OVERLAPPING GENERATIONS CAN PROMOTE ALTRUISTIC BEHAVIOR

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Abstract.—We use an inclusive fitness model to study the evolution of altruism in a patch-structured population in which there is positive probability of breeder survival from one generation to the next. We find first that breeder survival promotes altruism and second that there is a marked difference between benefits of fecundity and benefits of survival. Under the first altruism is more strongly favored, and under the second altruism is less strongly favored than in a randomly mixing population.

Key words.—Altruism, fecundity, overlapping generations, population structure, prisoner's dilemma, survival.

Over the past 20 years there has appeared an enormous body of literature on the evolution of social behavior in a spatially structured population. A major theme has been the evolutionary tension between cooperation and competition among neighbors. Much of the work focuses specifically on altruistic behavior, but it is also recognized that other forms of behavior, such as dispersal of offspring and sex allocation, can also be regarded as lying along a cooperate-compete axis. For example, if there is a survival cost to dispersal and a dispersing offspring, if successful, will find a patch that is on average no better than its native patch, then dispersal entails a sacrifice in personal fitness. Nevertheless dispersal can be selectively favored if it reduces competition among relatives that are left behind (Hamilton and May 1977).

A powerful and illuminating modeling approach for these problems is the inclusive fitness formulation of Hamilton (1964). This method assesses the evolutionary status of an action by adding up the effects of the action on the fitness of all individuals in the population, each effect weighted by the relatedness of the actor to the individual. If the resulting sum is positive, then the action is selectively favored. A difficulty with this formulation is that the offspring of close relatives are often in competition with those of the actor, so that an increase in the fitness of a relative may not benefit the actor as much as might be supposed. This difficulty is inherent: the tendency of offspring to move quite slowly from their native habitat (called population viscosity by Hamilton 1964) makes it likely that an actor will interact with close relatives and at the same time tends to brings the offspring of these relatives into conflict with those of the actor.

For an inclusive fitness analysis to account for such competitive interactions, it must subtract the fitness of potential offspring who are displaced as breeders by the extra offspring created by the behavior of the actor. This is most easily done when the model is set in a well-defined population structure, for example, a patch or a lattice structure. In this case, inclusive fitness can be calculated as a careful count of offspring who succeed in breeding in the next generation.

When this is done in models of altruism, a surprising result is obtained. In a class of simple population structures, the altruistic benefits and resulting competitive effects exactly balance one another, and the inclusive fitness of the actor is given by the net direct effect on its own fitness (Taylor 1992a,b; Wilson et al. 1992). In these cases, altruistic behavior is selected only if the same behavior would be favored in a randomly mixing population.

However, recent simulation studies with a number of spatial structures and types of altruistic behaviors have shown substantial departures from this exact balance (Nakamaru et al. 1997, 1998; Mitteldorf and Wilson 2000), often finding altruism to be more highly favored than expected. There are a number of ways in which these models depart from the simple assumptions of the models of Wilson et al. (1992) and of Taylor (1992a,b), and our purpose here is to investigate one of these departures, that of generation overlap. In the original studies of Wilson et al. (1992) and Taylor (1992a,b), there was no overlap between generations, but in most of the more recent studies in which altruism was unexpectedly favored, some generation overlap is found. This occurs, for example, in lattice-structured populations in which residents have a certain mortality, and offspring only colonize sites that become vacant. Here we present a simple general model in which overlap between generations can give a significant boost to altruism.

Specifically this paper studies the standard altruism model in a patch-structured population with some survival, *s,* of breeders to the next generation. We obtain two main results.

Result 1: the effect of benefit type.—There is a distinction between benefits of fecundity and benefits of survival. Under the first altruism is more strongly favored, and under the second altruism is less strongly favored than in a random-mixing population.

Result 2: the effect of overlapping generations.—For both types of benefit, the greater is *s,* the more strongly an altruistic trait is favored. Thus, generation overlap tends to promote altruism.

A Patch Structure with Overlapping Generations

We work with the simplest possible structure that displays the effect. Consider an infinite asexual haploid population, distributed on patches with *N* individuals per patch located on breeding spots. Each individual has a large number of (clonal) offspring who either disperse to a distant patch (with probability *d*) or remain on their native patch (with probability $1 - d$). We assume that dispersal incurs a cost, *k,* that is, only a fraction $1 - k$ of dispersing offspring successfully find a new patch. The next generation is formed as follows.

