Behav Ecol Sociobiol (1992) 30:201–206

Behavioral Ecology and Sociobiology

Egg cannibalism by sticklebacks: spite or selfishness?

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Received July 11, 1991 / Accepted December 1, 1991

Summary. Although it is generally agreed that humans can be spiteful, there are few if any, unambiguous examples of spite by non-human animals. Data are presented suggesting that female threespine sticklebacks show spiteful behaviour. In the field, they seek out conspecific eggs to attack while largely ignoring those of a closely-related sympatric species, the blackspotted stickleback. This occurs despite the fact that the latter's nests are more abundant and less well protected. In the laboratory, female threespine sticklebacks attack the eggs of conspecifics more than those of blackspotted sticklebacks, those of sympatric conspecific females more than those of allopatric females, and older eggs more than younger ones. Because there was no evidence of greater energetic or nutritional advantages from eating conspecific rather than heterospecific eggs, or older eggs rather than younger ones, threespine sticklebacks may be spiteful. Alternative proximate and evolutionary hypotheses to explain this discriminant egg-eating are discussed.

Introduction

A spiteful animal is one that will harm itself in order to harm another conspecific individual even more (Hamilton 1970, 1971). However, Hamilton stated that behaviour which harms other without benefit to the self may also be called spiteful. Hamilton (1971) labelled the former acts as "strongly" spiteful. He also distinguished spite from selfish behaviour, defining the latter as an act which benefits the individual while harming others. Hamilton (1970, 1971) was not able to list any unambiguous example of a spiteful animal and there is still considerable controversy about what behaviours should be accepted as spite. Wilson (1975) accepted both of Hamilton's (1970) definitions of spite (see pp. 117–119 and p. 595): however, he was also unable to provide a single clear-cut example of its occurrence. Theoreticians agree that both forms of spite might evolve in some circumstances; e.g. spite is most likely to be selected if populations are not very large and matings are random (Hamilton 1970, 1971; Knowlton and Parker 1979; Rothstein 1979).

Accepting Hamilton's (1970) broader definition of spite, Pierotti (1980) argued that when adult gulls kill a neighbour's chick (without necessarily consuming it), they are being spiteful. Waltz (1981) disagreed that Pierotti's (1980) gulls were spiteful. He opined that only behaviour which reduces the fitness of both the perpetrator and the recipient of action should be called spite. Pierotti (1982) was not convinced by Waltz's (1981) arguments to limit the term spite to those cases where the actor harms itself. He listed two problems with the narrow definition. First, it is quite possible that situations could arise where the cost to the actor is cancelled by a benefit, although perhaps not in a precise caloric sense. Second, an individual could perform an act that involves a high risk of death or serious injury and yet escape unharmed. How is its investment measured? Pierotti (1982) argued, in my opinion convincingly, "that an individual which took such a risk to harm a conspecific would be spiteful, even if the costs of the specific act turned out to be low relative to the benefits, either immediate or potential" (see also Trivers 1985).

Whatever definition one accepts, examples of spite are rare. Aside from Pierotti's (1980) spiteful gulls, the only other examples of spiteful animals that I know of, are monkeys and mountain goats (see Trivers 1985, pp 57–61). Cannibalistic species may be good candidates for being spiteful because of the danger of inadvertently eating one's relatives or because the cannibal may retaliate (Polis 1981). Cannibals could be acting spitefully if they consume conspecifics in preference to heterospecificis. Unfortunately, it is difficult to show that an individual consumes conspecific prey only for spite. This is because conspecifics may be a more economical (cost/benefit ratio) meal than heterospecifics. A possible exception to this generalization is egg-eating in fishes. Egg-eating *per se* will not be spiteful but *discriminant* egg-eating may be. Eggs of closely related species have similar energy values (Scrimshaw 1945; Hislop and Bell 1987) and similar costs associated with hunting and consuming the prey because the eggs are often relatively defenseless (discussed below). Thus, if individuals are spiteful, they should prefer to eat conspecific eggs. Similarly for species with a wide geographic distribution, spiteful individuals should prefer to attack eggs from within their population more than those from a distant population because the impact on the inclusive fitness of potential competitors will be greater. This assumes that allopatric and sympatric eggs are of similar energy value. A third prediction is that if individuals are eating eggs for spite rather than primarily for food, they should preferentially consume older eggs because of their greater reproductive value (*sensu* Fisher 1930). However, if they are cannibalizing eggs for energy they should prefer younger eggs because these are a more valuable food because they contain a higher proportion of yolk (Scrimshaw 1945; Gilbert 1985). Scrimshaw (1945) presented data for a variety of fishes indicating that about a third of the initial weight of the egg is used for maintenance during development.

