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Group selection in density-regulated populations revisited

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ABSTRACT

Recent theoretical studies have indicated that the evolution of cooperation can be severely constrained by the spatial scales over which density regulation acts. If density regulation occurs on a local scale within a group, variation in productivity among groups is suppressed and the among-group component of selection is eliminated. Here, I present the results from a simple model that shows that there is more scope for the evolution of cooperation under density regulation than previously thought. This statement, however, is conditioned upon the fact that the traits under selection are themselves involved in the density-regulating process. Furthermore, the results also suggest that traits directly involved in the density-regulating process, such as various competitive strategies or interference behaviours, are likely candidates for evolution through group selection, since they are not constrained by the ecological population structure to the same degree as other traits are. Laboratory experiments on group selection may provide some support for this hypothesis, since many traits that have been shown to be involved in the response to group selection are either directly or indirectly responsible for determining the strength of intraspecific competition.

Keywords: cooperation, competition, hard selection, intrademic selection, soft selection, structured demes.

INTRODUCTION

Many social behaviours not only influence an individual's own fitness but also the fitness of conspecific group members. One example of such behaviours are various cooperative behaviours, that is, behaviours that increase the fitness of conspecifics while at the same time incurring a fitness cost to the performer. The evolution of cooperation has formally been shown to include two (or more) hierarchical levels of selection (Wade, 1996), so that what ultimately determines whether a cooperative behaviour evolves is the balance between the relative strengths of selection within groups favouring non-cooperative behaviours and selection among groups favouring cooperation (Wade, 1985; Wilson, 1987).

Recent theoretical studies have indicated that the evolution of cooperative behaviours can be severely constrained by ecological processes, for example intra- and interspecific

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competition (Wade, 1996). In particular, the spatial scale over which density regulation occurs strongly affects when cooperation is expected to evolve (Boyd, 1982; Kelly, 1992a, 1994, 1997). If density regulation occurs locally within groups, groups with high mean fitness will experience stronger intraspecific competition than groups of lower mean fitness (Boyd, 1982; Kelly, 1992a). If density regulation is strong enough, differences in mean absolute fitness among groups (i.e. group size) will be diminished or completely eliminated by the density-regulating process (Wade, 1985; Kelly, 1992a). Since group selection is critically dependent upon the differential productivity of groups, strong local density regulation may either reduce or completely eliminate the among-group component of selection (Boyd, 1982; Wade, 1985; Kelly, 1992a,b).

Selection in subdivided populations has usually been analysed by contrasting the two simple models of soft (Levene, 1953) and hard (Dempster, 1955) selection, since these two models differ in the level at which density regulation occurs. Soft selection has been conceptually linked to local density regulation, whereas in models of hard selection, density regulation occurs on a global scale in the population (Levene, 1953; Dempster, 1955; Christiansen, 1975; Wade, 1985; Kelly, 1997). While the soft/hard selection dichotomy has primarily been studied from the perspective of the maintenance of genetic variation in spatially heterogeneous environments (e.g. Christiansen, 1975), it is clearly relevant for understanding the evolution of cooperation through group selection (Wade, 1985, 1996; Kelly, 1997). In fact, most models of the group selection process implicitly assume a population structure where density regulation occurs at a global scale in the population, thus implying hard selection (Wade, 1978; Michod, 1982; Wilson, 1983). Therefore, if local density regulation is the norm in natural populations, as ecological theory seems to suggest, the conditions under which we can expect cooperation to evolve will be severely constrained (Wilson *et al.*, 1992). Knowing the spatial scale over which density regulation occurs is thus crucial for understanding when cooperation can evolve in a subdivided population (Kelly, 1997).

