

Dedicated to the memory of William Donald Hamilton

Spite: Hamilton's unproven theory

Kevin R. Foster^{1*}, Tom Wenseleers² & Francis L. W. Ratnieks³

¹⁾ *Laboratory of Apiculture and Social Insects, Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK*

^{*} *Current address: Department of Ecology and Evolutionary Biology, Rice University, MS 170, 6100 Main, Houston, Texas 77005, USA (e-mail: krfooster@rice.edu)*

²⁾ *Laboratory of Entomology, Zoological Institute, Katholieke Universiteit Leuven, Naamsestraat 59, B-3000 Leuven, Belgium*

³⁾ *Laboratory of Apiculture and Social Insects, Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK*

Received 6 January 2001, accepted 28 May 2001

Foster, K. R., Wenseleers, T. & Ratnieks, F. L. W. 2001: Spite: Hamilton's unproven theory. — *Ann. Zool. Fennici* 38: 229–238.

Thirty years ago Hamilton showed that spite, an action that harms a recipient at no direct benefit to the actor, could evolve if interactants were negatively related. Wilson later showed that spite could also evolve by indirect benefits to a third party. Since then, many selfish actions that are particularly harmful to the recipient have been called 'spite' but no convincing examples have been found. Here we discuss three examples of spite from the social insects: worker policing, sex allocation biasing by workers and green beard queen killing in the fire ant. All examples are Wilsonian spite and the last example is also Hamiltonian spite. Spite will be harder to identify in other animals because actions that seem mutually harmful may have delayed reproductive benefits. Spite may prove to be more common at the genetic level than the individual level because negative relatedness can more easily arise. Two possible examples, cytoplasmic incompatibility and maternal-effect lethal distorter genes, are discussed.

Introduction

Social actions can be categorised in terms of their costs and benefits to interactants (Hamilton 1964a, Wilson 1975, Gadagkar 1993) (Fig. 1). Selection for selfishness and mutualism are straightforward in this context because both

confer a direct reproductive advantage to the actor. Why an animal should be altruistic, that is help another at a cost to itself, is less obvious. Hamilton (1964a, 1964b), however, showed that altruism could be selected for if the actor and recipient were related because the action would then increase the frequency of copies of the

| | | EFFECT ON RECIPIENT | |
|-----------------|--------|---------------------|-------------|
| | | + | - |
| EFFECT ON ACTOR | + | Mutualism | Selfishness |
| | - or 0 | Altruism | Spite |

Fig. 1. The four types of social action based on their effect on the direct fitness (lifetime personal reproduction) of the actor and recipient (e.g. Hamilton 1970, 1971). Definitions are based on the individuals that are physically involved in the action and not those that are indirectly affected after the event (e.g. Wilson 1975). Altruism and spite can either have zero or a negative fitness effect on the actor ('weak' and 'strong'; Hamilton 1971, Gadagkar 1993). Behaviours that have no fitness effect on the recipient are not considered.

actor's genes shared by the recipient. Specifically, Hamilton showed that an altruistic action would be favoured if $rb > c$, where b is the direct reproductive benefit to the recipient, c the direct reproductive cost to the actor and r the relatedness of actor to recipient. However, why an individual would be spiteful and harm another at no benefit to itself was more enigmatic. Hamilton initially considered spite non-selectable (Hamilton 1964a) but after discussions with George Price (Frank 1995, Hamilton 1995) showed that spite could evolve based on the reverse of altruism, harm to negatively related individuals (Hamilton 1970, 1971). Harm directed to a negatively related recipient ($r < 0$) could be selected for even without benefit to self. Negative relatedness occurs when a recipient is less likely to share the actor's genes than a randomly chosen individual in the population. A spiteful action between negatively related individuals, therefore, is selected for because it reduces the frequency of competing alleles in the gene pool. Wilson proposed an alternative mechanism for the evolution of spiteful behaviour (Wilson 1975, Foster *et al.* 2000). He considered the effect of

the action on a non-interacting third party. If a related third party receives a benefit from the spiteful action that outweighs the costs to actor and recipient then spite can evolve.

Although Hamilton and Wilson envisaged scenarios under which spite could be selected for, both thought it would be of little biological importance. In Hamilton's case, this stemmed from the restrictive requirements for its evolution: negative relatedness, accurate kin discrimination and little or no cost to the actor (*see* below). Since Hamilton's and Wilson's work, spite has suffered a chequered history. A wide range of behaviours that are not spite have been associated with the term (Table 1). Although these behaviours often involve serious harm to the recipient, the actor probably benefits from the action. Indeed, Hamilton (1970) pre-empted such interpretations and argued that they were merely selfish (Table 2).

