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Simple Models of Assortment through environmental feedback

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Abstract

Social evolution depends critically on assortment, or segregation versus mixing, between cooperators and non-cooperators in interacting groups. Altruistic traits, which reduce the absolute fitness of their bearers, cannot be selected for without positive assortment (above-random segregation of altruists from non-altruists). The question of how positive assortment can arise has been controversial, but most evolutionary biologists believe that common descent is the only effective general mechanism. Here I investigate another recently proposed mechanism for generating non-random assortment, termed “environmental feedback”. This requires only that two forms of a trait affect the quality of the local environment differently in such a way that all individuals are more likely to leave lower quality locales. Experiments with simple computational models confirm that environmental feedback generates significant levels of genetic similarity among non-kin within locales. The mechanism is fairly general, and can under some conditions produce levels of genetic similarity comparable to those resulting from close genealogical relationship. Environmental feedback can also generate the negative assortment necessary for the evolution of ‘spiteful’ traits. Environmental feedback is expected to create positive frequency-dependent selection, and thus to favor any social trait that becomes common in the population. Results from this stylized model suggest that environmental feedback could be important in the evolution of both cooperation and spite, within as well as between species.

Introduction

Assortment, or the degree of segregation of different types of individuals into different groups, plays a central role in social evolution. Here I consider the context of “trait groups”, or sets of individuals with mutual effects on each other’s fitness [16]. Altruistic traits that reduce the direct fitness of their bearer but increase the fitness of recipients of the act are selectively favored only under positive assortment, or above-random segregation of altruists and non-altruists into different trait groups. In contrast, spiteful traits, which reduce the fitness of both the actor and the recipient, can spread only under negative assortment, or excess mixing of types (here spiteful and non-spiteful types) [5].

Different mathematical frameworks for studying social evolution use different terminology, but all agree on the central role of assortment. In the framework of inclusive fitness theory [4], social evolution is critically sensitive to genetic similarity (or relatedness) between actors and the recipients of acts affecting fitness. In the mathematically equivalent framework of multilevel selection theory [11], the partitioning of genetic variation into within- and between-group components plays a similar role. These two frameworks (which can be inter-converted [6, 14, 15,] both agree that outcomes of social evolution are critically sensitive to assortment [9]. When individuals of the same type are concentrated together within the same trait groups (positive assortment), variance between groups is increased at the expense of variance within groups, and individuals are on average more genetically similar to other members of their trait group than to the population at large (i.e., relatedness within groups is high). Negative assortment leads to low variance between groups, and low genetic similarity of actors to recipients (low relatedness within trait groups).

The question of what mechanisms can generate non-random assortment for social traits has been controversial. Although W. D. Hamilton focused on the mechanism of genealogy or

common descent in his early work [4], he later took the position that, “Kinship should be considered just one way of getting positive regression of genotype [positive relatedness]... Thus the inclusive fitness concept is more general than ‘kin selection’.” [6]. However, most subsequent authors have concluded that, “other reasons for genetic similarity between neighbors seem likely to be unimportant” [7], and that, “The only plausible cause of genetic similarity among group members is common ancestry.” [2].

Based on an agent-based ecological model [10], it has recently been claimed that a relatively general mechanism, termed “environmental feedback”, can generate either positive or negative assortment in the absence of common descent, individual recognition, memory, or other special cognitive abilities. This mechanism requires only that a social trait alters the quality of the local environment in some way, and that all individuals are more likely to leave lower quality environments. In this paper I investigate a much simpler representation of the same process. I find that the necessary conditions for environmental feedback are few and rather general, and that higher levels of non-random assortment than reported previously [10] can arise under biologically plausible conditions.

