

Individual Selection with Mutation for Cooperative Group Formation

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1 Introduction

Powers, Penn, and Watson [2007] show that environmental conditions need not be externally imposed in order to promote the evolution of cooperative traits. They present a model which permits suitable conditions to arise via individual selection, and show that even in environments that initially select for selfish behaviour, a niche construction process can allow for cooperative behaviours to be ultimately successful. This paper reimplements the algorithm described, and extends the model to show not only that the process is accelerated by the introduction of mutation to the model, but also that a side-effect of the niche construction process then favours selecting against individuals that are able to mutate, resulting in a more stable niche.

2 Reimplementation

In Powers et al. [2007], an algorithm is presented which demonstrates that under the right circumstances, individuals can select for environments that promote cooperation. Using the trait-group aggregation and dispersal model presented in Wilson [1975], individuals are permitted to select for control both over individual strategy and initial group size. Large groups receive a resource bonus [Allee, 1938], but are also more susceptible to exploitation by selfish individuals. Groups are formed according to individual size preferences, and with a random but globally proportionate composition of strategies. Individuals in groups are then reproduced over a number of generations, with shares of the group's resources (r_i) allocated according to the proportion of individuals with a particular genotype within that group. When using the parameters in Appendix A, this should result in individuals selecting away from the resource bonus of the larger groups in favour of an environment where the cooperative trait has greatest individual fitness. In small groups, stochastic between-group variation ultimately globally favours the growth of groups with a higher proportion of cooperative individuals.

After initialising the migrant pool with N individuals, Powers et al. [2007] present the following algorithm as an implementation of the trait-aggregation model. The steps represent a single cycle, and should be repeated for T generations.

1. **Aggregation:** Assign individuals in the migrant pool randomly to groups according to their size preference - each group will have a random composition of strategies, but the average should be proportionate to the global ratios. Surplus individuals may be discarded.
2. **Reproduction:** Perform reproduction within groups - eq. 1 gives the resource share that each genotype population receives, and eq. 2 gives the resulting change in population size. Repeat for t generations.
3. **Dispersal:** Return the progeny of each group to the migrant pool.
4. **Scaling:** Rescale the migrant pool back to size N , retaining the proportion of individuals with each genotype.

$$r_i = \frac{n_i G_i C_i}{\sum_j (n_j G_j C_j)} R \quad (1)$$

$$n_i(t+1) = n_i(t) + \frac{r_i}{C_i} - K n_i(t) \quad (2)$$

2.1 Representation

In the reimplementaion, individuals are represented as aggregate populations by genotype. Each individual can specify two genes: one for size, and one for strategy, and each gene can take one of two values, large/small and cooperative/selfish, respectively. This results in four possible genotypes, and so a migrant pool is maintained of the total count of each of the four types. Each group formed also maintains only the total count of each genotype within it, and aggregation, reproduction, dispersal and scaling operations are all carried out by population rather than individually.

The algorithm has no explicit fitness function - rather, an individual's fitness may be approximated by the total resource share of its genotype within the population as a whole. There is no crossover, but the algorithm could be said to be generational, as after each aggregation/dispersal round the whole population is rescaled back to a nominal 'carrying capacity' (N). The rescaling can force populations below their minimum group sizes and hence to extinction when they are significantly outcompeted.

2.2 Results

When the reimplemented algorithm is run using the parameters in Appendix A, the output closely follows the original findings (Figures 1 and 2).

