The Evolution of Cooperation in an Ecological Context: An Agent-Based Model

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1 INTRODUCTION

The social and behavioral sciences have a long-standing interest in the factors that foster selfish (or individualistic) versus altruistic (or cooperative) behavior. Since the 1960s, evolutionary biologists have also devoted considerable attention to this issue. In the last 25 years, mathematical models (reviewed in Wilson and Sober 1994) have shown that, under particular demographic conditions, natural selection can favor traits that benefit group members as a whole, even when the bearers of those traits experience reduced reproductive success relative to other members of their group. This process, often referred to as "trait group selection" (D. S. Wilson 1975) can occur when the population consists of numerous, relatively small "trait groups," defined as collections of individuals who influence one another's fitness as a result of the trait in question. For example, consider a cooperative trait such as alarm calling, which benefits only individuals near the alarm caller.[1] A trait group would include all individuals whose fitness depends on whether or not a given individual

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[1]For this chapter, we define "cooperation" to include any behavior 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. Within evolutionary biology, such

gives an alarm call. If the cooperative trait confers sufficiently large reproductive benefits on the average group member, it can spread. This is because trait groups that happen to include a large proportion of cooperators will send out many more offspring into the population as a whole than will groups containing few, or no cooperators. Thus, even though noncooperators out reproduce cooperators *within* trait groups (because they experience the benefits of the presence of cooperators without incurring the costs), this advantage can be offset by differences in rates of reproduction *between* trait groups. Numerous models of group selection (Wilson and Sober 1994) show that whether cooperative traits (as defined in footnote 1) can spread depends on the relative magnitude of fitness effects at these two levels of selection (within and between trait groups). In addition, there is a growing body of empirical evidence for the operation of group selection in nature (e.g., Colwell 1981; Breden and Wade 1989; Bourke and Franks 1995; Stevens et al. 1995; Seeley 1996; Miralles et al. 1997; Brookfield 1998) and under experimental conditions (reviewed in Goodnight and Stevens 1997).

These developments have highlighted two critical factors that combined determine the strength of between-group selection. The first of these is the structuring of fitness effects, i.e., which individuals are affected by the expression of the trait, to what extent, and in which direction. The second important factor is the genetic structure of trait groups, i.e., the extent to which individuals who influence one another's fitness through a particular trait are more likely to share the alleles underlying that trait than members of the population at large. Kin-directed behavior is the most biologically important source of genetic structure, and it has received the most attention from evolutionary biologists (Hamilton 1964). Because kin-directed behavior facilitates between-group selection by decreasing genetic variance within trait groups and increasing it between trait groups, some evolutionary biologists, including W. D. Hamilton, the formulator of kin selection theory, have regarded kin selection as a special case of group selection (Hamilton 1975:337; Futuyma 1986:264; Breden 1990; Queller 1991). Others have argued that kin selection is an alternative to group selection. According to this view, although group selection can occur without kin selection in theory, the necessary conditions are so stringent as to make it unimportant in nature (e.g., Maynard Smith 1964, 1976; Williams 1966; Grafen 1984; Alexander 1989). Over the last 30 years, the debates about group versus individual selection and kin selection have played a central role among those interested in social evolution and the functioning of small-scale societies (e.g., E. O. Wilson 1975; Trivers 1985; Alexander 1987; Cronin 1991;, Wilson and Sober 1994; Sober and Wilson 1998).

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behaviors are often referred to as "altruistic." We avoid this term because it has been used in different ways by different authors, generating considerable confusion (Wilson and Dugatkin 1992). Ours is a very specific definition of the term cooperation that does not necessarily correspond to the way it is used by other researchers. For example, "cooperation" is sometimes employed to refer to joint actions (e.g., cooperative hunting) that *raise* the fitness of cooperators relative to other group members.

Formal mathematical models have clarified the role of local fitness effects and population genetic structure as causal factors in group selection but have almost completely failed to address how they can arise within an ecological context. Fitness effects and population structure are often represented in ways that have more to do with the exigencies of equation-based modeling than with how organisms behave in nature. Such models demonstrate that cooperation can evolve under the specified conditions, but they leave unexplored the critical question of whether the kinds of local fitness effects and genetic population structure they assume are realistic, and how they might come about. Here we describe a model in which both local fitness effects and population genetic structure emerge through the actions of individuals following simple yet plausible rules of behavior in spatially varying environments. We use the model to explore three interrelated questions raised by approaching multilevel selection from an ecological perspective:

1. How easily can ecological variation alone generate local fitness effects and genetic structure sufficient to drive the evolution of cooperation through trait group selection?
2. Given reasonable ecological assumptions, does between-group selection require association among kin in order to be effective, or can cooperation spread even in the absence of kin selection?
3. Do the answers to questions 1 and 2 vary depending on the nature of the cooperative trait in question?

To address the third question, we investigate the evolution of two different cooperative traits with long histories in the literature on the evolution of cooperation: alarm calling and feeding restraint. Alarm calling is perhaps the classic example of altruistic behavior among nonhumans and was one of the first to be extensively studied in the field (e.g., Sherman 1977; Hoogland 1983). 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).

Virtually all published quantitative models of group selection are based on systems of equations. However, such models have several critical limitations for modeling multilevel selection. First, they require simplifying assumptions, such as homogeneous randomly mixed populations and infinite population sizes, that can limit the possible outcomes in important ways. Second, in equation-based models, population structure (the division of a population into more or less discrete groups, or the absence of such divisions), must be assumed a priori. Many authors have argued that unlike those found in mathematical models, groups in the real world do not act as vehicles of selection strongly enough to affect evolutionary outcomes 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).

