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Spite, egotism, population stability, and resource conservation

William L. Vickery[1] and Joel S. Brown[2]

[1]*Département des Sciences biologiques et Groupe de recherche en écologie comportementale et animale, Université du Québec à Montréal, Montréal, Québec, Canada and*
[2]*Department of Biological Sciences, University of Illinois at Chicago, Chicago, Illinois, USA*

ABSTRACT

Questions: What effects does the presence of spiteful behaviour (a behaviour that risks harm to the actor in order to harm others) within a population have on population dynamics? Can these population-level effects influence interactions with prey? Do changes in prey abundance have feedback effects on the frequency of spiteful behaviour? Does altruism (a behaviour that helps others at the risk of harming the actor) also have population-level effects?

Mathematical methods: A game theory model of the evolution of spite within a population is combined with a model of predator–prey dynamics.

Key assumptions: Our analysis applies to cases where spite reduces individual fitness without destroying resources (prey). Predators, which may be spiteful, consume prey with a type II functional response. Prey experience logistic growth. Predator growth depends on prey consumption.

Predictions: If spite can invade a population, the resulting conflict within the population reduces its consumption of prey and thus lowers prey mortality. This results in an apparent conservation of resources. This reduction in prey consumption can increase the stability of the predator–prey interaction. Surprisingly, the addition of spite to a predator population may increase its equilibrium density at the predator–prey equilibrium. Through its effect on population dynamics, spite can lead to an interaction between evolutionary and ecological dynamics resulting in an evolutionarily stable equilibrium with a mixture of spiteful and non-spiteful strategies. Behaviours whose harm to others exceeds their benefits to the actor can also stabilize predator–prey interactions. Altruism (a behaviour that risks harm to the actor in order to benefit others) can have the opposite effect of spite at the population level.

Keywords: altruism, egotism, natural selection, population size, population stability, resource conservation, spite.

Correspondence: W.L. Vickery, Département des Sciences biologiques et Groupe de recherche en écologie comportementale et animale, Université du Québec à Montréal, C.P. 8888, Succ. 'Centre-Ville', Montréal, Québec H3C 3P8, Canada. e-mail: vickery.william@uqam.ca
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INTRODUCTION

A long-standing question in ecology is: Why don't organisms consume all of their resources? In a classic paper, Hairston *et al.* (1960) proposed that carnivores prevent herbivores from exhausting their food supply. Brown (1988) explained the phenomenon in terms of foraging costs and benefits. Krivan and Eisner (2003) related it to prey switching and optimal diet choice by predators. Post *et al.* (2002) cited complex interspecific dynamics. Numerous authors (see, for instance, Downes and Shine, 1998; Brodie *et al.*, 2002; Dietl, 2003) have proposed that predators and their prey are co-evolving in ways that ensure that prey do not go extinct. This apparent resource conservation by self-regulating predators has even been described in group-selectionist terms (Ulevicius and Balciauskas, 2000).

Here, we propose a simple mechanism by which such 'population self-regulation' and 'prudent predation' can evolve under individual rather than group selection and can lead to the apparent conservation of food resources. This mechanism can induce stability in the 'self-regulated' population, and in some cases can cause it to achieve higher abundances. Furthermore, effects at the population level can feed back on the evolutionary dynamics within the population.

MODELLING THE EFFECT OF SPITE

Our mechanism relies on behaviours that may increase or decrease the fitness of the individual that exhibits the behaviour and have negative effects on the fitness of other individuals within its population. Consider an extreme case, spiteful behaviour (Hamilton, 1970), in which an individual harms others without getting any direct benefit itself. Spite can evolve in a finite population when it costs less to be spiteful than the average negative impact of the spite on others (Vickery *et al.*, 2003). Let us suppose that such conditions occur in a population. When spite is 'profitable', all members of the population should become spiteful, and the evolutionarily stable strategy (ESS) cannot contain a mixture of co-existing spiteful and non-spiteful strategies (Vickery *et al.*, 2003). What will the impact of this spite be on population growth, size, and stability?