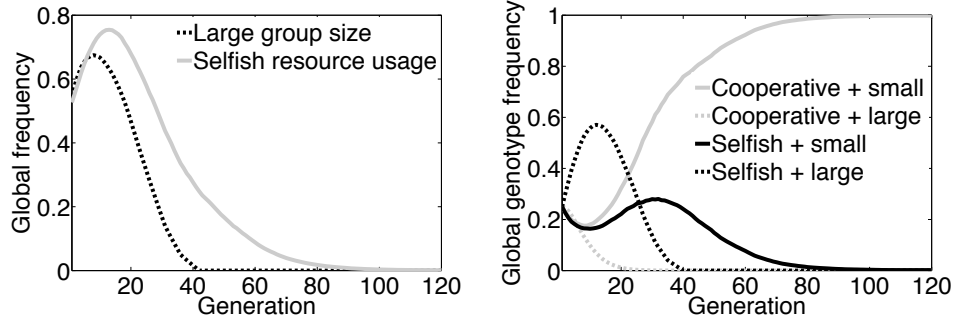


Figure 1: Left: average environment and strategy through time. Right: change in genotype frequencies over time. [Powers et al., 2007]

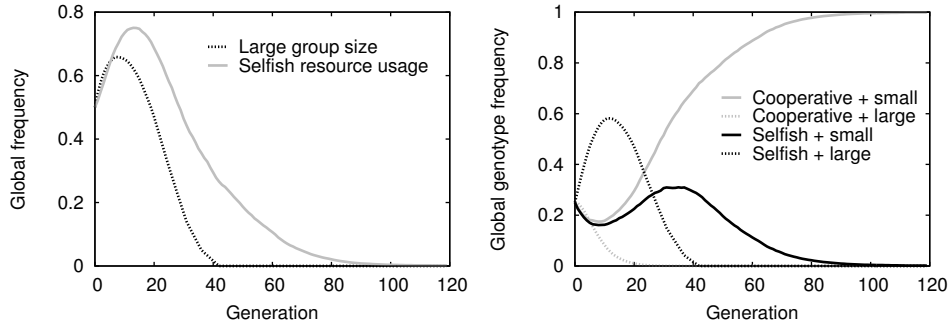


Figure 2: Results provided by reimplemented algorithm, as above. The plots match to a high degree of accuracy, showing accurate reimplementaion.

As in Powers et al. [2007], large individuals initially benefit from the resource bonus, with large + selfish individuals flourishing as expected for the first few generations. Without a healthy population of large + cooperative individuals to exploit, the selfish individuals begin to decrease in frequency. Among the small groups, between-group variance exerts a selective pressure against groups containing selfish individuals [Powers and Watson, 2011], eventually driving the selfish allele extinct and allowing the cooperative + small genotype to fix in the population at equilibrium.

3 Extension

The original result can be shown to be quite robust: even in the case of severe imbalance in the initial genotype distribution, it is generally seen that the cooperative + small genotype successfully forms a niche and eventually fixes (Appendix B, figure 6). However, this is only possible when there exists a critical minimum population of cooperative + small individuals that between-groups variation can select in favour of. In the model as presented, if a particular genotype dies out or does not exist in the initial distribution, then it is never possible for it to (re)enter the gene pool. In certain situations, this can be seen as disadvantageous - for example, if in the original model the cooperative + small individuals were able to form large groups again once the selfish allele had been eradicated, then they could reap the resource bonus without exploitation by selfish individuals.

As an extension to the original model, this paper then presents analysis of cases where individuals may occasionally spontaneously change their size preference or strategy. An additional gene is introduced to each individual which both controls and is subject to these spontaneous changes, in a manner similar to a low rate of mutation across the whole population [Smith and Fogarty, 1996]. The expectation is that the addition of mutable individuals will make the niche construction process possible in a wider range of more initially hostile populations.

3.1 Representation

Once again, individuals are represented by genotype as populations of identical clones. As there are three distinct genes, there are now eight separate combinations of alleles representing populations in the migrant pool and in each group. The reproduction code has been modified to respect the possibility of newly mutated individuals present in a group size different to that specified by their genotype. Mutation potentially occurs after each within-group reproduction cycle.

