

Original Article

Evolution of parochial altruism by multilevel selectionJulián García^{a,b,*}, Jeroen C.J.M. van den Bergh^{c,d,1}^a*Faculty of Economics and Business Administration, VU University, Amsterdam*^b*Center for Experimental Economics in Political Decision Making, University of Amsterdam, Amsterdam, The Netherlands*^c*ICREA, Barcelona, Spain*^d*Institute of Environmental Science and Technology and Department of Economics and Economic History, Universitat Autònoma de Barcelona, Spain*

Initial receipt 29 June 2009; final revision received 20 July 2010

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.

© 2011 Elsevier Inc. All rights reserved.

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 disproportionately 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

* Corresponding author.

E-mail address: j.garcia@feweb.vu.nl (J. García).¹ Also affiliated with the Faculty of Economics and Business Administration, and the Institute for Environmental Studies, VU University Amsterdam, The Netherlands.

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 (<i>A</i>) | (<i>C</i> , <i>C</i>) |
| Parochialist (<i>P</i>) | (<i>C</i> , <i>D</i>) |
| Traitor (<i>T</i>) | (<i>D</i> , <i>C</i>) |
| Egoist (<i>E</i>) | (<i>D</i> , <i>D</i>) |

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.

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

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

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 $1-\alpha$). 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.

3. The origin of discriminate strategies

We take as a starting point that altruistic traits originate from a random mutation in a world of egoists. It is not evident whether it is easier for a single altruist to take over a population of egoists, or for a single parochialist to take over a population of egoists. To shed some light on this issue, we analyze the stability of egoism in the face of altruist and parochial mutants. We assess the probability that a group with an altruist or parochialist mutant will be victorious in group conflict.² Consider the social dilemma game given by matrix A , for $b > c > 0$.

$$A = \begin{pmatrix} b - c & -c \\ b & 0 \end{pmatrix}$$

This is a PD game with strategies cooperate (C) and defect (D). Discriminatory behavior yields the extended strategy space presented in Table 1 in Section 2. We study a finite population of m groups, each consisting of n individuals. Individuals are randomly matched to play the game. With probability α , a pair is chosen from the same group. Inside groups, strategies reproduce in proportion to the payoff obtained in the game, following a Moran process. In a subsequent phase, a number of groups from the population probabilistically engage in conflict. More specifically, κ determines the average frequency of groups involved in conflict, at every generation. If κ is .5, on average, half of the groups will take part in a conflict. The group whose sum of fitness values over individuals is larger wins the conflict (Bowles et al., 2003). The losing group disappears, and its place is taken over by a copy of the winning group. Note that while the occurrence of conflict is probabilistic, winning is deterministic. In Section 4, where we use computer simulations, we will relax the latter assumption and examine the consequences of probabilistic winning.

3.1. Indiscriminate altruism

Consider first the case of non-discriminatory strategies, that is, egoism and indiscriminate altruism. There is one single altruist in Group 1. All other groups $j=2, \dots, m$ consist entirely of egoists. We assume that every individual interacts once. If Group 1 goes to conflict, the outcome of the confrontation is completely determined by who the single mutant altruist interacted with. With probability α , she interacted with an ingroup member and the conflict is won, and with probability $1-\alpha$, she interacted with an outgroup member, in which case the conflict is lost. To see this, note that if the single altruist helps an ingroup member the total payoff of Group 1 is $G_1 = b - c$, where the benefit b accrues to the ingroup egoist, and the cost c to the single altruist. The total payoff of other groups is zero in this case. Hence,

conflict is won by Group 1. On the other hand, if the mutant altruist helped an outgroup individual, the total payoff of Group 1 is $G_1 = -c$, given the cost felt by the mutant altruist. The total payoff of one of the egoist groups will be b , while the remaining groups will have a total payoff of zero. Therefore Group 1 loses any conflict. If Group 1 is involved in conflict, it will win with a probability equal to α , or:

$$P_A(\text{winning} | \text{being in conflict}) = \alpha \quad (1)$$

The main insight is that a group with altruists does not necessarily outperform groups consisting entirely of egoists. Winning depends on whether or not altruists are matched with ingroup members. Mutant altruists are more likely to invade a population of egoists when group conflict is frequent and interactions with outgroup members are rare.

3.2. Discriminate strategies

Assume a single parochialist in Group 1, and the rest of the population being made up of egoists. The single parochialist will only help another individual if interaction occurs inside the group. In this case, the total payoff of Group 1 is $G_1 = b - c$, where the benefit b accrues to the ingroup egoist, and the cost c to the single parochialist. When more parochialists are added to Group 1, the performance of this group increases. The total payoff of groups other than 1 is zero, so conflict is won by Group 1. On the other hand, if the single parochialist interacts with an outgroup member, the total payoff of all groups will be zero. In this case, we assume that conflicting groups win with equal probability. The probability that Group 1 wins a conflict is then:

$$P_P(\text{winning} | \text{being in conflict}) = \alpha + \frac{1}{2}(1 - \alpha) \quad (2)$$

which is strictly larger than α , the probability that a group with a mutant altruist wins a conflict, if $\alpha < 1$. The only possibility for Group 1 to lose a conflict is that the single mutant parochialist interacts with an outgroup member and with probability 0.5 its group loses the conflict. The other discriminate strategy that has to be considered is treason. Using a similar reasoning as above, it is easy to see that with group conflict, traitorous behavior is always maladaptive when surrounded by egoism. Traitors will disappear as they make their groups lose conflicts, because their help is limited to out-group members. Concluding, parochialism in the form of discriminatory altruism means that help will not be wasted on outgroup members, so that groups of parochialists will spread. Traitors are not relevant since they are maladaptive and likely to vanish along with their group. Selection for discriminate and indiscriminate helping behavior may also result from assortative interactions. This happens when interactions among altruist or parochialist mutants occur more frequently than interactions by them with egoists.

