

# Dynamic-persistence of cooperation in public good games when group size is dynamic

Marco A. Janssen<sup>a,\*</sup>, Robert L. Goldstone<sup>b</sup>

<sup>a</sup>School of Human Evolution and Social Change and School of Computing and Informatics, Arizona State University, P.O. Box 872402, Tempe, AZ 85287-2402, USA

<sup>b</sup>Department of Psychological and Brain Sciences and Program in Cognitive Science, Indiana University, Bloomington, IN 47405, USA

Received 13 April 2006; received in revised form 12 June 2006; accepted 16 June 2006

Available online 20 June 2006

---

## Abstract

The evolution of cooperation is possible with a simple model of a population of agents that can move between groups. The agents play public good games within their group. The relative fitness of individuals within the whole population affects their number of offspring. Groups of cooperators evolve but over time are invaded by defectors which eventually results in the group's extinction. However, for small levels of migration and mutation, high levels of cooperation evolve at the population level. Thus, evolution of cooperation based on individual fitness without kin selection, indirect or direct reciprocity is possible. We provide an analysis of the parameters that affect cooperation, and describe the dynamics and distribution of population sizes over time.

© 2006 Elsevier Ltd. All rights reserved.

**Keywords:** Evolution of cooperation; Group structure; Public good games

---

## 1. Introduction

The study of cooperation between individuals of species has led to a variety of interesting proposed explanations. The theory of kin selection focuses on cooperation among individuals who are closely related genetically (Hamilton, 1964), whereas theories of direct reciprocity focus on the selfish incentives for cooperation in repeated interactions (Trivers, 1971; Axelrod, 1984). Theories of indirect reciprocity and costly signaling show how cooperation in larger groups can emerge when cooperators can build reputations (Alexander, 1987; Nowak and Sigmund, 1998; Lotem et al., 1999; Wedekind and Milinski, 2000; Leimar and Hammerstein, 2001; Zahavi, 1977; Gintis et al., 2001).

Empirical studies show evolution of cooperation among *Homo sapiens* (Kagel and Roth, 1995), other higher organisms (Dugatkin, 1997), and microorganisms (Travissano and Velicer, 2004). A recent study has shown that cooperative, isogenic-respirer strains of yeast can prosper

when mixed with "cheater", respiro-fermenter strains in a spatially heterogeneous environment (MacLean and Gudelj, 2006). A basic model of biological cooperation must, therefore, not rely only on the high-level cognitive capacity of the individual agents.

Another line of explanation focuses on group selection (Wade, 1977, 1978; Wilson, 1983; Wright, 1945). A group that includes more altruistic agents derives higher average fitness for its members, which may lead to more offspring of agents in the successful group even though within each group the altruistic agents are less fit than their selfish neighbors. It is known that low demographic mobility is a crucial factor for the evolution of altruistic traits (Wright, 1945; Killingback et al., 2006).

Many models in the study of group selection build on the "haystack model" of Maynard Smith (1964). In haystack models, agents are divided into a number of groups in which games are played, and asexual reproduction takes place within each group. At the end of the reproductive phase there is a dispersal phase, where the entire population is pooled and new groups are randomly formed from the pooled population. For haystack models where the games are prisoner dilemmas, the only stable equili-

\*Corresponding author. Tel.: +1 480 965 1369; fax: +1 480 965 7671.

E-mail addresses: [Marco.Janssen@asu.edu](mailto:Marco.Janssen@asu.edu) (M.A. Janssen), [rgoldsto@indiana.edu](mailto:rgoldsto@indiana.edu) (R.L. Goldstone).

brium is one of mutual defection (see Bergstrom, 2002; Cohen and Eshel, 1976).

Our model differs from the haystack model because the reproduction and dispersal phases are combined. In fact, our model resembles trait-group selection where a trait can be negatively selected in each and every local group of a global population and yet be positively selected in the population overall (Wilson, 1975). As with trait-groups, we imagine a world with subpopulations (groups) that are enclosed in areas smaller than the boundaries of the deme. In each generation the individuals in each group play a public good game, which determines the individual fitness of the agents. Agents generate offspring in their group based on their relative fitness within the whole population of all groups. Thus, cooperative groups tend to produce higher offspring rates than less cooperative groups, but non-cooperative agents in cooperative groups bear more offspring than cooperative agents. In agreement with studies like Wright (1945) and Killingback et al. (2006), low demographic mobility proves to be the most crucial factor for the evolution of altruistic traits. We will also explore systematically other factors such as group size and mutation rates.

## 2. Model

Assume a population of  $N$  agents and  $M$  groups in which the agents can be located. At each time step, all agents may contribute to the public good in their group, and the created public good is evenly divided among the agents in the group. Each agent  $i$  contributes all or nothing to the public good, and therefore the income of agent  $i$ ,  $\pi_i$ , is defined as

$$\pi_i = 1 + \frac{x \cdot B}{N_{G_i}} \text{ for a selfish agent} \quad (1a)$$

and

$$\pi_i = \frac{x \cdot B}{N_{G_i}} \text{ for an altruistic agent,} \quad (1b)$$

where  $x$  is the fraction of cooperators and  $B (>1)$  is the multiplier of the investment in the public good to produce the public good.  $G_i$  is the set of agents who are in the same group as agent  $i$ .  $N_{G_i}$  is the number of agents in set  $G_i$ .

The fitness of an agent is equal to the individual's income. The agents in the next round are generated by replicating agents in the current round, where the probability of an agent being replicated is based on the fitness of the agent proportional to the fitness of the other agents.

According to Cohen and Eshel (1976), a cooperative equilibrium will be derived when  $B/N_{G_i} < 1$ , and an equilibrium of defectors will evolve when  $B/N_{G_i} > 1$ .

