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Diminishing returns in social evolution: the not-so-tragic commons

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social insects;
tragedy of the commons;
vampire bats.

Abstract

A challenge for evolutionary theory is to understand how cooperation can occur in the presence of competition and cheating, a problem known as the tragedy of commons. Here I examine how varying the fitness returns from reproductive competition or cooperation affects the negative impact of competition on a social group. Varying linear returns does not affect the impact of competition. However, diminishing returns, where additional investments in either competition or cooperation give smaller and smaller rewards, reduce the effects of competition on the group. I show that diminishing returns are common in many systems, including social vertebrates, microbes, social insects and mutualisms among species. This suggests that the tragedy of the commons is not so tragic and that the disruptive effects of competition upon social life will often be minor.

Introduction

'…what keeps competition from destroying the common good that could be created by cooperating?' Egbert Leigh Jr (Leigh, 1999)

This question is considered one of the fundamental problems in evolutionary biology (Leigh, 1977, 1983, 1999; Buss, 1987, 1999; Frank, 1995; Maynard Smith & Szathmáry, 1995; Wilson, 1997a; Michod, 1999a, b; Reeve & Keller, 1999; Foster & Ratnieks, 2001a). It goes under several names including the freeloaders paradox, N-person prisoner's dilemma and perhaps most famously Garrett Hardin's tragedy of the commons (Hardin, 1968; Leigh, 1977; Frank, 1995; Michod, 1999a; Hauert *et al.*, 2002; Wenseleers & Ratnieks, 2004). Hardin observed that in a commons pasture open to many herdsmen, the best strategy for each herdsman is to add as many cattle as possible, although this eventually causes the demise of the pasture. The tragedy arises because the benefit of adding a cow goes directly to the owner, while the cost is shared amongst all herdsmen (Hardin, 1968). Similarly, in social groups, natural selection is predicted to favour selfish replicators that pursue their own interests and disrupt group function (Leigh, 1977; Leigh, 1983; Frank, 1995; Michod, 1999a). A number of solutions have been proposed for this problem, which I divide into four nonmutually exclusive classes (i) selfish benefits of cooperation, (ii) preferential association of cooperators, (iii) enforcement and (iv) optional participation.

The tragedy of the commons is reduced when cooperation enhances the personal reproduction of the actor. Most simply, there is no tragedy for social traits that improve the actor's reproduction as well as other individuals ('by product benefits' Connor, 1995; Dugatkin, 1998, 2002; Sachs *et al.*, 2004). An example is Hamilton's selfish herd where the anti-predator benefits of grouping improve both the fitness of individuals and the group (Hamilton, 1971). A subtly but significantly different type of individual benefit occurs when an actor receives a share of the group benefit of cooperation (Wilson, 1975), such as with extracellular feeding enzymes in bacteria (Brown, 1999; Crespi, 2001). Here, there is still a tragedy of the commons because an individual can benefit from not producing the enzyme and freeloading on the others' enzyme production. However, because freeloading lowers the total enzyme level, there is also an individual cost which, particularly in small groups, will favour some enzyme production through trait group selection (Wilson, 1975, 1977, 1980, 1990; Dugatkin, 1998, 2002; Avilés, 2002). This is also known as Simpson's paradox (Sober & Wilson, 1999; Semmann *et al.*, 2003).

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The effect can be modelled in a kin selection framework by including relatedness to self in the measure of group relatedness (Frank, 1996; Brown, 1999; Pepper, 2000), but it is not strictly kin selection because the benefits of cooperation do not come from helping kin.

Competition is also reduced by factors that cause cooperators to preferentially associate, because this prevents their exploitation by noncooperative cheaters. Famously, high relatedness ensures that the action of genes for cooperation benefits other individuals carrying the same genes (Hamilton, 1964; Frank, 1995). An association formally comparable with relatedness (Frank, 1994a) is generated when unrelated individuals or species have a shared fate ('partner fidelity', Bull & Rice, 1991; Sachs *et al.*, 2004). Relatedness can be generated by kinship (Hamilton, 1964), while population viscosity (Nowak & May, 1992; Killingback *et al.*, 1999; Mitteldorf & Wilson, 2000; Le Galliard *et al.*, 2003, but see West *et al.*, 2002a) or physical linkage such as genes on chromosomes (Bull & Rice, 1991; Frank, 1994a) can generate partner fidelity or maintain kinship relatedness. In addition, Pepper & Smuts (2002) showed that individuals distributing in response to the environment can produce positive associations of cooperators. The strongest associations occur when cooperators are able to directly identify each other. This can arise through a cooperative gene identifying an identical copy in another individual (Hamilton, 1964, 'green beard genes' Dawkins, 1976) or more generally through 'partner choice' where individuals identify and interact only with individuals with a cooperative phenotype (Axelrod & Hamilton, 1981; Bull & Rice, 1991; Noë & Hammerstein, 1994; Sachs *et al.*, 2004). In a similar vein, reciprocal altruism can promote preferential interactions among cooperators through behaviours such as Tit for Tat, where individuals help those that help them (e.g. Axelrod & Hamilton, 1981; Brembs, 1996; Dugatkin, 2002). Reciprocal altruism is restricted to organisms that conditionally respond based upon recognition and/or memory of previous interactions (e.g. Dugatkin, 2002; Pepper & Smuts, 2002) but is notable because cooperation can be maintained through chaotic dynamics (Nowak & Sigmund, 1993). Indirect reciprocity can also drive cooperation in human societies when helping others improves reputation and increases the probability that an individual will receive help in the future (Nowak & Sigmund, 1998).

Enforcement mechanisms can prevent competition and the tragedy of the commons (Leigh, 1977; Alexander, 1979, 1987; Maynard Smith, 1988; Ratnieks, 1988; Frank, 1995, 2003; Foster & Ratnieks, 2001a). Most simply, some individuals may enforce the cooperation of others when power is unevenly distributed. This occurs in the mutualism between the fluorescent bacteria *Vibrio fischeri* and the squid *Euprymna scolopes*, which uses the bacteria for bio-illumination (Sachs *et al.*, 2004). Visick *et al.* (2000) showed that bacteria which did not produce the light production enzyme luciferase were prevented from growing in the squid light organ. This is also an example of partner choice (Sachs *et al.*, 2004). Mutual policing, where group members invest in the suppression of each other's reproduction, is another potentially important mechanism of conflict suppression (Frank, 1995; Keller, 1999). Mutual policing occurs in the social insects (Ratnieks, 1988; Ratnieks & Visscher, 1989; Foster & Ratnieks, 2001a), while recombination (Haig & Grafen, 1991) and meiosis (Hurst & Pomiankowski, 1991) may reflect the policing of selfish genetic elements within a 'parliament of genes' (Leigh, 1977).

Finally, optional participation may reduce competition. A recent game theory model (Hauert *et al.*, 2002) and experiment (Semmann *et al.*, 2003) has shown that if some individuals opt out of sociality (loners), then cooperation is promoted. This occurs through a rock-paper-scissors dynamic where cooperators are invaded by defectors, and defectors are invaded by loners, which in turn, can be invaded by cooperators. The negative effect that the loners have on the defectors facilitates the maintenance of cooperators in the population.

Selfish benefits, associations of cooperators, enforcement, and optional participation, therefore, can all limit the tragedy of the commons. However, the tragedy is still often expected to be severe, particularly in low relatedness groups that lack effective enforcement (Frank, 1995; Keller, 1999). Here I show that even under such conditions the negative effects of competition can be minor. A model is examined in which group members can either invest in selfish reproductive competition or in a cooperative group trait. I alter the rate of return from reproductive competition and cooperation and examine how this affects predictions. Models of cooperation typically assess sociality from how much each group member invests in cooperation (e.g. Brown, 1999; Killingback *et al.*, 1999; Avilés, 2002; Hudson *et al.*, 2002; Le Galliard *et al.*, 2003). Here I focus instead on group performance to measure of the impact of competition and specifically address the problem posed by the tragedy of the commons. For each case, I ask how similarly does the group perform to a group free from competition?

The model

The model describes a social group in which individuals have a fixed amount of resources that they can either invest in reproductive competition or in a cooperative group trait. I take reproductive competition to mean any activity that increases personal reproduction relative to other group members. Cooperative traits are those that increase the fitness of other group members. The key variable in the model is z, which is the proportion of personal resources that group members invest in reproductive competition, where $1 - z$ is the proportion that group members invest in a cooperative trait. This follows the fundamental assumption of the tragedy of the commons that investment in reproductive competition will decrease investment in cooperation and lower group performance. Examples that fit this scenario include release of foraging enzymes in bacteria (Crespi, 2001), sentinel behaviour in vertebrates (Trivers, 1971), nest building in eusocial hymenoptera (Wilson, 1971) and stalk formation in the slime mould *Dictyostelium discoideum* (Kessin, 2001).

