

Larval marbled salamanders, *Ambystoma opacum*, eat their kin

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Abstract. The effect of kinship on larval cannibalism was examined in the marbled salamander. In separate behavioural trials, cannibalistic larvae were presented with two smaller conspecifics (a 'prey group'), matched for size, that were (1) siblings of the cannibal, (2) non-siblings and (3) one sibling and one non-sibling (i.e. a mixture of two sibling groups); larvae were allowed to consume only one conspecific during each trial. This experiment was repeated in 2 consecutive years with larvae from two different populations. In both years, significantly fewer cannibals ate a non-sibling from the mixed sibship group than from groups composed of two non-siblings. In contrast, the number of cannibals that ate a larva from the pure sibling prey group did not significantly differ from the number that ate their sibling from the mixed sibship prey group. Thus, small larvae were significantly more vulnerable to cannibalism by their siblings than by non-siblings. The availability of unrelated individuals as alternative prey did not deter cannibals from eating their siblings, even though cannibals readily consumed prey of either genotype when the alternative one was absent. This kinship-biased cannibalism apparently was not due to size-selective predation or to differences among sibships in their propensity to cannibalize siblings. Moreover, the behaviour of potential prey did not differ towards related versus unrelated cannibals during initial observations of larval interactions. Cannibals required similar amounts of time to capture and process both sibling and non-sibling prey. To our knowledge, our results provide the first evidence of sibling cannibalism when unrelated individuals are available as alternative prey.

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Based on Hamilton's (1964a, b) kinship theory, if all else is equal, individuals should preferentially direct harmful behaviour away from close relatives. However, for inclusive fitness to be maximized, animals must often balance the conflicting consequences of their behaviour to direct and indirect fitness. Such fitness trade-offs may selectively favour harmful behaviour among close relatives in some instances (i.e. when the benefits to direct fitness exceed the costs to indirect fitness), despite the apparent paradox that such cases present to adaptationist models of behaviour. Indeed, numerous examples of harmful (even fatal) aggressive behaviour among close kin have been documented (e.g. Mumme et al. 1983; Mock 1984; Hoogland 1985; Mock et al. 1990; Fraser & Thompson 1991). Thus, depending upon the relative costs and benefits to inclusive fitness, both

altruistic and selfish behaviour patterns among close kin may be consistent with Hamilton's kinship theory (Hamilton 1970; Mumme et al. 1983).

Because the gregarious behaviour of many anuran tadpoles has implications for cooperative social behaviour, these amphibians have been model systems for examining the mechanisms of kin discrimination (reviewed in Blaustein et al. 1987a; Blaustein 1988; Waldman 1991; Blaustein & Waldman 1992; Blaustein & Walls, in press). Larval amphibians have also been exemplary subjects for evaluating aggression and cannibalism among kin (Walls & Roudebush 1991; Pfennig & Collins 1993; Pfennig et al. 1993, 1994; see review in Blaustein & Walls, in press). Studies of cannibalism are ideal for inspecting the consequences of behaviour to inclusive fitness, because the indirect costs of cannibalism (the death of kin) and its potential benefits to direct fitness (e.g. nutritional gain, enhanced growth, survival and reproduction; Crump 1992) are feasible to measure. Blaustein & O'Hara (1982) initially suggested that

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kin recognition may mediate cannibalism in larval amphibians. Walls & Roudebush (1991) further emphasized that kinship may be especially important to interactions among aggressive and cannibalistic salamanders of the genus *Ambystoma* (Ambystomatidae). This has subsequently been examined in the tiger salamander, *A. t. nebulosum* (Pfennig & Collins 1993; Pfennig et al. 1994), as well as in carnivorous tadpoles of the plains spadefoot toad, *Scaphiopus bombifrons* (Pfennig et al. 1993). Thus, kin recognition in cannibalistic larval amphibians may provide an example of recognition that has obvious and strong adaptive value.