The definition of spite has also had problems. The formulations of Hamilton and Wilson address when a loss of *direct* fitness (personal reproduction) in both actor and recipient can be selected for. However, some later authors have described spite in terms of a loss of *inclusive* fitness (reproduction through all that share copies of the actor's genes) in both parties, which is never favoured by natural selection (e.g. Pierotti 1980, Waltz 1981, Trivers 1985: p. 57). In addition, it has been suggested that spite can evolve due to a delayed direct reproductive benefit (Pierotti 1982) or a benefit to the offspring (FitzGerald 1992). However, as with the empirical examples above (Table 1) a direct benefit to reproduction means that these mechanisms are not spite but selfishness. Most recently, Gadagkar (1993) discussed examples in which no fitness benefit could be found (Table 1) suggesting that such examples could prove to be spiteful. However, Keller *et al.* (1994) later argued, as had Hamilton (1970) (Table 2), that such examples were better interpreted as selfishness. On this basis, Keller *et al.* (1994) concluded that "spiteful animals [are] still to be discovered".

Table 1. Behaviours described as spiteful that probably have a direct reproductive benefit to the actor.

| Species | Description of behaviour | Why action is not spiteful |
|---|--|--|
| Western gull (<i>Larus occidentalis</i>) (Gadagkar 1993, Pierotti 1980, 1982) | Males that pirate food from neighbours do not reproduce | Pirate males have low direct fitness but lose offspring before the action so pirating is not causing low fitness (Keller <i>et al.</i> 1994) |
| Western and herring gulls (<i>L. argentatus</i>) (Pierotti 1980, 1982) | Killing others' chicks without eating them | Energy loss but decreased reproductive competition will increase direct fitness (Keller <i>et al.</i> 1994) |
| Threespine stickleback (<i>Gasterosteus aculeatus</i>) (FitzGerald 1992; Gadagkar 1993) | Females cannibalise broods of conspecifics | Possible energy and competitive benefits (FitzGerald & van Havre 1987, Vickery <i>et al.</i> 1988, Belles-Isles <i>et al.</i> 1990, Keller <i>et al.</i> 1994) |
| Vervet monkey (<i>Cercopithecus aethiops</i>) (Horrocks & Hunte 1981) | Destroy competitors' food source | Energy loss but competitive gain |
| Old World monkeys (Pagel 1994) | Male post-copulatory mate guarding | Prevents sperm competition (Pagel 1994) |
| Old World monkeys (Pagel 1994) | Females invest in oestrous advertisement and increase male competition | Attracts best males and increases reproductive success (Pagel 1994) |
| Old World monkeys (Radwan 1995) | Females deplete male sperm reserves by multiple matings | Decreases competing females' reproduction (Radwan 1995) |
| Mountain sheep (<i>Ovis canadensis</i>)* (Trivers 1985) | Harassing injured competitor | Energy loss but competitive gain |
| Langur (<i>Presbytis entellus</i>)* (Trivers 1985) | Female harassment of copulating couples | Energy loss but competitive reproductive advantage by decreasing the fertility of the mating pair |
| Stumptail macaques* (<i>Macaca arctoides</i>) (Brereton 1994) | Harassment of copulating couples | Energy loss but competitive gain (Brereton 1994) |
| Macaque monkeys* (Trivers 1985) | Adult females harass infant and juvenile daughters of others | Energy loss but competitive gain |
| Fireflies (<i>Photinus macdermotti</i>) (Thornhill & Alcock 1983; Greenfield 1994) | Disruption by males of competing males' female-attraction signal | Energy loss but competitive gain |
| Red-sided garter snakes (<i>Thamnophis sirtalis parietalis</i>) (Shine <i>et al.</i> 2000, Marchant 2000) | Female mimicry by males | Diminishes the cost of courtship (Marchant 2000) |

*Described as "return-benefit spite"

Here we discuss the evolution of spite using three examples from the recent literature (Foster *et al.* 2000). We adopt the original definition of spite used by Hamilton (1970, 1971) and extended by Wilson (1975) and show that examples of both can be found in a group of organisms already famous for altruism: the social insects.