In an effort to overcome these problems, researchers in a growing number of fields are turning to an approach called "agent-based" or "individual-based" modeling. The essence of this approach is that instead of using equations that apply uniformly to the entire system, the model consists of individuals or "agents" that interact according to an explicit set of rules of behavior. Advantages include the ability to represent the behaviors and interactions of individuals in a more direct and natural way, to incorporate variation over space and time, and to incorporate nonlinear dynamics (Huston et al. 1988; Judson 1994; Belew et al. 1996). In addition, agent-based models require no starting assumptions about the nature of groups or nonrandom interactions among individuals; instead, population structure can be generated by simple rules of interaction. Moreover, recent advances in object-oriented programming techniques have greatly facilitated the use of agent-based models of biological processes (Judson 1994; Reynolds and Acock 1997; Sequeira et al. 1997). Despite their success in other areas, agent-based models have been used surprisingly little in evolutionary biology. This chapter is a first step in applying the tools of agent-based modeling to the long-standing problem of multilevel selection.

Our goal in this preliminary study was not to produce a realistic representation of any specific system, but rather to construct a "minimal model" of multilevel selection in an ecological context, one which leaves out as much as possible while still capturing the essential properties of interest (Roughgarden et al. 1996). Our hope is that understanding the dynamics of a simple (and relatively manageable) model will help generate useful new hypotheses about when and how group-beneficial traits can evolve in nature.

2 THE MODEL

The computer model included resources (plants) growing in two-dimensional space, and agents (foragers) moving about, eating food, interacting, reproducing, and dying. We assumed only that individuals showed some very simple behaviors, such as a tendency to move toward food. We then explored the question of whether individuals, by pursuing unevenly distributed resources, would generate sufficient population structure to drive significant levels of between-group selection. Like those in the real world, the groups that formed in this model did not have discrete boundaries, either in space or time. Instead these "trait groups" were characterized by shared fitness effects that varied continuously in strength over both space and time.

2.1 THE MODEL WORLD

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.

TABLE 1   Standard parameter settings.

Parameter	Value
All experiments	
Minimum number of plants	500
Plant maximum size (energy units)	10
Starting number of foragers	40
Forager starting energy (energy units)	50
Forager metabolic rate (energy units)	2
Forager fertility threshold (energy units)	100
Alarm-calling experiments	
Plant linear growth rate (energy units)	1
Forager feeding restraint (% left uneaten)	1%
Probability of predator attack	0.02
Alarm-calling range (# of cells)	5
Feeding restraint experiments	
Plant logistic growth rate r	0.2
Forager feeding restraint (% left uneaten)	1% or 50%
Probability of predator attack	0

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, while foragers moved about seeking and eating plants, reproducing, and dying. In each run, all plants were identical except for the amount of energy they started with (see Table 1 and below), but foragers could include two types differing in their tendency to cooperate. During each time step each agent (plant or forager) was activated once in random order.

A plant's energy store 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. For simplicity we assumed that feeding transferred energy from plants to foragers with 100% efficiency.

Runs that included both cooperative and noncooperative foragers began with equal numbers of each.[2] At the start of a run each initial forager was endowed with an energy level chosen as a uniform random number between zero

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[2]Because our experiments started with equal numbers of selfish and cooperative foragers, they did not address what has been termed the "problem of origination": that some cooperative traits cannot spread through selection unless they first reach a minimum threshold frequency. Wilson and Dugatkin (1997) have argued that this apparent obstacle is an artifact of the simplifying assumption of discrete traits. When traits are modeled instead as varying along a continuous spectrum (like most real traits), the problem of origination disappears. We plan to investigate this question in future studies.

and the fertility threshold, and placed on a randomly chosen cell containing a plant. At each time step, foragers could gain energy by eating plants, increasing their own energy store by the same amount they reduced the plant's. They also lost energy each time step as a fixed metabolic cost, regardless of whether or not they moved. If their energy store reached zero they died, but they did not have maximum life spans. If a forager's energy level reached an upper fertility threshold it reproduced asexually, creating an offspring with the same heritable traits as itself (e.g., tendency to cooperate). At the same time the parent's energy store was reduced by the offspring's initial energy. 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.

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 to a randomly chosen adjacent cell if any were unoccupied. 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.

We examined two forms of cooperation, alarm calling and feeding restraint. Each trait was controlled by a single haploid locus with two alleles that did not mutate, so that offspring always inherited their parent's trait. In each experiment, we allowed cooperative foragers to differ from selfish foragers in just one trait. The standard parameter settings shown in Table 1 were used in each run unless otherwise noted.

2.2 RESOURCE DISTRIBUTION

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 population (hereafter simply referred to as a "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 1 illustrates the patchy plant distribution pattern resulting from one setting of these parameters.
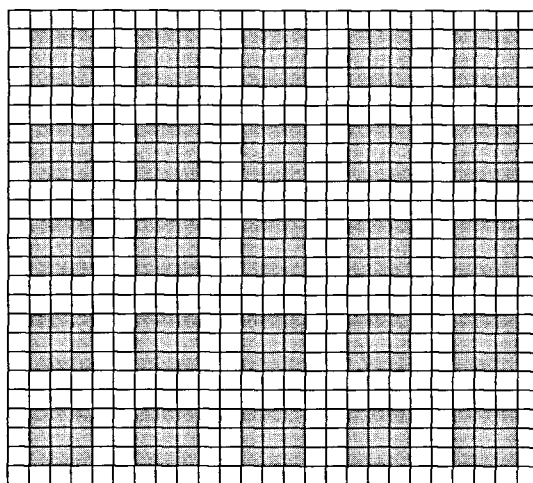
FIGURE 1   A representative resource distribution pattern. Filled squares represent cells occupied by a plant, and unfilled squares represent empty cells. This world was generated by setting the minimum number of plants to 200, the patch width to 3, and the gap width to 2. To create a uniform square world, the program increased the actual number of plants to 225 to create 25 patches, each consisting of 9 plants.

2.3   ALARM CALLING

For experiments on alarm calling we added predation to the model. With each time step, each forager experienced a 2% chance of being targeted by a predator. When a currently active forager was targeted other nearby foragers could give an alarm call, depending on their genotype. Alarm callers always called when a "neighbor" (any individual within the calling range of five cells) was targeted. (Targeted individuals themselves never called.) Calling had two effects: it reduced the chance that the predator would make a kill, and also exposed the caller to the risk of death. Noncallers never called, but benefited from having alarm callers nearby when they were targeted. Once a forager had been targeted, the probability of a kill was $1/(n + 1)$, where $n = $ the number of alarm calls. (One was added to the denominator to avoid a denominator of zero when no callers were present.) If the predator did make a kill, its victim was chosen with equal probability from among its original target and any neighbors that called. Note that under these rules, as the local density of callers increased, the benefit to the group increased and the cost to each caller (in terms of risk of death) decreased. For these experiments we employed a simple food growth rule of the type used in previous agent-based models (e.g., Epstein and Axtell 1996). Plants grew at the constant rate of 1 energy unit per time step, up to the maximum of 10 energy units.