Parochial individuals who happen to be in groups with more parochialists leave more offspring than those in groups

² Section A in the supplementary Web material presents analytical derivations of group performance based on expected total payoff.

of uncooperative individuals. This issue has been dealt with in the literature (e.g., Eshel and Cavalli-Sforza, 1982; Bergstrom, 2003).

4. Dynamics of multilevel selection

The analysis in Section 3 allows one to see how discriminate strategies can arise from small mutations in homogeneous populations when group conflict drives selection, but it does not capture the interaction between within-group and between-group selection. To study this problem, we introduce a stochastic model with within- and between-group selection.

4.1. An extended model

Traulsen and Nowak (2006) Traulsen and Nowak formulated a model for the evolution of cooperation by multilevel selection. This model considers finite groups that split when reaching a certain threshold size. A splitting group generates two daughter groups that take over the places of the parent group and another group chosen at random. Successful reproduction of individuals leads to larger groups that split more often, so that higher level selection emerges from selection within groups. Individuals reproduce according to a birth-death stochastic process. There are no mutations, and in every generation, only one individual has the chance to produce offspring. The main conclusion from Traulsen and Nowak (2006) is that a single cooperative mutant attains fixation when the benefit–cost ratio underlying the social dilemma game is above a threshold value. This threshold is proportional to the splitting size, and inversely proportional to the number of groups. In other words, the presence of many small groups favors cooperative behavior. We take Traulsen and Nowak (2006) as a starting point and add three elements to it: direct conflict between groups, individual intergroup encounters, and discriminate strategies. Direct conflict makes our model different from those based only on assortment (Lehmann et al., 2007). Intergroup encounters and discrimination allow for the evolution of the behavior described by Bernhard, Fehr and Fischbacher (2006b). We will present three model versions: one in which evolution is driven by only assortment, one with direct conflict only, and one with both of these mechanisms. Consider a prisoner's dilemma game with discrimination, as given by the game matrices presented in Section 2. Matrix A_{in} determines the payoff if the encounter occurs between members of the same group. Matrix A_{out} determines the payoff if the interaction occurs between members of different groups. Interactions are pairwise, and matching is performed in such a way that everybody plays the game at least once and on average twice. Following Traulsen and Nowak (2006), the fitness is computed as a linear transformation of the payoffs:

$$f_i = 1 - w + wg_i \quad (3)$$

where g_i is the payoff of the game. Values of b , c and w are chosen so that $f_i \geq 0$ and $b > c > 0$. The value of w determines the intensity of selection. The resulting model can be summarized as follows: We start with a population of m groups of size n , where all individuals are egoists except for a mutant altruist or parochialist. Each agent plays the game with an ingroup member with probability α , and with an outgroup member with probability $1 - \alpha$. The fitness of each agent is computed according to Eq. (3). Groups grow in the following manner: a single individual is selected for duplication with a probability equal to her fitness divided by the sum of the fitness values of all individuals in the population. The duplicated individual is added to the group to which the parent belongs with probability $1 - \lambda$ or migrates to another group with probability λ . Next, pairs of groups are selected for conflict. Parameter κ represents the average fraction of groups involved in conflict. At most, every group enters a conflict once in every generation (see Section B of the supplementary information). In a pair of conflicting groups, the one having the highest sum of payoffs has a higher chance of winning [as specified later in Eq. (4)]. The winning group is duplicated, and replaces the losing group. If the groups selected for conflict have the same sum of payoffs a random one is chosen as winner with probability 0.5. This conflict specification is similar to the one in Bowles et al. (2003), but here, we guarantee that the frequency of conflicts in the population remains constant for any number of groups.³ Next, if the size of a group increases beyond n , we split the group with probability q , by randomly assigning individuals from the parent group to two new daughter groups. One of the new groups replaces the parent group, while the other replaces a randomly chosen group. With probability $1 - q$ the group does not split, but a randomly picked individual is eliminated, in order to keep group size from growing larger than n . Fitness values are computed again, and the whole process is repeated until a homogeneous population is reached, that is, the mutant attains fixation or is driven out by the incumbent strategy. A more detailed description of the lifecycle can be found in the supplementary web material, Section B. Modeling conflict requires a number of specific choices. Different approaches have been explored in the literature (Guzmán et al., 2007; Bowles and Choi, 2003; Choi and Bowles, 2007). The conflict specification used here is based on Bowles et al. (2003) and van Veelen and Hopfensitz (2007). In these studies, groups at war are randomly picked, while the outcome is deterministic (based on group payoff). The winner duplicates and the loser disappears. We use a similar procedure, which allows for both probabilistic and deterministic conflict outcomes. Let G_i

³ An even number of groups is required for conflict. If conflict involves an odd number of groups, then with equal probabilities (0.5) a random group is added to, or deleted from, this set of groups. In this way the average frequency of conflict does not depend on the number of groups.

and G_j be the total payoff of conflicting groups i and j . The probability that G_i wins the conflict is defined as:

$$P(G_i) = \frac{G_i^{1/z}}{G_i^{1/z} + G_j^{1/z}} \quad (4)$$

Function P is known, particularly in economics, as a contest success function. Conflict then resembles a contest in which participants (in our case groups) exert effort to increase their probability of winning a prize (Skaperdas, 1996). The specification means that the higher the total payoff of a group, the higher is the chance of winning, and the group with the highest total payoff has the highest chance of winning. When z tends to zero, small differences already guarantee winning. For $z \rightarrow 0$ we approach the deterministic case in which the group with the highest total payoff wins with probability 1 (as addressed in the previous section). If z equals 1, the chance of winning is proportional to the difference in total payoff between the groups. For $z \rightarrow \infty$ winners are randomly chosen regardless of their total payoff. In this case there is no selective pressure by means of group conflict. The larger z is, the more chance matters in determining who wins a conflict. Fig. 1 shows the chance that group i wins conflict as a function of $G_i - G_j$ for different values of z . For this graph, we have set $G_j = 10$, but the qualitative features shown in the graph are the same for any value of G_j . Two distinct mechanisms are at work in our model. The first one is assortment, resulting from splitting and limited dispersal, which biases the probability that altruists interact with each other. A possible interpretation of this mechanism is kin selection (Lehmann et al., 2007), but other interpretations are feasible as well. The second mechanism is direct conflict between groups, which aligns the interests of members of the same group. Although interactions are pairwise in this model, conflict entails a collective action component, given that when one individual helps, the increased chances of winning

a conflict are shared by all group members. This conflict component has no link with kin selection (van Veelen and Hopfensitz, 2007). The combination of these mechanisms makes our model nonreducible to either assortment or kin selection interpretations. We are particularly interested in examining and comparing model versions in which the higher level in multilevel selection emerges only from splitting and in which it is due to intergroup conflict.

