

Visualizing the Limitations of Multi-level Selection as an Explanation for Altruism

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Introduction

To the extent that altruistic behavior persists in biological populations, it is problematic to explain as a phenomenon of adaptation. For to be altruistic in the biological sense, an altruistic act must confer, in an immediate manner at least, a fitness detriment to the actor. Taking up the challenge to account for altruism as an adaption, some theorists have turned to multi-level selection theory for explanation.¹ Their central claim is that while altruism is detrimental to fitness as measured within any discrete social group, because having a high proportion of altruists greatly enhances a group's collective reproductive capacity, the altruistic phenotype can maintain a fitness advantage when measured against the population at large, and thus be favored by natural selection.

The purpose of this study is to design, run, and visualize evolutionary simulations to investigate the viability of altruism persisting in populations through the mechanism of multi-level selection. The model for simulations used, which is based on a simple model put forth by Elliot Sober and David Sloan Wilson,² involves populations comprised of groups of individuals, where individuals are either selfish or altruistic. Sober and Wilson use the model to demonstrate, by a single example, that given the right parameters the altruistic phenotype is fitter than the selfish phenotype. The results of this study reveal however that, in the context of the adopted model at least, the parameters required for multi-level selection to sustain the altruistic phenotype are surprisingly extreme. The results thus provide reason to doubt Sober and Wilson's multi-level selection account of altruism.

The model, as adapted for this study³

Each individual has a phenotype, of which only two occur in the model, *altruistic* and *selfish*. The population is divided into groups, and each group is comprised of asexually reproducing individuals. Proportions of altruistic and selfish phenotypes within a group are

¹ In this paper I specifically examine Sober and Wilson's (1998) defense of altruism as a trait that evolves through multi-level selection.

² Sober, Elliot, and David Sloan Wilson, *Unto Others: The Evolution and Psychology of Unselfish Behavior*, London: Harvard University Press, 1998, pp. 19-26.

³ Note that as implemented, the model is actually more flexible than described here. The description captures the manner in which it was used for most of the experiments conducted. Some extensions to the model's behavior are discussed later. See the codebase at github.com/wedgec/multilevel-selection-simulations for model's full specifications. There you can also access all scripts for running experiments, experimental data, Matlab scripts for visualizing results, and Matlab-generated visualizations.

variable. Assignment of individuals to groups occurs before the first round of a trial and in between rounds subsequently.

Each group undergoes two life cycle phases per round. The first is the playing of a social game with one's groupmates, and the second is a phase of reproduction and death. Reproduction is probabilistic, and an individual's expected fertility is governed by the results of the social game. Each individual begins the game with a probability of 1 of producing a baseline of one offspring, and zero opportunities for additional offspring at a probability fixed at the start of each simulation (call this parameter *extra reproduction probability*, or e for short). During the social game one's probability of producing the baseline first offspring can be reduced, and one's count of opportunities to produce additional offspring at probability e can increase.

The social game proceeds as follows: each altruistic individual takes one action, in turn. The altruist randomly selects a groupmate other than oneself and confers to it one additional reproduction opportunity. The altruist furthermore suffers a reduction in its probability of producing its baseline first offspring, the amount of which is fixed at the beginning of each trial (call this parameter *cost of altruism*, or c for short). Individuals of the selfish phenotype are passive. They may receive additional reproduction opportunities, but do not otherwise participate.

The death and reproduction phase begins with reproduction, where each individual's reproductive opportunities are cashed out according the changes in state accrued during the social game. Every offspring inherits its parent's phenotype. The death sub-phase, which follows reproduction, is simple. All members of the parent generation perish, while all members of the child generation survive.

