

Demography, altruism, and the benefits of budding

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Abstract

It is now widely appreciated that competition between kin inhibits the evolution of altruism. In standard population genetics models, it is difficult for indiscriminate altruism towards social partners to be favoured at all. The reason is that while limited dispersal increases the kinship of social partners it also intensifies local competition. One solution that has received very little attention is if individuals disperse as groups (budding dispersal), as this relaxes local competition without reducing kinship. Budding behaviour is widespread through all levels of biological organization, from early protocellular life to cooperatively breeding vertebrates. We model the effects of individual dispersal, budding dispersal, soft selection and hard selection to examine the conditions under which altruism is favoured. More generally, we examine how these various demographic details feed into relatedness and scale of competition parameters that can be included into Hamilton's rule.

Introduction

Explaining altruism is one of the greatest problems for evolutionary biology (Maynard Smith & Szathmáry, 1995; Hamilton, 1996; Frank, 1998). The problem is why should an individual carry out an altruistic behaviour that is costly to perform, but benefits another individual or the local group? In a series of classic papers, Hamilton (1963, 1964a, b, 1970) demonstrated that altruism can be favoured when social partners are related. What is needed is a large enough benefit (B) to the recipient, a small enough cost (C) to the actor, and sufficient relatedness (R) between the two such that Hamilton's rule ($R \times B > C$) is satisfied. Much of the work following up on this theory has focused on relatedness due to shared genealogy (kinship), which has been termed 'kin selection' (Maynard Smith, 1964; Hamilton, 1975; Frank, 1998). Hamilton (1964a, b, 1971) originally suggested that kin selection could favour the evolution of altruism through two scenarios: (1) direct kin recognition between individuals allowing preferential altruism towards closer relatives (kin discrimination); (2) limited dispersal ('viscous' population structure) leading to

genealogical closeness between social partners that could favour indiscriminate altruism.

Limited dispersal could potentially be a very important mechanism for favouring cooperation because it does not require any mechanism for kin discrimination (Hamilton, 1964a, b). Consequently, it could occur even in the simplest of organisms. This has led to limited dispersal being suggested as an important driving force in numerous specific cases, including the evolution of ATP pathways, the transition from single cells to multicellular organisms, cooperative behaviours in bacteria and other micro-organisms, the evolution of eusociality in social insects, cooperative breeding in vertebrates, and even mutualistic cooperation between species (Queller, 1992; Maynard Smith & Szathmáry, 1995; Crespi, 2001; Pfeiffer *et al.*, 2001; Griffin & West, 2002; West *et al.*, 2002a, b; Pfeiffer & Boenhoeffer, 2003).

However, a number of theoretical models have suggested that limited dispersal will not necessarily favour the evolution of cooperation (reviewed by Queller, 1992; West *et al.*, 2002a). The reason for this is that limited dispersal can also lead to competition between kin, which selects against altruism (Hamilton, 1971, 1975). Taylor (1992a, b) provided an elegant algebraic formulation of this problem. Low rates of dispersal result in genealogical closeness between social partners, but since the extra progeny created by altruism will compete locally for resources, altruistic groups will

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be characterized by more intense competition between individuals. Higher rates of dispersal reduce the severity of local competition, but reduce kinship as well. Taylor (1992a, b) showed that in the simplest possible case these two effects exactly cancel so that limited dispersal does not favour the evolution of altruism. Theory is required to examine the extent to which more complex and possibly biologically realistic assumptions can reduce this problem, and lead to limited dispersal favouring altruism (Kelly, 1992, 1994; van Baalen & Rand, 1998; Mitteldorf & Wilson, 2000; Taylor & Irwin, 2000; Pen & West, 2006).

Our first and major aim in this paper is to investigate the consequences of when individuals have the opportunity to disperse as groups, termed budding (Pollock, 1983; Goodnight, 1992; Wilson *et al.*, 1992). Reproduction by budding occurs in a diverse range of organisms, from unicellular life, through to groups of cooperatively breeding mammals such as meerkats (Clutton-Brock, 2002; Pfeiffer & Boenhoeffer, 2003). Budding could favour altruism if it decouples the positive and negative aspects of dispersal, i.e. the extra progeny created by altruism are exported to reduce local competition, yet they are exported together so their kinship is maintained. A possible role of budding has been suggested previously, but the selective forces are unclear and it has even been argued that budding could select against altruism (Pollock, 1983; Goodnight, 1992; Wilson *et al.*, 1992; Kelly, 1994).

Our second aim is to investigate the consequences of density dependent regulation before dispersal. This is the continuum between hard and soft selection and there appears to be confusion as to whether and how this could influence selection for altruism when there is limited dispersal, and how this might interact with budding (Wallace, 1968; Wade, 1985; Kelly, 1994). Our third aim is to relate our models to previous extensions of Hamilton's rule that allow for competition between relatives (Queller, 1994; Frank, 1998). For example, Frank (1998, ch7) added to Hamilton's rule a scale of competition parameter (a) that allowed competition to vary from local to global. This provided a clear heuristic overview of the area that has been very useful in explaining and comparing across biological examples (West *et al.*, 2001, 2002a, b; Griffin & West, 2002; West & Buckling, 2003; Gardner & West, 2004a, b; Gardner *et al.*, 2004; Giron *et al.*, 2004; Griffin *et al.*, 2004). However, it is not clear how this relates to specific processes such as individual dispersal, budding dispersal and hard or soft selection.