4.2. Parameter values and model versions

Our model describes an absorbing Markov chain (MC) with a state space composed of all possible population structures. Once the MC reaches a subset of states characterized by homogeneous populations, there is no way it can leave this subset. Given that there are no mutations, the chain is always absorbed into a population made up of the incumbent or the mutant strategy. The probability that the chain is absorbed into a population of mutants is known as the fixation probability. We use simulations to estimate such probabilities under a range of conflict frequencies, splitting probabilities, migration rates, and within-group interactions (parameters κ , q , λ and α) (Ross, 2001). Table 2 summarizes the explored ranges for the main parameters. Note that, for $\kappa \gg 0$, there are many more offspring due to reproduction after conflicts than due to reproduction by individuals being selected for duplication in the Moran process. In this sense, within-group selection is very weak compared with between-group selection when the conflict frequency is high. This is the result of the assumption that at each generation only one individual can produce offspring, whereas conflict entails that all individuals in a winning group can leave offspring after a conflict event. For this reason, we keep the conflict frequency close to zero. It is easy to compute how many group conflicts an individual is involved in during her average lifetime. Given that she is chosen to be replaced with probability $1/mn$ every generation, the average number of generations an individual lives is mn . The average number of conflicts in a lifetime is then κmn . For the largest values of conflict frequency and population size, this takes a value of 30, while for the benchmark parameter values, it equals 2.75. This range of values is consistent with the documented high frequency of inter-tribe conflicts in pre-state societies (Keeley, 1996).

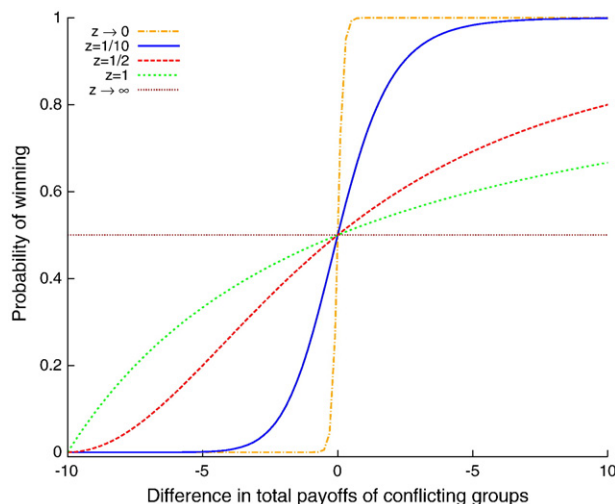


Fig. 1. Probability of winning a conflict for different values of z .

Table 2

Parameter values explored in the simulation model

| Parameter | Range (and default value) |
|--|---------------------------|
| Average frequency of groups in conflict (κ) | 0.0–0.1 (0.025) |
| Splitting probability (q) | 0–1 (0.01) |
| Group size (n) | 5–20 (10) |
| Number of groups (m) | 5–20 (10) |
| Benefit cost ration (b/c) | 1.5–5 (2.0) |
| Steepness of winning probability curve (z) | 0–1 (0.5) |
| Ingroup interaction frequency (α) | 0–1 (0.8) |
| Migration rate (λ) | 0–1 (0.0) |

In line with Traulsen and Nowak (2006), we have kept the splitting probability (q) small. Rare splitting implies that groups are almost always at their maximum group size, n . Increasing q would favor selection for cooperation. Also, in line with Traulsen and Nowak (2006), the intensity of selection w is set to 0.1. Choosing a low value of w has the advantage that a comparison with the fixation probability of a neutral mutant is meaningful and insightful. Note that for strong selection, fixation of a helping individual in a single uncooperative group will hardly ever happen, whereas a group of defectors will hardly ever take over a population of cooperative groups. Therefore, many attempts are required before reaching a homogeneous population. Both fixation probabilities of a cooperator and a defector then fall below the fixation probability of a neutral mutant, so that the comparison between the fixation probability of a neutral and a non-neutral mutant is not insightful (Traulsen et al., 2008). In the absence of fitness effects, every individual has the same chance of taking over the whole population. A neutral mutant will then fixate (i.e., due to drift only) with probability $1/mn$. Selection is working in favor of a certain trait if the fixation probability of a mutant bearing the trait is above the threshold $1/mn$. Likewise, selection is working against a certain trait if the fixation probability of a mutant bearing the trait is below $1/mn$. In the simulations, we will compare the fixation probabilities of altruists and parochialists with the fixation probability of a neutral mutant. This provides clear information on how selection is affected by discrimination. If the advantage for discrimination is large, we would expect the fixation probability of parochialists to pass the $1/mn$ threshold more quickly. In addition, we omit traitor strategies from the analysis. As discussed already in Section 3, and as can easily be shown numerically as well, traitorous behavior is selected against within and between groups. While a model in which successful groups split, and larger groups win conflicts, is realistic, these two elements add up to a degree of complexity which makes it hard to disentangle the forces of selection and to compare our results with the existing literature. We have thus two models of multilevel selection: one in which successful groups split, so that assortment is the driving force of selection (Traulsen and Nowak, 2006; Lehmann et al., 2007), and one in which conflict and assortment interact to determine between-group selection. We set a positive conflict frequency if splitting is zero and a positive splitting probability if there is no conflict. In addition, a version of the conflict model in which groups are randomly shuffled every generation is used to run simulations with the aim to examine evolution when the only driving force is group conflict.