Even though soft and hard selection models are conceptually linked to local and global density regulation, it may be somewhat misleading to assume that local density regulation always implies soft selection. If density regulation can occur locally without inducing soft selection, group selection can still be an effective force in the evolution of cooperation. The purpose of this paper is to point out that, under some conditions, selection can operate in a manner similar to hard selection even when density regulation is strictly local, contrary to what the soft/hard selection models seem to imply (Wade, 1985, 1996). An important set of characters for which this may be important are traits that are directly involved in the density-regulation process itself and thus determine the strength of intraspecific competition. Below I construct a simple model for the dynamics and evolution of a subdivided population and show that, for a broad range of conditions, group selection can favour the evolution of traits that reduce the strength of intraspecific competition, despite the occurrence of density regulation on a local scale.

GROUP SELECTION IN POPULATIONS WITH LOCAL DENSITY REGULATION

Consider a species with the following life-cycle: individuals mate randomly in a global population and each mating results in a group of C offspring that are full-sibs. The sib-groups remain as spatially subdivided groups during at least some portion of their development, during which viability selection and density regulation occur. Viability selection is assumed to occur only in relation to an individual's own genotype and thus does not depend on the genotypic composition of the group (see below). Density regulation thus constitutes a second round of natural selection that is distinct from viability and/or fertility selection (Kelly, 1997). After the period of population subdivision, groups dissolve and individuals disperse to form a global population, at which point mating and reproduction take place and the cycle repeats itself. The population structure of this example conforms to the intrademic group structure of Wade (1978), the structured deme model of Wilson (1977) and to the family structured models often used in studying kin selection (reviewed by Michod, 1982), with the exception that density regulation occurs locally, within groups.

This type of population structure is common for many organisms. For example, in many herbivorous insects, females often deposit eggs in spatially distinct clusters on the host plant (Grégoire, 1988; McCauley and Goff, 1997). The initial group structure, established by the oviposition behaviour of females, usually persists for at least the first couple of larval instars and ends after the larval period. Adults usually disperse some distance before mating and ovipositing to start the next generation (Grégoire, 1988). Similarily, many small mammals are territorial and live in kin groups during at least some part of their life (Chesser, 1991). If density regulation occurs during periods of group living, any variation in group size will tend to be reduced (or eliminated, depending on the strength of density dependence) by density regulation that occurs within larval groups.

Now, consider a trait such as resource consumption rate. It is easy to imagine that survival of individuals is positively correlated with resource consumption rate, so that higher resource intake translates into a higher survival rate. However, if resources are limited, only a certain number of individuals can survive at any given resource level. Thus, by reducing resource intake, individuals will suffer reduced survival. Hence individuals which reduce their feeding rate are selected against in competition with individuals that do not alter their feeding rate. On the other hand, by reducing resource intake, more individuals will be able to survive at any given resource level and groups with members with reduced feeding rates will, on average, be larger than groups without such individuals. Group selection will thus favour a reduced feeding rate. Clearly, there is a lower limit to the feeding rate that can evolve, and the feeding rate that ultimately evolves depends on the relative strengths of selection within and between groups and on the form of the relationship between feeding rate and survival.

A MODEL FOR THE EVOLUTION OF REDUCED INTRASPECIFIC COMPETITION

Consider further a locus with two alleles A_1 and A_2, that occur in frequencies q and p in the global population, $q = (1 - p)$. The three different genotypes A_1A_1, A_1A_2 and A_2A_2 are assumed to have viabilities W_{11}, W_{12} and W_{22}, respectively. As noted above, viability selection is assumed to occur within groups before density regulation occurs. If selection occurs only with reference to the local group, the allele frequency of allele A_1 after selection in group i is given by:

$$p'_i = \frac{f_{11(i)}W_{11} + \frac{1}{2}f_{12(i)}W_{12}}{\bar{W}_i} \tag{1}$$

where $\bar{W}_i = f_{11(i)}W_{11} + f_{12(i)}W_{12} + f_{22(i)}W_{22}$ is the mean fitness in group i with genotype frequencies $f_{11(i)}$, $f_{12(i)}$ and $f_{22(i)}$.