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Each of the N original females survives with probability s and in this case retains possession of her breeding spot. The offspring, native and immigrant, then compete on an equal basis for the vacated spots, with death to the offspring who do not win a spot, and the cycle begins again. In the model, the dispersal/cost parameters are both subsumed into the parameter:

$$h = \frac{1 - d}{1 - kd},$$ (1)

which is the probability that a breeding individual is native to the patch. Finally, we let r denote the relatedness (Michod and Hamilton 1980) of a breeding individual to a random offspring born on its breeding patch. This is also its relatedness to a random breeder on its patch (including itself) and it is calculated (Appendix) to be:

$$r = \frac{1 + s}{N(1 + s) - (N - 1)(2s + h - sh)h}.$$ (2)

It is important to note that this calculation assumes a monomorphic population with zero benefits and cost from the altruistic behavior. This assumption of ''weak selection'' is standard in inclusive fitness arguments. Essentially, we are ignoring the effects of the altruistic behavior on the distribution of alleles, and the resulting calculation will be valid to first order in the quantities b and c defined below (Taylor 1996). This patch-structured model with overlapping generations has recently been considered by Pen (2000) in a study of the fecundity-survival trade-off at equilibrium.

The General Altruism Model

We assume that just prior to breeding, the N individuals interact at random on the breeding patch and there is the possibility for individual behavior to be altruistic. Each altruistic act incurs cost, c, to the altruist and provides a total benefit, b, to the individuals on the patch. Thus, on average, each individual (including the altruist) gets benefit b/N from each altruistic act on the patch. These costs and benefits can represent changes in either fecundity or survival, and in fact this will give us two different versions of the model. We assume that costs and benefits are additive and that selection is weak, that is, b and c are small compared to the baseline fitness. Our objective is to find conditions on b and c for which the altruistic behavior is selectively favored.

The inclusive fitness approach (Hamilton 1964) requires us to make a count of all next generation individuals who are produced from or whose fitness is affected by an altruistic act, each one weighted by its relatedness to the actor. In this calculation, we must count the b extra individuals who are ''created,'' the c individuals who are ''destroyed,'' and, because of the viscous nature of the population, all other individuals whose fitness is affected by these $b - c$ extra individuals.

Fecundity Effects

We suppose that an altruistic act increases the fecundity of the recipient by a factor b and decreases the fecundity of the actor by a factor c. We let the average relatedness of the recipient to the altruist be r. Of course, the relatedness of the actor to itself is 1. Thus, the inclusive fitness effect of these extra offspring will be $(1 - s)(br - c)$. The factor $(1 - s)$ comes from the fact that this is the fraction of breeding spots that is available to offspring each generation. However, the effect of the action is to increase the number of patch offspring by the factor $b - c$, and in the inclusive fitness calculation, we must account for any related offspring that these extra offspring displace. Now, with probability $1 - h$ these extra offspring will wind up competing on a distant patch and will in that case have no effect on the fitness of a relative. However, with probability h they will compete on the natal patch and they will then displace $b - c$ random individuals who will be native to that patch with probability h and in this case will have average relatedness r to the actor. This gives an overall weighting of $(1 - s)h^2 r$ to each of these displaced individuals. The overall inclusive fitness effect is then:

$$W = (1 - s)(br - c) - (1 - s)(b - c)(h^2 r)$$
$$= (1 - s)[b(r - h^2 r) - c(1 - h^2 r)].$$ (3)

It is worth noting the different routes by which W depends on s. There is the direct effect of $(1 - s)$ and then the effect through relatedness (eq. 2), but there is also a third path. As we shall see later, h depends on the dispersal rate d and the evolutionarily stable strategy (ESS) value of d will depend on s. Thus, in practice, W has a complex dependence on s.