Models and analyses

Individual dispersal with soft selection

Taylor (1992a) used an inclusive fitness approach, based on the island model, to examine the impact of varying

degrees of individual dispersal (d_i) on the evolution of indiscriminate, 'whole-group' (Pepper, 2000) altruism. This is any helping behaviour that accrues a personal cost to the actor and also benefits the actor's group as a whole, with the group benefit shared equally among the group members—including the actor. This contrasts with 'others-only' (Pepper, 2000) altruism, where the direct benefits of the social behaviour do not accrue to the actor. Taylor demonstrated that the rate of individual dispersal is irrelevant in the asexual case, then reproduced this result for the sexual case, both for diploidy and haplodiploidy schemes. We now provide an explicit population genetic analysis of Taylor's model, focusing on the asexual case, and generalize the model by including an extra demographic parameter (s) that will describe the degree to which social group size is regulated before dispersal. The two extremes are soft selection ($s = 1$; Wallace, 1968) where group productivity is constant regardless of the social behaviour of its constituent individuals, and hard selection ($s = 0$; Wallace, 1968) where group productivity is the sum of absolute individual productivity. If hard selection is assumed the analysis is exactly equivalent to Taylor's model (Rousset, 2004)—the only differences are notational (all notation is summarized in Table 1).

Table 1 A summary of notation.

Symbol	Definition
R	Coefficient of relatedness in Hamilton's rule
B	Benefit component in Hamilton's rule
C	Cost component in Hamilton's rule
r	Kinship
b	Fecundity benefit of altruism for social partners
c	Fecundity cost of altruism for altruists
a	Scale of competition; proportion of competition occurring in the social group
A	Altruist
S	Selfish
i	Number of altruists in a social group
n	Social group size and bud size; the number of breeding spaces per patch
s	Degree of soft selection
d_i	Individual dispersal rate
d_B	Budding dispersal rate
m	Migration rate
$C_{A,i}$	Contribution of altruistic individuals to local progeny pool before soft selection
$C_{S,i}$	Contribution of selfish individuals to local progeny pool before soft selection
$P_{A,i}$	Number of offspring due to altruistic individuals after soft selection
$P_{S,i}$	Number of offspring due to selfish individuals after soft selection
K	Average number of offspring per individual in population after soft selection
t	Generation number
z	Altruism status of an individual: $z = 0$ (selfish), $z = 1$ (altruistic)
p	Frequency of altruists in the population, a vanishingly small quantity

A large population is composed of patches containing n individuals each. A vanishing proportion of individuals are altruists, whose altruism generates a fecundity benefit b shared equally over the individuals in their patch and incurs a fecundity cost c for themselves, in addition to baseline fecundity 1. Altruism implies $b, c > 0$ and, following Taylor, we will also assume weak selection ($b, c \ll 1$). The rest of the individuals in the population are selfish. After social interaction, all individuals in the population reproduce asexually (clonally) then die. The number of offspring in social groups is then regulated by random mortality according to the degree of soft (as opposed to hard) selection, s . After density-dependent regulation, offspring disperse individually with probability d_i to a random patch in the population, or else remain in their natal patch. After dispersal, n progeny in each patch are selected at random to live in that patch, and the remainder expire.

Individuals make large contributions to the local pool of progeny, according to their social behaviour (altruism, A ; selfishness, S) and the number of altruists (i) in their patch. An altruist occurring in a patch containing i altruistic and $n-i$ selfish individuals contributes:

$$C_{A,i} \propto 1 + \frac{i}{n}b - c, \tag{1}$$

and a selfish individual in a patch containing i altruists makes a contribution:

$$C_{S,i} \propto 1 + \frac{i}{n}b. \tag{2}$$

An individual parent will have a number of progeny surviving the soft selection process that depends on its contribution to the local progeny pool, the average contribution made by that social group, and the intensity of soft selection (s). For an altruist, this is:

$$P_{A,i} = K \frac{C_{A,i}}{s\{(i/n)C_{A,i} + [(n-i)/n]C_{S,i}\} + (1-s)C_{S,0}} \approx K \left\{ 1 + \frac{i}{n}[b - s(b-c)] - c \right\}, \tag{3}$$

where K is a large constant (we continue to assume a vast pool of progeny), and where the approximation is made on the assumption of weak selection ($b, c \ll 1$). The number of progeny produced by a selfish individual is

$$P_{S,i} = K \frac{C_{S,i}}{s\{(i/n)C_{A,i} + [(n-i)/n]C_{S,i}\} + (1-s)C_{S,0}} \approx K \left\{ 1 + \frac{i}{n}[b - s(b-c)] \right\}. \tag{4}$$

Lets consider a single focal altruist. A proportion d_i of this altruist's progeny is randomly dispersed into the population as a whole. Each dispersed progeny finds itself in a separate patch, competing with $(1-d_i)nK$ natives from that patch and d_inK immigrants to that patch, giving a total of nK competitors for the n breeding spaces on the patch. Since K is large, the probability that the progeny

successfully wins one of the n spots on the patch is approximately $1/K$, and hence the expected number of successful disperser progeny due to the focal altruist is:

$$d_i P_{A,i} \times \frac{1}{K} \approx d_i \left\{ 1 + \frac{i}{n}[b - s(b-c)] - c \right\}. \tag{5}$$

The focal altruist's nondispersing progeny compete with $(1-d_i)(iP_{A,i} + (n-i)P_{S,i})$ nondispersing natives (including themselves) and d_inK immigrants from elsewhere in the population. There are n spots available in the patch, so the expected number of successful non-dispersing progeny of the focal altruist is approximately:

$$n \times \frac{(1-d_i)P_{A,i}}{(1-d_i)[iP_{A,i} + (n-i)P_{S,i}] + d_inK} \approx (1-d_i) \left\{ 1 + (1-s)d_i \frac{i}{n}b - \left\{ 1 - \frac{i}{n}[1 - (1-s)]d_i \right\} c \right\}. \tag{6}$$

