

# Dynamic social networks and reciprocity: comparing agent-based models and behavioural studies

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21st April 2015

Phelps, S. (2013).

Emergence of social networks via direct and indirect reciprocity.

*Journal of Autonomous Agents and Multiagent Systems*, 27(3):355–374.

Russell, Y. I. and Phelps, S. (2013).

How do you measure pleasure? A discussion about intrinsic costs and benefits in primate allogrooming.

*Biology and Philosophy*, 28(6):1005–1020.

Phelps, S., Ng, W. L., Musolesi, M. and Russell, Y. (2015).

Grooming reciprocity in chimpanzees: evidence for delayed time matching.

*Proceedings of the Royal Society B: Biological Sciences*, [in submission].

# Grooming, Gossip and the Evolution of Language

Grooming plays a key role in maintaining “social cohesion” in primate societies

If extrapolated to humans then we would need to spend approx 40% of our time grooming.



Dunbar’s “***Social Brain Hypothesis***”:

Perhaps language, and gossip, are an efficient “grooming” mechanism for humans?

# “Social Cohesion” = Cooperation?

- How can we build a model to make some of these ideas more concrete and testable?
- The Prisoner’s Dilemma:

|           | Cooperate | Defect |
|-----------|-----------|--------|
| Cooperate | 3,3       | 0,5    |
| Defect    | 5,0       | 1,1    |

**Direct reciprocity:** copy the action chosen by your partner on the previous round of play.

a.k.a. ***Tit-For-Tat***

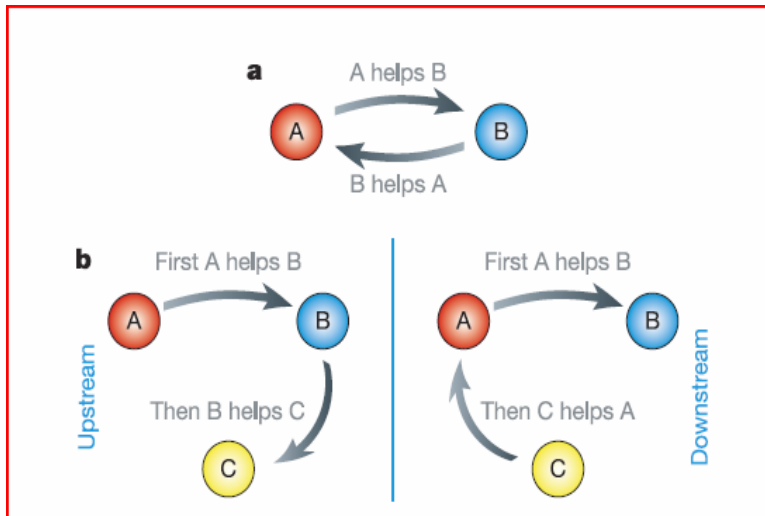
# Extending to groups $n > 2$

## - Public Goods Game

- Large group of players of size  $n > 2$
- Each player invests a certain amount in a global investment pool
- Payoff is  $(m \times \text{total contribution}) / n$
- Temptation to defect
- “Rational” solution is to invest nothing
  - a.k.a Free-riding
- Empirical behaviour in humans:
  - Cooperation persists but decreases over time
  - Cooperation decreases with increased group size

# Indirect reciprocity

Nowak and Sigmund demonstrated that cooperation can evolve in large groups via *indirect* reciprocity and conspicuous altruism



M. A. Nowak and K. Sigmund. The alternating prisoner's dilemma. *Journal of theoretical Biology*, 168:219-226, 1994.

M. A. Nowak and K. Sigmund. The dynamics of indirect reciprocity. *Journal of Theoretical Biology*, 194(4):561-574, Oct. 1998.

M. A. Nowak and K. Sigmund. Evolution of indirect reciprocity by image scoring. *Nature*, 383:537-577, 1998.

Agent A decides whether or not to help based on B's reputation for helping ("image score")

If some members of the group adopt the strategy "Help helpful agents" this can lead to widespread cooperation...

# Group cooperation: simple model

- Population of  $n$  agents
- Play is repeated over  $N$  rounds
- Agents paired randomly on each round:
  - 1st player chooses move (cooperate or defect)
  - 2<sup>nd</sup> player is passive – merely receives payoff

# Moves & Payoffs

- 1<sup>st</sup> player chooses investment
  - $\gamma = 0$  (defect)
  - $\gamma = 0.1$  (cooperate)
- Payoffs:
  - $-\gamma$  to 1<sup>st</sup> player
  - $10 \times \gamma$  to 2<sup>nd</sup> player
- Mutually beneficially provided players reciprocate
- Choice of  $u$  dependent on attributes of 2<sup>nd</sup> player:
  - $r$  = Reputation (“image score”) of 2<sup>nd</sup> player  $[-5, +5]$
  - 1<sup>st</sup> player cooperates if  $r \geq \sigma$
  - otherwise defects if  $r < \sigma$

# Strategies

- Unconditional cooperation:  $\sigma = -5$
- Unconditional defection:  $\sigma = +6$
- Discriminatory:  $\sigma = 0$

# Analysis

- Nowak and Sigmund analyse this game under the assumption that the group size  $n$  is large relative to the number of rounds  $N$ , therefore:
  - No need to take into account that agent cannot be paired with itself when deriving closed-form expression for expected payoffs
  - Can ignore the effect of strategies like Tit-For-Tat (T4T) which rely on a personal memory of interactions
- Under these assumptions the analysis is independent of group size or number of rounds..

