Evolutionary Ecology Research, 2011, **13**: 747–752

Altruism in viscous populations revisited: competition and altruism do not exactly cancel even in the island model

Michael C. Whitlock and J. David Van Dyken

Department of Zoology, University of British Columbia, Vancouver, BC, Canada

ABSTRACT

Background: Hamilton suggested that cooperation would evolve most readily in viscous (low dispersal) populations, because nearby individuals would have high genetic relatedness. However, Taylor (1992) found that the indirect fitness gains achieved by cooperation with relatives is exactly offset by local competition, preventing true altruism from evolving no matter the degree of relatedness or population viscosity.

Question: Does local density regulation exactly cancel the indirect fitness benefits of altruism in Taylor's model?

Mathematical method: Inclusive fitness theory following the derivation of Taylor (1992).

Key assumptions: Relatedness depends on the effective deme size, N_e, but the distribution of fitness benefits depends on its census size, N.

Conclusions: For Taylor's model, the exact cancellation of the indirect fitness benefits of altruism by local competition requires the special case where $N_e = N$, a condition not often observed in nature. Even in Taylor's model, the benefits of altruism depend on relatedness, rather than just direct benefits. When $N_e < N$, as is commonly observed, true altruism can evolve, and it is more likely to do so when populations are more viscous. Local competition is important, but it requires restrictive conditions to exactly negate the effects of cooperation among relatives in a viscous population.

Keywords: altruism, competition, cooperation, inclusive fitness, island model, viscosity.

Hamilton (1964) showed that the spread and maintenance of altruism requires high relatedness among social partners. This led him to suggest that altruism will be most favoured in 'viscous' populations, that is, in populations with low rates of juvenile dispersal from natal patches, although Hamilton also acknowledged that local competition will slow the evolution of altruism. In a seminal paper, Taylor (1992) provided a serious challenge to both the notion that viscosity promotes altruism, and to the possibility that true altruism can ever evolve. Specifically, Taylor (1992) showed that, in a version of Wright's (1931) infinite island model, true altruism cannot evolve, regardless of the rate of dispersal. This result

---

Correspondence: M.C. Whitlock, Department of Zoology, University of British Columbia, Vancouver, BC V6T 1Z4, Canada. e-mail: whitlock@zoology.ubc.ca

highlighted the two opposing effects of viscosity, namely that it increases relatedness but impedes exportation of altruistic benefits before density regulation negates them. Taylor showed that these opposing effects of viscosity exactly balance in the island model when density regulation follows dispersal, such that the condition for the evolution of cooperation is:

$$\frac{b}{N} - c > 0. \tag{1}$$

This is interpreted to suggest that 'altruism' can only evolve if its direct benefit to the actor, b/N, exceeds the direct cost to the actor, c (Taylor, 1992; West *et al.*, 2002; Rousset, 2004). If true, then the trait is not truly altruistic (West *et al.*, 2007): it evolves because of its direct benefits, not the advantage gained by recipients. Taylor's elegant analytical investigation was motivated, in part, by the simulation results of Wilson *et al.* (1992), who arrived at the same conclusion: true altruism cannot evolve in this life cycle.

Taylor's result has been extremely influential, showing as it does that the negative effects of competition among relatives can exactly offset the gains reached through cooperation. The paper has made the important point that the inclusive fitness benefits of cooperation cannot be considered in isolation, because the effects of competition among relatives can be just as strong. Moreover, Taylor (1992) has spawned a substantial body of work aimed at identifying conditions where the exact balancing of relatedness and competition does not occur. For example, it has been shown that Taylor's paradox is avoided with overlapping generations (Taylor and Irwin, 2000; Lion and Gandon, 2010), 'budding' or 'propagule' dispersal (Gardner and West, 2006; Lehmann *et al.*, 2006), benefits that persist over multiple generations (Lehmann, 2007, 2008), or when selection is 'hard', such that groups are not locally regulated (Wade, 1985; Kelly, 1992, 1994; van Baalen and Rand, 1998; Alizon and Taylor, 2008; Lion and Gandon, 2009; Platt and Bever, 2009; Van Dyken, 2010). The implication is that altruism requires special conditions to overcome Taylor's paradox.