I investigate the effect on group performance of altering the relationship between either investment in competition (z) or investment in cooperation ($1 - z$) and the resulting benefit. Group performance at equilibrium measures the impact of competition on cooperation and gives group productivity relative to a perfectly cooperative group without competition, such as a clonal group. The personal benefit from investment in competition is defined by the function $f(z)$ and the group benefit from investment in cooperation defined by $g(z)$. These are combined using the multilevel selection approach to social evolution developed by Price (1970, 1972). This partitions fitness into two components, one due to the differential success of individuals within groups (individual performance or within-group selection) and one because of the differential success of groups within the population (group performance or between-group selection, Wilson, 1975, 1977). The analysis uses the methods developed by Frank (1994b, 1995, 1996, 1998, Appendix A) and Taylor & Frank (1996) and assumes idealized social groups of constant size that come together each generation, do not mix and lack explicit spatial structure. Although this removes much of the complexity of biological systems, such models have value in highlighting the fundamental processes of evolution (e.g. Frank, 1995; Brown, 1999; Hudson *et al.*, 2002; West & Buckling, 2003). The fitness of an individual in a group (w_{ij}) can be written as:

$$w_{ij} = \overbrace{\frac{f(z_{ij})}{f(z_i)}}^{\text{individual performance}} \underbrace{g(z_i)}_{\text{group performance}} \tag{1}$$

where z_{ij} is investment in reproductive competition of the jth individual of the ith group, and z_i is average investment in reproductive competition in the ith group (Frank, 1994b, 1995). Table 1 summarizes the main notations used in the model. Investment in reproductive competition (z) ranges from 0 to 1 reflecting the finite level of resources that any group member can utilize. When $z = 1$, individuals invest all available resources in reproductive competition and when $z = 0$, individuals invest all of their resources into the group. The reproductive advantage given by competition is measured by $f(z_{ij})$, which describes the normally positive relationship between investment in competition and reproductive output, such that $f(z_{ij})/f(z_i)$ gives the relative reproductive success of the jth individual in the ith group. This component of the model determines the nature of selection *within* groups (Wilson, 1975, 1977; Frank, 1994b), which is then weighted by group performance $g(z_i)$ to give fitness. The function $g(z_i)$ gives the relationship between investment in the group and group performance and determines the nature of selection *between* groups (Wilson, 1975, 1977; Frank, 1994b). In some situations, individual performance may be better measured by absolute success rather than relative success such that $w_{ij} = f(z_{ij})g(z_i)$ (Brown, 1999; West & Buckling, 2003). However, all predictions were checked for both forms of individual performance and are qualitatively identical.

Table 1 Summary of the main notations.

Notation	Definition
w_{ij}	Fitness of the jth individual in the ith group
z_{ij}	Investment in reproductive competition of the jth individual in the ith group
z_i	Average investment in reproductive competition in the ith group
$f(z)$	Individual performance function
$g(z)$	Group performance function
z^*	Investment in reproductive competition at equilibrium
$1 - z^*$	Investment in the cooperative group trait at equilibrium
$g(z^*)$	Group performance at equilibrium. This is how similar group productivity is to a group without competition in which $g(0) = 1$.
$f(z^*)$	Absolute individual performance at equilibrium
r	Within-group relatedness (Appendix B)
r_p	Pairwise relatedness (Appendix B)
n	Number of group members
z_{opt}	Value of z that maximizes group performance

Model outputs – measuring cooperation and tragedy

Assessing the level of cooperation in a group can be done using at least two measures, the amount that individuals invest in cooperation or the degree to which cooperation is achieved as a group level trait (Dugatkin, 1998). Both of these measures can be predicted from the model by solving for the level of competition at equilibrium (see Appendix A). The first is z^*, which gives the average individual investment in reproductive competition at equilibrium and, conversely, the amount invested in the cooperative group trait ($1 - z^*$). The second measure of sociality is group performance at equilibrium $g(z^*)$; this is the productivity of the group relative to a group without competition for which $g(0) = 1$, which is equal to mean fitness in the group at equilibrium (w_i) because equilibrium individual performance $f(z^*)/f(z^*) = 1$. This predicts how much conflict affects group adaptation and measures the severity of the tragedy of the commons.

At first consideration, z^* and $g(z^*)$ seem equivalent measures of sociality and in the simplest case (Appendix A, eqn A1), group performance $g(z^*)$ is simply $1 - z^*$ which suggests that any factor that decreases reproductive competition at equilibrium z^* will increase group performance $g(z^*)$. However, changing the group performance function itself $g(z)$ can have different effects on reproductive competition and group performance making it important to distinguish between the two measures (see below).

Linear returns

The simplest way to alter the returns from investment in competition (z) or investment in cooperation $(1 - z)$ is to alter cost and benefits in a linear model (see Appendix A). The following analysis shows that linear changes can improve absolute group performance but do not reduce the overall impact of competition on cooperation. The benefit of competition vs. cooperation can be varied as follows:

$$w_{ij} = \frac{\overbrace{cz_{ij}}^{\text{individual performance}}}{cz_i} \underbrace{b(1 - az_i)}_{\text{group performance}} \qquad (2)$$

where z_{ij} is investment in reproductive competition of the jth individual of the ith group, and z_i is average investment in reproduction competition in the ith group (Frank, 1994b, 1995, Appendix A). The c term determines the individual cost of reducing reproductive competition to invest in cooperation, b determines the benefit from investing in the group, and a determines the group-level cost of competition. It is immediately obvious that c cancels and does not affect matters. Decreasing the benefit of investing in competition (c) affects all group members equally, so that the optimal level of competition is unaffected. At equilibrium, $z^* = (1 - r)/a$, where r is within-group relatedness (Appendix B) and z^* is the equilibrium investment in competition (Appendix A details the method used to produce this result). This shows that competition will reduce when it is costly to the group (high a). However, group performance is unaffected because competition reduces exactly in proportion to its increased group cost and the a term cancels when z^* is put into the group performance term giving $g(z^*) = br$. More intuitively, consider two species of meerkats where reproductive competition is twice as harmful to the colony in species A than in species B. The increased cost means that species A meerkats compete half as often over reproduction and so invest more of their resources in cooperation. However, the cost to the colony of each competitive event is double in species A so that the overall effect on the colony is the same in both species. This is an example of a factor that has different effects on investment in cooperation $(1 - z^*)$ and group performance $g(z^*)$, and illustrates that they are not always equivalent (see *Model outputs* above).

The equilibrium group performance $g(z^*) = br$ shows that absolute group performance will increase when there is a high benefit from investment in the group. In meerkats, this shows that a species whose ecology predisposes it to building well-defended nests will produce a better nest for a given investment than a species whose ecology makes nest building difficult. This basic benefit to cost ratio of a social trait, therefore, is an important factor in social evolution (Wilson, 1990) because it determines what is achieved for a given investment in the group. However, a predisposition towards sociality is not a factor in the tragedy of the commons because maximum group performance $g(0)$ is also increased by the b term so that $g(0) = b$. This means that the extent of the tragedy which is how a group performs compared with a perfectly cooperative group is $br/b = r$, as in Frank's original result (Appendix A). For example, if a sibling group of meerkats ($r_p = 0.5$) are predicted to invest 5 units in nest building with 300 units return then a perfectly cooperative group would invest 10 and gain 600 units, that is, there is still a tragedy with siblings despite the high returns.

Together, the parameters a and b determine how much the group benefits from cooperation and the relative strength of within-group selection to between-group selection (Wilson, 1975, 1977, 1990, 1997a; Frank, 1994b; Avilés, 2002). Wilson (1990) showed that a particular social trait is more likely to evolve when cooperation greatly benefits the group (strong between-group selection). The above analysis confirms this by showing that when the benefits to the group are high, the level of investment in cooperation (with high a) and absolute group performance (with high b) can increase, which both increase the likelihood that a social trait will evolve to a particular degree. However, the relative impact of competition on the social trait is unaffected by these factors so that they do not reduce the tragedy of the commons.

Nonlinear returns

The above model assumes that the returns from reproductive competition or the cooperative group trait are directly proportional to amount invested in the trait (eqn 2). Here I relax this assumption and investigate the effect of nonlinear relationships between investment and trait performance.

Individual performance function $f(z)$

The general effect of a nonlinear relationship between investment in and the benefit from reproductive competition can be investigated by analysing eqn 1 without specifying the form of the individual performance function:

$$w_{ij} = \frac{f(z_{ij})}{f(z_i)}(1 - z_i) \qquad (3)$$

Following Frank's (1994b) method outlined in Appendix A, this can be differentiated to find the equilibrium for z, with $z_{ij} = z_i = z^*$ and $dz_i/dz_{ij} = r$, where r is within-group relatedness (Appendix B).

$$\frac{dw_{ij}}{dz_{ij}} = \frac{(r-1)(z^*-1)f'(z^*)}{f(z^*)} - r = 0 \tag{4}$$

This equation can then be used to examine the effect of different forms of the individual performance function $f(z)$ on individual investment in reproductive competition z^* and group performance $g(z^*)$ at equilibrium (see *Model outputs* above). For this analysis, investment in reproductive competition and group performance are equivalent measures of sociality because $g(z^*) = 1 - z^*$ (eqn 3). This changes in the next section, which looks at the effect of changing the group performance function.

