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Evolution of Altruism in Stepping-Stone Populations with Overlapping Generations

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We study the evolution of altruism in one- and two-dimensional stepping-stone populations with discrete overlapping generations. We find that increasing survival probability facilitates the evolution of altruism, in agreement with recent results for a patch-structured population. We allow the altruistic behaviour to affect either fecundity or survival probability. In the first case, altruism is favoured compared to a randomly interacting population, but in the second case, altruism is less likely to evolve. We consider the iterated prisoner's dilemma as a description of an altruistic interaction and compare our results with recent simulations of lattice populations.   © 2001 Elsevier Science

Key Words: altruism; competition; inclusive fitness; prisoner's dilemma; overlapping generations; stepping-stone population.

1. INTRODUCTION

The evolution of altruism in spatially structured populations has a long history, repeatedly examined in the literature. Cooperative behaviours have been documented in an enormous variety of biological systems (e.g., Dugatkin, 1997) and are thought to have been essential to the major transitions in evolution—from the incorporation of organelles into cells and the development of multicellularity to the creation of social communities (Maynard Smith and Szathmáry, 1995). At the centre of the discussion is the tension between cooperation and competition. A key question is whether limited dispersal, creating what Hamilton (1964) called a viscous population, promotes or inhibits altruistic behaviour compared with a randomly mixing population. We consider a model in which altruists assist all the individuals in their interaction group and dispersal is limited so that

nearby individuals tend to be close relatives. Most of the benefit of altruism goes to relatives and therefore benefits the altruism gene. The benefit also leads to increased competition among relatives and thus inhibits the evolution of altruism. We use Hamilton's (1964) powerful inclusive fitness method to analyse this problem. This method determines the evolutionary fate of a behaviour by adding up the effects of the altruistic act on the fitness of all individuals in the population, weighted by the relatedness of the individual to the actor.

Hamilton's (1964) rule says that altruistic behaviour, which incurs cost c to the actor and bestows benefit b to the recipient, should be selectively favoured if $br > c$. This rule has been widely quoted and used, partly because it is mathematically simple, and partly because it has a strong intuitive character. However for the rule to hold, the fitness effects b and c and the relatedness r must be properly measured. Much work on inclusive fitness over the past 35 years has focused on the question of how these quantities should be calculated (Michod and Hamilton, 1980; Wilson *et al.*, 1992; Taylor, 1992a,b). In

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particular it has been noted that b and c must represent long-term realized fitness effects, rather than immediate consequences of the altruistic act. Much recent work has focused on structured populations and the central idea here is that the structure affects both the relatedness and the fitness effects; indeed, the structure holds the key for the correct measurement of both of these quantities.

A surprisingly simple result is obtained for some simple population structures with discrete nonoverlapping generations. The benefits of altruism exactly balance the changes in competitive effect and the inclusive fitness effect of the actor is simply the net direct effect of its behaviour on its own fitness (Wilson *et al.*, 1992; Taylor, 1992a,b). Thus, altruistic behaviour is selected exactly when it would be favoured in a randomly mixing population. Remarkably, this holds independently of the dispersal rate in these populations. The same result has also been found in finite deme-structured populations (Rousset and Billiard, 2000; Taylor *et al.*, 2000). Simulation studies of altruism in lattice populations have shown significant departures from this exact balance, often favouring the evolution of altruism. These simulations and the models of Wilson *et al.* (1992) and Taylor (1992a,b) differ in a variety of important ways. Instead of nonoverlapping generations and constant population densities, these calculations allow generations to overlap (Nowak *et al.*, 1994; Nakamaru *et al.*, 1997, 1998) or allow variable population densities by permitting some sites to remain vacant (Mitteldorf and Wilson, 2000). It's not clear from these studies whether the spatial structure of the population is the key ingredient which facilitates altruism or whether other features (e.g., precise details of the altruistic interaction, population density, generational overlap) are responsible. Variable population density may favour altruism, but we do not consider this in our model (Kelly, 1994; Mitteldorf and Wilson, 2000).

Recently it was shown that overlapping generations promotes the evolution of altruism in a patch-structured population (Taylor and Irwin, 2000). Furthermore, in this population structure there is a difference between altruistic acts which affect fecundity and those which affect survival. With the former, altruism is more strongly favoured and with the latter it is less strongly favoured than in a randomly mixing population. This difference persists throughout the entire range of survival probabilities. Here we present a model of altruism in one- and two-dimensional stepping-stone populations which extends the patch model of Taylor and Irwin (2000), and we obtain both of their results: overlapping generations promote altruism in stepping-stone populations, with a similar difference between altruistic gifts of fecundity and

survival. Finally, we use the iterated prisoner's dilemma as an alternative model of altruistic interactions and compare our results with recent simulations.

2. THE MODEL

We consider populations in a one-dimensional lattice with two nearest-neighbour sites and a two-dimensional lattice with four nearest-neighbours. The lattice is infinite with one asexually reproducing haploid individual per site. Prior to reproduction, nearest-neighbours interact with the possibility of altruistic behaviour. Each individual produces a large number of offspring which disperse to one of the neighbouring sites with total probability d. Dispersers incur a cost and only a proportion $1-k$ arrive at a new site. The effects of d and k are combined into a single variable p_{j-i} the probability an offspring competing on site j was born on site i,

$$p_{j-i} = \begin{cases} \dfrac{1-d}{1-kd}, & i = j \\[2ex] \dfrac{d(1-k)}{N(1-kd)}, & i, j \text{ are nearest-neighbours; } N \text{ is} \\ & \text{the number of nearest-neighbors} \\[1ex] 0, & \text{otherwise.} \end{cases} \tag{1}$$

Thus, p_0 is the probability that an offspring is native. After reproduction, each adult survives and breeds again in the next generation with probability s. On a site in which the resident adult dies, the offspring, both native and immigrant, compete on an equal basis for the vacant spot. Offspring which do not win a site die and the cycle begins again. Our notation is summarized in Table I.