We rewrite Vickery and colleagues' (2003) finite population model as a fitness-generating function (Vincent and Brown, 2005), where b is the negative effect of a spiteful individual on an average member of the population and c is the cost of delivering that spite:

$$G(v, u, N) = W_0 - \frac{b(uN - v)}{N - 1} - vc,$$

where G is the fitness of a focal individual, N is population size, W_0 is fitness in the absence of spite, v is the probability that the focal individual is spiteful, and u is the average level of the spiteful strategy within the rest of the population. In this fitness function, the first term is fitness in the absence of spite, the second is the negative effect of other individuals' spiteful behaviours on the focal individual (we remove the focal individual's level of spite from this calculation), and the third term is the cost of the focal individual's level of spite. The potential for spite ($u = 1$) or non-spite ($u = 0$) to be an ESS can be confirmed by differentiating G by v and evaluating the possibility of invasion by either strategy when evaluating the fitness gradient at $u = 0$ and then $u = 1$.

The above equation estimates both the evolutionary dynamics (through the fitness gradient) and the population dynamics (through the per capita growth rate of the

population, which is just the average fitness within the population). In terms of evolution, we can show that spite will exclude non-spite (which we will call 'normal') behaviour from the population if $1/(N-1) < c/b$ (Vickery *et al.*, 2003), confirming Hamilton's (1970) conclusion that spite can evolve in small populations. When this condition is satisfied, we have $v = 1 = u$ as the ESS. To investigate the effects on population dynamics, we must now specify W_0. Let us suppose that fitness, in the absence of spite, is a function of resource consumption. In this case, we choose Holling's (1965) disc equation (a type II functional response) and we define a parameter, e, as the efficiency of conversion of resources to offspring. Now the fitness-generating function, with $v = 1 = u$, becomes

$$G(.) = e\left[\frac{aR}{1+ahR} - d\right] - b - c,$$

where a is the per capita encounter rate between predators and prey, R is prey abundance, d is the amount of food required to meet basic energy needs, and h is handling time per prey. If we specify a per capita resource population growth rate, we now have a predator–prey (or consumer–resource) model. Here we suppose simple logistic growth for the resource (prey):

$$\frac{1}{R}\frac{\mathrm{d}R}{\mathrm{d}t} = \frac{r_0(K-R)}{K} - \frac{aN}{1+ahR},$$

where r_0 is the intrinsic rate of natural increase of the resource and K is its carrying capacity. This predator–prey model follows that of Rosenzweig and MacArthur (1963) (with density-dependence occurring via the consumption of resources) with the addition of spiteful behaviour. We need not specify whether spite has an effect on one individual at a time or many, even all members of the population. The parameters b and c are the average costs of spite per individual regardless of how spite is meted out.

To observe the effect of spite on the consumer population and on resource abundance, we solve for the equilibrium states of this interaction by setting the two per capita growth rates equal to zero. This occurs when resources and spiteful consumers have abundances of

$$R_{s,\mathrm{eq}} = \frac{ed+b+c}{a(e-h(ed+b+c))}$$

and

$$N_{s,\mathrm{eq}} = \frac{r_0 e[Ka(e-h(ed+b+c)) - (ed+b+c)]}{Ka^2\,(e-h(ed+b+c))^2},$$

respectively. We can compare these with the stable equilibrium of this interaction in the absence of spite:

$$R_{n,\mathrm{eq}} = \frac{d}{a(1-hd)},$$

$$N_{n,\mathrm{eq}} = \frac{r[Ka(1-hd)-d]}{Ka^2\,(1-hd)^2}.$$

By subtraction we get the impact of spite on the interaction:

$$R_{n,\mathrm{eq}} - R_{s,\mathrm{eq}} = \frac{(b+c)}{a(1-dh)(e-h(ed+b+c))},$$

$$N_{n,\mathrm{eq}} - N_{s,\mathrm{eq}} = \frac{r(b+c)[Kha(1-dh)(h(ed+b+c)-e)-(e-dh^2\,(ed+b+c))]}{Ka^2\,(1-dh)^2\,(e-h(ed+b+c))^2}.$$

Spite results in increased resource abundance whenever $R_{n,\mathrm{eq}} < R_{s,\mathrm{eq}}$, which occurs when $e/h > ed + b + c$, the ratio of conversion efficiency to handling time is greater than total losses due to spite and normal energetic needs. So, when organisms convert resources efficiently with little handling time, spiteful behaviour will produce resource conservation; it will result in a higher standing crop of resources. Low costs of spite (both in being spiteful and in receiving spite) will also favour resource conservation.