2.4   FEEDING RESTRAINT

For experiments on feeding restraint, we removed predation from the model so that foragers never gave alarm calls. Instead, the two types differed only in their feeding behavior. When 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, restrained foragers ate only half of the plant they fed on.[3]

To create a group benefit of feeding restraint, we altered the pattern of plant growth for these experiments. Instead of the linear growth pattern used in the alarm-calling experiments, plants followed a logistic growth pattern, with the logistic rate of growth set to 0.2 (Figure 2); as before, maximum plant size was limited to 10 units. The S-shaped logistic growth curve is typical of populations with growth limited by the environment's carrying capacity (Ricklefs 1990). Unlike resources that grow linearly, 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, 1998; Feeny et al. 1990).

2.5   IMPLEMENTATION

The program was written in the Objective-C language, using the Swarm library for agent-based modeling developed at the Sante Fe Institute (Minar et al. 1996). The program includes both an interactive graphical user interface and a batch mode. Multiple batch runs on a distributed network were controlled using the Drone program written by T. Belding at the University of Michigan's Program for the Study of Complex Systems. The program was run under Unix on Hewlett-Packard 9000 series workstations, but is also portable to Swarm environments on Windows platforms, and is available on request.

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[3]Note that this difference in feeding behavior affects the minimum size plant that will meet a forager's maintenance energy requirement, and thus that will be attractive. All foragers have the same metabolic rate of 2 energy units per time step. To gain this much energy unrestrained foragers must feed on a plant containing at least 2.02 units of energy $(2.02 \times 99\% = 2)$, whereas restrained foragers require a larger plant containing at least 4 units of energy $(4 \times 50\% = 2)$. Recall that in choosing a cell to move to, foragers find the accessible cell with the highest food yield, but if that yield falls below the starvation level they move randomly instead. Thus if the largest available plant contained between 2.02 and 4 energy units, an unrestrained forager would feed on it and grow, while a restrained forager would begin to starve and to wander randomly.
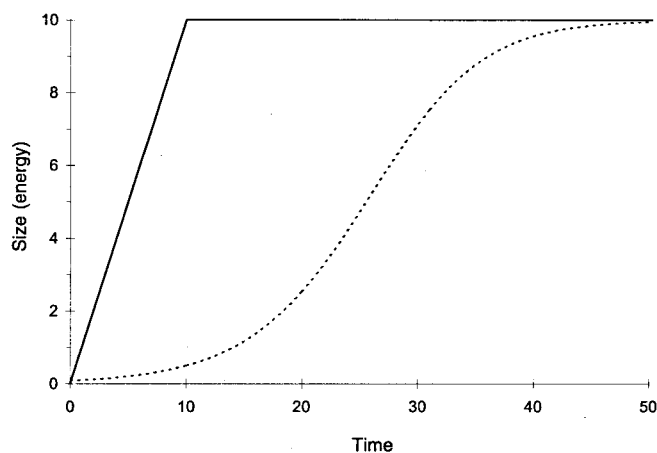
FIGURE 2   A comparison of linear growth (solid line) with logistic growth (dashed line). Under linear growth a plant increases its energy by a fixed amount each time step up to the maximum size. Under logistic growth, the increase per time step $= r * N * (K - N)/K$, where r = logistic growth rate, N = current size, and K = maximum size. The line shown represents a starting size of $N = 0.1$. In this model size corresponded to energy content, and the parameters r and K were set per Table 1.

3   THE EXPERIMENTS

3.1   PART 1: 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 every cell. For each form of cooperation, we compared the performance of cooperative and selfish foragers in both pure and mixed populations.

In experiments on alarm calling, pure populations of alarm callers experienced much less predation than noncallers, and as a result maintained larger populations (Figure 3). This showed that the increased death rate caused by alarm calling was more than offset by the protection afforded by neighboring foragers. However, when we included both alarm callers and noncallers in the same population, both callers and noncallers benefited from the presence of alarm-calling neighbors, while noncallers avoided the risks associated with calling. As a result, they survived better and consistently out-competed alarm callers, leading to fixation of the noncalling trait (Figure 4). The loss of alarm
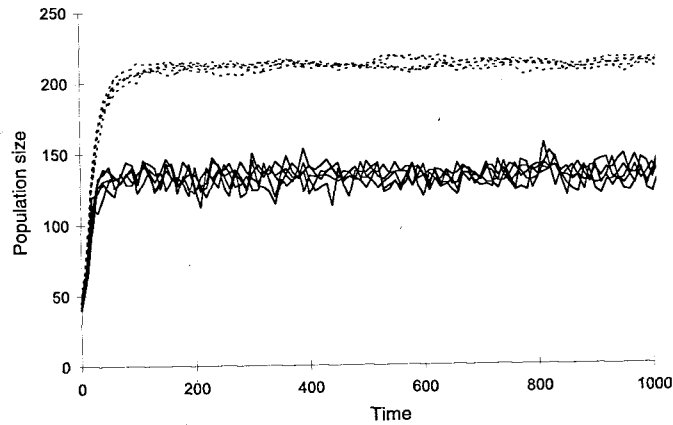
FIGURE 3 Population size as a function of time for pure populations of alarm callers (dotted lines) and noncallers (solid lines) in a uniform environment (single patch width = 529, gap width = 0). The five runs shown for each forager type used the same parameter settings (see Table 1) but different random number seeds.

callers from the population resulted in the same high predation rate and reduced population size shown by the initially pure population of noncallers (Figure 3).

In the experiments on feeding restraint, plants followed a logistic growth curve; consequently their growth 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 5). 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 5).