A linear model (Appendix A) predicts that at equilibrium, $z^* = 1 - r$ and $g(z^*) = r$. We are interested in which forms of the function $f(z)$ will result in improved group performance, which will means that the tragedy of the commons is lessened. That is, for what forms of $f(z)$ is $g(z^*) > r$, or equivalently when is reproductive competition reduced, $z^* < 1 - r$. This can be evaluated by rearranging eqn 4 to give r:

$$r = \frac{(z^*-1)f'(z^*)}{f'(z^*)(z^*-1) - f(z^*)} \tag{5}$$

Substituting this into the inequality $z^* < 1 - r$ gives:

$$z^* < 1 - \frac{(z^*-1)f'(z^*)}{f'(z^*)(z^*-1) - f(z^*)} \tag{6}$$

This rearranges to give that $z^* < 1 - r$ when:

$$f(z^*) > z^* f'(z^*) \tag{7}$$

Now, whenever the second derivative of the individual performance function is negative, then:

$$f'(z) > f'(z) + zf''(z) \tag{8}$$

because z is positive. If we integrate both sides of this inequality from 0 to z:

$$\int_0^z f'(z)dz > \int_0^z f'(z) + zf''(z)dz \tag{9}$$

$$f(z) > f(0) + zf'(z) \tag{10}$$

This shows that when $f''(z) < 0$ and $f(0) \geq 0$, inequality 7 is satisfied so that group performance [$g(z^*) = 1 - z^*$] is increased and reproductive competition (z^*) is reduced compared with a linear model. A negative second derivative occurs whenever the gradient of the individual performance function $f(z)$ is decreasing, that is the function is concave downwards. For $f(0) = 0$ and $f(1) = 1$, this describes a diminishing returns relationship between the amount an individual invests in reproductive competition and the benefit that they receive. Figure 1 demonstrates this for the diminishing returns function $f(z) = 1 - (1 - z)^x$, where x determines curvature. Figure 1c, d shows diminishing returns reducing equilibrium levels of investment in reproductive competition z^* and increasing group performance $g(z^*)$ for group-wise relatedness (r) between 0 and 1. The effects of diminishing returns on trait group selection in a group of five unrelated individuals are illustrated by a dashed line which shows z^* and $g(z^*)$ where $r = r_p(n - 1)/n + 1/n = 0.2$ (Appendix B). An associated conclusion from the analysis is that an *accelerating* returns relationship [when $f''(z) > 0$] will reduce group performance relative to the linear model and the tragedy of the commons will be worsened.

Group performance function *g*(*z*)

This section investigates the effects of a nonlinear relationship between individual investment in reproductive competition (z) and group performance $g(z)$:

$$w_{ij} = \frac{z_{ij}}{z_i} g(z_i) \tag{11}$$

Differentiating gives:

$$\frac{dw_{ij}}{dz_{ij}} = \frac{1-r}{z^*} g(z^*) + rg'(z^*) = 0 \tag{12}$$

As in the previous section, this can be used to examine the effect of different forms of the undefined function $g(z)$ on model predictions. The analysis in this case is slightly different, however, because the relationship between the two measures of social evolution, group performance $g(z^*)$ and individual investment in reproductive competition z^* (see *Model outputs* above), is not a simple linear relationship but depends on the form of the undefined function $g(z)$. This means that the effect of changing $g(z)$ on the equilibrium values z^* and $g(z^*)$ must be evaluated separately. The following analysis focuses on group performance at equilibrium $g(z^*)$ because this measures the extent of the tragedy of the commons (see *Model outputs* above).

A linear model predicts that group performance at equilibrium is equal to relatedness, that is $g(z^*) = r$ (Appendix A). Therefore, we are interested in which forms of the $g(z)$ function will cause group performance at equilibrium to be greater than relatedness, that is, which forms of $g(z)$ result in $g(z^*) > r$? Rearranging eqn 12 gives r:

$$r = \frac{g(z^*)}{g(z^*) - z^* g'(z^*)} \tag{13}$$

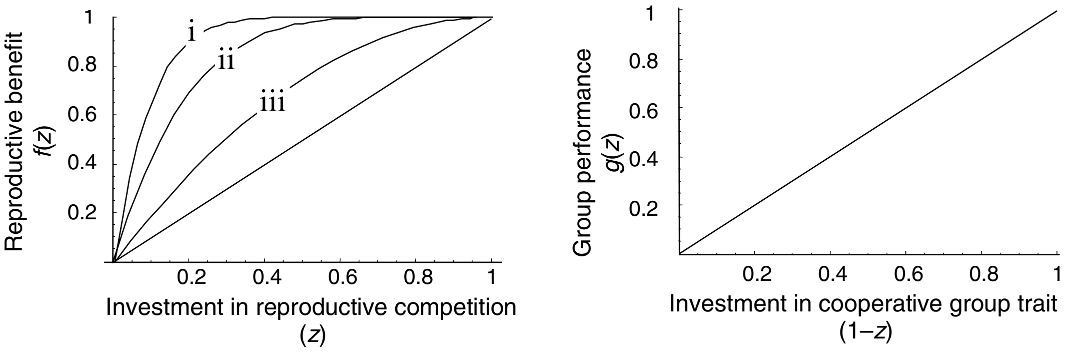
Therefore $g(z^*) > r$ when:

$$g(z^*) > \frac{g(z^*)}{g(z^*) - z^* g'(z^*)} \tag{14}$$

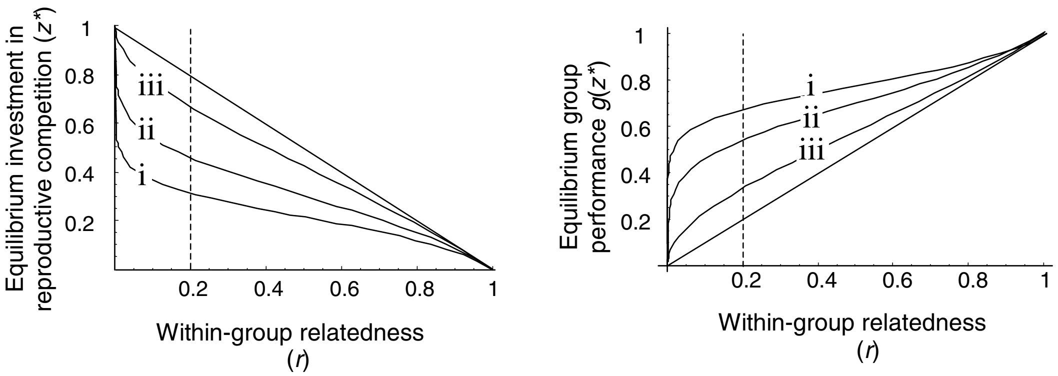
Inequality (15) will be true whenever the denominator of the right hand side is greater than one or when:

$$g(z^*) > 1 + z^* g'(z^*) \tag{15}$$

As with eqn 8, the following statement is true whenever the second derivative of the group performance function is negative:



(a) Individual performance function **(b) Group performance function**



(c) Predicted investment in competition **(d) Predicted group performance**

Fig. 1 Diminishing returns from investment in reproductive competition. (a) Relationship between investment in reproductive competition and the resulting reproductive benefit, $f(z) = 1 - (1 - z)^x$. Left to right the curves are for $x = 10, 5, 2, 1$ (eqn 1). (b) Relationship between investment in a cooperative group trait $(1 - z)$ and group performance $g(z) = 1 - z$. (c) Investment in reproductive competition (z^*) at equilibrium as a function of within-group relatedness. (d) Group performance at equilibrium $g(z^*)$ as a function of within-group relatedness (see *Model outputs*). This predicts how close group performance matches that of a perfectly cooperative group and measures the tragedy of the commons. The dashed lines in (c) and (d) show z^* and $g(z^*)$ that arise through trait group selection in an unrelated group of five individuals where $r = r_p(n - 1)/n + 1/n = 0.2$ (Appendix B).

$$g'(z) > g'(z) + zg''(z) \tag{16}$$

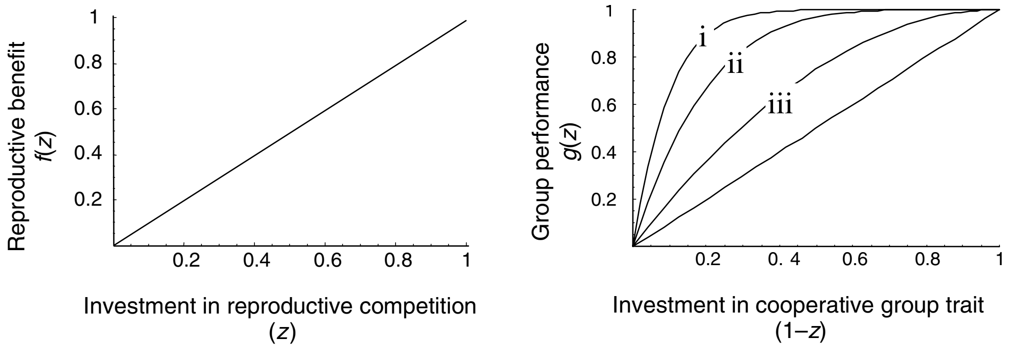
because z is positive. Integrating both sides of this equality from 0 to z gives:

$$\int_0^z g'(z)dz > \int_0^z g'(z) + zg''(z)dz \tag{17}$$

$$g(z) > g(0) + zg'(z) \tag{18}$$

This shows that inequality 15 is satisfied and $g(z^*) > r$ whenever $g''(z) < 0$ and $g(0) \geq 1$, which is a concave down function as occurred in the analysis of the individual performance term. This describes a $g(z)$ function where high levels of investment in selfish reproduction (z) is disproportionately costly to the group. This can be translated into the relationship between investment in the group and group performance by examining group performance as a function of $1 - z^*$, which gives the amount that an individual invests in the cooperative group trait (see *Model outputs* above). This reveals that it is again a diminishing returns relationship that promotes group adaptations. Figure 2b shows this for the candidate function $g(z) = 1 - z^x$ where x defines the degree of curvature. A significant difference to the effect of changing the individual performance function $f(z)$ (Fig. 1c) is that diminishing returns in the group performance function $g(z)$ increases investment in reproductive competition (z^*, Fig. 2c). This occurs because diminishing returns makes reproductive competition less costly at the group level. And assessing the evolution of cooperation through individual investment $(1 - z^*)$ would suggest that cooperation decreases. However, the decreased investment in cooperation does not fully compensate for the increased group benefit that comes with diminishing returns and overall group performance increases (Fig. 2d).