An altruistic act costs the actor and benefits its neighbours, affecting either fecundity or survival. For both fecundity and survival effects, an individual's fitness is its expected number of offspring which breed in the next generation plus its probability of breeding again. We will use Δw to measure fitness changes due to the altruistic behaviour. We denote by δ_i the direct effect of an altruist at any site j on the breeding individual at site $i+j$. In our fecundity model, δ_i is the multiplicative change in numbers of offspring and in our survival model δ_i is the multiplicative change in survival. In our stepping-stone population δ_0 is the effect on the actor, δ_1 the effect on each nearest-neighbour, and all other δ_i are zero. These effects δ_i are not changes in fitness but they alter the

TABLE I

Notation Used in the Main Altruism Model

d	Dispersal rate
δ_i	Effect of altruist at the origin on the fecundity or survival of an individual on site i
k	Dispersal cost; a fraction $1-k$ arrive at the new site
N	Number of neighbours
n_{ij}	Average number of offspring competing for site j who come from site i
$n_j = \sum_i n_{ij}$	Average number of offspring competing for site j
$p_{ij} = p_{j-i} = n_{ij}/n_j$	Probability an offspring competing for site j came from site i
$r_{ij} = r_{j-i}$	Equilibrium relatedness between an adult on site i and an adult at site j
s	The probability that an adult survives to breed in the next generation,
$w_i, \Delta w_i$	Fitness (and change in fitness due to the mutant) of an adult on site i

Note. In a homogeneous lattice, variables with two indices depend only on the separation between sites and are sometimes written to reflect this, e.g. $r_{j-i} = r_{ij}$. In two dimensions this is a vector difference and we index with these differences, e.g. $r_{0,\pm1} = r_{\pm1,0}$ is the relatedness of nearest-neighbours.

fitness of individuals by an amount which depends on dispersal and survival rate.

An inclusive fitness calculation adds up the fitness effects of a focal mutant weighted by the relatedness between the affected individual and the actor. We denote the relatedness between adults at sites i and j by r_{ij}. Our lattice is homogeneous so we often abbreviate this as r_{j-i} noting only the displacement between sites. Relatednesses for several pairs of nearby sites are computed using the lattice structure and stepping-stone dispersal pattern with no selection and this calculation is described in Appendix A. We assume that the costs and benefits are small (weak selection), so our inclusive fitness results are exact to first order in δ_i and will give reasonable approximations for small δ_i (Taylor, 1996). We assume dispersal at the ES dispersal rate which depends on survival rate (Appendix B).

In the following sections we find conditions on the δ_i which favour altruistic acts, considering first those which affect fecundity and then those which affect survival. Within each section we write a general expression for the inclusive fitness effect and find conditions in terms of the altruistic effects (δ_i) which select altruism in one- and two-dimensional stepping-stone populations. We then adapt our general results to another model of social interactions: the iterated prisoner's dilemma.

Fecundity Effects

We now analyse the effect of an altruistic mutant at site 0. The altruistic behaviour alters the fecundity of the mutant and individuals on neighbouring sites. Since there is some dispersal from sites ±1 to sites ±2, there will be an effect on the number of competing juveniles at sites ±2. Since some offspring born on sites ±3 will disperse to sites ±2, these offspring will experience a different amount of competition. Thus, the inclusive fitness effect includes fitness changes of individuals up to three steps away.

The inclusive fitness effect Δw_{IF} is (see Appendix C)

$$\Delta w_{IF} = (1-s)\left(\sum_i \delta_i r_i - \sum_{ijk} \delta_k p_{j-i} p_{j-k} r_i\right). \quad (2)$$

If $s = 0$, the relatedness recursion (A1) allows us to simplify (2), obtaining

$$\Delta w_{IF} = \delta_0 \left(r_0 - \sum_{ik} r_i p_k p_{k-i}\right) \quad (3)$$

(Taylor, 1992b). With nonoverlapping generations the inclusive fitness effect is independent of the effect of the mutant on other breeders ($\delta_i, i \neq 0$). This is a general result for any dispersal pattern or range of altruistic interactions on a lattice of arbitrary dimension.

One dimension. In a one-dimensional stepping-stone population the inclusive fitness effect (2) simplifies to

$$\Delta w_{IF} = r_0 \Delta w_0 + 2r_1 \Delta w_1 + 2r_2 \Delta w_2 + 2r_3 \Delta w_3, \quad (4)$$

where the net fitness effects on breeders at a distance i, Δw_i, are

$$\Delta w_0 = (1-s)(\delta_0(1-p_0^2-2p_1^2)-\delta_1(4p_0 p_1))$$
$$\Delta w_1 = (1-s)(-2\delta_0 p_0 p_1 + \delta_1(1-p_0^2-3p_1^2))$$
$$\Delta w_2 = -(1-s)(\delta_0 p_1^2 + 2\delta_1 p_0 p_1)$$
$$\Delta w_3 = -(1-s)\,\delta_1 p_1^2.$$

In the limit as $s \to 1$, the fitness effects approach 0 as expected.

