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**GROUP SELECTION AND THE EVOLUTION OF ALTRUISM**

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# GROUP SELECTION AND THE EVOLUTION OF ALTRUISM

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ABSTRACT. “Group selection” is often cited as an explanation for the survival of altruism. The idea of group selection is a controversial one — much effort has been expended on its justification (and refutation). Relatively little effort has gone into formally testing whether or not it can actually provide a *reasonable* explanation for altruistic behaviour. This paper concentrates solely on whether or not a group structure enables the survival of altruism in an evolving population. If altruism is to flourish either groups need to be isolated from each other for *multiple* generations, or groups themselves need to be constructed in a *positively assortative* manner. In the former case the size of the group, the relative benefit to cost of altruism and the number of generations in isolation play a crucial role in determining the survival chances of altruism. In the latter case, when groups are short-lived phenomena, a precise condition is given on the assortative mechanism for the survival of altruism in the long run. The probability distribution of the dispersion-rematching process and the group size are of critical importance in this case.

## 1. INTRODUCTION

“A tribe including many members who, from possessing in high degree the spirit of patriotism, fidelity, obedience, courage and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; [and this would be natural selection.]”  
Charles Darwin, *The Descent of Man* (1871)

These, perhaps rather over-used, lines are quoted by Wright (1994), Ridley (1997) and many others. They invariably precede an assault on group selection. The thrust of the attack concentrates upon the second phrase (in square brackets) — whilst the logic of the

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earlier part of the statement is left unchallenged. Whether or not group selection itself is rejected as a sensible theory of evolution, the idea that if only it *could* be accepted then it *would* provide a justification for the survival of altruism is not. Indeed, the intuition from the first part of the quote is freely admitted and reproduced over and over again.

**1.1. Group Selection and Altruism.** Group selection has a controversial history. Recently it has gained some degree of respectability, particularly through the work of Sober and Wilson (1998). Most often the theory is offered as a justification for altruistic behaviour. Even those who do not accept that group selection takes place claim it *would* explain altruism. Common of such claims is Ridley (1997, page 175): “[...] cooperative groups thrive and selfish ones do not, so cooperative societies have survived at the expense of others. Natural selection has taken place not at the level of the individual but at the level of the band or tribe.”, Dawkins (1989, page 7): “[...] a group, [...] whose individual members are prepared to sacrifice themselves for the welfare of the group, may be less likely to go extinct than a rival group whose individual members place their own selfish interests first. Therefore the world becomes populated mainly by groups consisting of self-sacrificing individuals.”, or Wright (1994, page 187): “[So] even though a tribe full of selfless people would prevail over a tribe full of selfish people, it is hard to see how a tribe would get full of selfless people in the first place. [...] Even if you magically intervened and implanted “sympathetic” genes in 90 percent of the population, these would steadily lose out to their less ennobling rivals.” The second part of this statement is typical. Indeed, Ridley (1997) goes on: “Selfless groups would be perpetually undermined by the selfishness of their individuals.”

Dawkins (1989) puts it even more forcefully: “[...] in the group of altruists, there will almost certainly be a dissenting minority who refuse to make any sacrifice. If there is just one selfish rebel, prepared to exploit the altruism of the rest, then he, by definition, is more likely than they are to inherit and have children. Each of these children will tend to inherit his selfish traits. After several generations of this natural selection, the ‘altruistic group’ will be over-run by selfish individuals, and will be indistinguishable from the selfish group. Even if we grant the improbable chance existence initially of pure altruistic groups without any rebels, it is very difficult to see what is to stop selfish individuals migrating in from neighbouring selfish groups and [...] contaminating the purity of the altruistic groups.”

The logic is always that group selection would work very nicely if only a group *full* of altruists could arise. Popular writers such as the above are in good company, Maynard Smith (1993, page 199) says: “[...] a group consisting entirely of altruistic individuals will do better than one consisting of entirely selfish ones [...] The problem is to explain how a

group comes to consist wholly of altruistic individuals in the first place, since in a mixed group altruism will be eliminated by selection.” There may be very good reasons for rejecting group selection (or there may not). This, however, is not one of them. Groups consisting *entirely* of altruists are not required for altruism to flourish in a population. On the other hand, group selection does not *always* favour altruists.

**1.2. Haystacks and Altruism.** All of the above writers (and many more) agree on two things; (i) altruists are perpetually undermined by the existence of selfish individuals within their groups and (ii) groups that are largely selfish in composition lose out to groups that are largely altruistic. This paper is an attempt to formalise this intuition and to calculate conditions under which altruism can survive in such a situation.

The literature this work most directly relates to, and follows from, is the “haystack” model of Maynard Smith (1964) and the subsequent reassessment of Wilson (1975) and (1987).<sup>1</sup> In the former, altruism’s survival does indeed depend entirely upon the existence of groups that are composed entirely of altruists. This is because (as Sober and Wilson, 1998, point out) mixed groups are eliminated immediately. It is not clear why a selfish/altruistic mix should be so detrimental to group survival. It is certainly not a necessary part of any definition of altruism. In the latter papers, this idiosyncrasy is resolved. Mixed groups do not immediately face extinction. Nonetheless, it remains full groups that drive the results. Individual agents are formed into groups only once, and it is possible for altruism to dominate the population. Therefore there must be at least one group which is composed entirely of altruists (where selfish behaviour can never take root) which comes to dominate the population. Mutation or migration would make such a scenario an extreme improbability. Here, this criticism is taken on board — mutations prevent homogeneous groups from prevailing.

This is not the only innovation in this paper. The initial group size, the number of groups, the number of generations spent within groups and the benefit to cost ratio of altruistic behaviour (along with its relationship to outside ‘non-interaction’ payoffs) are all parameters of the model. In this sense the model is more generally applicable to social as well as biological environments.