5. Simulation results

5.1. Results for assortment only

We will first analyze a model without conflict, in which selection is driven by assortment only. Selection at the level

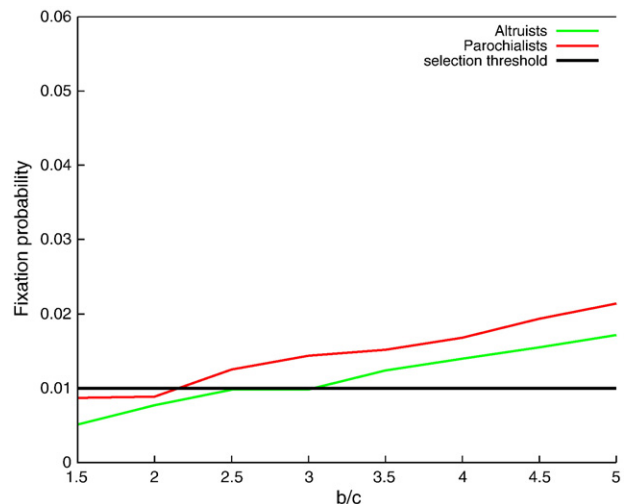


Fig. 2. Fixation probability as a function of b/c ($n=10$, $m=10$, $q=0.01$, $\alpha=0.8$).

of groups emerges from fast-growing groups splitting and taking over less successful groups. A differential advantage for groups occurs when helping individuals (discriminate or indiscriminate) assort, that is, when they are in the same groups. Intergroup interactions are harmful for altruists, but discrimination offers a chance for cooperative individuals to withstand the effects of interacting with outsiders. Figs. 2–5 show the fixation probabilities of mutant altruists and mutant parochialists as a function of different parameters. The green and red curves correspond to fixation probabilities of a mutant altruist and a mutant parochialist, respectively. The horizontal black lines mark the fixation probability of a neutral mutant and can be regarded as a selection threshold, as explained in Section 4.2. If the fixation probability of a strategy is above the black line, this strategy will be favored by selection. Likewise, if the fixation probability of a

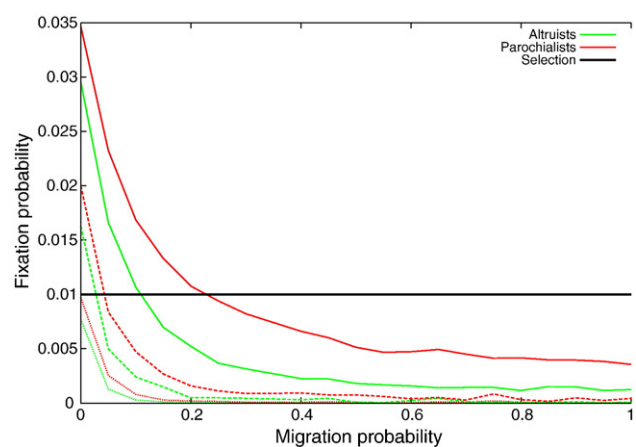


Fig. 3. Fixation probability as a function of λ for different b/c values ($b/c=10$ continuous lines, $b/c=5$ dashed lines, $b/c=2$ dotted lines; $n=10$, $m=10$, $q=0.01$, $\alpha=0.8$ for all b/c values).

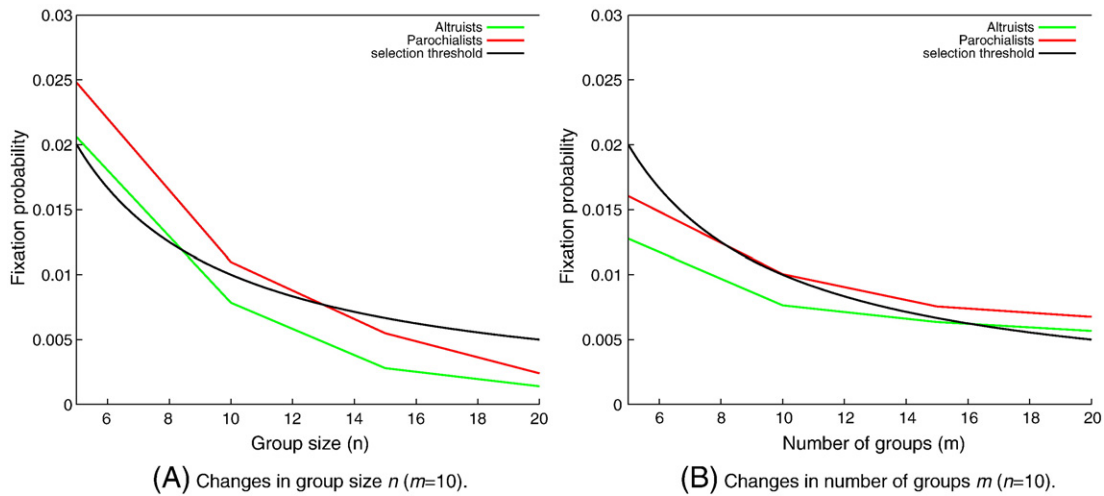


Fig. 4. Fixation probability as a function of group size n and number of groups m ($b/c=2$, $\alpha=0.8$, $q=0.01$).

strategy is below the black line selection will work against it. Therefore, if the mutant fixates, it is due to random drift and not to the fitness effects of bearing the trait in question. Whenever the green and red line are both below the black line, selection works against both discriminate and indiscriminate altruism. Parochial altruism has an edge over indiscriminate altruism, due to its ability to discriminate, whenever the red line is above the black line, while the green line remains below it. Fig. 2 shows the effect of varying the benefit-cost ratio. Discriminate and indiscriminate helping increase when b/c is higher, because helping behavior is cheaper. Parochialists are favored by selection at a smaller benefit-cost ratio than that required for altruists to be selected. This difference in benefit-cost ratios accounts for the edge that parochialists have over altruists, due to the former not being exploited when meeting outsiders. Fig. 3 shows the effect of different positive migration rates. Migration disrupts assortment by diminishing the chance

that similar individuals interact. Thus, larger migration rates require a higher b/c ratio for helping to be selected.