More interesting, because it is counterintuitive, is the possibility that spite increases the abundance of its own population ($N_{n,\mathrm{eq}} < N_{s,\mathrm{eq}}$). This is possible when resources are so abundant that per capita consumption increases to an extent that more than compensates for the losses due to spite. This necessary criterion is

$$K > \frac{e - dh^2\,(ed+b+c)}{ah(1-dh)(e-h(ed+b+c))}.$$

This interesting case is shown in Fig. 1. The population of spitefuls has a stable interaction with its prey and is more abundant at equilibrium than the equivalent population with non-spitefuls whose interaction with its prey leads to non-equilibrium population dynamics.

Thus, spite also affects the stability of the predator–prey interaction. Stability can be assessed by calculating the eigenvalues of the Jacobian matrix (the matrix of the first derivatives of the model with respect to R and N). The predator–prey system will have a stable equilibrium if both eigenvalues have negative real parts and if the carrying capacity of the prey, K, is large enough to avoid predator starvation. It turns out that this happens in populations without spite when

$$\frac{d}{(a(1-hd))} < K < \frac{(1+hd)}{ah(1-hd))}$$

and in populations of spiteful animals when

$$\frac{ed+b+c}{a(e-h(ed+b+c))} < K < \frac{e+h(ed+b+c)}{ah(e-h(ed+b+c))},$$

where K too small results in predator extinction, and K too large produces non-equilibrium population dynamics [paradox of enrichment (Rosenzweig, 1971)].

Whenever h, b, and c are small (less than 1), spite will increase both the lower bound and the upper bound at which stability is possible. The lower bound is increased by

$$\frac{b+c}{a(1-dh)(e-h(ed+b+c))}$$

and the upper bound by

$$\frac{2(b+c)}{a(1-dh)(e-h(ed+b+c))}.$$

Not only does spite increase the interval with a stable predator–prey interaction, but, for a given carrying capacity within that interval, populations of spiteful individuals return to equilibrium faster than normal populations.

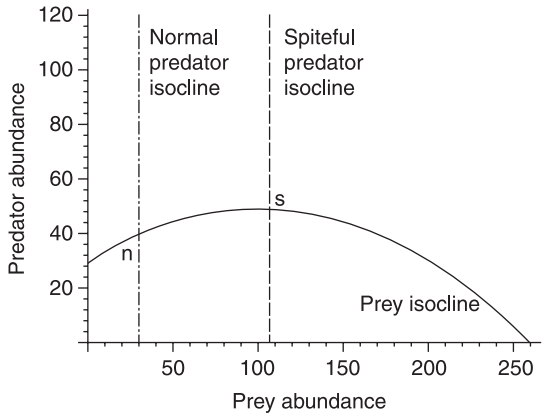

Fig. 1. Comparison of predator–prey isoclines with and without spite in the predator population. The left-most predator isocline represents the interaction when no spite is present and the right-most isocline when spite is present. The prey isocline does not differ between the two cases. Note that without spite the intersection of the two isoclines (point *n*) is to the left of the 'hump' in the prey isocline and so the interaction is unstable; with spite the intersection (point *s*) is to the right indicating stability. Furthermore, at equilibrium the spite-filled population is more abundant and has more abundant prey than the normal population. Parameters used in this example are $K = 260$, $e = 1/2$, $a = 1/60$, $h = 1$, $d = 1/3$, $r = 1/2$ and, for spite, $b = 1/7$, $c = 1/100$.

This result is not unique to the finite population model. Vickery *et al.* (2003) also propose a model in which spitefuls interact more often (with probability r') than chance alone with normals than with other spitefuls. This leads to the fitness-generating function:

$$G(.) = W_0 - (1 - r')bu - ur'b - vc\,.$$

When this function is combined with logistic resource growth and a type II functional response (the disc equation above), it produces exactly the same stable equilibrium as the finite population model. Thus, for both models of spite, the presence of spite in a population can lead to resource conservation and, in some cases, to greater abundances of spiteful individuals than would have occurred without spite.

The analysis so far deals only with the effects of spite. It is also worthwhile considering the effect of what we will call 'egotistical' behaviour. We define this as behaviour that benefits an individual while doing more harm to others than the benefit it receives itself. Like spite, the egotistical behaviour is not pareto-optimal but it can be the ESS. This situation fits easily into the models above by substituting $-c$ for c and specifying $|c| < b$ so that $-c$ is now a benefit (a negative cost) to the egotistical organism. Clearly, this change can also lead to resource conservation but the increase in resources will be less than in the case of spite. Similarly, the abundance of the population of egotistical organisms may also increase but not to the extent as in the case of spite.