The model

To capture the dynamics of environmental feedback in the simplest possible agent-based model, I assumed individuals were of two types, termed Cooperators and Defectors (non-cooperators), and that the environment consisted of discrete patches or locales. I used a non-spatial or “island” model of migration [8], in which all patches were equally accessible from one another. I assumed that the trait in question affected the quality of the local patch in some unspecified way, such that the set of individuals occupying a given patch constituted a trait group. The only parameters of the model were the number of patches (n), the total number of individuals ($N = (\sum c + \sum d)$), and the ratio of cooperators to defectors in the total population ($\sum c / \sum d$). The dynamics of the model were very simple: they consisted only of migration, and all individuals followed the same movement rule. Individuals could leave the patch they currently occupied and enter another patch, chosen with equal probability from all patches. The rate at which all individuals left any given patch was proportional to its relative abundance of defectors versus cooperators. This reflected the assumption that all individuals were more likely to leave lower-quality patches, and that group composition affected patch quality. I considered two kinds of cooperative traits: those that benefit all members of a trait group including the actor (“whole-group traits”), and those that benefit other individuals but not the actor (“other-only traits”). Both types of social traits are common in both theoretical and empirical studies [9]. The rate of emigration for whole-group traits was determined by the proportion of defectors in the patch as a whole, while for other-only traits it was determined by the proportion of defectors among the other group members, excluding the actor. This stylized model included no reproduction, death or selection, and the cooperative trait was represented only implicitly through its effects on emigration rates.

I implemented this conceptual model in an agent-based computer program. At the start of a run each individual was randomly assigned to one patch chosen with uniform probability. The simulation consisted of a single step iterated many times: A random individual was chosen with uniform probability, and left its current patch with probability p . For whole-group traits, this probability of emigration was equal to the proportion of defectors in the whole patch, including the potential migrator, while for other-only traits the probability of emigration was equal to the proportion of defectors among the other patch occupants, excluding the potential migrator.

Individuals that left their patch moved to a new patch chosen with uniform probability. (Thus they returned to their original patch with probability $1/n$, where n = number of patches). Because the number of patches had very little effect on the outcome, all results reported below are based on runs with $n = 100$ patches.

Quantifying assortment

I followed Pepper, 2000 [9] in measuring assortment in terms of the deviation of genetic similarity (r) within groups from the level expected under random mixing of cooperators and defectors, where r is defined as the regression coefficient of recipient genotype on actor genotype [5]. I defined the assortment index (r_a) as

$$r_a = r - r_s, \quad (1)$$

where r_a is the “excess” genetic similarity between actors and recipients caused by non-random assortment, r is total observed genetic similarity, and r_s is the genetic similarity expected if cooperators and defectors are distributed randomly among groups, i.e., if the composition of groups represents unbiased sampling from the population [9]. Positive values of r_a indicate excess segregation of cooperators from defectors, while negative values indicate excess mixing of the two types within groups.

To calculate a regression coefficient involving just two types of individuals, one need only assume that all cooperators have one genotypic value and all defectors have another (e.g., 1 and 0 respectively). Because r is calculated between actors and recipients, it is important to be explicit about who is included among the recipients of a trait. For whole-group traits the recipients of the act include the actor, while for other-only traits they do not. Because relatedness to self is always 1, r is higher for whole-group than for other-only traits. Expected levels of relatedness under random assortment are given by:

$$r_s = \frac{-1}{N-1} \quad (2)$$

for other-only traits, and

$$r_s = \frac{g-1}{N-1} \quad (3)$$

for whole-group traits, where g = number of groups (occupied patches), and N = total population size [9]. When groups are discrete and non-overlapping, eqn. (3) can be rewritten as

$$r_s = \frac{N - \bar{n}}{\bar{n}(N-1)}, \quad (4)$$

where \bar{n} = average group size, so that under infinite population size $r_s = 0$ for other-only traits, and $1/\bar{n}$ for whole-group traits [9].

Experiments

Experiment 1: Whole-group social trait

Whole-group traits affected patch quality for all group members including the actor. The probability of emigrating was therefore $p = d / (c+d)$, where c and d are the number of cooperators and defectors in the patch including the chosen ‘actor’ individual. Simulations started with random assortment, but assortment fairly quickly stabilized (with random fluctuations) around a non-zero value (Fig. 1).

