Journal of Theoretical Biology 344 (2014) 49–55

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Partner choice promotes cooperation: The two faces of testing with agent-based models

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HIGHLIGHTS

- We developed an agent based model of cooperation based on partner choice.
- Our model reproduced important features of cooperation in group living animals.
- Partner choice based on benefits received can sustain the evolution of cooperation.

ARTICLE INFO

Article history:
Received 24 April 2013
Received in revised form
14 November 2013
Accepted 25 November 2013
Available online 4 December 2013

Keywords:
Social relationships
Proximate mechanisms
Evolution

ABSTRACT

Reciprocity is one of the most debated among the mechanisms that have been proposed to explain the evolution of cooperation. While a distinction can be made between two general processes that can underlie reciprocation (within-pair temporal relations between cooperative events, and partner choice based on benefits received), theoretical modelling has concentrated on the former, while the latter has been often neglected. We developed a set of agent-based models in which agents adopted a strategy of obligate cooperation and partner choice based on benefits received. Our models tested the ability of partner choice both to reproduce significant emergent features of cooperation in group living animals and to promote the evolution of cooperation. Populations formed by agents adopting a strategy of obligate cooperation and partner choice based on benefits received showed differentiated "social relationships" and a positive correlation between cooperation given and received, two common phenomena in animal cooperation. When selection across multiple generations was added to the model, agents adopting a strategy of partner choice based on benefits received outperformed selfish agents that did not cooperate. Our results suggest partner choice is a significant aspect of cooperation and provides a possible mechanism for its evolution.

1. Introduction

The exchange of cooperative behaviours is a common feature of animal societies. This is particularly true for those species that form stable social groups, where exchanges of cooperative behaviours such as grooming, tolerance around resources or aggressive coalitions are frequently observed (Dugatkin, 1997; Cheney, 2011). The analysis of how group-living animals distribute their cooperative behaviours among group mates has revealed some common features that can be observed across a variety of settings and species. First, group-living animals show differentiated social relationships, meaning that each group member interact/cooperate frequently with some group mates and rarely, if ever, with others. As a result, pairs of animals belonging to the same social group differ widely in their frequency of interaction. Second, a positive relation is often found across pairs between cooperation given and received (Schino, 2007; Schino and Aureli, 2008; Seyfarth and Cheney, 2012).

Among the several hypotheses that biologists have proposed to explain the evolution of cooperative behaviours (West et al., 2007) reciprocity is perhaps the most debated, and reviews of its empirical evidence have reached widely diverging conclusions (Cheney, 2011; Clutton-Brock, 2009; Schino and Aureli, 2009). Part of this confusion stems from a failure to appreciate that two different processes can underlie reciprocation. The first process, that we call "temporal relations between events", is a strictly

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http://dx.doi.org/10.1016/j.jtbi.2013.11.019

within-pair process: subject A behaves cooperatively towards B in relation to how B has previously behaved towards A. Each A–B pair is conceptually isolated from all others, that is, the presence and behaviour of other individuals do not affect the behaviour of the A–B pair. This is essentially equivalent to Bull and Rice (1991) "partner-fidelity model", to Noë (2006) "partner control model" and to classical reciprocal altruism (Trivers, 1971). The classical iterated prisoner's dilemma belongs to this category of models. The second process, that we call "partner choice based on benefits received", is an across-pair process with a strong comparative component: subject A behaves cooperatively towards B rather than C in relation to a comparison of how B and C have behaved towards A. This is essentially partner choice based on outbidding competition (Noë and Hammerstein, 1994) and is equivalent to Bull and Rice (1991 and to Noë (2006) "partner-choice model", see (Eshel and Cavalli-Sforza, 1982) for an earlier study]. Empirical evidence shows reciprocal exchanges of cooperative behaviours depend more commonly on partner choice based on benefits received than on within-pair temporal relations between events (Tiddi et al., 2011; Fruteau et al., 2011).