We examined whether kinship mediates larval cannibalism in the marbled salamander, a species in which individuals exhibit cannibalism and modify their agonistic behaviour towards siblings (Walls & Roudebush 1991). Larvae of this species do not possess specialized, cannibalistic morphologies. However, cannibalism may result from differences in larval body size that are generated from variation in initial egg size (Kaplan 1980a, b) and dates of hatching (Jackson et al. 1989; Scott 1990). If size-related differences in growth rate continue to increase the disparity in size throughout the larval period (Kaplan 1980a), the potential for size-dependent cannibalism may be greatly enhanced. By using this potential for size variation, we experimentally manipulated relative body sizes to facilitate larval cannibalism. We tested the hypothesis that large larvae discriminate and cannibalize smaller conspecifics based on the genetic relatedness between predators and their potential prey.

METHODS

Collection and Rearing of Test Animals

In autumn, female *A. opacum* deposit their eggs underneath objects covering the dry basins of temporary ponds; after oviposition, females remain with their developing clutch until winter rains flood the nests, which causes the larvae to hatch (Noble & Brady 1933). During two consecutive autumn breeding seasons, we collected *A. opacum* from two different populations: from 11 to 15 November 1991, we collected four clutches of embryos from one breeding site (population 1); from 5 to 9 November 1992, we collected five clutches from another site (population 2).

These two populations, located near Chicot State Park in Evangeline Parish, Louisiana, are 8.2 km apart and are the same as those examined in previous studies of kin recognition in this species (Walls 1991; Walls & Roudebush 1991). Females may oviposit communally, which may mix larvae from different sibling groups (Noble & Brady 1933; Petranka 1990). Thus, we only collected clutches that were associated with a single brooding female and that were spatially separated from other clutches. Each brooding female was replaced in her original position after removal of her clutch. From the time of collection until hatching, each sibling group was maintained individually on moistened paper in covered dishes (9.2 cm diameter, 4.6 cm deep).

To ensure sufficient variation in relative body sizes so that cannibalism could potentially occur, we manipulated the dates on which larvae hatched. For each sibling group, we obtained larvae to function as potential cannibals by placing individuals in dechlorinated tap water and manually hatching them once they reached the hatching stage (stage 45; Harrison 1969). Smaller larvae, used as potential prey, were obtained by hatching the remainder of each clutch 2 weeks after their larger conspecifics. In year 1, potential cannibals were housed individually in opaque plastic containers (9.3 × 9.3 × 6.2 cm) filled with 400 ml of dechlorinated water. In year 2, we reared potential cannibals in mesh screen boxes (16.5 × 12.0 × 13.0 cm) that were each divided (both length-wise and width-wise by perforated partitions) into four equal-sized compartments. We then randomly assigned a single larva to each compartment, such that two of the four compartments each contained an individual from one clutch and the other two each contained an individual from a second clutch. Each mesh screen chamber was housed separately in a plastic box (28 × 19 × 8 cm) filled with 2.5 litres of dechlorinated water. Chambers were replicated such that all possible pairs of sibling groups were housed together.

In both years of the experiment, we reared smaller larvae that functioned as potential prey in 38-litre glass aquaria which were partitioned in half width-wise by fibreglass mesh screen (mesh size = 2 mm) and contained 19 litres of dechlorinated water. We reared 10–15 larvae from one clutch on one side and 10–15 larvae from another clutch on the opposite side. This procedure is

sufficient to familiarize individuals with water-borne chemical cues of both siblings and non-siblings and thus may prevent biasing prey behaviour towards either type of cannibal (Walls & Roudebush 1991). We replicated aquaria such that all possible pairs of sibling groups were reared together. Throughout the experiment, we fed brine shrimp nauplii, *Artemia salina*, to the larvae ad libitum, once per day. After 1 month, potential cannibals were also fed live *Tubifex*, ad libitum, depending upon availability. All cannibals received the same diet on any given day. We maintained larvae on a 12:12 h light:dark photoperiod at 15°C. Aquaria and chambers housing larvae were cleaned and replenished with fresh dechlorinated water every 7–10 days.

