

An Agent-Based Model of Group Selection

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Introduction

Mathematical models have shown that under some conditions natural selection can favor cooperative traits that benefit groups as a whole, but reduce individual fitness relative to the rest of their group (Sober and Wilson 1998). Unlike those in mathematical models however, groups in the real world may not be significant vehicles of selection because they are too few in number, too long in generation time, or too amorphous and ephemeral (e.g., Williams 1966; Dawkins 1982, p. 100; Dawkins 1989, p. 297).

To address this issue we used an agent based approach that did not impose group structure on the population, but let it arise in an ecologically plausible way through interactions with the environment. Cooperation was represented as a difference in feeding restraint, such that some individuals maximized their individual food intake and overexploited resources to the detriment of all individuals in the area, while other individuals reduced their consumption and thereby increased the food supply for all individuals in the area.

We used this model to address two questions: 1) Can spatial heterogeneity alone generate the local fitness effects and population structure necessary to drive group selection? 2) Does group selection require association among kin in order to be effective?

The Model

The model world was a two-dimensional grid, wrapped to form a torus. It contained food resources (plants) with fixed locations, and foragers that moved about, ate plants, reproduced, and died. Each cell in the grid could contain up to one plant and one forager. During each time step each agent (plant or forager) was activated once in random order.

Each plant was assigned a permanent location at the start of a run, and its energy store set to a uniform random number between zero and a fixed maximum. When a plant was activated it grew, increasing its energy content according to the logistic growth function

$$\Delta N = rN(K-N)/K,$$

where ΔN = size increase per time step, N = current size, r = logistic growth rate, and K = maximum size. Under this growth pattern, which is characteristic of natural populations, growth is fastest at intermediate sizes and drops off rapidly at lower sizes.

At the start of a run each forager was placed on a randomly chosen cell containing a plant, with its energy

store set to a random number between zero and the fertility threshold. When a forager was activated it moved according to the following rules: It examined its current and eight adjacent cells, and from those not occupied by another forager chose the cell containing the largest plant (with ties broken randomly). If this cell offered enough food to meet its metabolic cost it moved there. If not, it moved instead to a randomly chosen cell adjacent to its current cell (if any were unoccupied). This prevented foragers from staying at an inadequate food source until they starved. After moving, the forager fed on the plant in its current cell if there was one. This reduced the energy of the plant and increased the forager's energy by the same amount. The forager's energy level was then reduced by a fixed metabolic rate. If the resulting energy level was above the fertility threshold, the forager created an offspring, reducing its own energy store by a fixed amount that became the offspring's initial energy level. Newborn offspring occupied the cell nearest to their parent that was not already occupied by a forager (with ties broken randomly). If a forager's energy level was zero or below at the end of a time step, it died and disappeared from the world.

There were two types of foragers, differing only in their feeding behavior. When "unrestrained" foragers ate they took 99% of the plant's energy. In contrast, "restrained" foragers ate only half of the plant they fed on. Foragers inherited their restraint level from their parents without mutation. The standard parameter settings shown in Table 1 were used in each run unless otherwise noted.

Parameter	Value
Plants	
Minimum number of plants	500
Logistic growth rate r	0.2
Maximum size (energy units)	10
Foragers	
Starting number of foragers	40
Birth energy level (energy units)	50
Metabolic rate (energy units)	2
Fertility threshold (energy units)	100
Feeding restraint (% left uneaten)	1% or 50%

Table 1. Standard parameter settings.

The Experiments

Uniform environments

In the first set of experiments plants were distributed uniformly, one per cell. Pure populations of unrestrained feeders first went through a phase of near-exponential growth, followed by a collapse in food productivity and a forager population crash, usually resulting in extinction. In contrast, pure populations of restrained foragers persisted indefinitely, and at a much higher carrying capacity than pure populations of unrestrained foragers (Figure 1).

Combining equal numbers of restrained and unrestrained feeders in the same population resulted in the same initial boom and bust seen in pure populations of unrestrained foragers. Because restrained foragers extracted less energy than unrestrained foragers from plants of the same size, they were unable to compete and disappeared from the population in every run. Unrestrained feeders either died out as well, or recovered to establish a relatively small population (Figure 2). Thus feeding restraint benefited the populations in which it occurred, but within mixed populations it was out-competed by unrestrained feeding.

Patchy environments

In a second set of experiments on mixed populations the spatial distribution of plants was varied. Plants were arranged in evenly spaced square patches with one plant in each cell. The “patch width” parameter controlled how

many cells wide each patch was in each axis, and “gap width” controlled the distance between patches in each axis. The program first placed the specified minimum number of plants into patches, and then added any additional plants and empty cells required to create a uniform square world without any partially filled or unevenly spaced patches. Runs started with equal numbers of restrained and unrestrained feeders.

In patchy environments an unrestrained forager that colonized an empty patch accumulated energy rapidly, and unless the patch was quite small, quickly began reproducing. The resulting local population explosion typically exhausted all plants in the patch before they had time to regenerate. The foragers then dispersed, leaving behind an empty and unproductive patch of plants that took many time steps to regenerate.