The size of group i after viability selection is then $C_i' = \bar{W}_i C_i$. After viability selection, density regulation occurs without respect to an individual's own genotype (but it may depend on the genotypic composition of the group; see below) and thus the local gene frequencies remain unchanged by the density-regulating process. Let the size of group i after density regulation, C_i'', be determined by:

$$C_i'' = C_i' g(C_i') \tag{2}$$

where g is a function describing the strength and form of density regulation as a function of the local group size after viability selection (C_i').

The global population size in the following generation is given by:

$$N^* = \sum_{i=1}^{n} C_i'' \tag{3}$$

The global allele frequency is given by:

$$p^* = \sum_{i=1}^{n} \frac{C_i''}{N^*} p_i' \tag{4}$$

It is worth noting that, if the fertility is the same for all genotypes (i.e. C is constant), the assumption of random mating after dispersal guarantees Hardy-Weinberg proportions among newly produced offspring in the following generation.

If the pattern of density regulation is the same in all groups – that is, g is independent of the local allele frequency – we have $C_i'' = \hat{C}$ for all i, and equation (4) reduces to:

$$p^* = \sum_{i=1}^{n} \frac{\hat{C}}{N^*} p_i' \tag{5}$$

where $\hat{C}/N'$ is constant for all groups, as expected under soft selection (Christiansen, 1975; Wade, 1985).

This implies that even though both allele frequencies and mean fitness may vary among groups, differential productivity of groups does not occur (i.e. $\mathrm{cov}(C_i'',p_i') = 0$; Wade, 1985). However, if the density-regulation regime is a function of the local allele frequency (i.e. g depends on p_i'), then the assumption of $\mathrm{cov}(C_i'',p_i') = 0$ is generally not true and equation (5) no longer holds (Wade, 1985). In this case, selection can no longer be considered to be soft, even though density regulation is strictly local within groups, and group selection for reduced intraspecific competition is possible.

To model density regulation when the density regime depends on the genetic composition of the local group, let the function g in equation (2) be given by (Hassell, 1975):

$$g(C_i') = \frac{1}{(1 + aC_i')^b} = \frac{1}{(1 + a\bar{W}_i C_i)^b} \tag{6}$$

Here, a is a parameter related to the group size after density regulation and b is a parameter that determines the strength and type of intraspecific competition (Bellows, 1981). This model is very flexible in modelling various density-dependent processes and, depending on the value of the parameter b, equation (6) can describe anything from density independence ($b = 0$) to strong over-compensation ($b \gg 1$) (Fig. 1; see also Bellows, 1981). Equation (6)

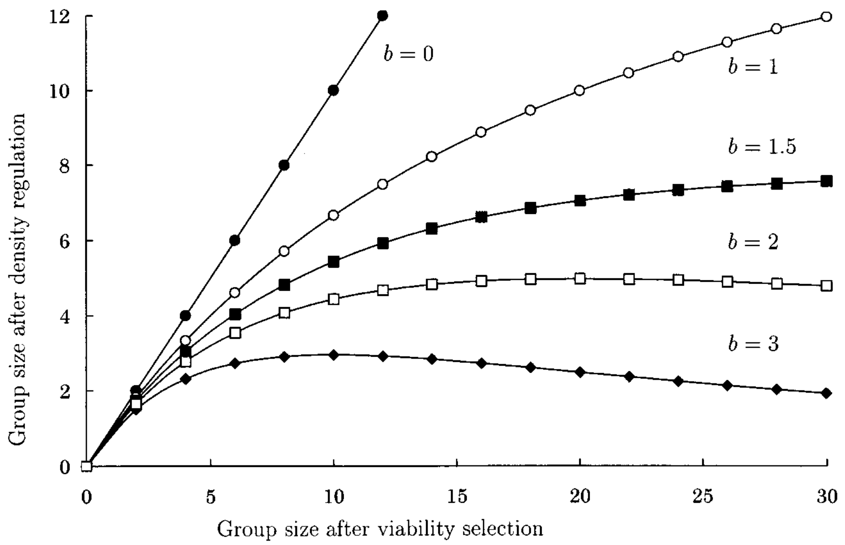

Fig. 1. The density-dependence function g used in the example in the text. Increasing values of b correspond to increasing strength of intraspecific competition.

is also less heuristic than many other models of density dependence, such as the logistic equation, since it is based on parameters that are, at least in principle, estimable (see Bellows, 1981, for a more detailed discussion).