Ochoa et al. [2000] notes that ‘optimal per-locus mutation rates depend mainly on $1/L$ (the reciprocal of the genotype length)’. In this model, the length of each individual’s genotype is 3, and a mutation rate of $1/3$ is high enough to cause no significant solution to arise. However, the original reasoning behind the heuristic leads to a more effective value for mutation within the model. The use of a mutation rate of $1/L$ is intended to result in an average of one change to one gene in an individual per reproduction - in the model presented, the desired mutation rate is on the order of one change

of one group per cycle of reproduction, and so a value of $1/\text{num_groups}$ is more appropriate. Though the actual number of groups fluctuates based on prevailing group size preference, 550 groups may be taken as a reasonable approximation¹. A mutation rate M of $\frac{1}{550} \approx 0.002$ is therefore used throughout the rest of the paper.

3.2 Results

In order to investigate the specific scenario detailed above, individual mutation was initially restricted to act upon the size gene only.

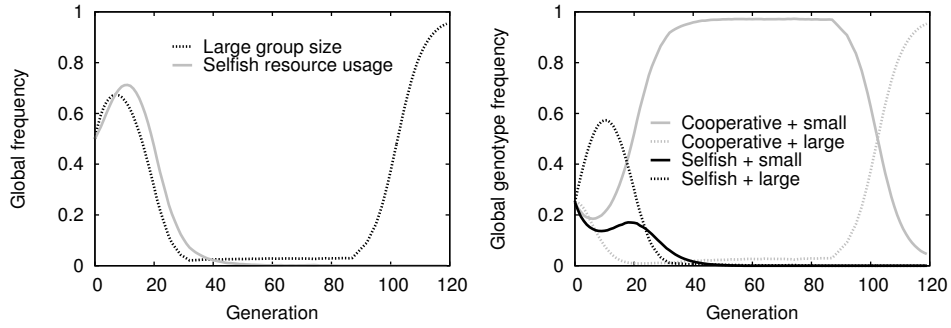


Figure 3: Mutation on the size gene allows the cooperative + large genotype to reappear and then eventually flourish once the selfish allele has died out.

The initial plot was then recreated using an equal distribution of all eight genotypes, and therefore an equal proportion of mutable to non-mutable individuals - shown on these plots as a separate aggregate proportion.

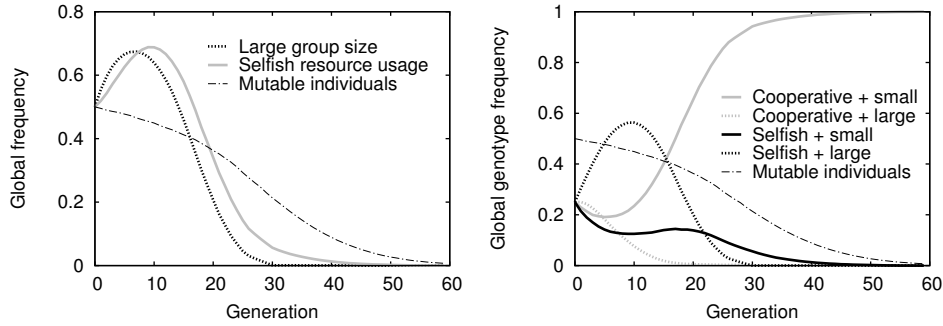


Figure 4: In this case, the addition of mutable individuals leads to the same outcome more quickly, and the mutable individuals die out.

¹ using the parameters in table 1 with equal distribution of genotypes: $\frac{2000}{40} + \frac{2000}{4} = 550$

Finally, with a high proportion of mutable individuals it is possible to start with an initial population distribution consisting of only a single genotype, and still demonstrate the niche creation process leading to the small + cooperative genotype dominating the population.

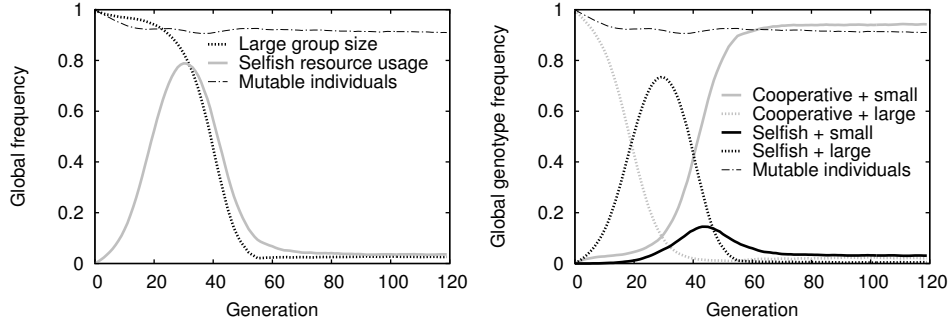


Figure 5: The population still contains a high proportion of mutable individuals after 120 generations, and so unlike in Figure 4 it is still possible that another genotype could later come to dominate, as in Figure 3.