In contrast, groups of restrained feeders did not over-exploit their patches, but followed a pattern of sustainable harvest. After plants were reduced to below the forager maintenance requirement, making them unattractive, they recovered enough to sustain foragers again within only a few time steps. As a result, patches larger than a single cell that were occupied only by restrained feeders did not become exhausted and were not abandoned. Instead, birth and immigration into the patch was balanced by dispersal as foragers occasionally failed to find sufficient food and wandered out of the patch. This pattern continued until an unrestrained forager invaded the patch and consumed the plants at a much higher rate, reproducing along the way if the patch was large enough. The patch then became unprofitable and was typically abandoned.

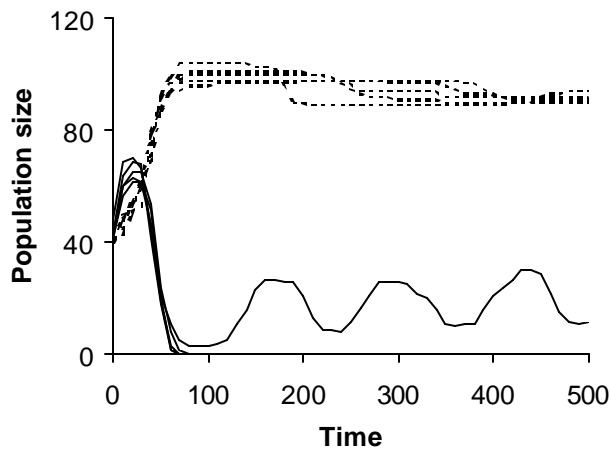


Figure 1. Population size over time for pure populations of restrained (dotted lines) and unrestrained (solid lines) feeders in a uniform 23 x 23 cell environment. Five runs for each forager type used the same parameter settings but different random number seeds. Populations of unrestrained feeders usually crashed to extinction, but occasionally recovered to establish a stable oscillation caused by time-lagged negative feedback.

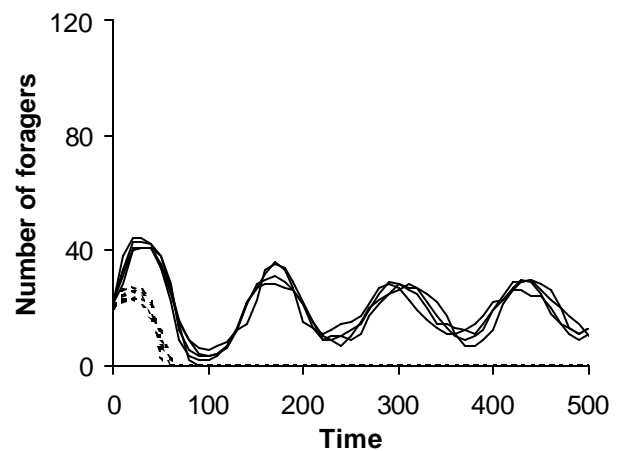


Figure 2. Number of restrained (dotted lines) and unrestrained (solid lines) foragers for mixed populations in a uniform 23 x 23 cell environment. Five runs are shown with the same parameter settings but different random number seeds. The restraint allele was always lost, leading either to extinction (in one run) or to a pure population of unrestrained feeders that oscillated in size, as in Figure 1.

Patch width	Gap width									
	1	2	3	4	5	6	7	8	9	10
1	0	*	*	*	*	*	*	*	*	*
2	0	0	0	*	*	*	*	*	*	*
3	0	0	1	1	1	1	1	1	1	1
4	0	0	0	1	1	1	1	1	1	1
5	0	0	0	0	0	1	1	1	1	1
6	0	0	0	0	0	0	0	1	1	1
7	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0

Table 2. Final frequency of restrained feeders as a function of patch and gap width. One run of 10,000 time steps was performed at each parameter setting. Averages over the last 1000 time steps are shown. Asterisks indicate that both forager types went extinct.

In patches containing both restrained and unrestrained foragers, unrestrained foragers gained more energy because they ate almost twice as much from plants of the same size. Thus within patches occupied by both forager types, unrestrained foragers had higher fitness. Both the size and spacing of patches affected the outcome of selection. Restrained feeding spread to fixation only when food patches were small and widely separated (Table 2).

Kin selection and group selection

Did association among kin drive group selection in this model? Offspring were born next to their parents, and tended to remain nearby for some time after birth, especially when food patches were small and isolated. Spatial association among relatives could thus be crucial for the evolution of cooperation in this model, because it allowed the benefits of cooperation to go mainly to relatives that were also cooperators. To test this we repeated the mixed population experiments summarized in Table 2 with one modification: Instead of newborn foragers starting in the nearest open cell to their parents, their birth location was chosen randomly from all unoccupied cells in the grid. Under these conditions feeding restraint evolved in a smaller region of parameter space than when offspring were born next to their parents. However, restraint still spread to fixation under some resource distribution conditions (Table 3).