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 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 6).
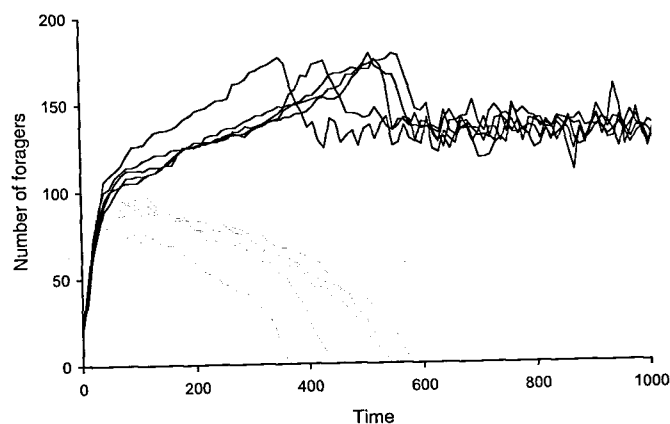
FIGURE 4   Number of alarm callers (dotted lines) and noncallers (solid lines) over time in mixed populations in a uniform environment (single patch width = 529, gap width = 0). Five runs are shown, each using the same parameter settings (see Table 1) but different random number seeds. The drop in the number of noncallers in each run immediately follows the loss of alarm callers from the population in the same run.
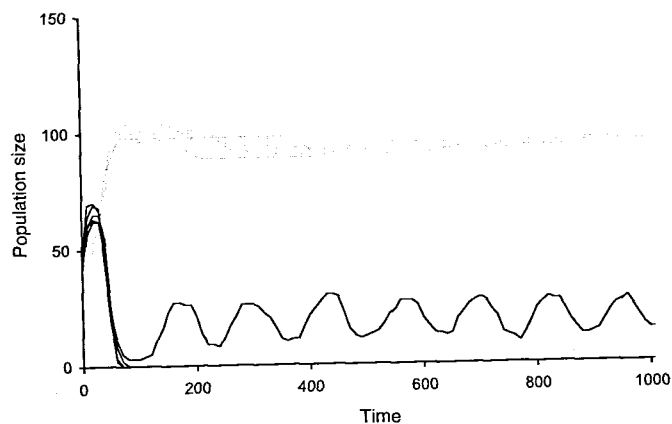

FIGURE 5   Population size as a function of time for pure populations of restrained (dotted lines) and unrestrained (solid lines) feeders in a uniform environment (single patch width = 529, gap width = 0). The five runs shown for each forager type used the same parameter settings (see Table 1) but different 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 producitivity of plants, leading to starvation and a reduced population size. Reduced feeding then led to increased food population and higher birth rates, repeating the cycle. Such oscillations are typical of some natural populations (Ricklefs 1990).
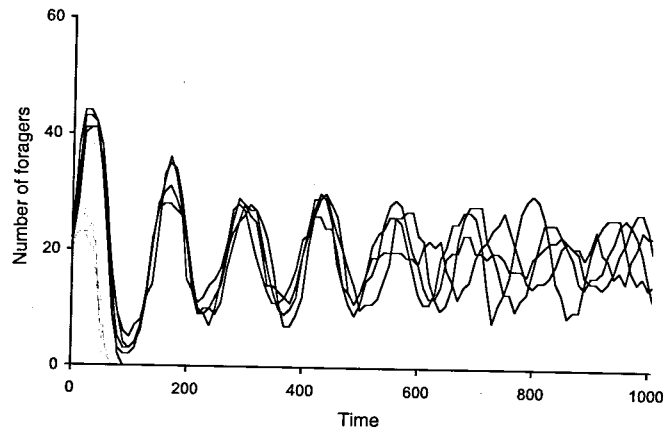
FIGURE 6   Number of restrained (dotted lines) and unrestrained (solid lines) for-
agers over time in mixed populations in a uniform environment (single patch width
= 529, gap width = 0). Five runs are shown, each using the same parameter settings
(see Table 1) but different random number seeds. The 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 5.

To summarize, in uniform environments a similar pattern emerged for
both forms of cooperation. In each case, cooperation benefited the popula-
tions in which it occurred. However, within mixed populations cooperation of
either form was inevitably out-competed and replaced by its selfish counter-
part, to the detriment of the population as a whole. The rest of our experi-
ments concern the effects of nonuniform environments on evolution in mixed
populations.

3.2   PART 2: RESOURCE DISTRIBUTION AND THE EVOLUTION OF ALARM CALLING

To investigate ecological influences on the evolution of alarm calling, we exam-
ined mixed populations of callers and noncallers in patchy environments. We
varied patch width from 1 to 10, and gap width from 1 to 10, for a total of 100
different parameter settings. None of these plant distribution patterns com-
pletely precluded migration between patches, as even newborn foragers could
traverse up to 25 cells without eating before starving to death (50 energy units
at birth/2 units metabolic cost per time step, Table 1).

When plants were concentrated into discrete patches, foragers spent most
of their time within patches, typically leaving them only after most plants were
consumed to below the minimum yield for forager subsistence (see footnote 3).
Moreover, when patches were widely separated, foragers leaving a patch were
more likely to either return to it or starve while wandering randomly than

TABLE 2 Final frequency of alarm callers 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 1,000 time steps are shown. Boldface indicates frequencies > 0.5. There was no evidence of stable equilibria, so that all of these runs would presumably have gone to fixation given sufficient time. *Population went extinct.

Patch width	Gap width 1	2	3	4	5	6	7	8	9	10
1	0	*	*	*	*	*	*	*	*	*
2	0	*	*	*	*	*	*	*	*	*
3	0	0	0	0.3	**1**	**1**	**1**	**1**	**1**	**1**
4	0	0	0	0	0	0	0	**0.6**	**0.6**	**0.8**
5	0	0	0	0	0	0	0	0	0.1	0.2
6	0	0	0	0	0	0	0	0	0.1	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

they were to successfully disperse to a new patch. Within a given patch, non-callers had higher survival rates than alarm callers for two reasons. First, they avoided the increased risk of death associated with calling, and secondly, they also paradoxically received more protection through alarm calls. To illustrate this latter effect, assume that all occupants of a patch are within calling range of each other and that no other foragers are. Then if the patch holds N callers, each caller is protected by $N - 1$ calls when targeted by a predator, whereas each noncaller is protected by N calls. Because of their survival advantage, noncallers tended to quickly take over mixed patches. However, patches with a lower frequency of callers were more vulnerable to predation, and those occupied only by noncallers were often emptied by predation, leaving an opportunity for later colonization by either type. In contrast, patches occupied only by callers were rarely emptied by predation unless they were very small.