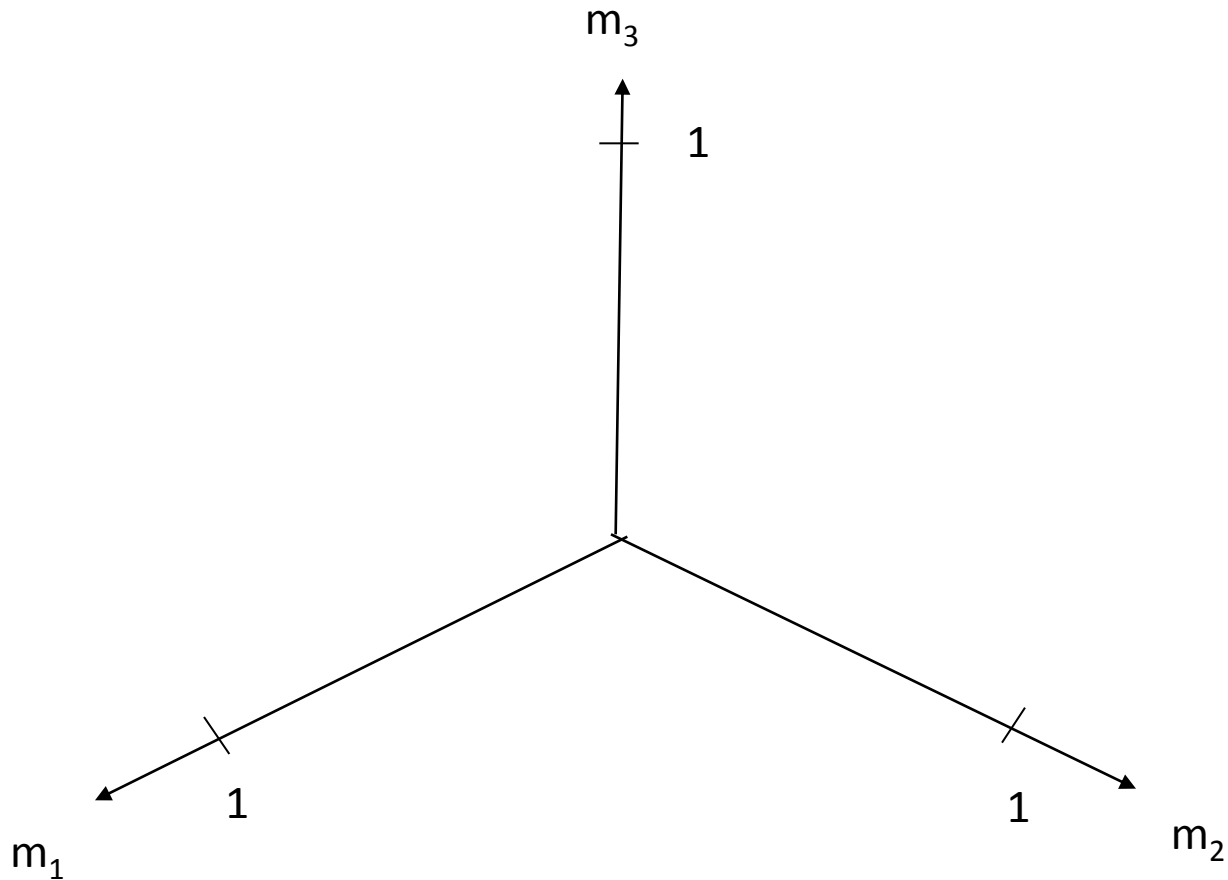
# Evolutionary Game Theory

- Use Maynard Smith's *replicator dynamics* to model adjustment to equilibrium

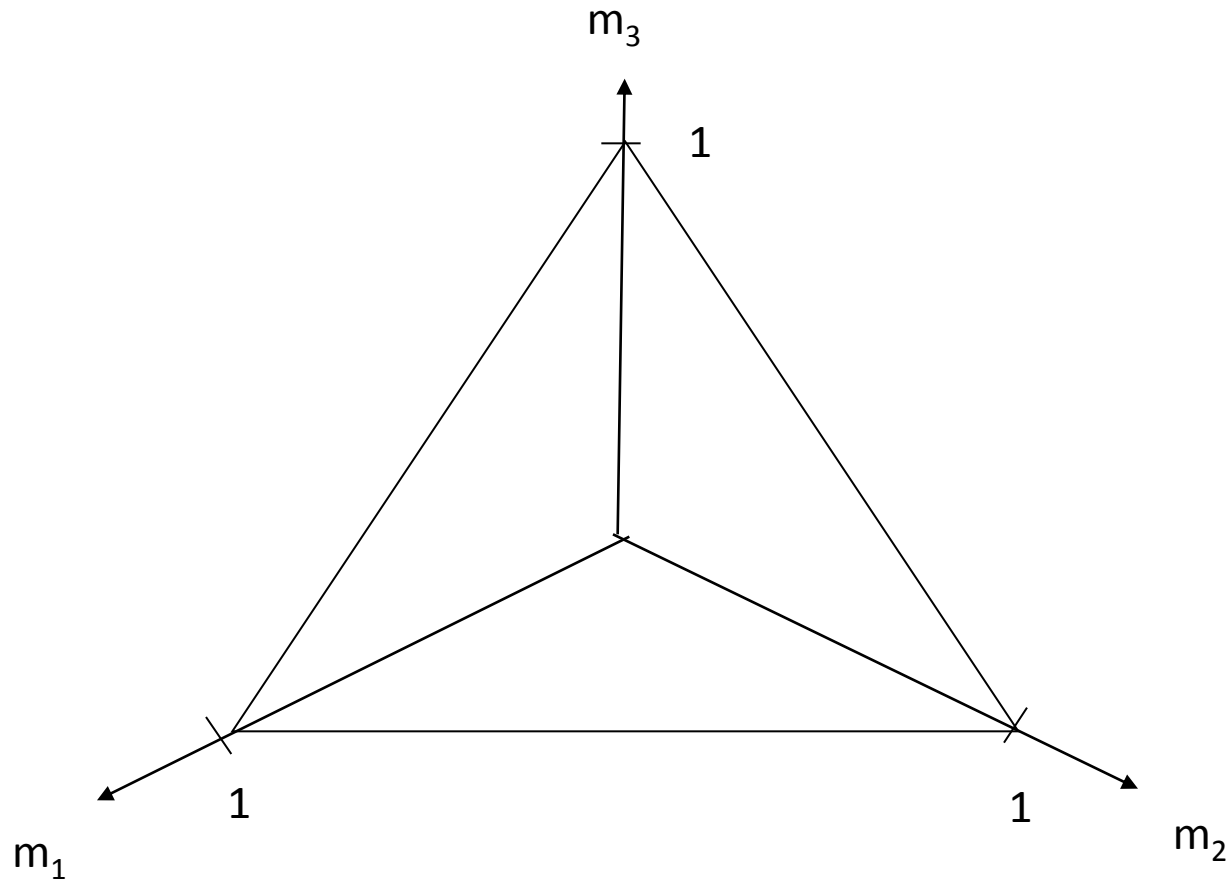
$$dm_i/dt = [u(e_i, \mathbf{m}) - u(\mathbf{m}, \mathbf{m})]m_i$$

- $\mathbf{m}$  is vector of population frequencies eg  
( $m_1, m_2, m_3$ ) proportion of population playing cooperate, defect or discriminate respectively
- $u(\mathbf{m}, \mathbf{m})$  is population average payoff (fitness)
- $u(e_i, \mathbf{m})$  is expected payoff to an individual adopting pure strategy  $i$  against a population consisting of  $\mathbf{m}$
- Plays similar role to fitness-proportionate selection in a Genetic Algorithm