The altruistic behaviour is favoured if $\Delta w_{IF} > 0$, which can be written as

$$2\delta_1 \left[\frac{r_1 - r_3 - p_0(4r_0 - 7r_1 + 4r_2 - r_3)}{2(r_0 - r_2 + p_0(3r_0 - 4r_1 + r_2))} \right] + \delta_0 > 0. \quad (5)$$

The quantity in square brackets is an altruism threshold: the cost–benefit ratio $-\delta_0/(N\delta_1)$ must be smaller than this, assuming $\delta_1 > 0$, for altruism to be favoured. Survival probability does not appear explicitly in this threshold, but is felt through the relatedness r_i.

Two dimensions. In two dimensions, the inclusive fitness effect involves terms from the six kinds of sites identified in Fig. 1,

$$\Delta w_{IF} = r_{0,0}\Delta w_{0,0} + 4r_{0,1}\Delta w_{0,1} + 4r_{1,1}\Delta w_{1,1} + 4r_{0,2}\Delta w_{0,2}$$
$$+ 8r_{1,2}\Delta w_{1,2} + 4r_{0,3}\Delta w_{0,3}, \quad (6)$$

where the net fitness effects on breeders at a distance i, Δw_i, are

$$\Delta w_{0,0} = (1-s)(\delta_0(1 - p_0^2 - 4p_1^2) - \delta_1(8p_0 p_1))$$
$$\Delta w_{0,1} = (1-s)(\delta_0(-2p_0 p_1) + \delta_1(1 - p_0^2 - 9p_1^2))$$
$$\Delta w_{1,1} = -2(1-s)(\delta_0(p_1^2) + \delta_1(2p_0 p_1))$$
$$\Delta w_{0,2} = -(1-s)(\delta_0(p_1^2) + \delta_1(2p_0 p_1))$$
$$\Delta w_{1,2} = -3(1-s)\,\delta_1 p_1^2$$
$$\Delta w_{0,3} = -(1-s)\,\delta_1 p_1^2.$$

The altruistic behaviour is favoured if $\Delta w_{IF} > 0$, which can be written as

$$4\delta_1 \left[\frac{\begin{array}{c} 7r_{0,1} - 6r_{1,2} - r_{0,3} - p_0(8r_{0,0} - 25r_{0,1} \\ + 16r_{1,1} + 8r_{0,2} - 6r_{1,2} - r_{0,3}) \end{array}}{\begin{array}{c} 4(3r_{0,0} - 2r_{1,1} - r_{0,2} \\ + p_0(5r_{0,0} - 8r_{0,1} + 2r_{1,1} + r_{>0,2})) \end{array}} \right] + \delta_0 > 0. \quad (7)$$

Survival Effects

Now we want the altruistic behaviour to have an effect on survival probability, not on fecundity. Assuming a nonzero survival probability ($s > 0$), the inclusive fitness effect of the mutant is (Appendix C)

$$\Delta w_{IF} = s \left(\sum_i r_i \delta_i - \sum_{ij} r_i \delta_j p_{j-i} \right). \quad (8)$$
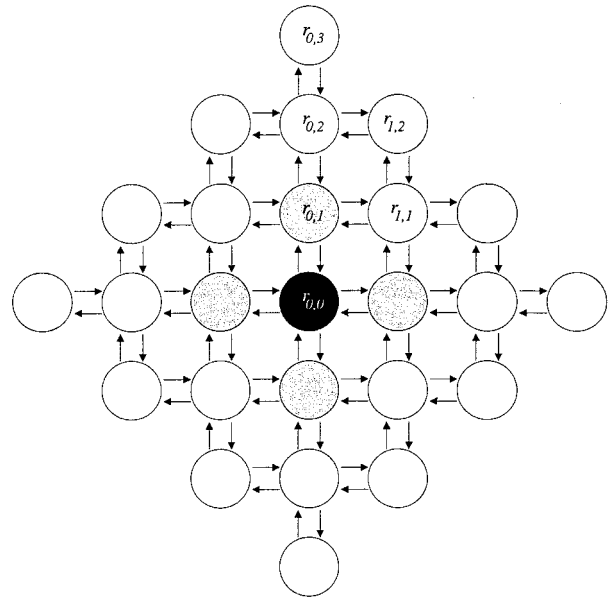

FIG. 1. Site classes on the two dimensional stepping-stone lattice labelled with relatedness to the centre (black) site. Shaded sites are in the interaction neighbourhood of an individual on the centre site.

One dimension. The inclusive fitness effect (8) in one dimension is

$$\Delta w_{IF} = \Delta w_0 + 2r_1 \Delta w_1 + 2r_2 \Delta w_2, \quad (9)$$

where the changes in fitness of the mutant and four nearest-neighbours are

$$\Delta w_0 = s(\delta_0(1 - p_0) - 2\delta_1 p_1)$$
$$\Delta w_1 = s(-\delta_0 p_1 + \delta_1(1 - p_0))$$
$$\Delta w_2 = -s\delta_1 p_1.$$

The altruistic act is favoured if

$$2\delta_1 \left[\frac{r_0 - 2r_1 + r_2}{2(r_1 - r_0)} \right] + \delta_0 > 0. \quad (10)$$