Expressions (5) and (6) can be added together to give the total number of successful offspring due to the focal altruist. If the average number of offspring over all altruists exceeds 1 (the population average) then altruism is favoured by selection. This allows us to write a condition for the increase of the frequency of altruism:

$$r\{b - [s + (1-s)(1-d_i)^2](b-c)\} > c, \tag{7}$$

where r denotes the expectation of i/n (averaging over altruists rather than over patches), which is the average kinship of an individual with its social partners (including itself; see appendix for details). Following Taylor, we can express kinship in terms of the model parameters if we make the assumption that the system has reached an equilibrium kinship. The expected kinship between an individual and its social group (including itself) in any generation (t) is a function of dispersal rate (d_t), patch size (n) and kinship in the previous generation ($t-1$). This can be broken down into several components: (1) with probability $1/n$ a randomly-chosen social partner is the focal individual itself, and kinship here is simply 1; (2) with probability $(n-1)/n \times (1-d_t)^2$ the social partner is not the focal individual, and neither of them dispersed from their natal patch, so their kinship is simply the kinship of their parents in the previous generation in that patch, i.e. r_{t-1} ; finally, (3) if the two are distinct individuals, and at least one of them dispersed away from its natal patch, their kinship is zero. Adding together these components, we have:

$$r_t = \frac{1}{n} + \frac{n-1}{n}(1-d_t)^2 r_{t-1}. \tag{8}$$

Equilibrium kinship satisfies $r = r_{t-1} = r_t$, yielding:

$$r = \frac{1}{n - (n-1)(1-d_t)^2}. \tag{9}$$

Thus, the model is closed, and differs from open models in which r is treated as an input parameter.

Substituting (9) into expression (7), we may write a full condition for the evolution of altruism in terms of only the model parameters (n, d_I, s, b, c) and not emerging quantities such as kinship (r). This is:

$$\frac{b - (s + (1 - s)(1 - d_I)^2)(b - c)}{n - (n - 1)(1 - d_I)^2} > c. \quad (10)$$

Expression (10) simplifies to give the condition:

$$\frac{1 - s}{n - s} b > c. \quad (11)$$

Note that the left-hand side of condition (11) is a decreasing function of s , so that whole-group altruism is increasingly disfavoured as the degree of soft selection is increased. This can be understood from a group-selection point-of-view: soft selection abolishes between-group differences in productivity, reducing the group benefit of altruism (Fig. 1a; Hamilton, 1964a; Wade, 1985; Rousset,

2004). For the special case of hard selection ($s = 0$), we recover Taylor's result: $b/n > c$. In a fully dispersing population ($d_I = 1$), b/n is the fitness benefit accruing to the actor due to its own altruism (its share of the group benefit b) and c is the fitness cost to the actor, so in this context the condition $b/n > c$ means that the whole-group altruism can be viewed as individual selfishness (Taylor, 1992a; Rousset, 2004), or 'weak altruism' (Wilson, 1990). Taylor's result shows that viscosity ($d_I < 1$) does not promote the evolution of whole-group altruism. Increased dispersal allows the export of the extra offspring produced by altruistic groups, relaxing competition within these groups, and in this way, it favours altruism. Yet, individual dispersal erodes the genealogical relationship between social partners, and in this way it disfavours altruism. The net result is the exact cancellation of these two effects, so that the rate of individual dispersal is irrelevant to the evolution of

