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Genetic relatedness in viscous populations

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Summary

Hamilton's inclusive fitness rule shows that the evolution of altruism is facilitated by high genetic relatedness of altruists to their beneficiaries. But the evolution of altruism is inhibited when the beneficiaries are also close competitors of the altruist, as will often be true in structured or viscous populations. However, Hamilton's rule still gives the correct condition for the evolution of altruism if relatedness is measured with respect to the local competitive neighbourhood.

Keywords: relatedness; altruism; viscous population; kin selection; Hamilton's rule

Selection on social interactions depends on both the fitness consequences of the behaviour and on the relatedness of the actor to the individuals affected. According to Hamilton's (1964a,b) inclusive fitness rule, an altruistic behaviour is favoured if $r_{xy} b - c > 0$, where c is the cost to the altruist, b is the benefit to the beneficiary, and r_{xy} is the relatedness of the altruist (x) to the beneficiary (y).

From the very beginning, two distinct means of benefiting relatives have been distinguished (Hamilton, 1964). First, relatives might be distinguished from other individuals that are encountered. This could be accomplished through genetic markers or through transitory patterns of association, such as being hatched in the same nest. Alternatively, Hamilton argued that limited dispersal would lead to what he called population viscosity, elevating local relatedness sufficiently to allow altruism towards neighbours in general.

Recently it has been discovered that this second mechanism does not necessarily work (Taylor, 1992a,b; Wilson *et al.*, 1992). While population viscosity does elevate relatedness towards neighbours, it also increases the extent to which neighbours are competitors. It has been recognized for some time that altruism may be harder to evolve if beneficiaries are close competitors (Alexander, 1974; West-Eberhard, 1975; Boyd, 1982; Pollock, 1983; Grafen, 1984; Wade, 1985). Specific examples include the devaluation of sons that compete with each other for mates, resulting in female-biased sex ratios (Hamilton, 1967), and the difficulty of evolving altruism among siblings competing for limited parental resources (Macnair and Parker, 1979; Metcalf *et al.* 1979). But it has only recently been shown, by computer simulation (Wilson *et al.* 1992) and analytical models (Taylor, 1992a,b), that the relatedness-enhancing and competition-enhancing effects of viscosity population exactly cancel under a variety of viscous population structures. Population viscosity often cannot lead to the evolution of unconditional post-dispersal altruism towards neighbours. (Altruism can still evolve if it occurs prior to dispersal (Taylor 1992a). It is also still possible for certain conditional post-dispersal behaviours (Goodnight, 1992; Queller, 1992a) and if dispersal is uncoupled from population regulation (Kelly, 1992; Taylor, 1992b)).

At first, this result may seem surprising from the standpoint of inclusive fitness theory. Taylor (1992a), following a general approach outlined by Grafen (1985), has shown that it is perfectly consistent. The trick is to use Hamilton's rule as intended, but to remember to explicitly include all individuals whose fitness is affected by a behaviour. If you help a neighbour to produce more

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offspring, then you are ultimately hurting someone else, whose offspring are displaced by the increased competition. Thus, for an altruistic behaviour resulting in *b-c* additional offspring, Hamilton's rule is correctly written as:

$$r_{xy}\, b - c - r_{\mathrm{xe}}\,(b - c) > 0 \tag{1}$$

where r_{xe} is the altruist's relatedness to the $b-c$ individuals in its economic neighbourhood displaced by competition (this is equivalent to the dispersal neighbourhood of Wilson *et al.* (1992)). When competition is global, $r_{\mathrm{xe}} = 0$, because the displaced individuals are a genetically random sample of the population. But when competition is local, the displaced individuals are expected to be relatives and must be included in the analysis.

An alternative way to incorporate these effects might be to put them all into the relatedness coefficient. Relatedness coefficients measure genetic similarity, expressed as deviations from the population mean. This is clear from the regression definition of relatedness, and even clearer when relatedness is expressed in a more general form due to Grafen (1985):

$$\mathrm{r} = \frac{\sum_x (p_y - \bar{p})}{\sum_x (p_x - \bar{p})} \tag{2}$$

Here $\bar{p}$ is the population frequency of an altruism allele, p_x is the frequency of the allele in all performers of altruism and P_y is the frequency in their beneficiaries. The summation is over all performers of the behaviour, indexed by x. Grafen's relatedness measure is closely akin to the more traditional covariance and regression measures, but is slightly more general in that for $\bar{p}$ it uses the actual population mean allele frequency rather than the mean frequency in potential altruists $\bar{p}_x$ and potential beneficiaries, $\bar{p}_y$ (Grafen, 1985). Selection, as always, really depends on the selected individuals being different from the population mean. Relatedness is simply the ratio of this difference for the beneficiaries and altruists. It is easy to adapt this measure to estimating relatedness from neutral marker alleles by letting each marker allele in turn stand in for an altruism allele (Queller and Goodnight, 1989).