Fig. 4 shows the effect of changes in group size (a) and number of groups (b). Increasing group size makes invasion of cooperative mutants less likely, but discrimination allows parochialists to be favored by selection in larger groups. Increasing the number of groups diminishes the chances that mutants will invade. However, the presence of more groups causes the selection threshold to decrease faster than the fixation probabilities of mutants. This means that increasing m favors discriminate and indiscriminate cooperation, but parochialists are favored by selection for smaller values of m . A small n and a large m imply that cooperation is selected. This is in agreement with the results reported by Traulsen and Nowak (2006). Fig. 5 shows the effect of changes in the frequency of interactions with members of other groups. The fixation probability of altruists reaches a maximum when all interactions take place inside groups ($\alpha=1$). Without outsiders to discriminate, parochial altruism has no advantage over indiscriminate altruism. On the other hand, for α equal to zero, ingroup interactions are absent, which gives an edge to parochialists since altruists no longer gain from being in groups with other altruists. For $\alpha=0$, the fixation probability of parochialists equals that of a neutral mutant, as then both egoists and parochialists always defect, resulting in equal fitness values. The ability of parochialists to switch to defection when interacting with outgroups makes their fixation probability to be unaffected by the frequency of intergroup encounters.

5.2. Results for group conflict, with and without assortment

Next we consider a model in which selection is driven by conflict between groups and assortment. Altruists and parochialists are likely to be selected for if the frequency of intergroup conflicts is sufficiently high. Since groups stick together, there is limited dispersal, which causes assortment

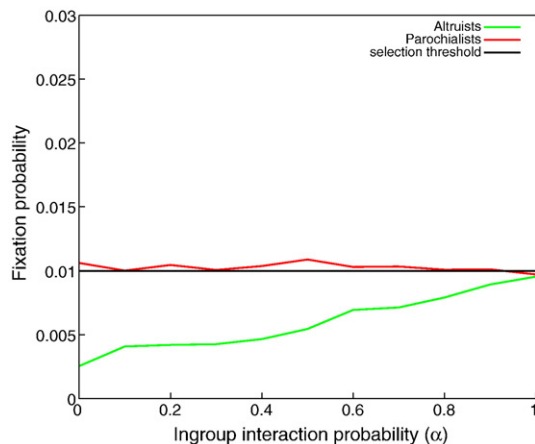


Fig. 5. Fixation probability as a function of α ($b/c=2$, $n=10$, $m=10$, $q=0.01$).

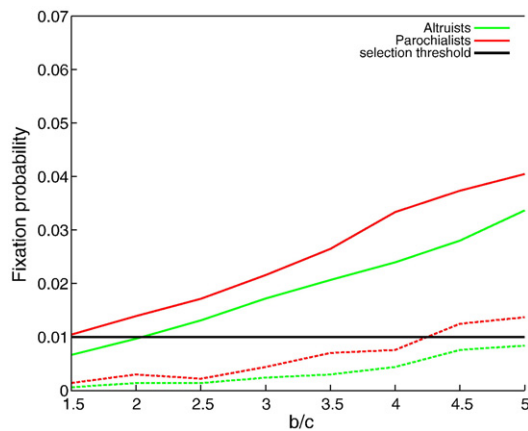


Fig. 6. Fixation probability as a function of b/c ($n=10$, $m=10$, $\kappa=0.025$, $z=0.5$). Note: broken lines, conflict only; continuous lines, conflict and assortment.

to also play a role in selection. That is, cooperative individuals will tend to interact disproportionately with others of their own type. The effect of assortative interactions can be switched off by reshuffling the groups at every generation. In this manner, there is no assortment, so that selection is driven by conflict only. Shuffling allows us to inspect how much of selection comes about by the mutualism induced by group conflict and how much comes from individuals assorting in groups with limited dispersal. Figs. 6–11 show the fixation probability of mutant altruists and mutant parochialists as a function of different parameters. Selection is driven by group conflict and assortment (continuous lines), or by group conflict alone (broken lines). In Fig. 6, we see that indiscriminate and parochial altruism evolve easily when assortment and conflict act together. Taking out the effect of assortment decreases cooperation.

However, conflict alone can select for helping without assortment if cooperation is cheap enough. The difference between the b/c ratios at which parochialism and indiscriminate altruism are selected reflects the edge that discrimination gives to parochialists. Note that, if we would include a cost for discrimination, parochialism would be selected for as long as the difference between the benefit-cost ratios of parochialists and altruists would compensate for the cost of discrimination borne by parochialists.

Fig. 7 shows the effect of different positive migration rates. As in the case of only assortment, larger migration rates require a higher b/c ratio for helping to be selected. However, the probability of fixation decreases more slowly than in the case where only assortment plays a role; with positive migration rates, fixation probabilities are larger when conflict is included. Since migration disrupts assortment, in the case of only conflict, there is no effect of positive migration rates; this makes sense since groups are reshuffled every generation and migration is therefore rendered meaningless since individuals occupy different