**1.3. An Evolutionary Game Theoretic Interpretation.** The crucial features of altruistic behaviour are well captured by a prisoners’ dilemma game. This is a common technique for modelling altruism in both biology (see Nowak, Sigmund and Sedy, 1995,

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<sup>1</sup>There is also a connection with the “kin selection” literature initiated by Hamilton (1963) and (1964). A discussion of the differences between group selection and kin selection is beyond the scope of the current paper. For an interesting summary see Maynard Smith (1976) and, more recently, Grafen (1984).

amongst many others) and the social sciences, for example Stark (1995). Agents are matched by some assortative process into groups. Once in their groups they interact for a number of generations, before a further dispersion takes place and all the agents are rematched into new groups. The groups are *isolated* in the sense that agents can only play against other agents in the same group. The interaction can be interpreted either as a game played by randomly assigned pairs, or as a game played by the entire group.<sup>2</sup>

The model is first analysed when there is only one period of interaction within groups before dispersion (in Section 2) and a precise condition is derived on the assortative process for the survival of altruism. Then, with the aid of simulations, a model of multiple generations is explored. Here assortment takes the form of random matching. Section 3 gives the details. Mutations are introduced for modelling realism and remove the artificial effect of groups composed entirely of altruists. As the results of Section 4 show, altruism can still survive. The parameters of the model determine the survival chances of altruism in an intuitive way. In a model with multiple dispersion phases, Section 5 demonstrates that altruism and selfishness can actually co-exist in the long run. Neither is driven to extinction. Section 6 concludes.

## 2. THE ANALYTICAL MODEL

The model can be seen as an attempt to formalise the framework described in Sober and Wilson (1998). Figure 1 depicts the dynamic of interest. A similar picture can be found in Sober and Wilson (1998, page 69). The number of groups (and generations) in Figure 1 is purely for illustrative purposes. In general, suppose a population of size  $N$  is divided equally into  $m$  groups, each with  $n$  agents. How the agents are assorted into the different groups is left open for the moment. The agents are one of two types —  $A$ , altruistic or  $S$ , selfish. Within a particular group  $i$  the proportion of altruists is given by  $p_i$ . In the population as a whole the proportion of altruists is written  $P$ .

Having been sorted into their groups the agents interact *only* with other members of their group. In particular, selfish types always increase in proportion at the expense of altruists. However, a group with many altruists grows at the expense of groups with fewer altruists. In this way there is both intra- and inter-group evolution. This continues for  $g$  generations. Interest lies in the proportion of altruists in the population as a whole.

Analytical results are available for the case when the population is immediately rematched (dispersed) after one “round” of interaction ( $g = 1$ ). The simulations of Section 3 allow a discussion of the more complex case when agents stay in their particular groups for

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<sup>2</sup>To be precise, the game is a 2-player or  $n$ -player prisoners’ dilemma.

more than one generation ( $g > 1$ ). The simulations also generate results when there is a (small) probability of mutations taking place and for multiple dispersion phases.

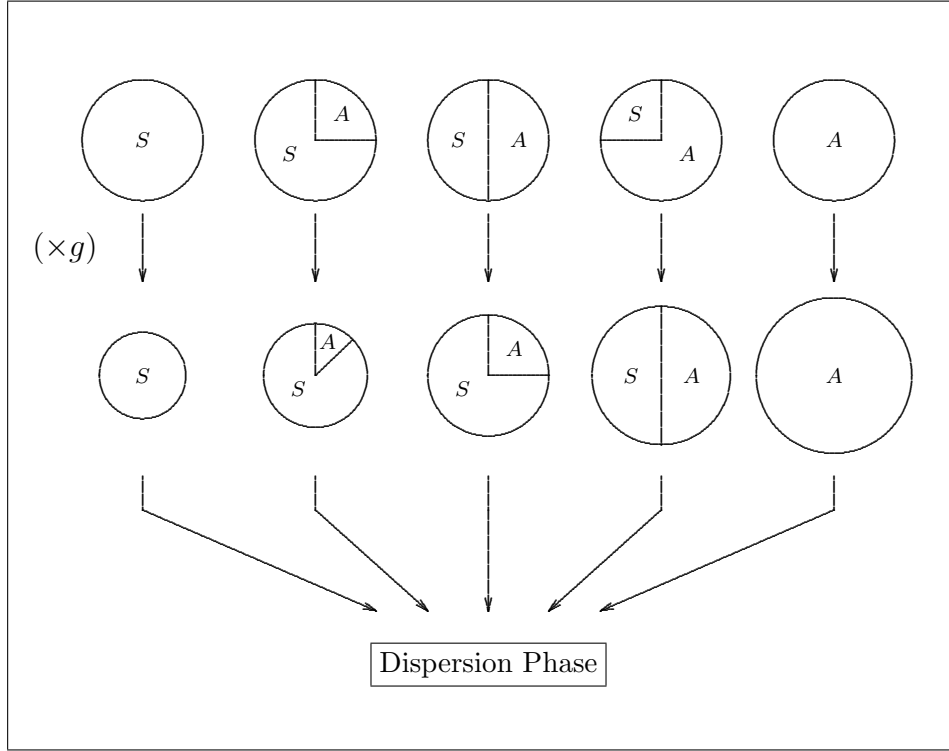


FIGURE 1. Groups and Altruists.

**2.1. The Game.** An agent in a particular group interacts with other agents *in that group*. The way in which this occurs can be given a micro game theoretic justification although this is by no means necessary. Suppose each agent within a group meets at random another agent from that group and plays a  $2 \times 2$  game with them. An altruist incurs a cost  $c$  to themselves whilst giving a benefit  $b$  to their opponent. Selfish types neither incur the cost nor give the benefit. This interaction is naturally a prisoners' dilemma and can be represented by the following normal form game:

	$A$	$S$
$A$	$b - c$ $b - c$	$b$ $-c$
$S$	$-c$ $b$	$0$ $0$

It is assumed throughout that  $b > c > 0$ . The only equilibrium of this game is  $\{S, S\}$ . Indeed, in the absence of the group structure, evolutionary game theory would predict

the extinction of altruists. The group structure not only allows altruists to survive but, under certain conditions, to flourish.