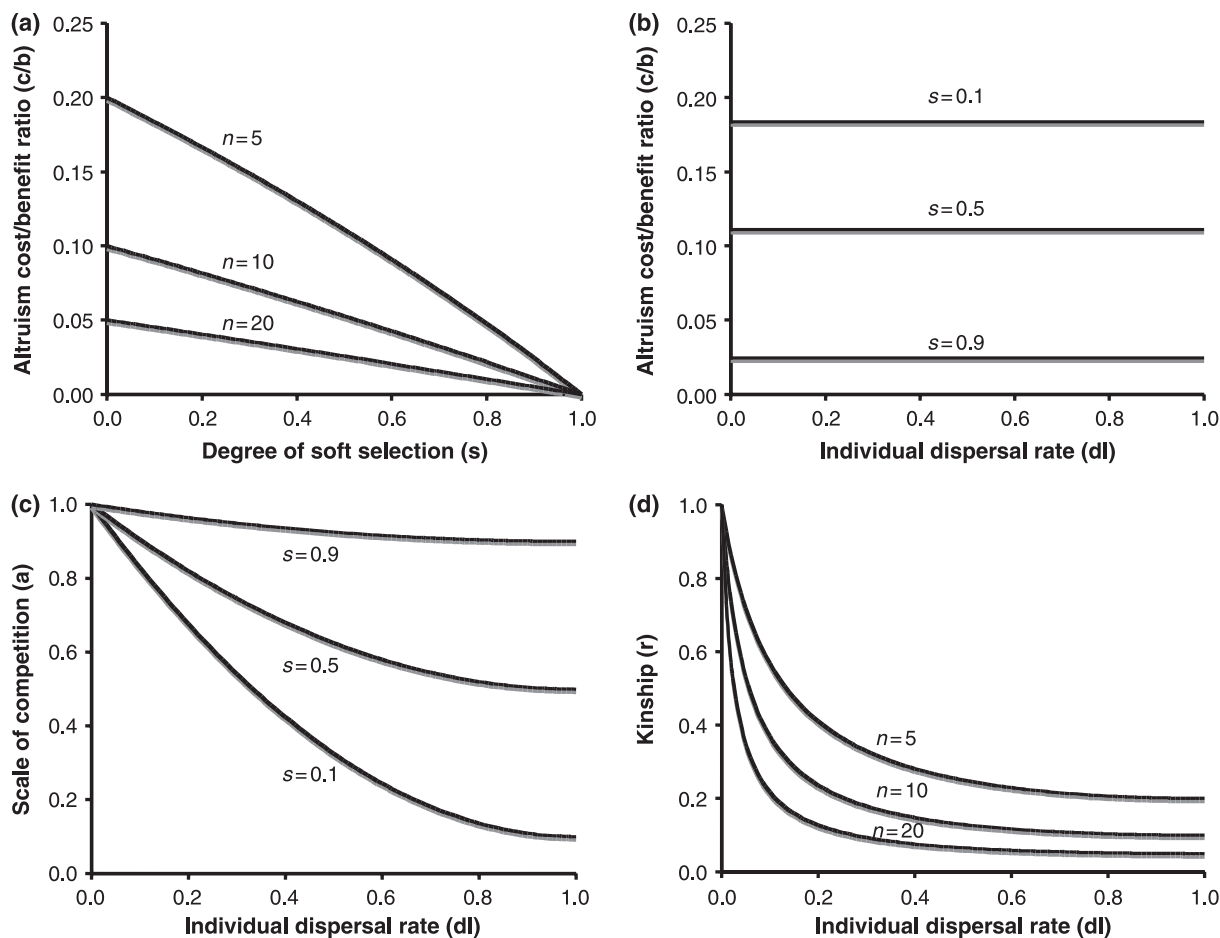


Fig. 1 Individual dispersal model. (a) The cost/benefit ratio (c/b), below which altruism is favoured and above which altruism is disfavoured, is a decreasing function of the degree of soft selection (s). Thus, soft selection inhibits the evolution of altruism. Numerical examples are given for group sizes $n = 5, 10$ and 20 individuals. (b) Individual dispersal (d_I) does not affect the evolution of altruism. Numerical examples are given for $n = 5$ individuals and $s = 0.1, 0.5$ and 0.9 . (c) Increased individual dispersal (d_I) reduces the scale of competition (a). Numerical examples are given for $s = 0.1, 0.5$ and 0.9 . (d) Increased individual dispersal (d_I) reduces equilibrium kinship (r). Numerical examples are given for $n = 5, 10$ and 20 individuals.

indiscriminate whole-group altruism (Fig. 1b). We have shown that this result holds more generally, over the continuum of hard to soft selection ($0 \leq s \leq 1$).

Budding dispersal with soft selection

We now consider a model of 'budding-viscosity' (Pollock, 1983; Goodnight, 1992; Wilson *et al.*, 1992; Kelly, 1994). Goodnight (1992) considered such details as sex, sexes and diploidy, which rendered his model intractable to mathematical analysis. The present model is idealized yet retains all the relevant biology required to address the consequences of budding, and has the advantage of being fully amenable to mathematical exploration. This is essentially the same model as described in the previous section, however it is now groups rather than individuals that disperse. We will consider that, immediately following predispersal regulation of patch productivity (soft selection), the surviving progeny on each patch are randomly organized into batches ('buds') each of n individual progeny, and that each bud disperses with a probability d_B and otherwise remains on the natal patch. Buds, and not individuals, then compete for patch ownership, with all or none of the individuals within a bud successfully winning a breeding spot in the contested patch. In general, bud size could be different from group size n . This model is intended to be illustrative rather than fully general, and so bud size of n is assumed for ease of analysis. We also allow for some exchange of individuals between groups (random migration at rate m) after density dependent regulation has returned all group sizes to n but before social interactions have occurred. This migration allows maintenance of within-group variation; some interesting results are obscured if we allow this to be exhausted. Migration also plays a role related to that of individual dispersal in the previous model, as we will see. Following the same procedure as in the previous section, we obtain a condition for whole-group altruism to be favoured:

$$r\{b - [s + (1-s)(1-d_B)^2](b-c)\} > c. \quad (12)$$

Applying the usual recursion method gives an expression for equilibrium kinship between individuals within patches:

$$r = \frac{1}{n - (n-1)(1-m)^2}. \quad (13)$$

Note that in the absence of migration between patches ($m = 0$) the equilibrium kinship is $r = 1$. Increasing the rate of migration after density-dependent regulation reduces the kinship between social partners. As before, we may express the condition for altruism to be favoured in terms of the model parameters (n , d_B , m , s , b and c):

$$\frac{b - (s + (1-s)(1-d_B)^2)(b-c)}{n - (n-1)(1-m)^2} > c. \quad (14)$$

As in the previous section, this condition can be re-written in form:

$$\frac{(1-s)(1-(1-d_B)^2)}{n-s-(n-1)(1-m)^2 - (1-s)(1-d_B)^2} b > c. \quad (15)$$

Again, we find that the left-hand side of (15) is a decreasing function of s (for $m > 0$), so that altruism is increasingly favoured as the degree of soft selection is increased (Fig. 2a). For $s < 1$, the left-hand side of (15) is an increasing function of d_B , thus altruism is increasingly favoured as budding dispersal is increased (Fig. 2b). This is because, like individual dispersal, budding dispersal has the benefit of allowing the export of excess productivity of altruistic groups, but unlike individual dispersal, budding dispersal does not cause dissociation of genealogical kin. This latter effect of individual dispersal is equivalent to the migration (m) of individuals between groups in the present model and, for this reason, the left-hand side of (15) is a decreasing function of m . Indeed, when the rate of budding dispersal and migration are constrained to be equal ($d_B = m$), the cancelling of these two effects occurs, and we obtain condition (11) from the previous section. In the absence of migration ($m = 0$), condition (15) simplifies to $b > c$, provided $s < 1$ and $d_B > 0$. The reason for this is that in this situation the equilibrium kinship between social partners is $r = 1$, and thus altruism is favoured if it gives any net benefit to the group. Because budding dispersal decouples the altruism-promoting and altruism-inhibiting effects of individual dispersal, enjoying the former without the latter, it allows indiscriminate whole-group altruism to evolve.