(a) Individual performance function **(b) Group performance function**



(c) Predicted investment in competition **(d) Predicted group performance**

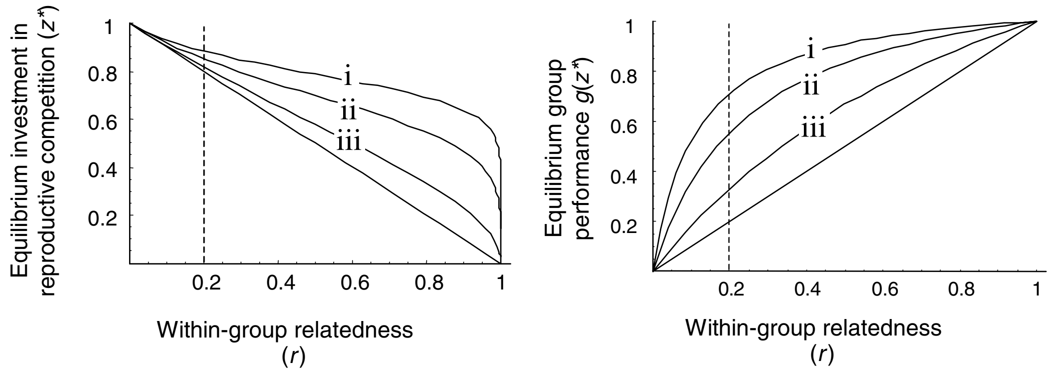


Fig. 2 Diminishing returns from investment in a cooperative group trait. (a) Relationship between investment in reproductive competition and the resulting reproductive benefit, $f(z) = z$ (eqn 1). (b) Relationship between investment in a cooperative group trait $(1 - z)$ and group performance $g(z) = 1 - z^x$. Left to right the curves are for $x = 10, 5, 2, 1$. See Fig. 1 legend for details of (c) and (d).

Optimal performance with partial investment

The above models assume that an individual's share of reproduction in the group is maximized by complete investment in reproductive competition, and that the group performance is maximized by complete investment in the group trait. This will often not be the case. For individual performance (Fig. 3), an optimum with reduced investment in competition can occur when a cooperative trait has associated selfish benefits, such as if vertebrate sentinels gain a survival advantage (Bednekoff, 1997). Too greater investment in a group trait may also carry costs (Fig. 4). For example, in microbes, release of a cooperative enzyme may be toxic above a certain level so that a perfectly cooperative group produces a low level of the enzyme.

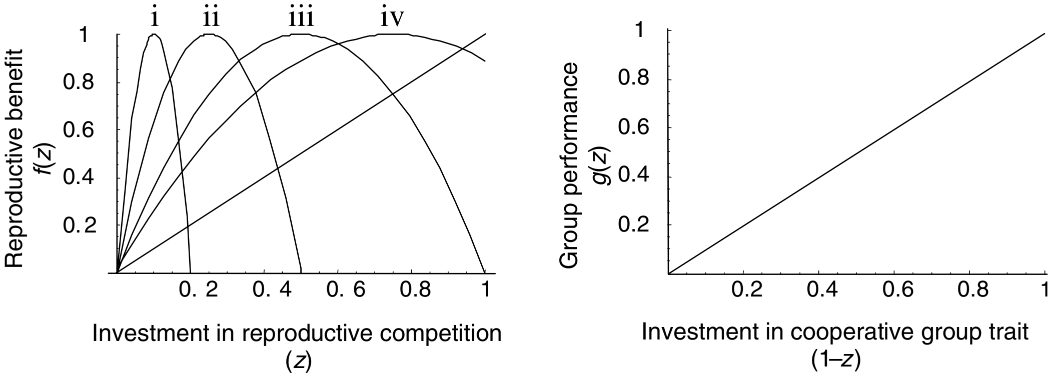
An intermediate optimum in either reproductive competition or the cooperative group trait further reduces the tragedy of the commons (Figs 3 and 4). This occurs because optima with partial investment bring group and individual interests closer together and lessens the zone of conflict. The effects of an intermediate optimum will now be formally shown for the group performance function. Qualitatively identical results can be obtained for the individual performance function but are not presented. An intermediate optimum can be incorporated into the group performance function by using a maximum (z_{opt}) where $0 < z_{\mathrm{opt}} < 1$ and $g(z_{\mathrm{opt}}) = 1$. For group performance, $z^* > z_{\mathrm{opt}}$ because below z_{opt} increasing reproductive competition (z) increases both group performance and individual performance so there will be no stable equilibrium (Fig. 4). Rearranging eqn 12 for z^* shows this:

$$z^* = -\frac{(1-r)}{r} \cdot \frac{g(z^*)}{g'(z^*)} \tag{19}$$

There are no positive solutions for z^* when $g'(z^*)$ is positive meaning there are no biologically relevant equilibria below z_{opt}. This is important for the next calculation because it means that integration from z_{opt} to z, rather than 0 to z, is appropriate.

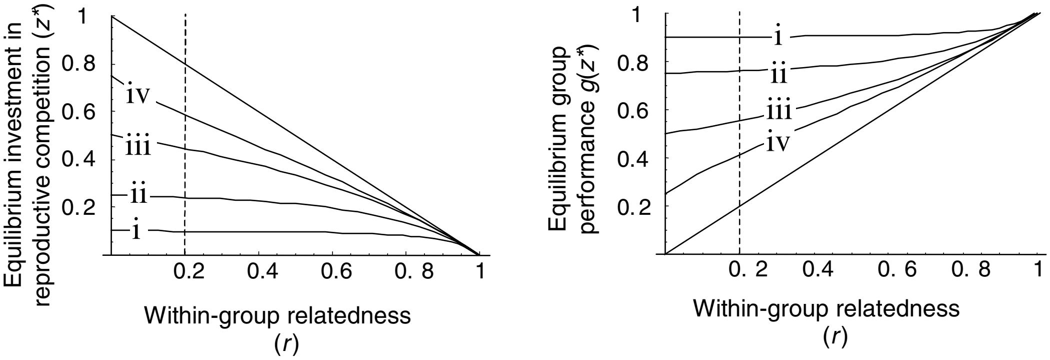
Diminishing returns also improves group performance for intermediate optima

An intermediate optimum means that the group performance function at the very least will be diminishing function



(a) Individual performance function

(b) Group performance function



(c) Predicted investment in competition

(d) Predicted group performance

Fig. 3 Optimal individual performance with partial investment in reproductive competition. (a) Relationship between investment in reproductive competition and the resulting reproductive benefit, $f(z) = 1 - a(1 - z - b)^2$. Left to right the parabolas are for $a = 100$, $b = 0.9$; $a = 16$, $b = 0.75$; $a = 4$, $b = 0.5$; $a = 1.75$, $b = 0.25$. (b) Relationship between investment in a cooperative group trait $(1 - z)$ and group performance $g(z) = 1 - z$. See Fig. 1 legend for details of (c) and (d).

of investment close to the optimum. Diminishing returns increases group performance with an intermediate optimum as it does for an optimum at $z = 0$ (eqn 18). This is shown by integrating eqn 16 between z_{opt} and z.

$$\int_{z_{\text{opt}}}^{z} g'(z)dz > \int_{z_{\text{opt}}}^{z} g'(z) + zg''(z)dz \tag{20}$$

$$g(z) > g(z_{\text{opt}}) + zg'(z) \tag{21}$$

which is identical to the result for an optimum at $z = 0$ (eqn 18) because $g(z_{\text{opt}}) = 1$.

