

MINI REVIEW

Spite and the scale of competition

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Abstract

In recent years there has been a large body of theoretical work examining how local competition can reduce and even remove selection for altruism between relatives. However, it is less well appreciated that local competition favours selection for spite, the relatively neglected ugly sister of altruism. Here, we use extensions of social evolution theory that were formulated to deal with the consequences for altruism of competition between social partners, to illustrate several points on the evolution of spite. Specifically, we show that: (i) the conditions for the evolution of spite are less restrictive than previously assumed; (ii) previous models which have demonstrated selection for spite often implicitly assumed local competition; (iii) the scale of competition must be allowed for when distinguishing different forms of spite (Hamiltonian vs. Wilsonian); (iv) local competition can enhance the spread of spiteful greenbeards; and (v) the theory makes testable predictions for how the extent of spite should vary dependent upon population structure and average relatedness.

Altruism and spite

Social behaviours can be categorized according to the direct fitness consequences they entail for the actor and recipient (Fig. 1; Hamilton, 1964, 1970, 1971). A behaviour increasing the direct fitness of the actor is mutualistic if the recipient also benefits, and selfish if the recipient suffers a loss. It is easy to see how such behaviours can be favoured by natural selection. Behaviours which reduce the direct fitness of the actor – altruism if the recipient enjoys a benefit, spite if the recipient suffers a loss – are less easy to explain. Hamilton (1963, 1964) introduced the concept of inclusive fitness and showed that while certain behaviours are detrimental to the individual, they may result in a net increase in the actor's genes in the population. Altruism can be favoured by natural selection despite a direct fitness cost (C) to the actor if the benefit (B) accruing to the recipient is sufficiently large and if the genetic relatedness (R) of the recipient to the actor is sufficiently positive.

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Specifically, when Hamilton's (1963, 1964) rule, $RB > C$, is satisfied. A spiteful behaviour, entailing a negative benefit ($B < 0$) to the recipient and a positive cost ($C > 0$) to the actor, is similarly favoured if $RB > C$, which would require a negative relatedness ($R < 0$) between actor and recipient.

Relatedness and spite

Hamilton (1963) argued that under the assumption of weak selection the appropriate measure of relatedness (R) coincides with Wright's (1922) correlation coefficient of relationship. Wright's coefficient is a function of the association between individuals and the association within individuals with respect to their genes at a given locus. Since these associations have popularly been interpreted in terms of Malécot's (1948) probability of identity by descent, and negative probabilities are not permitted, negative relatedness seems to be mathematically impossible (Hamilton, 1970, 1996; although see Wright, 1969, p. 178). Yet Hamilton (1963) understood that relatedness (R) was in principle a regression coefficient – a fact which is now generally appreciated (reviewed by Seger, 1981; Michod, 1982; Grafen, 1985; Queller, 1985, 1992; Frank, 1998) – and this was first made explicit in his elegant

		Effect on recipient	
		+	-
Effect on actor	+	mutualism	selfishness
	-	altruism	spite

Fig. 1 A classification of social behaviours.

reformulation of Hamilton's (1970) rule using Price's (1970) equation. Specifically, relatedness is the regression (slope) of the recipient's genetical breeding value on that of the actor (Hamilton, 1970, 1972; Taylor & Frank, 1996; Frank, 1997a, 1998). As regressions can be negative as well as positive (and zero), relatedness can feasibly take any real value (from negative infinity to positive infinity). Discussions with Price led Hamilton to acknowledge that negative relatedness can plausibly arise between social partners, and hence spite can be favoured by natural selection (Hamilton, 1970, 1996; Frank, 1995).

How does negative relatedness arise? Grafen's (1985) geometric view of relatedness reveals that relatedness between an actor and a potential recipient depends crucially upon the genetical composition of the whole population. This can be illustrated by assuming that a recipient carries the actor's genes with average frequency p , and the population frequency of the actor's genes is \bar{p} . If the recipient carries the actor's genes at a frequency greater than the population frequency of those genes ($p > \bar{p}$) then an increase in its reproductive success translates into increased frequency of the actor's genes in the population, and hence a positive inclusive fitness benefit to the actor ($RB > 0$; Fig. 2a). Conversely, if the recipient carries the actor's genes at a frequency lower than the population frequency of those genes ($p < \bar{p}$) then an increase in its reproductive success translates into decreased frequency of the actor's genes in the population, and hence a negative inclusive fitness benefit for the actor ($RB < 0$; Fig. 2b). The point here is that the difference between these two situations can arise purely due to variation in the frequency of the actor's genes in the population (variable \bar{p}), even with a fixed proportion of genes shared between the actor and recipient (fixed p): relatedness is relative, with the population as a whole providing the reference.