Both the size of patches and the distance between them affected the evolution of cooperation. If food patches were too small and widely separated they could not support any foragers for long, and the population went extinct. Subject to this constraint however, the evolution of alarm calling was promoted by small and widely spaced patches (Table 2).[4]

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[4]In the implementation described here, alarm calling was very costly because it put the caller at as much risk as the original target. As a result, alarm calling evolved only within a narrow range of plant distribution patterns (Table 2). In another version of the model in which the cost of calling was energetic rather than through risk of death, alarm calling was favored under a much wider range of ecological conditions. We suspect that reducing the risk of calling to a more realistic level would similarly broaden the range of conditions under which calling would evolve.

3.3 PART 3: RESOURCE DISTRIBUTION AND THE EVOLUTION OF FEEDING RESTRAINT

To investigate ecological effects on the evolution of feeding restraint, we performed a second sweep of the 10×10 parameter space for plant distribution patterns, this time starting with equal numbers of restrained and unrestrained feeders. There was no predation, and plant growth was logistic.

In a patchy environment, an unrestrained forager first colonizing a new 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 of them had time to 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.

In contrast, patches inhabited only by restrained feeders were not overexploited 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 that were occupied only by restrained feeders did not become exhausted and were not abandoned. Instead, birth and immigration into the patch was approximately 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.

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. The fact that restraint could spread to fixation under some conditions (Table 3) therefore demonstrated that it was favored by the greater productivity of patches occupied by restrained foragers. As with the alarm-calling trait, 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 3).

3.4 PART 4: KIN SELECTION AS A COMPONENT OF BETWEEN-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;

TABLE 3   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 1,000 time steps are shown. Boldface indicates frequencies > 0.5. *Population 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

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 for discriminating kin from nonkin, it nonetheless held the potential for significant levels 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. Both forms of cooperation 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 any spatial association between kin, we repeated the experiments in Parts 2 and 3 above with one modification: instead of newborn foragers being placed in the nearest open cell to their parents, their birth location was chosen randomly from all unoccupied cells in the grid. When we repeated the experiment on alarm calling (Table 2) with birth locations randomized, alarm calling never spread. Instead the noncalling trait went to fixation under every resource distribution pattern. In contrast, when we repeated the experiment on feeding restraint with randomized birth locations, restraint did spread to fixation under some resource distribution conditions. However, the conditions for the evolution of restraint were more restricted without parent-offspring association than when offspring were born next to their parents (Tables 3 and 4).

TABLE 4   Final frequency of restrained feeders with offspring dispersing randomly. All parameters were set as in Table 3, 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. Boldface indicates frequencies > 0.5. *Population 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	0.1	**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

3.5 PART 5: 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. Of course this requires that we explicitly define the groups involved, but that was not a simple task for trait groups in our model. Because trait group membership was not imposed as an assumption of the model, the boundaries of fitness effects between individuals shifted with each interaction. Moreover, in the case of feeding restraint it was not clear, even in principle, how to determine trait group boundaries, because an individual's current fitness depended on the actions of other individuals many time steps in 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. Patches corresponded well to trait groups when they were well separated, and in the case of alarm calling, when they were small enough to be entirely within the calling range of any patch occupant. 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.

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 (1970, 1972) covariance formula for partitioning change

in the frequency of an allele[5]:

$$\Delta p = \frac{\mathrm{cov}_n(w_g, p_g)}{w} + \frac{\mathrm{ave}_n, [\mathrm{cov}(w_{gi}, p_{gi})]}{w}. \tag{1}$$

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 = total change in allele frequency in population; w_g = group fitness (mean progeny per member of the gth group); p_g = allele frequency within the gth 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 ith individual in the gth group; p_{gi} = allele frequency within the ith individual in the gth group (either 0 or 1); cov = covariance among individuals within the gth 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.

Figures 7 and 8 illustrate the application of this formula to one run of the model for alarm calling and feeding restraint, respectively, under the same plant distribution pattern. The allele for each type of cooperation 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 experiments in Parts 2 through 4 using this analysis, and found that for both forms of cooperation 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.

4   DISCUSSION

The model captured the essential properties of opposing levels of selection, in that each form of cooperation was favored by between-group selection but diminished in frequency 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 varying outcomes we observed as we modified plant distribution patterns provided interesting answers to the three questions posed in the intro-