We can assess the stability of a group of cooperative agents which is founded by cooperators only. When all other groups are selfish agents and each cooperative agent in a group of cooperators derives a payoff equal to  $B$ , the

relative fitness of a group of cooperators,  $f(x)$ , is equal to

$$f(x) = \frac{x \cdot B}{x \cdot B + (1 - x)} \quad (2)$$

When there are  $x$  cooperators in the group, the fitness of individuals in the cooperative group is equal to  $B (>1)$ . The selfish agents in the other groups derive a payoff equal to 1.  $f(x)$  is the share of the cooperative group. When there is no mutation or migration, the group of cooperators will dominate the whole population.

However, when there is a probability  $\eta$  that cooperative agents mutate into selfish agents, or when the migration rate is equal to  $\mu$ , a cooperative group cannot persist. Only when a cooperator starts at a new location can cooperation persist until mutation or migration leads to invasion of defectors into the cooperative group. Sella and Lachmann (2000) analysed a spatial model of agents that play prisoner dilemma games, and can migrate to neighboring cells. They show that cooperators can only persist in the population when the migration is within a certain specific range.

Models which distinguish only cooperators and defectors are limited in terms of understanding the evolution of cooperation. Cooperative and defective behavior is relative (Sella and Lachmann, 2000, p. 478). Therefore, we assume a continuous variable  $x_i$  which defines the relative level of cooperation of agent  $i$ .

We assume that each agent  $i$  contributes a continuous level  $x_i \in [0, 1]$  to the public good (Mar and StDenis, 1994; Killingback et al., 1999). We assume a population of  $N$  agents and  $M$  groups in which the agents can be located. The income of agent  $i$ ,  $\pi_i$ , is therefore defined as

$$\pi_i = 1 - x_i + \frac{B}{N_{G_i}} \cdot \sum_{j \in G_i} x_j. \quad (3)$$

The fitness of an agent is equal to its individual income. The agents in the next round are generated based upon the fitness of the agent proportional to the fitness of the other agents in the total population (not just the agent's group). In particular, we generate  $N$  agents for each generation, and for each of these agents, the probability of selecting an agent in generation  $T$  for replication in generation  $T+1$  is

$$p_i = \frac{\pi_i}{\sum_{j=1}^N \pi_j}. \quad (4)$$

The offspring is not a perfect copy of its parent agent because a perturbation from a normal distribution with mean 0 and variance  $\eta$  is added to the cooperation level. There is also a probability  $\mu$  for each agent that it migrates to a randomly selected group.

One can easily see that there is no cooperative equilibrium with positive values of  $\eta$  and  $\mu$ . Suppose there is an equilibrium  $\hat{x}$ , and an invasion of a lower  $x$  due to mutation or migration, then the fitness of  $x$  is always higher than that of agent type  $\hat{x}$ , increasing the number of agents of type  $x$  in the next generation. Hence  $\hat{x}$  cannot be an equilibrium.

Note that for each group there is a dilemma between individual and group rationality. However, if  $B \geq N_{G_i}$  the agent will receive positive returns on its own contribution, thus it would always be beneficial to contribute. In fact, the unrestricted game only becomes a public good dilemma when the group size exceeds a certain level ( $N_{G_i} > B$ ). This echoes the observation of scholars that cooperation can only be derived in sufficiently small groups (Olson, 1965). Nevertheless, we also include the situation in our analysis with a stricter condition, such that

$$\pi_i = 1 - x_i + \sum_{j \in G_i} x_j \quad \text{if } B \geq N_{G_i}. \quad (5)$$

For this stricter condition, it is always to an individual's advantage to contribute nothing to the group, and the game always presents a true dilemma.

### 3. Results

We discuss first the basic dynamics of the model.<sup>1</sup> We use a reference case with  $N = 1000$ ,  $M = 10$ , and  $B = 10$ . With initial values of  $x$  drawn from a uniform distribution between 0 and 1, the average value of  $x$  in a group changes over time. A group will tend to grow when the average  $x$  of the group is higher than other groups. However, when agents with low levels of contribution  $x$  enter the group, the average value of  $x$  starts to drop because these less cooperative agents have a relatively high fitness within the group and total population. As a consequence of the lower average contribution to the group, the relative fitness of the group among all the groups declines, and the group size will drop. Therefore, we see that population levels of groups fluctuate significantly over time (Fig. 1). The average value of  $x$  for a group, initially around 0.5, decreases when the number of agents within the group is high. When enough agents with high  $x$  values migrate to other locations and can start new groups, cooperation can persist within the whole population.

Fig. 1 shows results for  $\eta = 0.006$  and  $\mu = 0.006$  for both the cases with and without Eq. (5). The group size dynamics is different. When the constraint of Eq. (5) is not included, small groups (up to 10 agents with  $B$  equal to 10) always have a benefit and attract new agents. Some of these small groups receive cooperative agents and then may become large groups. When we include Eq. (5), a single cooperator by itself or in a small group with less cooperative agents will be unlikely to prosper. This leads to the complete depopulation of some groups. Only when several cooperators migrate together to a depopulated group can a new group grow in size.

We now focus on the dynamics of the groups. As we mentioned in the discussion of the results above, groups are never stable, and often groups that are successful, measured in terms of population, will become prone to a

mutation that leads to less cooperative agents who temporarily free-ride on the cooperative agents, until the group's population collapses, and members in other groups out-compete the once-successful group, yielding higher offspring rates. If a group cooperates to a higher level than other groups, it will tend to drive out the others. Therefore, we can see our model as an arms race of cooperation. The only way for collapsed groups to reliably come back to life is to be seeded with migrating agents that happen, due to mutation, to be more cooperative than the group that they left. Although the tendency is always for cooperation within a group to decrease, new groups will only take hold of a population if they exceed the average cooperation level of other groups, and consequently cooperation ratchets upwards due to inter-group competition.