However, the fact that the effects of local competition and benefits of altruism exactly balance has perhaps been over-interpreted. We show in this paper that the exact cancelling observed in Taylor's model is the result of the very specific assumptions made in that model. Altruism does not require special conditions to overcome Taylor's paradox; rather, Taylor's paradox itself requires special conditions. The model could be adjusted in many ways to allow either competition or altruism to gain the upper hand, but here we show that a very small change in the model towards biological realism demonstrates that the cancelling is not exact.

Taylor's derivation uses N in two separate ways: (1) as the number of individuals sharing the benefits and (2) as an index of the amount of genetic drift in the population. The latter is appropriate under the restricted and stated assumptions of Taylor's model, where he assumes that each individual is equally and independently likely to give rise to each offspring individual. In general, however, genetic drift is not measured by the census population size, but instead by the effective population size, N_e, because in natural populations potential parents differ in their realized reproductive success more than predicted by assignment of offspring to parents in an equal and independent way, as assumed by ideal population conditions. The two numbers, N and N_e, are almost never equivalent in nature; in theory, N and N_e are equal only when the expected variance in reproductive success is exactly one (for haploids), and there is no biological reason for this variance to hold. (Note that N_e is usually different from N even with 'homogeneity' assumptions; the key parameter is the variance in realized reproductive success of each parent, not that each parent has an identical distribution of potential offspring.) In empirical studies, N_e is almost always much smaller than N. One estimate suggests that N_e is on average about 0.1 N across studies of multiple species (Frankham, 1995). Thus, in reality, the N that controls the distribution of benefits is different from the N_e that controls the magnitude of genetic drift and therefore relatedness to recipients.

We follow Taylor's original derivation to make clear the impact of this difference, using the simple haploid case. Taylor (1992) imagined an island model with a large number of populations, each of size N, each contributing and receiving a fraction m of its members to and from a migrant pool each generation. Before migration, adult individuals may interact with each other in a potentially altruistic way. Each individual that contributes to this interaction has its fitness reduced by a cost c, while increasing the fitness of each of the N members of the deme (including the contributor itself) by an amount b/N. Taylor's model is an example of 'whole-group' cooperation (Pepper, 2000), because the individual cooperator gets a share of the benefits itself. Thus the direct fitness effect to the contributor for this cooperation, exclusive of any indirect fitness effects, is $b/N - c$. After migration, local individuals compete for space, returning each population to be of size N. Importantly, Taylor implicitly assumed that each of the local populations behaved as an ideal population, such that the effective size N_e of each population was also N.

Taylor used $s = 1 - m$ to refer to the probability that an individual remains on its natal patch. Taylor showed that the marginal inclusive fitness (W) is given by

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

where R is the relatedness of a female to a randomly chosen offspring born in her population. It is useful to break this down to its component parts:

$$W = -c + \frac{b}{N} + bR_0 \frac{(N-1)}{N} - \frac{s^2 (b-c)}{N} - s^2 (b-c) \frac{(N-1)}{N} R_0, \tag{3}$$

where R_0 is the relatedness of two *different* randomly chosen females in the same deme at the time of the cooperative act. The five terms in this equation correspond to: (1) the direct fecundity cost to the focal individual for performing the act; (2) the fertility benefit to the focal individual gained by her share of the whole-group benefit of the act; (3) the fertility gain to related other females in the deme because of their share of the whole-group benefit; (4) the reduced survivorship of the focal individual's offspring as a result of the increased competition resulting from the changed fecundity in the deme, weighted by the probability s that an individual offspring remains resident and s that an extra competitor also remains resident at the time of population regulation; and (5) the effect of that competition on the offspring of related females. The role N plays in equation (3) is to describe how the benefits, b, are divided equally among the N individuals present in the population, independent of their relatedness status.

In Taylor's model, R_0 can be bundled in with the recurrence for R, because with an ideal population the probability that an individual is derived from the same parent (an important factor in determining the relatedness of two different individuals) is proportional to $1/N$. However, when $N_e \neq N$, that probability of co-ancestry is determined by $1/N_e$ instead.

