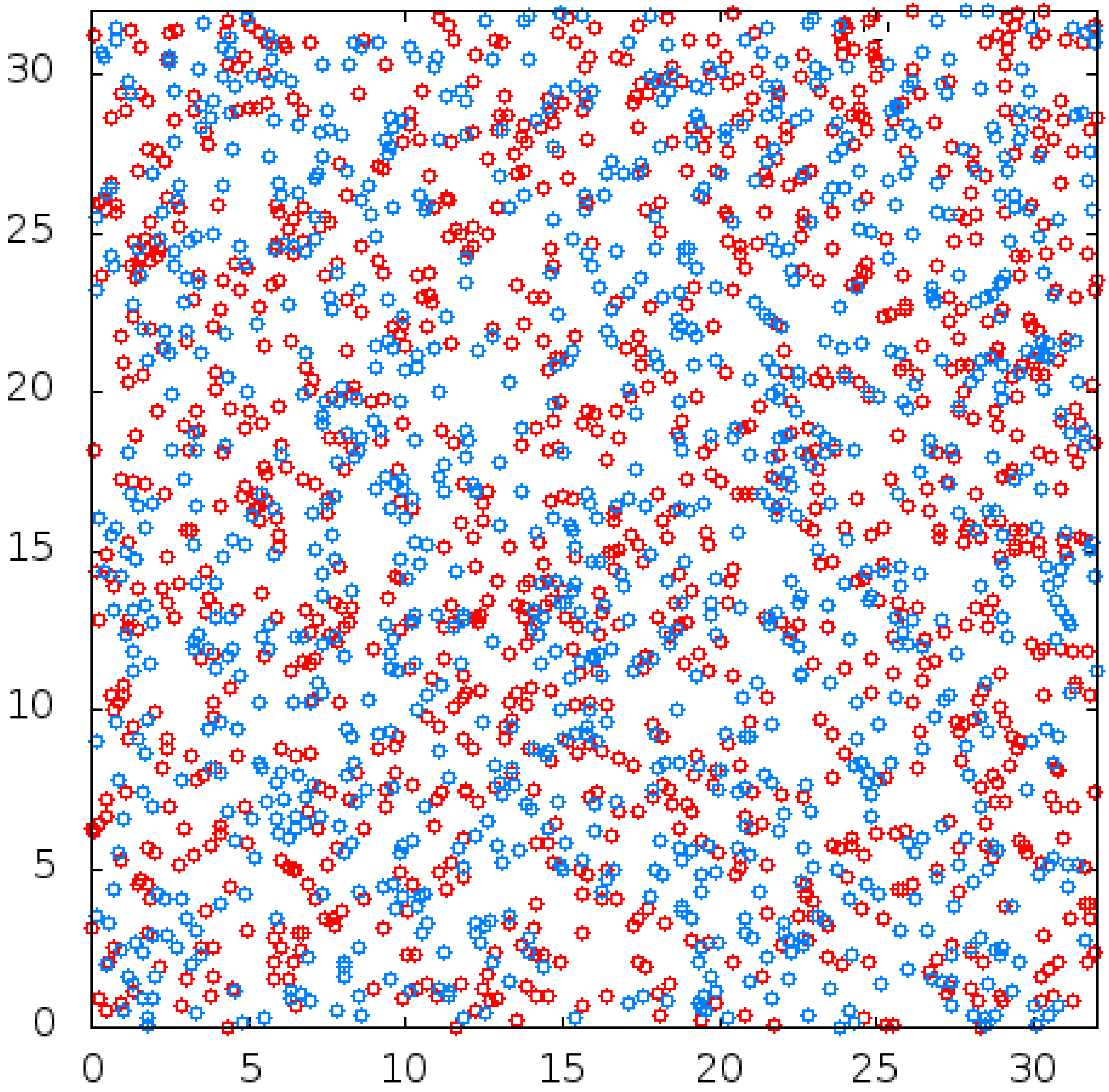
Numerical simulation (fixed x=50%)