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[5]Our notation follows Grafen (1985), but we have added Price's (1972) explicit notation for weighted statistical functions. Hamilton (1975) left the weighting of covariance out of his notation, mentioning it only in the text, and some later authors dropped it entirely (Grafen 1985; Bourke and Franks 1995). As a result their formulas are not strictly correct unless all groups are assumed to be the same size
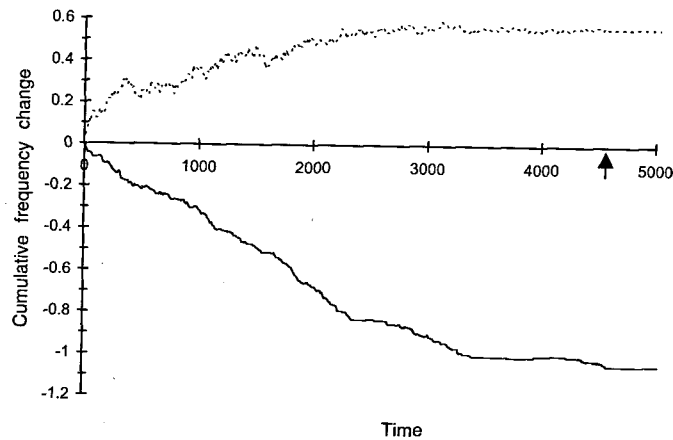
FIGURE 7   Cumulative change in the frequency of the alarm-calling allele during
one run due to within-patch selection (solid line) and between-patch selection (dot-
ted line). Because the allele began at a frequency of 0.5, the total frequency change
represented by the sum of the two lines equaled −0.5 when noncalling reached fixa-
tion (at arrow). Note that substantial between-group selection for alarm calling was
outweighted by stronger within-group selection against calling. Patch width = 4,
gap width = 5, and all other parameters were set as per Table 1. Calculations were
based on Eq. (1).
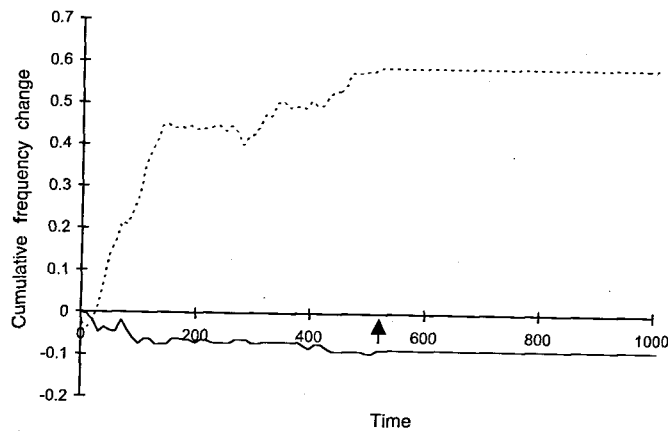
FIGURE 8   Cumulative change in the frequency of the feeding restraint allele due to
within-patch selection (solid line) and between-patch selection (dotted line). Because
the allele began at a frequency of 0.5, the total frequecy change represented by the
sum of the two lines equaled 0.5 when restraint 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).

duction. First, they showed that variation in an ecological factor—the patchiness of food distribution—can by itself create sufficient population structure to generate significant between-group selection, leading to the spread of group-beneficial cooperative traits. Second, we found that between-group selection could lead to the spread of the cooperative trait of feeding restraint even without positive assortment among kin. Third, the dynamics of selection on the two traits we examined showed both similarities and differences. Both cooperative traits were more likely to spread under similar ecological conditions (small patches separated by large gaps), but the mechanisms differed to some extent for the two traits.

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, and then explore similarities and differences in how they affected the evolution of each trait.

4.1   RESOURCE DISTRIBUTION AFFECTED TRAIT GROUP SIZE

It is important to keep in mind that trait groups are defined not in terms of geographical clustering, but in terms of fitness effects—specifically whether the fitness of some individuals is affected by the genotypes of others. Thus even if individuals do not form spatial clusters, trait groups come into existence whenever a trait expressed by one individual affects the fitness of a subset of other individuals in the population. In those runs in which foragers clustered within discrete food patches, the resulting spatial groups corresponded more or less closely with trait groups, but did not exactly coincide with them. The fitness effects of the trait could either extend beyond the patch, or apply to only a subset of the patch's inhabitants. Indeed, even when resources (and thus foragers) were evenly distributed, trait groups existed with respect to alarm calling or feeding restraint because these traits affected the fitness of a set of nearby individuals.

Although resource distribution did not define trait groups, it did influence them. Patch size affected the average number of foragers within a given radius, 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. When patches were close together the occupants of different patches affected one another's fitness, so that trait groups could encompass the occupants of multiple patches. Thus small patches and large gaps both decreased average trait group size.

Smaller trait groups in turn 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 compo-

nents, 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 both forms of cooperation.[6]

4.2 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 two different mechanisms, one involving the genetic make-up of trait groups, and the other involving the distribution of the benefits of cooperation. Each mechanism had important effects on only one of the two forms of cooperation we examined.

4.2.1 Population Mixing Reduced the Genetic Variance Between Trait Groups.   One effect of population mixing in our model 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 nonkin, and thus to interact more. Positive assortment of kin into trait groups (termed "kin selection") (Maynard Smith 1964) is important for the same reasons outlined above; it increases genetic variance between groups and reduces it within groups. In nature, kin selection often involves organisms recognizing their kin and actively directing cooperative behaviors toward them, but it need not. In all our experiments except part 4, offspring were born near their parents, creating spatial association and thus higher rates of interaction among kin than non-kin. However, in the absence of kin recognition, 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

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[6]Note that trait groups have a fixed size in some models of cooperation, such as the "Prisoner's Dilemma," in which all groups are of size two (Axelrod 1984). In such models resource distribution would not affect trait group size, but could still influence the evolution of cooperation through its effects on population mixing (see below).

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.[7]

Eliminating positive assortment among kin affected the two cooperative traits differently. Kin-based interaction was necessary for the evolution of alarm calling, as consistent with considerable empirical evidence (e.g., Sherman 1977; Hoogland 1983). However, it was not necessary for the evolution of feeding restraint (section 4 above). This result is particularly significant given that some workers view group selection as an alternative formulation of kin selection (Bell 1997:530; Maynard Smith 1998). To understand the difference between these two forms of cooperation, we must distinguish group-beneficial traits that reduce their bearer's fitness relative to the population as a whole from those that reduce individual fitness only relative to the rest of the trait group. To distinguish between these alternatives, Wilson (1979, 1980) coined the terms "strong altruism" and "weak altruism," respectively. For strongly altruistic traits, the net effect of dispensing group benefits is to lower the bearer's reproduction relative to the population as a whole. Therefore such traits can spread only if their bearers more than offset this disadvantage by receiving more than their share of the benefits dispensed by other cooperators (usually kin). Such inclusive fitness effects arise only if there is positive assortment, meaning that altruists are more likely than nonaltruists to interact with other altruists. In other words, the genetic variance between groups must be higher than expected if groups were random samples of the population (Bell 1997:526). In contrast, weakly altruistic traits lower the bearer's fitness relative to the trait group, but not relative to the population as a whole. As a result, they can spread without positive assortment (Hamilton 1975; D. S. Wilson 1975, 1979, 1990).