Experimental Procedure

We began our experiment 7 or 10 weeks (in 1992 and 1993, respectively) after the larger larvae had hatched. In 1992, we tested 20 large 'focal' larvae (i.e. potential cannibals; snout-vent length (SVL) = 28.1 ± 3.01 mm), using nine larvae from each of two sibling groups and one individual from each of two others. In 1993, we tested 28 larvae (SVL = 27.6 ± 3.01 mm), with between two and eight larvae used from each of five sibling groups. The number of individuals tested per sibling group varied because of random mortality that occurred prior to the start of the experiment. In sequential cannibalism trials, we presented each larva with three different groups of smaller conspecifics ('stimulus' larvae that were potential prey) in a randomized order. Each stimulus group consisted of a pair of larvae that were similar to each other in size (see below). Pairs were either from a single sibship, i.e. siblings of the larger focal larva (group 1), or non-siblings of the focal individual but siblings to each other (group 2), or were from a mixture of two sibships, i.e. one sibling and one non-sibling of the focal larva (group 3).

To identify stimulus larvae correctly, in 1992 we toe-clipped each individual on either the left or right front foot, at least 1 h prior to beginning a trial. These marks had no detectable effect on a larva's movement or its survival. For pairs of stimulus larvae that were unrelated (group 3), the side on which each larva was clipped was randomized with respect to its sibship. This marking regime was unnecessary in 1993, because we could

identify individuals by their patterns of bite injuries (either a missing front foot or toes). In both years, we only used prey that were missing toes or a foot to control for the potential effects of these injuries on subsequent larval survival.

Varying levels of hunger could influence the cannibalistic tendencies of focal larvae (Pfennig et al. 1993). Thus, we standardized the time of feeding and the quantity that each larva was fed by providing each individual with live *Tubifex*, ad libitum, 48 h before testing, then fasting them for 24 h. To minimize prey choice based on the body sizes of stimulus larvae, we measured their total length (to 0.5 mm precision) at least 1 h prior to a trial and then non-randomly paired them according to size. Between 1800 and 1900 hours, we placed focal larvae individually into test chambers (16.5-cm-diameter plastic bowls containing 1.0 litre of dechlorinated water) to acclimatize for 30 min. Simultaneously, we habituated the two stimulus larvae used in each trial to the testing environment by placing each into separate cups (7.3 cm diameter, 6.3 cm high, and filled with 150 ml of dechlorinated water) that were floated within the test chamber. After 30 min, we allowed the stimulus larvae to swim out into the test chamber.

We conducted our observations at night under a 15-W incandescent lamp, because larval *Ambystoma* are more active at this time (Branch & Altig 1981). For 30 min after acclimatization, we observed the frequency with which all three larvae exhibited the following types of behaviour (as defined by Walls & Jaeger 1987; Walls & Semlitsch 1991): (1) Move toward: one individual approaches another such that continued movement in that direction would result in contact between the two larvae; (2) Move away: a larva retreats from an approaching individual such that the distance between the two larvae is increased; (3) Lunge: an attempt at cannibalism, initiated as rapid and abrupt movement by the focal individual toward a stimulus larva. Additionally, we recorded the following types of behaviour for cannibals: (1) Prey capture: a rapid opening and closing of the mouth, resulting in the capture and ingestion of a conspecific; (2) Handling time: following a successful prey capture, the elapsed time (min) from the beginning until the cessation of gill and gular movement. For the following 24 h, we checked each test chamber every 3–4 h for disappearance of one of the stimulus prey. All

observations were blind with respect to the genetic relatedness of focal and stimulus animals. Trials ended once one prey had been consumed; we then noted the identity of the surviving prey. We terminated trials in which no prey were eaten after 24 h.

