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## AGENT-BASED MODELING OF MULTILEVEL SELECTION: THE EVOLUTION OF FEEDING RESTRAINT AS A CASE STUDY

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*Abstract.* Evolutionary biologists are increasingly interested in the dynamics of multilevel selection, or selection acting simultaneously at more than one level in a hierarchy of reproducing entities (e.g., gene, chromosome, organelle, cell, organism, social group, multi-species community). Systems of linear equations are the usual tool for studying evolution, but are limited in their ability to capture important dynamics of multilevel selection. Here we use an agent-based model to study the evolution of cooperation in spatially structured populations. This work addresses the long-standing controversy over the role of “group selection”, or natural selection between versus within groups of interacting individuals. In an ecologically plausible setting, cooperative individuals with lower rates of food consumption compete reproductively against selfish individuals with higher rates of consumption. The results show that changing the spatial distribution of food, and thus the distribution of the individuals seeking it, can determine whether or not cooperation evolves. In this model cooperation evolved under a fairly wide range of parameter values, even without the kinship effects and discrete mixing phase that are sometimes thought to be necessary. We suggest that integrating equation-based analysis tools into agent-based models is a powerful way to study selection in systems with complex dynamics.

### INTRODUCTION

Evolutionary biologists have a long-standing interest in the evolution of selfish versus cooperative behavior. Here we define “cooperation” as any trait that raises the fitness, or

average reproductive success, of the group in which it occurs, but decreases the actor’s fitness relative to other group members. Mathematical models have shown that under some conditions natural selection can favor traits that benefit group members as a whole, even when individuals with those traits have reduced reproductive success relative to other members of their group (reviewed in Wilson and Sober 1994). This process, often referred to as trait group selection, can occur when the population consists of multiple “trait groups”, or groups composed of individuals that influence one another’s fitness though the trait in question (D. S. Wilson 1975). This is because trait groups with a high frequency of cooperators will send out more offspring into the population as a whole than will groups containing few cooperators. Thus, even though non-cooperators out-reproduce cooperators *within* trait groups (because they experience the benefits of cooperation without incurring the costs), this advantage can be offset by differences in rates of reproduction *between* trait groups. Whether a cooperative trait spreads depends on the relative magnitude of fitness effects within versus between trait groups. There is a growing body of empirical evidence for the operation of group selection both in the laboratory (Goodnight and Stevens 1997) and in nature (Sober and Wilson 1998, Keller 1999).

One critical factor affecting the strength of between-group selection is the population’s genetic structure, i.e., the extent to which cooperators interact with each other as opposed to random members of the population. The most common source of such biased interactions is limited dispersal of offspring, leading to increased

interactions among related individuals (Hamilton 1964). Some evolutionary biologists regard such “kin selection” as a special case of group selection (Hamilton 1975:337; Futuyma 1986:264; Breden 1990; Queller 1991). Others view it as an alternative to group selection, arguing that although in theory group selection can occur without kin-biased interactions, in practice the necessary conditions are so stringent they are rarely met (e.g., Maynard Smith 1964, 1976; Williams 1966; Grafen 1984; Alexander 1989). Such debates about group versus individual and kin selection have played a central role in studies of social evolution (e.g., E. O. Wilson 1975; Trivers 1985; Alexander 1987; Cronin 1991; Wilson and Sober 1994; Sober and Wilson 1998).

Although formal mathematical models have demonstrated that cooperation can evolve through selection among groups under certain conditions, they do not address whether the required kinds of local fitness effects and genetic population structure are plausible, or how they might come about. In particular, some authors have argued that unlike those in mathematical models, groups in the real world are not 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 1982:100, 1989:297). To address this issue we used an agent-based approach that made no *a priori* assumptions about the nature of groups, local fitness effects, or non-random interactions among individuals. Instead, these system-level characteristics were allowed to emerge through the actions of individuals following simple yet plausible rules of behavior in spatially varying environments (Pepper & Smuts 2000).

The form of cooperation we chose to model has a long history in the literature on the evolution of cooperation. Feeding restraint was proposed by Wynne-Edwards (1962) as a widespread behavior that evolved through group selection, but his arguments were not well supported either theoretically or empirically. More recently the issue of feeding restraint or “prudent predation” has been revisited for specific cases (e.g., Hart et al. 1991; Frank 1996; Hemptinne and Dixon 1997; Miralles et al. 1997).