The altruistic trait will spread if $W > 0$ which, using equation (2), can be written (after some algebra) as:

$$\frac{b}{c} > N - (N - 1)\frac{2hs}{(1 + h)(1 + s)}.$$ (4)

If the last term in the inequality is zero, the condition reads:

$$\frac{b}{c} > N,$$ (5)

which is just the condition that the direct benefit b/N to the altruist exceed the cost c. There are three ways that this can happen—if $N = 1$, $h = 0$, or $s = 0$. The first two are expected. In case $N = 1$, the altruist has no one to interact with except itself and its inclusive fitness is $b - c$. In case $h = 0$, all offspring disperse, interactions are essentially at random in the whole population, and the only relative that the altruist interacts with is itself.

The third condition, $s = 0$, is unexpected and is interesting. This is the case of nonoverlapping generations, and equation (4) tells us that in this case the benefit conferred on relatives is exactly balanced by the competitive effects of the extra offspring created. This is the result discovered by Wilson et al. (1992) in a simulation study of a lattice-structured population and verified analytically in a patch-structured population and a one-dimensional lattice by Taylor (1992a,b).

The significant finding of equation (4) is that, if none of these conditions hold, that is, if $N > 1$, $h > 0$ (dispersal is incomplete), and $s > 0$ (some probability of breeder survival), then altruism can be favored with a cost c that exceeds the direct benefit b/N to the altruist. This provides the first case of our result 1.

Survival Effects

Here we suppose that an altruistic act increases the survival of the recipient by a factor b, and decreases the survival of the actor by a factor c. Then an average of $s(b - c)$ individuals will survive because of the act, and the offspring who are displaced from a vacant spot in these instances will be native with probability h and in this case will have average relatedness r to the actor. Thus, each of these displaced individuals gets a weighting of hr. The overall inclusive fitness effect is:

$$W = s(br - c) - s(b - c)(hr)$$
$$= s[b(r - hr) - c(1 - hr)]. \qquad (6)$$

The altruistic trait will spread if $W > 0$ which, using equation (2), can be written as:

$$\frac{b}{c} > N + (N - 1)\frac{2h(1 - s)}{(1 + s)}. \qquad (7)$$

As above, when $N = 1$ or $h = 0$, the condition reduces to condition (5) and for altruism to be favored we need the direct fitness effect on the altruist to be positive. This will also be true in the biologically unrealistic case that $s = 1$. But in all other cases, the last term in the inequality exceeds zero and a gift of survival is actually less beneficial to the actor than it would be in the complete mixing case ($h = 0$). This provides the second case of our result 1.

The Fecundity/Survival Trade-off for Cost

According to the above analysis, extra fecundity displaces "related" offspring at rate h^2r, whereas extra survival displaces offspring at the larger rate hr. For altruism to have the best chance of succeeding, one might think that the *benefit* should be given in fecundity, but the *cost* should be borne in survival, giving us the inclusive fitness:

$$W = (1 - s)b(r - h^2r) - sc(1 - hr) \qquad (8)$$

However, this argument fails. In fact, as long as the altruist has an evolutionarily stable balance between survival and fecundity, it makes no difference whether the cost is incurred in units of fecundity or survival. This follows from a recent analysis of Pen (1999), which we now summarize.

As we have seen above, a relative change of Δ_S units of survival counts $s\Delta_S(1 - hr)$ towards inclusive fitness and a relative change of Δ_F units of fecundity counts $(1 - s)\Delta_F(1 - h^2r)$ toward inclusive fitness. At evolutionary equilibrium for survival-fecundity trade-off within the altruist, these should be equal, so that:

$$s\Delta_S(1 - hr) = (1 - s)\Delta_F(1 - h^2r). \qquad (9)$$

In equation (8), the cost c is playing the role of Δ_S—let's call it c_S. If we want to convert it to a fecundity cost, c_F, then equation (9) tells us we must replace $sc_S(1 - hr)$ by $(1 - s)c_F(1 - h^2r)$ and that gives us equation (3). So (8) is really equivalent to (3); they just provide two different ways of measuring cost.