Using the life cycle described by Taylor (for which the altruistic act would occur after dispersal in the life of an organism), the relatedness R_0 evolves according to the recurrence equation

$$R_0' = s^2\left(\frac{1}{N_e} + \frac{N_e - 1}{N_e} R_0\right). \tag{4}$$

Note that in this equation, N_e plays the role of determining the probability that two randomly chosen different offspring share the same parent. This probability is increased if some parents have a higher probability of reproductive success than others. The change in the probability of co-ancestry turns out to be proportional to the variance in reproductive success (Caballero, 1994).

At equilibrium, R_0 is given by:

$$\hat{R}_0 = \frac{s^2}{N_e - s^2(N_e - 1)}. \tag{5}$$

The condition for the evolution of the altruism allele is that the fitness effect W be greater than 0. This occurs when

$$b\,\frac{N_e + (N - N_e)\,s^2}{N_e N + (N - N_e)\,s^2} - c > 0. \tag{6}$$

In contrast, Taylor's result was that $b/N - c > 0$. Equation (6) reduces to Taylor's result in the special case where $N_e = N$, or when $s = 0$ (all individuals disperse). However, in the more biologically realistic case where $N_e < N$, there is an effect of relatedness that makes the evolution of altruism easier.

Equation (6) further demonstrates that selection for altruism in this model depends on the drift component of relatedness, N_e, as well as the dispersal component, s. Thus, the original interpretations that neither relatedness nor dispersal affects selection in this model do not hold when $N_e \neq N$. Population viscosity promotes kin selection in this model, provided that $N_e < N$.

These equations are not limited to the haploid case. Similar equations for the whole-group case can be derived, as did Taylor (1992) for diploidy with similar results (except that N_e is replaced by $2N_e$ in equations 4–6).

With variance in reproductive success, the cost term c needs to be modified by a coefficient that includes the effects of 'bet-hedging' (Lehmann and Balloux, 2010). However, if the variance in reproductive success is the same for all genotypes, this extra consideration only modifies the value of c and otherwise has no effect on our conclusions.

Previous workers (e.g. Kelly, 1994; Queller, 1994; Van Dyken, 2010) have derived an 'effective' coefficient of relatedness (West *et al.*, 2002), which expressed the relatedness of recipients of cooperation relative to average competitors (and standardized by a similar terms for the relatedness of the focal individual to competitors). The competition effective relatedness is given by

$$R_e = \frac{(1 - a)\,R}{1 - aR}, \tag{7}$$

where in this case a, the proportion of competition that is local, is equal to s^2(Van Dyken, 2010) and

$$R = \frac{1}{N} + \left(1 - \frac{1}{N}\right) R_0, \tag{8}$$

where R is the relatedness between two adults chosen with replacement from the same deme. Thus the contribution of the benefit to inclusive fitness is proportional to the competition effective relatedness, meaning that a form of Hamilton's rule can be retained: $bR_e - c > 0$.

Local competition greatly reduces the net fitness benefits of cooperation between local individuals. This insight was given great strength and mathematical rigour by Taylor's (1992) excellent exposition, which dramatically showed that competition effects can be as strong as the inclusive fitness effects through cooperation with relatives. However, the specific model in Taylor (1992) has a particular quirk, not mirrored in biology, which equates the amount of drift causing local relatedness with the effects of sharing of benefits. That quirk results in a model where two different effects seem to cancel out.

When N_e is much less than N, which seems to be the norm in biological systems (Frankham, 1995), the conditions for evolution of cooperation are greatly relaxed. In addition, more viscous populations will facilitate greater altruism, as found in some experiments with microbes (Kummerli *et al.*, 2009; Le Gac and Doebeli, 2010). Taylor's (1992) model is mathematically correct for its specific assumptions, but the specific conclusions that (1) competition cancels the effect of indirect selection and (2) viscosity does not promote altruism are sensitive to these specific assumptions. Local competition can greatly attenuate the benefits of cooperation, but exact cancellation of their effects requires specific conditions that are unlikely to hold generally in nature.

ACKNOWLEDGEMENTS

This work was support by a Discovery Grant from the Natural Science and Engineering Research Council (Canada) to M.C.W. and an NSF Postdoctoral Fellowship to J.D.V.D. We are very grateful to Peter Taylor and anonymous reviewers for very helpful comments on the manuscript.