This also illustrates how negative relatedness can arise. As both situations described above involve a positive benefit ($B > 0$) to the recipient, the coefficient of relatedness which transforms recipient success into inclusive fitness of the actor must be positive in the former instance ($R > 0$; Fig. 2a) and negative in the latter ($R < 0$;

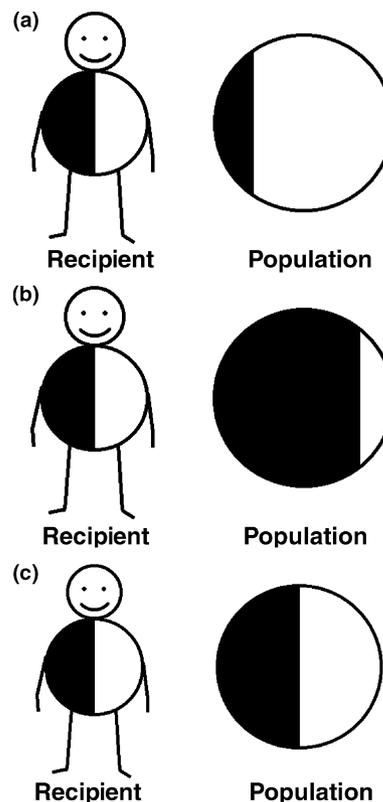


Fig. 2 The geometric view of relatedness. The actor's genes (shaded) are present in the recipient at frequency p and in the population as a whole at frequency \bar{p} . Enhancing the direct fitness of the recipient ($B > 0$) pushes the population gene frequency towards p , and so if $p > \bar{p}$ (a) the frequency of the actor's genes increase, giving a positive inclusive fitness benefit ($RB > 0$) which implies positive relatedness ($R > 0$) between actor and recipient. If $p < \bar{p}$ (b), then the population frequency of the actor's genes decreases, giving a negative inclusive fitness benefit ($RB < 0$) and hence negative relatedness ($R < 0$). When $p = \bar{p}$ (c) the population frequency does not change, giving no inclusive fitness benefit ($RB = 0$) and hence zero relatedness ($R = 0$).

Fig. 2b). The other possibility is that relatedness is zero when the recipient carries the same frequency of the actor's genes as does the population as a whole ($p = \bar{p}$), so that relatedness to the average population member (and hence to the population itself) is zero (Fig. 2c).

But, how large a negative relatedness is likely to arise? Consider an individual who lives in a population of size N , and who is then related to a fraction $1/N$ of the population (i.e. itself) by an amount 1 and is related to the other fraction $(N - 1)/N$ by an amount R . The relatedness to the population as a whole must be zero (Grafen, 1985), and hence must satisfy $(1/N) + [(N - 1)/N]R = 0$. Rearrangement gives $R = -1/(N - 1)$, i.e. the average relatedness between the actor and its social partners is negative (Hamilton, 1975; Grafen, 1985; Pepper, 2000). If the focal individual can identify, and refrain from being spiteful to, a number of positively related genealogically close social

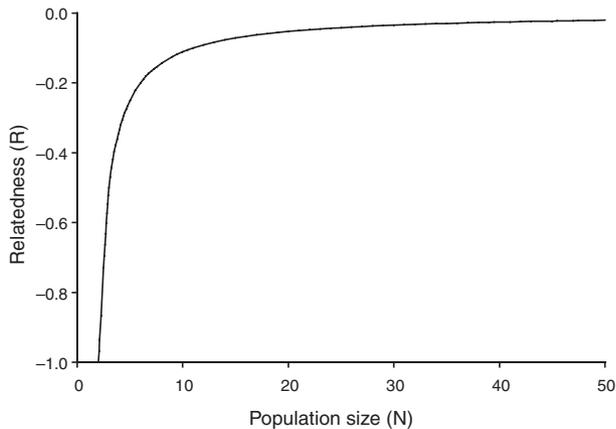


Fig. 3 The average relatedness (R) between population members as a function of population size (N), when there is no kin discrimination. Since relatedness by any member to the population as a whole is zero, and this includes positive relatedness to itself, relatedness to the other individuals is necessarily negative, specifically $R = -1/(N - 1)$. This is minimized at $R = -1$ when $N = 2$, but quickly tends to zero as N increases towards more plausible values.