For any group at the beginning of a round, we can model the expected number of offspring per phenotype with two simple equations:

Let A = the number of altruists in the parent generation

Let S = the number of selfish individuals in the parent generation

Let $N = S + A$ = the total number of individuals in the parent generation

Expected altruistic offspring: $E_A = A * ((1 - c) + e * \frac{A-1}{N-1})$

Expected selfish offspring: $E_S = S * (1 + e * \frac{A}{N-1})$

Notice that compared to selfish individuals, the within-group fitness of altruists suffers in two ways. The more obvious disadvantage is the loss in probability of producing the baseline first offspring, represented by c . The second, subtler disadvantage is that altruists collectively have A fewer opportunities for extra offspring, as each altruist is excluded from its set of potential beneficiaries. Thus the $A-1$ term in the altruism equation—each altruist has only as many chances to benefit from altruism as there are other altruists in the group. The -1 term in the denominators are present for the same reason—since an altruist cannot select itself as its beneficiary, the number of potential beneficiaries is always the total group size less one for the altruist currently acting.

It follows straightforwardly from the above equations that the proportion of altruists within a group is always expected to decline within a round, and vice-versa for selfish individuals. Sober and Wilson point out that nonetheless, through the vehicle of multi-level selection the global proportion of altruists can increase or remain stable. How does this work? Here are three necessary conditions: one, there must be multiple groups. Two, e must be greater

than c . And three, there must be variance between groups in their respective proportions of phenotypes. Basically, the idea is that under the right conditions groups with proportionally many altruists will greatly outreproduce groups with very few. While within these more prolific groups, selfish individuals will net more offspring per capita, altruists represent a bigger piece of the overall reproductive pie, and so the altruistic phenotype will be the dominant beneficiary of that group's fecundity. Groups dominated by the selfish phenotype will of course greatly favor selfish offspring, but since these groups' overall productivity will be less, their influence can be more than counterbalanced by the influence of the more productive, more altruistic groups. More formally, if A_g is the global proportion of altruists leading into a round, the proportion of altruists is expected to increase or remain stable when the following is true:

$$\left(\sum_{k=1}^G E_{A_k}\right) \div \left(\left(\sum_{k=1}^G E_{A_k}\right) + \left(\sum_{k=1}^G E_{S_k}\right)\right) \geq A_g,$$

where k is an index representing a unique group in the population of groups, and G is the total number of groups.^{4,5}

Another condition necessary for multi-level selection to favor altruism is that groups do not exist in isolation. Rather, individuals must be allowed to migrate from group to group. Given that within a group, altruist proportions are guaranteed to decline from a round's beginning to its end, it is obvious that this condition is required. Without it, over arbitrarily many generations, selfish phenotypes are expected to infinitely approach 100% representation in all groups they are present. How migration is implemented in this study's model is an important experimental condition,⁶ and will be discussed later in tandem with experimental designs.

There are a few other details of the model worth briefly noting. One, the starting number of groups is a parameter of the model, and is set to 10 for every experiment conducted. The number of rounds played is also a parameter of the model, and for these experiments is always set to 30.⁷ Next, there is a parameter for the seed proportion of altruists, the proportion of altruists that occurs in the population prior to the first round of play. This parameter is specified as a decimal, and if there is no integer number of altruists that satisfies the decimal proportion given the initial population size, the starting number of altruists is simply rounded up. All experiments in this study give altruists a seed proportion of .53, a slight edge over the selfish phenotype. Lastly is the parameter for target group size, which is an experimental condition for some of the experiments of this study. All groups begin the simulation with this number of individuals per group. In between rounds, when individuals are reassigned to groups, as many groups are initialized as the floor of the population divided by the target group size. The total population of individuals are then distributed among the groups as evenly as possible. Thus the target group size is a lower bound on the size of groups leading into a round, one less than twice the target group size is an upper bound, and every group has a size within one of the size of any other group. In practice, because the population size tends to greatly exceed the target group size,

⁴ See pages 23-26 of Sober and Wilson (1998) for a detailed example of selection for altruism in a simple scenario with only two groups.