Suppose there is a fixed payoff  $f$  gained independently of this interaction. This accrues to agents regardless of their types and represents the payoff agents get from other sources. It is assumed  $f \geq c$  to avoid the possibility of negative payoffs. The expected payoffs to each type within a typical group can be calculated. Suppose a group is of size  $n$  and has a proportion of altruists equal to  $p$ . The expected payoffs to altruists and selfish types in this  $n$ -player game are  $u_A$  and  $u_S$  respectively where:

$$u_A = \frac{np-1}{n-1}b + f - c \quad \text{and} \quad u_S = \frac{np}{n-1}b + f \quad (1)$$

Clearly,  $u_S > u_A$  for all  $p$ , so that survival of altruists is impossible without the group structure. These two equations could have been written down immediately without recourse to the particular  $2 \times 2$  game above. Nonetheless it is useful to write down this game as it provides a simple way in which to compare the current model with the previous literature. Notice also that the payoffs in Equation (1) only apply when there is at least one agent of the respective types in the population — so that  $u_A \geq f - c$  and  $u_S \leq b + f$ .

**2.2. Group Evolution.** After each agent receives their payoff (fitness) the new group size (say  $n'$ ) is given by the following natural expression:

$$n' = pnu_A + (1-p)nu_S = n \{f + p(b-c)\} \quad (2)$$

The proportion of altruists in the group after interaction is  $p'$  where:

$$p' = \frac{pnu_A}{n'} = p \left\{ f - c + \left( \frac{np-1}{n-1} \right) b \right\} / \{f + p(b-c)\} \quad (3)$$

It is trivial to check that the proportion of altruists will fall within every group after a round of interaction:  $p' < p$  for all  $p \in (0, 1)$ . Of course, if  $p = 0$  then  $p' = 0$ . Likewise if  $p = 1$  then  $p' = 1$ . Groups that are composed entirely of either altruists or selfish types are not of particular interest, however. Mutations (although not explicitly modelled until Section 3) would make such groups extremely unlikely to arise. The results are not driven by the existence of homogeneous groups and would not be completely convincing if they were. Naturally, although each group sees a fall in the proportion of altruists, the population as a whole may see a rise (see Simpson, 1951). The next section investigates.

**2.3. Population Evolution.** First consider the size of the population after one interaction.  $N' = \sum_i n'_i$  where  $n'_i$  is the new size of group  $i$  given by Equation (2).

$$N' = N \{f + P(b-c)\} \quad (4)$$

$P = \sum_i n_i p_i / N$  and hence the new population proportion, after one interaction is  $P' = \sum_i n'_i p'_i / N'$ . After some rearrangement and noting that  $n_i = n$  this becomes:

$$P' = P \left\{ f - c + \frac{n}{n-1} \left( \frac{\sum_i p_i^2}{\sum_i p_i} - \frac{1}{n} \right) b \right\} / \{f + P(b - c)\} \quad (5)$$

It is then straightforward to obtain the following condition for growth in the proportion of altruists in the population after one interaction. By rearranging Equation (5):

**Lemma 1.**  $P' > P$  if and only if:

$$\left\{ \frac{n}{n-1} \left( \frac{\sum_i p_i^2}{\sum_i p_i} - \frac{1}{n} \right) - P \right\} / (1 - P) > \frac{c}{b}$$

In this form the condition is difficult to interpret. However, the inequality can be rewritten in terms of the distribution of altruists and selfish types across the groups. In particular, suppose  $\Pr(X = x)$  is the probability that there are exactly  $x$  altruists in a group. The only possible proportions of altruists,  $p_i$ , in any group  $i$  are in the set  $\{0, \frac{1}{n}, \dots, \frac{n-1}{n}, 1\}$ .  $X_i$  is the number of altruists in group  $i$ . Hence  $X_i = np_i \in \{0, 1, \dots, n\}$ . There are  $m$  groups in the population (hence  $N = mn$ ). So:

$$\frac{1}{m} \sum_{i=1}^m p_i^2 = \frac{1}{m} \sum_{i=1}^m \left( \frac{X_i}{n} \right)^2 = \frac{1}{mn^2} \sum_{i=1}^m X_i^2 = \frac{1}{mn^2} \sum_{j=0}^n j^2 \Delta_j$$

Where  $\Delta_j$  is the number of groups with exactly  $j$  out of  $n$  altruists in them. Hence  $\sum_{j=0}^n \Delta_j = m$  and  $\Delta_j \in \{0, 1, \dots, m\}$ . Now,  $\Delta_j \doteq m \Pr(X = j)$ .<sup>3</sup> Finally:

$$\frac{1}{m} \sum_{i=1}^m p_i^2 = \frac{\mathbb{E}(X^2)}{n^2} \quad \text{and} \quad \frac{1}{m} \sum_{i=1}^m p_i = \frac{\mathbb{E}(X)}{n}$$

The second equality follows analogously. Assembling these facts together:

**Proposition 1.**  $P' > P$  if and only if:

$$\frac{n}{n-1} \left\{ \frac{\text{Var}(X)}{\mathbb{E}(X)(n - \mathbb{E}(X))} - \frac{1}{n} \right\} > \frac{c}{b}$$

*Proof.* Rearrange the inequality of Lemma 1 after substituting;

$$P = \frac{\sum_i n_i p_i}{N} = \frac{n \sum_i p_i}{N} = \frac{\sum_i p_i}{m} = \frac{\mathbb{E}(X)}{n}$$

and similarly  $\sum_i p_i^2 / m$  for  $\mathbb{E}(X^2) / n^2$  which will yield the above inequality.  $\square$

<sup>3</sup>The notation  $a \doteq A$  is taken to mean that the probability limit of  $a$  is  $A$ . In fact, the approximation here becomes exact since  $N$  gets very large endogenously. Alternatively, the rematching dispersion phase could be just *defined* to produce  $\Delta_j$  groups with exactly  $j$  altruists.

**2.4. Dispersion.** The way in which the population is *dispersed* determines the distribution of  $X$ . In this section two such mechanisms are briefly considered. The first of these is the hypergeometric distribution. This corresponds to “uniform” matching of the population after each interaction phase. The entire population is mixed and reallocated to groups randomly. The probability of choosing exactly  $x$  out of  $n$  altruists in any group is given by:

$$\Pr(X = x) = \binom{NP}{x} \binom{N(1-P)}{n-x} / \binom{N}{n}$$

The expected value and variance of the hypergeometric with parameters  $N$ ,  $NP$  and  $n$  are  $E(X) = nP$  and  $\text{Var}(X) = nP(1-P)(N-n)/(N-1)$ . Substituting into the crucial expression of Proposition 1 yields the following:

$$-\frac{1}{N-1} > \frac{c}{b} \quad \text{if and only if} \quad P' > P$$

This can never occur. Therefore, unsurprisingly:

**Corollary 1.** *Suppose agents are immediately and randomly rematched after only one generation of within group interaction. Then the proportion of altruism in the population as a whole collapses to zero.*

This is unsurprising since immediate and random rematching gives the group structure no role whatsoever in the survival of altruism. This is the case where each agent is facing the entire population every period — a standard evolutionary framework.<sup>4</sup> However, this negative result is of importance. If altruism is to survive at all, either there needs to be more than one generation of within group interaction or there needs to be a non-random assortative process that makes it more likely for altruists to find themselves in groups with other altruists. The former case is the main focus of the current paper and is explored fully in Section 3. The latter case is also of interest and is explored in the special case of  $n = 2$  in Cooper and Wallace (1998) and (2000).