Here I present the results of a series of experiments designed to test these predictions by examining ovo-cannibalism in threespine stickleback (*Gasterosteus aculeatus*) which are voracious egg eaters (Whoriskey and FitzGerald 1985a; FitzGerald et al. in press). Female threespine sticklebacks often attack the eggs in a male's nest, which is built on the substrate. In sticklebacks, only males care for the eggs and fry and females are free to forage throughout the habitat where, in addition to eggs, they consume a mix of various types of zooplankton and benthic invertebrates (Worgan and FitzGerald 1981). Predictions were derived with the broad definition of spite in mind, but it is also possible that ovo-cannibalism is costly (see background information) and that "strong" spite occurs in my system.

In order to show that egg-eating is spiteful, not merely selfish (*sensu* Hamilton 1970), it is necessary to determine if females eating conspecific eggs obtain greater fitness benefits [e.g. indicated by greater fecundity and (or) better physical condition] than ones eating heterospecific eggs. Therefore I also conducted a "diet" experiment to determine if there were greater fitness effects associated with eating conspecific eggs than heterospecific ones.

Methods

Background information. In tide pools near Isle Verte, Québec (48° 0′, 69° 21′), high densities of threespine and blackspotted sticklebacks (*G. wheatlandi*) breed sympatrically. Their nests may be as close as 15 cm and most are in open areas of the pools where they are easily found by human observers. On average there are twice as many blackspotted stickleback nests as threespine stickleback nests (FitzGerald 1983). However, despite the many hours of field observations by myself and others annually since 1977, we have rarely seen female threespine sticklebacks attack the nests of blackspotted sticklebacks. In contrast, they consume large quantities of conspecific eggs, and in some high-density pools, all of the eggs may be eaten (Whoriskey and FitzGerald 1985a). This observation of differential predation on conspecific eggs could occur for reasons other than spite. First, the eggs of blackspotted sticklebacks are readily eaten with no obvious ill-effect when given to female threespine sticklebacks in the laboratory. Second, while it is possible that female threespine sticklebacks cannot find the nests of blackspotted sticklebacks, I consider this unlikely because male threespine sticklebacks often find and attack blackspotted stickleback nests. In some pools up to 66% of the *G. wheatlandi* nests are destroyed by male *G. aculeatus* (Gaudreault and FitzGerald 1985). I interpret this latter behaviour as male interspecific competition for nest sites.

For those readers who will only accept the narrower definition of spite, i.e. the actor must suffer some cost, I suggest there are two ways a female could reduce her fitness by ovo-cannibalism. First, females may inadvertently eat their own eggs. The pools are small and females are never far from the site where they spawned their eggs. Females cannot recognize their own eggs if a nest contains clutches from other females (Smith and Whoriskey 1988). Because many nests do contain several clutches (Whoriskey 1984), there is a considerable risk that a female might eat her own eggs when she participates in a nest raid. Second, bird predation on adult sticklebacks is high (about 30% of all fish entering the marsh are eaten) (Whoriskey and FitzGerald 1985b) and there may be considerable risk to fish during a raid. I have not been able to measure this risk, but fish are more easily caught by humans during a raid on a nest than at other times (personal observation).

Behavioural experiments. In a series of three experiments, female threespine sticklebacks were given a choice between attacking (1) conspecific and blackspotted stickleback eggs, (2) eggs obtained from members of their own population and those from an allopatric population, (3) unfertilized (freshly stripped) and fertilized (48 h old) conspecific eggs. Because female threespine sticklebacks can sometimes discriminate their own eggs from those of unrelated conspecifics and prefer to attack the latter (FitzGerald and van Havre 1987; but see Smith and Whoriskey 1988), I did not used eggs from the experimental females as test stimuli.

For the first two experiments, sexually mature gravid females were obtained from Isle Verte, and Ile d'Orleans, Québec and transported to the laboratory at Laval University. Although both populations breed in inshore areas of the S. Lawrence estuary, I assume they are distinct breeding populations as the two sites are over 200 km apart. Fish from the two populations were held in separate tanks consisting of several hundred fish. In the experiments testing predictions 1 and 3, only Isle Verte fish were used. Two days prior to an experiment, 30 females were randomly selected and placed singly in a rectangular 4.5-l tank which served as their home and test tank for the duration of the experiments which usually lasted about a week. Water temperatures ranged from 15 to 22° C and salinity was 15%. Natural lighting (about 16 L : 8 D) was available as the laboratory contained a series of large windows. The aquaria were aerated and all fish survived the experiments. All fish were fed once a day on a commercial dry food (Nutrafin) after the period of behavioural observations, at about 17 h. When fish were given eggs in the experiments they had been deprived of food for about 18 h.