partners (kin discrimination), then the relatedness to recipients becomes even more negative (Hamilton, 1975). For very small populations (small N ; Fig. 3), negative relatedness can be nontrivial, and hence individuals might be expected to pay reasonable costs in order to inflict damage to their social partners. Negative relatedness (and hence spite) is therefore possible, but this tiny population condition caused Hamilton (1971) to regard spite as merely the 'final infection that kills failing twigs of the evolutionary tree', and not a general phenomenon contributing to adaptive evolution (Hamilton, 1996).

Scale of competition

However, the situation may not be so bleak for spite. There has recently been much interest in how local competition between relatives can reduce and even remove selection for altruism between relatives (reviewed by Queller, 1992; West *et al.*, 2002). This work was spurred by the possibility that with limited dispersal in a viscous population, individuals would tend to associate with kin, so that kin selection theory might suggest positive relatedness between social partners, and hence conditions favourable for the evolution of altruism (Hamilton, 1964, 1971, 1972, 1975, 1996). However, this relies on the implicit assumption of density-dependent regulation being global (hard selection; Wallace, 1968), with no increased competition, due to increased productivity, within more altruistic groups (Boyd, 1982; Wade, 1985). In contrast, if density-dependent regulation occurs at the level of the social group (soft selection, Wallace, 1968; see also Haldane, 1924), then the increased success of the recipient must be paid for by the group. Without kin discrimination, the relatedness of the actor to the

other members of the group will have been equally raised by population viscosity. Hence, population viscosity will not necessarily favour indiscriminate altruism (Hamilton, 1971, 1975; Taylor, 1992a,b).

This effect of local competition between relatives can be incorporated into Hamilton's rule in a number of ways (Grafen, 1984; Queller, 1994; Frank, 1998; West *et al.*, 2002). Queller (1994) reformulated the coefficient of relatedness in order to take this into account, giving a new measure which he described as 'not just a statement about the genetic similarity of two individuals, it is also a statement about who their competitors are'. Here, relatedness between actor and recipient is a regression as before, however it is now defined relative to a reference population of competitors, a proportion of which are locals, and the remainder being average members of the global population. Obviously if all competition is global, the reference population is the global population, allowing for positive relatedness between social partners. At the other extreme, if all competition is at the level of the social group, relatedness to the average member of the social group will be zero. Frank (1998) chose not to redefine relatedness, but instead introduced a separate scale of competition parameter to be incorporated into the benefit component of Hamilton's rule in order to predict when social behaviours will be favoured by selection. This parameter (a) is simply the proportion of competitors which are local as opposed to global. Soft selection (local competition) had been relatively neglected in social evolution theory prior to these developments, and this contrasts with population genetics, where it has received much attention (Roughgarden, 1979).

Although the importance of the scale of competition in the application of kin selection to altruism is now acknowledged (see West *et al.*, 2002 for a recent review, and Griffin *et al.*, 2004 for an empirical example), its implications for spite are underappreciated. Increasingly local competition, as well as disfavouring altruism, can enhance selection for spite. Hamilton was correct when he stated that spite should be restricted to tiny populations; however, the 'population' of interest is that of the competitive arena. If competition is global, so that there is hard selection at the level of the social arena, then relatedness is measured with respect to the population as a whole. But as competition becomes increasingly local, the reference population shrinks towards the size of the social arena, which may contain only a few individuals (small N) and/or a significant proportion of identifiable positively related kin, such that the negative relatedness towards the other potential recipients is nontrivial, enhancing the selective value of spite.