Statistical Analyses

We compared the total number of trials in which (1) a sibling was consumed in single sibship versus mixed sibship pairs of stimulus larvae (i.e. groups 1 versus 3); (2) a non-sibling was eaten in single sibship versus mixed sibship prey pairs (groups 2 versus 3); and (3) a larva was consumed in sibling versus non-sibling pairs (groups 1 versus 2), using the McNemar test for the significance of changes, corrected for continuity (Siegel 1956). We reduced alpha to 0.025 according to Bonferroni's inequality, because each data set was used twice (Snedecor & Cochran 1980). We also examined whether stimulus larvae behaved differently towards larger siblings than to non-siblings, which could explain potential differences in the frequencies of sibling and non-sibling cannibalism. For trials involving mixed prey groups only (i.e. one sibling+one non-sibling), we used a 2×2 multivariate analysis of variance (MANOVA) to examine whether (1) relatedness to the cannibal (sibling versus non-sibling), (2) the eventual outcome for each larva (eaten or uneaten after 24 h) and (3) the interaction of these two factors influenced two simultaneous response variables of each prey (Move toward and Move away from cannibal). We combined the data from both years of the experiment because those from 1992 were too few to analyse separately. This factorial analysis allowed us to compare simultaneously the behaviour of (1) eaten siblings versus eaten non-siblings ($N=23, 10$, respectively), (2) uneaten siblings versus uneaten non-siblings ($N=10, 23$, respectively), (3) eaten versus uneaten siblings ($N=23, 10$, respectively) and (4) eaten versus uneaten non-siblings ($N=10, 23$, respectively). This analysis was conducted using the general linear models (GLM) procedure of the statistical analysis system (SAS 1990).

For the 'two sibling' and 'two non-sibling' prey groups that were matched for each focal larva, we compared the total number of trials in which the first pursued prey moved away from an attacking sibling versus an attacking non-sibling. These data were analysed using the McNemar test for the

significance of changes, corrected for continuity (Siegel 1956). In trials (from both years combined) in which one act of cannibalism occurred during our initial 30-min observations, we compared (1) the elapsed time (min) until prey capture and (2) the handling time (min) for sibling versus non-sibling prey using Mann-Whitney *U*-tests (Siegel 1956). Matched data sets were too few for analysis in accordance with our paired experimental design. Thus, we maintained independence of data by selecting one trial at random from the three conducted for each focal larva. Data for siblings (and, similarly, for non-siblings) were combined from pure and mixed prey groups. For trials (from both years combined) in which cannibalism occurred during the 24-h period following our observations, we compared the time (h) elapsed until disappearance of a prey. Information on the time of disappearance was sufficient to analyse only the 'two sibling' and 'two non-sibling' prey groups that were matched for each focal larva, using Wilcoxon matched-pairs signed-ranks tests (Siegel 1956). Last, we examined whether potential cannibals could have based their foraging preferences on any slight variations in prey size. For trials in which one stimulus larva was eaten, we compared the total length of the larva eaten with that of the larva not eaten using Wilcoxon matched-pairs signed-ranks tests. Except where otherwise noted, each year of the experiment was analysed separately, with $\alpha=0.05$, two-tailed.

RESULTS

Cannibals ate significantly fewer non-siblings in the mixed sibship group than in groups composed of two non-siblings (1992: $\chi^2=6.75$, $P<0.01$; 1993: $\chi^2=13.47$, $P<0.001$; Fig. 1). However, the total number of trials in which a cannibal ate a larva in prey groups composed of two siblings did not differ significantly from the number of trials in which it ate its sibling in the mixed sibship prey group (1992: $\chi^2=0.00$, $P>0.99$; 1993: $\chi^2=3.50$, $P>0.05$; Fig. 1). Statistically, the frequency of sibling cannibalism remained constant, even when cannibals were offered a choice of non-siblings as alternative prey. This outcome was consistent for both populations examined in the two different years of the experiment (Fig. 1), and indicates that small larvae were more vulnerable to cannibalism by their larger siblings than by non-siblings. In