Two dimensions. The fitnesses of individuals on fewer sites are affected with survival effects in two dimensions compared to fecundity effects. Individuals two steps from the mutant are affected because of the change in survival of individuals one step away. The inclusive fitness effect is

$$\Delta w_{IF} = \Delta w_{0,0} + 4r_{0,1}\Delta w_{0,1} + 4r_{1,1}\Delta w_{1,1} + 4r_{0,2}\Delta w_{0,2}, \quad (11)$$
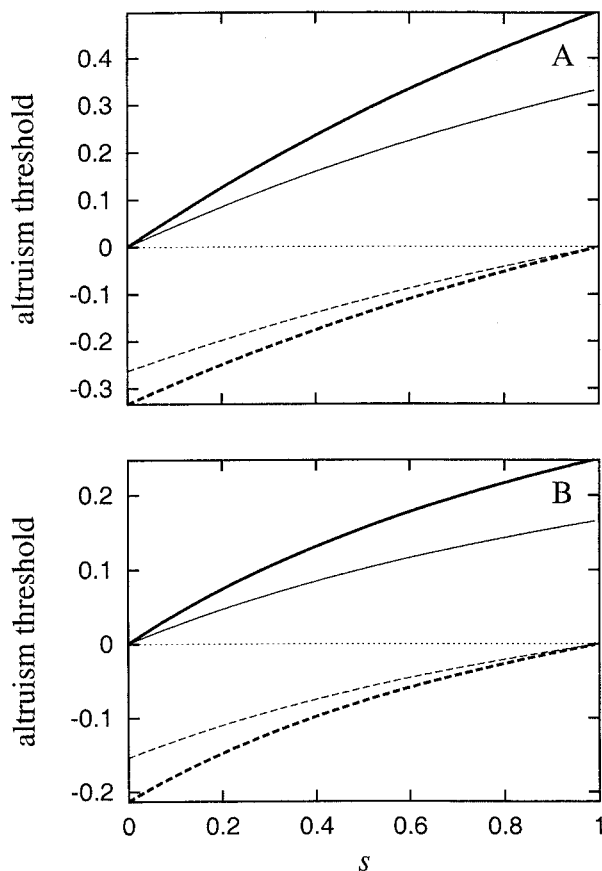
FIG. 2. Altruism threshold $-\delta_0/(N\delta_1)$ as a function of survival s. Results for fecundity (solid) and survival (dashed) effects in one (A) and two (B) dimensions. Thick lines are for zero-cost dispersal and thin lines for a small dispersal cost ($k = 0.2$). The horizontal dotted line is the altruism threshold for random-mixing populations or $s = 0$.

where the fitness changes (C9) are

$$\Delta w_{0,0} = s(\delta_0 - 4\delta_1 p_1 - \delta_0 p_0)$$

$$\Delta w_{0,1} = s(\delta_1 - \delta_0 p_1 - \delta_1 p_0)$$

$$\Delta w_{1,1} = -2s\delta_1 p_1$$

$$\Delta w_{0,2} = -s\delta_1 p_1.$$

The altruistic act is favoured if

$$4\delta_1 \left[\frac{r_{0,1} - 4r_{0,1} + 2r_{1,1} + r_{0,2}}{4(r_{0,1} - r_{0,0})} \right] + \delta_0 > 0. \quad (12)$$

Computational results. Figure 2 shows the altruism threshold $-\delta_0/(N\delta_1)$ as a function of survival s for one- ($N = 2$) and two-dimensional ($N = 4$) stepping-stone populations with both fecundity and survival effects. The horizontal line at 0 is the threshold for a randomly

interacting population; altruism is selected if the cost to the actor is in fact a direct benefit ($\delta_0 > 0$). With fecundity effects, the threshold increases with s from 0, allowing altruism to be favoured for increasingly large costs. With survival effects, the threshold also increases with increasing survival, but altruism is inhibited relative to a randomly interacting population and requires a large negative cost to overcome the benefit given to neighbours. In the limit as $s \to 1$, the threshold approaches 0. Adding a cost to dispersal (thin lines) pushes the threshold closer to that of a random-mixing population.

Iterated Prisoner's Dilemma

Our second example of social behaviour is the iterated prisoner's dilemma game (Trivers, 1971; Axelrod and Hamilton, 1981). A pair of individuals play a series of prisoner's dilemma games, each game followed by another with a constant probability w. We consider two pure strategies: tit for tat (TFT) and all defect (AD). If a player adopts TFT, it first cooperates and then repeats its partner's previous choice on subsequent interactions. AD players defect on each turn. The payoff matrix is shown in Table II. We are especially interested in the possibility of altruists invading a selfish population so we use mixed strategies characterized by the (initially small) probability of cooperative behaviour. A related approach varies costs and benefits as a function of a common "investment" parameter (Killingback *et al.*, 1999). We also note that although the iterated prisoner's dilemma is often used to describe complex organisms capable of long-term memory, the TFT and AD strategies are very simple, requiring very little sophisticated machinery.