Examples

Worker policing

Although typically unable to mate, workers in most hymenopteran societies (bees, ants and wasps) have functioning ovaries (Wilson 1971, Bourke 1988). This enables them to produce males since unfertilised eggs are male, while fertilised eggs are female (haplodiploid sex determination). Although workers produce males in some species, the norm appears to be that queens dominate male production (Bourke & Franks 1995). One reason for the reproductive monopoly of queens is the tendency of non-reproductive workers to prevent others from reproducing by aggression or egg eating. This 'worker policing', as it has been called (Ratnieks 1988), conforms to Wilson's model for the evolution of spite (Fig. 2). Workers invest time

and energy to kill other workers' sons at no direct reproductive benefit to themselves (Starr 1984, Ratnieks 1988). The action is selected because a third party, the queen's sons, indirectly benefits from the action. Worker policing by egg eating has been found in honeybees (Ratnieks & Visscher 1989, Barron *et al.* 2001) and Vespinae wasps (Foster & Ratnieks 2000, Foster & Ratnieks 2001, Foster *et al.* 2001). In addition, worker policing by direct aggression to reproductive workers occurs in queenless ants (Gobin *et al.* 1999, Kikuta & Tsuji 1999, Liebig *et al.* 1999, Monnin & Ratnieks 2001). This suggests that worker policing is widespread in the social insects (Foster & Ratnieks 2001) and, likewise, that Wilsonian spite is important.

Sex allocation biasing

Hymenopteran workers are more related to their sisters than their brothers because of haplodiploid sex determination. Therefore, workers are expected to attempt to increase female production and bias the sex ratio away from equality, which is the queen's optimum (Trivers & Hare 1976). Male killing by social insect workers to redirect colony resources to females has been found in several species (Sundström 1994, Evans 1995, Passera & Aron 1996) and, like worker

Table 2. Apparently spiteful actions which Hamilton interpreted as selfish.

| Species | Description of behaviour | Why Hamilton considered it selfish |
|---|---|---|
| Bower birds ¹ | Male wrecking of other males' bowers | Decreases reproductive success of competitors |
| Corn ear worm ¹ (<i>Heliothis zea</i>) | First caterpillar in an ear of maize (corn) eats all subsequent arrivals even though there is enough food for two or more | Behaviour may have evolved in the ancestral maize where there was not enough food for more than one larva |
| Mosquitos ¹ (<i>Toxorhynchites</i>) | Larvae kill but do not eat all other nearby larvae before pupating | Prevents actors being eaten by other larvae when they are helpless pupae |
| Fruit fly ² (<i>Drosophila</i>) | Insemination reaction that causes harm to the mated female | Prevents insemination by subsequent males and thus confers a competitive gain in mating success to the male |

¹) Hamilton (1970). ²) Hamilton (1971)

policing, represents Wilsonian spite (Fig. 2). Again, workers receive no direct benefit from their actions but instead benefit through increased production of their more related sisters. This example highlights the distinction made by Wilson's treatment of spite and altruism. The mechanism of sex allocation biasing could be direct help to sisters, which would be nepotistic altruism rather than spite. However, the empirical data demonstrates that workers bias sex allocation by selectively killing males rather than helping females (Evans 1995, Passera & Aron 1996, Sundström *et al.* 1996, Chapuisat *et al.* 1997).

Green beard queen killing in the fire ant

The most remarkable example of spite in social insects is the green beard gene in the red fire ant, *Solenopsis invicta* (Keller & Ross 1998, Hurst & McVean 1998, Foster *et al.* 2000). Heterozygous workers (*Bb*) that carry a certain allele (*b*) at the *Gp-9* (general protein-9) locus kill queens (*BB*) in the colony that lack it. It is referred to as a green beard gene because workers seem to be able to directly identify queens that do or do not possess the *b* gene. This matches the scenario described by Dawkins (1976) in which carriers of a gene for altruism also have green beards allowing them to identify each other. It is noteworthy that although Dawkins popularised green beard genes it was again Hamilton (1964a) who first discussed the concept. As with the previous examples of spite, green beard queen killing may be favoured by selection through a benefit to a third party (the queens in the colony that do carry the *b* allele, Fig. 2).

More interestingly, however, the fire ant system also has all the conditions predicted by Hamilton for the evolution of spite. First, there is negative relatedness (Fig. 3 and Box 1). The green beard allele *b* in a worker, which is the cause of the action, is negatively related to the *BB* locus in the queens that are killed. Second, there is powerful kin discrimination. Altruism requires that an actor can identify individuals that are more likely than average to share their

