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Original Article

Evolution of parochial altruism by multilevel selection

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Abstract

The evolution of parochial altruism is not well understood. We study this problem by considering a prisoner's dilemma game with four strategies: altruists who cooperate with everyone; parochialists who only cooperate with members of their own group; traitors who only cooperate with outgroup individuals; and egoists who never cooperate. We develop a model that allows for both assortment and conflict between groups. Individuals discriminate between in- and outgroup members. While assortment and conflict allow for the evolution of both indiscriminate and parochial altruism, discriminate behavior creates an advantage for parochialists over altruists, as the latter waste help on outgroup members. We use computer simulations to study the multilevel selection dynamics. The simulation model describes an absorbing Markov chain. We examine the absorption probabilities of altruists and parochialists. Three model versions are compared, with only assortment, with only group conflict, and with both mechanisms. We find that parochialism is selected for by group conflict as well as assortment. Discrimination allows for cooperation inside groups to withstand regular interactions with outgroup members.

Keywords: Discrimination; Group conflict; Multilevel selection; Parochialism

1. Introduction

Altruism can be regarded as a fitness transfer from altruistic individuals to recipients. If such a transfer is limited to donors and recipients belonging to the same group, we speak of parochial altruism. Human altruism seems to have a parochial component. A general tendency to favor group fellows over strangers is well documented (Bernhard et al., 2006a, 2006b; Hewstone et al., 2002). Although many models have been proposed to account for the evolution of (indiscriminate) altruism (e.g., Price, 1972; Hamilton, 1975; Frank, 1998; Lehmann and Keller, 2006; Nowak, 2006), ultimate or evolutionary explanations of parochial altruism have only recently received some attention (Bowles and Choi, 2004; Hammond and Axelrod, 2006; Choi and Bowles, 2007; Lehmann and Feldman, 2008). Models of group selection (e.g., Boorman and Levitt, 1972; Aoki, 1982; Bowles et al., 2003; Traulsen and Nowak, 2006; Lehmann and Keller, 2006) cannot explain the evolution of parochialism, since either intergroup interaction is limited or individuals employ identical strategies towards ingroup and outgroup members. We propose a multilevel selection model that provides an explanation for the evolution of parochial traits. Selection for group-contingent altruism stems from group competition and assortment. Group competition can favor individuals who help group fellows and harm strangers, while assortment favors such parochialists if limited dispersal allows them to disproportionally interact with each other. We disentangle these two mechanisms in examining the role of intergroup interactions in the evolution of helping behavior. Recently, Choi and Bowles, (2007) presented an agent-based simulation model that addresses the coevolution of war and parochial altruism. Parochial altruism has a different meaning here than in our approach: namely, willingness to sacrifice oneself in a conflict with other groups. Evolution in their model is driven by conflicts between groups, and conflict frequencies are made endogenous by assuming that the likelihood of engaging in conflict

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depends on the number of parochialists in a group. Group conflicts entail an explicit cost. A recent paper by Lehmann and Feldman (2008) also examines how individual traits may coevolve with intergroup conflicts and how the latter may have reproduction-enhancing effects for different life-history features such as migration and group size, as well as for sex in diploid individuals. The focus of these models is the evolution of hostility between groups. This fits the aim of providing an evolutionary explanation of warfare. Instead, we aim to explain the evolution of group-contingent altruism. We study the evolution of parochial traits by formalizing strategic interactions between individuals from different groups in a social dilemma game. The model includes two ingredients: assortative group formation and conflict between groups. Interactions resemble the experimental set-up of Bernhard et al. (2006a, 2006b), in which matching occurs with members of the own and other groups. Our model of the evolution of group-contingent altruism, in particular with variation in the importance of contacts with members of other groups, allows for empirical application to the evolution of early humans, who may have had few or many intergroup contacts. We first examine whether parochial behavior can arise in unstructured large populations. Next, we consider group conflict and assess the odds for a mutant parochial strategy to reach fixation in an egoist population. The interaction of discrimination, conflict and assortment is examined in detail by simulating a Moran process following the model presented by Traulsen and Nowak (2006). We examine three model versions, which emphasize different ingredients of the evolution of parochial behavior.

2. Within-group selection is insufficient

Consider a prisoner's dilemma (PD) game with strategies cooperate (C) and defect (D), and standard payoffs for the first player: $b-c$ for profile (C, C), $-c$ for (C, D), b for (D, C), and 0 for (D, D). As is common we set $b>c$. If players are assumed to have the capacity to differentiate between ingroup and outgroup members, and to condition their actions on who they interact with accordingly, the simplest possible representation of a strategy is a two-dimensional vector. Its components represent the strategies in response to encountering members of their own and other groups, respectively. This modified PD has four strategies, as listed in Table 1. The strategy space is given by $S=\{A, P, T, E\}$.

Table 1
Strategies in the modified PD

Strategy	In- and outgroup
Altruist (A)	(C,C)
Parochialist (P)	(C,D)
Traitor (T)	(D,C)
Egoist (E)	(D,D)

Our choice of strategies allows for the theoretical possibility of traitorous behavior. This is an automatic outcome of systematically matching discrimination and basic strategies of cooperation and defection. Traitorous behavior is quickly wiped out in all the model analyses presented in later sections. This is consistent with experimental evidence, which does not reveal such behavior (Bernhard et al., 2006a, 2006b; Hewstone et al., 2002). Let us first consider the one-shot interaction game. Here A_{in} represents the payoffs obtained if interaction takes place between members of the same group, and A_{out} the payoffs obtained if interaction takes place between members of different groups.

$$A_{\mathrm{in}} = \begin{pmatrix} b-c & b-c & -c & -c \\ b-c & b-c & -c & -c \\ b & b & 0 & 0 \\ b & b & 0 & 0 \end{pmatrix}$$

$$A_{\mathrm{out}} = \begin{pmatrix} b-c & -c & b-c & -c \\ b & 0 & b & 0 \\ b-c & -c & b-c & -c \\ b & 0 & b & 0 \end{pmatrix}$$

We define the payoff as the expected value resulting from interactions with individuals from the same group (with probability α) and other groups (with probability 1-α). This is a very implicit way of capturing population structure and intergroup interaction, which simplifies the analysis. For $\alpha\in(0,1)$, strategies A, P and T are strictly dominated by E. This is a straightforward consequence of $b>c>0$. Hence, provided that all strategies are present in the initial population, the only stable fixed point of the replicator dynamics is E, and we can conclude that within-group selection leads to egoism. It is not surprising that nonegoist strategies are wiped out here. The replicator dynamics assumes a very large unstructured population, so the probability of meeting any other strategy is independent of one's strategy. This means that nonrandom assortment is not possible. Moreover, there is no mechanism that makes nonegoist strategies beneficial to cooperative individuals as well (Clutton-Brock, 2002). Other possible explanations of parochialism include kin selection and reciprocity. As argued by Bernhard et al. (2006b), such individual selection models are unable to explain discriminate altruism. Instead, multilevel selection may explain parochialism. Group competition can foster parochial preferences while at the same time render indiscriminate altruism or egoism maladaptive. Quantitative analysis of the relationship between multilevel selection and parochial traits requires an explicit description of individual intergroup encounters. This covers the inclusion of occasional encounters between individuals of distinct groups, discriminate behavior towards outgroup members, and conflict between groups.