Another way of seeing this is by considering a crucial difference between altruism and spite. Within a social group, individuals with greater altruism than the group average have reproductive success lower than the group average, but if more altruistic groups are more productive, altruists may have higher absolute success than

nonaltruists when averaging over the whole population. When competition is global, fitness is proportional to absolute success, so that altruism can be a winning strategy. Increasingly local competition means that fitness is increasingly dominated by success relative to the social group average, and so altruism is less favoured. Conversely, spiteful behaviour incurs a direct cost and reduces the success of social partners, so that more spiteful individuals can have higher success relative to the group average, but suffer a reduction in absolute success. When competition is global and fitness is proportional to absolute success, spite cannot be favoured, but as competition becomes increasingly local fitness is increasingly determined by success relative to social partners, so that spite can be a winning strategy.

Illustrative overview

So far we have employed the standard approach of taking Hamilton's rule to be a given (for example, see Orlove, 1975) and using this as an entry point into the analysis of social evolution. However, it is often more appropriate and rigorous to derive the rule using a direct fitness approach, particularly when the aim is to resolve problematic conceptual issues. We use the direct (neighbour-modulated) fitness maximization techniques of Taylor & Frank (1996) and Frank (1998) to derive Hamilton's rule, in order to (i) distinguish two different forms of spite, and (ii) address the suggestion of Boyd (1982) that spite is often actually selfishness because it indirectly increments fitness through reducing the intensity of competition. The key to this is to distinguish possible direct benefits of spite that might accrue to positively related third parties, and indirect effects due to relaxed competition.

Let social groups comprise n equally abundant 'families', with kin recognition allowing discrimination of the proportion $1/n = k$ of the social group which are 'kin' from the remaining $1 - k$ which are 'nonkin'. Spite directed at nonkin carries a cost (some function c), inflicts a negative benefit upon the victim (b), and also potentially directly benefits (d) individuals within one's family, so that personal success might be written as:

$$S_{\text{focal}} = 1 + b[(1 - k)z] - c[x] + d[k(1 - k)y], \quad (1)$$

where x is the focal individual's spite strategy, y is the average strategy of its kin (including itself), and z is the average strategy played by the nonkin members of its social group. The local average and the average for the whole population are given by:

$$\begin{aligned} S_{\text{local}} &= 1 + k\{b[(1 - k)z] - c[y] + d[k(1 - k)y]\} \\ &\quad + (1 - k)\{b[(1 - 2k)z + ky] - c[z] + d[k(1 - k)z]\}, \\ S_{\text{global}} &= 1 + b[(1 - k)\bar{z}] - c[\bar{z}] + d[k(1 - k)\bar{z}], \end{aligned} \quad (2)$$

where \bar{z} is the average spite strategy played in the whole population. Following Frank's (1998) approach to including competition in models of social evolution,

fitness can be expressed as success relative to that of the average competitor, i.e.

$$w = \frac{S_{\text{focal}}}{aS_{\text{local}} + (1 - a)S_{\text{global}}}, \quad (3)$$

where the scale of competition parameter (a) is defined as the proportion of competition which occurs locally, i.e. at the level of the social group. Selection favours more spite whenever marginal fitness is positive ($dw/dx > 0$). As outlined by Taylor & Frank (1996), and Frank (1998), marginal fitness is given by the chain rule:

$$\frac{dw}{dx} = \frac{\partial w}{\partial x} + r_y \frac{\partial w}{\partial y} + r_z \frac{\partial w}{\partial z}, \quad (4)$$

where ∂ denotes a partial derivative, and $r_y = dy/dx$ and $r_z = dz/dx$ are the slopes of social partner phenotype on own phenotype (for kin and nonkin respectively). Assuming only minor variants ($x \approx y \approx z \approx \bar{z}$), and denoting $b' = db[\circ]/d\circ$, $c' = dc[\circ]/d\circ$ and $d' = dd[\circ]/d\circ$, we find that marginal fitness is positive ($dw/dx > 0$) when

$$\begin{aligned} &\{r_z - a[kr_y + (1 - k)r_z]\}(1 - k)b' \\ &+ \{r_y - a[kr_y + (1 - k)r_z]\}k(1 - k)d' \\ &> \{1 - a[kr_y + (1 - k)r_z]\}c'. \end{aligned} \quad (5)$$

Note that the relatedness to the average competitor relative to the whole population is $\hat{r} = a[kr_y + (1 - k)r_z]$, and the marginal costs and benefits of spite are $B = (1 - k)b'$, $C = c'$, and $D = k(1 - k)d'$. After making these substitutions, rearrangement of eqn 5 obtains the condition

$$\frac{r_z - \hat{r}}{1 - \hat{r}}B + \frac{r_y - \hat{r}}{1 - \hat{r}}D > C. \quad (6)$$