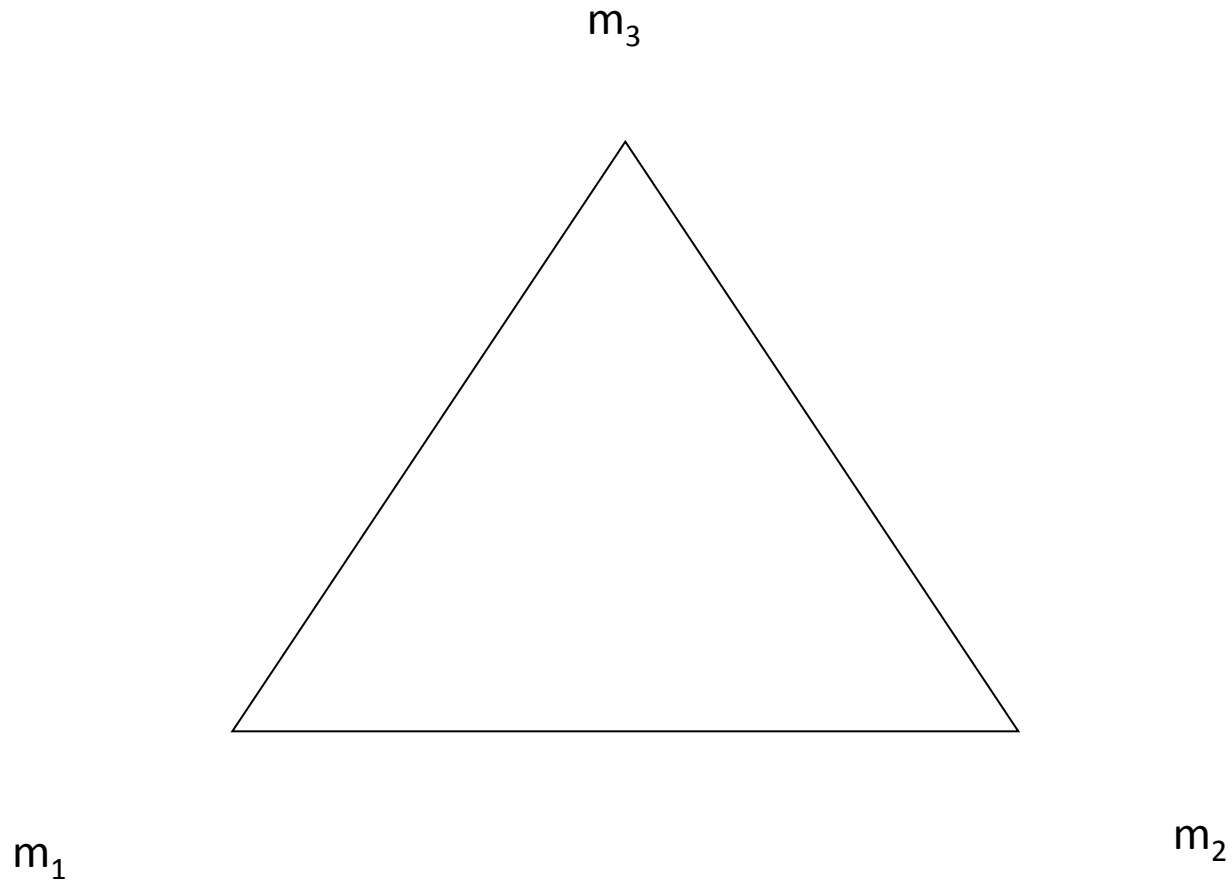
# Population frequencies in 3D

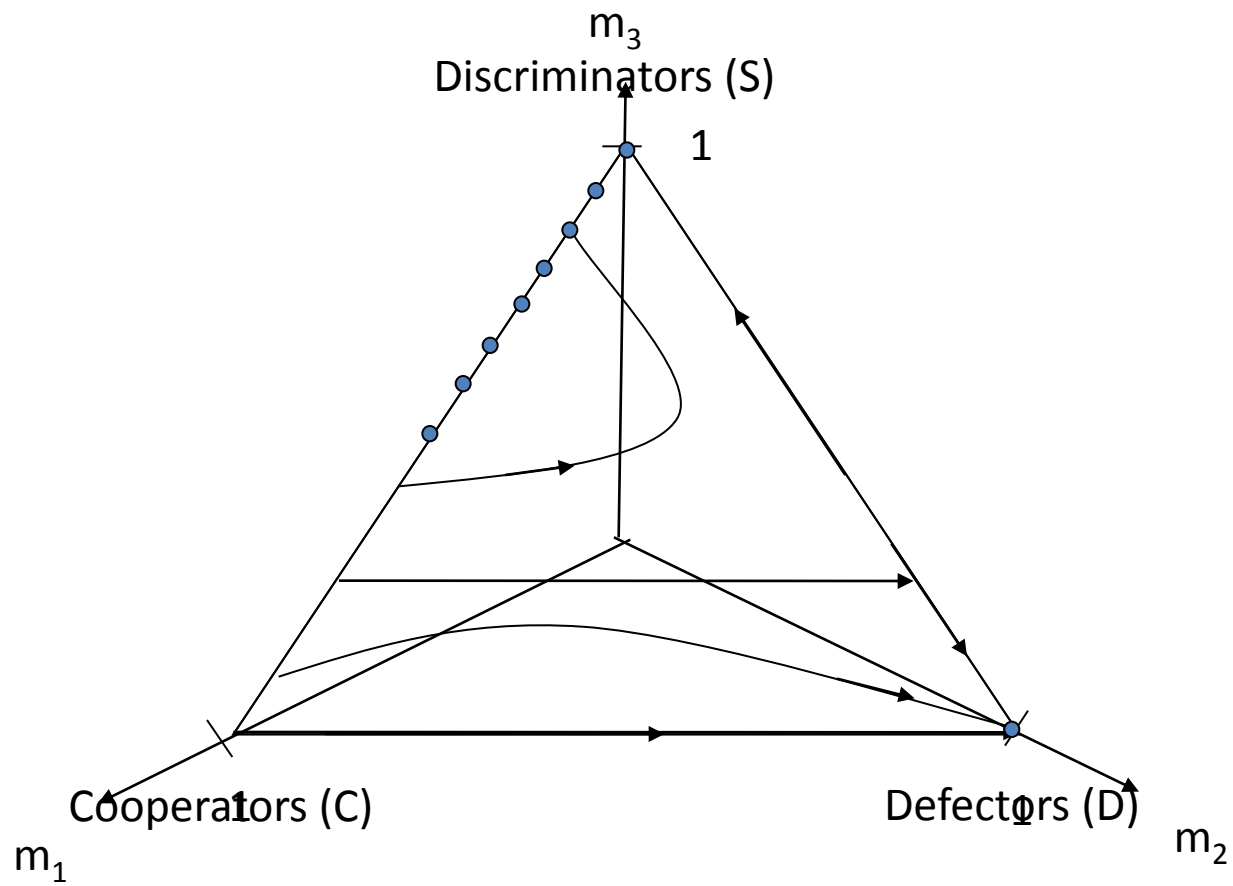


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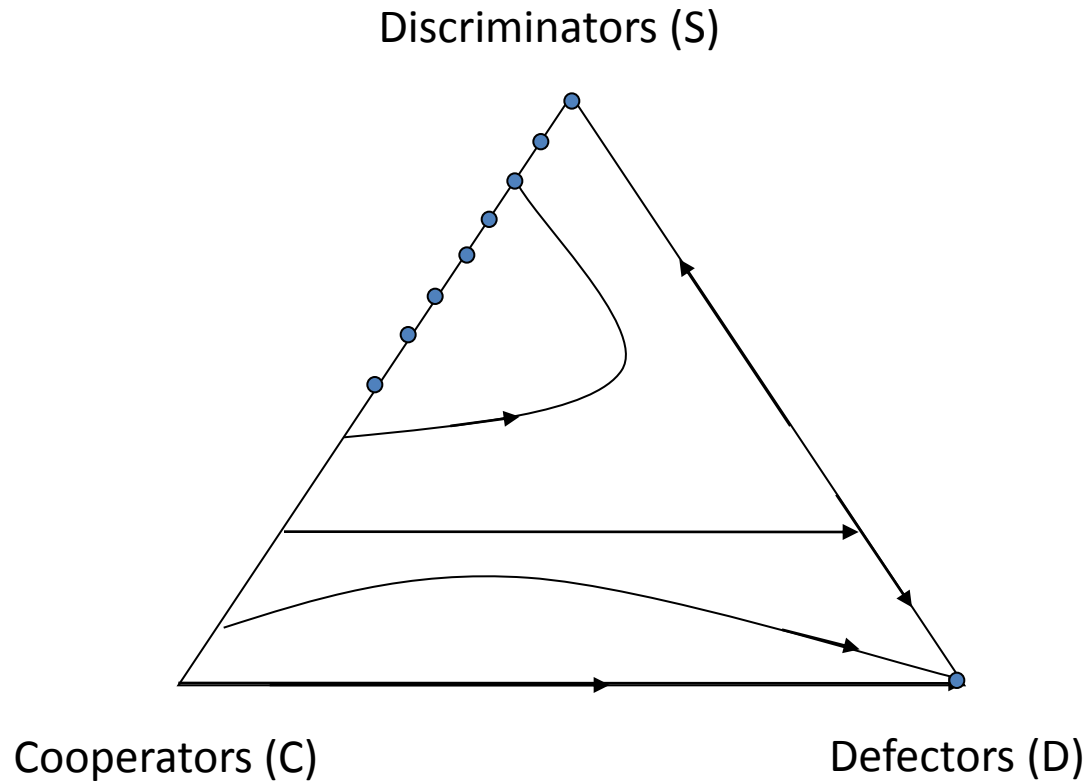


# Population frequencies in 2D



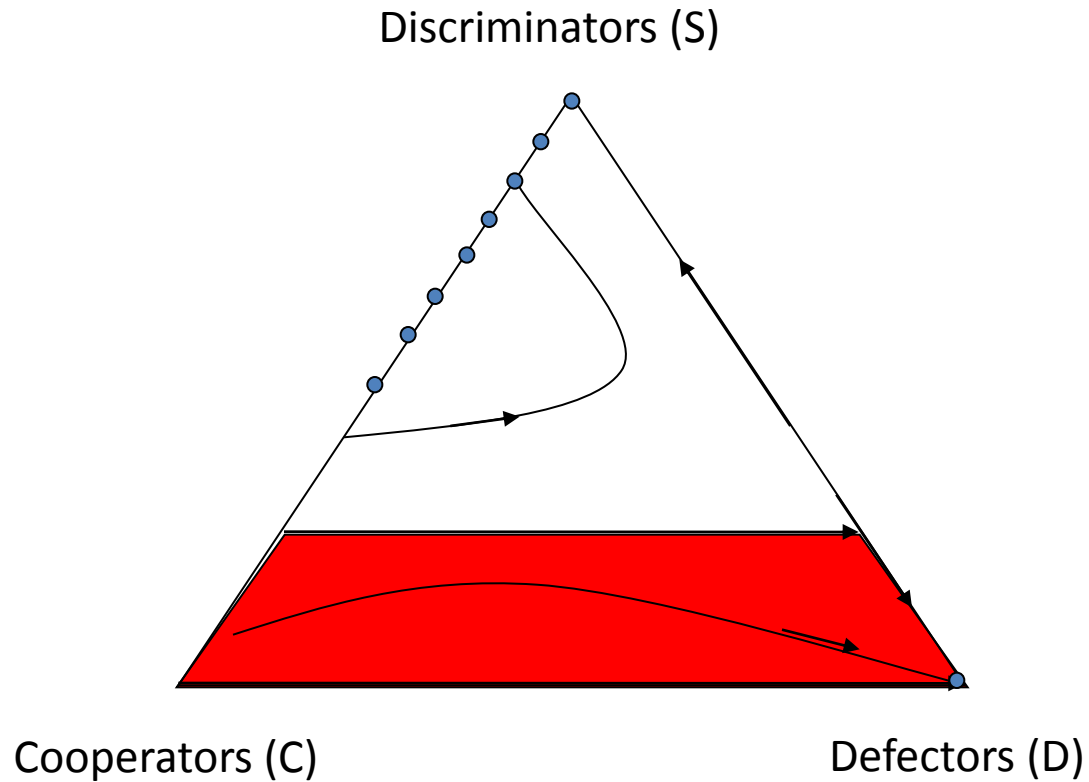


# Analytic results from Nowak and Sigmund



Outcome is independent of  $N$  or  $n$  (assuming large  $n$ )

## Basin of attraction for Defection (shaded red)



# Real interactions in nature

- Small group sizes  $n < 100$
- Structured interactions – more likely to interact with particular individuals than others
- Example: chimpanzee grooming interactions observed by Yvan Russell
  - Russell, Y. I. (2010). Third party grooming in a captive chimpanzee group. *Primates*, 51, 78-82.x

# What about smaller groups?

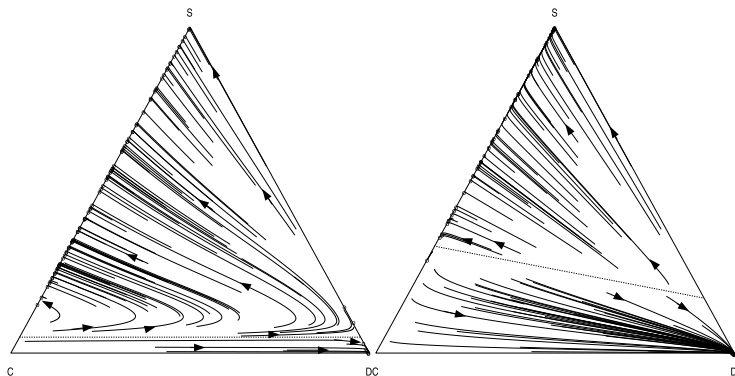
- What happens if we drop the assumption that  $n$  is very large relative to  $N$ ?
- More difficult to derive closed-form expressions for payoffs
- Therefore we estimate payoffs using simulation, and solve the RD equation numerically