Lowering optimal group investment increases equilibrium group performance

Lowering optimal investment in the group trait reduces the effect of competition on group performance for any function that monotonically decreases between z_{opt} and z^*, whether diminishing returns or otherwise (Fig. 4). Lowering optimal investment in the group means raising the group optimum for reproduction (z_{opt}). This increases the magnitude of both z^* and the gradient $g'(z^*)$ for any value of $g(z^*)$ (Fig. 4b). The effect of this can be seen by rearranging eqn 12 to give group performance at equilibrium $g(z^*)$:

$$g(z^*) = -\frac{r}{1-r} z^* g'(z^*) \tag{22}$$

In order to raise the magnitude of z^* and $g'(z^*)$ for any value of $g(z^*)$, relatedness must be reduced. Conversely, this means that $g(z^*)$ is increased for any value of relatedness. This effect is illustrated for the individual performance function (Fig. 3) and the group performance function (Fig. 4) using parabolic functions, which combine the effects of diminishing returns and optimal performance at an intermediate level of reproductive investment.

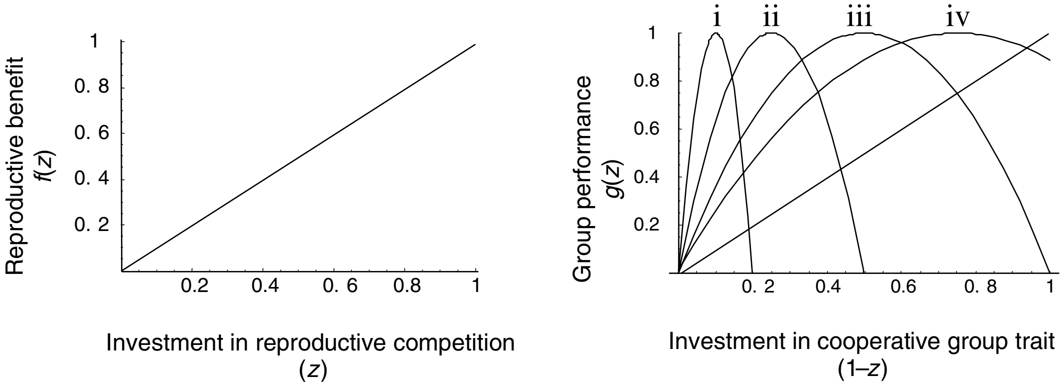
Discussion

Verbal summary of results

The selfish pursuit of reproduction directs resources away from cooperative group traits, which can disrupt cooperation and lead to an evolutionary tragedy of the

(a) Individual performance function

(b) Group performance function



(c) Predicted investment in competition

(d) Predicted group performance

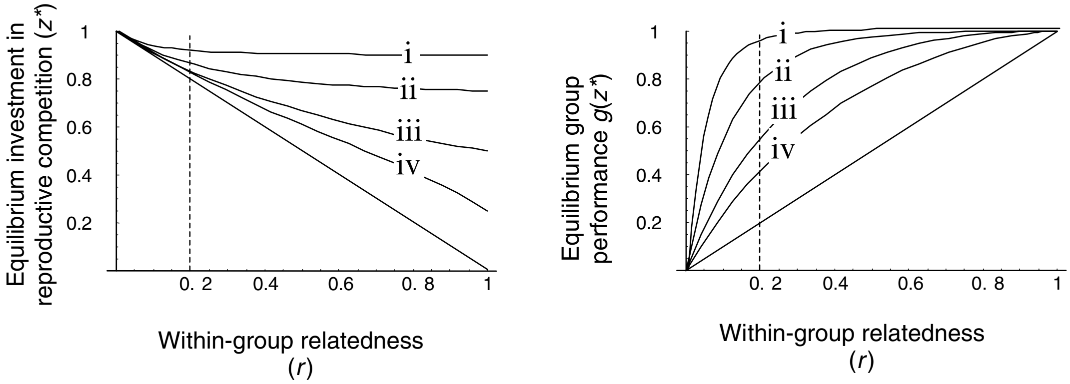


Fig. 4 Optimal group performance with partial investment in a cooperative trait. (a) Relationship between investment in reproductive competition and the resulting reproductive benefit, $f(z) = z$. (b) Relationship between investment in a cooperative group trait $(1 - z)$ and group performance $g(z) = 1 - a(z - b)^2$. Left to right the parabolas are for $a = 100$, $b = 0.9$; $a = 16$, $b = 0.75$; $a = 4$, $b = 0.5$; $a = 1.75$, $b = 0.25$. See Fig. 1 legend for details of (c) and (d).

commons (Leigh, 1977; Frank, 1995; Michod, 1999a). The models presented here show that the performance of a social group depends critically on the relationship between investment and benefit for both competitive and cooperative traits. The linear model (eqn 2) shows that the relative benefit of competition vs. cooperation sets the maximum possible group performance and, all else being equal, high returns from cooperation (strong between-group selection) means a more effective group adaptation (Wilson, 1990, 1997a). However, high returns from cooperation do not reduce the relative impact of competition on the group or the severity of tragedy of the commons.

The tragedy of the commons is lessened when investment in personal reproduction or a group trait provide diminishing returns. At the individual level, diminishing returns devalue high levels of investment in reproductive competition, which favours directing resources into the group (Fig. 1a). To give a hypothetical example, consider a wasp worker competing over reproduction in a nest where intensive competition disproportionately results in personal injury. This devalues intense competition and favours directing resources instead into cooperation, which will reduce the level of competition in the colony. A dynamic analysis and simulation of a spatially heterogeneous population by Le Galliard *et al.* (2003) predicted that altruism is most likely to invade when it has accelerating individual costs. Although phrased differently, an accelerating cost to altruism or cooperation is equivalent to diminishing returns from investment in reproductive competition. This can be seen by changing the x-axis in Fig. 1a from investment in reproductive competition (z) to investment in cooperation $(1 - z)$ by flipping it left to right, which reveals an accelerating decrease in individual performance $f(z)$ as investment in cooperation $(1 - z)$ increases. The effects of diminishing returns, therefore, are general and robust to very different forms of analysis.

The effects of diminishing returns from investment in the group (Fig. 2) are less intuitive because diminishing returns devalue high levels of investment in the group so that competition actually increases. However, diminishing returns also means that the effect of competition on cooperation is reduced and this outweighs the increased competition so that group performance increases overall. Consider again the wasp workers; say that there are extreme diminishing returns from investing in the colony so that working twice as hard provides little additional benefit to the colony. Workers will invest instead in egg laying and reproductive competition will increase. However, this egg laying uses resources that are of no use to the colony so that the competition has a negligible effect on colony performance and there is little tragedy. Note that this result is not simply a consequence of the diminishing function lying above the linear function (Fig. 2) because raising a linear function alone has no effect on the tragedy (parameter *b* in eqn 2).

A diminishing returns relationship can also lead to individual or group performance decreasing above a certain level of investment (Figs 3 and 4). For example, if worker competition was so injurious at high levels that it actually lowered a worker's reproductive output, then lowering competition to a certain level would be beneficial at the individual and group level. This lowers the scope and impact of reproductive competition by making the interests of the workers and the colony more similar. In some situations, individual and group interests will be perfectly aligned and cooperation will arise without conflict, through byproduct mutualism (Connor, 1995; Dugatkin, 1998, 2002; Sachs *et al.*, 2004).

Diminishing returns reduce the effects of competition through both trait group selection (Wilson, 1975) and kin selection (Hamilton, 1964). Dashed lines in Figs 1–4 illustrate the effects of diminishing returns on trait group selection in a group of five unrelated individuals (Appendix B). With rapidly diminishing returns, group adaptations can arise that are comparable with clonal groups (Figs 1–4). Diminishing returns similarly affect group adaptations that arise through kin selection, which suggests that the effects of competition can be minimized in low relatedness groups through this mechanism. While these results show that diminishing returns lessen the tragedy of the commons, an associated conclusion is that *accelerating* returns worsen the tragedy. It is important to my argument, therefore, that diminishing and not accelerating returns commonly occur in social systems.

Social vertebrates

Diminishing returns occur in the cooperative blood sharing of vampire bats (Wilkinson, 1984). After a blood meal, bats frequently feed others in the roost that have not managed to feed that night, which prevents them from starving. Reciprocal altruism and kin selection are thought to play a role in maintaining this feeding behaviour (Wilkinson, 1984; Nowak & Sigmund, 1993; Brembs, 1996; Dugatkin, 2002) but diminishing returns are also a key component. Wilkinson (1984) showed that when a bat is gorged with blood, it is unable to make efficient use of all of the blood. At the individual level, therefore, a bat experiences diminishing returns from retaining blood in terms of time until starvation (Fig. 5a, Wilkinson, 1984). This reduces the value of retaining the entirety of the blood meal and increases the likelihood the gorged bat will give up blood for starving nestmates. The group performance function is also diminishing returns because the each additional increment of blood received by a starving bat gives less additional survival time than the previous increment. Furthermore, only around 18% of bats fail to feed on a given night so the optimal mean donation among fed bats will be around 18% of a blood meal to produce an identical level of nutrition among group members that should optimize group survival. This means that it takes a relatively low level of investment into blood sharing to perform like a perfectly cooperative group.

A model of blood sharing in the vampires is shown in Fig. 5, which puts realistic functions for individual and group performance into eqn 1. Modelling the vampires this way assumes that fed bats do not discriminate among unfed bats when giving blood, that time to starvation is an indicator of nutritional status and ultimately reproductive performance, and that group survival depends upon blood exchange. Although simplistic, the results show the potentially powerful effects of diminishing returns and predict that above relatedness of around 0.05, blood sharing behaviour will not improve. Mean pairwise relatedness is between 0.08 and 0.1 in vampires (Wilkinson, 1984, 1988) suggesting that blood sharing will be near optimal even before nepotistic feeding or reciprocal altruism is considered.