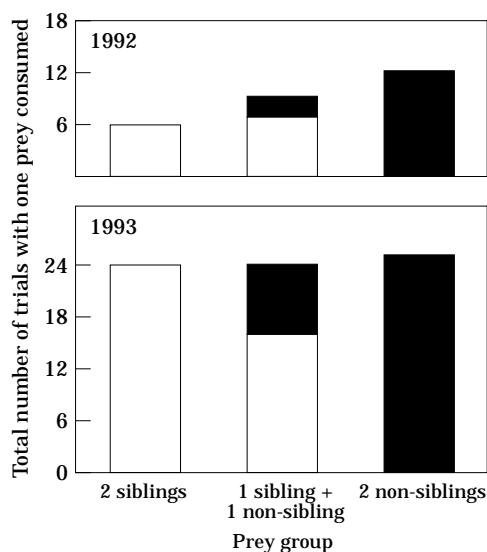


Figure 1. The total number of trials in which larval *A. opacum* cannibalized a sibling (□) versus a non-sibling (■) from single and mixed sibship pairs in each year of the experiment.

both years, there was no significant difference in the number of trials in which a larva was eaten in the 'two sibling' versus the 'two non-sibling' prey groups (1992: $\chi^2=3.12$, $P>0.05$; 1993: $\chi^2=0.00$, $P>0.99$; Fig. 1), indicating that both siblings and non-siblings were readily eaten (and at similar frequencies) in the absence of alternative prey.

One possible explanation for this greater vulnerability of siblings to cannibalism is that potential prey responded differently to the presence of a sibling than they did to a non-sibling, that is, smaller larvae may 'offer' themselves as prey to larger siblings. A MANOVA revealed that prey behaviour (i.e. their initial frequencies of Move toward and Move away), recorded during the first 30 min of larval encounters, was not significantly affected by the relatedness of prey to the cannibal, whether prey were eventually eaten, or by an interaction between these two factors (Fig. 2, Table I). During the first 30 min of each trial, we observed attempts at cannibalism (Lunge), in both the 'two sibling' and 'two non-sibling' prey groups, for seven focal larvae in 1992 and 12 larvae in 1993. The number of trials in which the pursued prey immediately moved away from the potential cannibal following its first attack did not significantly differ for the 'two sibling' versus the

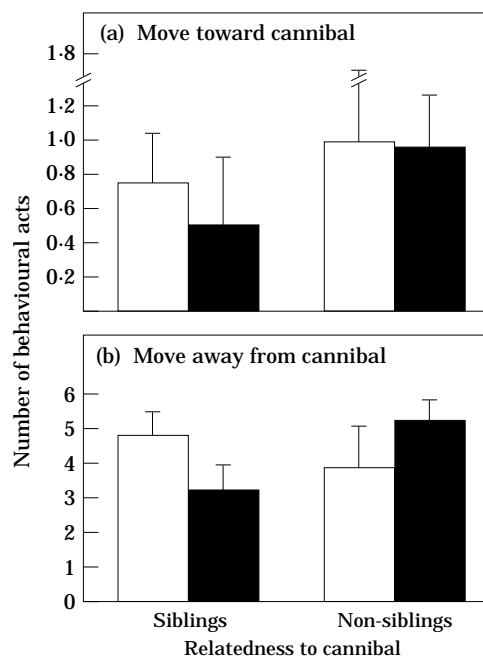


Figure 2. The number of behavioural acts ($\bar{X} \pm SE$) by stimulus larvae that were eventually eaten (□) or not eaten (■) by a sibling or a non-sibling. Responses are from the mixed prey group (one sibling+one non-sibling) and for 1992 and 1993 combined.

Table I. Summary of MANOVA for the effects of (1) relatedness of prey to cannibal, (2) experimental outcome (prey eaten or uneaten) and (3) a relatedness \times outcome interaction on two behavioural responses (Move toward and Move away from cannibal) of stimulus larval *A. opacum*

Source of variation	Wilks' lambda	$F_{2,61}$	P
Relatedness	0.99	0.42	0.66
Outcome	1.00	0.06	0.94
Relatedness \times outcome	0.96	1.38	0.26

'two non-sibling' prey groups in either year (1992: 7 siblings versus 6 non-siblings; $\chi^2=0.00$, $df=1$, $P>0.99$; 1993: 11 siblings versus 7 non-siblings; $\chi^2=2.25$, $df=1$, $P<0.25$).