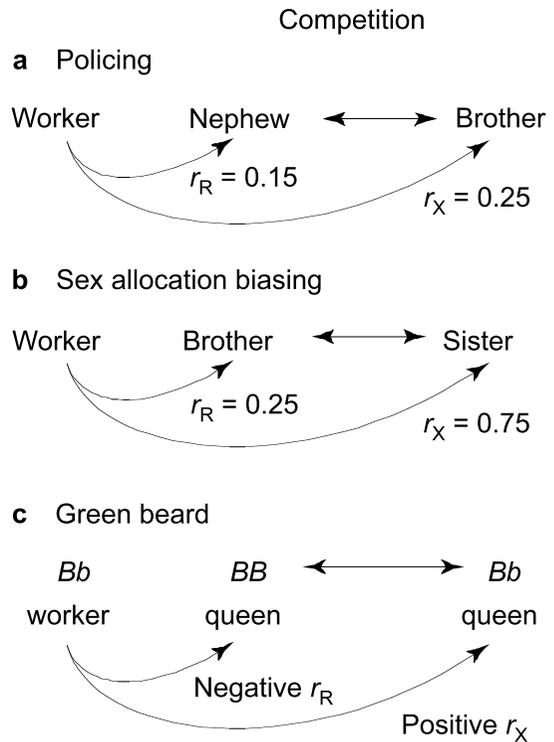


Fig. 2. Examples of spite from the social insects that all involve harm to recipients and possible benefits to a non-interacting third party. Such interactions are selected for when $c_A + c_R r_R < b_X r_X$, a three party extension of Hamilton's rule (Foster *et al.* 2000). Here, c and b denote costs and benefits and r denotes the actor's (life-for-life) relatedness to the recipient R and the third party X. In insect societies, cost to the actor c_A is negligible because of worker sterility. — **a**: For worker policing in the honeybee, r_R to nephews = 0.15, r_X to brothers = $1/4$, and $c_R = b_X$ because for every nephew killed, a brother is reared. — **b**: In worker-biasing of the sex ratio via fratricide, r_R to brothers = $1/4$, r_X to sisters = $3/4$. — **c**: In the fire ant, *Bb* green-beard workers eliminate non-carrier *BB* queens in the colony. The negative relatedness that arises in this system is explained more fully in Fig. 3 and Box 1.

genes, which can be achieved by association with kin. Hamiltonian spite, however, requires an actor to identify individuals that are *less* likely than average to share their genes. This is more challenging (Grafen 1990, 1991, Rozsa 2000) because although kinship information could be used to target non-kin, this generates only very slight negative relatedness (Box 1). In

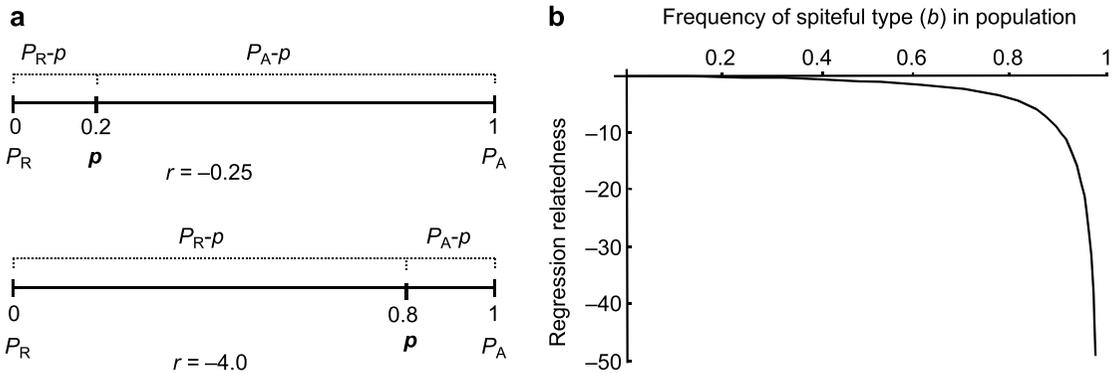


Fig. 3. Negative relatedness at a green beard locus, similar to that found in the fire ant. For simplicity, and as in Hamilton's original model (Hamilton 1971), we assume that the spiteful interaction occurs between haploid animals. Wild and spiteful types are denoted B and b . Relatedness is calculated as $(p_R - p)/(p_A - p)$ where p_R , p_A and p denote frequency of the spiteful b gene in recipients, actors and the population at large (Grafen 1985). With green beard recognition $p_R = 0$ and $p_A = 1$. — **a:** Relatedness between a b 'spiteful killer' and a B victim illustrated using Grafen's (1985) geometric view of relatedness, for b rare (top) and common (bottom). As b increases in frequency, the actor (b) becomes more like the population and the recipient (B) less like the population. This makes recipients less like actors relative to the population, increasing the magnitude of negative relatedness between actor and recipient. — **b:** Relatedness between a b 'spiteful killer' and a B victim, as a function of the frequency of the spiteful b type in the population. If the spiteful interaction occurs at a cost c_A to the actor and a cost c_R to the recipient, spite spreads in a population when $p > c_A/(c_A + c_R)$, a result first derived by Hamilton (1971).