groups every generation. Fig. 8 shows the effect of group size (a) and number of groups (b). Discrimination allows for cooperation to be sustained in larger groups than those in which indiscriminate altruism is selected for. On the other hand, more groups favor discriminate and indiscriminate cooperation, but discrimination allows for helping to be selected for in populations with fewer groups. Similar patterns, at lower fixation probabilities, appear when shuffling undercuts the effect of assortment. Fig. 9 shows the effect of the frequency of interactions inside the group. On the left side (a), we set the steepness of the conflict outcome probability (z) to 0.5. On the right side (b), z is set to 0.1 so that chance plays a smaller role in deciding conflict outcomes. For $\alpha=1$, when all interactions take place inside groups, there are no differences between the fixation probabilities of altruists and parochialists. On the other hand, for $\alpha=0$, indiscriminate cooperators almost never attain fixation. This makes sense, as assorted cooperators interact all the time with outgroup defectors. Discriminate cooperators always defect for $\alpha=0$ so their fixation probability equals that of a neutral mutant. These observations at the upper and lower bounds of α hold for both the model with assortment (continuous lines) and the model without assortment (broken lines), regardless of the value of z . The results for intermediate values of α vary considerably when including or excluding assortment, and depend on the values of z as well. Let us first analyze the assortative version (continuous lines). The fixation probability of parochialists remains rather constant for all values of α , when chance plays a large role in deciding who wins a conflict (left side of the figure). On the right side, when z equals 0.1, the fixation probability of parochialist individuals increases sharply. Fewer interactions with outsiders (larger α) increases the fixation probability of altruists. However, if z is small, this only happens beyond a certain critical value of α , namely 0.4 in Fig. 9(b). In the nonassortative version (broken curves),

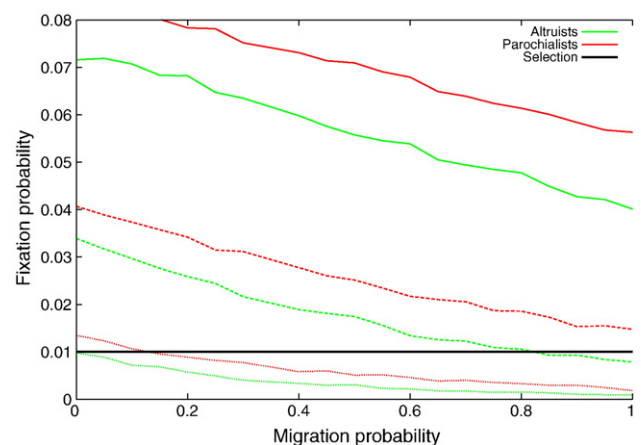


Fig. 7. Fixation probability as a function of λ for different b/c values ($b/c=10$ continuous lines, $b/c=5$ dashed lines, $b/c=2$ dotted lines; $n=10$, $m=10$, $q=0.01$, $\alpha=0.8$).

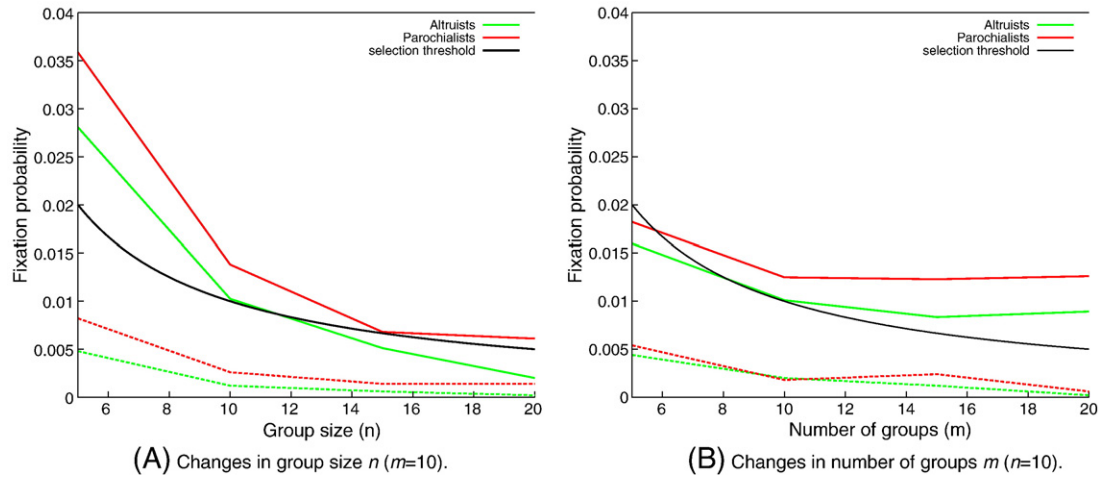


Fig. 8. Fixation probability as a function of group size n and number of groups m ($b/c=2$, $\alpha=0.8$, $\kappa=0.025$). Note: broken lines, conflict only; continuous lines, conflict and assortment.

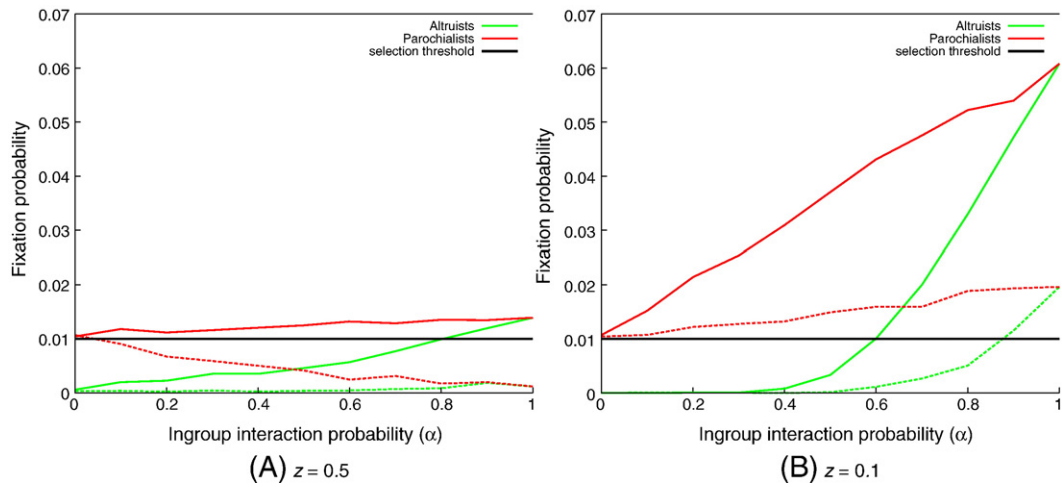


Fig. 9. Fixation probability as a function of α ($n=10$, $m=10$, $\kappa=0.025$). Note: broken lines, conflict only; continuous lines, conflict and assortment.