We used our model to address two main questions: 1) Can patchy environments alone generate the local fitness effects and population genetic structure necessary to drive the evolution of cooperation? 2) Does between-group selection require association among kin in order to be effective, or can cooperation spread even in the absence of kin selection? Our goal was not to produce a realistic representation of any specific system, but rather to construct a simple model that leaves out as much as possible while still capturing the essential properties of interest. Our hope is that understanding the dynamics of a simple model will help generate useful new hypotheses about when and how group-beneficial traits can evolve in nature.

### THE MODEL

The program was written in Objective C using the Swarm simulation library (Minar et al. 1996), and is available on request. Multiple batch runs on a distributed network were controlled using the Drone program written by T. Belding (<http://sourceforge.net/projects/drone>). The model consisted of food resources (plants) growing in two-dimensional space, and agents (foragers) moving about, eating food, reproducing, and dying. We assumed only that foragers showed some very simple behaviors, such as a tendency to move toward nearby food (see below). We then explored the question of whether individuals, by pursuing unevenly distributed resources, would generate sufficient population structure to drive selection among groups.

The model world was a two-dimensional grid, wrapped around in both axes to avoid edge effects. It contained two kinds of agents: plants and foragers. During each time step each agent (plant or forager) was activated once in random order. Because we wished to control the distribution of plants as an experimental variable, plants were created only at the start of a run, and did not move, die, or reproduce. A plant’s only behaviors were to grow and be eaten. In each run, all plants were identical except for their starting energy level, which represented the amount of food energy potentially available to foragers. At the

start of a run each plant's initial energy was set to a uniform random number between zero and a fixed maximum. During each time step a plant's energy could increase through growth, and decrease if a forager fed on it.

At the start of a run each forager's energy level was set to a uniform random number between zero and the fertility threshold, and foragers were placed on randomly chosen cells containing food. At each time step, foragers could gain energy by eating, increasing their own energy level and reducing the plant's by the same amount. They also lost energy each time step as a fixed metabolic cost, regardless of whether or not they moved. Foragers died if their energy level reached zero, but they did not have maximum life spans. If their energy level reached an upper fertility threshold they reproduced. This entailed creating an offspring with the same level of feeding restraint as its parent (without mutation), and reducing the parent's energy level 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. (Ties between equally close cells were broken randomly.) Newborn foragers were not activated (did not move or eat) until the time step after their birth. The standard parameter settings shown in Table 1 were used in each run unless otherwise noted.

**TABLE 1.** Standard parameter settings.

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

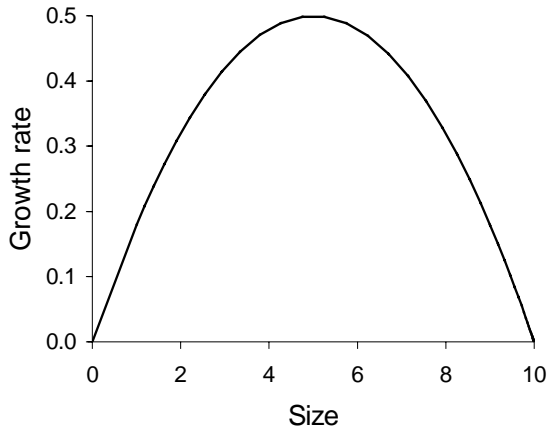
Foragers moved according to the following rules: They examined their current cell and the eight adjacent cells, and from those not occupied by another forager chose the cell containing the largest plant (with ties broken randomly). If the

chosen cell offered enough food to meet their metabolic costs for one time step they moved there; otherwise they moved instead to a randomly chosen adjacent cell. If all adjacent cells were occupied by other foragers, they stayed put. These rules simulated the behavior of individuals exploiting locally available resources as long as they can sustain themselves, but seeking a new food source instead when they cannot meet their minimum nutritional requirements.

Cooperative and selfish foragers differed only in their feeding behavior. When selfish or "unrestrained" foragers ate they took 99% of the plant's energy. (We set this parameter at less than 100% so that plants could continue to grow after being fed on, rather than being permanently destroyed.) In contrast, cooperative or "restrained" foragers ate only 50% of the plant they fed on. Feeding restraint qualified as a cooperative trait because it imposed an individual cost, in terms reduced food intake relative to other group members, and also created a group benefit, in terms of an increased rate of food production.

