

Kin recognition and cannibalism in spadefoot toad tadpoles

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Abstract. Tadpoles of spadefoot toads, *Scaphiopus bombifrons*, are polymorphic in nature: juveniles that feed on detritus develop into herbivorous omnivores, while those that feed on fairy shrimp sometimes become carnivores that are cannibalistic. The kin recognition abilities of both larval morphotypes were studied. In laboratory tests, omnivores preferentially associated with siblings, while carnivores from the same clutch preferentially associated with non-siblings. In follow-up studies, carnivorous tadpoles were observed to nip at conspecifics, and then either eat them, if they were non-siblings, or release them unharmed, if they were siblings. Carnivores became less selective when hungry, demonstrating that their level of kin discrimination was context-dependent. Three evolutionary hypotheses for avoidance of siblings by the carnivore morph were considered; of these, the most likely is that such behaviour resulted from kin selection.

Kin recognition is 'the differential treatment of conspecifics as a function of their genetic relatedness' (Sherman & Holmes 1985, page 437; see also Gamboa et al. 1991b). This topic has generated intense interest (e.g. Fig. 1 in Pfennig & Sherman 1992), due largely to the development of kin selection theory (Hamilton 1964) and optimal outbreeding theory (Bateson 1978). Both theories predict that organisms should recognize descendant and non-descendant kin. Spurred on by these conceptual advances, investigators have looked for, and found, remarkably precise kin recognition abilities in multiple vertebrate and invertebrate taxa and across the spectra of social and cognitive complexity (reviewed in Fletcher & Michener 1987; Waldman 1988; Hepper 1991).

Kin-biased behaviour often is assumed to indicate both that an animal can recognize kin and that selection favouring discrimination of different degrees of relatedness produced such behaviour. However, kin-biased behaviour may evolve for reasons that have nothing to do with identification of kin per se (Grafen 1990; Pfennig 1990a; Barnard 1991; Gamboa et al. 1991b). Instead, such behaviour may be an incidental effect of habitat, species, or group-member identification.

For example, many anuran tadpoles preferentially school with siblings (reviewed by Blaustein et al. 1987a; Waldman 1991). Such behaviour often is

assumed to implicate a history of kin selection (e.g. Blaustein et al. 1987b). But when Pfennig (1990a) investigated the adaptive significance of associations among larval New Mexico spadefoot toads, *Scaphiopus multiplicatus*, he found that these tadpoles aggregated with any conspecifics that had eaten the same food. Attraction to tadpoles bearing familiar, environmentally-derived cues has also been observed in larval wood frogs, *Rana sylvatica* (Gamboa et al. 1991a). In nature, eggs of both species are laid typically in clusters and siblings grow up side by side, so association with conspecifics bearing similar chemical cues usually results in aggregations of kin. However, selection for philopatry, rather than kin selection, may account for such discrimination (Pfennig 1990a). Clearly, whether or not an organism treats kin and non-kin differently is a separate issue from the evolutionary reasons it does so (Grafen 1990; Pfennig 1990a; Gamboa et al. 1991b).

We sought to disentangle these two questions by studying the kin preferences of plains spadefoot toad tadpoles, *S. bombifrons*. Spadefoot toads are desert-dwellers that breed in temporary ponds in North America (Bragg 1965). The tadpoles of at least three species (*S. bombifrons*, *S. intermontanus*, and *S. multiplicatus*) occur as two behaviourally and morphologically distinct phenotypes: omnivores and carnivores (Pomeroy 1981; Pfennig 1990b,

1992a). Omnivores have flat, keratinized mouthparts, feed primarily on detritus, and often aggregate with conspecifics. In contrast, carnivores have beak-shaped, keratinized mouthparts and enlarged buccal cavity muscles, feed on live animal prey, and are solitary (Bragg 1965; Pomeroy 1981; Pfennig 1989).

Carnivores and omnivores are environmentally-induced alternatives. In the laboratory, larvae become omnivores if they are fed plant material or detritus. Tadpoles from the same sibship can become carnivores if they are fed fairy shrimp or live conspecifics (Pomeroy 1981; Pfennig 1990b, 1992a). In nature, both morphs will consume conspecific tadpoles (Bragg 1965), but carnivores are markedly more cannibalistic than omnivores (Pfennig 1989, page 42). For example, a census of the stomach contents of field-caught tadpoles revealed that 22 of 56 carnivores (39%) had eaten conspecific tadpoles, whereas none of 60 omnivores had eaten conspecifics (D. W. Pfennig, unpublished data).

Given this difference between morphs in the propensity to engage in cannibalism, we wondered if omnivorous and carnivorous tadpoles would display different preferences for kin. In particular, we sought to determine whether the more cannibalistic carnivorous morph would, unlike omnivores, avoid close relatives. Our rationale was that cannibals that can recognize and avoid preying on individuals with whom they share genes by descent should be favoured over cannibals lacking this ability.

Our study therefore was designed to address the following question. Do the two tadpole morphs differ in how they treat relatives? Specifically, are carnivores less attracted to kin than omnivores, and do carnivores indeed avoid eating their close relatives?