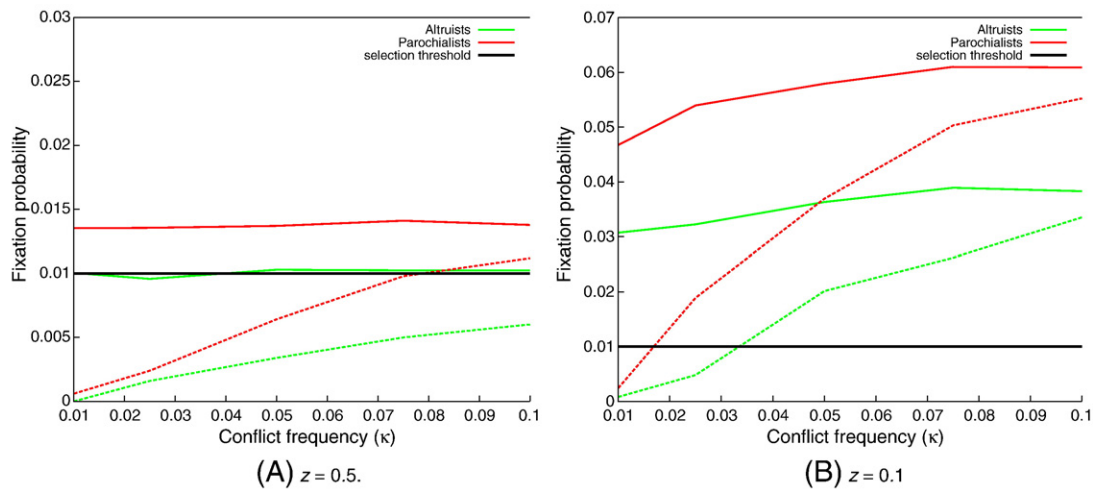


Fig. 10. Fixation probability as a function of κ and z ($n=10$, $m=10$, $b/c=2$). Note: broken lines, conflict only; continuous lines, conflict and assortment.

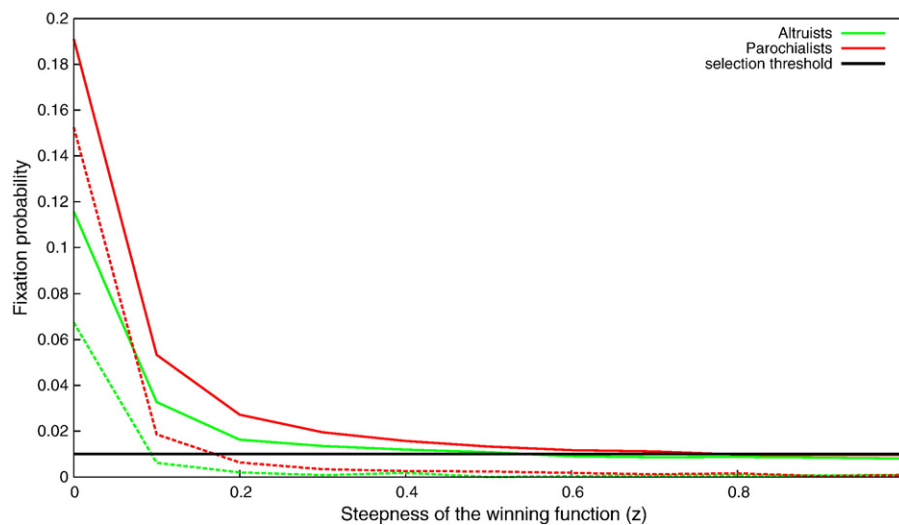


Fig. 11. Fixation probability as a function of z ($n=10$, $m=10$, $\kappa=0.025$, $b/c=2$). Note: broken lines, conflict only; continuous lines, conflict and assortment.

where only conflict matters, altruistic behavior has a very small chance of fixation for all values of α if z is high. Provided that chance plays a small role in deciding conflicts ($z=0.1$) altruists can be selected for if interactions with outsiders are uncommon. Parochialists, on the other hand, are harmed by more interactions inside the group when z is high. Shuffling at every generation makes ingroup fellows random, with the result that the fixation probability for parochialist mutants decreases because small differences in the outcomes of conflict translate into small probabilities of winning conflict. However, if z is small, parochialists are favored by selection at any frequency of ingroup interaction α . Fig. 10 shows the effect of different values of κ , the frequency of groups in conflict, and z , the steepness of the contest function that determines the probability of winning a group conflict. On the left side (a), for z equal to 0.5, differences in total group payoff matter more than on the right side (b), where a small difference in total payoff causes a larger difference in the probability of winning. Increasing the conflict frequency favors helping. The gain obtained by cooperators is evidently larger for a smaller z . The differences in fixation between altruists and parochialists are maximized when only conflict drives selection. As is shown also in Fig. 11, the value of z is very important in determining the effectiveness of conflict: fixation of cooperators attains the highest level when z is close to 0. Increasing z rapidly diminishes selection for helping, as well as the differences between selection for altruists and parochialists. As explained in the lifecycle description (Section 4.1 and section B in the supplementary web material), z determines the role of chance in a group conflict. For deterministic conflict ($z \rightarrow 0$) the advantage of discrimination is maximized, since the difference between altruists and parochialists is the largest. This difference decreases when $z \gg 0$ and chance matters more.