Hamilton's rule and demography

We will now explain the predictions of the previous sections with reference to the central conceptual result of social evolution theory—Hamilton's (1963, 1964a, 1970) rule. Frank (1998, ch. 7) allowed for competition between kin by incorporating into Hamilton's rule a parameter (a) that defines the extent to which local competition reduces the benefit of altruism. Using a direct fitness approach, Frank (1998, p. 115) derived a condition for when indiscriminate whole-group altruism is favoured by selection in the context of kin competition:

$$r(b - a(b-c)) > c. \quad (16)$$

The parameter a is the proportion of competition which occurs at the level of the social group (the remainder of competition is at the level of the global population), and which is therefore bounded between the extremes of local ($a = 1$) and global ($a = 0$) competition. Each altruist generates a local excess of progeny ($b - c$) due to their altruism, and localized competition destroys a proportion a of this, so in addition to the direct cost (c) and the kin selected benefit (rb) altruism is associated with an additional kin-competition cost ($ra(b-c)$). Frank (1998) subsumes this latter cost into the benefit component of Hamilton's (1963) rule:

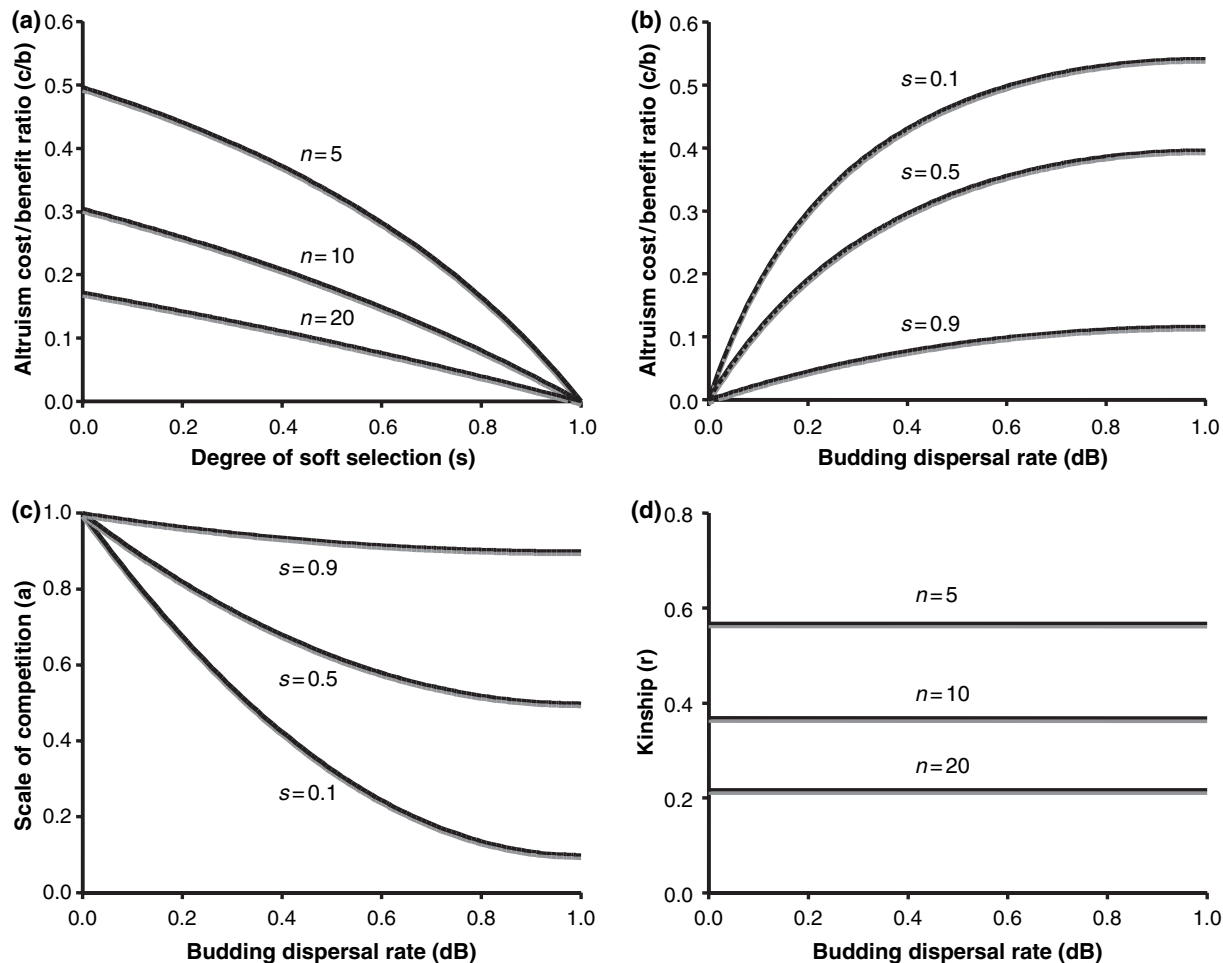


Fig. 2 Budding dispersal model. (a) The cost/benefit ratio (c/b), below which altruism is favoured and above which altruism is disfavoured, is a decreasing function of the degree of soft selection (s). Thus, soft selection inhibits the evolution of altruism. Numerical examples are given for group sizes (n) of 5, 10 and 20 individuals, budding dispersal rate $d_B = 0.5$ and migration rate $m = 0.1$. (b) Increased budding dispersal rate (d_B) increasingly favours the evolution of altruism. Numerical examples are given for $n = 5$ individuals, $s = 0.1, 0.5$ and 0.9 , and $m = 0.1$. (c) Increased budding dispersal (d_B) reduces the scale of competition (a). Numerical examples are given for $s = 0.1, 0.5$ and 0.9 . (d) Budding dispersal (d_B) does not affect equilibrium kinship (r). Numerical examples are given for $n = 5, 10$ and 20 individuals, and migration rate $m = 0.1$.