⁵ Notice that any particular altruist would have more expected offspring if its phenotype were instead of the selfish type. Thus the claim of multi-level selectionists is not that altruism enhances the fitness of particular altruists, but rather that it enhances the fitness of the altruistic phenotype, or of altruists collectively. In this way multi-level selection has much in common with kin selection, and indeed they are sometimes argued to be equivalent. See for example Lehtonen (2006).

⁶ See Pichugin, *et. al.* (2015) for a study that focuses specifically on different migration strategies and their role in multi-level selection.

⁷ The reason for such a low number of rounds is that for trials that favor altruism, population growth is exponential, resulting in memory overflow and slow computation above a certain threshold of rounds.

most groups begin each round with the target group size or one plus the target group size. Implicit in what has just been described is that as the population grows, it is primarily increases in the number of groups that absorb the growth, rather than increases in the size of each group.

Experiment I: multi-level selection through stochastic dynamics

As emphasized by Sober and Wilson, high variance in phenotype proportions among groups is correlated with selection for altruism. The intent of this first experiment is to test this hypothesis, and to establish a baseline combination of parameters in which multi-level selection is successful.

The means in which I attempt to achieve phenotype variance is stochastic. For this experiment, a special migration procedure for redistributing individuals between rounds was devised. In this procedure, which I shall refer to as *random migration*, all individuals are pooled together and then randomly redistributed across groups. In combination with varying the target group size, random migration can be used to stochastically influence phenotype variance. Random migration is expected to result in higher variance for groups of small size, and lower variance for groups of greater size.

Design

Two parameters are varied, target group size and extra reproduction probability. The former is varied from 2 to 21 in steps of 1, and the latter from 0 to .6 in steps of .05. All combinations of the two parameters are tested. The cost of altruism is invariant, and is set to .02.

For each trial, values of the two dependent variables are reported. The first variable is the final proportion of altruists in the global population, which is a proxy for altruism's fitness for that particular trial. The second is the average standard deviation in altruist proportions across all rounds. That is, for each round, the standard deviation of altruist proportions across groups is measured, and what is ultimately collected is the average of all such standard deviations. Also note that if at the end of a trial the final population count is less than its starting value, the values of both dependent variables are omitted before any plots are generated. The reason is that trials with an extremely low ending population tend to produce erratic, unreliable data. The dependent variables reported, and the omission of data presumed unreliable, is the same for all experiments in this study.

Results and Discussion



Figure 1. Effect of Target Group Size on Altruists' Fitness Under Random Migration.

Each line plotted represents all trials with the specified value of extra reproduction probability

The red reference line represents the starting proportion of altruists, and the black line represents a proportion of .5, the proportion at which altruists and selfish individuals are equally prevalent. These reference lines will recur in a number of figures.

Figure 1 shows the hypothesis of experiment 1 to be unsubstantiated. There is no apparent relationship between group size and the fitness of altruism under the given parameters, although it is the case that trials with smaller groups have a greater variance in final altruist proportions compared to larger