The r terms denote relatedness of individuals with respect to their spite phenotypes, relative to the population average, \bar{z} . If R is used to denote relatedness *sensu* Queller (1994), i.e. measured relative to the average competitor, then eqn 6 is simply

$$R_1B + R_2D > C. \quad (7)$$

This is the three-party extension to Hamilton's rule for spiteful interactions given by Foster *et al.* (2000), although here it is the consequence of an analysis rather than the starting point. R_1 is the relatedness to the victims of spite, and R_2 is the relatedness to the third party which receives any direct benefits. A major source of confusion over Hamilton's rule involves the meaning of the terms B and C (and in the above expression, D), and so it is worth pointing out that these are not fixed parameters – they are marginal values.

This form of the rule can be used to discriminate Hamiltonian and Wilsonian forms of spite (Hamilton, 1970, 1971; Wilson, 1975; Foster *et al.*, 2000, 2001). Feeling that negative relatedness was implausible, Wilson (1975) proposed that spite directed against non-negatively related individuals could be favoured if it also delivered a benefit to a sufficiently positively related

third party. In terms of the above notation, such Wilsonian spite occurs when $D > 0$ and $R_2 > 0$, and does not require a negatively related victim ($R_1 < 0$). Hamiltonian spite occurs when the victim is negatively related ($R_1 < 0$, and hence $R_1 B > 0$; Hamilton, 1970, 1971), and hence a direct benefit to positive relations ($D > 0$) is not always required in order for the spite to be favoured. From eqn 6 we can see that: (i) negative relatedness depends on the ability to discriminate individuals who are less related than the average competitor (so that $r < \hat{r}$); and (ii) the magnitude of this negative relatedness increases as competition becomes more localized (increasing a , and hence increasing \hat{r}). Clearly, there is potential for spiteful behaviours to involve both negative relatedness to victims and positive benefits to positive relations, and hence a mixture of Hamiltonian and Wilsonian spite (Foster *et al.*, 2000, 2001).

Related to this distinction, we can address the suggestion of Boyd (1982) that spite is actually less likely to occur under local competition, as the resulting relaxed competition gives an indirect benefit to spiteful individuals, so that many cases of spite would in fact be selfishness. Equation 7 reveals that the relaxation of competition due to spite is absorbed into the negative relatedness term, when relatedness is measured relative to the average competitor. Boyd's indirect benefit to the spiteful individual does not make the action selfish, in the same way that this indirect benefit accrued to other positive relatives does not mean that the spiteful behaviour is Wilsonian.

It is important to note that the above is not a general model for spite, but is rather an example included for the purpose of illustration. For instance, we have assumed additivity of fitness components, and equally abundant families. For this reason, it is always more rigorous to do a direct fitness analysis for particular models of interest in order to obtain the appropriate Hamilton's rule, rather than using the rule as a starting point.

Biological applications

Applying the theory to biological examples, we show: (i) that previous models which have successfully demonstrated selection for spite have tended to implicitly assume local competition; (ii) behaviours previously interpreted as indirect altruism or Wilsonian spite might turn out to involve negative relatedness and hence Hamiltonian spite; (iii) spiteful greenbeards are more likely to reach their threshold frequency, above which they are favoured by selection, when competition is localized; (iv) there are several general predictions which will help us identify situations where spite is likely to be found, and (v) these predictions are amenable to empirical testing.

Spiteful models assume local competition

Theoretical models that show that spiteful behaviour can be favoured often assume that some or all of competition

is local. However, this has rarely been acknowledged as an important factor contributing to the success of spite. For example:

1. Reinhold (2003) used an inclusive fitness analysis to investigate fatal fighting in fig wasps. This model shows selection for spite when competition is completely local. Some fig wasps have a lifecycle, such that wingless males hatch, mate and die within the confines of the fruit, and the mated females disperse to be the foundresses of new figs (Hamilton, 1979; Cook *et al.*, 1997). This leads to an asymmetric scale of competition, such that males compete locally (for mates) and females compete globally (for figs in which to lay eggs), the consequences of which for sex allocation theory have been much studied (Hamilton, 1967; Herre *et al.*, 2001). In some species, this local competition for mates is accompanied by lethal combat between heavily armoured males, which have mandibles capable of decapitating each other (Hamilton, 1979; Murray, 1987; West *et al.*, 2001). Reinhold (2003) predicted that if males could discriminate between relatives and nonrelatives (kin recognition) then they would be selected to fight with males who are nonrelatives. This cannot be explained simply as selfishness because there is generally a net direct fitness cost of fighting (the difference in the direct fitness component of Reinhold's equations 2.1 and 2.2 for the terms T_1 & T_2). However, it can be explained as Hamiltonian spite, because the local competition means there is a negative relatedness towards opponents. Following Reinhold's notation, n males compete locally for matings, including a focal actor who is related to a proportion y of the other males (his brothers) by r and to the remaining $(n-1)(1-y)$ males (nonkin) by zero. Rescaling such that the focal individual is related to competitors on average by zero, we find that the relatedness to his brothers is $[n(1-y)r - (1-ry)] / [(n-1)(1-ry)]$ and to the unrelated males is $-[1 + (n-1)ry] / [(n-1)(1-ry)]$, i.e. a negative quantity. The importance of spite in this system depends upon the possibility of kin discrimination between male fig wasps, which has yet to be tested for.

2. Gardner *et al.* (2004) presented a model of chemical (bacteriocin) warfare between microbes. Bacteriocins are the most abundant of a range of antimicrobial compounds produced by bacteria, and are found in all major bacterial lineages (Riley & Wertz, 2002). They are a diverse family of proteins with a range of antimicrobial killing activity including enzyme inhibition, nuclease activity and pore formation in cell membranes (Reeves, 1972; Riley & Wertz, 2002). They are distinct from other antimicrobials in that their lethal activity is often limited to the same species of the producer, suggesting a major role in competition with conspecifics (Riley *et al.*, 2003). As bacteriocin synthesis is energetically expensive and release can entail death of the producer cell (for instance, colicin production by *Escherichia coli*) production of bacteriocins is costly ($C > 0$). Bacteriocins kill susceptible bacteria, and hence these recipients suffer a negative

benefit ($B < 0$). Hence bacteriocin production can be regarded as a spiteful trait. As kin of the producer cell are immune to its bacteriocins, there is effective kin discrimination, and the potential for recipients to be negatively related to the producer. Specifically, this relatedness is $R = -(ak)/(1 - ak)$ where k is the proportion of the social group which are clonal kin of the producer, and a is the proportion of competition which occurs locally. This reveals the importance of local competition in the evolution of spiteful behaviour. Specifically, (i) spiteful bacteriocin production is only selected for when there is some local competition ($a > 0$; as $R = 0$ when $a = 0$), and (ii) as the degree of local competition (a) increases the evolutionary stable strategy (Maynard Smith & Price, 1973) is to increasingly allocate resources to spiteful bacteriocin production (Gardner *et al.*, 2004).

3. Cytoplasmic Incompatibility (CI), the phenomenon whereby maternally transmitted *Wolbachia* (and other) bacteria occurring in male hosts sterilize uninfected female hosts upon mating (O'Neill *et al.*, 1997), has been interpreted as a form of spite (Hurst, 1991; Foster *et al.*, 2001). Infected females are compatible with infected males, and so there is effective discrimination of carriers and noncarriers of the parasite. The question of whether it can be favoured by selection has received much attention (Prout, 1994; Turelli, 1994; Frank, 1997b). Frank (1997b) demonstrated that selection can favour CI in structured host populations. In his model, the sterilization of uninfected females relaxes competition for the infected progeny produced by the group. In particular, Frank highlighted the importance of kin associations, so that related bacteria are carried by several hosts within the group. Less emphasis was given to the assumption of density-dependent regulation at the group level, so that all competition is local ($a = 1$). Similar reasoning can be applied to the evolution of such selfish elements as maternal-effect lethal distorter genes (Beeman *et al.*, 1992; Hurst, 1993; Hurst *et al.*, 1996; Foster *et al.*, 2001), in which the killing of noncarriers relaxes competition among the carriers of the killer allele.