Quantifying group selection

To quantify selection among groups, we defined a group as the set of foragers occupying a given patch. Foragers not currently located in a patch were considered to be members

Patch width	Gap width									
	1	2	3	4	5	6	7	8	9	10
1	0	*	*	*	*	*	*	*	*	*
2	0	0	0	*	*	*	*	*	*	*
3	0	0	1	1	1	1	1	1	1	1
4	0	0	0	1	1	1	1	1	1	1
5	0	0	0	0	0	0	0	0	0.1	1
6	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0

Table 3. Final frequency of restrained feeders with offspring dispersing randomly. All parameters were set as in Table 2, but newborn offspring were placed at random locations.

of the last patch they had occupied. Foragers born outside of any patch were assigned to the patch their parent belonged to.

To measure selection within and between patches, we used Price's (1970, 1972) covariance formula for partitioning selection:

$$\Delta p = \frac{\text{cov}_n(w_g, p_g)}{w} + \frac{\text{ave}_{n'}[\text{cov}(w_{gi}, p_{gi})]}{w} \quad (1)$$

The first term on the right side of this equation represents the change in allele frequency caused by between-patch selection, and the second term represents the change due to within-patch selection. Definitions are as follows: Δp = change in allele frequency in global population, w_g = group fitness (mean progeny per member of the g 'th group), p_g = allele frequency within the g 'th group, cov_n = covariance among groups, weighted by group size in the parental generation, w = average population fitness (mean progeny per individual), w_{gi} = fitness of the i 'th individual in the g 'th group, p_{gi} = allele frequency within the i 'th individual in the g 'th group (either 0 or 1), cov = covariance among individuals within the g 'th group, and $\text{ave}_{n'}$ = average of the within-group covariances, weighted by progeny per group. Because life spans overlapped in our model, we defined a "generation" as a single time step of the model, and an individual's "progeny" as any offspring it produced, plus itself if it survived the time step.

Figure 3 illustrates the application of this formula to one run of the model. The allele for restraint increased in frequency through between-patch selection and decreased through within-patch selection. The overall change in allele frequency was the sum of these two effects, and thus the

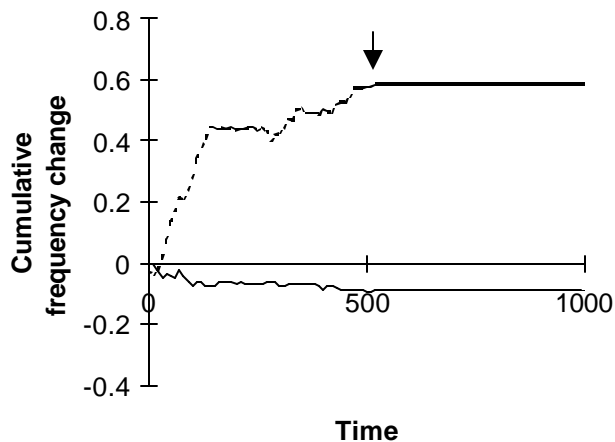


Figure 3. Cumulative change in the frequency of feeding restraint due to within-patch selection (solid line) and between-patch selection (dotted line), from equation (1). Because restraint began at a frequency of 0.5, the total frequency change represented by the sum of the two lines equaled 0.5 when restraint reached fixation (at arrow). Within-group selection against feeding restraint was outweighed by stronger between-group selection for restraint. Patch width = 4, gap width = 5, and all other parameters were set as per Table 1.

evolutionary outcome depended on their relative strengths. We repeated the above experiments using this analysis, and found that under all resource distribution patterns, within-patch selection decreased the frequency of cooperation. Thus cooperation spread to fixation only when positive between-patch selection was of greater magnitude than negative within-patch selection.

Discussion

The model captured the essential properties of opposing levels of selection, in that cooperation was selected for through between-group selection but simultaneously selected against through within-group selection. Thus the evolutionary outcome in a given run depended not on which form of selection was operating, but on their relative strengths.

The results showed that patchy food distribution can by itself create sufficient population structure to generate significant between-group selection, leading to the spread of a cooperative trait that reduced individual fitness relative to the rest of the group. This result is not specific to feeding restraint, as qualitatively similar results were obtained for a version of the model that used alarm calling instead of feeding restraint as the cooperative trait (Pepper and Smuts 2000). The results also showed that between-group selection could lead to the spread of feeding restraint even without spatial association among kin. This

contradicts the view sometimes expressed that group selection can be effective only when it is driven by kin interactions (Bell 1997, p. 530; Maynard Smith 1998).

A number of authors have dismissed between-group selection as a weak and relatively unimportant force in evolution (Grafen 1984, Dawkins 1989, Ridley 1996). This study suggests that that conclusion is premature. In a plausible ecological and behavioral setting, the requirements for cooperation to evolve through group selection did not appear unrealistically stringent. Ephemeral groups emerging through the behavior of individuals searching for food in patchy environments drove the evolution of group-beneficial traits, even in the absence of kin selection. This demonstrates that effective group selection does not depend on discrete and stable groups that may not be typical in nature.

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