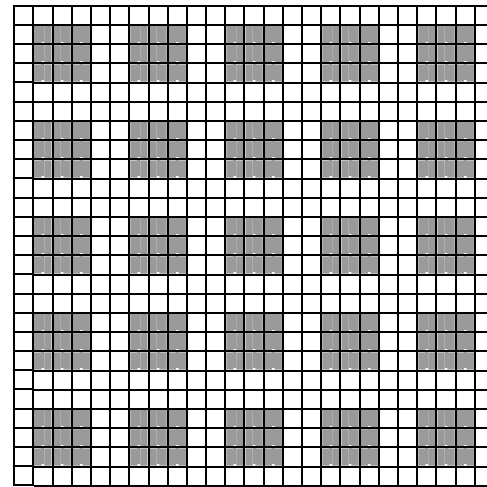
The group benefit followed from the fact that plants followed a logistic growth pattern (Figure 1). Logistic growth is typical of populations that are limited by environmental carrying capacity (Ricklefs 1990). Food sources with logistic growth can be over-exploited, leading to a sharply reduced growth rate or even the destruction of the resource. This situation, and the conflict between individual and group interests that drives it, has been referred to as the "tragedy of the commons" (Hardin 1968).

Runs that included both cooperative and non-cooperative foragers began with equal numbers of each. These experiments therefore addressed only the evolutionary spread of cooperation and not its origination.



**FIGURE 1.** Plant growth rate as a function of size (here equivalent to energy content). The increase in size per time step =  $rN(K-N) / K$ , where  $r$  = logistic growth rate,  $N$  = current size, and  $K$  = maximum size. Here  $r$  is set to 0.2 and  $K$  is set to 10, as per Table 1. Growth is slow for plants near their minimum and maximum size, and fastest at intermediate size ( $N = K/2$ ).

To examine the effects of resource distribution on the evolution of cooperation, we systematically varied the spatial distribution of plants using two parameters. At the start of a run, the program placed plants into 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. Figure 2 illustrates the patchy plant distribution pattern resulting from one setting of these parameters.



**FIGURE 2.** A representative resource distribution pattern. Filled squares represent cells occupied by a plant, and unfilled squares represent empty cells. This world was generated by setting the minimum number of plants to 200, the patch width to 3, and the gap width to 2. To create a uniform square world, the program increased the actual number of plants to 225 to create 25 patches, each consisting of 9 plants.

## THE EXPERIMENTS

### *Cooperation vs. Selfishness In Uniform Environments*

Our first set of experiments was designed to validate the model and to demonstrate that it successfully captured the tension between conflicting levels of selection. For these runs plants were not clumped into patches, but were instead distributed uniformly, one in each cell. We compared the performance of cooperative versus selfish foragers in both pure and mixed populations.

Because plants followed a logistic growth curve, their growth rate was severely reduced by unrestrained feeding. Pure populations of unrestrained feeders first went through a phase of near-exponential growth as they moved quickly from one plant to the next, consuming them almost entirely. However, this population explosion soon resulted in the over-exploitation of all available plants, causing a collapse in food

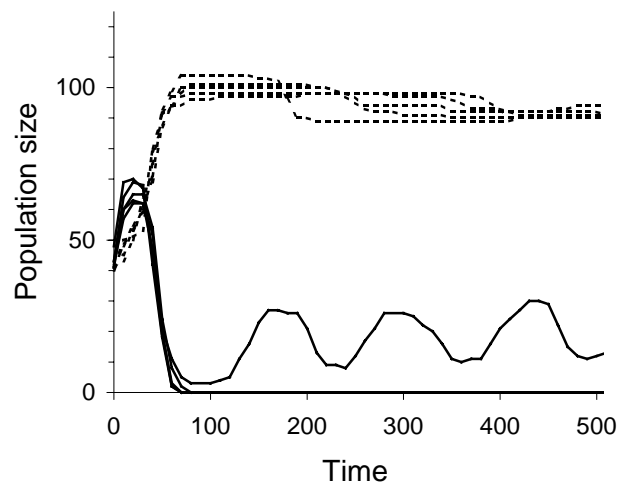
productivity followed by a crash in the forager population. This crash usually resulted in extinction, but in some runs foragers survived the initial population crash to enter a stable oscillation in population size (Figure 3). In contrast, pure populations of restrained feeders did not over-exploit plants to the point of being effectively unproductive. As a result, pure populations of restrained foragers persisted indefinitely, and at a dramatically higher carrying capacity than pure populations of unrestrained foragers (Figure 3).

