

Altruism in viscous populations – an inclusive fitness model

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Summary

A viscous population (Hamilton, 1964) is one in which the movement of organisms from their place of birth is relatively slow. This viscosity has two important effects: one is that local interactions tend to be among relatives, and the other is that competition for resources tends to be among relatives. The first effect tends to promote and the second to oppose the evolution of altruistic behaviour. In a simulation model of Wilson *et al.* (1992) these two factors appear to exactly balance one another, thus opposing the evolution of local altruistic behaviour. Here I show, with an inclusive fitness model, that the same result holds in a patch-structured population.

Keywords: altruism; inclusive fitness; competition; viscosity

Introduction

In genetic studies of the evolution of altruism it has been recognized that the selective advantage of an altruistic gene *A* depends on its opportunities to confer the benefits of its altruism disproportionately on other copies of *A* rather than on copies of its non-altruistic alleles. The 'viscosity' of a population, being the tendency of offspring to remain near their place of birth (Hamilton, 1964), both enhances and opposes the spread of an altruistic gene. It favours altruism because it promotes a clustering of the *A*-gene (Hamilton, 1964), such that a random neighbour of an *A*-gene is more likely to be *A*. But it also selects against altruism by promoting increased competition between the offspring of *A*-genes for reproductive resources (Grafen, 1984, p.80) – there's little point in giving a fellow *A*-gene more offspring if these offspring are going to compete with those of the donor for the same basket of resources. The question is, how do these two balance?

Wilson *et al.* (1992) have studied a simulation model in which breeding females are located on a grid and interact with neighbouring females, and have offspring which may disperse locally. Their results are that, in such a population, independently of the level of viscosity (that is, for any dispersal rate), the selective force on the altruistic gene is the same as it would be in a panmictic population: the altruism threshold occurs when the benefit to the altruist of her behaviour exactly equals the individual cost.

Here, I use an inclusive fitness argument to show that this same result holds in a patch-structured population. For any patch size *N* and dispersal rate *t*, the threshold for altruistic interactions among breeding females occurs when the cost just balances the individual benefit.

I consider an infinite population with non-overlapping generations. Mated females breed on patches with *N* females per patch. The offspring mate at random on each patch and then, with some probability *t*, $0 < t < 1$, disperse to distant patches. Finally, on each patch, the offspring,

native and immigrant, compete for the N breeding spots, and the cycle begins again. In more detail, the stages of the life cycle are as follows.

(1) Interaction. Mated females interact at random on the patch. Each altruistic act incurs cost c and provides a total benefit b to the females on her patch (including the altruist). Thus, on average, each female gets benefit b/N from each altruist on her patch. These costs and benefits translate directly into fecundity during the breeding stage. I assume that selection is weak, that is, b and c are small compared to the baseline fitness.

(2) Breeding. Each female has a large number of offspring determined by her fitness from the previous stage. The mothers die.

(3) Mating. The offspring on each patch mate at random. The males die.

(4) Dispersal. With probability t , each female disperses to a distant patch, distant enough that she will find no relatives there. With probability $s = 1 - t$, the female stays on her natal patch.

(5) Competition. On each patch, the mated females, native and immigrant, compete for the N breeding spots and the cycle begins again.

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

The argument for asexual (haploid) reproduction is simplest, and I treat it first. In this case, the mating stage 3 is absent, and offspring are genetically identical to their mother. The argument for sexual reproduction allows a diploid or a haplodiploid genetic system.

Asexual reproduction

Let R be the relatedness of a mother to a random offspring born on her breeding patch (including her own). The altruistic act creates b offspring with average relatedness R , and $-c$ offspring with relatedness 1. In addition, these $b - c$ extra offspring remain on the natal patch with probability s and will therefore displace $s(b - c)$ random individuals competing for the next generation breeding spots on that patch, and these will be native to that patch with probability s and in this case will have average relatedness R to the actor. Thus these displaced individuals will have average relatedness sR . The overall accounting is given in Table 1.

Table 1. Inclusive fitness change – asexual

Offspring	Relatedness
$-c$	1
b	R
$-s(b-c)$	sR

The marginal inclusive fitness is calculated as

$$W = -c + bR - s^2(b - c)R \tag{1}$$

The altruistic trait will spread if $W > 0$ which can be written

$$\frac{b}{c} > \frac{1 - s^2R}{R - s^2R} \tag{2}$$

To analyse condition 2 we need to calculate R , and this is done with the following recursive argument. First note that R is the average relatedness between two offspring born on the same patch. Choose two such offspring. With probability $1/N$ they are sibs, and have relatedness 1. With probability $(N - 1)/N$ they are not sibs and in this case, with probability s^2 , their mothers are both native to the patch and have relatedness R (at equilibrium the same value of R applies to each generation). This gives the recursion

$$R = \frac{1}{N} + \frac{N - 1}{N} s^2 R \tag{3}$$

which can be rearranged to read

$$N(R - s^2 R) = 1 - s^2 R \tag{4}$$

and if this is put into Condition 2, we get

$$\frac{b}{N} > c \tag{5}$$

This is just the condition that the altruist provide a net benefit to herself.

Sexual reproduction

The sexual argument is trickier because male and female offspring play different roles. I measure fitness in units of mated female offspring. If we let x denote the patch sex ratio (males/female) then there are x males produced for every female, but these males expect $1/x$ mates, so every female expects the same number of mated females through sons and daughters. I let r_m and r_f be the relatedness of a mother to a son and daughter, and let R_m and R_f be the relatedness of a mother to a random male and female offspring on the patch. The offspring count is given in Table 2. Here, relatedness is weighted by relative reproductive value in case this is different for the two sexes. In Table 2, v is the relative reproductive value of the female sex, and is 1 for diploidy and 2 for haplodiploidy (Price, 1970). Table 2 emphasizes the different roles of the two sexes: males simply compete with one another for matings with the existing females, whereas females provide a mating resource for patch males.