Variation in traits related to competitive ability or strategy can thus be modelled by making the parameter b in equation (6) depend on the genotypic composition of the population. Let genotype A_1A_1 be associated with a competitive strategy, b_{11}, that leads to a different intensity of intraspecific competition than that of the A_2A_2 genotype with strategy b_{22} (i.e. $b_{11} > b_{22}$). The heterozygote is assumed to have a competitive strategy equal to $b_{22} + h(b_{11} - b_{22})$, where h is the dominance of allele A_1, so that $b_{12} = b_{11}$ when $h = 1$ and $b_{12} = b_{22}$ when $h = 0$. The average competitive strategy in group i can then be found as:

$$\bar{b}_i = f'_{11(i)}b_{11} + f'_{12(i)}(b_{22} + h(b_{11} - b_{22})) + f'_{22(i)}b_{22} \tag{7}$$

where $f'_{(i)}$ are the genotype frequencies in group i after viability selection. Equation (2) is thus modified to:

$$C''_i = \frac{C'_i}{1 + (aC'_i)^{\bar{b}_i}} = \frac{\bar{W}_i C_i}{1 + (a\bar{W}_i C_i)^{\bar{b}_i}} \tag{8}$$

where $\bar{b}_i$ is now a function of the local allele frequency, p_i, as specified in equation (7).

If the increased competitive ability that allele A_1 confers to its bearer results in a survival advantage (or vice versa that the reduced competitive ability of allele A_2 results in lowered fitness, that is $W_{11} \geq W_{12} > W_{22}$ holds whenever allele A_1 is at least partially dominant, $h > 0$), allele A_1 will be locally favoured within each group by natural selection. However, a decrease in p_i within a group will lead to more intense competition within groups, so that groups with low p_i will, on average, experience more intense intraspecific competition. The local group size after density regulation is determined by the strength of density regulation within groups (parameter $\bar{b}_i$ in equation 8), and since $\partial C''/\partial p_i > 0$ over the range of interest, $\mathrm{cov}(C_i'',p_i')$ will be positive (i.e. group selection leads to an increase in p_i).

Since the ecological population structure no longer constrains $\mathrm{cov}(C_i'',p_i')$ to zero, this opens up possibilities for evolution of genotypes with ‘reduced’ competitive ability and/or more prudent exploitation of resources (Wade, 1985; Wilson, 1987). However, whether such cooperation evolves ultimately depends on the balance between the opposing forces of selection within and among groups (Wade, 1985; Wilson, 1987).

To explore this phenomenon, I simulated the system consisting of equations (1) and (8) above. In the simulations, groups were formed by assigning genotypic frequencies in proportion to the relative frequencies of six different kinds of families that can be produced in the global population (Table 1; Michod, 1982). Two individuals were drawn at random (with replacement) from the global population to determine the parents of any given sib-group. Each individual was assumed to produce, on average, one sib-group so that a total of N sib-groups were established each generation with an upper limit set to 3000 for computational reasons.