Similar to Axtell (1999) we look at the distribution of group sizes. These distributions lead to certain distinct regularities which enable us to understand the underlying dynamics of the groups. When we look at the group sizes, we may expect a normal distribution when agents are just randomly put into groups. Fig. 2 shows the distribution of group sizes over the 2000 time steps of the simulation for  $\eta = 0.006$  and  $\mu = 0.006$ . When Eq. (5) is included, there is a relative large frequency of small groups, with as few as zero or one agents. However, there is also a relatively high frequency of large groups. This distribution shows that agents cluster most of the time in a few large groups. As a consequence it is more difficult for cooperative agents to survive. Including Eq. (5) necessarily leads to a social dilemma when making a decision to invest in the public good, and therefore it is more difficult to initiate new groups of cooperative agents. When Eq. (5) is not included, there is a relatively high frequency of medium-sized groups. Agents are more spread over the groups, but not according to a normal distribution.

We conducted a systematic analysis of the model's parameter space. Each simulation consists of 2000 time steps, and we report the average cooperation value per time step during the last 1000 time steps of 100 runs. Explorations reveal that about 100 simulations are necessary to reduce the variability of our statistics to an acceptable level. We also explore the sensitivity of the cooperation level and average value of  $x$  to variation in the values of  $\eta$ ,  $\mu$ ,  $B$ ,  $N$ , and  $M$ . For each combination of parameters we report simulations with and without restriction on  $B$  (Eq. (5)). The default values which we use are  $\eta = 0.006$ ,  $\mu = 0.006$ ,  $B = 10$ ,  $N = 1000$ , and  $M = 10$ .

First we show the results of individual variation of the migration rate  $\mu$  for two different values of mutation rate  $\eta$ , with and without Eq. (5). Fig. 3 shows that for a low level of migration, high levels of contribution evolve. This is consistent with earlier studies on group structures (Wright, 1945; Killingback et al., 2006). When there is no migration, the levels of contribution are low, especially when there is also mutation. The case of both  $\eta$  and  $\mu$  being zero is a special case. Initially the groups compete, and the most

<sup>1</sup>The model is implemented in java and the source code can be derived upon request from the first author.

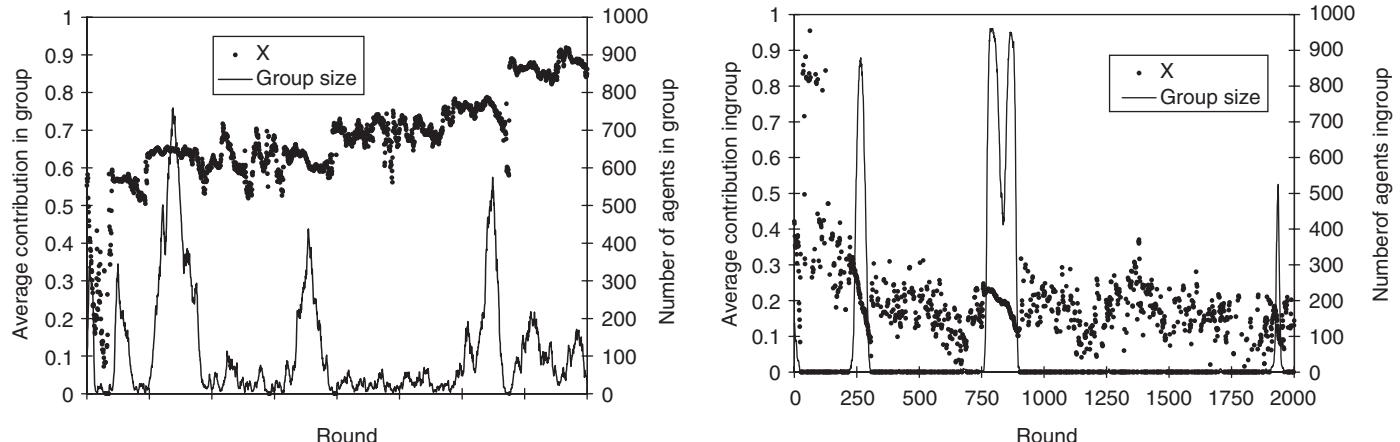


Fig. 1. Statistics of one arbitrarily chosen group over time. Average value of  $x$  of agents in that group and the number of agents in that group. Left figure is for a situation when Eq. (5) is not included, while the right figure, Eq. (5) is included.

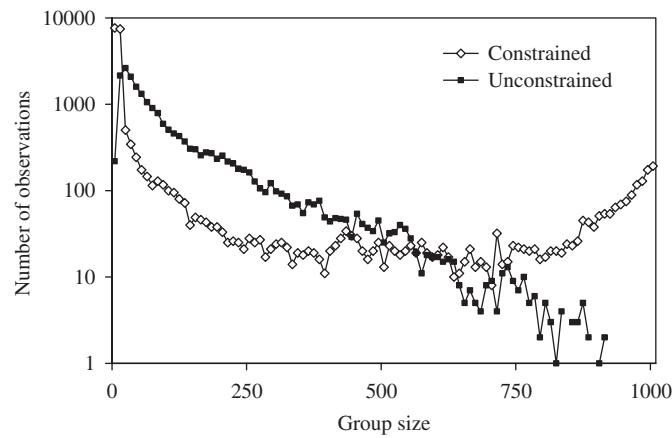


Fig. 2. Distribution of group sizes in a simulation of 2000 time steps, the data of simulations shown in Fig. 1. Eq. (5) is enforced for the constrained, but not unconstrained, condition.