Box 1. Negative relatedness, green beard genes and frequency dependence

The concept of negative relatedness is unfamiliar to many biologists and is rarely discussed because it is generally viewed as unimportant (Grafen 1985). This is because interacting with kin, the most familiar mechanism of generating a genetic association, causes only positive relatedness ranging from zero (random genetic association) to one (clones). A slight exception is if an individual uses kinship information to target non-kin, which generates negative relatedness. However, non-kin are typically many times more abundant than identifiable kin making them genetically very similar to the population average ($r = 0$). Such discrimination will, therefore, generate only very slight negative relatedness. With other mechanisms of genetic assortment relatedness between interactants can range from negative to positive infinity. Such mechanisms include green beard genes and interactions in highly viscous populations where nearby individuals are positively related while distant ones are negatively related. Green beard gene-based interaction also differs from kinship in that the level of relatedness depends on the frequency of the focal gene in the population. This is illustrated by Fig. 3 where the relatedness between a spiteful actor and its victim are plotted as a function of the frequency of the spiteful allele in the population. The figure also shows that the strength of selection on the spiteful allele (b) relative to the wild type (B) is dependent on the frequency of the spiteful allele in the population. As the b allele spreads, selection for the green beard trait becomes relatively stronger. Or conversely, as the B type becomes rarer, harm has relatively more impact on its frequency and so benefits b individuals more. This system is equivalent to measuring the relatedness between the green beard allele b in a killing fire ant worker and the BB locus in a killed queen (Keller & Ross 1998, Hurst & McVean 1998). In the fire ant, however, selection will also be affected by the lethality of the bb genotype and possible third-party benefits (above).

the fire ant negative relatedness is achieved by the green beard effect which represents the direct identification of non-gene carriers, independent of kinship. Finally, Hamilton predicted that a spiteful action would have little or no direct fitness cost because the benefits from spite are likely to be small. Fire ant workers are sterile, so they suffer no direct cost from their action.

Are there other examples of spite in animals?

Selection for spite, particularly as Hamilton described, requires much rarer conditions than selection for altruism. We can, therefore, expect spite to be rarer than altruism. However, the examples from the social insects have shown that, contrary to prediction (Hamilton 1964a, 1964b, 1995, Wilson 1975), spite can be an important phenomenon. Establishing just how important spite is outside the social insects will be challenging. In most species, the potential exists for delayed direct reproductive benefits from actions. This is particularly true in vertebrates where helpers may often become reproductives at a later time ('hopeful reproductives', Krebs & Davies 1991). A harmful action in such animals may appear spiteful but may later incur a direct fitness benefit rendering it selfish. Sterile or effectively sterile social insect workers are, therefore, a particularly easy group in which to identify spite. With the molecular analysis of kinship now routine, however, another way to proceed could be to look out for negative relatedness: the landmark trait of Hamiltonian spite (Box 1). Hamilton (1971) suggested that mating partners might sometimes be selected to be spiteful towards each other since inbreeding avoidance causes slight negative relatedness between them (Wright 1965, Storz 1999; Table 2). However, Hamilton (1971) could not find any convincing examples (Table 2). This is consistent with the prediction that selection for spite based on harm to non-kin will generally be weak (Box 1) and only significant when the actor can harm many non-kin at a low cost. One example where harm to non-kin may experience significant selection is when animals are chronically

infected with a parasite (Rózsa 2000). Such individuals can potentially infect and seriously harm many non-kin at little direct fitness cost, given that their own reproductive potential is already seriously depleted by the infection itself. Host traits that increase parasite transmission such as increased dispersal may, therefore, sometimes represent host-parasite cooperation rather than parasite manipulation, which is normally assumed.

Spite in genetic conflicts

Spite has also been discussed in the context of intragenomic conflict. Hurst (1991) called cytoplasmic incompatibility caused by the intracellular bacterium *Wolbachia* spiteful. *Wolbachia* is an endosymbiont that lives in the cells of many arthropods and is known to manipulate host reproduction in ways that enhance its own spread (reviewed by O'Neill *et al.* 1997, Rousset & Raymond 1991, Werren 1997). Cytoplasmic incompatibility is one strategy that has been widely documented in insects (O'Neil *et al.* 1997). *Wolbachia* occurring in males sterilise uninfected female hosts upon mating. Hurst (1991) observed that this system resembles Hamilton's scenario for the evolution of spite because the sterilising *Wolbachia* in males benefit their clonemates by removing non-carriers' offspring from the population (Frank 1997). Because *Wolbachia* is vertically transmitted via egg cytoplasm, a male is a dead end. Therefore, as in the fire ant, the action has no reproductive cost to the acting *Wolbachia*. However, in this system the 'spiteful' action is between two different species: the *Wolbachia* in the male and the female insect. This raises the question of whether it is useful to extend definitions of social actions to interspecific interactions (Frank 1994). The field of social evolution in interspecific interactions is still in its infancy, so we leave this decision open here.