In this model, alarm calling was "strongly altruistic" because it conferred only costs and no benefits on its bearer. Thus it could not spread without positive assortment, and in our model, spatial proximity between parents and their offspring was the only way this could come about. In contrast, feeding restraint conferred benefits as well as costs on its bearer, by increasing plant productivity and thus later food availability. Thus feeding restraint was not necessarily strongly altruistic—if the benefits of restraint exceeded the costs for the individual expressing it, that individual's fitness increased. (Whether this actually occurred depended on the frequency of restraint among the patch's inhabitants.) Thus the spread of alarm calling depended on kin selection because it was always strongly altruistic, while this was not true of

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[7] Our model would be a more realistic representation of social behavior in humans and other primates if we added kin recognition, and the tendency both to preferentially associate with kin and to direct cooperative acts toward them. These features would greatly facilitate the evolution of cooperation, and in this sense our model was conservative in leaving them out.

feeding restraint. Note, however, that feeding restraint was always at least "weakly altruistic"—i.e., it reduced individual fitness relative to the rest of the trait group—because neighbors (other trait group members) reaped the benefits of another's restraint without paying the cost.

Given the importance of genetic structure for between-group selection, it may seem surprising that feeding restraint could evolve so readily when offspring dispersed to random locations, preventing positive assortment of kin among patches (Table 4). The explanation lies in the difference between cooperative traits that benefit the entire trait group including the actor (those with "whole-group effects"), versus traits that benefit only other group members (those with "other-only group effects"). In a large randomly assorting population, the average genotype of the "recipients" of an act (those individuals included in its group-level effect) is uncorrelated with that of the actor if the trait has other-only-group effects. In contrast, if the trait has whole-group effects, then as trait groups become smaller the actor itself constitutes an increasing proportion of the act's recipients, causing an increasingly positive correlation between the genotype of the actor and the average genotype of the recipients (Figure 9). This is another mechanism, in addition to positive assortment, by which the benefits of cooperation can be directed disproportionately to cooperators. Cooperative traits with other-only-group effects (such as alarm calling) are necessarily strongly altruistic, and thus cannot evolve without positive assortment. Those traits with whole-group effects (such as feeding restraint) will be only weakly altruistic if the actor's share of the group benefit exceeds the individual cost of the act. Under these conditions positive assortment is not necessary for the trait to spread.

4.2.2 Population Mixing Reduced the Acquisition of Delayed Benefits. For feeding restraint specifically, population mixing tended to prevent the evolution of cooperation for a second reason unrelated to genetic structure. The cost of feeding restraint was immediate, but the potential benefits of improved food supply 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, and also how much benefit accrued.

In freely mixing populations, the individual paying the cost of an act of restraint was rarely among those reaping the benefits. A forager that showed restraint was likely to move away before its restraint paid off in an improved local food supply. As a result restraint became strongly altruistic, and could not evolve without the positive assortment of kin that was absent from freely mixing populations. 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 was only weakly altruistic and could evolve without positive assortment of kin.

A second consequence of the delayed benefit of restraint was that the size of its ultimate payoff depended on the social environment. Refraining from
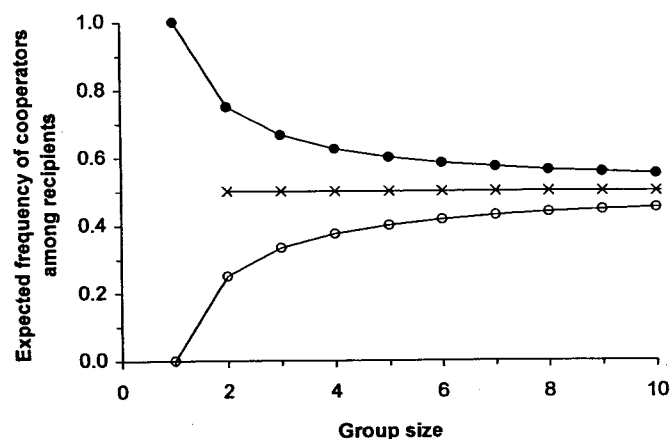
FIGURE 9   Effect of actor's genotype on the average genotype of a social act's recipients in a randomly assorting population. If a cooperative trait has a group effect that excludes the actor (cross marks), the frequency of cooperators among recipients is uncorrelated with the genotype of the actor. In contrast, if the trait's group-level effect includes the actor, the frequency of cooperators among recipients depends increasingly on the genotype of the actor as group size falls. In small groups the recipients of cooperative acts (filled circles) are biased toward cooperators, while the recipients of selfish acts (open circles) are biased toward selfish individuals. This figure assumes haploid single-locus control of the trait, with cooperative and selfish alleles at frequencies of 0.5, and infinite population size.

destroying a plant's productivity could potentially yield benefits for many time steps into the future. However, if the same plant was over-exploited two time steps later, the benefits would have little time to accumulate. Thus the full benefits of restraint were only realized in small isolated patches where clusters of restrained feeders could persist for some time without invasion by unrestrained feeders. In freely mixing populations, even if a restrained feeder stayed nearby to reap the delayed benefits of sustainable harvesting, the chances were high that an unrestrained feeder would soon arrive and terminate those benefits by over-exploiting the plant and destroying its productivity. Thus it was an important feature of the model that the benefits of restraint were not fixed as they typically are in equation-based models, but varied with the social environment in a realistic way.

Small, isolated patches were more favorable to restraint through their effects on selection at both levels. At the between-group level, patchy environments increased the total payoff of restraint to all trait group members, increasing between-group selection for cooperation. At the within-group level, patchy environments allowed restrained foragers to collect a larger share of the

payoff from their own restraint, thus reducing within-group selection against them. A variant of our model showed that the combined effect of these two factors was decisive. We gave foragers exclusive access to a floating "territory" consisting of the cells they had visited during the last several time steps. As a result population mixing was greatly reduced, and the benefits of restraint were both larger and directed primarily to the restrained individual. Under these conditions, feeding restraint spread rapidly even in uniform environments.