Phelps, S., Nevarez, G., & Howes, A. (2009). The effect of group size and frequency of encounter on the evolution of cooperation. LNCS, Volume 5778, ECAL 2009, Advances in Artificial Life: Darwin meets Von Neumann (pp. 37-44). Budapest: Springer. doi:10.1007/978-3-642-21314-4\_5

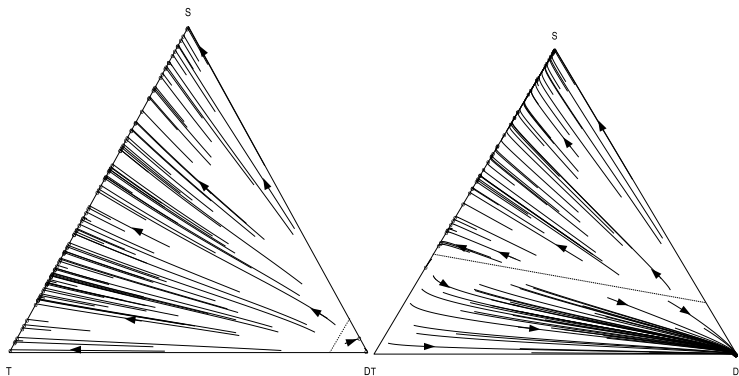
# Heuristic Payoff Matrix

| $n(T4T)$ | $n(S)$ | $n(D)$ | T4T    | S     | D     |
|----------|--------|--------|--------|-------|-------|
| 0        | 0      | 3      |        |       | 0.0   |
| 0        | 1      | 2      |        | -0.03 | 0.015 |
| 1        | 0      | 2      | -0.006 |       | 0.03  |
| 0        | 2      | 1      |        | 0.15  | 0.03  |
| 1        | 1      | 1      | 0.26   | 0.28  | 0.04  |
| 2        | 0      | 1      | 0.45   |       | 0.06  |
| 0        | 3      | 0      |        | 0.9   |       |
| 1        | 2      | 0      | 0.9    | 0.9   |       |
| 2        | 1      | 0      | 0.9    | 0.9   |       |
| 3        | 0      | 0      | 0.9    |       |       |

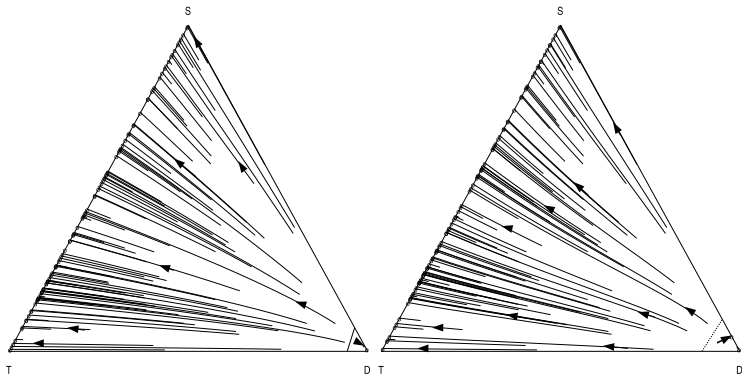
Table : Heuristic payoff matrix for  $n = 3$  agents and  $N = 100$  iterations



**Figure:** Direction field for  $n = 10$  agents and  $N = 100$  pairwise interactions per generation (left) compared with  $N = 13$  (right).  $C$  denotes unconditional altruists,  $D$  unconditional defectors and  $S$  discriminators who cooperate in the first round. Each line represents a trajectory whose termination is represented by an open circle. The arrows show the direction of change.

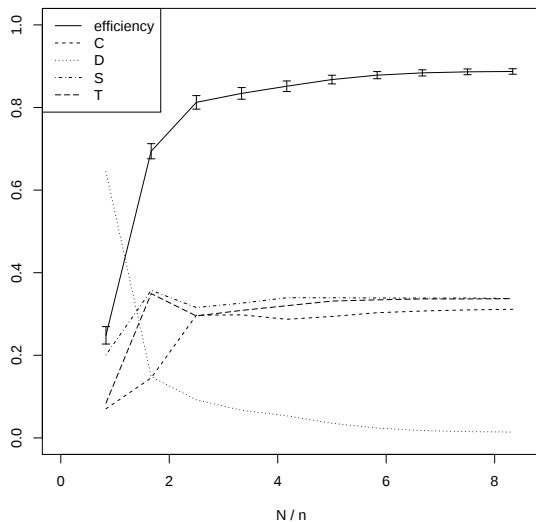


**Figure:** Direction field showing the interaction between the strategies  $T$ ,  $S$  and  $D$  for  $n = 10$  agents and  $N = 100$  pairwise interactions per generation (left) compared with  $N = 13$  (right).

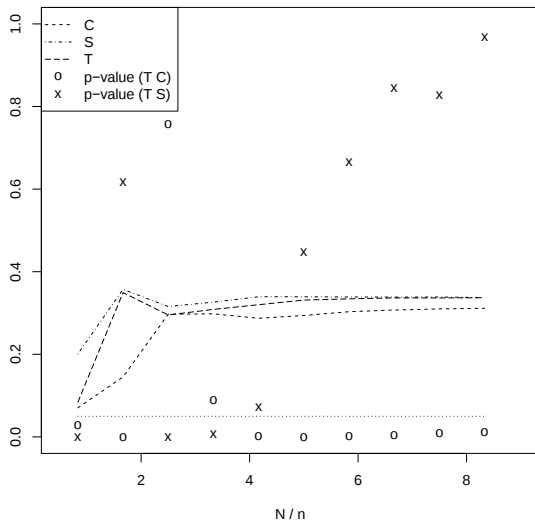


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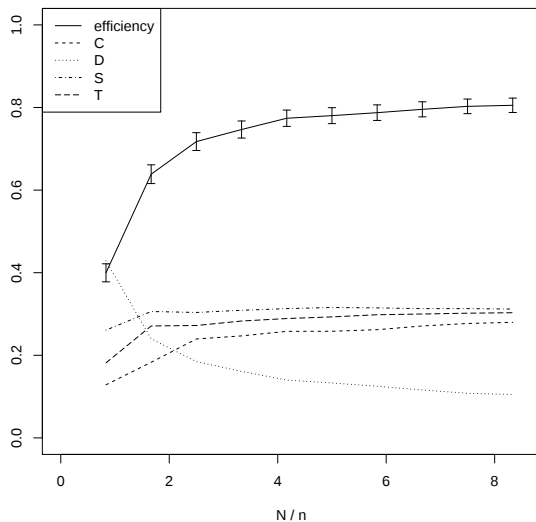
# Mean frequency in equilibrium weighted by basin size



## p-values (t-test)



# Results under conformist bias



# Cooperation over networks

- What effect do networks have?
- Two existing approaches:
  - Static: generate network then allow play
  - Dynamic: agents can adjust their ties

F. C. Santos, et al. (2006). 'Cooperation Prevails When Individuals Adjust Their Social Ties'. *PLoS Comput Biol* **2**(10): e140. doi:10.1371/journal.pcbi.0020140.

F. C. Santos, et al. (2006). 'Graph topology plays a determinant role in the evolution of cooperation'. *Proceedings of the Royal Society B: Biological Sciences* **273**(1582):51–55.

F. C. Santos, et al. (2006). 'Graph topology plays a determinant role in the evolution of cooperation'. *Proceedings of the Royal Society B: Biological Sciences* **273**(1582):51–55.