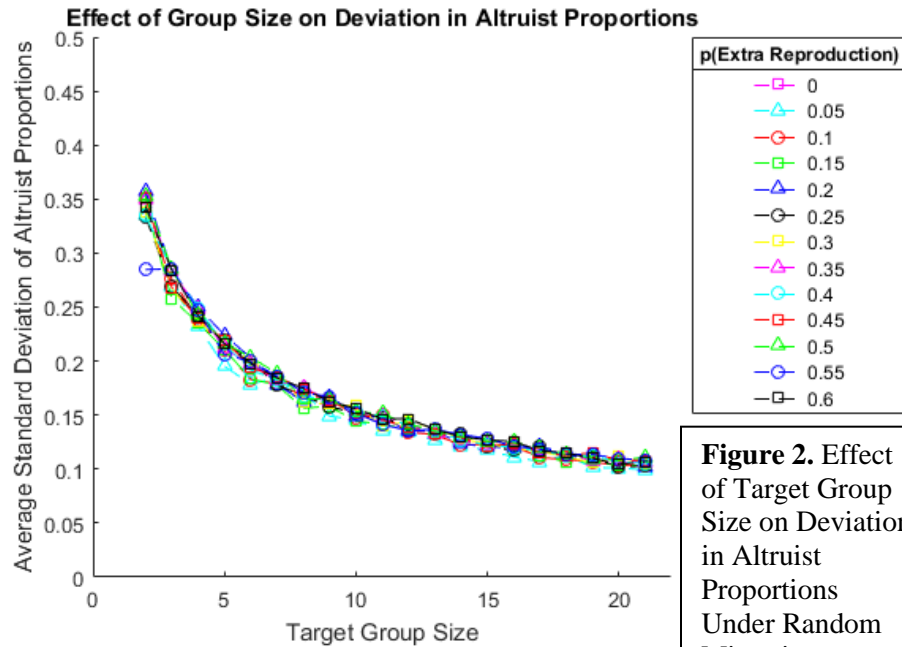


Figure 2. Effect of Target Group Size on Deviation in Altruist Proportions Under Random Migration.

groups. Notice furthermore from Figure 2 that the reason no relationship was found is not a failure of stochastic dynamics to create variance in altruist proportions among groups. As Figure 2 demonstrates, altruist variance is high for small groups, and declines sharply as group size increases. Also interesting, altruist proportions declined below 50% in almost every trial, even though the cost of altruism was set to a very low value of .02. Thus the experiment failed to establish a successful combination of parameters for realizing multi-level selection.

This is what I suspect explains the results: while multi-level selection is sensitive to altruist proportions, as group size decreases another factor is introduced that countervails the benefit conferred by high variances in phenotypes. Recall the last fractional terms in the equations for E_A and E_S , which represent the probability that an individual of the associated phenotype will benefit from any single altruistic act, all multiplied by the number of

opportunities in which an individual of that phenotype is a potential beneficiary of altruism. In E_A the term is $\frac{A-1}{N-1}$, and in E_S the term is $\frac{A}{N-1}$. What happens as the target group size decreases is that the size of the disadvantage represented by the -1 term in E_A 's numerator increases. For the smaller N is, the larger is $\frac{1}{N}$. And furthermore the marginal difference between $\frac{1}{N}$ and $\frac{1}{N+1}$ is very high among small values for N . In terms pertaining to the social game modeled, we can put the point this way: as group size decreases, the penalty that altruists pay for not being potential beneficiaries of their own altruism becomes more consequential, and this countervails the benefit from increased phenotype variance characteristic of small groups.

Experiment 2: weak multi-level selection control of experiment 1

Experiments 2 and 3 aim to respectively isolate and test the two competing effects of group size hypothesized. Experiment 2 introduces a control on experiment 1 to eliminate the disadvantage altruists face due to their ineligibility to benefit directly from one's own altruistic act. This is achieved by modifying the behavior of the social game. In the version of the game employed for experiment 2, an altruist has the same probability of benefitting from its altruistic act as everyone else. In the multi-level selection literature, this type of altruism is called *weak altruism*, whereas the altruism exhibited in the previous version of the game is called *strong altruism*.⁸ Since the stochastic effect of varying group size on phenotype variance should not be effected by the adoption of weak altruism, the hypothesis of experiment 2 is like that of experiment 1: altruists' fitness will be inversely correlated with group size.