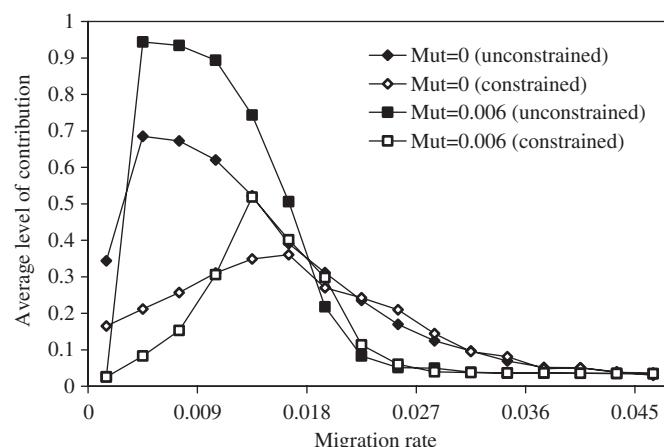


Fig. 3. The average level of contribution for different migration rates, different rates of mutation, and with or without Eq. (5).

cooperative group will dominate the population. Then the individuals within the most cooperative group will compete, and the least cooperative agent type will tend to dominate. So the emerging cooperation level in this situation is the lowest cooperation level within the most cooperative group. This explains the relatively high levels of cooperation when  $\eta$  and  $\mu$  are zero compared to near values, as can be seen in Fig. 3. The differences between the constrained and unconstrained simulations is caused by the different relative fitnesses of the agents when their groups drop below level  $B$ , which favors small groups who have eliminated low contributors.

When migration is beyond 0.02 the evolved levels of contribution is low. Groups with cooperative agents are more frequently invaded by agents who have low contribution levels. When the multiplier for the public good is not constrained, higher levels of contribution will evolve. The effect of mutation is less obvious. In some conditions it increases the level of contribution while in others it decreases cooperation. Therefore, we performed a systematic analysis varying both mutation and migration rates.

Fig. 4 depicts the values when  $\eta$  and  $\mu$  are varied. For small levels of migration a high level of cooperation can be achieved. Higher levels of migration lead to more frequent intrusions of selfish agents who break down cooperative groups. Small levels of migration, however, are beneficial, because migration of cooperative agents to small groups can establish new successful groups. If no migration is possible, then the simulation is more accurately interpretable as several simultaneous replications of a single-group simulation. As discussed with Fig. 1, high levels of cooperation occur in very dynamic environments where cooperative groups increase in size, but eventually break down due to the invasion of selfish agents, while other groups simultaneously increase in fitness and cooperation due to the migration of cooperators. Non-cooperators

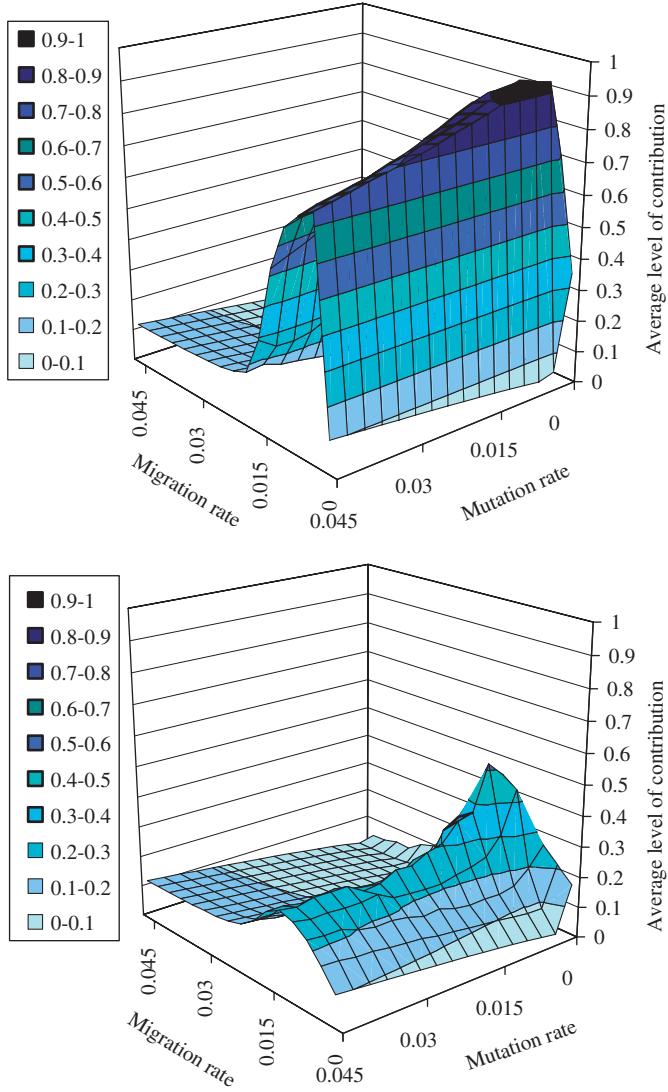


Fig. 4. Average level of contribution  $x$  for different values of mutation ( $\eta$ ) and migration ( $\mu$ ). Top figure without Eq. (5), lower figure including Eq. (5).

migrate as often as cooperators, but when they migrate into unpopulated groups, they are likely to die out rather than thrive as émigré groups of cooperators do.

When  $B$  is restricted (Fig. 4b), the levels of cooperation are smaller because it is harder for small groups (smaller than  $B$  individuals) to cooperate. Nevertheless, we get cooperation levels of more than 25% for small levels of migration. The cooperation level drops significantly with higher levels of mutation. For higher levels of mutation, there is a high probability that more selfish agents enter a group of cooperators and break down the cooperation.