Selection against the allele favouring cooperation was imposed within groups by assigning genotypes A_1A_1, A_1A_2 and A_2A_2 viabilities 1, $1-hs$ and $1-s$, respectively, where $0 \le h \le 1$ is the dominance coefficient of allele A_1. It is possible to use other fitness functions, such as the additive fitness functions commonly used in kin-selection models (Wilson, 1977, 1987) or even more sophisticated fitness functions that take pairwise interactions among genotypes into account (Cockerham *et al.*, 1972; Anderson and Arnold, 1983). However, the actual fitness functions chosen do not qualitatively change the results as long as the allele for cooperative behaviour is always selected against within groups. In the simulations, the selection coefficient s against allele A_2 was varied between 0.0 and 0.5. The average strength of intraspecific competition was calculated using equation (7) and density regulation was imposed locally in each group by using equation (8). In all simulations, b_{22} was assigned a fixed value of 1, while b_{11} varied between 1 and 3. After viability selection and density regulation, the global allele frequency in the following generation was calculated from equation (4). Each simulation began with allele A_2 being introduced at a low frequency ($q = 0.01$). The cycle described above was repeated every generation and simulations were run until the introduced allele had either been lost or driven to fixation.

Table 1. All possible family types, their frequencies under random mating and the offspring array within each family

Family type	Frequency	Offspring array
$A_1A_1 \times A_1A_1$	p^4	A_1A_1
$A_1A_1 \times A_1A_2$	$4p^3q$	$\frac{1}{2}A_1A_1$, $\frac{1}{2}A_1A_2$
$A_1A_1 \times A_2A_2$	$2p^2q^2$	A_1A_2
$A_1A_2 \times A_1A_2$	$4p^2q^2$	$\frac{1}{4}A_1A_1$, $\frac{1}{2}A_1A_2$, $\frac{1}{4}A_2A_2$
$A_1A_2 \times A_2A_2$	$4pq^3$	$\frac{1}{2}A_1A_2$, $\frac{1}{2}A_2A_2$
$A_2A_2 \times A_2A_2$	q^4	A_2A_2

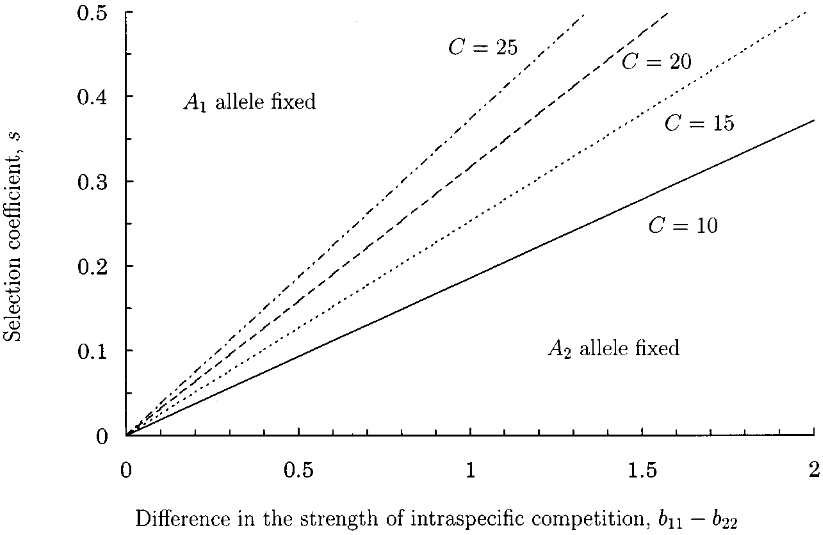

Fig. 2. Outcome of the evolution of cooperation via traits that reduce the strength of intraspecific competition in a population subdivided into sib-groups. Combinations of parameters that allow the evolution of reduced intraspecific competition fall to the right of the corresponding line, in the region marked 'A_2 allele fixed'. Increasing the clutch size C increases the range over which reduced intraspecific competition can evolve. The four lines correspond to $C = 10$, $C = 15$, $C = 20$ and $C = 25$. Other parameter values were $a = 0.025$, $h = 0.5$ and $b_{22} = 1$. Lines were fitted to simulated data using the least-squares method.