REFERENCES

Alizon, S. and Taylor, P. 2008. Empty sites can promote altruistic behavior. *Evolution*, **62**: 1335–1344.

Caballero, A. 1994. Developments in the prediction of effective population size. *Heredity*, **73**: 657–679.

Frankham, R. 1995. Effective population size/adult population size ratios in wildlife: a review. *Genet. Res.*, **66**: 95–107.

Gardner, A. and West, S.A. 2006. Demography, altruism, and the benefits of budding. *J. Evol. Biol.*, **19**: 1707–1716.

Hamilton, W.D. 1964. The genetical evolution of social behaviour. I. *J. Theor. Biol.*, **7**: 1–16.

Kelly, J.K. 1992. Restricted migration and the evolution of altruism. *Evolution*, **46**: 1492–1495.

Kelly, J.K. 1994. The effect of scale dependent processes on kin selection: mating and density regulation. *Theor. Popul. Biol.*, **46**: 32–57.

Kummerli, R., Griffin, A.S., West, S.A., Buckling, A. and Harrison, F. 2009. Viscous medium promotes cooperation in the pathogenic bacterium *Pseudomonas aeruginosa. Proc. Biol. Sci.*, **276**: 3531–3538.

Le Gac, M. and Doebeli, M. 2010. Environmental viscosity does not affect the evolution of cooperation during experimental evolution of colicigenic bacteria. *Evolution*, **64**: 522–533.

Lehmann, L. 2007. The evolution of trans-generational altruism: kin selection meets niche construction. *J. Evol. Biol.*, **20**: 181–189.

Lehmann, L. 2008. The adaptive dynamics of niche constructing traits in spatially subdivided populations: evolving posthumous extended phenotypes. *Evolution*, **62**: 549–566.

Lehmann, L., Perrin, N. and Rousset, F. 2006. Population demography and the evolution of helping behaviors. *Evolution*, **60**: 1137–1151.

Lion, S. and Gandon, S. 2009. Habitat saturation and the spatial evolutionary ecology of altruism. *J. Evol. Biol.*, **22**: 1487–1502.

Lion, S. and Gandon, S. 2010. Life history, habitat saturation and the evolution of fecundity and survival altruism. *Evolution*, **64**: 1594–1606.

Pepper, J.W. 2000. Relatedness in trait group models of social evolution. *J. Theor. Biol.*, **206**: 355–368.

Platt, T.G. and Bever, J.D. 2009. Kin competition and the evolution of cooperation. *Trends Ecol. Evol.*, **24**: 370–377.

Queller, D.C. 1994. Genetic relatedness in viscous populations. *Evol. Ecol.*, **8**: 70–73.

Rousset, F. 2004. *Genetic Structure and Selection in Subdivided Populations*. Princeton, NJ: Princeton University Press.

Taylor, P. 1992. Altruism in viscous populations – an inclusive fitness model. *Evol. Ecol.*, **6**: 352–356.

Taylor, P.D. and Irwin, A.J. 2000. Overlapping generations can promote altruistic behavior. *Evolution*, **54**: 1135–1141.

van Baalen, M. and Rand, D.A. 1998. The unit of selection in viscous populations and the evolution of altruism. *J. Theor. Biol.*, **193**: 631–648.

Van Dyken, J.D. 2010. The components of kin competition. *Evolution*, **64**: 2840–2854.

Wade, M.J. 1985. Soft selection, hard selection, kin selection, and group selection. *Am. Nat.*, **125**: 61–73.

West, S.A., Pen, I. and Griffin, A.S. 2002. Cooperation and competition between relatives. *Science*, **296**: 72–75.

West, S.A., Griffin, A.S. and Gardner, A. 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J. Evol. Biol.*, **20**: 415–432.

Wilson, D., Pollock, G. and Dugatkin, L. 1992. Can altruism evolve in purely viscous populations? *Evol. Ecol.*, **6**: 331–341.

Wright, S. 1931. Evolution in Mendelian populations. *Genetics*, **16**: 97–159.