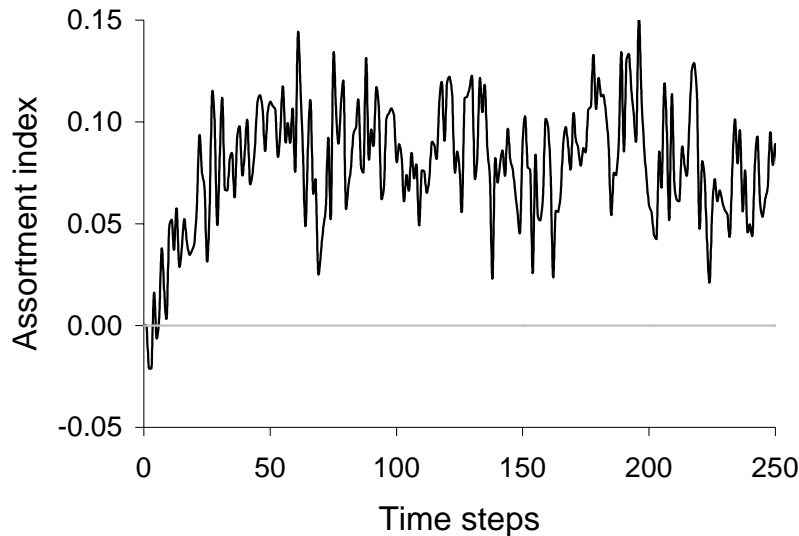


Figure 1. Assortment as a function of time, starting with a random distribution of individuals into patches. One run is shown, using a density of 1 individual per patch on average, and equal numbers of cooperators and defectors (50 each).

The magnitude of departure from random assortment depended on population density. In runs with many individuals per patch, assortment was close to zero, or random. At lower population density the stationary level of assortment could be either positive or negative, depending on the relative proportions of cooperators and defectors in the population (Fig. 2).

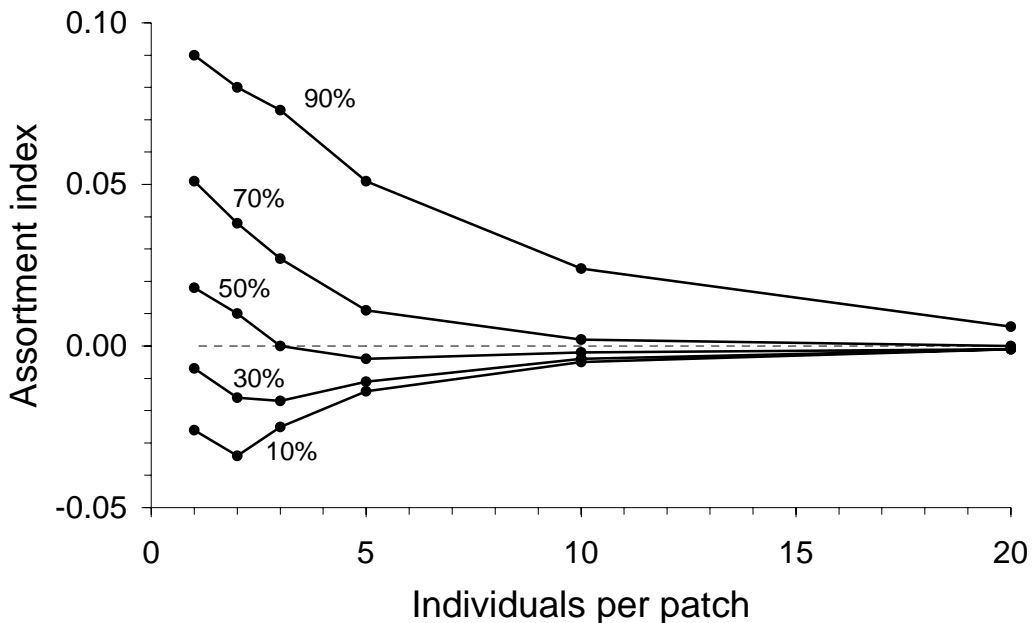


Figure 2. Average levels of assortment for different proportions of cooperators in the population. The number next to each line indicates the proportion of cooperators. Each data point shows the mean over 3 runs with different random number seeds. Each run was represented as the average assortment value over 10,000 time steps