We observed 14 independent acts of cannibalism ($N=7$ for both sibling and non-sibling trials) during these initial observations. The elapsed time (min) until prey capture did not significantly differ between sibling ($\bar{X} \pm SD=17.6 \pm 8.5$) and non-sibling prey (16.9 ± 7.1 ; $U=52$, $P>0.05$).

Table II. Total length (mm; $\bar{X} \pm \text{SE}$) of larval *A. opacum* eaten versus those not eaten, by larger conspecifics in three experimental groups of prey per year in 2 years

Larval group	Length of larva eaten	Length of larva not eaten	<i>N</i>	<i>N</i>	<i>T</i>	<i>P</i>
1992						
2 siblings	27.9 ± 1.25	29.0 ± 1.47	6	5	—	—*
2 non-siblings	21.8 ± 0.89	23.2 ± 1.20	10†	8	6	>0.05
1 sibling+1 non-sibling	24.6 ± 1.11	25.2 ± 1.20	9	8	13	>0.05
1993						
2 siblings	23.3 ± 0.32	24.0 ± 0.39	19†	17	74	>0.05
2 non-siblings	22.9 ± 0.38	23.4 ± 0.50	24†	24	127	>0.05
1 sibling+1 non-sibling	24.2 ± 0.41	23.6 ± 0.37	24	23	101.5	>0.05

N=Number of independent trials in which one larva was eaten; *N*=statistical sample size (non-tied scores) for the Wilcoxon matched-pairs signed-ranks test.

**N* was insufficient to conduct the Wilcoxon analysis; Siegel 1956.

†Some pure sibship trials could not be analysed because identifying marks of surviving prey were eliminated during those trials.

Cannibals also spent similar amounts of time (min) handling sibling and non-sibling prey (4.4 ± 2.2 versus 4.2 ± 3.0 ; $U=43$, $P>0.05$). During the 24-h post-observational period, the maximum time required for a prey to disappear from the matched 'two sibling' and 'two non-sibling' prey groups was known for eight focal larvae. The elapsed time (h) until prey disappearance was similar for sibling and non-sibling prey (10.1 ± 3.4 h versus 5.7 ± 4.5 h; $T=7$, $P>0.05$).

There were no significant differences in the sizes (total lengths) of larvae eaten versus not eaten for any of the three prey groups in either of the two years (Table II). Therefore, differential cannibalism does not appear to be a consequence of selective foraging based on the relative body sizes of alternative prey. We also evaluated whether our results might be due to a bias in only one or a few sibling groups in their propensity to cannibalize siblings. For the seven sibling groups (two populations combined) for which at least two focal larvae were tested, we calculated the proportion of each sibling group that ate a sibling in the mixed sibship prey group (group 3). A chi-squared test for proportions (Zar 1984) revealed no significant difference among these seven sibling groups in their propensity to eat siblings (proportions=0.0, 0.5, 0.5, 0.71, 0.80, 0.83, 0.86; $\chi^2=7.34$, $df=6$, $P<0.50$).

DISCUSSION

Our study demonstrates that small larvae of *A. opacum* are more vulnerable to cannibalism by

their larger siblings than by non-siblings. Under the conditions of our experiment, this sibling cannibalism did not appear to result from size-selective foraging by the cannibal or differences among the sibships in the propensity for larvae to cannibalize siblings, the latter of which has been found in larval *A. tigrinum* (Pfennig et al. 1994). We cannot conclusively evaluate whether differences in the behaviour of the prey (over a 24-h period) may have influenced their vulnerability to cannibalism, because we observed individuals for the first 30 min of each trial only. Prey behaviour during these initial observations, however, did not appear to influence the outcome of the cannibalistic event. Cannibals required similar amounts of time to capture and handle both siblings and non-siblings. Nevertheless, we tentatively propose that our results indicate *preferential* cannibalism of siblings.