Table 2. Inclusive fitness change – sexual

	Offspring	Value-relatedness
Through sons	$-c$	r_m
	b	R_m
	$-(b - c)$	R_m
Through daughters	$-c$	$v r_f + R_m$
	b	$v R_f + R_m$
	$-s(b - c)$	$s(v R_f + R_m)$

If we add everything up, we get a marginal inclusive fitness of

$$W = -c(r_m + v r_f + R_m) + b(2R_m + v R_f) - (b - c)(R_m + s^2(v R_f + R_m)) \tag{6}$$

and the condition, $W > 0$, for the altruistic trait to spread becomes

$$\frac{b}{c} > \frac{\bar{r} - s^2\bar{R}}{\bar{R} - s^2\bar{R}} \quad (7)$$

where $\bar{r} = (r_m + \nu r_f)/(1 + \nu)$ and $\bar{R} = (R_m + \nu R_f)/(1 + \nu)$ are average relatednesses, the average weighted by reproductive value. It remains to calculate these.

Diploidy

In a diploid population, the relatednesses r and R of mother to her own offspring and random patch offspring are independent of the sex of the offspring, and Condition 7 can be written

$$\frac{b}{c} > \frac{r - s^2R}{R - s^2R} \quad (8)$$

The argument to calculate the relatednesses mimics the haploid case, noting that r is the average relatedness between sibs, and R is the average relatedness between two offspring born on the same patch. We obtain the recursion

$$R = \frac{r}{N} + \frac{N-1}{N} s^2R \quad (9)$$

which can be rearranged as

$$N(R - s^2R) = r - s^2R \quad (10)$$

and if this is put into Condition 8, we get Condition 5, as before.

Haplodiploidy

Because of the genetic asymmetry between the sexes, the relatedness recursions are considerably more complicated, and are presented, for example, in Taylor (1988a). However, it can be shown from these recursions that the analogue of Equation 10

$$N(\bar{R} - s^2\bar{R}) = \bar{r} - s^2\bar{R} \quad (11)$$

holds and this gives us, again, Condition 5.

Discussion

In natural populations, we typically find the two definitive characteristics of the above patch-structured population: local interactions between individuals, and periodic flow of genetic material between neighbourhoods, often caused by dispersal of gametes or offspring. The viscous nature of this gene flow tends to promote positive coefficients of relatedness within neighbourhoods, and this would appear to favour altruistic interactions. But this same viscosity limits the capacity of the neighbourhood to export the benefits of altruistic behaviour, and this selects against altruistic interactions. The above result shows that, for a patch-structured population, regardless of the size of the interaction neighbourhood (controlled by N) or the average relatedness between interactants (controlled by $s = 1 - t$), these two factors balance, and selection will act as if the interactions are among non-relatives in a non-viscous population.

This result shows that altruistic interactions are not expected to evolve among the breeding females; however, I remark that altruistic interactions can be favoured at other points in the life cycle. For example, consider the haploid case, and suppose that each female has k offspring who interact just before the dispersal stage. It turns out that the condition for these interactions to be selectively favoured is still given by Inequality 5: $b/N > c$. Since the group size is now kN , the interactions are favoured when the individual benefit b/kN is at least $1/k$ times the cost c , and

when $k > 1$, we would certainly call this altruism. The point is that altruism can be favoured in this population if it occurs at the right moment. The general result appears to be that what determines the altruistic threshold is not the overall mixing in the population, but the timing of the altruistic interaction in a life cycle which alternates clumping (here the production of offspring) and mixing (dispersal). Conditions just prior to the mixing phase should be more favourable for the evolution of altruism.

The haplodiploid Equation 11 is quite interesting, because its formal equivalence with the diploid Equation 10 helps to explain why behavioural models for diploid and haplodiploid populations often give the same results. Indeed, it suggests that this might typically be the case in models of the behaviour of mated females (as opposed to models in which male and female behaviour are considered separately). An example of this is found in my model of the dispersal of offspring (Taylor, 1988b) in which the ESS dispersal rate for mated females turns out to be the same for both genetic systems, though this is not the case when dispersal precedes mating. I did not have Equation 11 at that time; otherwise I might have understood better why this is expected.

Proponents of the inclusive fitness approach to modelling behaviour have always made it clear that all affected relatives must be accounted for. An important special situation is found in viscous populations in which any change in local fitness (due for example to some mutant behaviour) will result in a change in the level of local competition for resources, and hence affect the fitness of everyone in the neighbourhood. The above model provides a simple illustration of how the inclusive fitness accounting can be done in a simple model of altruism. Other illustrations of this effect of viscosity on inclusive fitness calculations can be found in models of sex allocation and dispersal (Taylor, 1988a,b).

A general model of interactions between relatives in an asexual population (Taylor, in preparation) shows that, in a homogeneous structured population with partial dispersal between sites, the inclusive fitness of a breeding female is independent of her direct effect on the fitness of her neighbours. The mathematical argument has the same form as that given above: the inclusive fitness Equation 1 involves all neighbours, but when the recursion Equation 3 for equilibrium is plugged in, all fitness effects cancel except the direct effect of the actor on herself. This is a striking result because it suggests that there may be quite general conditions under which, in geographically structured populations, the fitness effects of direct interactions between neighbours are neutralized by the competition between their offspring.

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