The condition of Proposition 1 generally states a necessary and sufficient condition for the spread of altruism on the assortative process in the case of a one generation model. A distributive mechanism that can achieve this is one where each mixture of group is equally likely. In other words  $\Pr(X = x) = 1/(n+1)$ . Here the expectation and variance are  $E(X) = n/2$  and  $\text{Var}(X) = n(n+2)/12$  respectively.

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<sup>4</sup>Indeed, calculating the proportion of altruists in the population is straightforward and is given by:

$$P' = P \left\{ f - c + \left( \frac{NP-1}{N-1} \right) b \right\} / \{f + P(b-c)\}$$

This is identical to Equation (3). The entire population operates exactly like a single group.

**Corollary 2.** *Suppose agents are immediately rematched after only one generation of within group interaction in such a way as to make each proportion of altruists equally likely. Then the proportion of altruism in the population as a whole will increase to one if and only if  $b > 3c$ .*

In other words the benefit to others of altruistic actions has to be 3 times higher than the cost to oneself for altruism to flourish. How such an assortative environment might arise is beyond the scope of this paper, instead attention is restricted to the case of multiple generations of within group interaction. The next section investigates this question with the assistance of simulations.

### 3. THE SIMULATIONS

In this section the simulation methodology is described. The results are presented in Sections 4 (a single dispersion phase followed by repeated generations) and 5 (multiple dispersion phases each followed by a fixed number of generations). Two types of simulation were run side by side — “real” and “smoothed”.<sup>5,6</sup>

**3.1. “Real” Simulations.** A *dispersion phase* consists of the following steps:

- (1)  $N$  agents (of which a proportion  $P_0$  are altruists) are randomly assorted into  $m$  groups of size  $n$  (with a large population this process corresponds to the discussion in Section 2.4 with players distributed according to the hypergeometric).
- (2) Agents within these groups are matched together according to a uniform random matching algorithm.
- (3) Having played the game and received their associated payoffs the new proportion of altruists within each group is calculated and hence the proportion in the population as a whole.
- (4) Simulations are run with and without mutations. Mutations occur randomly at this stage — with probability  $\varepsilon$  an agent’s type is altered.
- (5) The population proportion is recorded and the process repeats itself *from step 2* for  $g$  generations.

<sup>5</sup>All simulations were run using SWARM routines (written in Objective C) — see Luna and Stefansson (2000) for an introduction. Details of the routines are available from the authors upon request.

<sup>6</sup>In each case time-averaged results are reported across 1000 runs of the simulation.

**3.2. “Smoothed” Simulations.** This type of simulation is very similar in structure. A dispersion phase consists of the following steps:

- (1)  $N$  agents (of which a proportion  $P_0$  are altruists) are randomly assorted into  $m$  groups of size  $n$ .
- (2) The proportion of altruists  $p_i$  in every group  $i$  is updated according to Equation (3) and the group size  $n_i$  is updated according to Equation (2).
- (3) Simulations are run with and without mutations. Group size is unaffected, but the proportion of altruists is altered according to the following:

$$p_i'' = p_i'(1 - 2\varepsilon) + \varepsilon = p_i'(1 - \varepsilon) + (1 - p_i')\varepsilon$$

where  $p_i'$  is the proportion of altruists in group  $i$  after step 2.

- (4) The population proportion is recorded and the process repeats itself *from step 2* for  $g$  generations.

**3.3. Parameter Values.** For each type of simulation a range of parameter values were examined. The parameters of interest are  $n$ , initial group size,  $g$ , the number generations spent within groups after dispersion, and  $b/c$ , the ratio of benefit to cost for altruism. All simulations were run for integer values of the parameters in the ranges  $n \in \{2, \dots, 10\}$ ,  $g \in \{1, \dots, 19\}$  (or  $g \in \{1, \dots, 29\}$  with mutations) and  $b \in \{2, \dots, 10\}$  ( $c = 1$  without loss of generality). Generation times were set high enough to allow convergence.

The real simulations were run with twenty groups ( $m = 20$ ). Smoothed simulations run much faster and hence allow the collection of higher quality data. They were run with  $m = 20$  (to check robustness) and with  $m = 100$ . All the results are reported for  $P_0 = 0.5$ ,  $\varepsilon = 0.01$  and  $f = 1$  with  $N$  set endogenously by  $N = nm$ .

**3.4. Multiple Dispersion Simulations.** Finally, results for a number of multiple dispersion phase simulations are reported. Here the smoothed simulation method was employed. After step 4 in Section 3.2 a further step takes place — dispersion (in the sense that the population is rematched into new groups of size  $n$ ). Then agents interact within their groups for another  $g$  generation cycle before dispersion takes place again. The process repeats itself until convergence. Again these simulations were run for a variety of parameter values. With the added perspective from the simulation results of Section 4 three such examples are reported in Section 5.

## 4. RESULTS

Real and smoothed simulations were run side by side. The results are much the same. Essentially the “real” simulations are used to check the robustness of the smoothed simulations which run substantially faster and therefore allow the collection of better quality data (1000 runs per parameter value combination). There are two minor differences between the real and smoothed simulation results. The first occurs for odd  $n$ . In this case, when agents within the group match to play the game, one agent is left out. As soon as groups begin to expand this problem disappears. The second arises due to the difference in the way in which mutations are introduced. Real mutations cause infrequent and large jumps in  $p_i$  — rather than the continuous small jumps associated with the smoothed simulations. Again this becomes less of a problem for larger population sizes. All the results reported here are from the smoothed simulations. The (key) results presented in Section 4.2 are for  $m = 100$  to minimise the effects of these two difficulties.