Next we look at the relation between number of groups and migration rate (Fig. 5). A larger number of groups and smaller migration rates (but not zero) lead to higher values of cooperation. With more groups, there is a greater chance that a group of cooperators is isolated from less cooperative agents. Cooperation thrives when groups are

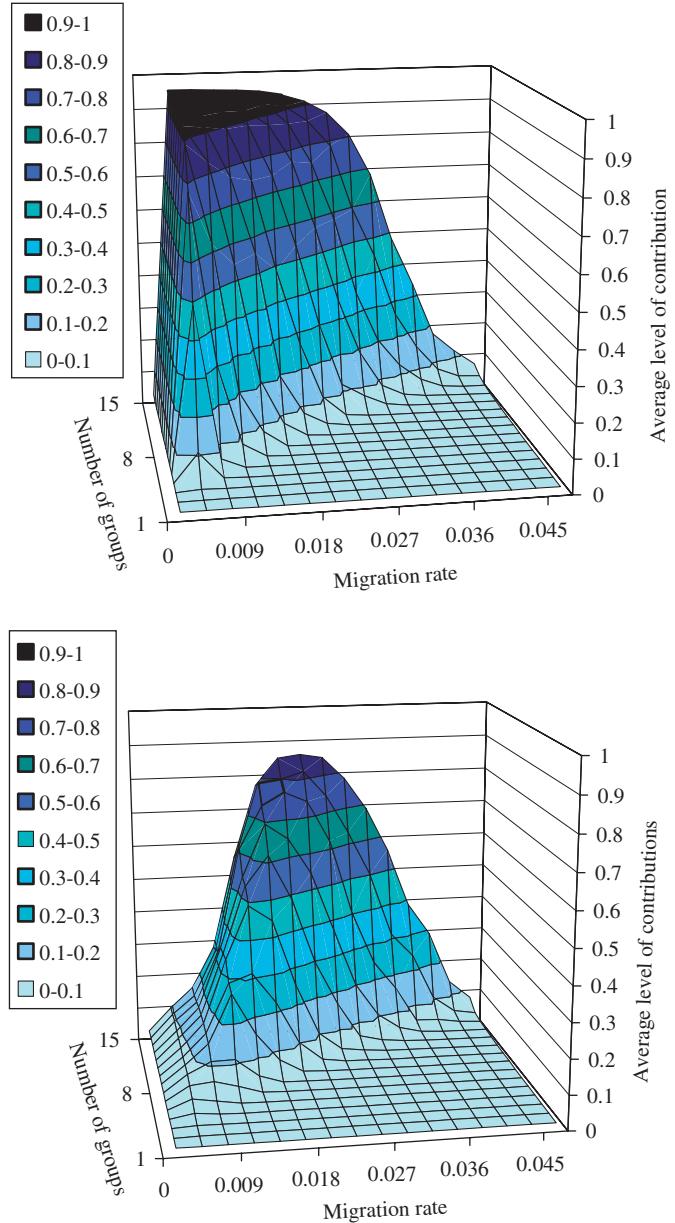


Fig. 5. Average level of contribution  $x$  for different values of migration ( $\mu$ ) and number of groups ( $M$ ). Top figure without Eq. (5), lower figure including Eq. (5).

well insulated by low migration rates, which prevents too much homogeneity among the groups. When homogeneity is too high, the population is essentially a single group rather than a collection of independent groups. Again, a restricted  $B$  (Fig. 5b) leads to lower but still significant levels of cooperation.

When we focus on the effect of mutation and number of groups (Fig. 6), we observe less sensitivity to variations in mutation rate and relatively more sensitivity to variations in the number of groups. There is a large difference between constrained and unconstrained multiplier levels of  $B$ . When unconstrained, more than five groups can lead to

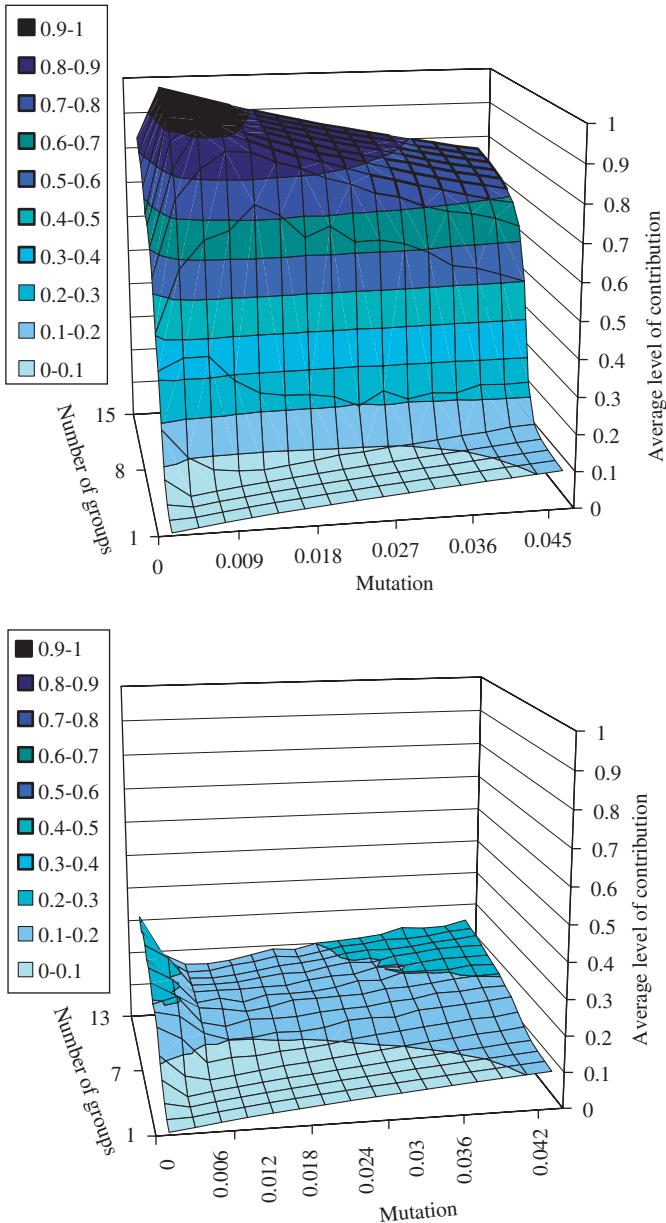


Fig. 6. Average level of contribution  $x$  for different values of mutation ( $\eta$ ) and the number of groups ( $M$ ). Top figure without Eq. (5), lower figure including Eq. (5).