The Effect of s on the Threshold b/c

If in equations (4) and (7) we only looked at the explicit dependence on s, then we observe that in (4) the absolute
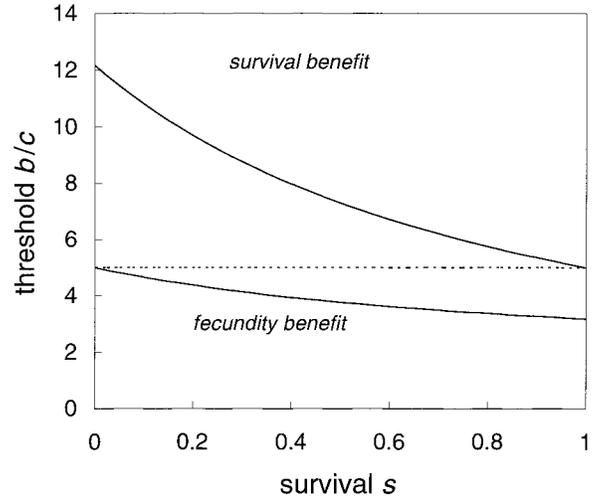
FIG. 1. The threshold benefit:cost ratio (above which altruism will be favored) plotted against the probability s that a breeder will survive to reproduce in the next generation. The graphs plotted are for fecundity benefit (eq. 4) and for survival benefit (eq. 7). The parameter values are $N = 5$ breeders on a patch and cost $k = 0.5$ of dispersal, giving a probability h that a breeder is native of around 0.85. Note that the random mixing model predicts a threshold b/c of $N = 5$, and this is the value obtained for $s = 0$ (fecundity benefit) and $s = 1$ (survival benefit). Note also that both graphs decrease, that is, higher survival promotes altruistic behavior.

value of the last term increases with s, and in (7) the absolute value of the last term decreases as s increases. In both cases, this implies that the threshold value of the benefit:cost ratio decreases with s. The conclusion would be that for either a fecundity or a survival benefit, increased overlap between generations promotes an increased level of altruism, this is our result 2. This simple conclusion would be valid if we assumed that the dispersal rate d, and thus h, is independent of the survival rate s.

However, in general we might expect the ESS value of d and therefore the ESS value of h (which we will call h^*) to depend on s. In the example below, we calculate the ESS condition for h^* (eq. 12), assuming a constant cost k of dispersal, and we use this equation to show that h^* decreases with s and thus the dispersal rate d increases with s (this is expected as dispersal is an altruistic behavior).

With this result, we can easily analyze the threshold value of b/c for the case of survival benefit (eq. 7). Because h^* and $(1 - s)/(1 + s)$ both decrease with increasing s, the right side of equation (7) decreases with s and so therefore does the threshold value of b/c. The same result holds for the case of fecundity benefits (eq. 4) although this is not immediately clear as h^* and s change in opposite directions (eq. A7). The decreasing relationship between the threshold b/c and s is illustrated in Figure 1 for the parameter values $N = 5$, $k = 0.5$.

The conclusion we arrive at is that for both fecundity and survival benefits, altruism becomes more favored as s increases. This gives us our result 2.

Example: Offspring Dispersal

As mentioned in the introduction, most forms of social behavior have altruistic components, and result 2, above, sug-

gests that such behaviors should equilibrate at a more altruistic level for larger *s*. Here we test this prediction with a standard model of dispersal of offspring. Because dispersal of offspring reduces the level of competition for neighbors, dispersal can be regarded as altruistic, and thus we would expect larger *s* to result in higher ESS dispersal levels.

Using a game-theoretic approach, Hamilton and May (1977) constructed the first model that showed that it was beneficial for a mother to disperse some of her offspring, even if that incurs a high mortality cost, the benefit accruing in reduced competition for resources at home. Hamilton and May worked with the patch-structured model described above with one breeder per patch ($N = 1$) and no generation overlap ($s = 0$). This model was extended by Comins et al. (1980), Frank (1986), and Taylor (1988) to allow $N > 1$ and to encompass sexual reproduction and more general genetic systems. Here we extend it further to allow $s > 0$.

