

Spite: altruism's evil twin

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A spiteful animal is one that will risk harm to itself in order to harm another (Hamilton 1970, 1971). Spite differs from selfish behaviour, acts which benefit the individual while possibly harming others. There are many examples of selfishness (Wilson 1975, Trivers 1985), but whether animals are spiteful is controversial (Gadagkar 1993, Keller et al. 1994). Verner (1977) argued that some birds might protect territories much larger than necessary for their own use (“superterritories”) in order to reduce the breeding success of other birds within the population. He argued that this increased the fitness of superterritory owners not directly, by increasing survival or breeding success, but indirectly, by limiting the mean breeding success of other birds within the population. As fitness is the ratio of an individual’s reproductive success to its population’s mean reproductive success, spite allows an organism to increase its fitness at the expense of others without any increase in its own reproductive success. Verner’s (1977) argument was criticized (Colgan 1979, Tullock 1979, Robertson et al. 1986) on the grounds that the spiteful exclusion of a potential breeder results in increased relative fitness for both spiteful and normal breeders while the cost of spiteful aggression is borne only by the superterritory owner; so spite should not evolve.

Efforts to model the possible evolution of spite have produced variable results. Hamilton (1964, 1970) suggested that spite may evolve but, only in dwindling or fragmented finite populations and that spiteful behaviour should be directed toward non-kin rather than kin. Models of spiteful territoriality (Verner 1977) suggest that spite can evolve only in small populations (Rothstein 1979) and that indiscriminate spite (directed indiscriminately at both kin and non-kin) may (Knowlton and Parker 1979) or may not (Rothstein 1979) evolve.

Theoretical analyses of the evolution of spite have dealt only with superterritory-type resource partitioning

(Knowlton and Parker 1979, Rothstein 1979) and the effects of kin selection (Hamilton 1964, 1970). Other types of spite are possible. Dobson et al. (2000) suggested that infanticide, particularly in ground squirrels, may be a spiteful strategy as females kill the offspring of others, reducing the total number of young produced and thus increasing their own proportional (but not absolute) contribution to the next generation. Brereton (1994) argued that stumptail macaques use sexual interference (interrupting copulations of others) in order to reduce the reproductive success of competitors. In host-parasite interactions, Rozsa (1999) predicted that dying infected individuals will evolve a strategy of emigration in order to infect non-kin rather than kin. Probably the most convincing case involves spiteful cannibalism (Polis 1981, FitzGerald 1992). FitzGerald (1992) showed that female threespine sticklebacks eat conspecific offspring even when food is superabundant. In fact they prefer to eat threespine stickleback eggs even when blackspotted stickleback eggs are more abundant.

Here we use a game theory model for the evolution of spite to show that the conditions under which spite may be able to evolve have parallels to those which may allow the evolution of altruism.

The model

We analyze spite using a simple matrix game analogous to that used to study the evolution of altruism.

		Opponent	
		Spiteful	Normal
Subject	Spiteful	$-b-c$	$-c$
	Normal	$-b$	0

Here \mathbf{b} is the effect of spite (fitness lost by an individual which receives a spiteful act) and \mathbf{c} is the cost (to the spiteful individual) of being spiteful. This matrix specifies the fitness of individuals according to the strategy that they adopt and the strategy of their opponents. The analogy with models of altruism is simple. In models of altruism, the strategy 'spiteful' is replaced by 'altruist' and the parameter \mathbf{b} has a positive sign rather than negative.

Initial analysis

For random interactions in an infinite population whose players have no memory of previous interactions, the best strategy is to play normal. Neither spite nor cooperation can evolve in a population of normal strategists. The normal strategy has the highest pay-off in each column, thus normal is the only ESS under these conditions.

Now we relax some assumptions of the game to evaluate conditions under which spite can invade a population of normal strategists and resist invasion by the normal strategy. For each scenario, we establish fitness functions for both strategies and evaluate which strategy produces higher fitness when normals are common (spite tries to invade) and when spite is common (normals try to invade).

