Spiteful animals still to be discovered

In a recent TREE article, Gadagkar1 raised the interesting question of whether or not spiteful behaviour exists in animals. The interaction between members of a species is termed spiteful when both the actor and the recipient suffer. Gadagkar also coined the term ‘weak spit’ for a behaviour that harms the recipient without benefit to the actor, and he claims that ‘at least two clear-cut examples of weak spit behaviour have been documented in the animal kingdom’. We suggest, however, that explanations other than spite may account for the results of the two studies cited by Gadagkar.

The first example comes from a study by Pierotti2 on the western gull (Larus occidentalis). Pierotti2 and Gadagkar suggest that pirating food from neighbours and attacking others’ chicks are examples of spite (or weak spit) behaviour. Pirate males have been shown to fledge fewer offspring than non-pirate males — hence the hypothesis for spite behaviour. However, Pierotti2 notes that the males that became pirates ‘had lost all or most of their offspring as eggs or in the first days after hatching’. Therefore, it should come as no surprise that pirate males fledged fewer offspring since they became pirates after having lost their offspring! Indeed, Waltz3 suggested that pirating might be an alternative foraging tactic by individuals which had been less successful in raising offspring and possibly obtaining food conventionally. Regarding the killing of neighbour’s chicks, no fitness loss to the perpetrator is demonstrated (or even suggested) in Pierotti’s paper2, and the fact that the chicks are not eaten does not prove that the motive of the attacks is spite. One possible benefit of this behaviour has been suggested by Pierotti2 himself, who states that decreasing the breeding success of other individuals may yield some benefits by decreasing the competition that one’s offspring ‘may face in the crucial first few weeks after becoming independent’. Interestingly, piracy was more common during the year when food supply was poor, suggesting that competitive interactions might indeed increase under harsher ecological conditions.

The second example is a study on threespine stickleback (Gasterosteus aculeatus) females, which frequently attack conspecific nests to eat eggs. FitzGerald4 argued that three predictions must be upheld for conspecific egging to be spiteful: 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 compared to younger conspecific eggs, since older eggs are being expected to be more valuable to their parent’s fitness. Since the three predictions were verified in choice experiments, FitzGerald4 and Gadagkar1 concluded that conspecific eggs eating by females is spiteful or weakly spiteful behaviour. This conclusion suffers, however, from at least two caveats. First, the rationale for prediction (2) is unclear, since females will never have a chance to feed on conspecific eggs, because the two selected populations were 200 km apart. Furthermore, a theoretical analysis5 showed that weak spit might be selected for under some restrictive conditions, but only when directed toward individuals having less-than-average relatedness (giving the opposite prediction to that of FitzGerald). Second, and most importantly, there is a simple alternative explanation to account for the observed egg preferences. In all three experiments, females may have preferred familiar food, a phenomenon documented in many fish species6. Since FitzGerald caught sexually mature, gravid females which had been used to eat conspecific eggs, conspecific eggs must have been more familiar than heterospecific ones. Sympatric eggs more than allopatric ones, and older eggs more familiar than freshly spawned ones. Furthermore, a female might prefer older eggs because freshly spawned ones are more likely to be hers under natural conditions.

In conclusion, although we agree with Gadagkar1 that apparently paradoxical behaviour should not be overlooked, we believe that ‘clear-cut’ examples of spite, or weak spit, behaviour are still to be discovered.

We thank the Swiss National Science Foundation for support.

L. Keller, M. Milinski, M. Frischknecht, N. Perrin, H. Richner and F. Triplet

Zoologisches Institut, Bern University, Ethnologische Station Hasli, Wohlenstrasse 50a, 3032 Hinterkappelen, Switzerland

References

Reply from R. Gadagkar

Keller et al. claim that spiteful animals are ‘still to be discovered’ because ‘explanations other than spite may account for the results of the two studies’ cited by me.

I believe that Keller et al. ignore the spirit of my article; my purpose was not so much to claim that we are sure of the spite in the cited examples, but to encourage people to investigate with particular care anything that even ‘smells’ of spite. I think I was pretty explicit about this when I said ‘if one wanted to be absolutely certain… one should not yet label the behaviour of the gulls and sticklebacks as spite,… it is possible that ultimately they may be explained as selfish behaviour’. As far as their criticism of Pierotti’s study of gulls2 is concerned, they say nothing really new compared to what Pierotti2, Waltz3 and I have already said. As for the points raised by them about FitzGerald’s study of sticklebacks1, one can very easily provide counter arguments against each of their points.

For example, Keller et al. argue that FitzGerald’s rationale for the predicted preference for conspecific eggs over heterospecific eggs is unclear, since females will never have a chance to feed on conspecific eggs. It is entirely possible that there is a continuous variation in, say, the smell of eggs with distance, and that this may be sufficient to drive the evolution of a preference for non-symaptic over symaptic eggs. There is no need for a previous direct experience with non-symaptic eggs. Secondly, they claim that Hamilton’s model7 leads to a prediction which is the opposite of what is used by FitzGerald. This is not at all obvious. In spite of Hamilton’s model, the prediction will depend on the details of population genetic structure, about which we know nothing. Finally, they claim that their alternative explanation of familiarity is sufficient because the fish FitzGerald used must have been used to eat conspecific eggs. The question, then, is why were the fish accustomed to eating conspecific eggs when heterospecific eggs were available? Keller et al. know as well as I do that these hair-splitting arguments (theirs and mine) are not going to take us very far, and that more controlled experiments are needed. But I wish to emphasize that their arguments against spite are not any stronger than those in favour of spite. If their conclusion is that we should therefore ignore spite on the grounds of parsimony, then I disagree, because I think that by admitting the possibility of spite we will pay more attention to these behaviours than if they are simply considered as more examples of selfish behaviour.

Raghavendra Gadagkar

Centre for Ecological and Sciences and Jawaharlal Nehru Centre for Advanced Scientific Research, Indian Institute of Science, Bangalore 560 012, India

References

TREES vol. 9, no. 3 March 1994

103