Here is a summary of the basic model. We measure fitness in terms of offspring (after dispersal) ready to compete for the available next generation spaces. A mother who keeps an extra offspring at home loses $1 - k$ offspring on a distant patch and gains one offspring at home. This extra offspring at home displaces another who will be a native with probability h and in this case will have average relatedness r to the mother. The overall inclusive fitness effect is:

$$W = -(1 - k) + (1 - hr) = k - hr. \quad (10)$$

Increased dispersal will be favored if this is negative, which gives the condition

$$hr > k. \quad (11)$$

This appears to say that dispersal is favored if h is sufficiently large (which means that the dispersal rate d is sufficiently small), but it is not quite that simple, because r itself depends on h. However, because $1/r$ is a quadratic polynomial in h (eq. 2), this condition can be solved explicitly for h, and thus for d, and it then tells us that dispersal will be favored if d is small enough, which gives us a stable intermediate dispersal rate, d^* (Frank 1986; Taylor 1988).

So far the argument is identical to the standard case of $s = 0$. The effect of breeder survival comes into play through the dependence of r on s (eq. 2). Our interest here is not so much in finding the equation for the ESS dispersal rate, as in showing analytically that this rate increases with *s*.

From equation (11), the ESS value of the parameter h is a solution to the equation:

$$h^*r = k, \quad (12)$$

where $r = r(h^*, s)$ is the value of the relatedness coefficient at the ESS. Differentiate equation (12) with respect to s:

$$\frac{dh^*}{ds}r + h^*\left[\frac{\partial r}{\partial s} + \frac{\partial r}{\partial h}\frac{dh^*}{ds}\right] = 0, \quad (13)$$

where r and its partial derivatives are evaluated at h^*. By rearranging:

$$\frac{dh^*}{ds}\left[r + h^*\frac{\partial r}{\partial h}\right] = -h^*\frac{\partial r}{\partial s}. \quad (14)$$

It is shown in the appendix (eqs. A4, A5) that both $\partial r/\partial h$ and

$\partial r/\partial s$ are positive, and it follows that dh^*/ds is negative. Because h is a decreasing function of dispersal rate d (from eq. 1), it follows that the ESS dispersal rate increases with *s*.

Example: The Iterated Prisoner's Dilemma

Sometimes a more natural model of altruistic behavior provides no direct benefit to the actor. As an example, we consider 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 bout being 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 1. Our inclusive fitness argument above can be adapted to this problem. Let individuals use TFT with probability p and AD with probability $1 - p$. Individuals who are slightly more likely to behave altruistically (i.e., play, TFT with probability $p + \delta$) are favored if p is greater than a certain threshold (eq. A9). If generations are non-overlapping ($s = 0$) and altruism affects fecundity or the population disperses completely ($h = 0$) TFT is evolutionarily stable for

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

assuming the numerical values for the payoffs from Table 1. This threshold value of p is shown as a dashed line for $w = 3/5$ in Figure 2. The solid lines are the threshold p for fecundity and survival effects. Arrows indicate the direction in which p will evolve. Our work shows that overlapping generations and patch structure together change the conditions for the evolution of altruism, although separately they have no effect. The pattern is the same as the earlier example: Increasing s enlarges the area where altruism is favored. A fecundity benefit favors altruism more in a patch-structured population than in an unstructured population, but survival benefits make it more difficult for altruism to evolve (for $s < 1$).

DISCUSSION

In natural populations, we typically find the two central characteristics of the above patch-structured population, local interactions between individuals and periodic flow of genetic

TABLE 1. Payoffs for the iterated prisoner's dilemma where TFT is tit for tat and AD is always defect. The parameters T, R, P, S are the payoffs for the prisoner's dilemma and satisfy $T > R > P > S$. The probability of playing again with the same partner is w. We use $T = 5, R = 3, P = 1, S = 0$ for numerical examples. If $w = 0$ the game reduces to the prisoner's dilemma.