Allowing for non-random interactions

Suppose that interactions are non-random and disassortative. Spitefuls avoid like strategies and seek unlike (normals). Let r' be the proportion of non-random interactions in which unlikes interact. Now $1 - r'$ is the proportion of interactions that occur at random with respect to strategy. If s is the proportion of spitefuls in the population, and W_o is fitness of normals in the absence of spite, then the fitness functions W_s , for spitefuls, and W_n , for normals are:

$$W_s = W_o - rc - (1 - r)[s(b + c) + c(1 - s)] \text{ and}$$

$$W_n = W_o - rb - b(1 - r)s$$

Spite will be advantageous, W_s will be greater than W_n , either when common or when rare provided $r' > c/b$. Hamilton (1970) showed that spite can evolve provided that individuals are spiteful to non-kin more often than to kin. Here we extend that result to the more general case of dis-assortative interactions.

This is the spiteful analogue of Hamilton's (1964) rule for the evolution of altruism. In Hamilton's rule, r is the degree of relatedness between strategists, while here r' is the probability of dis-assortative interactions. Our analysis suggests that Hamilton's rule can be ex-

panded. We can define r as the probability of assortative interactions (like interacts with like) rather than degree of relatedness in the altruism model. Analysis of such a game matrix shows that altruism should evolve when $r > c/b$. This extends the validity of Hamilton's rule for the evolution of cooperation to more general circumstances.

Hamilton (1970) has also showed that spite can evolve provided that individuals are spiteful to non-kin more often than to kin. Here we extend that result to the more general case of dis-assortative interactions.

Interactions in a finite population

Now assume that interactions are random but in a finite population of size N in which S individuals are spiteful and $N - S$ are normal. The fitness functions become:

$$W_s = W_o - (s - 1)(b + c)/(N - 1) - (N - S)c/(N - 1)$$

$$W_n = W_o - Sb/(N - 1)$$

Now spite can invade a population of normals and resist invasion by normals if $N - 1 < b/c$; population size is smaller than the ratio of the effect of spite to the cost of spite, plus one. Here we note that the probability of interacting with any given opponent is $1/(N - 1)$, so the necessary condition for spite to evolve is that this probability exceed the ratio of costs to effects of spite (i.e. $1/(N - 1) > c/b$). (Thus, $1/(N - 1)$ simply replaces r' as the probability of encounter in the previous analysis).

Allowing for repeated interactions

Allowing for repeated interactions with the same individual can lead to the evolution of spite via a strategy somewhat analogous to tit-for-tat (Brown et al. 1982). Consider a "bully" strategy in which bullies are spiteful on first encounter with strangers and thereafter always use the opposite tactic from that first used by the opponent. We call this strategy "bully" because it directs spite to non-bullies but not to known bullies.

This strategy produces a pay-off which approaches 0 when two bullies interact repeatedly but does not otherwise alter the pay-off matrix. Now both bully and normal are ESS. Thus either can dominate the population but cannot invade the other. However, this result predicts that spite will not be seen in nature as populations will contain either all bullies or all normals and normals are not spiteful while bullies don't use spite against other bullies.

A more interesting version of this game accepts that individuals are not always sure of the strategy of their

opponents (they may forget or they may wish to test opponents from time to time). Suppose that, for any interaction, an individual has a probability p of remembering its opponent's initial tactic; not remembering includes both forgetting and not having interacted before. Under these conditions, the pay-off matrix changes slightly. When bully strategists encounter each other, the pay-off becomes $(1 - p)(-b - c)$ while all other entries in the pay-off matrix remain the same. Clearly, normal is an ESS because bully cannot invade a population of normals as $0 > -c$. However, bully may also be an ESS because normals cannot invade against it when $p > c/(b + c)$. In this case, we expect to observe spiteful behaviour in a proportion $1 - p$ of interactions in the population.