The preceding analysis shows that the presence of spite in a population can alter population dynamics, possibly producing counterintuitive effects. A further surprising effect is also possible. The population dynamics generated by the presence of spite can feed back on the evolutionary dynamics of spite.

For spite to be the ESS, the population size must be sufficiently small. It is possible that the increase in population size caused by spitefuls actually nullifies spite as the ESS. The

equilibrium N of non-spitefuls favours spite, but the higher N of spitefuls favours non-spitefuls! This happens when a spiteful population has a higher equilibrium population size than a non-spiteful population and the population size below which spite will evolve falls between the two (Fig. 2). In this case, when spite invades a population it causes the population to grow. However, when the population reaches a critical size (the horizontal line in Fig. 2), spite is no longer profitable. The predator–prey system will reach neither the equilibrium with or without spite because at each of these points the opposite strategy is favoured. The system does have an equilibrium at the point where the horizontal line intersects the resource isocline. At this point, spite and non-spite co-exist.

Vickery *et al.* (2003) suggested that spite is altruism's evil twin because of contrasts in the conditions that favour their evolution. If this is the case, we should expect the presence of altruism in a population to have the opposite effect of that produced by spite. We explore this possibility by making the parameter b in our model positive rather than negative because the altruist helps conspecifics at its own expense, whereas the spiteful individual harms conspecifics at its own expense. If we repeat the predator–prey analysis above with b positive, we find that altruism can increase equilibrium population size but under some circumstances the converse will happen. Furthermore, intraspecific altruism can destabilize the predator–prey interaction (Fig. 3).

DISCUSSION

The results of this analysis may appear counterintuitive. At first glance, one might expect spiteful (harming others without generating any personal gain) and egotistical (harming others for personal gain) interactions at the individual level to have negative consequences at the population level. Although this can happen (populations can be reduced and extinction is possible when the lower bound of stability rises), there are unexpected and collateral benefits in populations in which prey handling is efficient and prey carrying capacity is sufficiently high. Spite (or egotism) can lead to increased prey (resource) abundance when these prey are not eaten because of negative interactions within the predator population. This produces more prey per predator. The ratio of prey to predator may rise several-fold at the equilibrium point of the predator–prey system. These additional prey can then support a larger spite-filled population (Fig. 1). The process amounts to shifting the predator isocline to the right in a predator–prey diagram (Rosenzweig and MacArthur, 1963).

Resource conservation occurs in this scenario even though the spitefuls have no direct effect on an individual's harvest of resources – the effects of our model occur through dynamical rather than behavioural feedbacks. The spiteful act in this model does not involve resource destruction. If, for instance, spite involved destroying the food of others, the resource conservation predictions of this model would not hold. In fact, just the opposite would occur: resource abundance would decrease and so would the size of the spite-filled population. Ironically, spite or egotistical behaviour helps avoid 'the tragedy of the commons' (Hardin, 1968), in which individuals benefit from consuming ever more resources even as their population suffers lower growth rates because of the reduced resource availability. Although this might appear like 'prudent predation', it is not. The spite or egotistical behaviours that benefit the predator population are simply the ESS of a behavioural game among the predators.

Behaviours that could induce conservation include the pre-emption of excess resources (e.g. guarding excessively large territories), fighting for resources, and even killing or