$RB > C$, where $B = b - a(b - c)$, $C = c$, and $R = r$ (here kinship provides the appropriate coefficient of relatedness). Although this has provided a useful heuristic method for explaining cases when local competition between kin is and is not important (see Introduction), it often is not clear how the parameter a relates to specific demographic processes. Here, we show how it relates to the models developed above.

In our analysis of the individual dispersal model, we encountered a Hamilton's rule (expression (10)) of Frank's form. Here, the scale of competition parameter is given by $a = s + (1 - s)(1 - d_i)^2$. Consequently, the scale of competition is the proportion of extra group productivity lost due to density-dependent regulation before dispersal (soft selection, s) plus the proportion lost due

to density dependent regulation after limited dispersal ($(1 - s)(1 - d_i)^2$), where $(1 - d_i)^2$ is the probability that two competitors for places in a patch are both native to that patch (i.e. neither dispersed). Thus, local competition increases as individual dispersal is reduced, countering the increase in kinship between social partners in increasingly viscous populations. Examining the model of budding dispersal, we derived a Hamilton's rule of the same form (expression (14)). Here the scale of competition parameter is given by $a = s + (1 - s)(1 - d_B)^2$ where d_B denotes the rate of dispersal of buds. Again, the intensity of local selection is given by the proportion of excess productivity that is eliminated by the predispersal regulation of group size, plus the proportion that survives this but is destroyed due to limited dispersal generating competition between

kin. The form of dispersal (individual or budding) is irrelevant in terms of the scale of competition (compare Figs 1c and 2c).

However, individual and budding dispersal impact on relatedness in entirely different ways. In the first model, increasing the rate of individual dispersal reduces equilibrium kinship between social partners (expression (9)), from $r = 1$ when $d_I = 0$ to $r = 1/n$ when $d_I = 1$ (Fig. 1d). But because kinship is preserved within buds, in the second model budding dispersal does not reduce kinship, so $r = 1/(n - (n - 1)(1 - m)^2)$ for the whole range of d_B (Fig. 2d). Thus, budding dispersal achieves the benefits of individual dispersal (reducing local competition) without incurring the costs (reducing kinship), and so it is more favourable to altruism. Note that the expressions for equilibrium kinship in the two models are equivalent, with m taking the place of d_I in the budding dispersal model. In the budding dispersal model, d_B stands in for d_I within the scale of competition parameter, and m stands in for d_I within the relatedness parameter. The two models are equivalent when $d_B = m = d_I$, and the second model additionally allows decoupling of the scale of competition and relatedness effects of dispersal by having d_B and m vary independently (Fig. 3).

An alternative methodology for incorporating the effects of localized competition into models of social evolution has been suggested by Queller (1994); see also Kelly (1994). The idea here is to incorporate local competition into the definition of relatedness itself. Rearranging Frank's form of Hamilton's rule (expression (16)), we obtain a Hamilton's rule of the Queller form:

$$\frac{r - ar}{1 - ar} b > c. \quad (17)$$

Here, we have the condition $RB > C$ where $B = b$, $C = c$ and $R = (r - ar)/(1 - ar)$. Queller's scheme measures relatedness not with respect to the average population member, but with respect to one's average competitor. If a proportion a of competition occurs at the level of the social group, and social partners (including self) have average kinship r , whereas individuals drawn from the population as a whole have average kinship of zero, then the average competitor has average kinship ar . Here, relatedness is the kinship of a social partner relative to oneself, measured with respect to the kinship of one's average competitor: $R = (r - ar)/(1 - ar)$.

In the individual dispersal model of the first section, we obtained an equilibrium kinship $r = 1/(n - (n - 1)(1 - d_I)^2)$ and a scale of competition parameter $a = s + (1 - s)(1 - d_I)^2$. Substituting into Queller's relatedness we have $R = (r - ar)/(1 - ar) = (1 - s)/(n - s)$, and the Hamilton's rule given by condition (11). In the budding dispersal model of the previous section, we obtained $r = 1/(n - (n - 1)(1 - m)^2)$ and $a = s + (1 - s)(1 - d_B)^2$, which gives a Queller relatedness $R = (1 - s)(1 - (1 - d_B)^2)/(n - s - (n - 1)(1 - m)^2)$