The outcome of our study resembles several other examples of harmful (even fatal) acts of aggression among close kin. For example, female prairie dogs, *Cynomys ludovicianus*, and acorn woodpeckers, *Melanerpes formicivorus*, kill the offspring of close kin (Mumme et al. 1983; Hoogland 1985). Similarly, domestic piglets use their elaborate dentition as weaponry against sibling competitors (Fraser & Thompson 1991). Brood reduction due to siblicide may be a common strategy among the nestlings of many species of birds (cf. reviews by Mock 1984; Mock et al. 1990). These examples, however, involve organisms that live in family groups, at least during

particular stages of development in which individuals would not normally encounter unrelated individuals (except for chicks of colonially nesting birds, which may encounter non-siblings; e.g. Mock 1984). Thus, to our knowledge, our results are the first demonstration of an apparent cannibalistic preference for siblings when non-siblings are available as alternative prey.

Our results contrast with those obtained in a previous study of kin recognition in larval *A. opacum* (Walls & Roudebush 1991), as well as with those of other behavioural studies of cannibalistic larval amphibians (spadefoot toad tadpoles, *Scaphiopus bombifrons*: Pfennig et al. 1993; tiger salamanders, *A. tigrinum*: Pfennig et al. 1994). Walls & Roudebush (1991) demonstrated that larval *A. opacum* of similar body size (and from the same populations examined in the present study) reduce aggression and increase submission towards siblings, compared with non-siblings. Similarly, larvae of *S. bombifrons* and *A. tigrinum* minimize cannibalism of siblings (Pfennig et al. 1993, 1994). Many other animals also avoid cannibalizing kin, such as insects (flour beetles and waterstriders: Wade 1980; Nummelin 1989), larval ascidians (Young 1988) and several species of fishes (reviewed in FitzGerald & Whoriskey 1992) and rodents (reviewed in Elwood 1992; but see Baur 1987, 1990 and Miller 1989 for lack of kin discrimination in cannibalistic snails and spiders, respectively).

A likely explanation for the divergence of our results from those of other behavioural studies of larval *Ambystoma* is the context-dependent nature of kin discrimination (e.g. Blaustein et al. 1987b; Reeve 1989; Waldman 1991). For *A. opacum*, kin discrimination might depend upon the relative body size of larvae. For example, harmful aggression may decrease among siblings of similar size, if similarly sized individuals have equivalent fitness, because aggression could be costly to indirect fitness. Conversely, the costs to indirect fitness of eating a stunted sibling may be low, compared with the nutritional benefits gained by the cannibal, because small individuals may have a low expectancy of survival in the temporary ponds they inhabit (Waldman 1982, 1991; Crump 1992). From the victim's perspective, a small individual might profit more (in terms of indirect fitness) by restraining from competition with its larger siblings or, in particularly harsh environments, by being cannibalized by them (Waldman 1982,

1991). The magnitude of variation in kin discrimination in *A. opacum* (from reduced aggression towards siblings of similar size to 'preferential' cannibalism of siblings of smaller size) is similar to that reported in other species: both prairie dogs and acorn woodpeckers may switch from harming to aiding kin within a short period of time (Hoogland 1985, 1989; Stanback & Koenig 1992). Kin-biased behaviour patterns in prairie dogs and blue-footed boobies, *Sula nebouxii*, tend to vary with the intensity of intraspecific competition (Hoogland 1986; Drummond & Garcia Chavelas 1989).

We are uncertain whether kin-biased cannibalism in *A. opacum* is adaptive, or is an epiphenomenon (Grafen 1990; Pfennig 1990). The adaptive value of kin discrimination has become a contentious issue, partly because it is not clear what is being identified in the discrimination process: genetic relatedness per se or species or group membership (e.g. Grafen 1990; Blaustein et al. 1991). Because sibling cannibalism may pose a paradox to adaptive explanations of behaviour, this phenomenon illustrates a particular need to explore alternative hypotheses for the evolutionary significance of kin discrimination in cannibalistic species.

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