It may seem quite counter-intuitive that within each patch all individuals followed exactly the same movement rule, yet the global population ended up assorting non-randomly, which would seem to require behavioral differences between Cooperators and Defectors. This is an instance of the statistical phenomenon known as Simpson's paradox [12, 13]. When individual behavior is influenced by conditions that vary among groups, the average behavior of two types of individual can be quite different even though both types behave exactly the same way within each group. Because most cooperators were in groups with a low proportion of defectors, they tended to migrate at low rates on average, while most defectors were in groups with a high proportion of defectors, and so they migrated at a higher average rate.

Why did the magnitude of non-random assortment fall as population density increased? The dynamics of environmental feedback were driven by differences among patches in the local proportion of defectors. As population density increased, so did average size of the trait groups. As a result, the variance among trait groups in their proportion of defectors fell according to the central limit theorem, removing the variance among patches that drove environmental feedback.

Another striking question arising from Fig. 2 is: how did the same migration dynamics create negative assortment when defectors were more common, but positive assortment when cooperators were more common? I hypothesized that this resulted because migration by the two types created opposing influences on assortment. All individuals tended to leave patches

containing mostly defectors and move to other patches with more typical group composition (lower proportion of defectors). When cooperators did this, it led to excess segregation of the two types, or *positive* assortment. When defectors did the same thing, it led to excess mixing of the two types, or *negative* assortment. Which influence dominated the outcome depended on which type had more migration opportunities. In the foregoing experiment individuals of each type had equal opportunities to move, so that when one type was more common, migration opportunities for that type were also more common. Thus an excess of cooperators led to positive assortment, and an excess of defectors led to negative assortment. To test this hypothesis, I conducted an experiment in which the proportions of the two types were held constant at 50%, but the probability of individuals being chosen for potential migration was varied as a function of their type. As predicted, assortment became increasingly positive as cooperators were selected more often, and increasingly negative as defectors were selected more often (Fig. 3).