high levels of contribution irrespective of the mutation rate because groups are not significantly affected by variations in mutation levels.

When we look at the trade-off between migration and  $B$ , we see that for higher levels of  $B$  it is easier to establish high levels of cooperation in the unrestricted case (Fig. 7a). This is not surprising given that higher values of  $B$  mean that there is a relatively strong benefit for cooperation compared to the benefit for free-riding.

When  $B$  is restricted, we see that cooperation does not appear beyond a certain level of  $B$ . The reason for this is that small groups ( $N_G < B$ ) do not benefit from high values of  $B$  since they are cut off to  $B = N_G$ . This will benefit

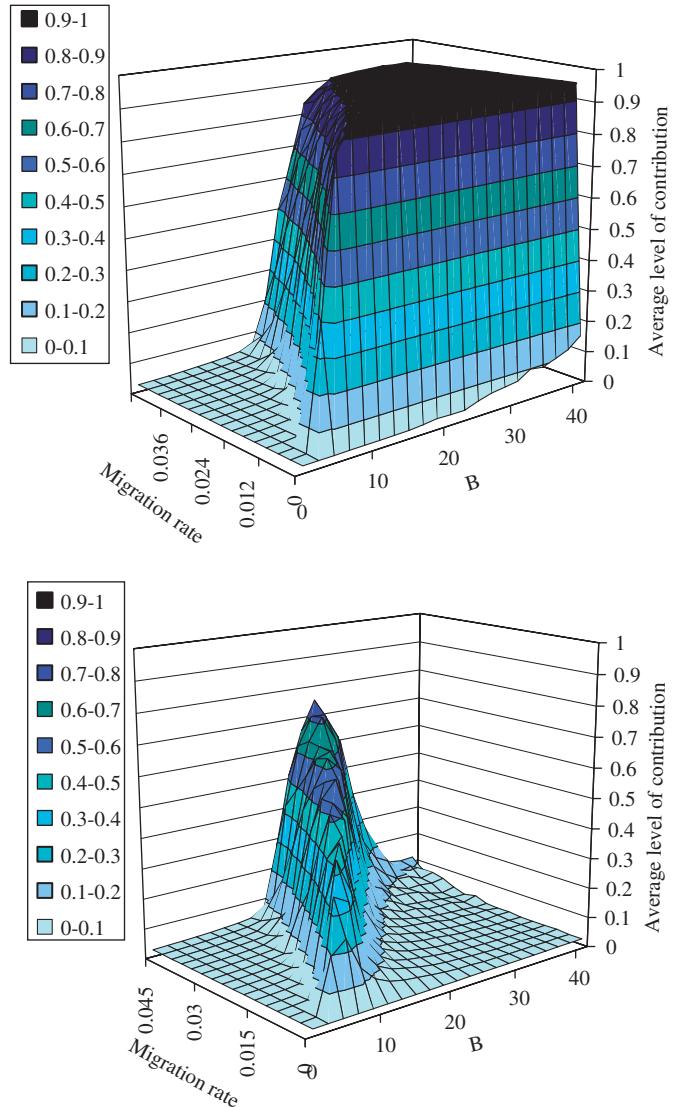


Fig. 7. Average level of contribution  $x$  for different values of migration ( $\mu$ ) and  $B$ . Top figure without Eq. (5), lower figure including Eq. (5).

larger groups, but these are also likely to be the groups that have defectors. When  $B$  is not restricted, a collapse of a populous group leads to small groups that all benefit from the large values of  $B$ , and new cooperative groups emerge. When  $B$  is restricted, the collapse of a large group will bring the population back to a number of small groups that each depends upon the existence of sufficient cooperation to grow again. Thus, with a restricted  $B$  (according to Eq. (5)) and a low migration rate, there is only a small probability that cooperative agents move to other (smaller) groups at a sufficient rate for new cooperative groups to become established before the larger groups collapse due to invasion and propagation of selfish agents.

When we vary the number of agents  $N$  in the simulation, we increase the number of time steps to  $2000 * (1000/N)$  in order to derive comparable results with the other figures. With a smaller number of time steps, the populations

