Can Animals Be Spiteful?
Raghavendra Gadagkar

LOGIC SUGGESTS that when members of a species interact with each other at least nine kinds of consequence are possible, because both actors and recipients may benefit (+), suffer (−) or experience no effect (0) (Box 1). When both the actor and the recipient benefit from an interaction (+,+), it is termed cooperation; this is widespread in the living world. When the actor benefits and the recipient suffers (+,−), the interaction is termed selfishness, which is even more abundant in the living world. When the actor suffers while the recipient benefits (−,+), the interaction is termed altruism. Compared to cooperation and selfishness, altruism is less common; nevertheless there are many examples of it in the animal kingdom. Altruism is not so easy to explain as cooperation or selfishness, but much has been learnt about its evolution in the last 25 years.

We now understand two mechanisms by which altruistic behaviour can evolve. Hamilton’s rule1, which states that the benefit to the recipient devalued by the genetic relatedness between actor and recipient should be greater than the cost to the actor, specifies a set of precise conditions for the evolution of altruism. An alternate mechanism for the evolution of altruism, pointed out by Trivers, is reciprocity2−4: If altruistic behaviours performed by an individual are reciprocated at some future time, such altruism may be favoured by natural selection.

What all of this means, of course, is that there is no real altruism and that all behaviour is really selfish in the long run or at the genetic level. But there is no doubt that the apparent paradox associated with altruism was largely responsible for the attention this behaviour has received and for the consequent revolutionary changes in the study of animal behaviour4−6.

If both the actor and the recipient suffer as a result of an interaction (−,−), it is called spite. Conventional wisdom has it that to be spiteful is the prerogative of humans alone. It is true that there is no unequivocal example of interaction between animals where both actor and recipient clearly suffer. With no clear-cut real-life examples known, theoreticians have not been too active in this area. Puzzled by the absence of good examples of spite in natural populations, Hamilton7 (1970) suggested a softening of our definition so that ‘behaviour which harms others without benefit to the self may well be called spiteful’. More detailed investigations of examples of potential spite, even by this softened definition, are likely to enhance our understanding of the evolution of animal behaviour greatly, much as altruism has done in the past and continues to do so today.

At least two clear-cut examples of such ‘weak spite’ (see Box 1) have been demonstrated in the animal kingdom. The first came from a study of the western gull Larus occidentalis and the herring gull, L. argentatus in Newfoundland, Canada, a decade ago8−10. The gulls showed two kinds of behaviours that probably represent weak spite and have been interpreted as such by Pierotti8−10. The first behaviour, called piracy or kleptoparasitism, was directed at conspecific neighbours rather than to members of other species (as is usually the case...
with other birds\textsuperscript{11,12}. The second behaviour is to attack fledged or just-fledged chicks of conspecifics and kill them but without eating the dead chicks. The negative fitness effects to the recipients in these interactions are quite clear but the consequences to the actors are not. It appears that the actors should benefit at least in the case of piracy, but there seems to be a correlation between being a pirate and having very few or none of one’s own chicks fledging. This correlation was found not only across individuals but even within the same individuals across years. Of course it is not clear which is the cause and which is the effect: does piracy lead to loss in personal fitness or does loss in personal fitness lead to piracy? In either case, however, there is no strong suggestion of a personal benefit from piracy. In the case of the killing of conspecific chicks without eating them, the case for personal gain is even weaker.

The second example comes from a recent study of the threespine stickleback (\textit{Gasterosteus aculeatus}) by Gerard J. FitzGerald\textsuperscript{13}. In the area of study, threespine sticklebacks coexist with a related species, the blackspotted stickleback (\textit{G. wheatlandi}) and the latter are more common. This study appears to have been prompted by the observation that threespine sticklebacks do not attack nests of the blackspotted stickleback but instead attack conspecific nests and consume large quantities of conspecific eggs. To show that egg-eating by threespine stickleback is spiteful and not merely selfish, FitzGerald argued that three premises must be upheld: the fish must prefer (1) conspecific eggs over heterospecific eggs, (2) conspecific eggs from a sympatric population compared to those from an allopatric population and (3) older conspecific eggs over younger ones. The third and perhaps the strongest prediction arises from the fact that young eggs are expected to be more nutritionally valuable than older ones, while older eggs are expected to be more valuable to their parent’s fitness than younger eggs. The preference for what is less valuable to themselves but more valuable to others over what is more valuable to themselves and less valuable to others would be a very good reason to label this behaviour as spite.