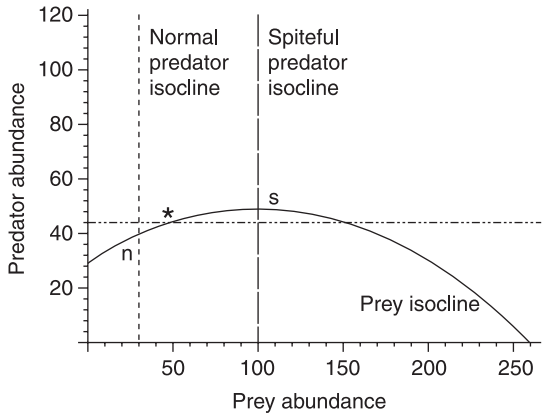

Fig. 2. Interacting effects of predator–prey dynamics with the evolution of spite. Both predator–prey equilibrium points are unstable. Without spite (left-most isocline) the equilibrium predator population (point *n*) is small enough that spite is profitable; with spite (right-most isocline) the equilibrium predator population (point *s*) is too large to make spite profitable. We then expect a stable equilibrium at the point * along the spite–normal isocline generated by the game controlling the evolution of spite. In this case, the predator–prey dynamics will lead to a mixture of spite and normal behaviour. Parameters used in this example are $K = 260$, $e = 1/2$, $a = 1/60$, $h = 1$, $d = 1/3$, $r = 1/2$ and, for spite, $b = 1/7$, $c = 1/300$.

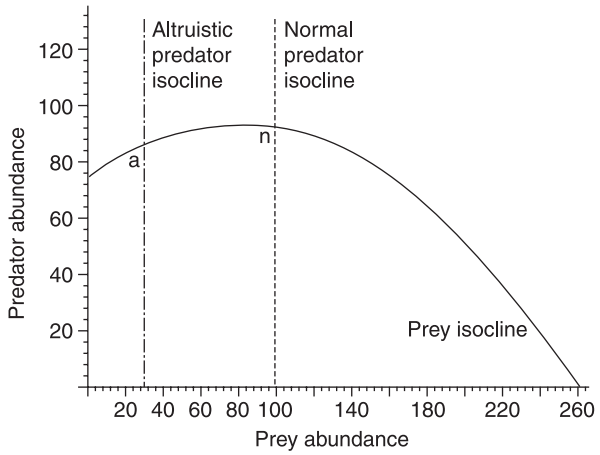

Fig. 3. Comparison of predator–prey isoclines with and without altruism in the predator population. The predator isocline for altruists (to the left of the figure) represents the interaction when altruism is present and the other isocline (to the right) when altruism is absent. The prey isocline does not differ between the two cases. Note that without altruism the intersection of the two isoclines is to the right of the 'hump' in the prey isocline and so the interaction is stable; with altruism the intersection is to the left indicating instability (and reductions in both predator and prey populations). Parameters used in this example are $K = 260$, $e = 1/2$, $a = 1/150$, $h = 3/2$, $d = 1/3$, $r = 1/2$ and, for altruism, $b = 1/10$, $c = 1/100$.

sterilization of conspecifics. Pre-emption of resources – possibly a spiteful act (Verner, 1977) – is especially interesting as it impacts progressively more conspecifics as population size grows, giving it a large potential for stabilizing population size. Cannibalism, which may be either spiteful (Polis, 1981; FitzGerald, 1992) or egotistical if some benefit is derived from eating conspecifics, is likely to produce less benefit to the cannibal than the cost to the individual eaten. Fighting over resources can have a similar effect. This can be particularly interesting when organisms engage in a 'war of attrition' that can lead to total costs exceeding benefits (Maynard Smith, 1982). In each of these cases, costs are imposed on members of the consumer population without consuming resources – thus they have the potential to induce resource conservation (even increased consumer abundance) indirectly.

Spiteful behaviour has been demonstrated among bacteria (Iwasa *et al.*, 1998; Gardner *et al.*, 2004; Engelstädter and Charlat, 2006) and in some insects (Gardner *et al.*, 2007). Bacteria use a form of chemical warfare to harm conspecifics (Iwasa *et al.*, 1998; Gardner *et al.*, 2004), while among parasitoid wasps sterile soldier castes kill conspecifics (Gardner *et al.*, 2007). Thus, although Hamilton (1970) found the conditions of the evolution of spite rather restrictive, it appears that spite has evolved. Whenever spite does evolve there is the potential to produce resource conservation by direct impacts on the fitness of conspecifics, which should reduce consumption rates of their resources. This should stabilize the abundance of the spiteful population. Whether mutual stabilization at the population and evolutionary levels will occur depends on specific parameter values that will have to be measured to test this model.

Our model makes no assumptions as to whether these negative acts affect one individual (as is the case for cytoplasmic genes among arthropods), many (the case for chemical warfare among bacteria) or the entire population. It suffices that spite is able to invade the population and to resist invasion from normals. This requires either a small predator population size, $1/(N-1) < c/b$, or disassortative interactions where the probability that a spiteful will direct its spite towards normals is high ($r' > c/b$). If one of these is true, then spite will dominate in the population (Vickery *et al.*, 2003). When it does, resource availability will increase provided that $e/h > ed + b + c$.