The two analyses of the bully strategy show that it can maintain spite in a population once it has invaded via one of the previous mechanisms. For instance, spite might invade a small population and then persist at higher population sizes via the Bully strategy. It is theoretically possible that the Bully strategy might eliminate normals even when the cost of spite exceeds its effect; it is possible that $p > c/(b + c)$ even when $c > b$.

Spite affecting the whole population

Spite may manifest itself in a way that the simple game presented earlier cannot evaluate. A spiteful act may harm an entire group rather than a single individual. In this case, we analyse an n -player game instead of a two player game. Hoarding excess resources may produce this effect. Suppose the spiteful act has a cost c but that its effect, b , is shared equally among the other members of a group of size N . If S members are spiteful then the two strategies have fitness:

$$W_s = W_o - c - (S - 1)b/(N - 1)$$

$$W_n = W_o - Sb/(N - 1)$$

Thus spite will evolve to exclude normals if $N - 1 < b/c$, which is the same condition found in the two-player game with finite population size.

Discussion

This game shows that spite, a behaviour that provides no direct benefits and that incurs a cost, can evolve in natural populations if it harms others to an extent that is substantially greater than its expected cost. This counter-intuitive conclusion results from the fact that fitness is a comparative measure within a population. Thus, an animal that harms the average member of the population more than it harms itself can, under some circumstances, benefit from spiteful behaviour.

Colgan (1979), Tullock (1979) and Robertson et al. (1986) have all argued that simply doing more harm to others than one incurs oneself is not enough to give spiteful individuals an advantage because normal individuals who are not impacted by the spiteful behaviour will benefit more from it than will the spiteful individuals. This result is seen clearly in our initial analysis in which spite could not evolve; normal behaviour is the only ESS of the game. Spite will only occur under specific circumstances. Here, we have shown that disassortative interactions, finite population size, spite affecting the entire population and a bully strategy in repeated interactions can lead to the evolution of spite.

Spite can invade small populations when its cost/effort ratio is low. Previous studies of superterritories (Maynard Smith 1982, Trivers 1985) and kin selection (Hamilton 1964) suggested that spite can only invade small populations. Here we show small population size is a sufficient but not a necessary condition (dis-assortative interactions do not require small population size) for the evolution of spite. Also, the bully strategy does not require small population size in order to favour spite. While the latter cannot allow spite to invade a population of normals, it can contribute to the spread of spite once it has invaded by another mechanism.

Dis-assortative interactions may play a role in allowing spite to evolve. Such interactions may come about in populations where juvenile emigration is common. It has often been argued that juveniles emigrate from their parental home range in order to avoid inbreeding. If so, they also will avoid future interactions with kin and thus possibly avoid interactions with like phenotypes, in this case, other spitefuls. Rozsa (1999) has taken this idea one step further by suggesting that infected host organisms may use a strategy of emigration in order to avoid passing the infection to kin living nearby. This emigration would then put them in contact with non-kin, presumably more likely to use strategies other than their own, and thus create conditions favourable to the evolution of spite.

A bully strategy has also been modelled by Pontier et al. (2000) in a non spite context, a hawk-dove-bully interaction. While their model and ours contain a bully strategy (one that backs away from aggressive opponents) they differ in that our bully actually gains no direct advantage from its behaviour, theirs can potentially gain resources.

Our bully model assumes, as does the tit-for-tat model for the evolution of altruism, that individuals can recognize each other and remember past interactions. Animals unable to recognize and remember conspecifics will be unable to use the bully (or the tit-for-tat) strategy unless they evolve the requisite recognition and memory abilities simultaneously, a process which may be very slow. Our series of models does suggest a way in which the latter may occur in a stepwise fashion. If spite invades a population via non-

random interactions a selection pressure may be created favouring individuals who recognise spiteful strategists and avoid interacting with them. Once this recognition ability becomes common, the bully strategy may evolve.