4 Conclusion

The addition of mutable individuals increases stochasticity - particularly for the ultimate proportion of mutable individuals. As it has no inherent effect on fitness, it is self reinforcing. Often the algorithm will select towards non-mutability as there is bias in that direction. The increase or decrease in proportion of mutable individuals is highly self-reinforcing, and though the ultimate outcome is largely stochastic, exhibits a generally non-mutable bias.

One area for further investigation would be to allow mutation on size preference to act in a more granular manner, as suggested in Powers [2010].

Selfish behavior

(Appendix B, figure 7)

References

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Appendix A Algorithm parameters

Behaviour parameters	Cooperative	Selfish	Global parameters	Value
Growth rate, G_i	0.018	0.02	Population size, N	4000
Consumption rate, C_i	0.1	0.2	Generations, T	120
Size parameters	Large	Small	Reproductions, t	4
Group size, S_i	40	4	Death rate, K	0.1
Resource influx, R_i	50	4		

Table 1: Parameters from Powers et al. [2007], used throughout.

Appendix B Additional graphs

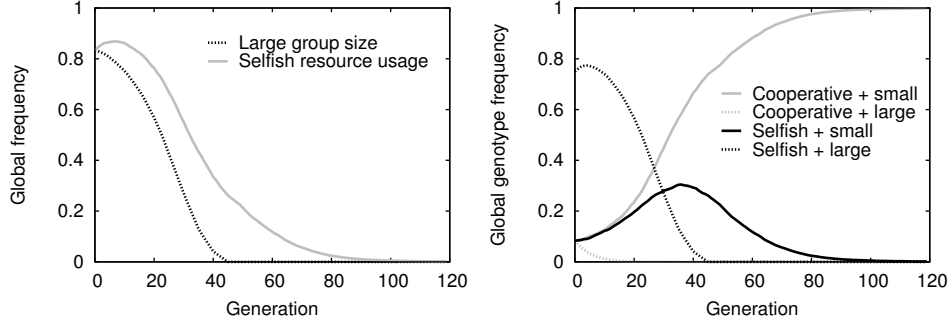


Figure 6: The model presented in Powers et al. [2007] is robust even in the face of severe imbalance in the initial genotype distribution.

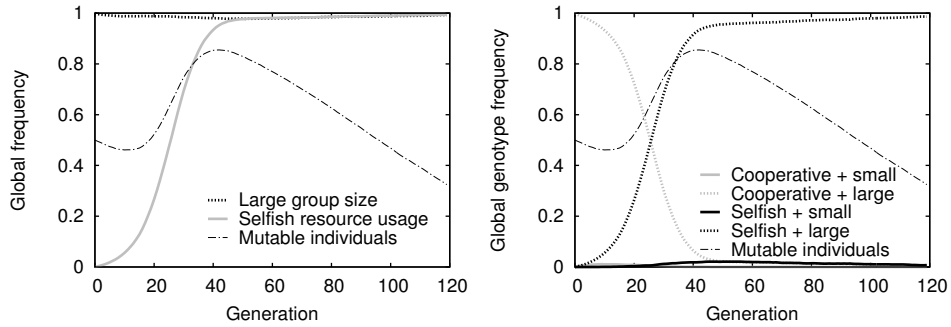


Figure 7: Compare to Figure 5. The initial distributions differ only in the proportion of mutable individuals, yet provide startlingly different outcomes.

Appendix C Source code

`base.html`

`further.html`