We chose to model Hamiltonian and not Wilsonian (Gardner and West, 2004) spite, defining spite based on direct fitness effects and not inclusive fitness (Lehmann *et al.*, 2006), because in doing this we avoid arguments that spiteful behaviour is also altruistic (Lehmann *et al.*, 2006) and we avoid definitional problems as to whether what we define as spite can really be called spite if it has indirect fitness benefits.

An interesting interaction is possible between population dynamics and the evolution of spite. In some cases where normals produce an equilibrium abundance small enough to allow spite to invade, the presence of spite can increase predator abundances to the point where normals have an advantage over spitefuls and can thus invade the spite-filled population. Thus we can get a mixed ESS, which is not predicted under the effect of natural selection alone (Vickery *et al.*, 2003), through the interaction of natural selection and population dynamics! Furthermore, the evolutionary dynamics have a stabilizing effect on the size of the spiteful population.

Throughout this paper, we refer to individuals as being either spiteful or not spiteful. We do this because Vickery *et al.* (2003) suggest that a given population should evolve to contain only spiteful individuals or no spiteful individuals. However, if a mixed ESS does occur, it could contain either a mixture of pure strategies (each being either always spiteful or never spiteful) or individuals playing a mixed strategy (spiteful with a certain probability).

The condition $e/h > ed + b + c$ is of interest because it ensures both that resources will increase in the presence of spite and that there will be a stable equilibrium when spite is present. Thus, if a stable equilibrium exists in the presence of spite, it will contain more resources than when spite is absent. On the other hand, it is possible that the arrival of spite in the population will drive the system to extinction. This will occur when $dh < 1$ (the condition necessary for co-existence in the absence of spite) and $e/h > ed + b + c$. The latter will arise if the cost of spite is high compared with the ratio e/h.

Stability in the presence of spite does not ensure an increase in abundance for the spiteful population. An increase in abundance requires first that resources increase and second that $e/h < dh(ed + b + c)$. This latter requirement ensures that resources increase so much that they sustain additional consumers. When this latter inequality is not satisfied, the abundance of the consumer population will decrease (possibly, but not necessarily, to extinction) in the presence of spite.

Spite shifts the interval of K values (carrying capacity of prey) over which the predator–prey system remains stable. Thus, spite may drive its population to extinction (if its prey has a low carrying capacity) or it may stabilize a population that would otherwise cycle with its prey around an unstable equilibrium point (if the prey carrying capacity is high). Spite also makes this interval of stability larger as the upper end of the interval shifts twice as much as the lower end. Furthermore, in this upper range where spite induces stability, it also increases the size of the spite-filled population for all values of K beyond the midpoint of the upper shift. Hence, spite can produce an exception, in terms of stability, to the paradox of enrichment [as can having relatively invulnerable prey (Abrams and Walters, 1996)].

We note that Engelstädter and Charlat (2006) propose that spite can have a stabilizing effect on population dynamics and even cause increases in population size. Their model is based on mate competition while ours, which is based on resource competition, also shows the potential for resource conservation, which may look like prudent predation. Our results also have a parallel with those of Coolen *et al.* (2007), who showed that the reduction of predator efficiency involved in the producer–scrounger game can have a stabilizing effect at the population level and, in some cases, lead to resource conservation and larger populations of producers and scroungers than expected if all animals searched for their own food. It is interesting that these three models all suggest that the evolution of a strategy that harms other individuals in a population can produce stability in the population and possibly even increase population size. It may be worthwhile searching for a general pattern.

If we look at the other side of the coin, altruism and exploitation by producing more benefits to the exploiter than costs to its exploited conspecific should have the opposite effects of spite. Altruism would then stabilize populations exploiting prey with low carrying capacity and destabilize those exploiting prey with high K (see Fig. 3). At high K, altruism could even lead to declines in population size in altruist-filled populations. Vickery *et al.* (2003) suggested that spite is the 'evil twin of reciprocal altruism' because of similarities in the conditions necessary for their evolution. At the population level, we can expect these similarities to persist. So, at least in some cases, at the population level, altruism may be the evil twin of spite!