N=2048

dens= 2

nu= 0

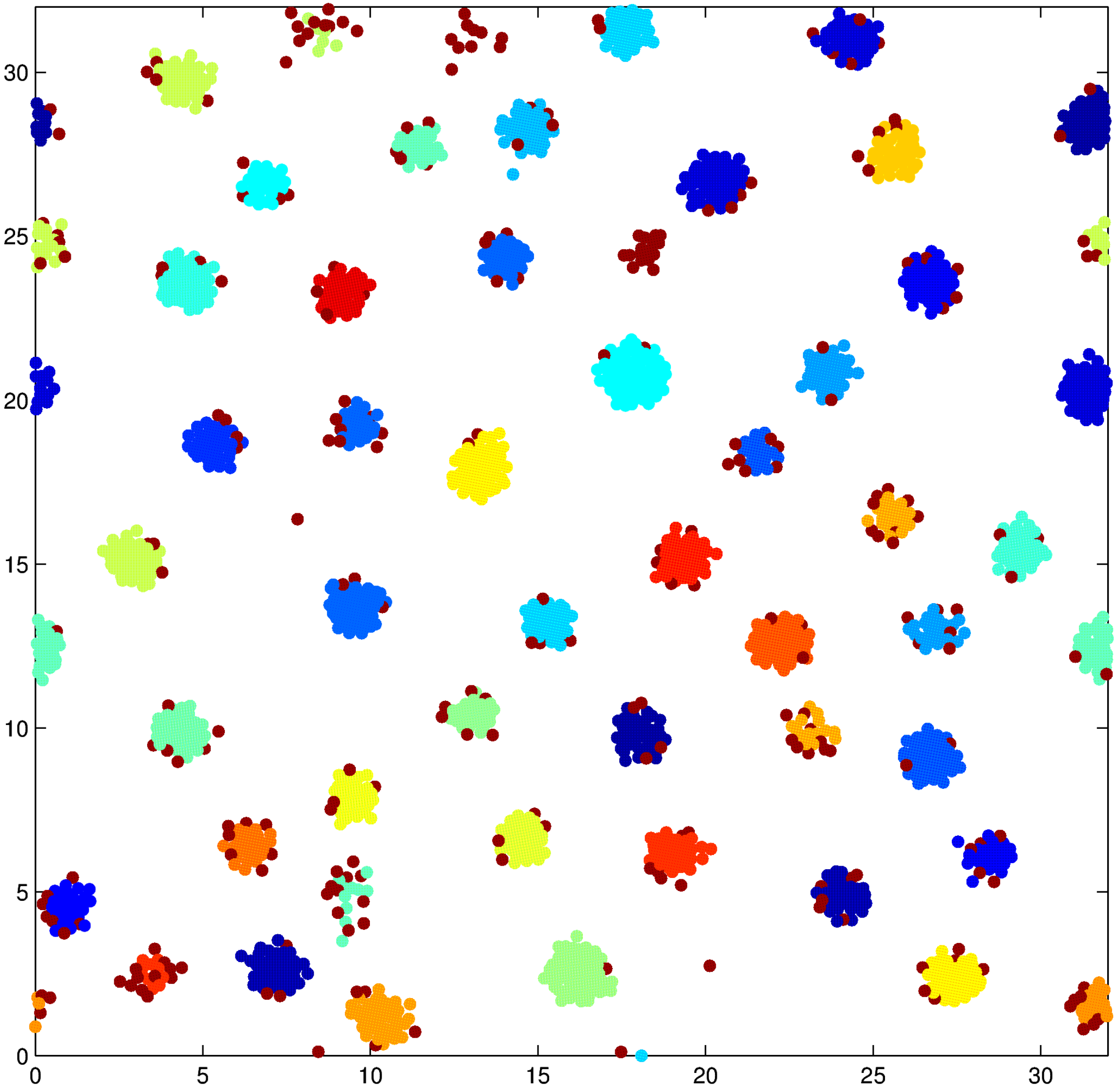
t= 1