The sentinel behaviour of many mammals and birds (Bednekoff, 1997) is another cooperative trait where diminishing returns are likely to be important. Clutton-Brock *et al.* (1999) showed that meerkats most often become sentinels when they are well fed. This suggests that, like the vampires, sentinel behaviour uses excess resources that cannot efficiently be channelled into reproduction (Bednekoff, 1997; Clutton-Brock *et al.*, 1999). Individuals will, therefore, experience diminishing returns from retaining resources for personal reproduction. There are also diminishing returns in investment in sentinel behaviour because group vigilance does not rise linearly with number of sentinels (Trivers, 1971; Roberts, 1996; Bednekoff, 1997). Moreover, sentinels may gain a survival benefit if they are the first to escape predators, which would favour some sentinel behaviour at the individual level (Fig. 3, 'safe selfish sentinels' Bednekoff, 1997; Clutton-Brock *et al.*, 1999). In combination, these effects will greatly limit the impact of conflict on the sentinel system.

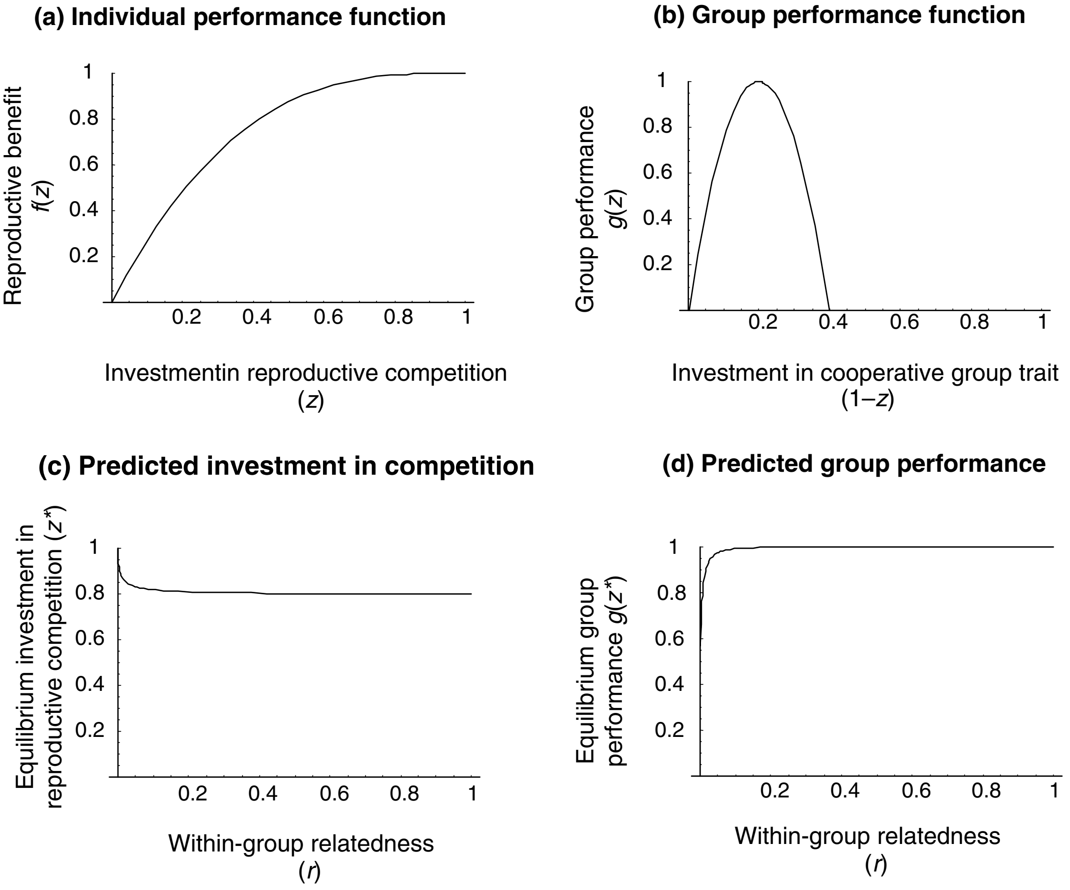


Fig. 5 Blood sharing in vampire bats as an example of diminishing returns in a social trait. (a) Individual performance function $f(z) = 1 - (1 - z)^3$ based upon the empirically determined relationship between proportion of blood meal retained (investment in self) and time to starvation (Wilkinson, 1984), which is used as a proxy for reproductive benefit. The curve closely approximates Fig. 2 in Wilkinson, 1984 after the axes have been normalized to a 0–1 range. (b) Relationship between investment in reproductive competition and group performance $g(z) = 1 - a(z - b)^2$ where $a = 25$, $b = 0.8$. This is based on the observation that around 20% of bats do not feed each night so that the remaining bats will have to donate on average 20% of their resources for all bats to have equal survival probability, which is assumed to maximize group survival. Note that the possibly unrealistic behaviour of the function to the right of the optimum does not affect predictions because $z^* > z_{\mathrm{opt}}$ so that the z^* is always to the left [see *Optimal performance with partial investment,* (c)]. See Fig. 1 legend for details of (c) and (d).

Social insects

Relatedness and enforcement, in the form of queen and worker policing, both limit reproductive competition in insect societies (Hamilton, 1964; Ratnieks, 1988; Bourke & Franks, 1995; Foster & Ratnieks, 2001a; Wenseleers *et al.*, 2003). However, diminishing returns are also likely to moderate the costly effects of conflict. As discussed above, if intense reproductive competition carries a disproportionately high risk of personal injury, then competition will provide diminishing rewards (Fig. 1a). Indirect support that injury is disproportionately likely with intense competition comes from the vespine wasps, where there is a sharply accelerating relationship between predicted queen–worker conflict intensity (worker–worker relatedness) and queen mortality across species (Foster & Ratnieks, 2001b). Furthermore, insect societies typically have diminishing returns between group size and group productivity (reviewed by Michener, 1964; Reeve, 1991; Clouse, 2001). If adding an individual to a colony has similar effects to another working twice as hard, this means that the majority of insects societies also experience a diminishing returns relationship between investment and group performance (Fig. 2b). This suggests that the moderate amount of reproductive competition that occurs in many societies (Bourke & Franks, 1995) will not seriously affect colony productivity.

Microbes

In addition to high relatedness (Crespi, 2001), diminishing returns are likely to be important in microbial cooperation. The commonest form of cooperation in microbes is the release of an extracellular product that benefits all members of a group (Crespi, 2001). Examples include the foraging enzymes of *Myxococcus xanthus* (Crespi, 2001), invertase production by yeast (e.g. Mortimer & Hawthorne, 1969), siderophore production in bacteria (West & Buckling, 2003), and the production of protective chemicals such as slime production in biofilms (Crespi, 2001) and the polysaccharide sheath of the slime mould *Dictyostelium discoideum* (Kessin, 2001). Diminishing returns are likely to be common with extracellular products because their benefit will saturate beyond a certain level of production. For example, the release of extracellular enzymes will cease to increase growth rate when factors such as uptake and other nutrients become limiting. Some microorganisms also form multicellular structures. Around one fifth of cells in aggregates of *D. discoideum* sacrifice themselves to form a stalk that holds reproductive spores aloft (e.g. Kessin, 2001). However, the benefit of raising the spores above the soil will decrease above the height that enables spore dispersal by water or insects (Bonner, 1982; Huss, 1989; Hudson *et al.*, 2002). This devalues high investment in the stalk, which will reduce the impact of conflict (Fig. 2). Finally, some microbial cooperation will also have group performance optimum with partial investment, if the production of enzymes and protective chemicals become harmful at high levels (Fig. 4).

Direct measurements of the shape of individual and group performance functions should be possible in microbial systems. The group benefit from a cooperative product can be assessed by removing or adding the product to a knockout strain that does not synthesize it e.g. adding different levels of invertase to a yeast mutant that does not make it. And the individual cost of production might be assessed by comparing the reproductive rate of mutants that produce different levels of the cooperative product in a saturated environment.

Cooperation between species

The models presented here are most relevant to cooperation within a species. However, trait group selection can also drive among-species cooperation when helping a cooperative partner results in personal benefits (Wilson, 1997b). Furthermore, most mechanisms for cooperation among-species and genes *(egalitarian transitions*, Queller, 2000), including spatial association (Frank, 1994a), partner fidelity (Trivers, 1971; Axelrod & Hamilton, 1981; Bull & Rice, 1991) and partner choice (Axelrod & Hamilton, 1981; Bull & Rice, 1991; Noë & Hammerstein, 1994), involve generating a genetic correlation between cooperative genotypes of each species that is formally comparable with relatedness within conspecific groups (Frank, 1994a; Pepper & Smuts, 2002). This suggests that diminishing returns may have a comparable effect in among-species interactions.