As can be seen from Fig. 2, evolution favours reduced intraspecific competition under a broad range of conditions. Combinations of parameters that allow the evolution of reduced intraspecific competition fall to the right of the corresponding line, in the region marked 'A_2 allele fixed' in Fig. 2. Increasing the clutch size, C, leads to an increased range over which cooperation is favoured (compare the four different lines in Fig. 2). This is not surprising, since an increase in clutch size will lead to more intense competition within groups, thus magnifying the effect of among-group variation in p on group size after density regulation (see Fig. 1).

DISCUSSION

Even though the model presented here is somewhat simplified, it clearly shows that even when density regulation occurs strictly on a local scale, evolution of cooperation through group selection can occur. Thus, there is a broader range under which cooperation can evolve through group selection, even with local density regulation, than has previously been thought (Boyd, 1982; Kelly, 1992a, 1994). However, this statement is conditioned upon the fact that the traits under selection are themselves involved in the density-regulating process, and it is this novel mechanism that makes evolution of cooperation possible in the model described here.

The resulting selective regime can be classified as hard selection, even though density regulation occurs within groups, since (1) selection leads to variation in group sizes and (2) the local group size is a function of local allele frequency (i.e. $\mathrm{cov}(C_i'', p_i') \neq 0$). This is somewhat counterintuitive, since local density regulation has been conceptually linked to soft selection (Christiansen, 1975; Wade, 1985; Kelly, 1997). However, as pointed out by Kelly (1997), the distinction between the models of soft and hard selection is only one way of representing variation in the ecological population structure. Soft and hard selection are thus only two ends of a continuum of possible ecological population structures and, as the present example clearly shows, soft and hard selection cannot generally be equated to local and global density regulation, respectively. In fact, soft selection represents an extreme form of local density regulation in the sense that density regulation is as strong as it possibly can be so that variation in productivity among groups is completely suppressed. It is also worth pointing out here that based on the assumptions made above (i.e. that individuals with reduced competitive ability are selected against within populations), evolution of reduced intraspecific competition of the form discussed here cannot evolve in an unstructured population, since it is critically dependent on among-group variation in productivity.

A similar situation was considered by Wilson (1987) for the evolution of altruism in mendelian populations derived from sibling groups. Wilson concluded that when local population size (K in Wilson's terminology) was independent of the local allele frequency of the altruistic allele, group selection could not operate and altruism would hence not evolve. When K was some function of local allele frequency, Wilson found that altruistic behaviours could evolve even though density regulation set an upper limit to the local population size, but he did not explore the implications of this further.

The scenario outlined above suggests that traits which are involved in the density-regulating process itself might be likely candidates to respond to group selection, since these traits are not constrained by the ecological population structure to the same degree as other traits might be (Wilson, 1980; Kelly, 1992a). It is interesting to note that many traits that have been shown to respond to group selection in laboratory experiments were either directly or indirectly involved in determining the strength of intraspecific competition. Such traits include competitive ability (Wade, 1980b, 1988; Dawson, 1982), cannibalism rates (Wade, 1979, 1980a; McCauley and Wade, 1980) and susceptibility to competition (Wade, 1979; McCauley and Wade, 1980). Thus, laboratory experiments on group selection may provide some possible support for the model presented here, since many traits that were involved in the response to group selection were either directly or indirectly responsible for determining the strength of intraspecific competition. Whether the same is true under more natural conditions is unclear and more field studies are required before we can assess the importance of group selection in the evolution of competitive strategies in natural populations.

Finally, it is interesting to note that the model presented here shares many similarities with Wilson's models of evolution of adaptive indirect effects between different species (Wilson, 1980, 1986). Both differ from the classic kin/group selection models in that they depend on the spatial scales of density regulation in exactly the opposite way. The evolution of adaptive indirect effects and the evolution of reduced intraspecific competition, as modelled here, both rely on density regulation acting on a local scale, while traditional kin/group selection models require density regulation to occur over the scale of the global population (Kelly, 1992a). These differences highlight the need to take the ecological population structure into account when studying the evolution of social behaviours in structured populations.

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