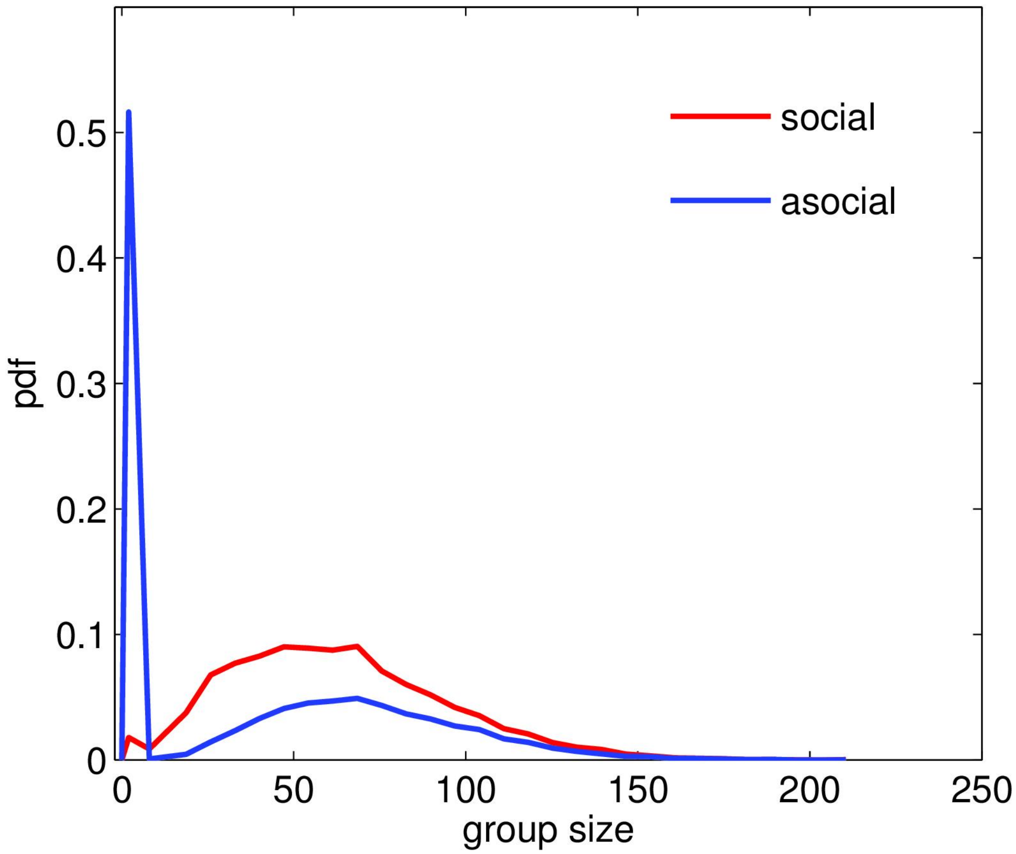
Socials

Asocials

Numerical simulation (fixed x=50%)