**4.1. No Mutations.** The results in this section refer to Figure 2. Each individual simulation run corresponds with one of the types illustrated in the figure.

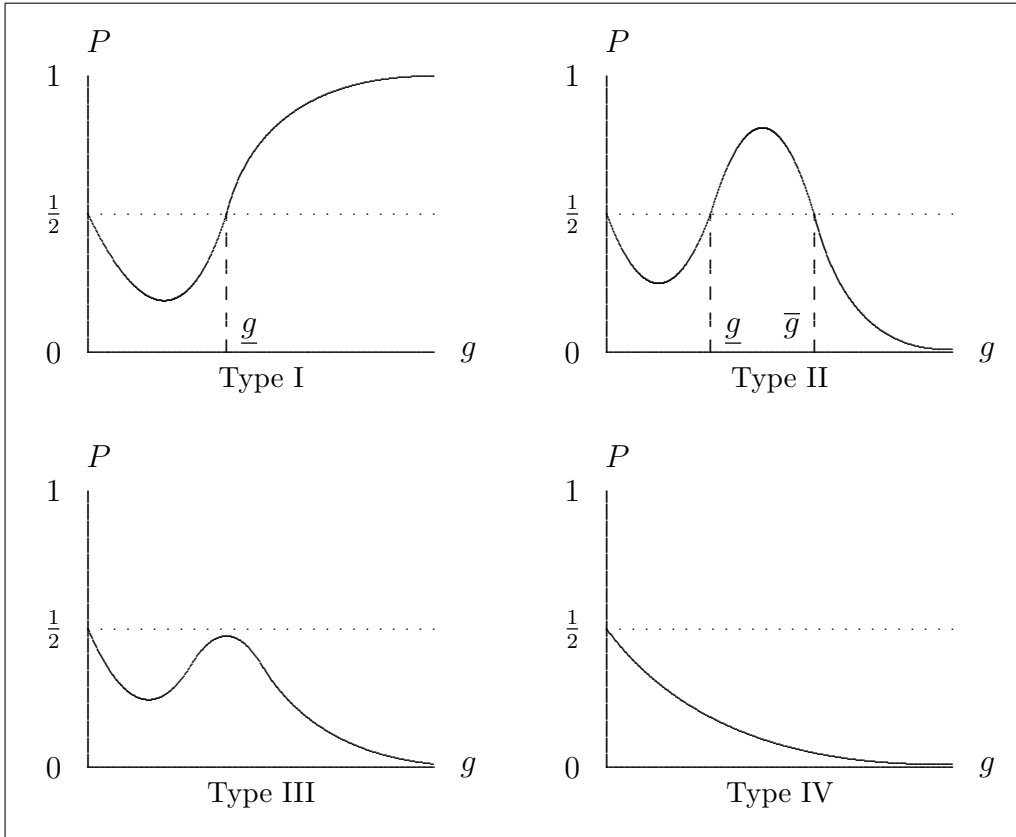


FIGURE 2. The Evolution of Altruists.

**Type I:** These runs ended with altruism dominating the population. The proportion of altruists in the population,  $P$ , first falls (as it must, see Corollary 1) but then *recovers* after  $\underline{g}$  generations of within group interaction, to  $P = 0.5$ . Following recovery the proportion of altruists tends to one until eventually they dominate the population.

This only occurs because there is positive probability that at least one of the initial groups is *full* of altruists. From Equation (3),  $p' = p = 1$  in such groups. Moreover they grow faster than mixed groups and eventually dominate the population. This would not happen if there were mutations. Type I runs are not observed at all when there are mutations; they only happen when groups full of altruists are allowed to stay that way.

Indeed, for a given parameter combination, the number of Type I runs (out of 1000) corresponds exactly with the probability that there is at least one group entirely composed of altruists. The probability any given group is full of altruists is given by:

$$\Pr(X = n) = \binom{NP}{n} \binom{N(1-P)}{0} / \binom{N}{n} = \frac{(N/2)!}{(N/2 - n)!} \frac{(N - n)!}{N!}$$

(Recall  $P = 0.5$ ). This probability is well-approximated by:

$$\Pr(X = n) \approx \left(\frac{1}{2}\right)^n \quad \text{hence} \quad \Pr(X < n) \approx 1 - \left(\frac{1}{2}\right)^n$$

For large  $m$  (and hence  $N$ ) the probability that there are no groups completely full of altruists after the dispersion phase is well approximated by:

$$\Pr(X < n \text{ for all groups}) \approx \left[1 - \left(\frac{1}{2}\right)^n\right]^m$$

So  $1000 \times \{1 - [1 - (1/2)^n]^m\}$  gives a good approximation of the number of type I simulation runs to be expected. This number does not depend on  $b/c$  and matches well with the simulation results. Certainly a more reasonable model (with mutations) would not include any type I runs. This is why the results of Section 4.2 are more important.

**Type II:** This is the crucial run type. The proportion of altruists in the population at first falls (as it must), then recovers to its initial proportion (0.5) at  $\underline{g}$  before finally falling again. Eventually it falls below the initial proportion (at  $\bar{g}$ ) and asymptotes to 0.

Given certain parameter values altruism can, and does, recover. This result does not depend upon there being any groups completely composed of altruists. In fact, there are none (otherwise the proportion would asymptote to 1 as above). However, the number of generations spent interacting within groups must lie in a critical range:  $g \in [\underline{g}, \bar{g}]$ . Too little time within groups does not allow altruism to give the group an advantage in the population. Too many generations allow selfish individuals the time to dominate the group. If dispersion takes place too soon *or* too late, altruism cannot survive.

Section 4.2 has a full discussion of the relationship between this critical range and the other parameters of interest, particularly  $n$  and  $b/c$ . Section 5 examines the evolution of the population when there are multiple dispersions. Clearly, for altruism to stand a chance in such cases, dispersion must take place within the critical range.

**Type III:** These simulation runs see a fall in altruism to begin with (as always) and then a rise. However, the proportion of altruists in the population does not recover to its initial level before it begins to fall again (and asymptotes to 0). Altruism will not survive regardless of the timing of the dispersion phase.