Hamiltonian and Wilsonian spite

Equation 7 can be used to discriminate between Hamiltonian and Wilsonian forms of spite, and assess their relative importance when both occur (i.e. when spite is directed at negatively related individuals but also accrues a net inclusive fitness benefit by directly enhancing the success of positive relations). In particular, using measures of relatedness that take into account the effects of competition, we can reinterpret many putative examples of Wilsonian spite as Hamiltonian spite or a mixture of the two. For instance, Foster *et al.* (2000, 2001) present two spiteful behaviours presented by the eusocial insects which they describe as Wilsonian: worker policing and sex allocation manipulation.

Often in eusocial hymenopteran societies, worker individuals do not have the opportunity to mate, but nevertheless have functioning ovaries, and can therefore produce unfertilized eggs which may develop as haploid males (Wilson, 1971; Bourke, 1988). Worker policing, the phenomenon whereby workers eat the eggs of other workers in their colony (Ratnieks, 1988), is well documented (Ratnieks & Visscher, 1989; Foster & Ratnieks, 2000, 2001; Barron *et al.*, 2001; Foster *et al.*, 2002). Foster *et al.* (2000, 2001) argue that this costly policing behaviour enhances the inclusive fitness of the actor as it frees up resources for the queen's sons (their brothers), to which they are more related than the sons of other workers (their nephews), and hence the spite is of the Wilsonian form. However, given that competition between the progeny for resources is within the colony, it is appropriate to measure relatedness with respect to this local competitive arena when assessing the inclusive fitness consequences for this particular behaviour. This means that the victim of the policing (a nephew) is less related than average (all brothers and nephews) and hence negatively related to the actor (i.e. $R_1 < 0$). Consequently, if relatedness is measured at the scale of competition, worker policing can be interpreted as involving Hamiltonian spite.

The haplodiploid genetics of the hymenoptera means that in eusocial species the workers can be more related to their diploid sisters than their haploid brothers. This means that, while the queen prefers equal sex allocation among reproductives, the workers would rather there was a female bias (Trivers & Hare, 1976). In some species the workers create this bias by killing male progeny (Passera & Aron, 1996; Sundström *et al.*, 1996; Chapuisat & Keller, 1999; Hammond *et al.*, 2003). Foster *et al.* (2000, 2001) suggest this killing of male progeny is Wilsonian spite that benefits the colony's female progeny. However, the local competition for resources within the colony, plus the fact that males are devalued relative to females in terms of relatedness, means that the recipient of the spite is negatively related to the actor ($R_1 < 0$). Again, this behaviour may be reinterpreted involving Hamiltonian spite.

Application of the theory should also allow reinterpretation of behaviours which have not been considered spiteful (Hamiltonian or otherwise) in the past. Precocious larval development in polyembryonic parasitoid wasps (Godfray, 1992; Grbic *et al.*, 1992; Hardy *et al.*, 1993; Ode & Strand, 1995) seems to constitute a previously overlooked example of spite. Typically, two eggs, one male and one female, are laid on or in the body of the host insect, which then divide asexually to produce a brood of genetically identical brothers and genetically identical sisters. Local competition for resources limits the number of adult wasps emerging from the host, suggesting that there is scope for negative relatedness between the sexes within the brood. Upon inspection, some of the larvae that have not emerged as

adults are found to have developed precociously, giving up their own future reproduction in order to murder opposite-sex siblings developing in the same host. Asymmetric dispersal (which generates a sex difference in the scale of competition), and asymmetric relatedness (brothers are more related to sisters than vice versa) seem to be responsible for evolutionary resolution of this conflict in favour of the sisters, such that most precocious larvae are female.