Sticklebacks are highly cannibalistic even when satiated with other foods (FitzGerald and van Havre 1987). Thus my test is probably a conservative one because discrimination should wane as fish get hungrier.

For the behavioural experiments, eggs were obtained by stripping them from two randomly chosen females to give eggs of each type. Stripping was done by exerting a light pressure upon the abdomen. This procedure is a standard technique of fisheries biologists and aquaculturists and causes no harm to either the female or the eggs. All stripped eggs were stage 4 (Nikolsky 1963). The eggs of threespine and blackspotted sticklebacks used in the tests were similar in size (average diameter 1.67 ± 0.05 and 1.65 ± 0.04 mm respectively). Batches of 50 eggs were placed in an opaque, perforated plastic tube, 3.5 cm long and 1 cm diameter, and kept at 4° C until ready for use, within 12 h.

In experiment 3, care was taken to ensure that masses of fertilized and unfertilized eggs were equal by weighing them (mg). The eggs were put into opaque perforated tubes to keep the odour stimulus of the eggs before the females while denying them the opportunity to remove the stimulus by eating it. Thus they could receive the chemical cues, and they could respond unambiguously, but the cue remained.

On the day of the trial, two tubes were attached to the corner walls of the short end of the test tank (15 cm apart). Each tube was 5 cm above the tank floor allowing the fish to attack the sides and bottom of the tubes.

In a control experiment, 20 females were presented with two empty tubes. Most (17/20) females never attacked the empty tubes and the three that did so only made a total of three attacks. To eliminate the possibility that the results could be due to a preference for attacking tubes on one side of the tank more often than on the other side, the positions of the tubes were switched after 5 min.

The number of bites directed against each of the two tubes during a 10-min trial was recorded. Bites were easily scored because when the fish's mouth contacted the plastic, a sharp "pinging" sound was easily heard. Fish were tested once per day for a total of 20 min of observation per female. Because a preliminary analysis (t-test, $P > 0.05$) showed no differences between the two observation periods, data were pooled.

For experiment 3, batches of fertilized (old) eggs were obtained by allowing eggs to develop until they were 48 h old. At this time the eggs contain much less yolk than stripped eggs (Wootton 1976).

Diet experiment. To determine if females obtain greater energetic/nutritional advantages from eating conspecific rather than heterospecific eggs, I conducted a diet experiment. Several hundred fish were collected as Isle Verte with a beach seine, transported to the laboratory at Laval University, and housed as described above. After a week of acclimation to laboratory conditions, 36 female threespine sticklebacks were randomly chosen from the stock tanks. Care was taken to match the females for size (Table 1). Each fish was placed on one of three diets. These consisted of a mix of dry food and eggs. The commercially-prepared dry food was a mix of *Tubifex* worms, brine shrimp *Artemia*, and zooplankton *Euphasia pacificia* (Nutrafin, Hagen, Montréal). In addition to the dry food, fish received a ration of either (fertilized or unfertilized) conspecific or (unfertilized) heterospecific eggs. Dry food was used as a supplement because we were unable to raise enough other females to supply the experimental fish with a pure egg diet. All fish were fed twice daily, once about 0800 and once about 1600 h. Fish were given 20 min to feed, and any excess food remaining was then collected with a small net, dried, and weighed. This allowed us to determine if actual food consumption differed among the groups.

Groups 1 and 3 were fed daily reactions of 50 non-fertilized conspecific eggs and 50 fertilized conspecific eggs, respectively. These eggs were about 48 h old. Group 3 received 50 unfertilized blackspotted stickleback eggs each day. This amount of eggs corresponded to 10% of their daily ration and females can easily consume this many eggs during a raid in nature (Whoriskey and FitzGerald 1985a). All fish consumed all eggs given. All groups received a total of 0.30 g of food per day, a ration determined as adequate for normal egg production for this population (Bolduc and FitzGerald 1989; Boulé and FitzGerald 1989).