Our inclusive fitness argument above can be adapted to this problem. The population-wide strategy is to use

TABLE II

Payoffs for the Iterated Prisoner's Dilemma Where TFT Is the Cooperative Strategy "Tit-for-Tat" and AD Is "Always Defect"

Actor	Partner	
	TFT	AD
TFT	$R/(1-w)$	$S + Pw/(1-w)$
AD	$T + Pw/(1-w)$	$P/(1-w)$

Note. The parameters T, R, P and S are the payoffs for the prisoner's dilemma and satisfy $T > R > P > S$. The probability of playing the prisoner's dilemma again with the same partner is w. We use $T = 5$, $R = 3$, $P = 1$, and $S = 0$ for numerical examples. If $w = 0$ the game reduces to the prisoner's dilemma.
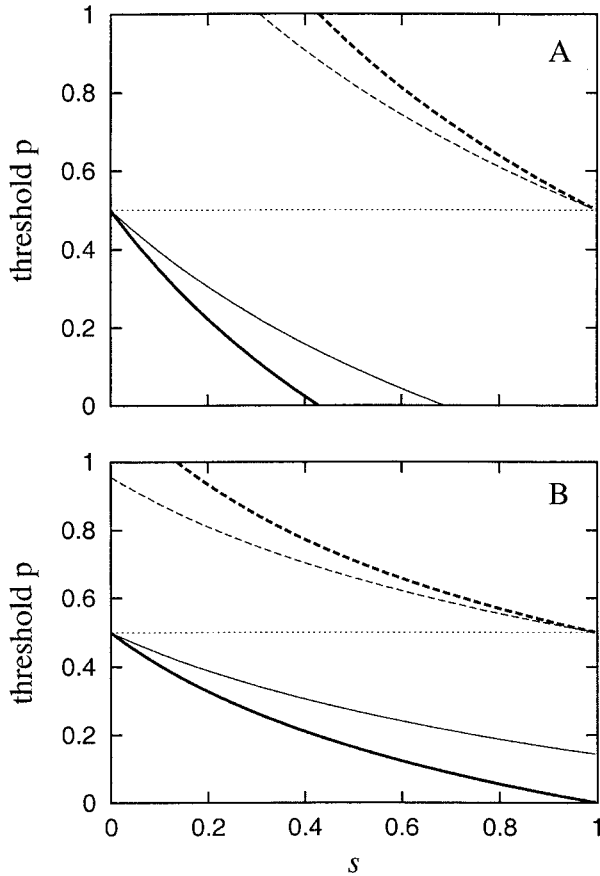
FIG. 3. Threshold values of TFT frequency p as a function of survival s for the iterated prisoner's dilemma game with a probability of re-encounter of $w = 3/5$ in one- (A) and two-dimensional (B) stepping-stone populations. The horizontal dotted line is the threshold for random-mixing populations (11) or $s = 0$ and other lines are as in Fig. 2. Increased frequency of TFT is favoured above the appropriate line. For no-cost dispersal in one dimension, TFT can't be invaded by AD for $s > \frac{3(P-S)}{2T-3P+S} = \frac{3}{7}$ with fecundity effects and AD can't be invaded by TFT for $s < \frac{9-13w}{1+3w} = \frac{3}{7}$ with survival effects.

TFT with probability p and AD with probability $1-p$ while a mutant uses a deviant strategy $p' = p + \delta$ (Appendix D). An actor's score (δ_0) is the average payoff it receives from interactions with all of its neighbours (not including itself). If the population-wide probability of playing TFT p is greater than a threshold (D5), then individuals with greater p' are selected. In randomly mixing populations (and populations with fecundity effects and nonoverlapping generations), the threshold (D5) takes a simpler form, independent of the size of the interaction neighbourhood,

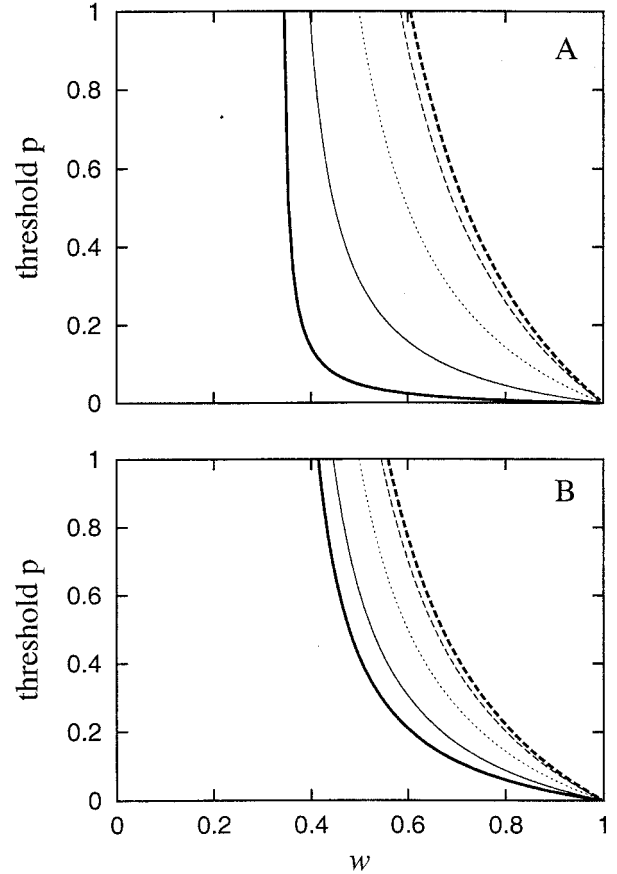$$p > \frac{1-w}{3w-1} \quad \text{and} \quad w > \frac{1}{3}, \tag{13}$$

FIG. 4. Threshold values of TFT frequency p as a function of the probability of re-encounter w for the iterated prisoner's dilemma game with survival probability of $s = 2/5$ in one- (A) and two-dimensional (B) stepping-stone populations. The dotted line is the threshold for randomly-mixing populations (13) or $s = 0$ and other lines are as in Fig. 2. Increased frequency of TFT is favoured above the appropriate line.

assuming the numerical values for the payoffs from Table II.