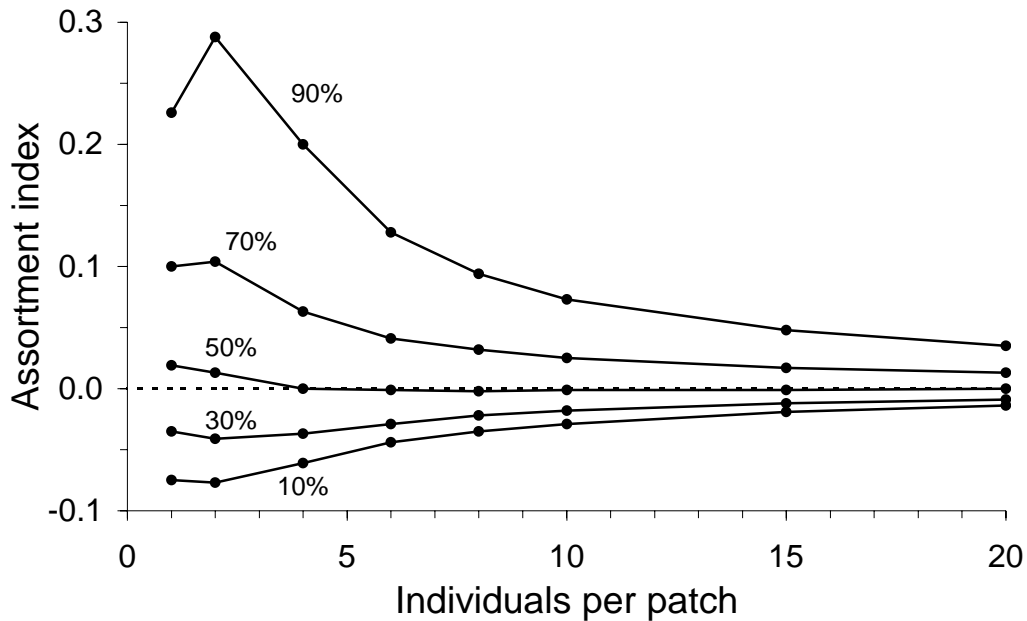


Figure 3. Average levels of assortment under varying relative mobility of cooperators versus defectors. All runs used 50% cooperators and a density of 1 individual per patch. Numbers next to each line indicate the proportion of migration opportunities that went to cooperators. Each data point shows the mean of 10 runs, each represented by the average assortment over 10,000 time steps.

Experiment 2: Other-only social trait

Other-only traits affect patch quality for other group members but not the actor. To represent this situation, the probability of emigrating from the i -th patch was $p = d_i / (c_i + d_i - 1)$ for cooperators, and $p = (d_i - 1) / (c_i + d_i - 1)$ for defectors, where c_i and d_i are the number of cooperators and defectors in patch i . Because this expression was undefined for solitary individuals, they instead moved with a probability given by the global frequency of defectors: $p = \Sigma d / (\Sigma c + \Sigma d)$.

The magnitude of assortment (either positive or negative) generated by environmental feedback was substantially higher for other-only traits than for whole-group traits (Fig. 4). This is consistent with the fact that non-random assortment generated by any mechanism has more scope to affect relatedness for other-only than for whole-group traits [9].

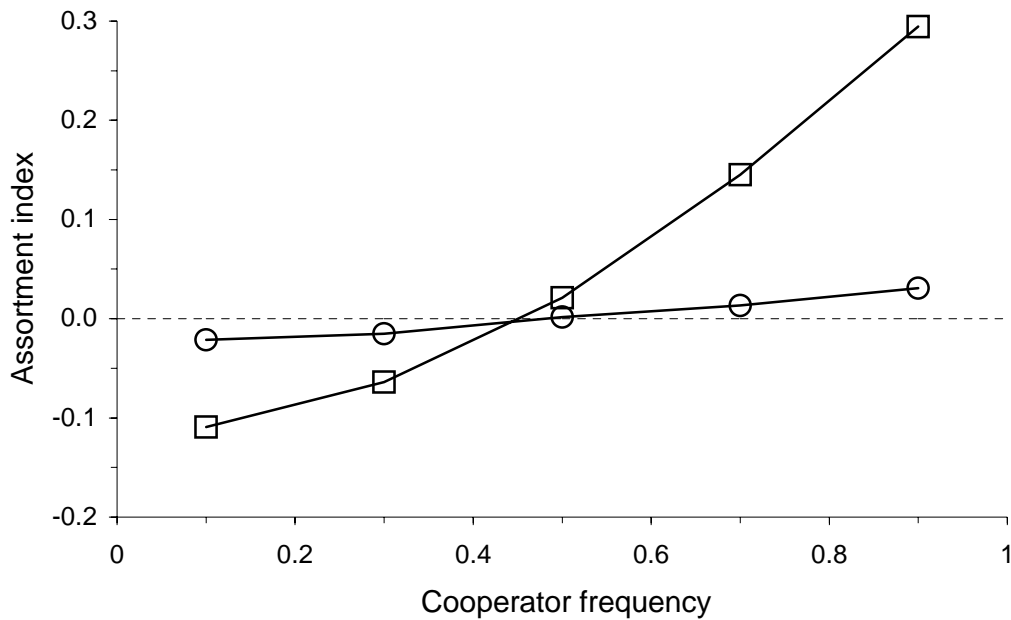


Figure 4. Comparison of average levels of assortment resulting from the whole-group movement pattern (circles) versus the other-only movement pattern (squares). Each data point shows the mean over 10 runs, each with a population density of 1 individual per patch. The assortment index is based on average relatedness of individuals to their whole group.