		Partner	
		TFT	AD
Actor	TFT	$\dfrac{R}{1-w}$	$S + \dfrac{Pw}{1-w}$
	AD	$T + \dfrac{Pw}{1-w}$	$\dfrac{P}{1-w}$

FIG. 2. Threshold frequency of TFT p in the iterated prisoner's dilemma as a function of survival s using the payoffs in Table 1. Increased altruism is favored above the lines (arrows pointing upward) and selected against below the lines (arrows pointing downward). The height of the dashed line, $p = (1 - w)/(3w - 1)$, gives the threshold p for nonoverlapping generations ($s = 0$) and with a fecundity benefit. The two solid curves are for fecundity and survival benefits (eq. A9). The parameter values are $N = 5$, $h = 0.8$, and $w = 3/5$.

material between neighborhoods, which is often caused by dispersal of gametes or offspring. The viscous nature of this gene flow tends to promote positive coefficients of relatedness within neighborhoods, and this would appear to favor altruistic interactions. But this same viscosity limits the capacity of the neighborhood to export the benefits of altruistic behavior, and this selects against altruistic interactions. This was already understood by Hamilton in his 1964 paper and 20 years later Grafen (1984) observed that, in a group-structured population, altruistic acts can be selectively favored only to the extent that an altruistic group is able to export some fraction of the benefits it generates, specifically, some of the extra offspring produced must compete with individuals of relatively low relatedness.

In recent years, considerable attention has been paid to this tension of opposite effects, and a number of mechanisms that might promote altruism in a structured population have been investigated. We mention three of these.

The Timing of Altruism

Suppose that in the above model, the interaction is among the offspring just before dispersal. Because the relatedness between offspring born on the same patch is still r, conditions (4) and (7) still apply, and in case $s = 0$, they give us $b/N > c$. But in this case the benefit of the altruist to itself is no longer b/N, but is b/fN, where f is the expected number of offspring per breeder, and the condition that the net direct benefit to altruist be positive is $b/fN > c$. If $f > 1$, the condition for altruism to be favored is less stringent than this. The point is that in a life cycle that alternates clumping (here the production of offspring) and mixing (dispersal), conditions just prior to the mixing phase will generally be more favorable for the evolution of altruism.

Population Elasticity

Hamilton (1964) observed that in populations that are subdivided into ''standard-sized batches,'' each of which is allotted a ''standard-sized pool of reproductive potential,'' the progress of an altruistic gene will be slowed. He credited the original observation of this phenomenon to a paper of Haldane (1923) on sib competition. Hamilton (1971, p. 91) again asserted that ''the most 'system-like' version of an 'isolation-by-distance' model, which is supposed to preclude long-range migration and elastic expansion from vigorous areas, is rather hostile to altruism.''

The key concept here is that of elastic expansion, by which is meant the capacity of the environment to expand to accommodate (and give reproductive potential to) extra offspring produced by the altruistic behavior. This seems to make sense; a model that allowed an elastic patch size, so that a patch with a high proportion of altruists will be permitted a higher density, should provide an extra benefit to altruism. A recent simulation study of this problem was run by Mitteldorf and Wilson (2000) for a lattice-structured population, but a comprehensive theoretical analysis of this question remains to be done. The interesting question for us is whether result 2, the enhancement of altruism with s, will continue to hold in an elastic population. There are many different ways to model elasticity and we are currently investigating this phenomenon more generally, but here we mention some preliminary results.

It seems to us that there are two different pathways through which elasticity might act; through a positive correlation first between allele frequency and patch density, and secondly between allele frequency and patch density growth rate. Of course, in general both of these factors might act together. First, suppose that patches with more altruists have a higher density. Then provided that these patches received no more than the normal number of immigrants, the pool of offspring competing for next generation spots will have a higher than normal frequency of altruists, and altruists will get more than their share of such spots. Note that if patches with more altruists are simply *larger,* say 5%, and get 5% more immigrants because of this, then this effect disappears. Our initial results (P. D. Taylor and A. J. Irwin, unpubl. data) show that in this case, our result 2, that increased survival promotes altruism, will continue to hold in case the benefits of altruism are through fecundity, but may not hold when the benefits are through survival. In the latter case, this is because the increased density effect works through offspring fitness and increased survival reduces the offspring share. Second, suppose that patches with more altruists have a higher growth rate. Then altruists will clearly get more than their share of next generation spots, either through survival or offspring or both, and our results show that increased survival will typically promote altruism.

Overlapping Generations

Positive survival of breeders from one generation to the next tends to increase the within-patch relatedness, r. Another way to think about this is that it tends to increase the between-group genetic variance, because the ''mixing'' effects of dispersal are reduced, even with the same offspring dispersal

rate. Now higher relatedness between interactants does not necessarily favor altruism; it is also required that there not be a corresponding increase in competitive interactions between their offspring. In fact, this is the case in our model. If the dispersal rate remains the same, then the competition between offspring native to the same patch will not increase, in the sense that breeders have the same probability h of being native.