Combining 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 that oscillated in size indefinitely (Figure 4). Thus feeding restraint benefited the populations in which it occurred, but within mixed populations it was out-competed by unrestrained feeding, to the detriment of the population as a whole.

#### *Effects Of Patchy Resource Distribution*

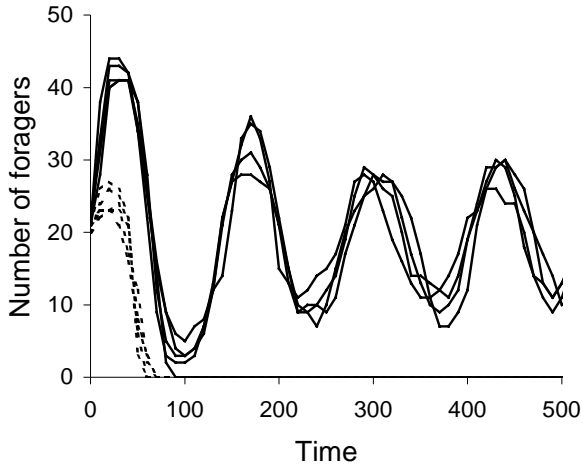
To investigate ecological effects on the evolution of feeding restraint, we performed a second set of experiments on mixed populations of restrained and unrestrained feeders, this time varying the spatial distribution of plants. Each run started with equal numbers of restrained and unrestrained feeders, placed in an environment in which plants occurred in patches of a fixed size and spacing.

In patchy environments an unrestrained forager first colonizing 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 any had time to



**FIGURE 3.** Population size as a function of time for pure populations of restrained (dotted lines) and unrestrained (solid lines) feeders in a uniform environment (single patch width = 23, gap width = 0). The five runs shown for each forager type used the same parameter settings (Table 1) but different random number seeds. Populations of unrestrained feeders usually crashed to extinction, but occasionally survived the initial crash to establish a stable size oscillation caused by time-lagged negative feedback. In this cycle high population density reduced the productivity of plants, leading to starvation and a reduced population size. Reduced feeding then led to increased food production and higher birth rates, repeating the cycle. Such oscillations are typical of simple ecological models and some natural populations (Ricklefs 1990).

regenerate. This resulted in the dispersal of hungry descendants in all directions, leaving behind an abandoned and unproductive patch of plants that did not regenerate for many time steps.



**FIGURE 4.** Number of restrained (dotted lines) and unrestrained (solid lines) foragers over time in mixed populations in a uniform environment (single patch width = 23, gap width = 0). Five runs are shown, each using the same parameter settings (see Table 1) but different random number seeds. The restraint allele was always lost, leading either to the population’s extinction (in one of the five runs) or to a pure population of unrestrained foragers that oscillated in size, as in Figure 3.

In contrast, patches inhabited only by restrained feeders were not over-exploited to the point of becoming unproductive, but instead established 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 and occupied only by restrained feeders remained productive and were not abandoned. Instead, births were 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 first for restrained foragers, then for unrestrained foragers, and was typically abandoned by both.

The restrained foraging trait spread to fixation under some but not all conditions. 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 ( $99\% / 50\% = 1.98$ ). Feeding rate was an accurate proxy for fitness because it was the only factor determining both survival and reproduction. Thus, within patches occupied by both forager types, unrestrained foragers always had higher average fitness. Restraint could spread to fixation only because of the greater productivity of patches occupied by restrained foragers. Both the size and spacing of patches affected the outcome of selection. Feeding restraint went to fixation only when food patches were small and widely separated (Table 2). Although a few runs did not reach fixation within 1000 time steps, they always did with longer runs, and there was no evidence for stable polymorphisms between the two trait types.

**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. Shading indicates frequencies > 0.5. Asterisks indicate that both forager types went extinct.