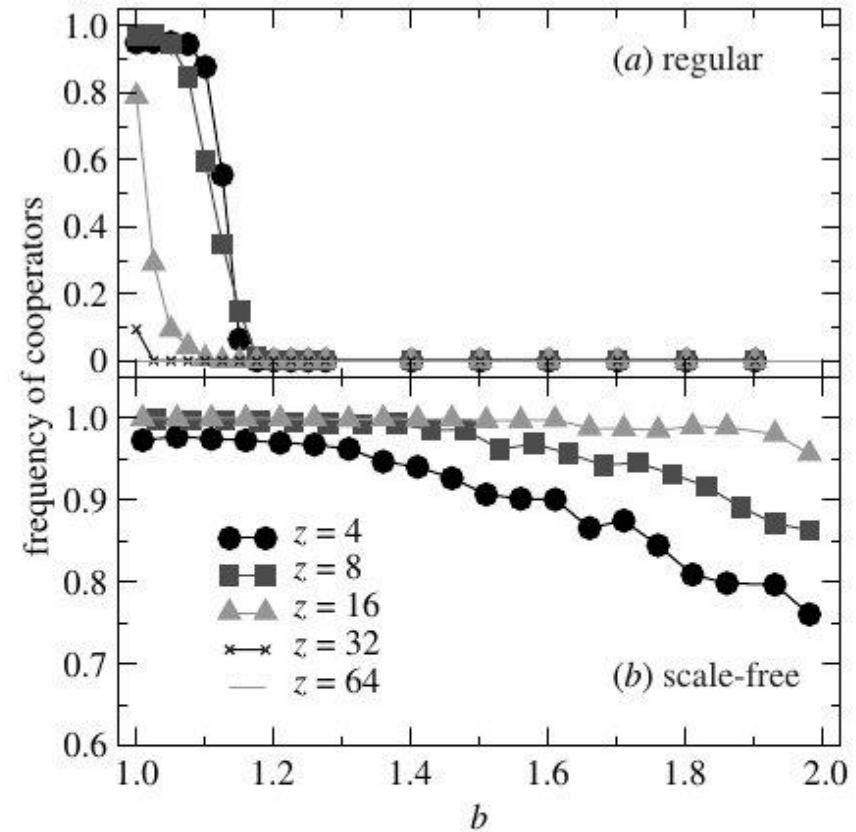
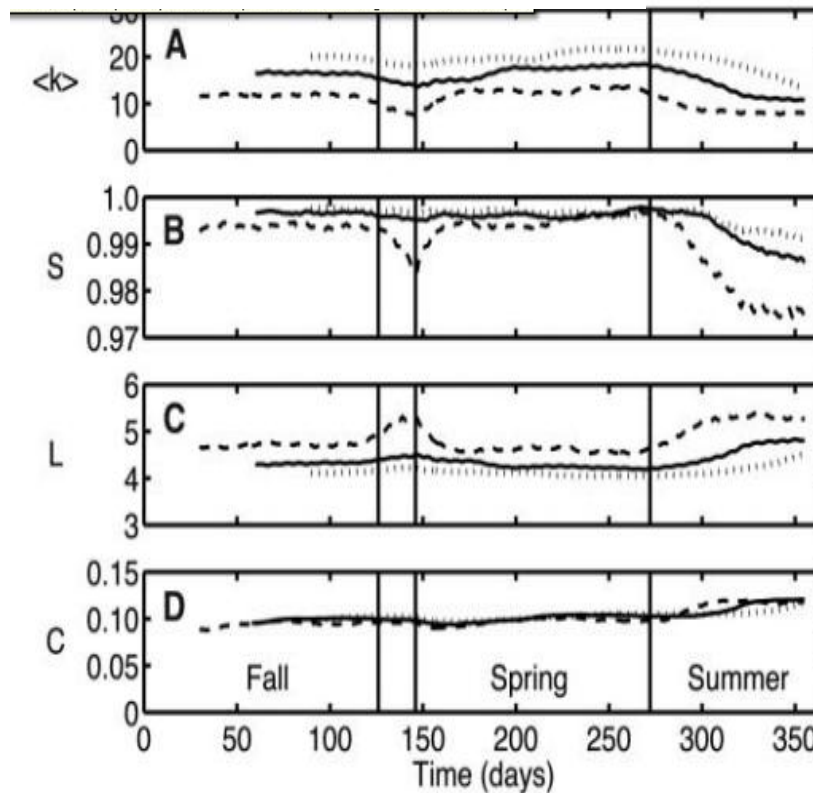


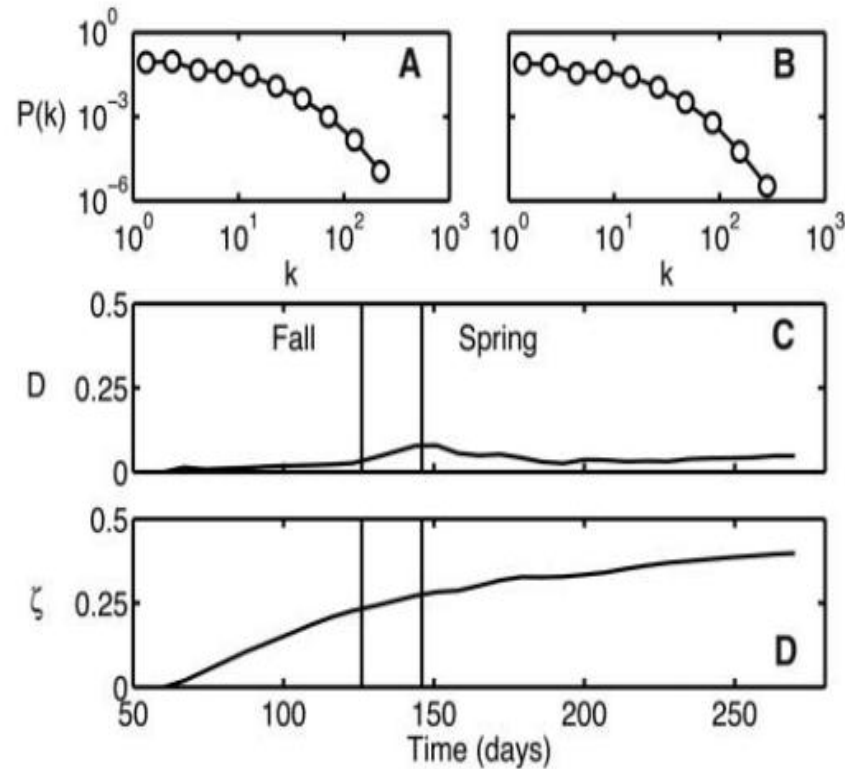
Figure 1. Frequency of cooperators on different NOCs. Results for the PD shown as a function of the cheating advantage  $b$ . Results for (a) regular NOCs and different values of the average connectivity  $z$ ; (b) scale-free NOCs and different values of  $z$ . In all cases,  $N=10^4$ . Cooperation hardly dominates on regular networks, but clearly dominates for all values of  $b$  on scale-free NOCs generated including growth and preferential attachment.