Experiment 3: Limited patch capacity

In the next experiment I considered the effect on assortment of limited patch capacity, where migrating individuals could not join a patch that was already full. All patches had the

same maximum occupancy m . The rate of immigration into a patch was unaffected by the number of individuals occupying it until it reached full capacity, $c_i + d_i = m$ (where c_i and d_i are the number of cooperators and defectors, respectively in patch i) at which point no further immigration was possible until after an individual left the patch. Thus migrating individuals entered a patch randomly chosen from those that were not full.

In this modified version of the model, as long as $\sum c_i \geq m$, so that there were enough cooperators in the population to completely fill a patch, it was inevitable that given sufficient time a patch would eventually become completely filled with cooperators. Those individuals would never leave, and that patch would no longer participate in the migration dynamics. This would be repeated in successive patches until all cooperators were in pure-cooperator patches (or more precisely, until all but $(\sum c_i \text{ modulus } m)$ cooperators were in pure-cooperator patches). After a sufficiently long time, the population would approach maximum positive assortment with $r_a = r \approx 1$. This outcome is not realistic though, because it relies on perfect adherence to the movement rules, with no stochastic events. I therefore added some stochastic noise in the form of a probability u that the selected individual moved regardless of its current group composition. As expected, the resulting levels of assortment were quite sensitive to u . With low values of u , positive assortment was substantially stronger with more limited patch capacity (lower m) (Fig. 5).

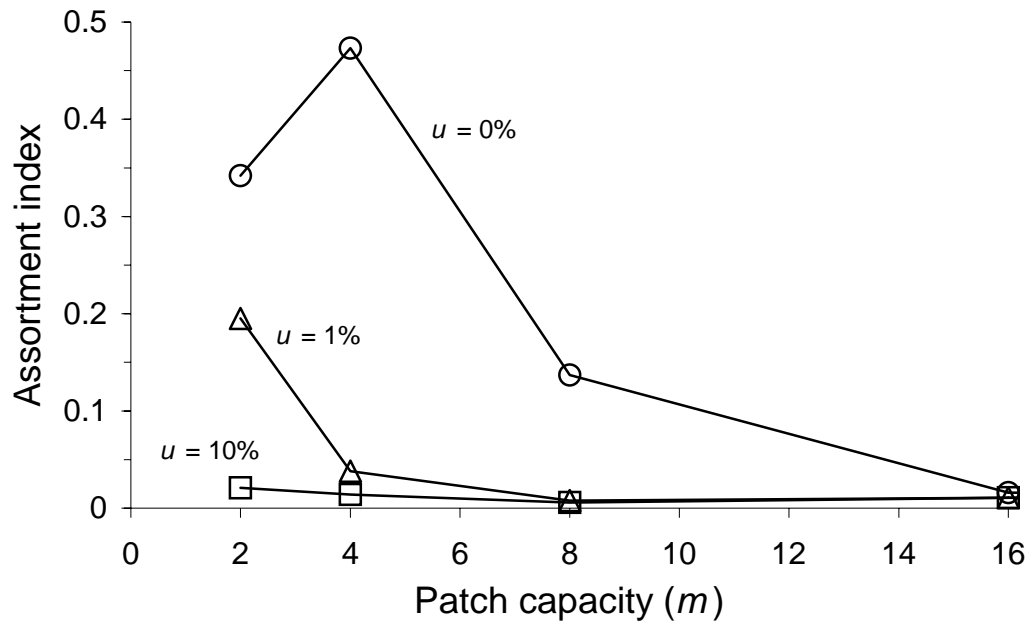


Figure 5. Effect of limited patch capacity on levels of assortment. Labels indicate the frequency of unconditional moves (u). All runs used 50% cooperators and a density of 1 individual per patch. Each data point shows the mean of 10 runs, with each run represented as the average assortment value over 10,000 time steps

Discussion

The results presented here confirm that environmental feedback can be an effective source of both positive and negative assortment, and that the process is independent of the details of the earlier ecological model [10]. Thus Hamilton was apparently correct, at least in principle, in claiming that relatedness can arise through mechanisms other than common ancestry [6]. These results also show that much higher levels of relatedness than reported previously [10] can arise through environmental feedback under any of several plausible assumptions, including traits that affect the fitness of other group members but not the actor (Fig. 4), and habitat patches that can hold only a limited number of individuals (Fig. 5).