Design

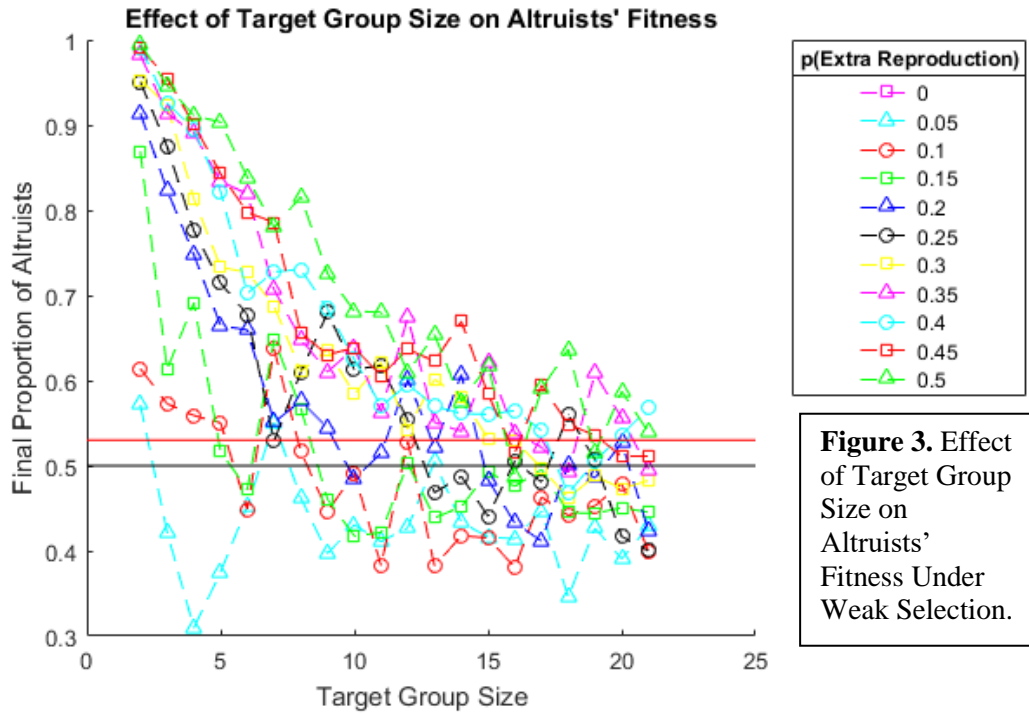
Besides modifying the social game to support weak altruism, the only difference in design from experiment 1 is that the parameter extra reproduction probability is incremented only to .5 instead of to .6. This was done because with higher values of e , the population growth was too great, resulting in memory overflow.

Results and Discussion

The control introduced by experiment 2 appears to be successful, and the hypothesis is supported by the results. Observe how sharply the final proportion of altruists decreases as group size increases, shown by Figure 3. Note furthermore that compared to strong selection, weak selection is in general far more favorable to altruism, although as group sizes increases the relative benefit conferred by weak selection is expected to become less and less.⁹

⁸ See Pichugin, *et. al.* (2015), page 148, for a discussion of strong vs. weak altruism.

⁹ While the results are not pictured here, experiment 2 resulted in a similar relationship between group size and average phenotype variance as did experiment 1.



Experiment 3: phenotype-stratified migration control of experiment 1

Experiment 3 introduces another control on experiment 1, this time to eliminate the other hypothesized effect of group size. That is, experiment 3 aims to neutralize the effect of group size on phenotype variance, while maintaining the disadvantage that strong selection imposes on groups of smaller size. I attempt this through the use of a migration function that biases the reassignment of individuals to groups in such a manner that groups tend to maintain a consistently high variance.¹⁰ Call this function *phenotype-stratified migration*. The hypothesis of experiment 3 is that with this control in place, altruists' fitness will be directly correlated with group size.

Design

Besides substituting the migration function, the only difference in design from experiment 1 is that the parameter extra reproduction probability is incremented only to .5 instead of to .6.

Results and Discussion

The hypothesized direct relationship between group size and altruists' fitness was not observed, as is clear from Figure 4. Looking at Figure 5 however, we see that while there is a diminishment in the rate at which phenotype variance decreases with increasing group size, and while variance is in general greater than for experiment 1, the phenotype-stratified migration procedure fails to adequately enforce a consistent variance across group sizes. Unfortunately, this

¹⁰ See module src/migration.py for the details of this migration procedure.

the experiment is therefore inconclusive. The results of experiment 3 will be discussed further in the general discussion section.