Threshold values of p are shown as a function of s and w in Fig. 3 and 4, respectively. Fecundity thresholds (solid lines) are below the random-mixing threshold (dotted line) and survival effects (dashed lines) are above the random-mixing threshold. Results for one (A) and two (B) dimensions are shown as well as zero-cost dispersal (thick lines) and dispersal with a small cost ($k = 0.2$, thin lines). Populations with p above the corresponding line favour increasing p, that is larger probabilities of playing TFT. Increasing dispersal cost k moves the thresholds closer to the random-mixing threshold (13), inhibiting altruism with fecundity effects and favouring it with survival effects. The pattern is the same as the previous altruism example: increasing s enlarges the area in parameter space where

altruism is favoured. A fecundity benefit favours altruism more in a stepping-stone-structured population than in an unstructured population, but survival benefits make it more difficult for altruism to evolve.

3. DISCUSSION

Much recent attention has been focused on the effect of the population structure on the evolution of a behavioural trait as this affects not only the relatedness between interactants, but also the realized fraction of potential fitness changes. Less attention has been paid to the question of what exactly is traded in a fitness interaction, for example, fecundity vs survival, but recent work has shown that this can have a nontrivial effect on the selective advantage of the trait. We find such an effect here; benefits of survival increase the level of competition among offspring and reduce realized fitness more than benefits of fecundity.

The population model used in the paper is a stepping-stone structure with overlapping generations, and our primary interest is the effect of the survival rate of breeders on the selective advantage of altruism. We have three main results. First, there is a distinction between benefits of fecundity and survival. Under the former, altruism is more strongly favoured and under the latter altruism is less strongly favoured than in a random-mixing population. Second, there is an effect of overlapping generations. For both types of benefit, an increased survival probability promotes altruism. Third, although the stepping-stone model describes a much richer population structure than a simple island population, our results here show the same qualitative results found in an island population (Taylor and Irwin, 2000). This indicates that the precise details of a population's spatial structure may not be very important.

We use an inclusive fitness model to measure the effects of altruism, and in order for this to predict the course of genetic evolution, we need to assume that selection is "weak," that is that altruistic behaviour has a small selective effect, which means that the costs and benefits are small (Taylor, 1996). There are several reasons for this assumption, but an important one is that our calculation of relatedness (Appendix A) is valid only when the allele causing the altruistic behaviour is neutral. The selective advantage of altruism that we calculate is then actually the rate at which the fitness of this allele increases as the effect of the allele is increased above zero.

When breeder survival s is zero and there is no overlap between generations we find that, independent of the dispersal rate of offspring, the altruism threshold occurs where the direct effect δ_0 of the altruist on itself is positive (3). This is expected in a random-mixing population, but the point is that it is also obtained when dispersal of offspring is only partial in both one- and two-dimensional stepping-stone populations. However, if breeder survival is positive, so that there is overlap between generations, a decrease in the dispersal rate does have an effect on the threshold level of altruism. But here there is a striking difference between gifts of fecundity and gifts of survival—relative to a random-mixing population, altruism is promoted under a fecundity benefit, but discouraged under a survival benefit. This is illustrated in Fig. 2. The difference between these two cases is easily understood. A survival benefit can be regarded as a special class of extra offspring that have the appropriate probability of winning a site, but that do not disperse, so they must remain on their home site. This increases the local competition among offspring and reduces the advantage of altruism.

The altruism threshold decreases as breeder survival s increases, favouring higher levels of altruistic behaviour. The analysis of this effect is complicated because the threshold depends on both s and the dispersal rate d, and the ES value of d itself increases with s (Irwin and Taylor, 2000). This latter relationship, the increase of dispersal rate with s, is an example of the phenomenon we are discussing—increased altruism with higher s.

Increasing the cost of dispersal has different effects on the altruism threshold for fecundity and survival effects (Fig. 2). First, with fecundity effects, increasing dispersal cost reduces the ES dispersal rate and inhibits altruism. This is because the increased cost reduces the proportion of immigrant offspring on a patch and thus increases competition among native offspring, resulting in a reduced benefit from the altruistic act. In contrast, a survival benefit increases competition on neighbouring sites. This affects the recipient's fitness only through its offspring which disperse to these sites. If dispersal cost is higher, a smaller fraction of offspring disperse, so the cost has less effect on the recipient.

Several recent studies of social behaviour in lattice-structured populations are worth comparing to our results. Nowak *et al.* (1994) simulated the prisoner's dilemma game on a lattice with fecundity effects and found that cooperators do better in models with overlapping instead of nonoverlapping generations. Nakamaru *et al.* (1997, 1998) studied the iterated

prisoner's dilemma on the lattice with both survival and fecundity effects. They simulated populations of TFT and AD strategists in one-and two-dimensional stepping-stone populations. There are several differences between their model and ours: they assume complete dispersal ($d = 1$, an empty site can only be colonized by a neighbour, and not the offspring of the dead individual) and they use continuously overlapping generations—only one individual on the lattice dies per time-step. Despite these differences they obtained similar results, including a difference between fecundity and survival effects, except that while we found altruism benefitting a neighbour's fecundity to be favoured, in their model the same effect could work in either direction. Nakamaru *et al.* (1997, 1998) attribute their results to population structure, but in our example of nonoverlapping generations the results are identical in both structured and randomly mixing populations. In their model with sufficiently long games (w near 1), TFT is able to invade a population of AD individuals. In one dimension their result was especially striking: their threshold in the survival effect and the fecundity effect could be shown as a vertical line at $w = 3/5$ and $w = -3/7$, respectively, in our Fig. 4A. One of their derivations of the vertical threshold used a "pair-edge" analysis of the velocity of the interface between clusters of TFT and AD (Ellner *et al.*, 1998, Nakamaru *et al.*, 1998). A critical assumption in this calculation is that adjacent sites on the interface can't die (and potentially be replaced with the other strategy) in the same generation. This is approximately true in our model only at high survival rates.