**Type IV:** Finally, in type IV simulation runs, altruism collapses monotonically to zero. These last two cases are discussed in more detail in the next section. Interest lies in the values of the key parameters for which a type II simulation will occur and moreover the critical range of  $g$  for which altruism recovers.

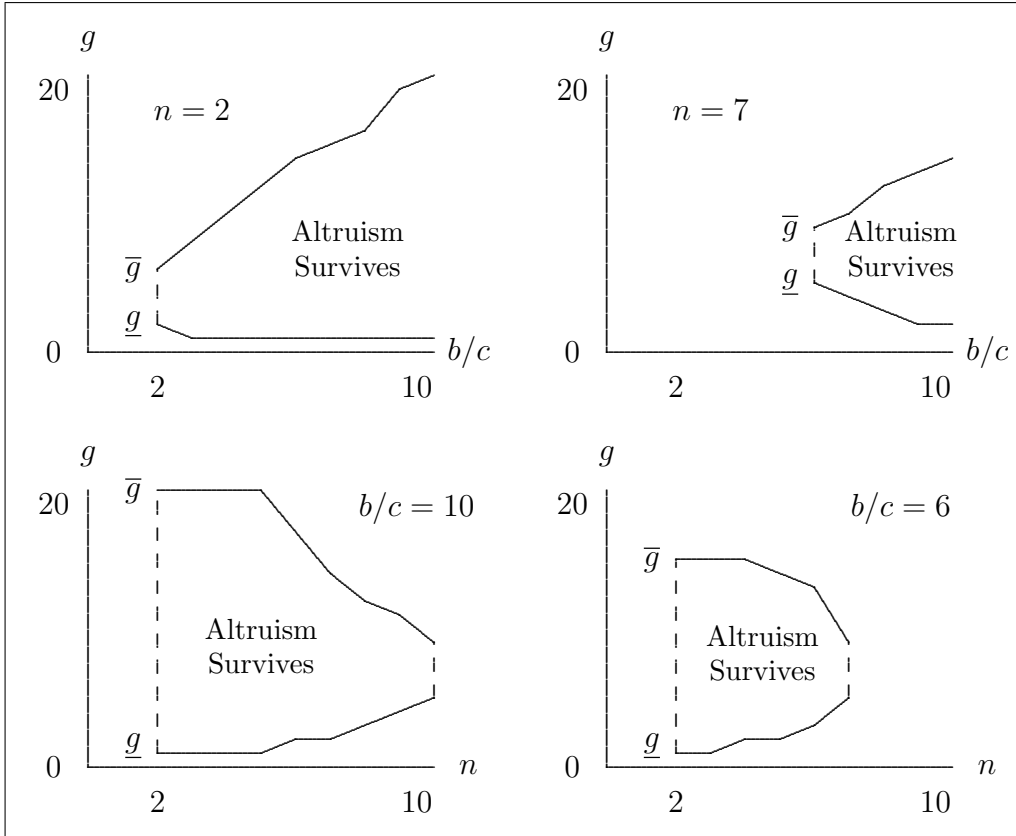


FIGURE 3. The Survival of Altruism.

**4.2. Mutations.** Mutations are introduced for the sake of modelling realism. They have the expected effect of removing homogeneous groups (both of altruists and of selfish types). Type I simulations are no longer observed. All the results correspond to types

II, III or IV. This is much more convincing.  $P \rightarrow 0$  in the long run — the dispersive and assortative phase is *required* for the survival of altruism. Isolated groups *cannot* be enough in themselves to provide a justification for altruism.<sup>7</sup> The two key issues are:

- (1) For which parameter values does a type II run occur?
- (2) What is the critical range  $[g, \bar{g}]$  for which altruism can recover?

For fixed  $n$ , as  $b/c$  rises type II runs become more likely. For fixed  $b/c$ , as  $n$  falls type II runs become more likely. More precisely the results can be characterised as follows:

- (1) Fix  $n$ :  $\underline{g}$  is weakly decreasing in  $b/c$  and  $\bar{g}$  is weakly increasing in  $b/c$ .
- (2) Fix  $b/c$ :  $\underline{g}$  is weakly increasing in  $n$  and  $\bar{g}$  is weakly decreasing in  $n$ .
- (3) Fix  $g$ :  $\bar{n}$  is weakly increasing in  $b/c$ .<sup>8</sup>

These three statements together allow the construction of a three dimensional plot of  $b/c$  and  $n$  against  $g$ . For each  $b/c$  and  $n$  combination a range  $G = [\underline{g}, \bar{g}]$  can be plotted such that a dispersion phase taking place at any  $g \in G$  can result in the survival of altruism. Figures 3 and 4 illustrate cross sections of this three dimensional plot for a few of the parameter values. Notice that, in Figure 3, the area denoted “Altruism Survives” for  $n = 7$  would fit inside the analogous area for  $n = 2$ . This is generally true. Denote  $G_{n,b}$  as the range  $[\underline{g}, \bar{g}]$  for a particular  $n$  and  $b/c$ . Then  $G_{n+1,b} \subseteq G_{n,b}$  and  $G_{n,b} \subseteq G_{n,b+1}$ .

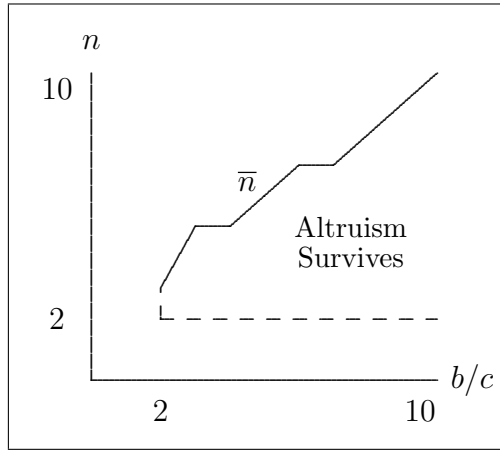


FIGURE 4. Survival:  $\bar{n}$  and  $b/c$  with  $g = 6$ .

Figure 4 shows  $\bar{n}$  for a given  $g$ , it equally shows the minimum value of  $b/c$  in terms of  $n$  (given  $g$ ) for the survival of altruism. The line labelled  $\bar{n}$  rises and then falls as  $g$  increases. The maximum occurs at around  $g^* = 8$ . This approximately corresponds

<sup>7</sup>Simply because the entire population is itself a “group” and altruism will go extinct in such a situation.