Local competition can enhance the success of spiteful greenbeards

Greenbeards are phenotypic markers for genetic composition that allow individuals to identify positive relations more effectively than through discrimination of genealogical kin from nonkin (Hamilton, 1964, 1971; Dawkins, 1976). A greenbeard gene causes three things: (i) a phenotypic trait, (ii) recognition of this trait in others, and (iii) preferential treatment of those recognized – see Queller *et al.* (2003) for an example of a single gene which satisfies these three conditions. From the perspective of the greenbearded actor, social partners displaying the phenotype carry his gene and hence are positively related to him, and those who do not display the phenotype do not carry his gene, and are therefore negatively related to him, with respect to that locus. Greenbeards can therefore increase in frequency either by directing altruism towards the positive relations or else by directing spite towards the negative relations. However, nontrivial negative relatedness is only possible when the greenbeard allele is at a substantial frequency in the population, as Hamilton (1971) understood, making it difficult to imagine how a spiteful greenbeard could initially be selected. This problem is not felt by altruistic greenbeards, which have maximal relatedness between bearers of the gene even when the greenbeard is at low frequency in the population. The understanding that is the arena of competition that provides the appropriate reference, rather than the population as a whole, means that the spread of spiteful greenbeards can be more easily understood, and the attainment of the threshold frequency does not have to rely upon assumptions such as extreme stochastic fluctuations.

Foster *et al.* (2000, 2001) discuss the example of the red fire ant (*Solenopsis invicta*; see also Keller & Ross, 1998 and Hurst & McVean, 1998), in which workers with genotype Bb, under the influence of their greenbeard (b) gene, murder negatively related BB queens and hence increase the frequency of the b gene in the population (homozygotes for the greenbeard gene are absent as the bb genotype is lethal). It is easy to see how the frequency of the b allele among the small number of locally competing queens could, through sampling error, exceed the threshold even as the global frequency approaches zero.

Where should we expect spite?

The extensions to spite theory, and biological examples of spite discussed above, suggest several clues as to where we should expect such behaviours to occur. Hamilton (1970, 1971) noted that spite should be more prevalent when actors are in a position to inflict damage to others at little cost to themselves, and so it is unsurprising that many examples turn up among nonreproductives in the eusocial insects, those individuals who have little or nothing to lose with respect to their direct fitness (Foster *et al.*, 2000, 2001). A major factor which has received much attention is the ability to identify one's negative relations. This can be achieved through recognition of genealogically close individuals (kin discrimination) or by means of phenotypic markers for genetic composition (greenbeards). We also emphasize that spite should be looked for in situations where competition is mostly local (among social partners), and in viscous populations.

Empirical testing of spite theory

Previous debate over spite has focused primarily on whether spite occurs. However, some of the more recent examples, such as worker policing in the eusocial insects and bacteriocin production by bacteria, provide possibilities for testing whether the relative occurrence of spite varies as predicted by social evolution theory. Indeed, much of the data from the eusocial insects fits well with the predictions of the theory (Chapuisat & Keller, 1999; Ratnieks *et al.*, 2001). Here we emphasize two general points.

1. We used Hamilton's rule to give an overall conceptual view. However, if particular cases are to be analysed, then it is often much easier and more rigorous to start with an equation for direct (neighbour-modulated) fitness based upon the relevant biology, and then derive predictions (Taylor & Frank, 1996; Frank, 1998). Hamilton's rule in some form usually appears as a consequence of such an approach, and provides a conceptual tool that can be used for interpretation of the results (Frank, 1998; Pen & Weissing, 2000; West & Buckling, 2003; Gardner *et al.*, 2004).

2. A relatively general prediction that arises from different models is that the incidence of spite should be dome shaped in relation to the degree of kinship within a social group. If the proportion of kin (including oneself) in the group is vanishingly small then no spite is favoured, as the nonkin recipients of spite will have the same relatedness, on average, as the average group member (i.e. zero). Similarly, when the actor associates solely with clonal kin, spite is also not favoured, as there are no negatively related individuals present. However, when the degree of kinship takes intermediate value, some degree of spite might be favoured because some individuals will necessarily be less related to the actor than others, such that some will have below-average

(and hence negative) relatedness. This result was found in both the bacteriocin (Gardner *et al.*, 2004) and fig wasp mortal combat (Reinhold, 2003) examples discussed above. The relatedness differential also selects for spiteful sex allocation manipulation (brothers are less related than sisters) and worker policing (nephews are less related than sons and brothers) discussed above. As well as suggesting where we might find spite occurring in nature, these models give predictions that could be tested with observational or experimental studies.

Conclusion

Spite has been neglected by social evolution theory because a common, implicit assumption (global competition) in evolutionary models tends to diminish its selective advantage. We have demonstrated that many previously analysed behaviours can be readily interpreted as involving spite. Furthermore, theory has been developed to such a degree that we can make testable predictions about where spite is likely to be found and how it relates to the degree of competition and kinship between social partners.

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