An interesting application of this might be found in eusocial behavior for which the queen's life expectancy is often longer than that of workers. This is typically considered to be a derived trait, one that followed the introduction of eusociality. Our analysis suggests that this might in some cases have been reversed, namely that where generations are overlapping, and the ''survivor'' plays the role of the queen, eusociality might evolve more easily as long as the altruistic acts are such that they increase the number of the queen's offspring. (We are grateful to one of the reviewers for pointing out this interesting possibility.)

The population model used in the paper is the standard patch structure with overlapping generations, and our interest is in the effect of the survival rate of breeders on the selective advantage of altruism. We use an inclusive fitness model to measure this advantage; for this to predict the course of genetic evolution, we need to assume that selection is ''weak,'' that is, that altruistic behavior has a small selective effect, which means that b and c are small (Taylor 1996). There are a number of reasons for this assumption, but an important one is that our calculation of relatedness, r (eq. 2), is valid only when the allele causing the altruistic behavior 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.

In case breeder survival s is zero and there is no overlap between generations, we obtain the results of Taylor (1992a) that, irrespective of the rate of dispersal of offspring, the altruism threshold occurs where the cost to the altruist is exactly balanced by the direct benefit it receives ($[b/N] - c = 0$). This is of course exactly what one would expect in a randomly mixing population ($d = 1$), but the point is that it is also obtained when dispersal of offspring is only partial. However, in case 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—altruism is promoted under a fecundity benefit (eq. 4), but discouraged under a survival benefit (eq. 7). This is illustrated in Figure 1. The difference between these two cases can be easily explained. 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 that the site they occupy will necessarily be at home. This increases the local competition among offspring, and thereby reduces the advantages of altruism.

We show that the threshold benefit:cost ratio decreases as breeder survival, s, increases. Thus, higher s results in higher levels of altruistic behaviors. The analysis of this effect is slightly complicated because the threshold b/c depends on both s and the dispersal rate d, and the ESS value of d itself

increases with s. This latter relationship, the increase of dispersal rate with s, is in fact a particular example of the phenomenon we are discussing—increased altruism with higher s.

Finally we apply our result to the iterated prisoner's dilemma, and obtain analogous results. We expect that the qualitative results of this paper will continue to hold for other population structures, for example, a lattice in one or two dimensions. Several recent studies of social behavior in a lattice-structured population with overlapping generations 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. Fecundity effects are more favorable to the evolution of altruism, although, unlike our results, survival effects sometimes inhibited the evolution of altruism and sometimes facilitated it. In their model with sufficiently long games ($w \simeq 1$), AD was no longer evolutionarily stable, a result not found in our analysis. Nakamaru et al. (1997, 1998) attribute their results to population structure, but our results for $s = 0$ and fecundity effects are identical to the unstructured population. Competition between two strains of *Escherichia coli*, one producing a toxin (colicin) with a fecundity cost and the other sensitive to the colicin with a survival cost, shows results qualitatively similar to the Nakamaru et al. (1997, 1998) studies (Durrett and Levin 1997; Iwasa et al. 1998). The threshold survival cost of the colicin necessary for colicin producers to displace the colicin-sensitive strain in the structured population is different than in the unstructured population. Additionally, the structured population creates situations in which colicin producers can invade colicin-sensitive populations when invasion is impossible in unstructured populations. These models show some of the same features as ours, although they have not examined explicitly the effect of variable survival rates.