# Real networks are dynamic: Global properties

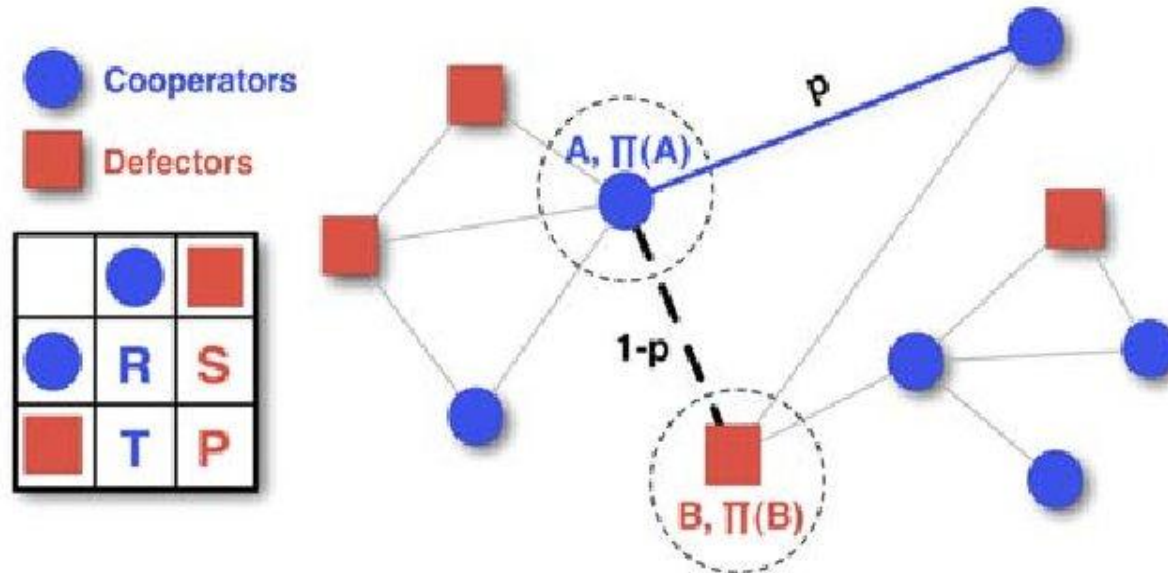


G. Kossinets & D. J. Watts (2006). 'Empirical Analysis of an Evolving Social Network'. *Science* **311**(5757):88–90.

# Empirical Social Networks: Local properties



G. Kossinets & D. J. Watts (2006). 'Empirical Analysis of an Evolving Social Network'. *Science* **311**(5757):88–90.

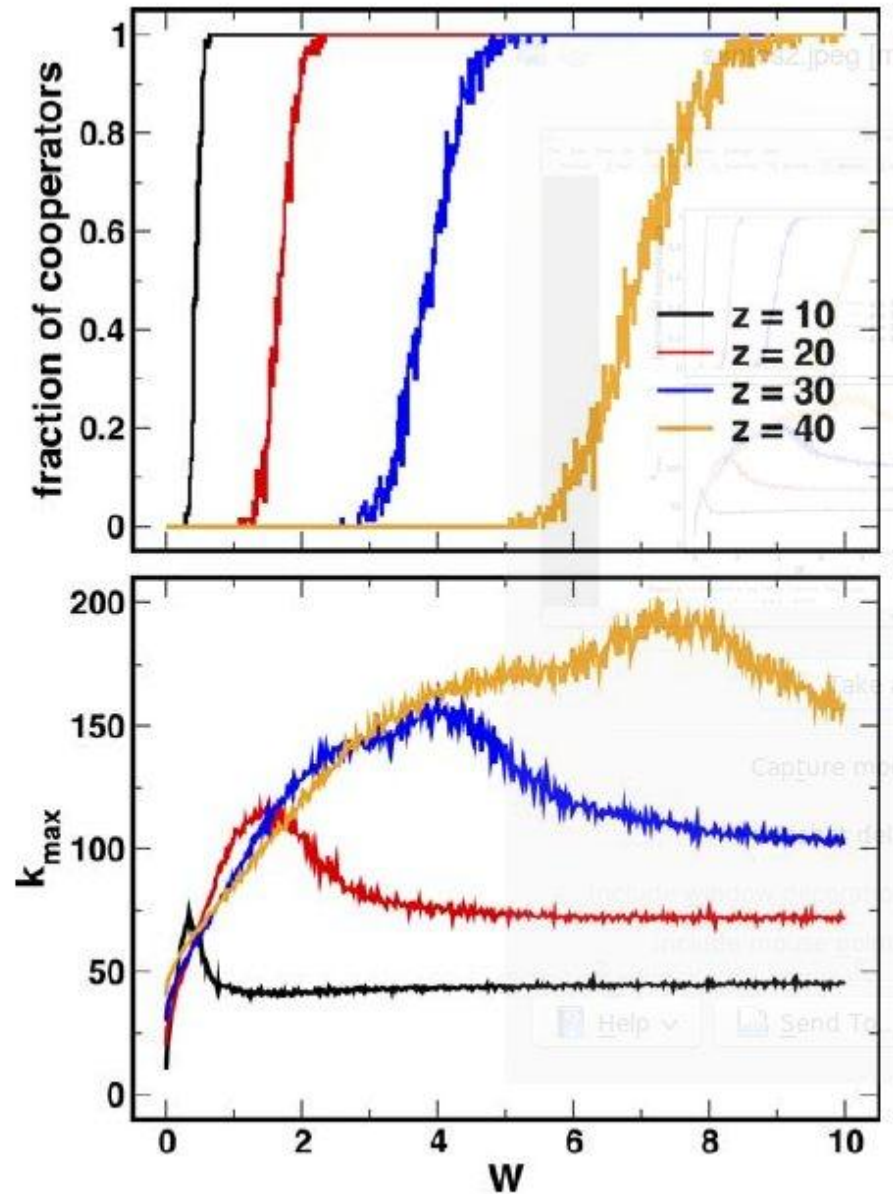


**Figure 1.** Evolving the Neighbourhood

Cooperators and defectors interact via the edges of a graph. B (A) is satisfied (dissatisfied), since A (B) is a cooperator (defector). Therefore, A wants to change the link whereas B doesn't. The action taken is contingent on the fitness  $\Pi(A)$  and  $\Pi(B)$  of A and B, respectively. With probability  $p = [1 + e^{-\beta[\Pi(A) - \Pi(B)]}]^{-1}$  (where  $\beta = 0.005$ , (see Materials and Methods)), A redirects the link to a random neighbor of B. With probability  $1 - p$ , A stays linked to B. Other possibilities occur: whenever both A and B are satisfied, nothing happens. When both A and B are dissatisfied, rewiring takes place such that the new link keeps attached to A with probability  $p$  and attached to B with probability  $1 - p$ .

DOI: 10.1371/journal.pcbi.0020140.g001

F. C. Santos, et al. (2006). 'Cooperation Prevails When Individuals Adjust Their Social Ties'. *PLoS Comput Biol* **2**(10).



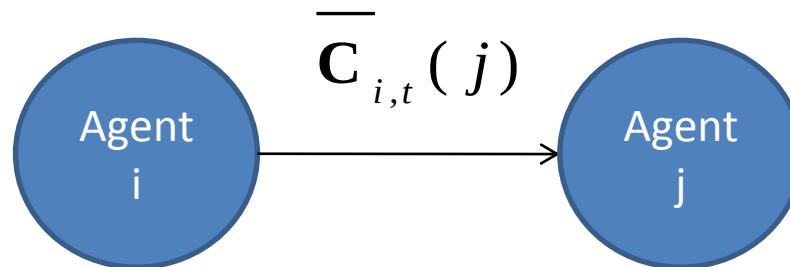
**Figure 3.** Co-Evolution in the PD for Different Time Scales  
PD with  $b/c = 2$  ( $T = 2, S = -1$  and  $\beta = 0.005$ ).

# Real networks again

- Real interactions occur in small groups  $n < 100$
- Santos et al. results only hold for  $n > 1000$
- There is clear evidence that animals use information when forming new “links”
- We need a model that works for small group sizes, and also incorporates intelligent partner selection – e.g. indirect reciprocity

# The Nowak & Sigmund model as a network

- Network is a Directed Graph whose vertices are the agents and whose edges are the EMA of historical investment between  $i$  and  $j$



- Network structure *emerges* from interactions rather than *driving* interactions

# Emergent network model

- All agents interact simultaneously
- Just as with public goods games and previous model there is an initial endowment and a multiplier  $m$
- Agents choice is how to distribute their endowment amongst the other agents as a function of available information
- Agents choose a portfolio vector...

$$\mathbf{C}_{i,t} = (w_1, w_2, \dots, w_n) \quad (1)$$

which obeys the constraints:

$$\mathbf{C}_{i,t}(j) \in [0, 1] \subset \mathbb{R} \quad \forall_{i,j} \quad (2)$$

$$\mathbf{C}_{i,t}(i) = 0 \quad \forall_i \quad (3)$$

$$\sum_{j=0}^n \mathbf{C}_{i,t}(j) \leq 1 \quad \forall_i \quad (4)$$

Payoff to agent  $i$  at time  $t$ :

$$U_{i,t} = \sum_{j=1}^n C_{j,t}(i) \cdot \gamma \cdot m - \sum_{j=1}^n C_{i,t}(j) \cdot \gamma \quad (5)$$

Reputation of agent  $i$ :

$$r_{i,t} = \sum_{j=1}^n C_{i,t-1}(j) \quad (6)$$

History of reputation and investments available as an exponential moving average of past values:

$$\bar{r}_{i,t} = \alpha \cdot r_{i,t} + (1 - \alpha) \cdot \bar{r}_{i,t-1} \quad (7)$$

$$\bar{C}_{i,t}(j) = \alpha \cdot C_{i,t}(j) + (1 - \alpha) \cdot \bar{C}_{i,t-1}(j) \quad (8)$$

# Strategies

Defect (D)  $C_{i,t}(j) = 0 \quad \forall a_j \in A$

Cooperate (C)  $C_{i,t}(j) = \frac{1}{n-1} \quad \forall a_j \in A: j \neq i$

Reputation-weighted (RW)  $C_{i,t}(j) = \frac{\bar{r}_{j,t-1}}{\sum_{k=1}^n r_k} \quad \forall a_j \in A: j \neq i$

Tit4Tat (T4T)

$$\bar{C}_{j,t-1}(i) > T \Rightarrow C_{i,t}(j) = \frac{\bar{C}_{j,t-1}(i)}{\sum_{k: \bar{C}_{k,t-1}(i) > T} \bar{C}_{k,t-1}(i)}$$

# Learning



$$Q_{i,t}(s_{i,t-1}) = \alpha \cdot (U_{i,t-1} + \beta \cdot Q_{i,t}^*) + (1 - \alpha) \cdot Q_{i,t-1}(s_{i,t-1})$$

Roth, A. E. & Erev, I. (1995). 'Learning in extensive form games: experimental data and simple dynamic models in the intermediate term'. *Games and Economic Behavior* **8**:164–212.