APPENDIX A

Relatedness Coefficients

A recursion for the relatedness between an adult at site i and at site j in the next generation (denoted by $'$) in terms of relatedness in the current generation is

$$r'_{ij} = \begin{cases} \sum\limits_{k,m} r_{km}\, \tilde{p}_{ki}\, \tilde{p}_{mj}, & i \neq j \\ 1, & i = j \end{cases} \quad \text{(A1)}$$

where the sums range over all sites and the probability that an offspring competing on site j was born on site i is

$$\tilde{p}_{ij} = \begin{cases} 1-d-\mu, & i = j \\ \dfrac{d}{N}, & i, j \text{ are nearest-neighbours; } N \text{ is the number of nearest-neighbors} \\ \mu, & i \text{ or } j = \infty \\ 0, & \text{otherwise.} \end{cases} \quad \text{(A2)}$$

In the absence of any long-range dispersal or mutation these equilibrium relatednesses are all 1 (in one and two dimensions only), so we introduce as a technical device an additional dispersal μ from the birth site to sites with unrelated individuals at infinity. Equations (A1) and (A2) do not include effects of overlapping generations or costly dispersal. These can be incorporated with a change of variables, replacing d and μ in (A2) with $\hat{d}$ and $\hat{\mu}$,

$$\hat{d} = d(1-s)\left(\frac{1-k}{1-k(d+\mu)}\right)$$
$$\hat{\mu} = \mu(1-s)\left(\frac{1-k}{1-k(d+\mu)}\right) \quad \text{(A3)}$$

(Irwin and Taylor, 2000). With these substitutions $\tilde{p}_{ij}$ becomes $\hat{p}_{ij}$ and its interpretation changes to the that probability site j is won by an offspring or adult survivor from site i.

The solution of recursion (12) in one dimension is described by Kimura and Weiss (1964) and for overlapping generations by Irwin and Taylor (2000). The coefficients r_j which we need are (dropping terms $O(\mu)$)

$$r_0 = 1$$
$$r_1 = 1 - \Phi$$
$$r_2 = 1 - 4\,\frac{\sqrt{1-\hat{d}}-(1-\hat{d})}{\hat{d}}\,\Phi \quad \text{(A4)}$$
$$r_3 = 1 - \frac{16(1-\hat{d})\left(1-\dfrac{\hat{d}}{2}-\sqrt{1-\hat{d}}\right)+\hat{d}^2}{\hat{d}^2}\,\Phi,$$

where

$$\Phi = \sqrt{\frac{2\hat{\mu}}{\hat{d}(1-\hat{d})}}\ .$$

In two dimensions, the equilibrium relatedness between adults separated by the vector (j, k) is

$$r_{j,k} = c(A_{j,k}(z_1) + (-1)^{j+k} A_{j,k}(z_2)), \qquad \text{(A5)}$$

where

$$A_{j,k}(z) = \frac{1}{(2\pi)^2 \hat{d}} \int_0^{2\pi} \int_0^{2\pi} \frac{\cos(j\theta_1)\cos(k\theta_2)}{z - \cos\theta_1 - \cos\theta_2} d\theta_1 d\theta_2$$

and

$$\begin{aligned} z_1 &= 2\left(1 + \frac{\hat{\mu}}{\hat{d}}\right) \\ z_2 &= 2\left(\frac{2 - \hat{\mu}}{\hat{d}} - 1\right) \end{aligned} \qquad \text{(A6)}$$

and the constant c is determined by $r_{0,0} = 1$ (Weiss and Kimura, 1965; Irwin and Taylor, 2000). Malécot (1975) uses a similar method to obtain results for both finite and infinite stepping-stone populations.

We evaluate the $A_{j,k}(z)$ in two ways. If $j = k$ then we can simplify the integrals using special functions eventually obtaining forms involving the complete elliptic integrals $K(\cdot)$ and $E(\cdot)$ (Abramowitz and Stegun, 1964),

$$A_{0,0}(z) = \frac{2}{\pi z} K\left(\frac{2}{z}\right) \qquad \text{(A7)}$$

$$A_{1,1}(z) = \frac{1}{\pi}\left(z - \frac{2}{z}\right) K\left(\frac{2}{z}\right) - \frac{z}{\pi} E\left(\frac{2}{z}\right). \qquad \text{(A8)}$$

Off-diagonal elements are evaluated with algebraic manipulations and trigonometric identities, obtaining

$$A_{0,1}(z) = -\frac{1}{2} + \frac{z}{2} A_{0,0}$$

$$A_{0,2}(z) = 2z A_{0,1} - 2A_{1,1} - A_{0,0}. \qquad \text{(A9)}$$

If the mutant affects the fecundity of the nearest-neighbours, two more relatedness coefficients are needed:

$$A_{1,2}(z) = z A_{1,1} - A_{0,1}$$

$$A_{0,3}(z) = 2z(A_{0,0} + A_{0,2}) - 2A_{1,2} - 5A_{0,1} - 2. \qquad \text{(A10)}$$

APPENDIX B

Dispersal

Evolutionarily stable dispersal rates can be calculated with an inclusive fitness argument analogous to the calculation in this paper. In fact, dispersal can be thought of as an altruistic act because dispersers incur a cost of dispersal and benefit offspring which remain behind by reducing competition among relatives. The results we need are below and derivations can be found in Irwin and Taylor (2000).