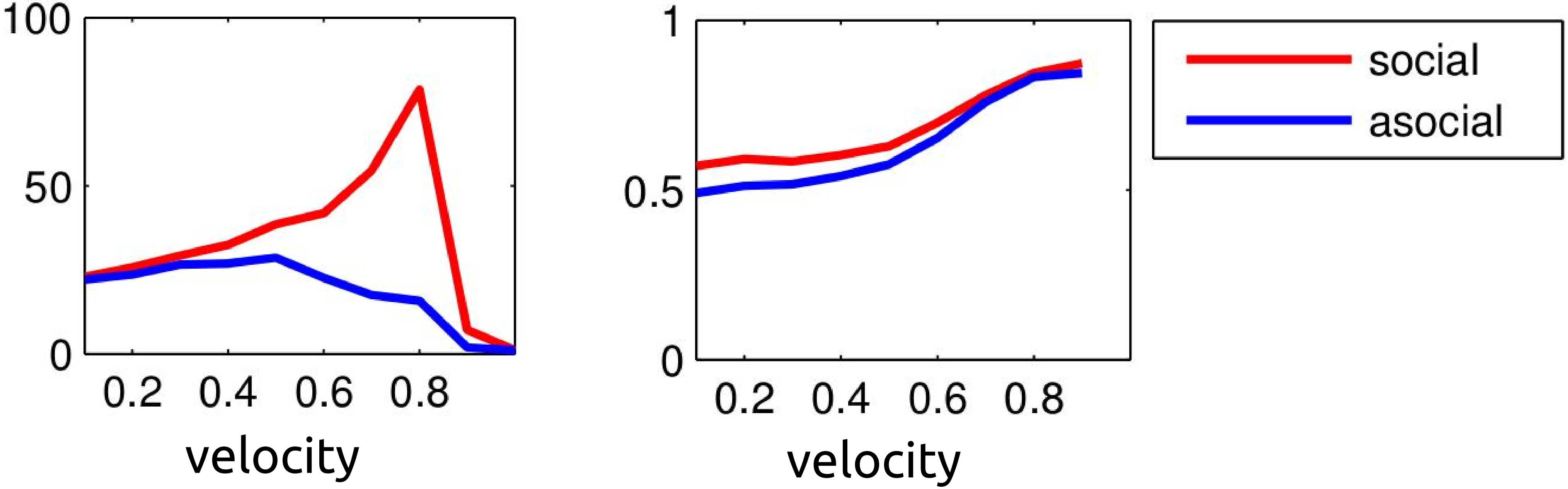


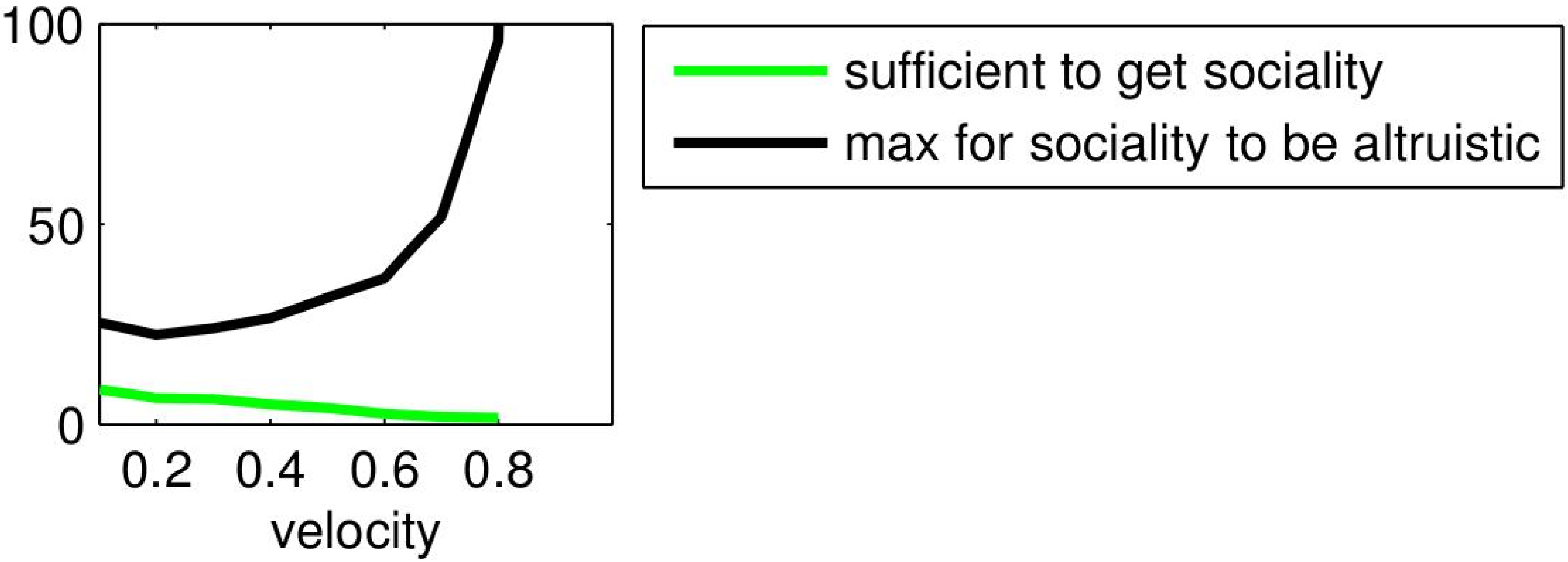
Group size distribution



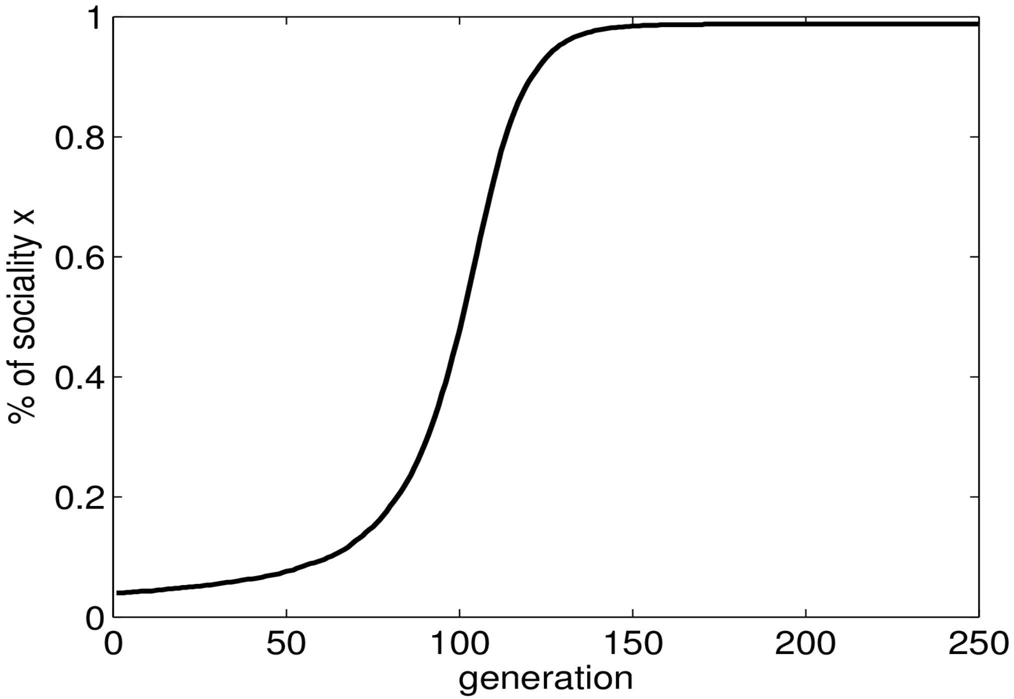
Asocials are more often alone

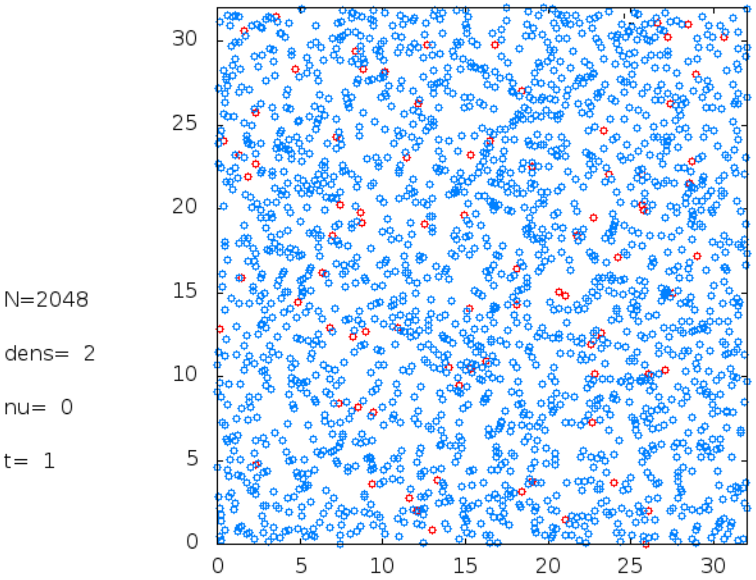
Exploration of parameter space

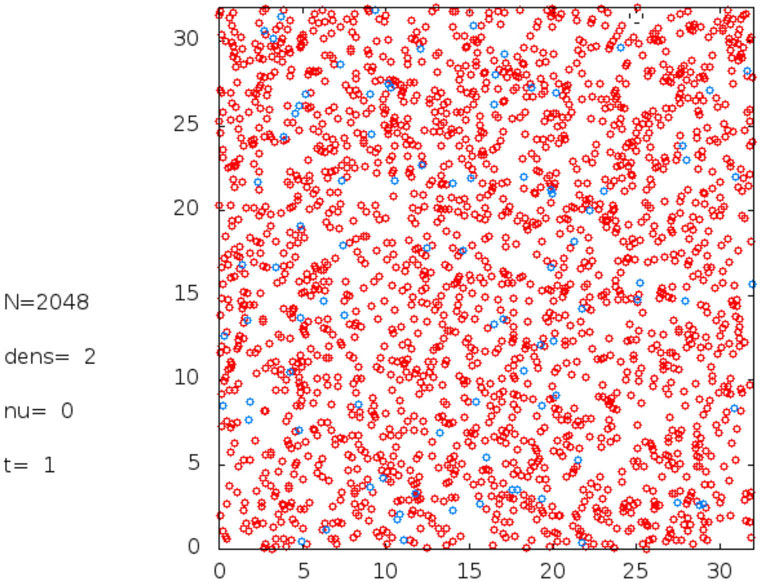




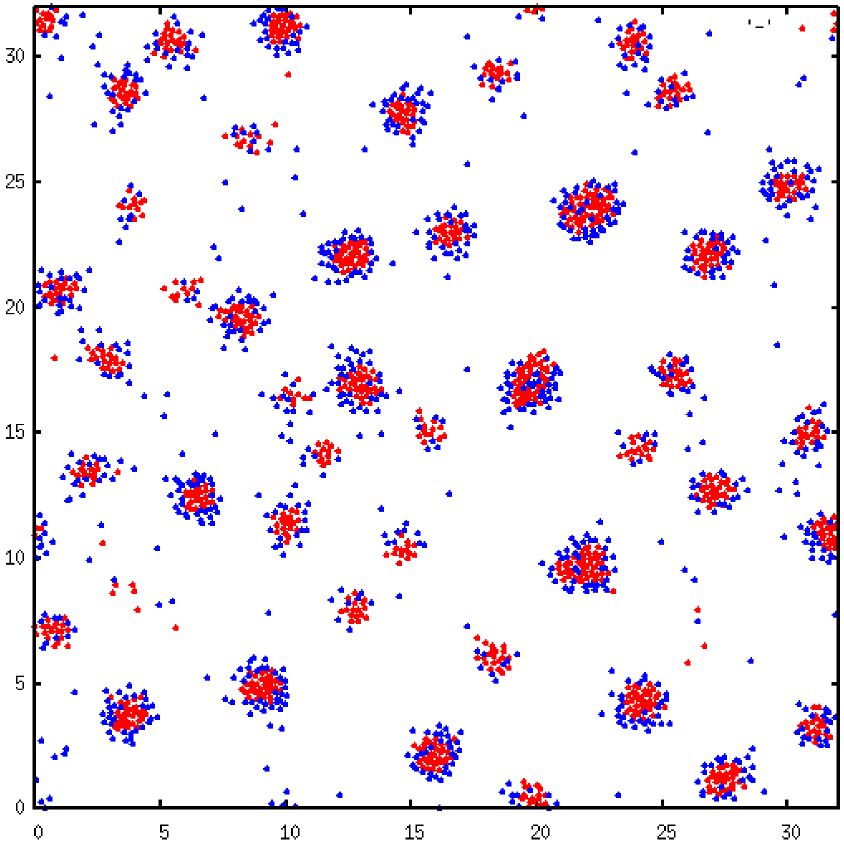
Evolutionary dynamics







Within-group structure



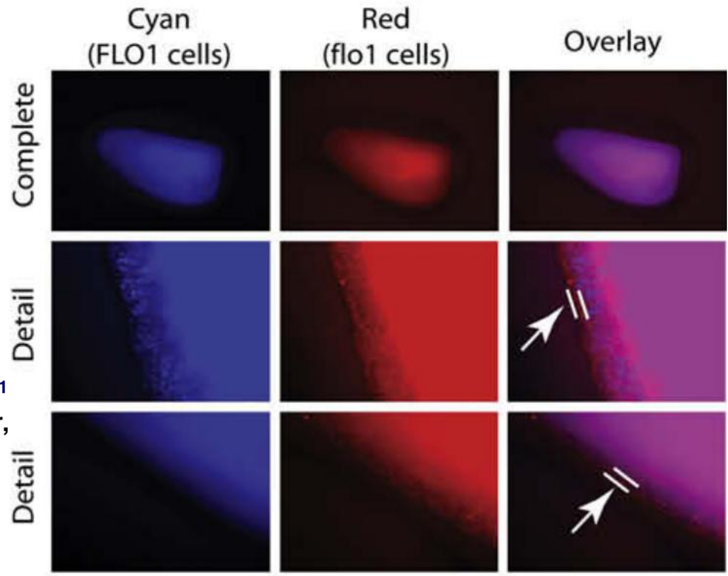
Asocials

Socials

FLO1 Is a Variable Green Beard Gene that Drives Biofilm-like Cooperation in Budding Yeast