Mutualisms probably commonly feature diminishing returns (Doebeli & Knowlton, 1998), particularly when they provide cooperators with a limiting resource. Legume plants obtain nitrogen from rhizobial bacteria in their roots in return for photosynthate (Denison, 2000; West *et al.*, 2002b). The exchange is to some extent driven by partner fidelity and trait group selection because, by helping the plant, the rhizobia indirectly benefit themselves and *vice versa*. And recent work suggests that plant sanctions are also important (Kiers *et al.*, 2003). However, there are also diminishing returns because rhizobia allow the plants to overcome nitrogen-limiting environments (Denison, 2000), and the benefit of nitrogen production will rapidly diminish as nitrogen ceases to limit plant growth (Fig. 2a). The effects of competitive interactions between the species, therefore, may not be severe so long as sufficient nitrogen is supplied to prevent it limiting plant growth.

Diminishing returns are common in social systems and act in addition to factors such as relatedness, trait group selection and enforcement. The importance of diminishing returns depends critically on the curvature of the relationship between investment and benefit. However, even a modest curvature can drive a group performance several times the level expected by a linear model, an effect amplified when an intermediate level of investment is optimal for reproductive competition or the cooperative trait. Under these conditions, the tragedy of the commons is not so tragic and the disruptive effects of competition upon social life are greatly reduced.

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References

Alexander, R.D. 1979. *Darwinism and Human Affairs*. Pitman Ltd, London.

Alexander, R.D. 1987. *The Biology of Moral Systems*. Aldine de Gruyter, New York.

Avilés, L. 2002. Solving the freeloaders paradox: genetic associations and frequency-dependent selection in the evolution of cooperation among nonrelatives. *Proc. Natl. Acad. Sci. USA* **99**: 14268–14273.

Axelrod, R. & Hamilton, W.D. 1981. The evolution of cooperation. *Science* **211**: 1390–1396.

Bednekoff, P. 1997. Mutualism among safe, selfish sentinels: a dynamic game. *Am. Nat.* **150**: 373–392.

Bonner, J.T. 1982. Evolutionary strategies and developmental constraints in the cellular slime moulds. *Am. Nat.* **199**: 530–552.

Bourke, A.F.G. & Franks, N.R. 1995. *Social Evolution in Ants*. Princeton University Press, Princeton, NJ, USA.

Brembs, B. 1996. Chaos, cheating and co-operation: potential solutions to the Prisoner's Dilemma. *Oikos* **76**: 14–24.

Brown, S.P. 1999. Cooperation and conflict in host-manipulating parasites. *Proc. Roy. Soc. London B* **266**: 1899–1904.

Bull, J.J. & Rice, W.R. 1991. Distinguishing mechanisms for the evolution of cooperation. *J. Theor. Biol.* **149**: 63–74.

Buss, L.W. 1987. *The Evolution of Individuality*. Princeton University Press, Princeton, NJ, USA.

Buss, L.W. 1999. Slime molds, ascidians and the utility of evolutionary theory. *Proc. Natl. Acad. Sci. USA* **96**: 8801–8803.

Clouse, R. 2001. Some effects of group size on the output of beginning nests of *Mischocyttarus mexicanus* (Hymenoptera: Vespidae). *Fla Entomol* **84**: 418–425.

Clutton-Brock, T.H., O'Riain, M.J., Brotherton, P.N.M., Gaynor, D., Kansky, R. & Manser, M. 1999. Selfish sentinels in cooperative mammals. *Science* **284**: 1640–1644.

Connor, R.C. 1995. Altruism among non-relatives: alternatives to the 'Prisoner's Dilemma'. *Trends Ecol. Evol.* **10**: 84–86.

Crespi, B.J. 2001. The evolution of social behaviour in microorganisms. *Trends Ecol. Evol.* **16**: 178–183.

Dawkins, R. 1976. *The Selfish Gene*. Oxford University Press, New York.

Denison, R.F. 2000. Legume sanctions and the evolution of symbiotic cooperation by rhizobia. *Am. Nat.* **156**: 567–576.

Doebeli, M. & Knowlton, N. 1998. The evolution of interspecific mutualisms. *Proc. Natl. Acad. Sci. USA* **95**: 8676–8680.

Dugatkin, L.A. 1998. Game theory and cooperation. In: *Game Theory and Animal Behaviour* (L. A. Dugatkin & H. K. Reeve, eds), pp. 38–63. Oxford University Press, Oxford.

Dugatkin, L.A. 2002. Animal cooperation among unrelated individuals. *Naturwissenschaften* **89**: 533–541.

Foster, K.R. & Ratnieks, F.L.W. 2001a. Convergent evolution of worker policing by egg eating in the honey bee and common wasp. *Proc. Roy. Soc. London B* **268**: 169–174.

Foster, K.R. & Ratnieks, F.L.W. 2001b. Paternity, reproduction and conflict in vespine wasps: a model system for testing kin selection predictions. *Behav. Ecol. Sociobiol.* **50**: 1–8.

Frank, S.A. 1994a. Genetics of mutualism: the evolution of altruism between species. *J. Theor. Biol.* **170**: 393–400.

Frank, S.A. 1994b. Kin selection and virulence in the evolution of protocells and parasites. *Proc. Roy. Soc. London B* **258**: 153–161.

Frank, S.A. 1995. Mutual policing and the repression of competition in the evolution of cooperative groups. *Nature* **377**: 520–522.

Frank, S.A. 1996. Policing and group cohesion when resources vary. *Anim. Behav* **52**: 1163–1169.

Frank, S.A. 1998. *Foundations of Social Evolution*. Princeton University Press, Princeton, NJ, USA.

Frank, S.A. 2003. Repression of competition and the evolution of cooperation. *Evolution* **57**: 693–705.

Haig, D. & Grafen, A. 1991. Genetic scrambling as a defence against meiotic drive. *J. Theor. Biol.* **153**: 531–558.

Hamilton, W.D. 1964. The genetical evolution of social behavior I and II. *J. Theor. Biol.* **7**: 1–52.

Hamilton, W.D. 1971. Geometry for the selfish herd. *J. Theor. Biol.* **31**: 295–311.

Hardin, G. 1968. The tragedy of the commons. *Science* **162**: 1243–1248.

Hauert, C., De Monte, S., Hofbauer, J. & Sigmund, K. 2002. Volunteering as red queen mechanism for cooperation in public goods games. *Science* **296**: 1129–1132.

Hudson, R.E., Aukema, J.E., Rispe, C. & Roze, D. 2002. Altruism, cheating, and anticheater adaptations in cellular slime molds. *Am. Nat.* **160**: 31–43.

Hurst, L.D. & Pomiankowski, A. 1991. Maintaining Mendelism: might prevention be better than cure? *BioEssays* **13**: **489–490.**

Huss, M.J. 1989. Dispersal of cellular slime moulds by two soil invertebrates. *Mycologia* **81**: 677–682.

Keller, L. (ed.) 1999. *Levels of Selection in Evolution*. Princeton University Press, Princeton, NJ, USA.

Kessin, R.H. 2001. *Dictyostelium. Evolution, Cell Biology, and the Development of Multicellularity*. Cambridge University Press, Cambridge.

Kiers, E.T., Rousseau, R.A., West, S.A. & Denison, R.F. (2003) Host sanctions and the legume-rhizobia mutualism. *Nature* **425**, 78–81.

Killingback, T., Doebeli, M. & Knowlton, N. 1999. Variable investment, the continuous Prisoner's Dilemma, and the origin of cooperation. *Proc. Roy. Soc. London B* **266**: 1723–1728.

Le Galliard, J., Ferrière, R. & Dieckmann, U. 2003. The adaptive dynamics of altruism in spatially heterogeneous populations. *Evolution* **57**: 1–17.

Leigh, E.G. Jr 1977. How does selection reconcile individual advantage with the good of the group? *Proc. Natl. Acad. Sci. USA* **74**: 4542–4546.

Leigh, E.G. Jr 1983. When does the good of the group override the advantage of the individual? *Proc. Natl. Acad. Sci. USA* **80**: 2985–2989.

Leigh, E.G. Jr 1999. Levels of selection, potential conflicts, and their resolution: the role of the 'common good'. In: *Levels of Selection in Evolution* (L. Keller, ed.), pp. 15–30. Princeton University Press, Princeton, NJ, USA.

Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.

Maynard Smith, J. 1988. Evolutionary progress and levels of selection. In: *Evolutionary Progress* (M. H. Nitecki, ed.), pp. 219–230. University of Chicago press, Chicago.

Maynard Smith, J. & Szathmáry, E. 1995. *The Major Transitions in Evolution*. Freeman, New York.

Michener, C.D. 1964. Reproductive efficiency in relation to colony size in Hymenopterous societies. *Insectes Soc.* **4**: 317–342.

Michod, R.E. 1999a. Individuality, immortality, and sex. In: *Levels of Selection in Evolution* (L. Keller, ed.), pp. 53–74. Princeton University Press, Princeton, NJ, USA.

Michod, R.E. 1999b. *Darwinian Dynamics. Evolutionary Transitions in Fitness and Individuality*. Princeton University Press, Princeton, N.J.

Mitteldorf, J. & Wilson, D.S. 2000. Population viscosity and the evolution of altruism. *J. Theor. Biol.* **204**: 481–496.