Maternal-effect lethal distorter genes (such as *Medea* in *Trilobium*, Beeman *et al.* 1992 and *Scat+* in mice, Hurst 1993) have been proposed as a candidate for *intraspecific* spite (Frank 1995). When present in a female (D+) these nuclear genes kill offspring that do not carry

them (D-) (reviewed by Hurst *et al.* 1996). The death of progeny might provide direct benefits to surviving sibs (although perhaps not in *Tribolium*, Smith 1998), which would render the action selfish. However, even without such benefit, selection is still expected to favour the action due to the negative relatedness between the distorter gene and the killed offspring. This would be an instance of Hamiltonian spite, formally comparable to the green beard gene in the fire ant (cf. Wade 2000). Hamiltonian spite may prove to be common in genetic conflicts, especially as negative relatedness can more easily arise. Identifying non-gene carriers in direct genetic interactions can be based on simple toxin/anti-toxin systems (Haig 1996), whereas interactions at the organismal level are likely to require more elaborate recognition systems (Hurst & McVean 1998).

Wilsonian spite and parental punishment

Several authors, including Hamilton (1964a, 1964b), have compared parental care to altruism because helping an offspring reduces reproductive allocation to other offspring in the same way as helping a sibling. Given this, parental punishment (Clutton-Brock 1995, Mock & Parker 1998) could be considered an example of Wilsonian spite. In moorhens, for example, parent birds punish offspring that persistently demand food (Leonard *et al.* 1988). Here the harm caused by the parent (actor) to the punished offspring (recipient) is presumably favoured by a benefit to the other offspring (third party). This example highlights the difference between a direct fitness (e.g. Gadagkar 1993) and phenotypic definition (e.g. Alexander 1979) of social behaviour. Treating parental punishment as spite represents a phenotypic definition in that the phenotypes of both parties (parent and offspring) are harmed. However, by the original direct fitness definition of spite of Hamilton and Wilson then parental punishment is not spite because the action increases the overall direct fitness of the parent.

Conclusion

The history of the use of the term spite shows that a precise definition is critical to any discussion. In this paper we have shown that behaviours by social insect workers formally match the original definitions of spite of Hamilton (1970, 1971) and Wilson (1975). Wilson's conditions for the evolution of spite are less stringent than those of Hamilton, which is perhaps reflected in the larger number of examples. Indeed, Wilson's spite is less distinct from other social actions than Hamilton's spite and has been interpreted as an indirect form of altruism (M. J. West Eberhard pers. comm., P. K. Visscher pers. comm.). Nevertheless, Wilson's definition of spite is useful because it separates two distinct mechanisms by which an individual can gain an inclusive fitness benefit: by directly helping a relative or by harming a relative's direct competitor (Example 2). However, Hamilton's spite will remain the most distinctive, with its unique and fascinating ingredient: negative relatedness.

References

- Alexander, R. D. 1979: *Darwinism and human affairs*. — University of Washington Press, Seattle. 40 pp.
- Barron, A., Oldroyd, B. P. & Ratnieks, F. L. W. 2001: Worker policing and anarchy in *Apis*. — *Behav. Ecol. Sociobiol.* 50: 199–208.
- Beeman, R. W., Friesen, K. S. & Denell, R. E. 1992: Maternal-effect selfish genes in flour beetles. — *Science* 256: 89–92.
- Belles-Isles, J.-C., Cloutier, D. & FitzGerald, G. J. 1990: Female cannibalism and male courtship tactics in threespine sticklebacks. — *Behav. Ecol. Sociobiol.* 26: 363–368.
- Brereton, A. R. 1994: Return-benefit spite hypothesis: an explanation for sexual interference in stump-tail macaques (*Macaca arctoides*). — *Primates* 35: 123–136.
- Bourke, A. F. G. 1988. Worker reproduction in the higher eusocial Hymenoptera. — *Quart. Rev. Biol.* 63: 291–311.
- Chapuisat, M., Sundström, L., & Keller, L. 1997: Sex-ratio regulation: the economics of fratricide in ants. — *Proc. R. Soc. Lond. B* 264: 1255–1260.
- Clutton-Brock, T. H. & Parker, G. A. 1995: Punishment