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

***Kin Selection And Group Selection***

Although it is sometimes contrasted with group selection (e.g., Maynard Smith 1976; Dawkins 1982:288; Frank 1988:37; Alexander 1989), kin selection is now generally recognized as fitting within the framework of group selection theory (Hamilton 1975; Wade 1985; Futuyma 1986; Breden 1990; Queller 1991; Frank 1995; Sober and Wilson 1998). Groups composed of genetic relatives facilitate group selection because genetic variance within groups is lower and genetic

variance between groups is higher compared with populations containing groups of random composition. Was association among kin an important component of group selection in our model?

Although the model did not include any mechanism by which foragers could recognize relatives, it nonetheless held the potential for a significant degree of kin selection. Offspring were born next to their parents, and tended to remain so for some time after birth, especially when food patches were small and isolated. Feeding restraint affected only nearby individuals, and so could be directed disproportionately toward relatives bearing the same gene for cooperation. Spatial association among relatives could thus be a key element of selection for cooperation in this model.

To examine whether cooperation could evolve without spatial association among kin, we repeated the mixed population experiments above with one modification: instead of newborn foragers being placed in the open cell closest to their parents, they dispersed at birth to a randomly chosen unoccupied cell. Under these conditions feeding restraint evolved in a smaller region of parameter space than when offspring were born near their parents (Table 2). However, restraint still spread to fixation under some resource distribution conditions (Table 3).

**Quantifying Multilevel Selection**

To move beyond verbal descriptions and arguments about levels of selection, it is necessary to actually quantify selection at each relevant level. This requires that we explicitly define the groups involved, but that was not a simple task for trait groups in our model. Trait group membership was not imposed as an assumption of the model. Instead, the boundaries of fitness effects between individuals shifted with each interaction, and an individual’s current fitness depended on the actions of other individuals many time steps into the past.

Given these difficulties, we chose to measure selection within and among patches as a proxy for selection within and among actual trait groups. Foragers not currently located in a patch were considered to be members of the last patch they

had occupied. Foragers born outside of any patch were assigned at birth to the patch their parent currently belonged to.

**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. One run of 10,000 time steps was performed at each parameter setting. Averages over the last 1000 time steps are shown. Shading indicates frequencies > 0.5. (Smaller non-zero values indicate runs in which feeding restraint would presumably have disappeared if the run had continued longer.) Asterisks indicate that both forager types went extinct.

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	.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

To measure selection within and between patches, we used a powerful approach that underlies much of modern multilevel selection theory (Frank 1995). This is Price’s (1972) covariance formula for partitioning change in the frequency of an allele:

$$\Delta p = cov_n(w_g, p_g) + ave_n[cov(w_{gi}, p_{gi})]. \quad (1)$$

This equation represents the total change in allele frequency across one generation as the sum of two components: between-group selection (the first term on the right) and within-group selection (the second term on the right). Definitions are as follows:  $w_g$  = relative group fitness (mean progeny per member of the  $g$ ’th group, relative to other

groups),  $p_g$  = allele frequency within the  $g$ 'th group,  $cov_n$  = covariance among groups, weighted by group size in the parental generation,  $w_{gi}$  = fitness of the  $i$ 'th individual in the  $g$ 'th group relative to other group members,  $p_{gi}$  = allele frequency for the  $i$ 'th individual in the  $g$ 'th group (either 0 or 1),  $cov$  = covariance among individuals within the  $g$ 'th group, and  $ave_{n'}$  = average of the within-group covariances, weighted by progeny per group.