Figure 4. Effect of Target Group Size on Altruists' Fitness Under Phenotype-stratified Migration.

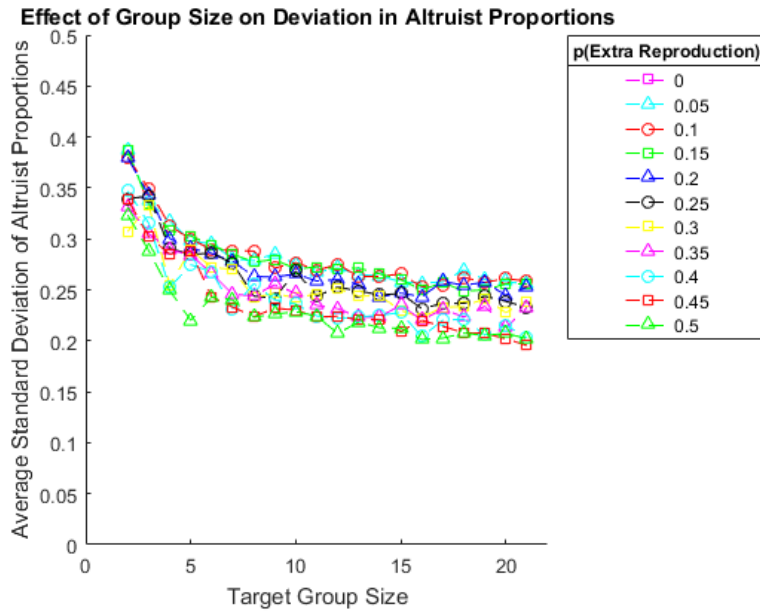


Figure 5. Effect of Target Group Size on Deviation in Altruist Proportions Under Phenotype-stratified Migration.

Experiment 4: the limits of strong altruism by multi-level selection

Simulations similar to experiment 1, not shown here, suggest that there are virtually no ways to parameterize the model to cause the selection of altruism if strong altruism and random migration are among the parameters.¹¹ The purpose of experiment 4 is to investigate the viability

¹¹ This is demonstrated best by the visualizations for experiment 5, available on the project's GitHub repository.

of multi-level selection in promoting strong altruism when the model's migration function is phenotype-stratified migration. Since we have already seen that phenotype-stratified migration increases average phenotype variance, it is expected that selection for altruism will be reasonably successful under these parameters.

Design

The migration function selected for the model is phenotype-stratified migration. The group size used is simply ten, as experiments 1 and 3 suggest that group size is not a consequential parameter when strong altruism is in play. Only two parameters are varied, cost of altruism and extra reproduction probability. The former is varied from 0 to .2 in steps of .01, and the latter from 0 to .5 in steps of .05. All combinations of the two parameters are tested.

Results and Discussion

Figure 6 makes clear the unsurprising facts that altruism cost is negatively correlated with selection for altruism, while extra reproduction probability is positively correlated with selection for altruism. What is surprising is just how high the ratio of extra reproduction probability to altruism cost needs to be for multi-level selection to favor altruism. Even with phenotype-stratified migration, extra

reproduction probability needed to be about four times greater than the cost of altruism in order for the final proportion of altruists to exceed .5.