Mortimer, R.K. & Hawthorne, D.C. 1969. Yeast Genetics. In: *The Yeasts* (A. H. Rose & J. S. Harrison, eds), pp. 386–460. Academic Press Inc. Ltd, London.

Noë, R. & Hammerstein, P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav. Ecol. Sociobiol.* **35**: 1–11.

Nowak, M. & May, R.M. 1992. Evolutionary games and spatial chaos. *Nature* **359**: 826–829.

Nowak, M. & Sigmund, K. 1993. Chaos and the evolution of cooperation. *Proc. Natl. Acad. Sci. USA* **90**: 5091–5094.

Nowak, M. & Sigmund, K. 1998. Evolution of indirect reciprocity by image scoring. *Nature* **393**: 573–577.

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

Pepper, J.W. & Smuts, B.B. 2002. Assortment through Environmental Feedback. *Am. Nat.* **160**: 205–213.

Price, G.R. 1970. Selection and covariance. *Nature* **277**: 520–521.

Price, G.R. 1972. Extension of covariance selection mathematics. *Ann. hum. gen.* **35**: 485–490.

Queller, D.C. 2000. Relatedness and the fraternal major transitions. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **355**: 1647–1655.

Ratnieks, F.L.W. 1988. Reproductive harmony via mutual policing by workers in eusocial Hymenoptera. *Am. Nat.* **132**: 217–236.

Ratnieks, F.L.W. & Visscher, P. K. 1989. Worker policing in the honeybee. *Nature* **342**: 796–797.

Reeve, H.K. 1991. Polistes. In: *The Social Biology of Wasps* (K. G. Ross & R. W. Matthews, eds), pp. 99–148. Cornell University Press, Ithaca.

Reeve, H.K. & Keller, L. 1999. Levels of selection: burying the units of selection debate and unearthing the crucial new issues. In: *Levels of Selection in Evolution* (L. Keller, ed.), pp. 3–15. Princeton University Press, Princeton, NJ, USA.

Roberts, G. 1996. Why individual vigilance declines as group size increases. *Anim. Behav.* **51**: 1077–1086.

Sachs, J.L., Mueller, U.G., Wilcox, J.P. & Bull, J.J. 2004. The evolution of cooperation. *Q. Rev. Biol.* (in press).

Semmann, D., Krambeck, H. & Milinski, M. 2003. Volunteering leads to rock-paper-scissors dynamics in a public goods game. *Nature* **425**: 390–393.

Sober, E. & Wilson, D.S. 1999. *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Harvard University Press, Harvard, MA, USA.

Taylor, P.D. & Frank, S.A. 1996. How to make a kin selection model. *J. Theor. Biol.* **180**: 27–37.

Trivers, R.L. 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**: 35–57.

Visick, K.L., Foster, J., Doino, J., McFall-Ngai, M. & Ruby, E.G. 2000. *Vibrio fischeri lux* genes play an important role in colonization and development of the host light organ. *J. Bacteriol.* **182**: 4578–4586.

Wenseleers, T. & Ratnieks, F.L.W. 2004. Tragedy of the commons in *Melipona* bees. *Proc. R. Soc. Lond. B* **79**: 135–160.

Wenseleers, T., Ratnieks, F.L.W. & Billen, J. 2003. Caste fate conflict in swarm-founding Hymenoptera: an inclusive fitness analysis. *J. Evol. Biol.* **16**: 647–658.

West, S.A. & Buckling, A. 2003. Cooperation, virulence and siderophore production in bacterial parasites. *Proc. Roy. Soc. London B* **270**: 37–44.

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

West, S.A., Kiers, E.T., Simms, E.L. & Denison, R.F. 2002b. Sanctions and mutualism stability: why do rhizobia fix nitrogen? *Proc. Roy. Soc. London B* **269**: 685–694.

Wilkinson, G.S. 1984. Reciprocal food sharing in the vampire bat. *Nature* **308**: 181–184.

Wilkinson, G.S. 1988. Reciprocal altruism in bats and other mammals. *Ethol. Sociobiol.* **9**: 85–100.

Wilson, E.O. 1971. *The Insect Societies*. Harvard University Press, Cambridge, MA, USA.

Wilson, D.S. 1975. A theory of group selection. *Proc. Natl. Acad. Sci. USA* **72**: 143–146.

Wilson, D.S. 1977. Structured demes and the evolution of group advantageous traits. *Am. Nat.* **111**: 157–185.

Wilson, D.S. 1980. *The Natural Selection of Populations & Communities*. Menlo Park, Benjamin Cummings.

Wilson, D.S. 1990. Weak altruism, strong selection. *Oikos* **59**: 135–140.

Wilson, D.S. (ed.) 1997a. Multilevel selection. *Am. Nat.* **150**: S1–S134.

Wilson, D.S. 1997b. Biological communities as functionally organized units. *Ecology* **78**: 2018–2024.

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Appendices

The appendices review Frank's (1994b, 1995, 1996, 1998) model and associated concepts, which form the foundation for the analyses presented above.

Appendix A – Frank's model

Frank's (1994b, 1995 model is the simplest form of eqn 1, which assumes that investment and the benefit received are equivalent so that $f(z_{ij}) = z_{ij}$, $f(z_i) = z_i$, and $g(z_i) = 1 - z_i$:

$$w_{ij} = \frac{z_{ij}}{z_i}(1 - z_i) \qquad (A1)$$

where z_{ij} is the level of reproductive competition of the jth individual of the ith group, and z_i is average reproductive competition in the ith group (Frank, 1994b, 1995). The aim of the model is to find the level of reproductive competition at equilibrium (z^*) that maximizes the fitness of the focal individual w_{ij}. This represents the evolutionarily stable strategy (ESS; Maynard Smith, 1982) because it is the value of z from which any deviation decreases the focal individual's fitness. In practice, z^* is found by differentiating eqn A1 to find dw_{ij}/dz_{ij}, which gives the change in fitness (w_{ij}) for each change in reproductive competition (z_{ij}):

$$\frac{dw_{ij}}{dz_{ij}} = \frac{1}{z_i} - \frac{z_{ij}}{z_i^2} \cdot \frac{dz_i}{dz_{ij}} - 1$$

This can be simplified because at equilibrium all individuals in the group converge on the same level of competition and $z_{ij} = z_i = z^*$. Furthermore, dz_i/dz_{ij}, which is the regression of average group phenotype on the focal individual's phenotype, is equivalent to within-group relatedness (r, Appendix B). The value of z^* which maximizes fitness w_{ij} is found by exploiting the mathematical fact that at the maximum, the derivative (dw_{ij}/dz_{ij}) will be zero:

$$\frac{dw_{ij}}{dz_{ij}} = \frac{1 - z^*}{z^*} - r\frac{1}{z^*} = 0$$

By rearrangement, this gives $z^* = 1 - r$ (Frank, 1994b, 1995, 1996, 1998; Taylor & Frank, 1996), where r is within-group relatedness. This predicts that group performance is proportional to relatedness, $g(z^*) = 1 - z^* = r$ and that reproductive competition will limit group adaptation unless relatedness is high (Leigh, 1977, 1983; Frank, 1995, 1996). This occurs because of strong selection from the individual performance term (z_{ij}/z_i) to increase competition. With zero relatedness, increasing competition always improves an individual's total fitness, irrespective of the harm incurred by the group ($1 - z_i$), which ultimately results in zero group performance at equilibrium, that is, $1 - z^* = 0$. This is the tragedy of the commons.

When group members are related, individual and group behaviour is correlated so that cooperative individuals occur together, which increases the benefit of cooperation and lowers competition, resulting in the $z_{ij} = 1 - r$ equilibrium. This equilibrium is used as the basis for comparisons in the analyses above, which investigate the conditions that increase group performance relative to this prediction. In calculating the level of competition, the model assumes there is no feedback effect of competition upon relatedness.

Appendix B – Relatedness

The relatedness that emerges from the model (eqn 1 and A1) is the regression of average group phenotype on the focal individual's phenotype, where importantly the group phenotype includes the actor (Frank, 1996). Such 'within-group relatedness' includes relatedness of the focal individual to themselves and is appropriate for modelling actions that benefit all group members including the actor, such as nest building, sentinel behaviour and extra-cellular enzymes in bacteria (whole-group traits, Pepper, 2000). A different measure of relatedness is needed for social traits that benefit all group members except the actor, such as allogrooming (other-only traits, Pepper, 2000). Here 'pairwise relatedness' is appropriate, which is equivalent to average kinship in the group and excludes the relatedness of the actor to themselves where $r = [r_p(n - 1)/n]+1/n$, where r is Frank's within-group relatedness, r_p is mean pairwise relatedness in the group, n is group size (Frank, 1995; Pepper, 2000). Zero cooperation is always predicted with zero within-group relatedness (r). However, with zero pairwise relatedness (r_p), whole-group cooperative traits can evolve through relatedness to self. This can be seen by substituting r_p into the equilibrium value of group performance from eqn A1 for $r_p = 0$, which gives $g(z^*) = r = 1/n$, and is the mechanism by which trait group selection can result in cooperation among unrelated individuals (Wilson, 1975; Dugatkin, 1998, 2002; Avilés, 2002).