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REFERENCES

Abrams, P.A. and Walters, C.J. 1996. Invulnerable prey and the paradox of enrichment. *Ecology*, **77**: 1125–1133.

Brodie, E.D., Jr., Ridenhour, B.J. and Brodie, E.D., III. 2002. The evolutionary response of predators to dangerous prey: Hotspots and coldspots in the geographic mosaic of coevolution between garter snakes and newts. *Evolution*, **56**: 2067–2082.

Brown, J.S. 1988. Patch use as an indicator of habitat preference, predation risk and competition. *Behav. Ecol. Sociobiol.*, **22**: 37–47.

Coolen, I., Giraldeau, L.-A. and Vickery, W.L. 2007. Scrounging behaviour regulates population dynamics. *Oikos*, **116**: 533–539.

Dietl, G.P. 2003. Interaction strength between a predator and dangerous prey: Sinistrofulgur predation on Mercenaria. *J. Exp. Mar. Biol. Ecol.*, **289**: 287–301.

Downes, S. and Shine, R. 1998. Sedentary snakes and gullible geckos: predator–prey coevolution in nocturnal rock-dwelling reptiles. *Anim. Behav.*, **55**: 1373–1385.

Engelstädter, J. and Charlat, S. 2006. Outbreeding selects for spiteful cytoplasmic elements. *Proc. R. Soc. Lond. B*, **273**: 923–929.

FitzGerald, G.J. 1992. Egg cannibalism in sticklebacks: spite or selfishness. *Behav. Ecol. Sociobiol.*, **30**: 201–206.

Gardner, A. and West, S.A. 2004. Spite and the scale of competition. *J. Evol. Biol.*, **17**: 1195–1203.

Gardner, A., West, S.A. and Buckling, A. 2004. Bacteriocins, spite and virulence. *Proc. R. Soc. Lond. B*, **271**: 1529–1535.

Gardner, A., Hardy, I.C.W., Taylor, P.D. and West, S.A. 2007. Spiteful soldiers and sex ratio conflict in polyembryonic parasitoid wasps. *Am. Nat.*, **169**: 519–533.

Hairston, N.G., Smith, F.E. and Slobodkin, L.B. 1960. Community structure, population control, and competition. *Am. Nat.*, **94**: 421–425.

Hamilton, W.D. 1970. Selfish and spiteful behaviour in an evolutionary model. *Nature*, **228**: 1218–1220.

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

Holling, C.S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Ent. Soc. Can.*, **45**: 1–60.

Iwasa, Y., Nakamura, M. and Levin, S.A. 1998. Allelopathy of bacteria in a lattice population: competition between colicin sensitive and colicin producing strains. *Evol. Ecol.*, **12**: 785–802.

Krivan, V. and Eisner, J. 2003. Optimal foraging and predator–prey dynamics III. *Theor. Pop. Biol.*, **63**: 269–279.

Lehmann, L., Bargum, K. and Reuter, M. 2006. An evolutionary analysis of the relationship between spite and altruism. *J. Evol. Biol.*, **19**: 1507–1516.

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

Polis, G.A. 1981. The evolution and dynamics of intraspecific predation. *Annu. Rev. Ecol. Syst.*, **12**: 225–251.

Post, E., Stenseth, N.C., Peterson, R.O. and Vucetich, J.A. 2002. Phase dependence and population cycles in a large-mammal predator–prey system. *Ecology*, **83**: 2997–3002.

Rosenzweig, M.L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science*, **171**: 385–387.

Rosenzweig, M.L. and MacArthur, R.H. 1963. Graphical representation and stability conditions of predator–prey interactions. *Am. Nat.*, **97**: 209–223.

Ulevicius, A. and Balciauskas, L. 2000. Scent marking intensity of beaver (*Castor fiber*) along rivers of different sizes. *Zeits. Saug. Int. J. Mamm. Biol.*, **65**: 286–292.

Verner, J. 1977. On the adaptive significance of territoriality. *Am. Nat.*, **113**: 769–775.

Vickery, W.L., Brown, J.S. and FitzGerald, G.J. 2003. Spite: altruism's evil twin. *Oikos*, **102**: 413–416.

Vincent, T.L. and Brown, J.S. 2005. *Evolutionary Game Theory, Natural Selection and Darwinian Dynamics*. Cambridge: Cambridge University Press.