# Epsilon-greedy action selection

- For small  $\varepsilon \in [0,1]$

Random variate  $\eta_t \sim U(0,1)$

Exploit with  $P(1-\varepsilon)$   $\eta_t > \varepsilon \Rightarrow \text{choose}(s_t^*)$

Explore with  $P(\varepsilon)$   $\eta_t \leq \varepsilon \Rightarrow \text{choose}(s \sim U(1, n_s))$

# Data collection

- ▶ Chimpanzees (*Pan troglodytes*)
- ▶ 26 members, mean age 18.7 years (SD = 11.4), range 2-38 years
- ▶ 18 adults (4 male, 14 female), 6 subadults (all female), and two juveniles (1 male, 1 female).
- ▶ Observed for 82 days (402.5 hrs), 2003-2004, by Yvan Russell



- ▶ Scan sampling, recorded to nearest second
- ▶ Recording grooming cliques (identity of groomers, direction of grooming) within 10m of chosen focal animal
- ▶ Here, subset of 59.8 hours was analyzed



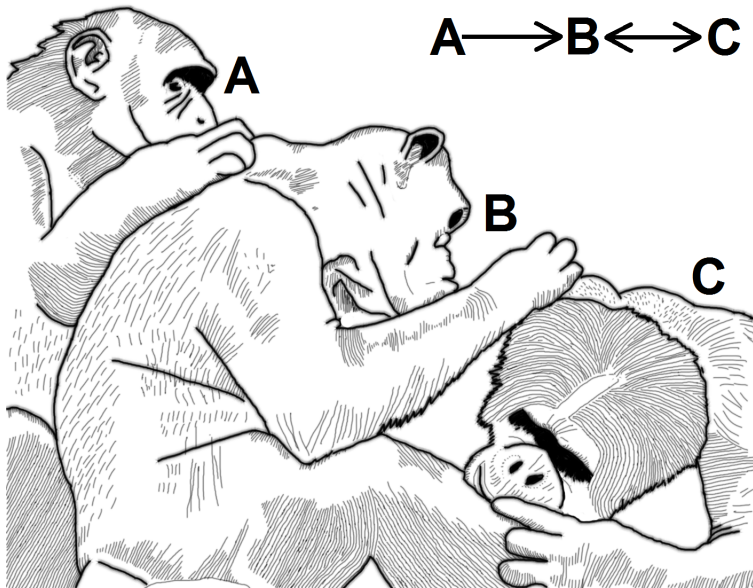
[Russell, 2007]



[Russell, 2007]



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# Research questions

- ▶ **Is grooming reciprocated?**
- ▶ Is there direct reciprocity?
- ▶ Is there indirect reciprocity?
- ▶ What is the time horizon for tracking debts?
- ▶ Are results distinguishable from a null model of random grooming behaviour?

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# Reciprocity analysis - traditional approach

668 L. Barrett and others *Grooming reciprocity in female baboons*

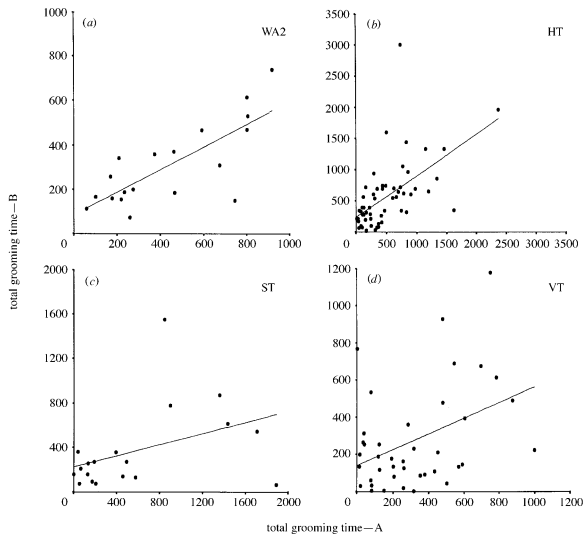


Figure 2. The degree of time matching within reciprocated grooming bouts.

[Barrett et al., 1999]

# Immediate reciprocation

*“Henzi et al. (1997) showed that within-bout reciprocation is essential for the maintenance of grooming dyads over time, suggesting that there is something critically important about the capacity to respond to grooming immediately. Given this, and the problem of determining a priori the period over which to measure responses to non-reciprocated bouts (minutes, hours or days), the analyses were based only on immediately reciprocated bouts . . .”*

[Barrett et al., 1999][p. 666]

# Reciprocity analysis - longitudinal approach

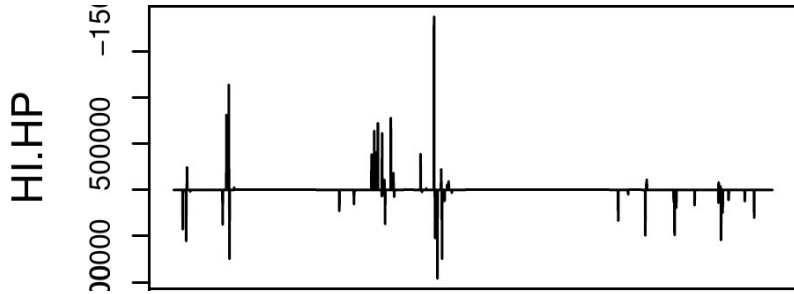
- ▶ Grooming events consist of a dyad, start time, direction and duration.
- ▶ Let  $g_{(i,j,t)}$  represent an event in which  $i$  groomed  $j$  starting at time  $t$ . The value  $g$  represents the total duration of this event, and the sign of  $g$  represents the direction.
- ▶ Events are partitioned into time windows each of duration  $\Delta t$ .
- ▶ The cumulative totals over each window give us the *grooming imbalance*:

$$G_{(i,j,t_0)} = \left| \int_{t_0}^{t_0 + \Delta t} g_{(i,j,t)} dt \right| \quad (1)$$

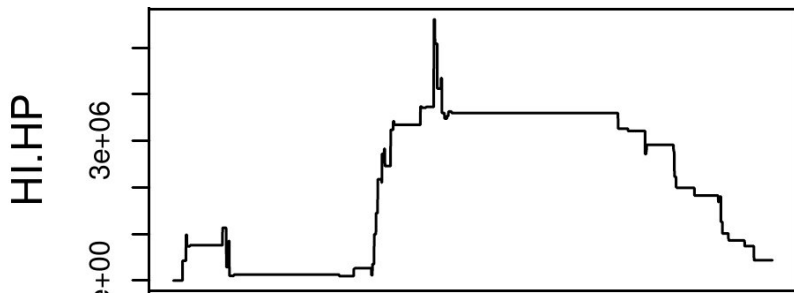
Table : Observation sessions

| No. | Date   | Start time | End time | Duration (minutes) |
|-----|--------|------------|----------|--------------------|
| 1   | Nov 4  | 9:52       | 11:26    | 94                 |
| 2   | Nov 4  | 11:50      | 14:26    | 156                |
| 3   | Nov 5  | 10:43      | 12:41    | 118                |
| 4   | Nov 5  | 13:06      | 15:40    | 154                |
| 5   | Nov 6  | 10:18      | 14:24    | 246                |
| 6   | Nov 6  | 14:50      | 16:06    | 76                 |
| 7   | Nov 7  | 10:45      | 13:30    | 165                |
| 8   | Nov 7  | 14:04      | 16:06    | 122                |
| 9   | Nov 11 | 10:42      | 14:30    | 228                |
| 10  | Nov 11 | 15:15      | 16:10    | 55                 |
| 11  | Nov 12 | 10:20      | 13:37    | 197                |
| 12  | Nov 12 | 13:59      | 14:14    | 15                 |
| 13  | Nov 12 | 14:30      | 16:05    | 95                 |
| 14  | Nov 13 | 13:40      | 15:26    | 106                |
| 15  | Nov 14 | 9:55       | 11:15    | 80                 |
| 16  | Nov 14 | 11:48      | 12:45    | 57                 |
| 17  | Nov 16 | 13:05      | 14:05    | 60                 |
| 18  | Nov 19 | 10:11      | 15:30    | 319                |
| 19  | Nov 21 | 10:23      | 13:46    | 203                |

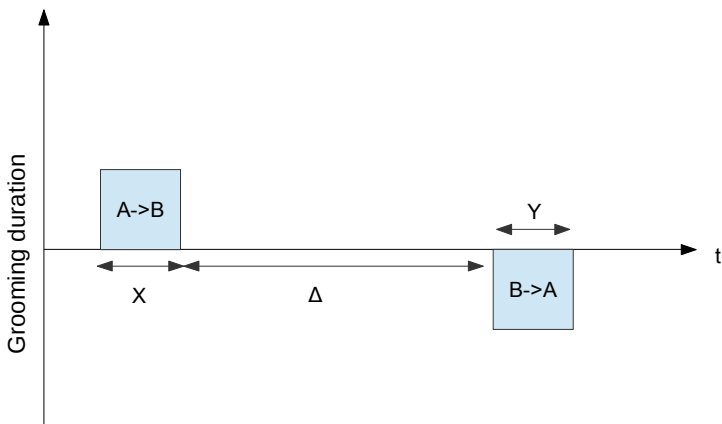
## Individual reciprocity metrics: $g$



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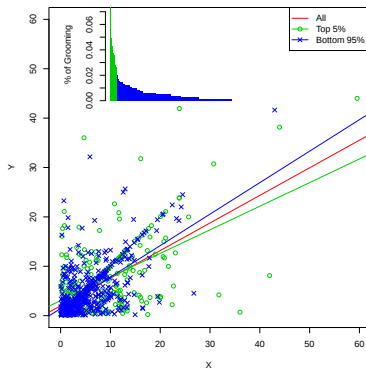


Consecutive or simultaneous pairs of grooming events between any given dyad  $\{A, B\}$  are represented in our data-set by triples  $(X, Y, \Delta)$ , where:  $X$  represents the time that  $A$  spent allogrooming  $B$ ;  $Y$  represents the time that  $B$  spent allogrooming  $A$  and  $\Delta$  represents the time that elapsed between (i)  $A$  finishing grooming  $B$ , and (ii)  $B$  starting to groom  $A$ . Simultaneous grooming is recorded using negative values of  $\Delta$ .