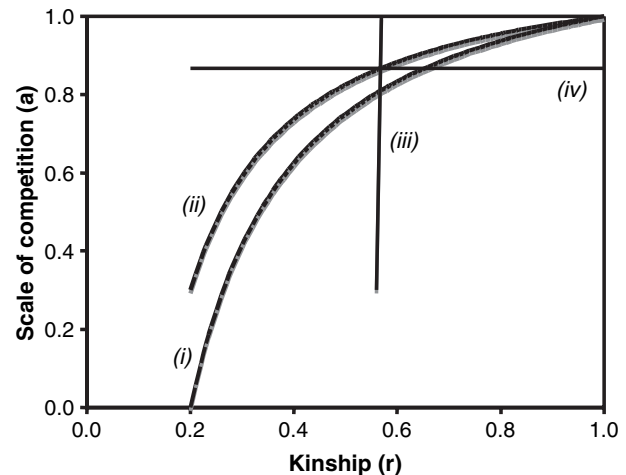


Fig. 3 In closed models, the relationship between the scale of competition and relatedness is determined by specific life-history assumptions and their parameter values (see text). We illustrate this with four examples: (i) Taylor's island model, for group size $n = 5$ individuals, and a range of individual dispersal rate, d_I (lower d_I leads to higher r and a). (ii) General individual dispersal model, for degree of soft selection $s = 0.3$, $n = 5$, and a range of d_I (lower d_I leads to higher r and a). (iii) Budding dispersal model, for migration rate $m = 0.1$, $s = 0.3$, $n = 5$, and a range of budding dispersal rates, d_B (higher d_B leads to lower a , and does not influence r). (iv) Budding dispersal model, for $d_B = 0.1$, $s = 0.3$, $n = 5$, and a range of migration rates, m (higher m leads to lower r , and does not influence a). The point at which (ii), (iii) and (iv) intersect corresponds to $d_I = 0.1$ in the individual dispersal model, and $d_B = 0.1$ and $m = 0.1$ in the budding dispersal model.

$-(1 - s)(1 - d_B)^2)$ and an associated Hamilton's rule given by condition (15).

These two methods are both correct, and represent different ways of conceptualizing the problem. The Hamilton's rules of Frank's (1998) form [conditions (12) and (20)] show clearly how demographic processes impact upon scale of competition and relatedness, helping to conceptualize why demography impacts upon social evolution in the way it does. The Hamilton's rules of Queller's (1994) form [conditions (13) and (21)] reveal the net effect of demography in a single measure of how individuals value their social partners (R), and are useful in that they highlight such results as that the rate of individual dispersal is irrelevant to the evolution of indiscriminate whole-group altruism.

Discussion

Budding, density dependence and the evolution of altruism

Hamilton (1964a, b) suggested that limited dispersal could lead to kin interacting and hence favour the evolution of altruism. However, it is now well

appreciated that limited dispersal can also increase competition between kin, which can reduce or negate this selection for altruism (Wilson *et al.*, 1992; Taylor, 1992a; Queller, 1992; West *et al.*, 2002a). We have shown that: (1) density-dependent regulation of patch size before dispersal (soft selection) selects against whole-group altruism, because it increases local competition between kin and hence reduces the local benefit of altruism (Fig. 1a; Wade, 1985); (2) groups of individuals dispersing together (budding) selects for whole-group altruism because it reduces local competition, whilst allowing a high kinship to be maintained. Budding could be an important mechanism for favouring altruism because it occurs in a diverse range of organisms, from unicellular life to cooperatively breeding vertebrates. In addition we used our models to show how conceptual overviews in this area provided by Frank (1998) and Queller (1994) can be related to specific demographic parameters.

The impact of budding (and other forms non-independent dispersal) on the genetic structure of populations has received some attention (Whitlock & McCauley, 1990; Wade *et al.*, 1994). The consequences of budding dispersal for the evolution of altruism have been considered previously by Pollock (1983), Goodnight (1992), Wilson *et al.* (1992) and Kelly (1994), usually from a group selection perspective. Pollock (1983) provided a deterministic argument that budding selects against altruism because while altruistic groups would proliferate, they are inevitably overrun from within by selfish variants. Ultimately between-group variation in altruism would be exhausted, yet within-group selection would continue to ensure that each generation was more selfish than their parents. In contrast, Goodnight (1992) demonstrated that stochastic sampling error resulting from finite group size would continue to generate between-group variation so that altruism could result as a response to group selection. Goodnight's (1992) model was considered too complicated for a full analytical treatment, so he employed a simulation study. We have explored a much simpler model that can be analysed using a kin selection framework, but nevertheless retains all the crucial elements of the argument. It should be noted that, for a whole-group trait such as the indiscriminate altruism considered in this article, the kin selection coefficient of relatedness is equal to the proportion of trait variance that is between-group as opposed to within-group, thus there is an equivalence between the group selection and kin selection approaches (Price, 1972; Hamilton, 1975; Wade, 1985; Frank, 1986, 1998; Queller, 1992).

We have followed the aforementioned studies in using the term 'budding dispersal' to describe the partitioning of groups into randomly sampled daughter groups, and subsequent long-range dispersal of these daughters. However, budding has somewhat different connotations in the social insects world, where it is contrasted with alternatives such as 'group fissioning' according to how

the daughter group is derived from the parent, and how far it disperses (Bourke & Franks, 1995), details with clear implications for both relatedness and scale of competition. In the microbial world, a bud produced by an individual or colony might normally be thought of as comprising clones derived from the same parental cell, and this will have a large impact on relatedness structure and altruism evolution. We emphasize that the present article is intended only as an illustration of a broader principle, and to highlight that the pattern of dispersal does have important consequences for the evolution of social behaviours. Specific models for specific organisms would be very useful.