Each day that female appeared ready to spawn, as evidenced by their willingness to court models of males placed in their tanks, they were stripped of eggs. Females were weighed before and after stripping to obtain the wet weight of the clutch. All eggs were counted and a random sub-sample of 10 eggs were used to measure egg diameter (mm) under a binocular microscope (10 ×). Egg diameter is considered a good correlate of fitness in fish because larger eggs are more likely to hatch and larvae from bigger eggs are more likely to survive than ones from smaller eggs (Wootton 1990). Because wet and dry weights may not always be correlated, egg dry weights were obtained by drying eggs at 65° C for 24 h. The experiment lasted 39 days after which all females were quickly killed by immersion in hot water. Carcasses were dissected and the liver and gonads were separated. Wet and dry weights of the liver, gonads, and carcasses without these organs were obtained as described above in order to determine if any effects of diet upon physical and reproductive condition were evident. The weights of these organs are useful measures to evaluate the physical condition of a fish and together give a better indication of an animal's physical condition than a single measure (Black and Love 1988).

Several measures of reproduction, closely correlated with fitness, were used to estimate the seasonal breeding success of females. These were: the average clutch size per female, the average number of clutches spawned per female, the average diameter of the eggs produced per female and the average interspawning interval.

Statistical analysis

The behavioural data (number of attacks per 20 min) were analyzed with a one-tailed Wilcoxon matched-pairs signed ranks test. Differences in the numbers of fish that attacked one type of eggs more than the others were analyzed with a χ^2 test. The data from the diet experiment were analyzed with a one-way analysis of variance followed by a Scheffé multiple-comparisons test. This is appropriate as the three groups of females were homogeneous for weight and length and were randomly assigned to the experimental treatments (Table 1).

Results

Is there a preference for attacking conspecific eggs?

Twenty-three fish tested attacked conspecific eggs more often, four attacked heterospecific eggs more often, and three attacked both groups equally often ($\chi^2 = 8.97$, $df = 2$, $0.025 < P < 0.01$). (The numbers of fish that initially attacked one type of eggs rather than the other in all experiments did not differ significantly, indicating no bias due to "known odour", χ^2 tests). On average, females attacked conspecific eggs significantly more often than heterospecific eggs (mean 38.3, SD 7.5 vs. mean 11.9, SD 2.90; $P < 0.005$; Fig. 1A).

Is there a preference for attacking eggs of females from one's own population?

Twenty-one fish attacked sympatric eggs more often than the allopatric eggs, whereas five fish did the opposite. The other four fish attacked both types of eggs equally often ($\chi^2 = 18.2$ $df = 2$; $P < 0.005$). On average, fish attacked sympatric eggs more often than the allopatric eggs (mean 37.4, SD 8.4 vs. mean 16.4, SD 5.0; $P < 0.005$; Fig. 1B).

Is there a preference for attacking older eggs?

Seventeen fish made more attacks on older eggs, nine fish more attacks on younger eggs, and four fish made an equal number of attacks ($\chi^2 = 8.6$, $df = 2$; $0.025 < P < 0.01$). On average, older eggs were attacked more often than younger ones (mean 30.3, SD 5.2 vs. mean 14.7, SD 3.9; $P < 0.005$; Fig. 1C).

Does a diet supplemented with conspecific eggs confer greater fitness benefits than one supplemented with heterospecific eggs?

The three groups did not differ from any of the measures of reproductive success or physical condition (Table 1).

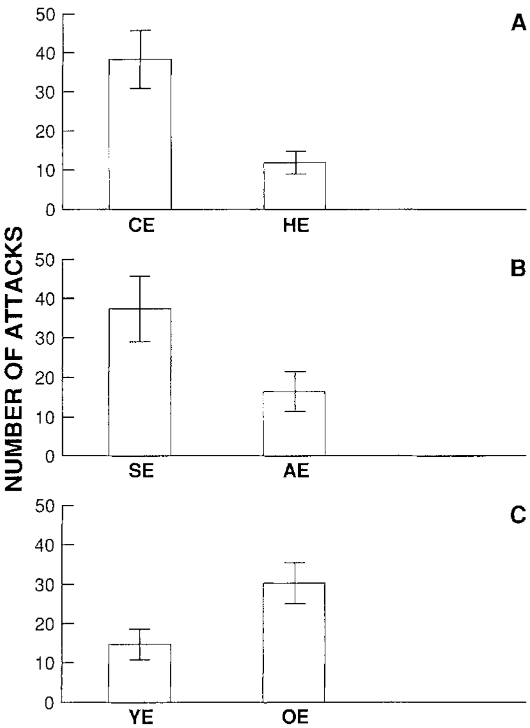

Fig. 1A–C. Mean (±1 SD) number of attacks per individual by 30 female threespine sticklebacks directed toward: **A** conspecific eggs (*CE*) and heterospecific (blackspotted stickleback) eggs (*HE*); **B** eggs from sympatric females (*SE*) and allopatric females (*AF*); and **C** young eggs (*YE*) and old eggs (*OE*)