- in animal societies. — *Nature* 373: 209–216.
- Dawkins, R. 1976: *The selfish gene*. — Oxford University Press, New York. 224 pp.
- Evans, J. D. 1995: Relatedness threshold for the production of female sexuals in colonies of a polygynous ant, *Myrmica tahoensis*, as revealed by microsatellite DNA analysis. — *Proc. Natl. Acad. Sci. USA* 92: 6514–6517.
- FitzGerald, G. J. 1992: Egg cannibalism by sticklebacks: spite or selfishness? — *Behav. Ecol. Sociobiol.* 30: 201–206.
- FitzGerald, G. J. & van Havre, N. 1987: The adaptive significance of cannibalism in sticklebacks (Gasterosteidae: Pisces). — *Behav. Ecol. Sociobiol.* 20: 295–300.
- Foster, K. R. & Ratnieks, F. L. W. 2000: Facultative worker policing in a wasp. — *Nature* 407: 692–693.
- Foster, K. R. & Ratnieks, F. L. W. 2001: Convergent evolution of worker policing by egg eating in the honeybee and common wasp. — *Proc. R. Soc. Lond. B* 268: 169–174.
- Foster, K. R., Wenseleers, T. & Ratnieks, F. L. W. 2000: Spite in social insects. — *Trends Ecol. Evol.* 15: 469–470.
- Foster, K. R., Gulliver, J. & Ratnieks, F. L. W. 2001: Worker policing in the European hornet *Vespa crabro*. — *Insects Soc.* [Accepted].
- Frank, S. A. 1994: Genetics of mutualism: the evolution of altruism between species — *J. Theor. Biol.* 170: 393–400.
- Frank, S. A. 1995: George Price's contributions to evolutionary genetics. — *J. Theor. Biol.* 175: 373–388.
- Frank, S. A. 1997: Cytoplasmic incompatibility and population structure. — *J. Theor. Biol.* 184: 327–330.
- Gadagkar, R. 1993: Can animals be spiteful? — *Trends Ecol. Evol.* 8: 232–234.
- Gobin, B., Billen, J. & Peeters, C. 1999: Policing behaviour towards virgin egg layers in a polygynous ponerine ant. — *Anim. Behav.* 58: 1117–1122.
- Grafen, A. 1985: A geometric view of relatedness. — *Oxford Surv. Evol. Biol.* 2: 28–89.
- Grafen, A. 1990: Do animals really recognize kin? — *Anim. Behav.* 39: 42–54.
- Grafen, A. 1991: Kin recognition in vertebrates — What do we really know about adaptive value — reply. — *Anim. Behav.* 41: 1085–1087.
- Greenfield, M. D. 1994: Cooperation and conflict in the evolution of signal interactions. — *Annu. Rev. Ecol. Syst.* 25: 97–126.
- Haig, D. 1996: Gestational drive and the green-bearded placenta. — *Proc. Natl. Acad. Sci. USA* 93: 6547–6551.
- Hamilton, W. D. 1964a: The genetical evolution of social behaviour. I. — *J. Theor. Biol.* 7: 1–16.
- Hamilton, W. D. 1964b: The genetical evolution of social behaviour. II. — *J. Theor. Biol.* 7: 17–52.
- Hamilton, W. D. 1970: Selfish and spiteful behaviour in an evolutionary model. — *Nature* 228: 1218–1220.
- Hamilton, W. D. 1971: Selection of selfish and altruistic behaviour in some extreme models. — In: Eisenberg, J. F. & Dillon, W. S. (eds.), *Man and beast: comparative social behavior*: 57–91. Smithsonian Press.
- Hamilton, W. D. 1995: *Narrow roads of gene land. Volume 1. Evolution of social behaviour*. — W.H. Freeman, New York. 552 pp.
- Horrocks, J. & Hunte, W. 1981: 'Spite'; a constraint on optimal foraging in the vervet monkey *Cercopithecus aethiops sabaues* in Barbados. — *Am. Zool.* 21: 939.
- Hurst, G. D. D. & McVean, G. A. T. 1998: Selfish genes in a social insect. — *Trends Ecol. Evol.* 13: 434–435.
- Hurst, L. D. 1991: The evolution of cytoplasmic incompatibility or when spite can be successful. — *J. Theor. Biol.* 148: 269–277.
- Hurst, L. D. 1993: *Scat+* is a selfish gene analogous to *Medea* of *Tribolium castaneum*. — *Cell* 75: 407–408.
- Hurst, L. D., Atlan, A. & Bengtsson, B. O. 1996: Genetic conflicts. — *Quart. Rev. Biol.* 71: 317–364.
- Keller, L., Milinski, M., Frischknecht, M., Perrin, N., Richner, H. & Tripet, F. 1994: Spiteful animals still to be discovered. — *Trends Ecol. Evol.* 9: 103.
- Keller, L. & Ross, K. G. 1998: Selfish genes: a green beard in the red fire ant. — *Nature* 394: 573–575.
- Kikuta, N. & Tsuji, K. 1999: Queen and worker policing in the monogynous and monandrous ant, *Diacamma* sp. — *Behav. Ecol. Sociobiol.* 46: 180–189.
- Krebs, J. R. & Davies, N. B. 1991: *Behavioural ecology: an evolutionary approach*. — Blackwell, Oxford. 3rd edition, 482 pp.
- Leonard, M. L., Horn, A. G., & Eden, S. F. 1988: Parent-offspring aggression in moorhens. — *Behav. Ecol. Sociobiol.* 23: 265–270.
- Liebig, J., Peeters, C. & Hölldobler, B. 1999: Worker policing limits the number of reproductives in a ponerine ant. — *Proc. R. Soc. Lond. B* 266: 1865–1870.
- Marchant, J. 2000: Faking it — in the snake world, cross-dressing is a smart sexual strategy. — *New Sci.* 165: 6.
- Mock, D. W. & Parker, G. 1998: *The evolution of sibling rivalry*. — Oxford University Press, Oxford. 480 pp.
- Monnin, T. & Ratnieks, F. L. W. 2001: Policing in queenless ponerine ants. — *Behav. Ecol. Sociobiol.* 50: 97–108.
- O'Neill, S. L., Hoffmann, A. A. & Werren, J. H. 1997: *Influential passengers: inherited microorganisms and arthropod reproduction*. — Oxford University Press, Oxford, New York, Tokyo. 226 pp.
- Pagel, M. 1994: Evolution of conspicuous estrous advertisement in old-world monkeys. — *Anim. Behav.* 47: 1333–1341.
- Passera, L. & Aron, S. 1996: Early sex discrimination