4.2.3 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" (nonmixing) populations, cooperation cannot easily evolve because groups that are sufficiently isolated for altruists to prosper are also too isolated to export their productivity. This is apparently true of Wright's (1945) early model of group selection (Sober and Wilson 1998:61), and also of models of plant-like organisms that do not move during their lifetimes, so that mixing is restricted to local dispersal of offspring (Wilson et al. 1992; Queller 1994).

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 (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.

In the current model there was no discrete mixing phase, yet local subpopulations 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. Instead of the migration rate between patches being a uniform parameter, as it typically is in equation-based models, the rate of emigration from a patch increased with its frequency of cooperators. This pattern, which increased the strength of between-group relative to within-group selection, emerged as a natural consequence of the foragers' movement rules.

Our results show that increasing mobility tends to reduce the effect of between-group selection through several mechanisms. However, some degree

of population mixing is also necessary for between-group selection to occur. This suggests that if gaps were too large, cooperative groups would become too isolated to export their productivity, and between-group selection would become ineffective. Further experiments with larger gap sizes have confirmed this. When gap width was increased to 30 cells, successful migration was almost impossible and each patch was effectively isolated. Under these conditions the overall frequency of cooperators in the population never rose significantly regardless of patch size. Instead it fell until all mixed patches had been taken over by selfish foragers. If mutation was added to the model, cooperation continued to decline in frequency until it disappeared.

4.3 CONCLUDING REMARKS

Many of the issues we examine in this chapter have been studied previously using equation-based approaches (reviewed in Wilson and Sober 1994). What can we gain by revisiting them using a new methodological paradigm? The agent-based approach offers several important advantages, all stemming from the fact that necessary assumptions concern the traits and behaviors of individuals rather than the global patterns that arise through their interactions. This makes it easier to evaluate the appropriateness of the assumptions and to adjust them to reflect the real world. It also means that the simplifying assumptions 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, which in turn can affect reproductive rates and thereby change emigration rates, which in turn feed back onto population structure. Such interactions may explain some of the differences between our conclusions and those of previous modeling studies.

Gilpin (1975) developed a model of predators and prey based on differential equations that is similar in spirit to our model of feeding restraint. Predators that hunted more efficiently out-competed less efficient hunters within the same patch, but were prone to over-exploiting local prey populations, leading to the local extinction of both predators and prey. Under some parameter settings between-group selection overwhelmed within-group selection, leading to the evolution of less efficient hunting (analogous to our feeding restraint). In particular, less efficient hunting was favored by small population size per patch, low migration between patches, and rapid extinction of a patch once

invaded. These parameters correspond to small patch width, large gap width, and low intrinsic rate of plant growth, respectively, in our model.

In an influential review, Maynard Smith (1976) re-analyzed Gilpin's rather complex model in simpler terms that apply in general to group selection models based on the differential extinction and colonization of patches. He concluded that whether altruism evolves depends on a single variable, M = the average number of selfish dispersers to leave a patch before it goes extinct and successfully colonize a patch not already containing selfish individuals. When $M > 1$ selfishness spreads, and when $M < 1$ altruism is favored. With a few adjustments (e.g., treating the abandonment of a patch as a local extinction), this analysis also describes the dynamics of our model.

Maynard Smith (1976:281) was cautious in evaluating the implications of these results for nature, commenting only that, "It is hard to say how often the condition $M < 1$ will hold in nature." Other authors have been less circumspect, however. According to Grafen (1984), "The final consensus on these models was that the conditions for A1 [altruism] to be successful were too stringent to be realistic." Dugatkin and Reeve (1994) express the same opinion regarding patch extinction-recolonization models. In his recent textbook, Ridley (1996) echoes this sentiment and extends his conclusion to all models of group selection. Regarding the condition $M < 1$, he asserts that, "This number is so small that we can expect selfish individual adaptations to prevail in nature. Group selection, we conclude, is a weak force." Surprisingly, none of these authors provide or cite evidence to support their conclusions. Our results suggest they may be premature even if limited to patch extinction-recolonization models. In a plausible ecological and behavioral setting, the requirements for the evolution of cooperation through between-group selection did not appear to be unrealistically stringent in any obvious way.

Other agent-based studies have concluded that even without an imposed group structure, including a spatial dimension can strongly affect the outcome of various forms of social and ecological interaction (e.g., Nowak et al. 1994; Colegrave 1997; Wilson 1998). In particular, localized interactions can facilitate the evolution of cooperation through reciprocal altruism (Ferriere and Michod 1996; Nakamura et al. 1997). However, we are not aware of previous studies showing that food distribution alone can generate sufficient population structure to permit group-beneficial traits to evolve, even in the absence of reciprocal altruism and kin selection. Interestingly, D. S. Wilson (1975:145) anticipated this result in an early formulation of trait group selection, in which he concluded that "...spatial heterogeneity, by partitioning the deme [population] spatially, may be expected to enforce trait-groups and enhance group selection."

Our preliminary work with this model has shown that groups emerging through the behavior of individual agents in patchy environments are sufficient to drive the evolution of group-beneficial traits, even in the absence of kin selection. 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 may not be typical in nature. In future studies we plan to explore the sensitivity of our results to various parameters and assumptions, as well as to extend the model in new directions.

The agent-based approach to modeling multilevel selection may prove useful for modeling real systems as well as exploring general principles. In particular, our model of feeding restraint may have applications in ecology, because patchy resource distribution and logistic growth of food resources are both ubiquitous in nature (Ricklefs 1990). These factors could conceivably generate strong enough between-group selection to produce observable levels of feeding restraint in real organisms. Recent empirical studies provide some support for this suggestion (e.g., Frank 1996; Hemptinne and Dixon 1997; Miralles et al. 1997). Further use of agent-based models may help to both guide and interpret the results of such empirical research. Similar models may also prove useful in helping us to understand the ecological and demographic conditions leading to sustainable resource management in small-scale human societies (e.g., Lansing and Kremer 1993; Lansing this volume) and the failures of sustainability that plague our planet today. Indeed, the global collapse of food resources in our model is closely analogous to the current global crash in fish populations as a result of unrestrained "feeding" by competing fishing fleets (Roberts 1997; McGinn 1998). Agent-based models may prove useful in both the research and public education needed to avert such tragedies of the commons in the future.

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