The ES dispersal rate in one dimension is

$$d^* = \frac{1}{2k} \frac{2(1 - \sqrt{1 - k(1-k)(1-s)}) - k(1-s)}{1 - \sqrt{1 - k(1-k)(1-s)} - k(1-s)} \qquad \text{(B1)}$$

and with no cost ($k = 0$),

$$d^* = \frac{3+s}{4}. \qquad \text{(B2)}$$

In two dimensions, the ES dispersal rate d^* is a solution of

$$2(2d^* sk - s - 1) K\left(\frac{(1-s)(1-k)d^*}{d^*(1 - s + k + sk) - 2}\right)$$

$$+ \pi(2 - d^*(1 - s + k + sk)) = 0, \qquad \text{(B3)}$$

where $K(\cdot)$ is the complete elliptic integral of the first kind (Abramowitz and Stegun, 1964).

APPENDIX C

Derivation of Inclusive Fitness Effects

Fecundity effects. The fitness of the adult on site i is the sum of 1 times the probability that the adult survives and the probability that its offspring out-compete other offspring on each site, $\sum_j p_{ij}$, times the probability that the resident adult dies,

$$w_i = s + (1-s) \sum_j p_{ij}. \qquad \text{(C1)}$$

The number of individuals from site i which compete on site j once the mutant has been introduced n'_{ij}, is the original number n_{ij} increased by a small relative change,

$$n'_{ij} = n_{ij}(1+\delta_i). \qquad (C2)$$

The average number of individuals competing for site j is $n_j = \sum_i n_{ij}$ and with the mutant this is

$$n'_j = \sum_i n'_{ij} = n_j\left(1+\sum_i \delta_i p_{ij}\right). \qquad (C3)$$

The new probability of an individual from site i obtaining a vacant breeding spot on site j is p'_{ij}, written to first order in δ

$$p'_{ij} = \frac{n'_{ij}}{n'_j} = p_{ij}\left(1+\delta_i - \sum_k \delta_k p_{kj}\right). \qquad (C4)$$

The fitness of the adult on site i with a mutant at site 0 is

$$w'_i = s+(1-s)\sum_j p'_{ij}, \qquad (C5)$$

and together with (C1) and (C4) we obtain the inclusive fitness effect of the mutant

$$\Delta w_{IF} = \sum_i \Delta w_i r_i = (1-s)\sum_{ij} r_i p_{ij}\left(\delta_i - \sum_k \delta_k p_{kj}\right). \qquad (C6)$$

Symmetry allows us to write $p_{ij} = p_{j-i}$ and $p_{-j} = p_j$; the probability of dispersal to a site depends only on the separation between the two sites and not the absolute position of the sites. The simplified expression is (2).

Survival effects. Writing the survival of an adult on site i as $s_i = s$ we can introduce an effect of the mutant, altering the survival probability by a small relative change δ_i,

$$s'_i = s_i(1+\delta_i). \qquad (C7)$$

We leave n_{ij} and p_{ij} as before, and note that p_{ij} can be interpreted as the probability that an individual from

site i wins on site j conditioned on the death of the individual at site j. The fitness of an individual on site i is

$$w_i = s_i + \sum_j p_{ij}(1-s_j) \qquad (C8)$$

and after a mutant is introduced at site 0, the fitness is

$$w'_i = \sum_j p'_{ij}(1-s'_j)+s'_i = \sum_j p_{ij}(1-s_j(1+\delta_j))+s_i(1+\delta_i)$$

$$= w_i - \sum_j \delta_j p_{ij} s_j + s_i \delta_i. \qquad (C9)$$

The inclusive fitness effect $\Delta w_{IF} = \sum_i r_i \Delta w_i$ is (8).

APPENDIX D

Iterated Prisoner's Dilemma

The average payoff to a p actor playing a q player is

$$W(p,q) = pq\left(\frac{R}{1-w}\right)+(1-p)\,q\left(T+\frac{Pw}{1-w}\right) \qquad (D1)$$

$$+p(1-q)\left(S+\frac{Pw}{1-w}\right)+(1-p)(1-q)\left(\frac{P}{1-w}\right). \qquad (D2)$$

The cost to an actor of using the mutant strategy $p' = p+\delta$ is

$$C = -(W(p',p)-W(p,p)) = -\delta_0 \qquad (D3)$$

and the benefit to its neighbours is

$$B = W(p,p')-W(p,p) = N\delta_1. \qquad (D4)$$

We use capital letters as a reminder that these are the net cost C to the actor and the benefit B which is divided, on average, among the N neighbours not including the actor. Substituting (D3, D4) into (5, 7, 10, 12) to obtain an altruism relatedness threshold $-\delta_0/(N\delta_1)$ and solving for p to first order in δ using the payoffs from Table II we obtain the threshold

$$p = \frac{1-w}{3w-1}\cdot\frac{\left(\dfrac{-\delta_0}{N\delta_1}\right)(3+N)-4}{1+\left(\dfrac{-\delta_0}{N\delta_1}\right)(N-2)}. \qquad (D5)$$

If $w > 1/3$ then increased altruism (frequency of playing TFT) is selected for p greater than this threshold and decreased altruism is selected for smaller p. If $w < 1/3$ then AD is the ESS.

ACKNOWLEDGMENTS

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