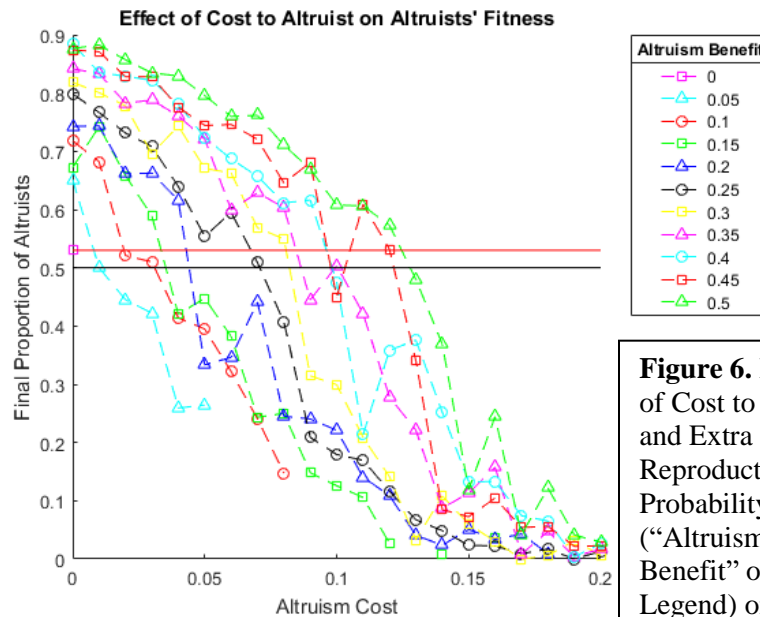


Figure 6. Effects of Cost to Altruist and Extra Reproduction Probability ("Altruism Benefit" on Legend) on Altruists' Fitness Under Phenotype-stratified Migration.

General Discussion and Conclusion

The experimental results of this study suggest that selection for altruism through multi-level selection is not very robust with respect to variation in parameters. Instead, parameters needed to be very much on the extreme end in order to produce the phenomenon. An initial difficulty was explored in experiments 1 through 3. What was found is that with strong selection and random migration, it was extremely difficult for multi-level selection to occur because group size is correlated with two factors that affect the success of multi-level selection, one with a positive correlation and one with a negative correlation. As group size increases, stochastic effects of migration cause phenotype variance to decrease, causing poorer fitness of altruism in turn. And furthermore as group size decreases, the relative disadvantage altruists face from not

being potential beneficiaries of one's own altruism becomes greater, also to the detriment of altruism's fitness. The net effect of these two factors appears to be a wash—group size has no apparent relationship with altruism, and whether small or large altruism is not selected for even when the remaining parameters are very favorable to altruism.

Of course we shouldn't be overconfident about the mechanism by which greater group size is unfavorable to altruism's selection, as experiment 3 was unsuccessful in controlling for phenotype variance. It is clear from the arithmetic characterizing the model that as group size increases, the magnitude of the altruist's disadvantage in not being a candidate for benefiting from its own altruism becomes less consequential. However, it is as of yet unproven whether the effect here is of the right magnitude to exactly countervail the detriment to altruism's fitness that results from reduced phenotype variance as group size gets larger. Notice though that both effects are marginally smaller in magnitude the larger group size is, which adds to the plausibility that one effect exactly countervails the other.

Introducing phenotype-stratified migration as a parameter improves the success of multi-level selection for altruism, but with some caveats. As we saw from experiment 4, even with the benefit of increased phenotype variance across groups, still the benefit from altruism had to greatly exceed its cost in order for altruism to be favored by selection. Furthermore, in actual biological populations, it might be problematic for a proponent of the multi-level selection view of altruism to account for the mechanism by which stratification of phenotypes occurs. The reason is that from the perspective of altruists and selfish individuals alike, it is most advantageous to be in a group with a high proportion of altruists. And if there was an evolutionary arms race between the selfish and the altruistic to identify and associate with altruists, and altruists won the arms race such that high phenotype variance is maintained, it's unclear we would classify the so-called altruists anymore as altruists *per sé*. After all they would have evolved a mechanism that encourages their prosocial acts to selectively benefit individuals of their own phenotype. Thus the relationship between the prosocial individuals would be better characterized as one of reciprocity than of altruism.

Of course with any study involving evolutionary simulations, there are many, many ways in which the model could be altered or parameterized that remain untested. It is beyond the scope of this paper to discuss the ways in which different behavior to the model might be more favorable to a multi-level selection account of altruism. Still, the results here provide some early motivation for skepticism.

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