An important demographic feature which has been left out of our and previous analyses is elastic population structure. Elasticity is the extent to which the capacity of a patch stretches to accommodate increases in local density of individuals (Hamilton, 1971; Taylor, 1992b). Although the present analysis considers the continuum of hard to soft selection, this concerns only the part of density-dependent regulation before dispersal, and the model is actually fully inelastic since all patch sizes are returned to n individuals after dispersal. At first glance, the ability of a population to make extra room for progeny created by altruism may seem implausible, yet it would feature in a range of situations. For example, altruistic alarm-calling will allow for a higher carrying capacity insofar as predation is an important regulator of population density (Clutton-Brock *et al.*, 1999); this highlights that the scale of competition will often be different for different traits (Gardner & West, 2004a). An extension to this model for arbitrary elasticity, and the impact of this on the scale of competition, would require fluctuating group sizes and hence a major departure from the classic island model. So as not to obscure the main results of this article with an overly complicated analysis, we leave elasticity as an open problem for the future.

Localized competition and Hamilton's rule

We have shown how the general extensions of Hamilton's rule provided by Queller (1994) and Frank (1998, ch7) can be related to specific demographic parameters. For example, Frank showed that the effect of competition between relatives could be incorporated in Hamilton's rule by having the marginal benefit of altruism reduced by an amount $a(b - c)$, where a is the spatial scale at which competition occurs, which varies from completely global ($a = 0$) to completely local ($a = 1$). This (and Queller's) formulation has been useful for discussing and generalizing across empirical examples ranging from chemical warfare and cooperative foraging in bacteria to lethal fighting in wasps to altruism in cooperative vertebrates (West *et al.*, 2001, 2002a; Gardner & West, 2004a, b; Gardner *et al.*, 2004; Giron *et al.*, 2004; Griffin *et al.*, 2004). However, it is often not clear what the parameter a explicitly represents. We have

shown that this is because the parameter a incorporates a range of demographic processes (e.g. the dispersal rate, whether budding occurs and the extent of soft and hard selection), and this could be extended to include other factors that have been shown elsewhere to influence the consequences of limited dispersal, such as when dispersal occurs, the form of density regulation, overlapping generations, or mating system (Kelly, 1992, 1994; Taylor, 1992a, b; Queller, 1992; Wilson *et al.*, 1992; Mitteldorf & Wilson, 2000; Taylor & Irwin, 2000; West *et al.*, 2002a, b; Pen & West, 2006). This emphasizes the general point that the simplicity of Hamilton's rule and extensions such as provided by Frank (1998, ch. 7) means that they hide a lot of detail. Consequently, they are best used for the interpretation of results and not as the starting point for a theoretical analysis, because it is not known a priori how parameters such as r and a will be correlated (Taylor & Frank, 1996; Frank, 1998; Fig. 3).

To conclude, our analyses also clarify the utility of two very different approaches in social evolution theory. The approach of Taylor (1992a, b), which we have used here, is to develop explicit closed models in which parameters such as kinship (r) are determined by the demographic assumptions and hence other parameters of the model (e.g. dispersal rate; Fig. 3). The advantage of this approach is that it allows specific questions to be answered. For example, given a specified life history, does limited dispersal favour the evolution of altruism? The alternative approach of Frank (1998, ch. 7) is to have a more general open model in which parameters such as relatedness and the scale of competition are left more nebulous and allowed to vary independently. This approach is useful for interpreting and relating the results of different closed models, as well as providing a single framework for discussing biological examples. Put another way, open models allow a general framework for discussing how relatedness and the scale of competition interact over the evolution of altruism, whereas closed models explicitly determine how these parameters and their consequences will be intertwined for specific cases (Fig. 3).

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Appendix

Earlier we substituted the expected fraction of altruists per social group, averaging over altruists, with the kin

selection coefficient of relatedness r . The coefficient of relatedness with respect to a particular trait is properly given by $r = \text{Cov}(z', z)/\text{Cov}(z, z)$, where z is a focal individual's trait value, z' is the trait value on average of the focal individual's social partners, and Cov is the covariance taken over all individuals in the population (e.g. Frank, 1998). We will take z to represent the presence ($z = 1$) or the absence ($z = 0$) of the altruistic allele, allowing us to write:

$$r = \frac{P[z' = 1 \& z = 1] - P[z' = 1]P[z = 1]}{P[z = 1 \& z = 1] - P[z = 1]^2}, \quad (\text{A1})$$

where P denotes a probability. $P[z = 1]$ is the probability that a randomly-chosen individual is an altruist, and this is simply p , the population frequency of altruists. $P[z' = 1]$ is the probability that a randomly chosen social partner is an altruist, unconditional on the altruism status of its associated focal individual, and again this is simply p . $P[z' = 1 \& z = 1]$ is the probability that both a randomly chosen focal individual and a randomly chosen social partner of this focal individual are altruists, which is equal to the probability that the focal individual is an altruist multiplied by the probability that the social partner is an altruist conditional on the focal individual being an altruist, $P[z = 1] \times P[z' = 1|z = 1] = p \times P[z' = 1|z = 1]$. Finally, $P[z = 1 \& z = 1]$ is the probability that a randomly chosen individual is an altruist and is also an altruist, i.e. simply the probability that it is an altruist, $P[z = 1] = p$. Substituting this in gives:

$$r = \frac{p \times P[z' = 1|z = 1] - p \times p}{p - p^2} = \frac{P[z' = 1|z = 1] - p}{1 - p}. \quad (\text{A2})$$

Under the assumption of vanishingly rare altruism, we can write $r \rightarrow P[z' = 1|z = 1]$ as $p \rightarrow 0$, so that the appropriate kin selection coefficient of relatedness is simply the probability that a randomly chosen social partner is altruistic conditional on the focal individual being an altruist. In other words, it is the expected proportion of altruists in an individual's social group, averaging over all altruistic individuals in the population. Thus, when we average the number of successful progeny [eqns (5) and (6)] over all altruistic individuals, we may replace the expectation of i/n (conditional on the focal individual being an altruist) with relatedness r .

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