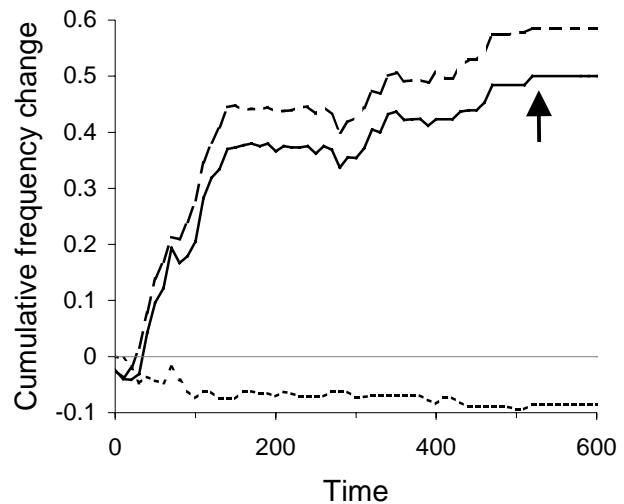
Because life spans overlapped in our model, we defined a "generation" as a single time step of the model, and an individual's "progeny" as any offspring it produced, plus itself if it survived the time step. Figure 5 illustrates the application of this formula to one run of the model. The allele for 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 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 effects we observed as we modified plant distribution patterns provided interesting answers to the questions we posed. They showed that variation in an ecological factor -- the patchiness of food distribution -- could by itself create sufficient population structure to generate significant between-group selection, leading to the spread of a group-beneficial cooperative trait. This result is not specific to feeding restraint, as

qualitatively similar results were obtained from a similar model in which cooperation took the form of alarm calling (Pepper & Smuts 2000). The results also showed that between-group selection could lead to the spread of the cooperative trait of feeding restraint even without spatial association among kin. This was due to that fact that actors were among the recipients of their own group-beneficial effects (Pepper 2000).



**FIGURE 5.** Total change in the frequency of feeding restraint (solid line) as the sum of within-patch selection (dotted line) and between-patch selection (dashed line). Because restraint began at a frequency of 0.5, total frequency change equaled 0.5 when restraint reached fixation (at arrow). Note that 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. Calculations were based on Eq. (1).

Changing the distribution pattern of plants affected whether cooperation evolved through two different causal mechanisms -- by changing the size of trait groups, and by changing their temporal stability. In the following sections we discuss each of these mechanisms in turn.

### ***Resource Distribution Affected Trait Group Size***

Trait groups come into existence whenever a trait expressed by one individual affects the fitness of other individuals. Patch size affected the number of nearby foragers, so that smaller patches led to smaller trait groups. Distance between patches was important in limiting trait groups to only those foragers within a single patch. Thus small patches and large gaps both decreased average trait group size.

Small trait groups increased the strength of between-group selection relative to within-group selection by changing the partitioning of genetic variance. Selection at any level requires that the units being selected vary genetically, and all else being equal, the strength of selection increases with the genetic variance among units. In a subdivided population, all variance among individuals can be partitioned into within- and between-group components, and the proportion of the total variance found at each level strongly affects the relative strength of within- versus between-group selection (Price 1972; Hamilton 1975; D. S. Wilson 1975). The smaller groups are, the more variance is shifted from within to between groups, and thus the stronger the between-group component of selection becomes relative to the within-group component. Because small isolated patches reduced trait group size, both small patches and large gaps facilitated the evolution of cooperation.

### ***Resource Distribution Affected Population Mixing***

Food distribution influenced not only how clustered or dispersed foragers were at any given moment, but also how freely the population mixed over time. Patchy environments effectively restricted foragers' movement patterns, causing them to repeatedly interact with the same individuals. Both environmental parameters played a role: Larger gaps inhibited migration between patches and kept foragers in the same patch longer, while larger patches let some patch inhabitants escape the influence of others, permitting trait group membership to shift as individuals moved within the patch. Thus small patches and large gaps both stabilized trait group

membership by reducing mixing. This facilitated the evolution of cooperation through effects both on the genetic make-up of trait groups, and on how the benefits of cooperation were distributed.

One effect of population mixing was that it reduced the tendency for kin (individuals with the same allele for cooperation due to common descent) to be together more often than non-kin, and thus to interact more. Positive assortment of kin into trait groups is important for the same reasons outlined above; it increases genetic variance between groups and reduces it within groups. In most of these experiments offspring were born near their parents, creating spatial association and thus higher rates of interaction among kin than non-kin. However, foragers tended to wander away from kin over time. The extent to which kin assorted positively within trait groups thus depended on the balance between births and population mixing. When patchy food distribution restricted movements largely to within patches, clusters of kin could arise and persist. In contrast, when food was distributed more uniformly, movements were less restricted and the population mixed constantly, removing the positive assortment of kin as fast as it was produced by new births.