<sup>8</sup> $\bar{n}$  is the maximum size of the group for which altruism survives.

to the value of  $g$  that maximises the proportion of altruists in a type II or III run (see Figure 2). This is the generation length  $g$  that is “kindest” to altruism — it maximises altruism’s survival chances.

In the next section the model is taken one step further. Multiple dispersion phases are introduced using a  $g \in G_{n,b}$  for various values of  $n$  and  $b/c$ . Altruism certainly could survive — does it? Can it eventually dominate the population even though there are no fully altruistic groups? Can altruistic and selfish types co-exist in a population, or must one always drive the other to extinction?

## 5. MULTIPLE DISPERSIONS

The results for three of the simulation runs with multiple dispersion phases are presented in this section. The timepaths illustrated are the averaged results of 1000 simulation runs. In the first example altruism will, on average, eventually dominate the population. In the second altruism either collapses to zero or explodes to one. This is a “bifurcation”. In the third (and most interesting) example the proportion of altruists locks into a regular cycle. Altruistic and selfish types co-exist in non-negligible proportions.

**5.1. Domination.** Consider Figure 5. In this simulation the parameters are  $b/c = 10$ ,  $n = 5$ ,  $g = 8$  and  $m = 20$ . Both the first and second simulations are run with  $\varepsilon = 0$ .

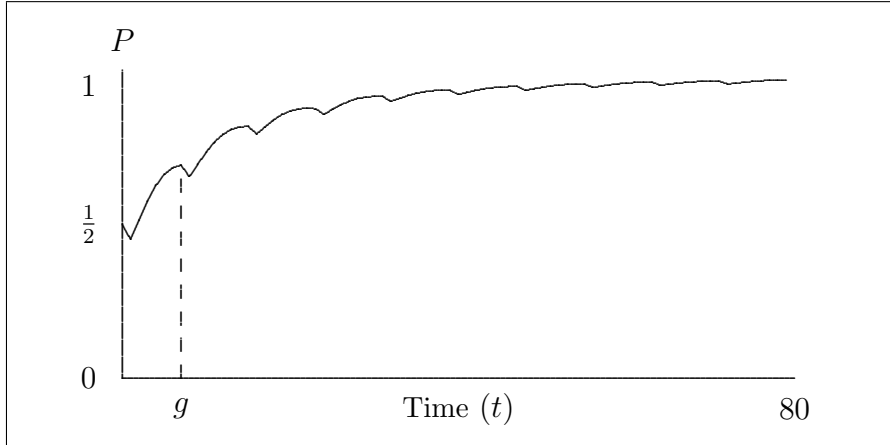


FIGURE 5. Multiple Dispersions: Eventual Domination.

The population is initially dispersed randomly into 20 groups. The agents interact within their groups for 8 generations and then a further dispersion phase occurs. The process repeats itself. Referring to the results discussed in the last section, the parameters for this simulation yield a type II run on average with  $\underline{g} = 2$  and  $\bar{g} = 15$ . Hence  $g \in G_{5,10}$ .

Nearly all of the runs result in altruism eventually dominating the population. The time averaged graph in Figure 5 shows this clearly. After each dispersion phase there is a drop in the proportion of altruists (as expected) but before the next dispersion takes place altruism has had enough time to recover to its initial level and beyond.

**5.2. Bifurcation.** Consider Figure 6. In this simulation the parameters are  $b/c = 6$ ,  $n = 8$ ,  $g = 9$  and  $m = 100$ . Again there are no mutations.

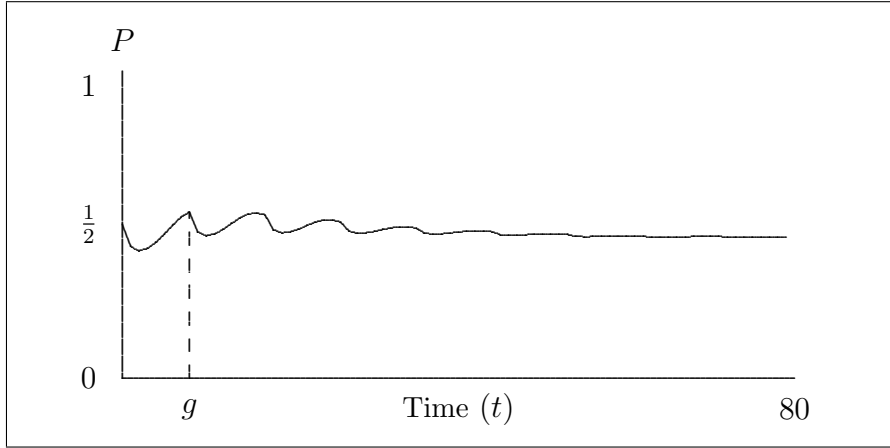


FIGURE 6. Multiple Dispersions: Bifurcation.

Exactly the same process takes place here with the new parameter values. This time the results of Section 4 suggest again a type II run on average. The critical values of  $g$  are  $\underline{g} = 7$  and  $\bar{g} = 10$ . Hence  $g \in G_{8,6}$ . However, 61% of the runs (with a single dispersion phase) were type III or IV whilst 31% were type I. Unsurprisingly then, in the simulations with multiple dispersion phases, the population either sees a rise in the proportion of altruists (asymptoting at 1) or a fall (asymptoting at 0). Figure 6 shows the average proportion of altruists in the population over time.

Whether altruism faces extinction or not depends mainly upon the existence of groups composed entirely of altruists. If the initial dispersion draws a group consisting only of altruists (with a probability of approximately 0.31) the proportion of altruists increases to a great extent in the first 9 generations. This makes it much more likely that a group with only altruists is constructed during the next dispersion phase, and so on. Again it is the presence of homogeneous groups that drives the results. Mutations remove this possibility and hence the simulations described in the next section are of more interest.