This suggests that the effects of local competition might be incorporated by adjusting the population mean in Equation (2). Instead of using the global mean, one might use instead the mean frequency of the allele in each altruist's economic neighbourhood, $\bar{p}_e$. It is easy to show that this is so. Substitution of relatedness coefficients of the form of Equation (2) into Hamilton's rule (Inequality (1)) yields:

$$\frac{\sum_x (p_y - \bar{p})}{\sum_x (p_x - \bar{p})}\,\mathrm{b} - \mathrm{c} - \frac{\sum_x (p_e - \bar{p})}{\sum_x (p_x - \bar{p})}\,(\mathrm{b} - \mathrm{c}) > 0. \tag{3}$$

Collection of the *b* and *c* terms, followed by algebraic simplification, gives:

$$\mathrm{r} = \frac{\sum_x (p_y - p_e)}{\sum_x (p_x - p_e)}\,\mathrm{b} - \mathrm{c} > 0 \tag{4}$$

which is simply Hamilton's rule with the global population mean replaced by a local population mean (which could differ for different altruists). This means that, instead of explicitly summing up all the indirect fitness effects due to competition, we can still summarize the effect of selection with a single relatedness coefficient that measures relatedness with respect to the economic neighbourhood.

Peter D. Taylor (personal communication) has shown that a parallel result can be obtained using a covariance measure of relatedness, at least if the population is divided into discrete competitive neighbourhoods. This is not surprising given that Grafen's measure is a slight generalization of the covariance forms. John K. Kelly (personal communication) has derived another parallel result using a group selection analysis which is also not unexpected given the close formal correspondence between analyses based on group selection and inclusive fitness (Queller, 1992 b, c).

Inequality (1) is based on the assumption that altruist and beneficiary have the same economic neighbourhoods. This may not exactly hold in a viscous population lacking true group structure (K.F. Goodnight, personal communication). Indeed, one advantage of helping a beneficiary some distance away may be to diminish local competition. If we let $e(x)$ and $e(y)$ index the economic neighbourhoods of the altruist and beneficiary, respectively, the derivation above can be modified to give:

$$\frac{\Sigma\,(p_{y_x} - p_{e(y)})}{\Sigma\,(p_{x_x} - p_{e(x)})}\,\mathrm{b} - \mathrm{c} > 0. \tag{5}$$

These results have been shown strictly only for inelastic populations in which adding *b-c* fitness units means *b-c* fitness units must also be taken away somewhere else. It would be interesting to see if similar results can be obtained for elastic populations (Taylor, 1992b) in which this requirement is relaxed, at least for some neighbourhoods at some times. Since no population can expand indefinitely, even elastic increases in local fitness must have some eventual effect on competitors and a proper accounting of these eventual effects might yield an appropriate population mean frequency to use in place of the global mean. Of course, the more these competitive effects are removed to more distant future generations, the more likely they are to be distributed more globally, so that the global mean may often be a good approximation.

In terms of practice, this result is useful because it allows the genetic effects of selection to be summarized by a single relatedness coefficient that can be estimated from genetic markers in the customary way (Queller and Goodnight, 1989), the sole change being in the mean frequencies used. It also reinforces and gives rigour to the view that decisions about the reference population are integral to the meaning of any relatedness estimates. In our own studies of relatedness using genetic markers (Queller *et al.*, 1988, 1990, 1992, 1993; Strassmann *et al.*, 1989, 1991, 1992), we have attempted to sample from areas that are as small as possible, in order to avoid inflating relatedness estimates because of allele frequency differences between different geographic areas that do not compete significantly with each other. Our implicit assumption was that these geographic areas would be differentiated only if most competition was relatively local, in which case relatedness should be measured locally. If there were no differences between geographic areas, then it wouldn't matter whether sampling is local or global, because the mean frequencies are the same.

Pamilo (1984, 1989) has devised hierarchical *r*-statistics, analogous to *F*-statistics, that measure relatedness at different levels in subdivided populations. The results of this paper give some guidance in selecting among these possible measures of *r* and also expand the set of choices to a continuum. Relatedness should usually be measured with respect to the local population, where most of the competition resides. However, if the investigator has reason to believe (based on intuition or data) that an individual displaces a deme-mate x of the time and displaces an individual in another deme 1-x of the time, these values can be used as weights to obtain appropriate values of $\bar{p}$ for relatedness estimates. More generally, the message that needs to be remembered is that relatedness is not just a statement about the genetic similarity of two individuals, it is also a statement about who their competitors are.

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