Discussion

The most obvious proximate explanation for the fact that threespine stickleback prefer to eat some types of eggs rather than other types is that they obtain more energy or some other nutritional advantages. However, the diet experiment suggests that this does not occur. I should have detected greater benefits from eating conspecific eggs rather than heterospecific ones and from eating younger eggs rather than older ones. One critique of my diet experiment is that sample sizes were insufficient to detect an effect of differential egg-eating. However Belles-Isles and FitzGerald (in press) found that female threespine sticklebacks fed equal amounts of conspecific eggs or a mix of zooplankton and worms, a regular food of this species, differed significantly in total seasonal fecundity and in egg size. Cannibalistic females produced almost twice as many eggs, and bigger eggs, than the non-cannibal group. The sample sizes and duration of the experiment in that study were similar to those in this one. Therefore, if conspecific eggs were a better food than heterospecific ones. I should have detected similar effects on reproductive performance or body condition in this study.

Experiment 2 showed that threespine sticklebacks preferred to attack sympatric eggs rather than allopatric ones. It is possible that the Isle Verte sticklebacks preferred to attack the sympatric eggs strictly because these eggs were of better quality. However egg sizes (diameter) were similar for females from the two populations (unpublished data). Both populations are the anadromous form of the species characterized by fully-developed body armor (see Wootton 1976). Although, I did not measure egg quality directly, the diets of both populations were similar (unpublished data); so there is no reason to suspect major differences in egg quality. Another possibility is simply that sympatric eggs were more

Table 1. Effect of diet (see text for details) on selected correlates of fitness in threespine sticklebacks

Variables	Group 1[1]	Group 2	Group 3	Test[3]
Initial wet weight	4.22 ±0.29	4.11 ±0.38	4.29 ±0.45	$P=0.53$
Initial length	7.5 ±0.1	7.5 ±0.1	7.5 ±0.2	$P=0.89$
Final wet weight	2.74 ±0.42	2.77 ±0.23	2.58 ±0.24	$P=0.28$
Final dry weight	0.684±0.136	0.707±0.108	0.612±0.095	$P=0.12$
Final length	7.5 ±0.1	7.6 ±0.1	7.5 ±0.2	$P=0.95$
Number of spawns	4.0 ±2.0	4.9 ±1.6	3.9 ±1.6	$P=0.31$
Clutch size	160 ±30	181 ±23	180 ±40	$P=0.20$
Egg diameter[2]	1.68 ±0.06	1.67 ±0.03	1.68 ±0.05	$P=0.77$
Interspawning interval (days)	6.6 ±2.3	6.9 ±1.7	7.2 ±2.1	$P=0.73$
Total egg production (*n*)	650 ±357	873 ±254	704 ±305	$P=0.20$
Dry gonad weight	0.082±0.036	0.067±0.025	0.061±0.025	$P=0.23$
Dry weight of each clutch	0.096±0.025	0.104±0.015	0.102±0.024	$P=0.70$
Wet weight of each clutch	0.65 ±0.13	0.71 ±0.08	0.68 ±0.15	$P=0.48$
Wet gonad weight	0.40 ±0.21	0.30 ±0.08	0.28 ±0.08	$P=0.08$
Dry liver weight	0.028±0.011	0.035±0.015	0.030±0.018	$P=0.52$
Wet liver weight	0.11 ±0.04	0.12 ±0.04	0.11 ±0.05	$P=0.80$

[1] Groups 1, 2 and 3 received unfertilized conspecific eggs, fertilized conspecific eggs and unfertilized blackspotted stickleback eggs respectively. Weights are in grams, lengths of fish are in cm
[2] Egg diameters are in mm
[3] *P* values are for a one-way anova followed by a Scheffé test

familiar to the test females than allopatric ones. However, in the behaviour tests, fish were equally likely to first attack either type of eggs, but once they discovered the sympatric eggs, these were preferred.