- and male brood elimination by workers of the Argentine ant. — *Proc. R. Soc. Lond. B* 263: 1041–1046.
- Pierotti, R. 1980: Spite and altruism in gulls. — *Am. Nat.* 115: 290–300.
- Pierotti, R. 1982: Spite, altruism, and semantics: a reply to Waltz. — *Am. Nat.* 119: 116–120.
- Radwan, J. 1995: On estrous advertisement, spite and sexual harassment. — *Anim. Behav.* 49: 1399–1400.
- 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.
- Rózsa, L. 2000: Spite, xenophobia, and collaboration between hosts and parasites. — *Oikos* 91: 396–400.
- Rousset, F. & Raymond, M. 1991: Cytoplasmic incompatibility in insects — why sterilize females? — *Trends Ecol. Evol.* 6: 54–57.
- Shine, R., Harlow, P., Lemaster, M. P., Moore, I. T. & Mason, R. T. 2000: The transvestite serpent: why do male garter snakes cour (some) other males? — *Anim. Behav.* 59: 349–359.
- Smith, N. G. C. 1998: The dynamics of maternal-effect selfish genetic elements. — *J. Theor. Biol.* 191: 173–180.
- Starr, C. K. 1984: Sperm competition, kinship, and sociality: a review of modern theory. — In: Smith, R. L. (eds.), *Sperm competition and the evolution of animal mating systems*: 427–464. Orlando.
- Storz, J. F. 1999: Genetic consequences of mammalian social structure. — *J. Mammal.* 80: 553–569.
- Sundström, L. 1994: Sex ratio bias, relatedness asymmetry and queen mating frequency in ants. — *Nature* 367: 266–267.
- Sundström, L., Chapuisat, M. & Keller, L. 1996: Conditional manipulation of sex ratios by ant workers: a test of kin selection theory. — *Science* 274: 993–995.
- Thornhill, R. & Alcock, J. 1983: *The evolution of insect mating systems*. — Harvard University Press, Cambridge, Mass. 547 pp.
- Trivers, R. 1985: *Social evolution*. — Benjamin/Cummings. 462 pp.
- Vickery, W. L., Whoriskey, F. G. & FitzGerald, G. J. 1988: On the evolution of nest-raiding and male defensive behaviour in sticklebacks (Pisces: Gasterosteidae). — *Behav. Ecol. Sociobiol.* 22: 185–193.
- Wade, M. J. 2000: Opposing levels of selection can cause neutrality: mating patterns and maternal-fetal interactions. — *Evolution* 54: 290–292.
- Waltz, E. C. 1981: Reciprocal altruism and spite in gulls: a comment. — *Am. Nat.* 118: 588–592.
- Werren, J. H. 1997: Biology of *Wolbachia*. — *Annu. Rev. Entomol.* 42: 587–609.
- Wilson, E. O. 1971. *The insect societies*. — Harvard Press, Cambridge, Mass.
- Wilson, E. O. 1975: *Sociobiology: the new synthesis*. — Harvard Press, Cambridge, Mass. 697 pp.
- Wright, S. 1965: The interpretation of population substructure by *F*-statistics with special regard to systems of mating. — *Evolution* 19: 395–420.