6. Conclusions

This article has studied the evolution of discriminatory strategies in a prisoner's dilemma game. We considered the interaction between four strategies, namely egoists, altruists, parochialists, and traitors. It was first argued that selection in a large unstructured population cannot explain the evolution of parochial altruism. Next, we analyzed the stability of egoists against altruist and parochialist mutants. The main result here is that egoist groups with parochialist mutants are more likely to win conflicts against purely egoist groups than egoists groups with altruist mutants. We developed a computational model with selection occurring at the levels of groups and individuals. We included discriminate strategies, intergroup interactions and conflict. We first studied a model version in which conflict is absent so that selection is exclusively driven by assortment. In a second model version selection is driven by group conflict and assortment. In a third model version, groups are reshuffled every generation so that there is no assortment, and selection is exclusively driven by conflict. Intergroup interactions harm the evolution of cooperation. Since early humans may have had few or many intergroup contacts, the ability to discriminate individuals from other groups is a possible mechanism that would allow cooperators to sustain cooperation inside their groups. This may explain some of the parochial features reported in human altruism. Fixation probabilities in the conflict model are higher than those obtained in the assortment model. This holds for the most conservative comparison, when fixation in the splitting model is at its highest (by setting $q=1$) and conflict is rare ($\kappa \rightarrow 0$). While qualitatively the two models give rise to the same patterns, the main difference is that the process of group conflict apparently always creates more intense competition between groups. In the group conflict scenario, differences in total group payoff are more of a determinant

in deciding which groups proliferate and which groups die out. Discrimination allows cooperation inside groups to be maintained when individuals interact regularly with outsiders. Group conflict as well as assortment select for parochial behavior. Selection for such behavior is strongest when the two selection mechanisms are both present, migration is low, and chance has a small influence on winning a conflict.

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.evolhumbehav.2010.07.007](https://doi.org/10.1016/j.evolhumbehav.2010.07.007).

Acknowledgments

This research was funded by the Netherlands Organization for Scientific Research, under the program “Evolution and Behaviour.” We thank Matthijs van Veelen for helpful comments and discussions.

References

- Aoki, K. (1982). A condition for group selection to prevail over counteracting individual selection. *Evolution*, 36(4), 832–842.
- Bergstrom, T. (2003). The algebra of assortative encounters and the evolution of cooperation. *International Game Theory Review*, 5(3), 211–228.
- Bernhard, H., Fehr, E., & Fischbacher, U. (2006a). Group affiliation and altruistic norm enforcement. *The American Economic Review*, 96(2), 217–221.
- Bernhard, H., Fischbacher, U., & Fehr, E. (2006b). Parochial altruism in humans. *Nature*, 442(7105), 912–915.
- Boorman, S., & Levitt, P. (1972). Group selection on the boundary of a stable population. *Proceedings of the National Academy of Sciences*, 69(9), 2711–2713.
- Bowles, S., Choi, J., 2003. The first property rights revolution. Workshop on the Co-evolution of Behaviors and Institutions, Santa Fe Institute, January, 10–12.
- Bowles, S., & Choi, J. (2004). The co-evolution of love and hate. Cultural diversity versus economic solidarity: Is there a tension? How must it be resolved. De Boeck Universiteit, Ch. 6. pp. 81–97.
- Bowles, S., Choi, J., & Hopfensitz, A. (2003). The co-evolution of individual behaviours and social institutions. *Journal of Theoretical Biology*, 223, 135–147.
- Choi, J., & Bowles, S. (2007). The coevolution of parochial altruism and war. *Science*, 318(5850), 636–640.
- Clutton-Brock, T. (2002). Breeding together: Kin selection and mutualism in cooperative vertebrates. *Science*, 296(5565), 69–72.
- Eshel, I., & Cavalli-Sforza, L. (1982). Assortment of encounters and evolution of cooperativeness. *Proceedings of the National Academy of Sciences*, 79(4), 1331–1335.
- Frank, S. (1998). *Foundations of social evolution*. Princeton University Press.
- Guzmán, A., Rodríguez-Sickert, C., & Rowthorn, R. (2007). When in Rome, do as the Romans do: the coevolution of altruistic punishment, conformist learning, and cooperation. *Evolution and Human Behavior*, 28(2), 112–117.
- Hamilton, W. (1975). Innate social aptitudes of man: an approach from evolutionary genetics. *Biosocial Anthropology*, 133–155.
- Hammond, R., & Axelrod, R. (2006). *The evolution of ethnocentrism. Journal of Conflict Resolution*, 50(6), 926.
- Hewstone, M., Rubin, M., & Willis, H. (2002). *Intergroup bias. Annual Review of Psychology*, 575–605.
- Keeley, L. (1996). *War before civilization*. USA: Oxford University Press.
- Lehmann, L., & Feldman, M. (2008). *War and the evolution of belligerence and bravery. Proceedings of the Royal Society B: Biological Sciences*, 275, 2877–2885.
- Lehmann, L., & Keller, L. (2006). *The evolution of cooperation and altruism—a general framework and a classification of models. Journal of Evolutionary Biology*, 19, 1365–1376.
- Lehmann, L., Keller, L., West, S., & Roze, D. (2007). *Group selection and kin selection: Two concepts but one process. Proceedings of the National Academy of Sciences*, 104(16), 6736–6739.
- Nowak, M. A. (2006). *Five rules for the evolution of cooperation. Science*, 314(5805), 1560–1563.
- Price, G. (1972). *Extension of covariance selection mathematics. Annals of Human Genetics*, 35(4), 485.
- Ross, S. M. (2001). *Simulation*. Third Edition. San Diego CA: Academic Press.
- Skaperdas, S. (1996). *Contest success functions. Economic Theory*, 7(2), 283–290.
- Traulsen, A., & Nowak, M. A. (2006). *Evolution of cooperation by multilevel selection. Proceedings of the National Academy of Sciences*, 103, 10952–10955.
- Traulsen, A., Shresh, N., & Nowak, M. (2008). *Analytical results for individual and group selection of any intensity. Bulletin of Mathematical Biology*, 70(5), 1410–1424.
- van Veelen, M., & Hopfensitz, A. (2007). *In love and war: Altruism, norm formation, and two different types of group selection. Journal of Theoretical Biology*, 249(4), 667–680.