Despite its prevalence, partner choice has been widely neglected as a general explanation for the evolution of cooperative behaviours (Sachs et al., 2004). Rather, theoretical modelling has focused mostly on the analysis of within-pair temporal relations between events, and a vast literature exists on the possible strategies that can promote the evolution of cooperation through this process (Bshary and Bronstein, 2011; Nowak, 2006; Nunn and Lewis, 2001; Lehmann and Keller, 2006; André and Baumard, 2011). In contrast, theoretical models of the evolution of cooperation by partner choice are comparatively rare. In some of the few existing examples, partner choice is based on the general tendency of potential partners to cooperate, rather than on actual cooperation received by each partner (Barclay, 2011; Roberts, 1998). As such, these models seem more relevant to indirect than to direct reciprocity. In other modelling attempts, partner choice is included in the form of the possibility to terminate a within-pair series of cooperative interactions (Sherratt and Roberts, 1998; Johnstone and Bshary, 2002). The relative paucity of models of partner choice based on benefits received is puzzling, considering its obvious relevance for group living animals.

When developing a theoretical model of a biological phenomenon, one can aim either at reproducing important features of the target system "as is" [for cooperative exchanges, see 26], or at modelling its evolution, i.e., at reproducing the changes that would occur across generations as a result of natural selection (Axelrod and Hamilton, 1981). Ideally, however, a good model should be able to reproduce both aspects of the phenomenon and if both tests are successful a stronger case for the relevance of the principles underlying the model in explaining the target system being modelled could be made. In this study, we developed a model of cooperation based on partner choice and explored its ability to explain both features of cooperation in group living animals and the evolution of cooperation. We took particular care in excluding alternative elements that could drive reciprocal cooperation in order to obtain a model based on "pure" partner choice.

2. Models

We developed our agent-based models using NetLogo 4.1. Wilensky, (1999); the source code of all the models is available upon request. Statistical analyses were conducted in R version 2.14.2 R Development Core Team, 2012.

2.1. "Single-generation" model

We developed this model to test whether a strategy of partner choice based on benefits received can reproduce significant emergent features of cooperation in group living animals.

Agents were created and equipped with a behavioural strategy and memory of past interactions. At each step of the simulation, all agents behaved cooperatively as explained below. First, an agent (the "actor") is randomly chosen from the population. Then, a subset of other agents (the "candidates") is randomly extracted among the remaining agents. The actor inspects its memory of past interactions and directs its cooperative behaviour towards the candidate that, in the previous steps of the simulation, had behaved most cooperatively towards it. If there is no memory of past interactions (i.e., when $t=0$) or if the actor's memory stores the same number of cooperative interactions received from more than one candidate, the choice between these candidates is made at random. The chosen candidate updates its memory of cooperation received. All agents in the population go through this sequence at each step of the simulation.

Size of the memory and number of candidates was varied systematically as summarized in Table 1.

The output of each simulation was a sociometric matrix showing the cooperation given by each agent to each other agent in the population. For each simulation, we calculated the within-subject linear regression between cooperation given and received to/by each other agent. We also produced figures representing the social networks of cooperation exchanged between agents. Finally, we evaluated how reciprocity developed by calculating the within-subject linear regression between cooperation given and received at different time steps during the simulation.

2.2. "Multi-generation" evolutionary models

We developed two evolutionary agent based models in order to test whether a strategy of partner choice based on benefits received can promote the evolution of cooperation. Agents were created and equipped with a behavioural strategy (see below) and memory of past interactions. Behavioural interactions had fitness costs and benefits, and the population composition varied generation after generation depending on the evolutionary success of the different strategies agents adopted.

2.2.1. First model

In a first evolutionary model, agents were created that adopted one of two different behavioural strategies, choosing cooperative or selfish. Choosing cooperators behaved as described in the single-generation model. Selfish agents never cooperated, but could be the recipient of cooperative behaviour by agents adopting the choosing cooperative strategy. At each step of the simulation, each agent behaved according to its own strategy.

Cooperation implied a cost for the actor and a benefit for the recipient. The fitness function used to evaluate individual success was calculated as the difference between the accumulated benefits received and costs incurred during a generation cycle.

Table 1
Parameters used to run the "single-generation" model.

Parameters	Values
Population size (*N* of agents)	50
Memory (*N* of previous steps)	0, 5, 100, 1000
Candidates for the interaction (*N* of agents)	2, 10, 25, 49
Number of steps per simulation	10000
Number of simulations (replicates)	100