Experiment 3 supported the prediction that females should preferentially attack older eggs. This choice is difficult to explain on purely energetic considerations as older eggs contain less yolk and should be a less valuable food (Scrimshaw 1945). However, although young eggs are supposed to be of higher energetic content than older ones, no advantage of eating younger eggs was detected in the diet experiment. This may be because 48 h was insufficient for the developing organism to have consumed much of the energy in the egg, or as argued by de Martini (1987), the energetic content of different-aged eggs is minimal in relation to the predator's needs. Interestingly, Kynard (1979) showed that cannibalism by threespine sticklebacks was generally greater on older eggs and fry than on younger eggs. However, other factors such as differences in access to the different eggs by cannibals were not controlled in his field study.

An evolutionary hypothesis to explain the ovo-cannibalism of female sticklebacks was offered by Vickery et al. (1988). They developed a model based on the assumption that high-quality males were a limiting resource for females. Their "sexual selection" model assumed that female sticklebacks raided nests to force males to rebuild their nests. Then the raider could spawn in the reconstructed nest. Any nutritional benefits were secondary. There is some support for this model (see Belles-Isles et al. 1990; FitzGerald and van Havre 1987) but one prediction of the model, that females should raid those nests containing the most eggs, was not supported. Thus not all cases of nest raiding and egg cannibalism can be explained as a consequence of competition for nests containing few eggs (Belles-Isles et al. 1990). For additional discussion see FitzGerald (in press) and FitzGerald and Whoriskey (1992). The Vickery et al. model (1988) ignored factors such as nutrition, differential predation upon non-cannibals, group selection pressures which may operate if cannibalism becomes so widespread as to threaten the extinction of the population as a whole, or spiteful behaviour.

Other evolutionary explanations for ovo-cannibalism are that the behaviour is either selfish or spiteful. The discriminant egg-eating described in this study is merely selfish if the benefits to the individual outweigh the costs. The nutritional benefit is obvious but whether this benefit outweighs the risk of eating one's own eggs and a possible increased risk of predation remains to be determined. I suggest that if nutrition was the driving force leading to the evolution of nest-raiding, then the threespine females should also raid heterospecific nests.

Could the sticklebacks be spiteful? The females are spiteful if they harm themselves to harm others more, or, if one accepts the narrow definition of spite, if they harm others without themselves gaining a bet benefit. Of course spite cannot evolve unless the cannibal's offspring receive an advantage. One benefit of eating others' eggs is that the cannibal reduces competition for its own young. Ovocannibalism could be spiteful in this system because the potential costs may often exceed the potential benefits *for the cannibal*. For example, the females often raid nests in groups consisting of several hundred individuals. However the nests usually contain less than 1000 eggs, so an individual, on average, may receive only a few eggs as her share. Thus her nutritional benefit is low relative to the risk that her eggs will be eaten.

However given the ambiguity of the concepts of spite and selfishness and disagreements over what behaviours should be labelled as spite (see Wilson 1975; Trivers 1985; Pierotti 1980; Waltz 1981; Pierotti 1982; Polis 1988), alternative explanations for the present results, as discussed above, cannot be excluded. Whether the behaviour described in this paper is labelled as "spiteful" or "selfish", it apparently occurs for other than strictly nutritional considerations.

How general are the findings of this study likely to be? I also found similar results for blackspotted sticklebacks (FitzGerald, unpublished) and Baur (1988) found that hatchlings of two species of land snails *Arianta arbustorum* and *Helix pomatia* had a strong preference for eating conspecific eggs over eggs from other snails. Intraspecific oophagy occurs in more than 100 species distributed over more than 80 families (Fox 1975; Polis 1981; Hausfater and Blaffer Hrdy 1984), and the fact that animals as disparate as snails and fish prefer to attack conspecific eggs suggests that the phenomenon may be widespread.

Acknowledgements. The research was supported by grants from the National Sciences and Engineering Research Council of Canada (NSERC) Grant and FCAR (Fonds pour la Formations de Chercheurs et l'Etude à la Recherche). Guylaine Gosselin and Francois Gagnon helped with the experiments. George Barlow, Jacques Bovet, Felix Breden, Buck Buchanan, Quan Dong, France Dufresne, Mart Gross, Héléne Lair, K.E. Linsenmair, Jeremy McNeil, Gary Polis, Bernie Roitberg, Bruce Waldman and an anonomyous reviewer kindly commented on various previous versions of the manuscript. The comments, discussion, and disagreements about definitions of spite with everyone were very useful. No one was spiteful. However, any errors of fact or interpretation are mine alone.

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