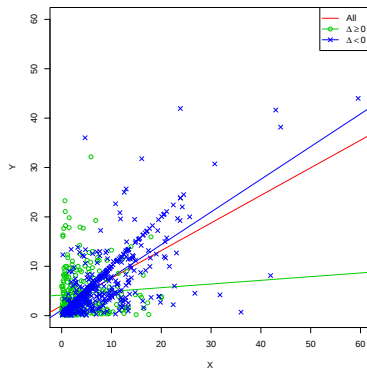


**Figure :** The model used for the longitudinal regression analysis.

# Longitudinal time-matching (i)

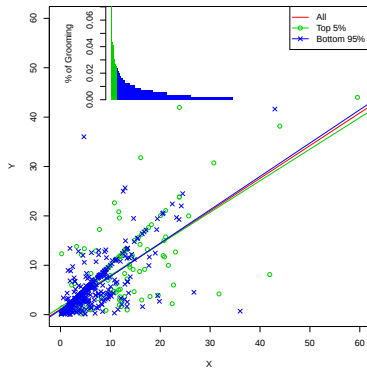


(a) Time-matching (all)

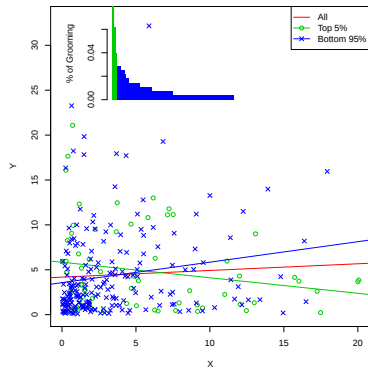


(b) Time-matching by  $\Delta$

# Longitudinal time-matching (ii)



(c) Within-bout time-matching  $\Delta < 0$

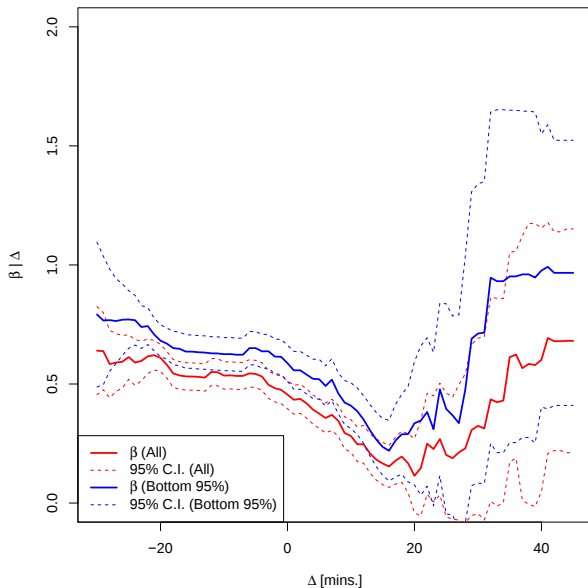


(d) Delayed time-matching  $\Delta \geq 0$

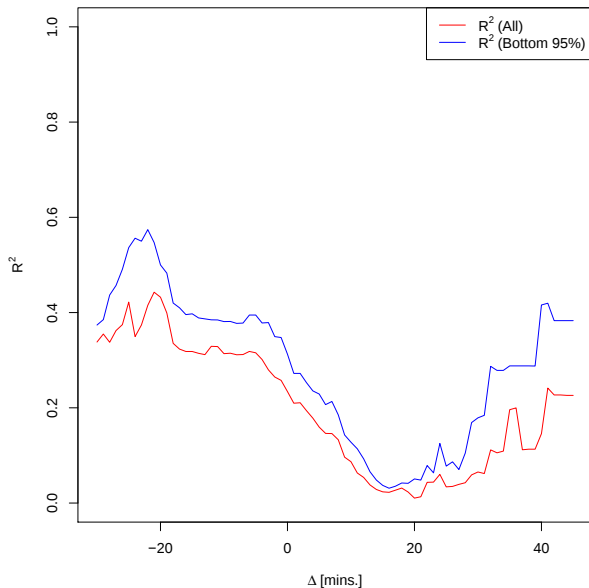
# Time-matching regression statistics

| <i>Figure</i> | <i>Condition</i>                 | $R^2$ | $\beta$ | $p$ -value              |
|---------------|----------------------------------|-------|---------|-------------------------|
| 2(a)          | <b>Overall time-matching</b>     |       |         |                         |
|               | All                              | 0.36  | 0.56    | $< 2 \times 10^{-16}$   |
|               | Top 5% grooming activity         | 0.30  | 0.48    | $< 2.2 \times 10^{-16}$ |
|               | Bottom 95% grooming activity     | 0.40  | 0.63    | $< 2 \times 10^{-16}$   |
| 2(c)          | <b>Within-bout time-matching</b> |       |         |                         |
|               | All                              | 0.53  | 0.66    | $< 2 \times 10^{-16}$   |
|               | Top 5% grooming activity         | 0.51  | 0.64    | $< 2 \times 10^{-16}$   |
|               | Bottom 95% grooming activity     | 0.50  | 0.68    | $< 2 \times 10^{-16}$   |
| 2(d)          | <b>Delayed time-matching</b>     |       |         |                         |
|               | All                              | 0.01  | 0.07    | 0.27                    |
|               | Top 5% grooming activity         | 0.04  | -0.17   | 0.11                    |
|               | Bottom 95% grooming activity     | 0.03  | 0.23    | 0.01                    |

# Coefficient of time-matching by $\Delta$



## $R^2$ of time-matching regression by $\Delta$



## Indirect reciprocity in Chimpanzees

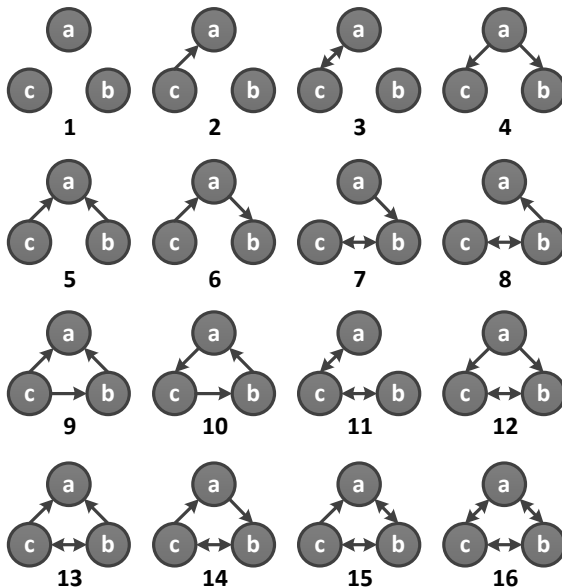
*"We tested for image scoring in chimpanzees, bonobos, gorillas, and orangutans. Subjects passively observed two types of incident: (i) a 'nice' person gave grapes to a human beggar, and (ii) a 'nasty' person refused to give. The subject witnessed both incidents in succession (but was unable to obtain the grapes). Shortly after, the ape had an opportunity to approach one or both human actors (nice/nasty), both of whom were now sitting side-by-side holding grapes. However, neither human offered their grapes if approached. The subject's expectation of which human was more likely to offer food was measured by comparing the proportion of time that subjects spent near each person. Chimpanzees ( $n = 17$ ) spent significantly more time at the 'nice' window compared to 'nasty'. Also, preference for 'nasty' declined as trials progressed. Results for other apes were not significant."*

[Russell et al., 2008]

# Indirect reciprocity

- ▶ Thus far our analysis has focused on dyads, i.e. subgraphs of size  $n = 2$
- ▶ Direct reciprocity can be detected by such an analysis
- ▶ However, to test for *indirect* reciprocity we need to examine subgraphs of size  $n > 2$
- ▶ Simplest such case is  $n = 3$ , i.e. triads

## Network motifs $n = 3$



# Motifs in bioinformatics

- ▶ Originally developed for bioinformatics and theoretical biology [Itzkovitz et al., 2003, Kashtan et al., 2004]
- ▶ Used to analyse transcriptional regulatory networks, gene networks or food webs [Mangan et al., 2003, Milo et al., 2002].
- ▶ Micro-foundations of network biology?
- ▶ To date, several interesting properties of large *biological* network structures were reinterpreted or discovered with help of motif analysis [Mangan et al., 2003, Vazquez et al., 2004, Young-Ho et al., 2006].

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# Summary

- ▶ Our models show the importance of both direct *indirect reciprocity* reciprocity in smaller populations
- ▶ Working towards testing these models against empirical data
- ▶ To this end, we have developed method for detecting direct reciprocity over different time periods
- ▶ Presented some early results on direct reciprocity in a Chimpanzee group
- ▶ Future work: detection of indirect reciprocity using motif analysis

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