Relatedness through common descent is known to have important effects on the evolution of social behavior for values of r in the range of 0.25 – 0.5 (e.g., for half or full sibs). The current results show that comparable levels of relatedness can arise without any role for common descent (Figs 4 & 5).

Exactly how does environmental feedback generate non-random assortment? As discussed above, the movements of cooperators tend to generate positive assortment, while those of defectors tend to generate negative assortment, with the outcome depending on the balance between these two processes. All else being equal, the more common type dominates the resulting assortment pattern. Thus when cooperators are common, environmental feedback generates positive assortment, which in turn favors the spread of cooperation. In contrast, when defectors are common environmental feedback generates negative assortment, which favors the spread of defection. Such positive frequency-dependence is expected to create a threshold effect for new mutations with either positive or negative effects on the local environment.

Consequently, environmental feedback will suppress novel social traits while they are rare, but if they reach high frequency through local stochastic events, it will stabilize them against invasion.

A mathematical analysis of the dynamics of environmental feedback has shown that it is critically dependent on the indivisibility of the individual (E. Smith, pers. comm.). Because this discreteness is central, the phenomenon cannot be easily represented or studied using any model of continuous populations. A paper describing these results is in preparation.

How biologically important is the concept of environmental feedback? An abstract model such as I present here can never demonstrate that a phenomenon is important in nature, but it can show, and has shown, that the mechanism is feasible and cannot be ruled out *a priori* as a biologically significant mechanism influencing social evolution, as has been done in the past.

The current model has been verified both by independently replicating the computer program and its main results, and through the numerical solution of a mathematical version of the same conceptual model (M. Lachmann, pers. comm.). A more complex spatial model has also demonstrated that environmental feedback can operate under more ecologically realistic assumptions [10]. Clearly though, the spatial scale of fitness effects is critical to the strength of this phenomenon. If the quality of the local environment is affected by many individuals (in the 10's or more), then environmental feedback may have weak and possibly negligible effects.

The potential scope of the model is rather broad. Local environmental quality can be interpreted either in terms of ecological factors, such as effects on the food supply [10] or production of toxic waste products or allelopathic chemicals, or in terms of behavioral factors, such as alarm calling or interference competition. Moreover, the model may apply to traits that affect mortality rather than movement. Low-quality local environments would plausibly cause higher local mortality rates, and re-labeling departures from patches as deaths rather than migrations would be compatible with the results reported here. This idea is supported by

preliminary studies of environmental feedback involving cooperative traits, such as alarm calling, that effect mortality rather than migration [10]

Because a wide range of social traits are likely to influence either the movements or survival of other individuals, environmental feedback could potential come into play in many contexts.

The mechanism studied here is not entirely unprecedented. Other workers have enquired into how cooperation among non-kin in a mobile population can persist in the face of cheating. A previous model by Aktipis [1] also showed that contingent movement can facilitate the evolution of cooperation. That model was based on a ‘prisoner’s dilemma’ payoff matrix for paired interactions, and assumed that individual movements were contingent on which of two facultative strategies was employed by the partner during the previous time step. The current study extends these results by showing that contingent movement can strongly favor cooperation even when interactions are not paired, and when the behavior or trait in question is obligate rather than facultative. Moreover, the current model emphasizes that generating non-random assortment does not require that the behaviors of other individuals are directly perceived or responded to. Like the current study, Hamilton & Taborsky [3], considered the situation in which decisions to change group membership are dependent on anonymous social experience. In a game-theoretic context based on paired interactions within larger groups, they concluded that a win-stay, lose-shift movement rule could favor the establishment of widespread cooperation in a population. This mechanism is highly similar to the ‘environmental feedback’ of Pepper & Smuts [10], and of the current model. Both of the above-mentioned papers also noted the key role of positive assortment in promoting cooperation in their models.

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