Scott Smukalla,[1,8] Marina Caldara,[1,8] Nathalie Pochet,[1,2,8] Anne Beauvais,[3] Stephanie Guadagnini,[4] Chen Yan,[1]
Marcelo D. Vinces,[1] An Jansen,[5,6] Marie Christine Prevost,[4] Jean-Paul Latgé,[3] Gerald R. Fink,[5] Kevin R. Foster,
and Kevin J. Verstrepen[1,6,7,*]

Cell *135*, 726–737, November 14, 2008



Conclusions

Group formation can create assortment and thus favour the evolution of social behaviour in simple settings

If the same trait plays a role both in group formation and in group function (e.g. stickiness), sociality and group size co-evolve

Sociality can evolve even if interactions are costly

Evolution of a 'social' trait based on individual-level selection

Multicellular groups re-form every generation, and assortment depends on the mechanism of group formation

But groups are not Darwinian entities (there is no reproduction and heredity at the group level)

Emergent groups and multicellularity

With Paul Rainey & Ellen Clarke

An evolutionary transition to multicellularity must imply a mechanism by which groups have a heritable variability in fitness

There may be different ways to get this (e. g. fission-fusion)

Some mechanism may be more efficient than other in order to get a 'Darwinian machine'

A general framework for the evolution of multicellularity?

TOWARDS A GENERAL THEORY OF GROUP SELECTION

Burton Simon,[1,2], Jeffrey A. Fletcher,[3] and Michael Doebeli[4]

Evolution 2012

$$\frac{\partial\theta_t}{\partial t}(\vec{x}) + \sum_{i=1}^{k} \frac{\partial(\theta_t\alpha_{ti})}{\partial x_i}(\vec{x}) = g_t(\vec{x}).$$

taille de la pop : N=2048

longueur du carré : L=32 => d'où densité = 2

vitesse : v = 0.05

nombre de pas de temps pour l'agrégation : 2000

bruit : 0.3

r0 = 0.2r1 = 1.00

f0 = 5e-3

beta_ss = 1.8

beta_aa = 1.0

beta_as = sqrt(beta_aa*beta_ss)

Les 3 vidéos sont faites pour x=0.05, x=0.50 et x=0.95