We note that no analogy to our finite-population model has been published for the evolution of altruism. In fact, the analogous altruism model would show that finite population size is not a sufficient condition for the evolution of altruism.

In conclusion, we show three ways in which spite can invade a population. It can invade small populations in which its effect is spread over the entire population or felt by only one individual if its effect greatly exceeds its cost. Spite can also invade large populations when interactions among spitefuls and normals are non-random and dis-assortative. When individuals interact repeatedly and remember opponent's strategies spite can increase in a population but this condition is insufficient to allow invasion by spite.

The evolution of spite shows close parallels to the evolution of altruism. Dis-assortative interactions rather than assortative or playing the opposite strategy against a known opponent rather than the same one, will favour spite rather than altruism. Emigration will favour spite while philopatry will favour altruism. This leads us to propose that spite is altruism's evil twin.

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References

- Brereton, A. R. 1994. Return-benefit spite hypothesis: an explanation for sexual interference in stump-tail macaques (*Macaca arctoides*). – *Primates* 35 (2): 123–136.
- Brown, J. S., Sanderson, M. J. and Michod, R. E. 1982. Evolution of social behaviour by reciprocation. – *J. Theor. Biol.* 99: 319–339.
- Colgan, P. 1979. Is superterritoriality stable? – *Am. Nat.* 114: 604–605.
- Dobson, F. S., Chesser, R. K. and Zinner, B. 2000. The evolution of infanticide: genetic benefits of extreme nepotism and spite. – *Ethol. Ecol. Evol.* 12: 131–148.
- FitzGerald, G. J. 1992. Egg cannibalism in sticklebacks: spite or selfishness. – *Behav. Ecol. Sociobiol.* 30: 201–206.
- Gadagkar, R. 1993. Can animals be spiteful. – *Trends Ecol. Evol.* 8: 232–234.
- Hamilton, W. D. 1964. The genetical evolution of social behaviour. – *J. Theor. Biol.* 7: 1–16.
- 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. and Dillon, W. S. (eds), *Man and beast: comparative social behavior*. Smithsonian Press, Washington, D.C., pp. 57–91.
- Keller, L., Milinski, M., Frischknecht, M. et al. 1994. Spiteful animals still to be discovered. – *Trends Ecol. Evol.* 9: 103.
- Knowlton, N. and Parker, G. A. 1979. An evolutionary stable strategy approach to indiscriminate spite. – *Nature* 279: 419–421.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. – Cambridge Univ. Press.
- Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. – *Annu. Rev. Ecol. Syst.* 12: 225–251.
- Pontier, D., Auger, P., De La Parra, R. B. and Sanchez, E. 2000. The impact of behavioral plasticity at individual level on domestic cat population dynamics. – *Ecol. Model.* 133: 117–124.
- Robertson, R. J., Gibbs, H. K. and Stutchbury, B. J. 1986. Spitefulness, altruism and the cost of aggression: evidence against superterritoriality in tree swallows. – *Condor* 88: 104–105.
- Rothstein, S. I. 1979. Gene frequencies and selection for inhibitory traits, with special emphasis on the adaptiveness of territoriality. – *Am. Nat.* 113: 317–331.
- Rozsa, L. 1999. Influencing random transmission is a neutral character in hosts. – *J. Parasitol.* 85: 1032–1035.
- Trivers, R. L. 1985. *Social evolution*. – The Benjamin/Cummings Publishing Company Inc., Menlo Park, California.
- Tullock, G. 1979. On the adaptive significance of territoriality: comment. – *Am. Nat.* 113: 772–775.
- Verner, J. 1977. On the adaptive significance of territoriality. – *Am. Nat.* 111: 769–775.
- Wilson, E. O. 1975. *Sociobiology: the new synthesis*. – Belknap Press of Harvard Univ. Press.