In three sets of experiments with 30 test fish per experiment, all three predictions were clearly upheld. A particularly fascinating aspect of the behaviour of the fish was that they did not seem to make their choice because of any previous familiarity. Their initial choice was random and it appears that after first tasting/smelling the two available categories of eggs, they showed the preferences described above. An essential control is to show that the observed preference is not a result of the higher nutritional value of the preferred category of eggs. In carefully controlled diet experiments, three groups of 13 fish were given, in addition to standard dry food, a supplement of young conspecific eggs, older conspecific eggs or young heterospecific eggs, equivalent to about 10\% of their diet. Using 16 measures of physical condition and/or reproductive success, FitzGerald failed to find any difference between the three groups. This suggests that there is no nutritional advantage of eating conspecific eggs but it also suggests that there is no particular advantage of eating younger eggs (as suspected).

Even though eggs make a nutritious meal, all of this suggests that the threespine stickleback females may be acting in a spiteful manner. Their behaviour is clearly detrimental to other members of their species. By preferring conspecific eggs in nature, they would run a significant risk of accidentally eating their own eggs because threespine sticklebacks are known to deposit their eggs in nests made by males and not to remain to care for their young\textsuperscript{14}. To the extent that there were no significant differences between the three groups of fish in the diet experiments, this is perhaps a (0,-) interaction rather than a (-,-) one, although there may be other disadvantages which may still make it a (-,-) interaction.

The definition of spite used here and the respective authors’ claims that the gulls and sticklebacks are behaving spitefully, even if weakly, are potentially controversial. If one wanted to be absolutely certain of the costs and benefits involved and/or insist on a (--) definition of (strong) spite then perhaps one should not yet label the behaviour of the gulls and sticklebacks as spite. But is that the kind of error that we need to urgently guard against? I think not. Instead, I think we are in a greater danger of overlooking potential examples of spite and perhaps delaying the development of an interesting new direction of enquiry in evolutionary biology. It is important that these apparently paradoxical behaviours receive more attention, even though it is possible that ultimately they may be explained as selfish behaviour – just as seems

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\textbf{Box 1. Consequences of Interactions where both actor and recipient can benefit (+), suffer (-) or have no change in fitness (0)}

Weak selfishness is where the actor benefits and there is no change in the fitness of the recipient (-,0). The interaction is either a weak form of cooperation [deviation from (+,+)] or a weak form of selfishness [deviation from (+,-)]; however, since the dominant element of a (-,0) interaction only benefits the actor, it is termed weak selfishness.

Weak altruism is either where the actor suffers but there is no change in the fitness of the recipient (0,--) or where the actor has no change in fitness but the recipient benefits (0,+). The former interaction is weak altruism [deviation from (+,-)] or weak spite [deviation from (-,-)]; but since the dominant element of a (0,-) interaction only causes suffering to the actor, it is labelled weak altruism. The latter interaction is either weak cooperation or weak altruism, but since a (0,+)-interaction only benefits the recipient it is termed weak altruism.

Weak cooperation is where both actor and recipient have no change in fitness as a result of an interaction (0,0), such interaction borders on the trivial and should perhaps not be called an interaction at all. But, for completeness, we may label it weak cooperation; certainly there is no element of selfishness, altruism or spite in it.

Weak spite is when the actor experiences no change in fitness while the recipient suffers (0,-). Such interaction is by definition weak selfishness [deviation from (+,-)] or weak spite [deviation from (-,-)]. But since the dominant element of a (0,-) interaction causes suffering to the recipient, it is called weak spite. Unlike weak selfishness; weak altruism and weak cooperation, which hold no great promise (because their strong counterparts have been well studied), this type of interaction deserves attention at both the theoretical and empirical levels.
to have happened with altruistic behaviour!

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