Population mixing also tended to prevent the evolution of feeding restraint for a second reason unrelated to genetic structure. The cost of feeding restraint was immediate, but the benefits were deferred for at least one time step and potentially many more. This delay affected which individual received the benefit from an act of restraint. In freely mixing populations the individual paying the cost of restraint was rarely among those reaping the benefits, because it was likely to move away before its restraint paid off in an improved local food supply. In contrast, when patches were isolated foragers tended to stay within them, and when patches were small they contained few competitors. Under these conditions the restrained individual was usually among those benefiting from its behavior, so that restraint directly benefited the actor. Patchy environments thus allowed restrained foragers to collect a larger share of the payoff from their own restraint, thereby reducing within-group selection against

them. For this reason, association among kin was not always necessary for feeding restraint to spread. This contradicts the view sometimes expressed that group selection can be effective only when it is driven by preferential interactions among kin (Bell 1997:530; Maynard Smith 1998).

### *Cooperation Evolved Without A Discrete Mixing Phase*

Because of its within-group disadvantage, cooperation can only spread through an advantage in founding new groups. Successful groups must be able to export their productivity from the local area, so that their reproductive success is not suppressed by local population regulation (Wilson et al. 1992). This creates a tension between the need for mobility in order to found new groups, and the need for isolation to prevent selfish immigrants from invading cooperative groups.

In some models of “viscous” (non-mixing) populations, cooperation cannot easily evolve because groups that are sufficiently isolated for altruists to prosper are also too isolated to export their productivity (Wilson et al. 1992, Queller 1994, Sober and Wilson 1998:61). In many group selection models this problem is overcome by alternating between an interaction phase, during which the population is structured into trait groups and fitnesses are determined, and a mixing phase, during which individuals or propagules are randomly recombined to create new groups (D. S. Wilson 1975, 1980). Indeed some authors have suggested that a discrete mixing phase is necessary for group selection to be effective (Dugatkin and Reeve 1994). Obviously, this would significantly limit the role of group selection in nature.

The current model included no discrete mixing phase, yet local sub-populations of cooperators were able to export their productivity and thereby escape local population regulation. This occurred because a patch approaching its carrying capacity became less attractive to its occupants as their feeding rates fell, leading some to disperse and eventually colonize new patches. As a result, cooperative groups continued to reproduce faster and send out more dispersers than selfish groups,

giving them an advantage in colonizing empty patches.

### CONCLUSIONS

Many of the issues we examine in this chapter have been studied previously using equation-based methods (reviewed in Wilson and Sober 1994). What can we gain by re-visiting them using an agent-based model? This approach offers several important advantages, stemming from the fact that the necessary assumptions concern traits and behaviors of individuals rather than the global patterns that arise through their interactions. This makes it easier to build a model on assumptions that reflect real world mechanisms. It also means that the simplifications necessary to make the model tractable are less likely to inadvertently bias the results. In particular, in equation-based models parameters critical to the outcome of multilevel selection, such as the benefits and costs of cooperative acts and the rates of migration between groups, are uniform and fixed. In this agent-based model the values of these parameters emerge through the interactions of individuals, and can thus vary over both space and time in realistic ways. Our results suggest that this local spatial and temporal variation can have important effects. Moreover, these critical parameters can interact with one another in complex ways impossible to incorporate into equation-based models. For example, ecological conditions can affect population genetic structure, which in turn can affect the magnitudes of costs and benefits. Such complex interactions may explain some of the differences between our conclusions and those of previous modeling studies. A hybrid approach such as that followed here combines the advantages of agent-based models for generating realistic nonlinear dynamics, and equation-based tools for quantifying and analyzing the resulting outcomes.

A number of authors have dismissed between-group selection as a relatively weak and unimportant force in evolution (Grafen 1984, Ridley 1996). Our results suggest that this conclusion is premature. In a plausible ecological and behavioral setting, the requirements for the

evolution of cooperation through between-group selection did not appear unrealistically stringent in any obvious way. Our work with this model has shown that groups emerging through the behavior of individual agents in patchy environments can drive the evolution of group-beneficial traits, even in the absence of kin selection and a discrete mixing phase. We have also found that the evolution of other forms of cooperation can similarly depend on how resource distribution shapes a population's spatial structure and dynamics (Pepper & Smuts 2000). This demonstrates that effective between-group selection does not depend on the kind of discrete and stable groups that are typical of equation-based models, but that may not be typical in nature.

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