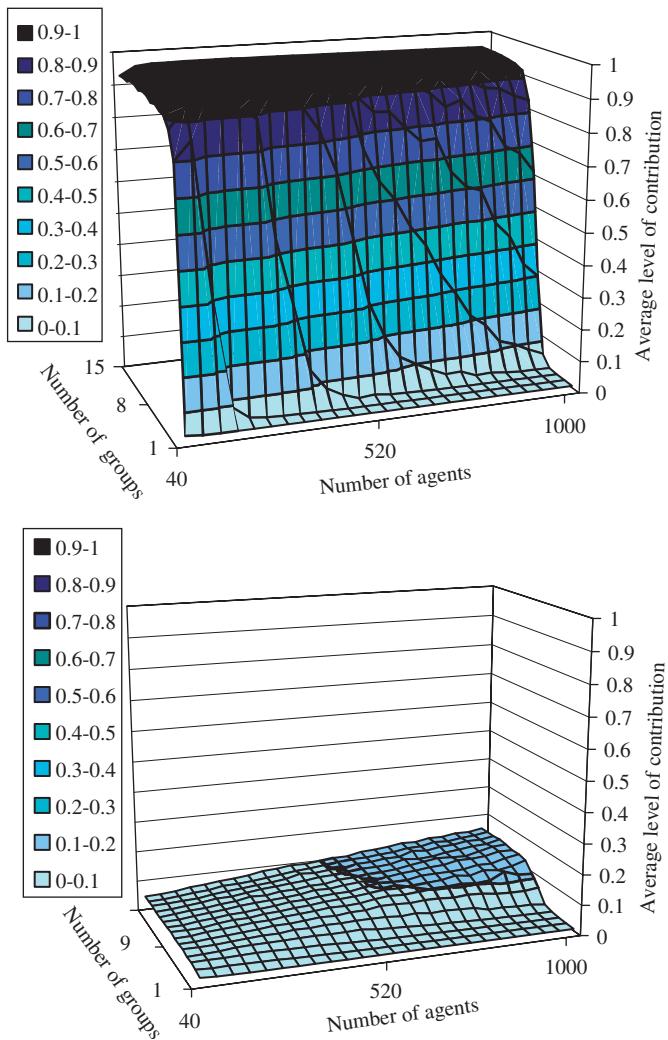


Fig. 8. Average level of contribution  $x$  for different values of number of agents ( $N$ ) and the number of groups ( $M$ ). Top figure without Eq. (5), lower figure including Eq. (5).

would experience less migration and mutation than the reference situation. Fig. 8 shows the trade-off of cooperation between different numbers of agents and groups. A large number of groups is beneficial for establishing high levels of cooperation because more groups lead to fewer opportunities for cooperative groups to be invaded by less cooperative agents. When the number of agents increases, more groups are necessary to derive the same level of cooperation. This relation is roughly linear, indicating that the level of cooperation achieved in a population is a function of the ratio of the population to the number of groups. It is harder to attain groups of cooperators for a restrictive  $B$  since small groups are also prone to the social dilemma that benefits selfish agents in cooperative groups.

#### 4. Discussion

We introduced a simple model that leads to the evolution of high levels of cooperation without kin selection,

perceptible markers of cooperation, indirect or direct reciprocity, or agents with cognitive abilities. Providing agents the opportunity to be divided into groups with modest migration between groups is sufficient for the evolution of cooperation in public good games. Our model differs from other approaches such as kin selection in subdivided populations (Maynard Smith, 1964), trait-group selection (Wilson, 1975), correlated markers (Burtsev and Turchin, 2006), and spatial public good games (Szabo and Hauert, 2002). Kin selection cannot explain our results because the agents do not differentially act in a manner that benefits other agents that are genetically similar. Our model is different from trait selection because groups are not assumed to have equal densities and mutation of cooperation levels and migration across groups are allowed. In models that use correlated markers (Burtsev and Turchin, 2006), cooperation has been shown to evolve provided that agents are capable of perceiving heritable external markers of other agents that may be correlated with a cooperative disposition. Our simple agents develop cooperation despite the absence of sensitivity to any markers. Finally, our model is different from spatial public good games, since no explicit spatial structure is assumed in which agents have fixed positions and interact only with their neighbors (Szabo and Hauert, 2002). Our model provides one mechanism for group selection (Wilson, 1983), or more generally, multi-level selection, in which alleles spread in a population because of the benefits they bestow on groups. This multi-level selection occurs even though each agent's reproduction rate depends only its individual fitness, because individual fitness depends upon the group's overall cooperation level.

Our paper resembles the modeling and results of Killingback et al. (2006) in a number of ways. Both of our models incorporate a public good problem with a total population divided into multiple groups, resource sharing within groups, competition for reproduction by agents across all groups, and parametric manipulation of the group benefit for cooperation, migration rate, and mutation rate. There are nevertheless important differences between our study and Killingback et al. (2006). We considered two types of public good games, and analysed in greater detail the temporal dynamics and the sensitivity of the level of cooperation to individual parameters and their interactions. The two types of games we distinguish are with a public good multiplier independent of group size, as also used by Killingback et al. (2006), and a stricter condition that the value of the public good multiplier always leads to a conflict between individual and group interests. This latter condition is particularly important because it shows that cooperation can emerge in a public good problem even when agents always face a social dilemma. Killingback et al.'s explanation of their results was that "reproduction in groups, combined with dispersal between groups, results in variations in group size, and for groups of sufficiently small size, the public goods game is

no longer a social dilemma" (p. 1480). We agree that the formation of small groups is the crucible for the emergence of cooperation, but argue that this can occur even when there is always a true social dilemma. It requires that mutation is not too fast, otherwise cooperation levels degrade before new pioneering colonies of cooperators can be formed. It also requires that migration be fast enough to regularly create clusters of cooperative pioneers, but not so fast as to constantly expose these colonies to less cooperative invaders.

Within these constraints, robust cooperation is reliably achieved. The fundamental mechanism is that once a particular cooperation level is achieved in a population, only newly forming groups that happen to have cooperation levels higher than this will thrive. As long as their group grows before they are invaded by defectors (how long they have to grow is determined jointly by migration and mutation rates), the agents that migrate out of the group to form new groups will possess this new, higher value of cooperation. In this manner, cooperation ratchets upwards in the population while ratcheting downwards within each of the groups. As noted by Killingback et al. (2006), the upward trend in population-wide cooperation is consistent with downward trends in each group, and is an example of Simpson's paradox. The resolution to the paradox stems from the highly unequal population sizes in the groups. As the cooperation level in a group decreases its global competitiveness and population size also decreases, with the result that newly founded cooperative groups will rapidly increase their relative share of the total population.