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APPENDIX

It is useful to define $\hat{r}$ to be the relatedness of a breeding individual to another breeder on its patch. Then r, which is the relatedness of the actor to a random breeder that can include the actor itself, is:

$$r = \frac{1}{N} + \frac{N-1}{N}\hat{r}. \qquad (A1)$$

Now consider two different individuals breeding on the same patch (who therefore have relatedness $\hat{r}$) and ask for the relatedness of their ''ancestors'' exactly one generation ago. With probability s^2 they were fellow breeders who survived, and in that case they also had relatedness $\hat{r}$. With probability $2s(1-s)$ one of them is a survivor and the other is a new offspring, in that case, the new offspring is native with probability h and thus its ancestor is a random breeder in the previous generation, giving us a relatedness of r. Finally, with probability $(1-s)^2$ neither are survivors; in this case, they are both offspring, each of which is native with probability h, and thus have relatedness r. This gives us the recursion equation:

$$\hat{r} = s^2\hat{r} + 2s(1-s)hr + (1-s)^2h^2r. \qquad (A2)$$

This is a recursion in the sense that the $\hat{r}$ on the left belong to the generation after the various r-values on the right, but at equilibrium, there should be no change from one generation to the next, and equations (A1) and (A2) can be solved to give equation (2). This equation was first obtained by Pen (2000).

For purposes of taking derivatives, equation (2) is most simply written as:

$$\frac{1}{r} = N - \frac{(N-1)}{1+s}[2sh + (1-s)h^2]. \qquad (A3)$$

We want to show that r increases with both h and s, and it is simplest to show that $1/r$ decreases. First differentiate (A3) with respect to h holding s constant:

$$\frac{d}{dh}\left[\frac{1}{r}\right] = -\frac{(N-1)}{1+s}[2s + 2h(1-s)], \qquad (A4)$$

which is clearly negative. This equation was first obtained by Pen (2000). Now we differentiate (A3) with respect to s holding h constant:

$$\frac{d}{ds}\left[\frac{1}{r}\right] = -(N-1)h\frac{d}{ds}\left[\frac{2s + (1-s)h}{1+s}\right]$$

$$= -(N-1)h\left[\frac{(2-h)(1+s) - 2s + (1-s)h}{(1+s)^2}\right]$$

$$= -\frac{2(N-1)h(1-h)}{(1+s)^2}, \qquad (A5)$$

which is clearly negative.

To show that the threshold b/c (eq. 4) decreases for fecundity effects, we compute its s derivative:

$$\frac{d}{ds}\left[\frac{b}{c}\right] = -2(N-1)\left(\frac{h^*(1+h^*) + s(1+s)\frac{dh^*}{ds}}{(1+h^*)^2(1+s)^2}\right). \qquad (A6)$$

Although dh^*/ds is negative, it is small in magnitude:

$$-\frac{dh^*}{ds} = \frac{h^*}{1+s} \cdot \frac{2h^*(1-h^*)}{\left(\frac{N}{N-1}\right)(1+s) + h^{*2}(1-s)} < \frac{h^*(1+h^*)}{s(1+s)}, \qquad (A7)$$

and it follows that the threshold b/c for fecundity effects decreases with increasing s.

Cost:Benefit Ratio in the Iterated Prisoner's Dilemma

The payoff to a p actor playing a q player is

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

$$+ p(1-q)\left(S + \frac{Pw}{1-w}\right) + (1-p)(1-q)\left(\frac{P}{1-w}\right). \qquad (A8)$$

The cost to an actor of switching from p to $p' = p + \delta$ is $C = -[W(p', p) - W(p, p)]$ and the benefit to its neighbors is $B = W(p, p') - W(p, p)$. We use capital letters for the net cost C to the actor and benefit B that is shared among the $N-1$ patch-mates. The change of variables that relates these new costs and benefits to the original c and b is $C = c - (b/N)$ and $B = (N-1)b/N$.

Using the payoffs from Table 1 and ignoring terms $O(\sigma^2)$, we obtain the following condition for increased altruism to be favored:

$$p > \left(\frac{1-w}{3w-1}\right)\left(\frac{1-4C/B}{1+C/B}\right) \quad \text{and} \quad w > 1/3, \qquad (A9)$$

where C/B is the threshold cost:benefit ratio obtained by repeating the inclusive fitness arguments in the main text. The C/B thresholds are:

$$\frac{C}{B} = \begin{cases} \dfrac{2hs}{[(1+h)(1+s)N] - [2hs(N-1)]} & \text{with fecundity effects} \\[4ex] -\dfrac{2h(1-s)}{[(1+s)N] + [2h(1-s)(N-1)]} & \text{with survival effects.} \end{cases}$$

$$(A10)$$