**5.3. Cycles.** Consider Figure 7. In this simulation the parameters are  $b/c = 3$ ,  $n = 4$ ,  $g = 8$  and  $m = 100$ . Mutations are present here, with  $\varepsilon = 0.01$ . Referring again to the results of Section 4, the critical region for this parameter combination is  $G_{4,3} = [\underline{g}, \bar{g}] =$

$[5, 10]$ . Hence  $g \in G_{4,3}$ . The proportion of altruists in the population as a whole locks into a recurrent cycle. After each dispersion phase the proportion falls (as it must) only to recover and begin to fall again before another dispersion takes place.

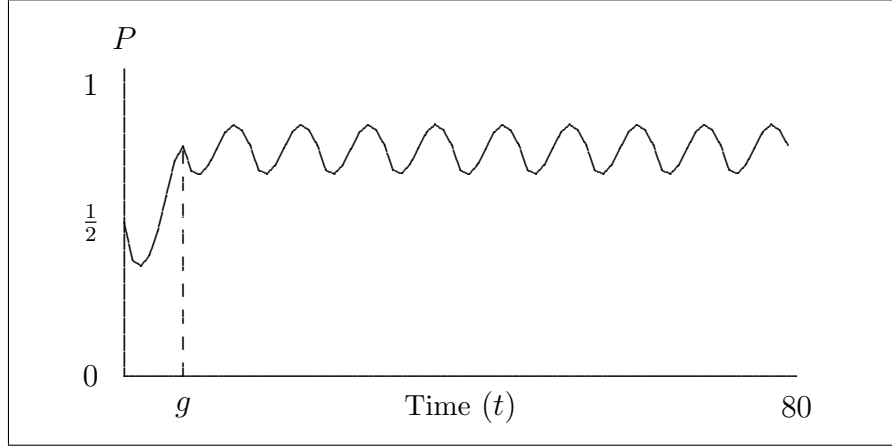


FIGURE 7. Multiple Dispersions: Co-existence.

In the first phase the proportion of altruists increases substantially — here this is *not* due to the existence of groups entirely composed of altruists. Mutations do not allow these groups to survive. After the second dispersion phase begins, the level of altruism in the population quickly stabilises into a cyclic formation. Figure 8 illustrates  $P_t$  against  $P_{t+1}$  for all generations  $t$ . The proportion of altruists varies between approximately 0.65 and 0.81. This kind of behaviour is a common feature of the system with mutations.

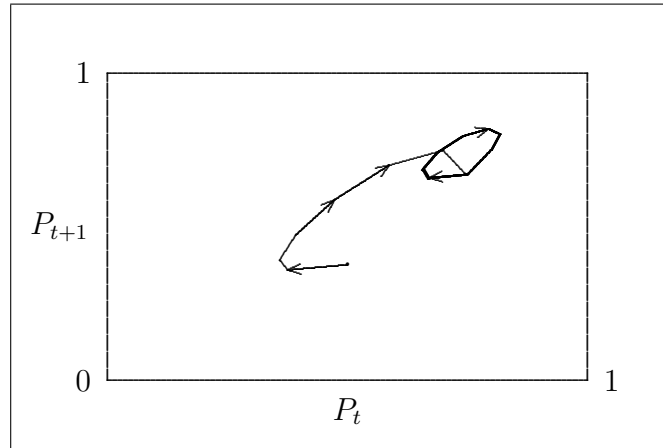


FIGURE 8. Cycles and Altruism.

The level around which the system cycles depends upon the parameters,  $b/c$  and  $n$ . The lower  $n$ , or the higher  $b/c$ , the more successful altruism will be (the higher the level). Of

course, it is essential that  $g$ , the number of generations spent interacting within groups, lies in the critical region  $G_{n,b}$ . If this were not the case, altruism could not survive in the first place. The next section offers some general conclusions drawn from both the analysis of Section 2 as well as the simulations.

## 6. CONCLUSIONS

Group selection can therefore provide a justification for the existence of altruism. However, it is by no means certain that altruism will survive given an evolutionary group structure alone. On the contrary, conditions on the size of groups, the benefit (to others) to cost (to oneself) ratio of altruistic behaviour and the length of time spent interacting within groups are critical. Also of crucial importance is the assortative process itself.

Altruism can only survive when there is either (i) positively assortative matching processes or (ii) multiple generations of within group interaction. The group structure is of no importance at all if agents are immediately rematched into new groups *at random* after *one round* of interaction (see Corollary 1).

Proposition 1 gives a necessary and sufficient condition on the distribution of the rematching process for the growth of altruism (when agents spend only one generation interacting within groups). The process must be positively assortative in the sense that altruists must be more likely to join groups containing high numbers of altruists. An example of such a distribution, when  $b/c$  is sufficiently large, is the uniform (see Corollary 2). How such a procedure might arise is left open.

The simulations explore the possibility that rematching remains random but individuals spend longer within groups. Here too altruism can survive. Without mutations and with just one dispersion phase, the simulations can be placed into four categories. However, type I simulations (see Section 4) would not arise in a more complete model including mutations. In fact, simulations where altruism eventually dominates the population only occur when there is at least one group consisting entirely of altruists. This situation would never arise if there was even a tiny probability of mutation or migration.

For this reason the simulations are also computed *with* mutations. Here the rather artificial type I runs do not occur. Altruism can still survive. After initially falling, the proportion of altruists in the population can recover to its initial level and beyond, before tending to zero in the limit (type II runs). The implied range of generation times for which the proportion is above its starting value is of key importance. As long as dispersion takes place at a generation which lies within this range altruism can survive. For each combination of group size and benefit to cost ratio such a range can be calculated. The lower bound of the range is decreasing in the benefit to cost ratio and increasing in

group size. The upper bound of the range is increasing in the benefit to cost ratio and decreasing in group size. The diagrams of Section 4.2 illustrate this result.

Simulations presented in Section 5 illustrate the process over a number of dispersion phases. The proportion of altruists in the population can become locked in a permanent cycle. Altruism need not evolve to dominate the population and it need not face extinction. Group selection can provide a justification for the co-existence of altruistic and selfish types in a given population. The models above yield predictions for the level of altruism observed in a particular population given a few key parameters — the most important being (i) the size of the isolated group, (ii) the length of time spent by agents interacting within groups and (iii) the benefit to cost ratio of the altruistic action.

Most interestingly, if group selection is to provide a reasonable justification for altruism, the length of time spent within groups before returning to match with the rest of the population must neither be too long *nor* too short. It has to be just right.

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