Our systematic analysis of the parameter space shows that a small level of migration is important, as well as more than a handful of groups. Interestingly, the optimal rate of migration for achieving cooperation is between 0% and 1%. Although no cooperative group is ever stable, a sufficient chance of migration of cooperative agents leads to frequent enough creations of new cooperative groups to stabilize the level of cooperation within the whole population. The higher the value of the public good multiplier, the higher the level of migration that is required to form larger groups that can match this multiplier.

Our model also relates to the firm model of Axtell (1999). In this model Axtell defines firms as a number of agents who are located in a group and who develop a "public" good, production, that is shared among all participants. Firms form, and as more defectors enter who free-ride on the more active agents, the more altruistic agents move out of the group. With this model he simulates the sizes of firms existing in a population, and is able to relate his simple model to observed firm distributions in the USA. The distribution of firm sizes is similar to the unconstrained situation shown in Fig. 2.

In sum we provided a simple mechanism which explains how agents without comprehensive cognitive abilities can evolve to cooperate in various public good games given the right group structure.

## Acknowledgments

Many useful comments and suggestions were provided by Neil Bearden, Filippo Menczer, Elinor Ostrom, Michael Wade, and an anonymous reviewer. This research was funded by National Science Foundation Grants BCS-0432894 and 052792, and Department of Education, Institute of Education Sciences Grant R305H050116.

## References

- Alexander, R.D., 1987. *The Biology of Moral Systems*. Aldine de Gruyter, New York.
- Axelrod, R., 1984. *The Evolution of Cooperation*. Basic Books, New York.
- Axtell, R., 1999. The emergence of firms in a population of agents: local increasing returns, unstable Nash equilibria, and power law size distributions. Center on Social and Economic Dynamics Working Paper No. 3, Brookings Institute, Washington.
- Bergstrom, T.C., 2002. Evolution of social behavior: individual and group selection. *J. Econ. Perspect.* 16 (2), 67–88.
- Burtsev, M., Turchin, 2006. Evolution of cooperative strategies from first principles. *Nature* 440, 1041–1044.
- Cohen, D., Eshel, I., 1976. On the founder effect and the evolution of altruistic traits. *Theor. Popul. Biol.* 10, 276–302.
- Dugatkin, L.A., 1997. *Cooperation Among Animals: an Evolutionary Perspective*. Oxford University Press, Oxford.
- Gintis, H., Smith, E., Bowles, S., 2001. Costly signaling and cooperation. *J. Theor. Biol.* 213, 103–119.
- Hamilton, W.D., 1964. Genetical evolution of social behavior I and II. *J. Theor. Biol.* 7, 1–52.
- Kagel, J.H., Roth, A.E. (Eds.), 1995. *The Handbook of Experimental Economics*. Princeton University Press, Princeton, NJ.
- Killingback, T., Doebeli, M., Knowlton, N., 1999. Variable investment, the continuous prisoner's dilemma, and the origin of cooperation. *Proc. R. Soc. B* 266, 1723–1728.
- Killingback, T., Bieri, J., Flatt, T., 2006. Evolution in group-structured populations can resolve the tragedy of the commons. *Proc. R. Soc. B* 273, 1477–1481.
- Leimar, O., Hammerstein, P., 2001. Evolution of cooperation through indirect reciprocity. *Proc. R. Soc. London B* 268, 745–753.
- Lotem, A., Fishman, M.A., Stone, L., 1999. Evolution of cooperation between individuals. *Nature* 400, 226–227.
- MacLean, R.C., Gudelj, I., 2006. Resource competition and social conflict in experimental populations of yeast. *Nature* 441, 498–5001.
- Mar, G., StDenis, P., 1994. Chaos in cooperation—continuous-values prisoners dilemmas in infinite logic. *Int. J. Bifurcation Chaos* 4 (4), 943–958.
- Maynard Smith, J., 1964. Group selection and kin selection. *Nature* 201, 1145–1147.
- Nowak, M.A., Sigmund, K., 1998. Evolution of indirect reciprocity by image scoring. *Nature* 393, 573–577.
- Olson, M., 1965. *The Logic of Collective Action*. Harvard University Press, Cambridge, MA.
- Sella, G., Lachmann, M., 2000. On the dynamic persistence of cooperation: how lower individual fitness induces higher survivability. *J. Theor. Biol.* 206, 465–485.
- Szabo, G., Hauert, Ch., 2002. Phase transitions and volunteering in spatial public goods games. *Phys. Rev. Lett.* 89, 118101.
- Travisano, M., Velicer, G.J., 2004. Strategies of microbial cheater control. *Trends Evol. Ecol.* 12, 72–78.
- Trivers, R., 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.* 46, 35–57.
- Wade, M.J., 1977. An experimental study of group selection. *Evolution* 31, 134–153.

- Wade, M.J., 1978. A critical review of the models of group selection. *Q. Rev. Biol.* 53, 101–114.
- Wedekind, C., Milinski, M., 2000. Cooperation through image scoring in humans. *Science* 288, 850–852.
- Wilson, D.S., 1975. A theory of group selection. *Proc. Natl Acad. Sci. USA* 72, 143–146.
- Wilson, D.S., 1983. The group selection controversy: history and current status. *Annu. Rev. Ecol. Syst.* 14, 159–187.
- Wright, S., 1945. Tempo and mode in evolution: a critical review. *Ecology* 26, 415–419.
- Zahavi, A., 1977. The cost of honesty (further remarks on the handicap principle). *J. Theor. Biol.* 67, 603–605.