METHODS

Subjects

We collected three pairs of *S. bombifrons* in amplexus from a pond 6.3 km west-southwest (WSW) of Rodeo, New Mexico, U.S.A. (31°48'N, 109°05'W) and allowed them to oviposit in buckets. We transferred the eggs to the laboratory and maintained them on a 14:10 h light:dark cycle at 30°C. One day before the eggs hatched (i.e. 1 day after they were laid), we separated each sibship into five groups of 100–200 embryos each. Each group was

then placed with its egg jelly into a separate 30-litre aquarium containing dechlorinated tap water. Siblings reared in separate aquaria were never exposed to each other. Rearing densities were within the range of tadpole densities in the field (see Pfennig et al. 1991b). Tadpoles were fed 0.20 g of live shrimp, *Artemia* sp., and 0.20 g of Carolina Biological Supply tadpole chow daily. We changed the tadpoles' water every third day. Within a week, one to five tadpoles transformed into carnivores in each aquarium. When most tadpoles reached Gosner's (1960) developmental stage 30, which occurred at 10 days post-hatching, we conducted experiments to answer three questions.

Experiment 1: Do Omnivores and Carnivores Differ in Tendencies to Aggregate with Siblings?

To investigate this, we employed testing procedures similar to those used in previous studies of tadpole kin associational behaviour (e.g. Blaustein & O'Hara 1981; O'Hara & Blaustein 1981; Cornell et al. 1989). Each trial consisted of giving a carnivore or an omnivore a choice of associating with unfamiliar non-siblings or with unfamiliar siblings (i.e. siblings reared in different aquaria). We divided a plastic tray measuring 38 × 15 × 5 cm into three equal-sized sectors with vertical 80-µm nylon mesh and flooded it with 750 ml of dechlorinated tap water. The nylon mesh effectively separated the compartments but allowed visual and olfactory exchange.

To start a trial, we placed omnivores ($N=16$) from separate sibships into each end compartment and allowed them to acclimatize for 10 min. Then a single test tadpole was placed at the centre of the tray. The test animal was an unfamiliar sibling to one group of stimulus animals and an unfamiliar non-sibling to the other group. After a 10-min acclimation period, an observer recorded the total time that the test animal spent on either side of the centre line for the next 10 min. This observer was the same person throughout the experiment; she was never aware of which end compartment contained the test animal's siblings, nor of the hypothesis being tested. After each trial, the test tray was rinsed thoroughly with dechlorinated tap water and rotated 180°.

For two-thirds of the trials, the test tadpole was a carnivore; these carnivores were selected from all three sibships. On every third trial, the test animal was an omnivore from the same sibship as the test

carnivores used in the two previous trials. Test animals were used only once. Stimulus animals were selected randomly from the rearing aquaria. Some of these tadpoles probably were used multiple times, although not in consecutive trials and not before having been returned to their rearing aquarium.

Experiment 2: Do Carnivores Avoid Consuming Siblings?

To answer this question, we offered carnivores a choice between unfamiliar omnivore siblings and unfamiliar omnivore non-siblings. Five small glass bowls (19.3-cm diameter) were filled 1.5 cm deep with dechlorinated tap water. We placed six similar-sized (0.6–0.8 cm, snout–vent length: SVL) omnivores, three from one sibship and three from another, in each bowl, along with a carnivore (1.1–1.9 cm, SVL; these were different carnivores than those used in experiment 1). The carnivore was an unfamiliar sibling of three omnivores and an unfamiliar non-sibling of the other three omnivores. To keep track of the omnivores, we used only those individuals that possessed sibship-specific pigmentation patterns. To control for any possible effects of the pigmentation itself, in two bowls the carnivore's siblings were the darker-pigmented animals, and in three bowls they were the lighter-pigmented animals. An observer, who again was unaware of which omnivores were the carnivore's siblings or of the question being addressed, recorded all encounters (physical contact) between carnivores and omnivores and cannibalism events for 30 min following the carnivore's introduction. The experiment was repeated three times using different omnivores each time.

We minimized the numbers of animals used in our study ($N = 5$ carnivores, and $N = 90$ omnivores) in light of the Animal Behavior Society's (1991) guidelines and Elwood's (1991, page 847) recommendation that, 'It should be a general aim in studies on aggression and predation to use experimental designs that keep numbers of animals to a minimum.'

Experiment 3: Do Carnivores' Food Preferences Differ with Hunger?

In nature, a carnivore's fitness can be affected adversely by failing to feed on one day, which may represent 7% of the animal's larval life (Pfennig

et al. 1991b). More successful foragers metamorphose more quickly (Pfennig et al. 1991b), and rapid development often enhances survival in the highly ephemeral breeding ponds occupied by *S. bombifrons* (Pfennig 1992b). Under such conditions, the benefits of feeding may outweigh the fitness costs of eliminating a relative (Eickwort 1973). If so, cannibals should become less choosy as they become hungrier.

To test this, the same five carnivores studied in experiment 2 were given a choice of cannibalizing omnivorous siblings and non-siblings after not having eaten for various lengths of time. The three trials in experiment 2 were conducted consecutively over a 96-h period. First, a carnivore was fasted for 24 h and a 30-min feeding trial was conducted; then the same animal was fasted for 48 h, and another trial was run; finally the animal was fasted for 24 h and tested again. The third test following the 24-h food deprivation interval controlled for changes in a carnivore's level of discriminatory cannibalism due to habituation or ageing. Again, a 'blind' observer recorded the proportion of light-coloured or dark-coloured omnivores consumed in 30 min.

Statistical Analyses

For the main effects, in experiment 1, the response variable was the proportion of time that each test tadpole spent on the half of the test tray nearer its siblings. In experiments 2 and 3, the response variable was the proportion of prey each carnivore ingested that were siblings. Two-tailed, one-sample *t*-tests were then used to examine the null hypothesis that the observed proportions were not equal to 0.5 (the expected proportion if the behaviour patterns of the tadpoles were random with respect to kinship). Before analysis, all proportions were transformed (arcsine square-root) to meet the parametric assumptions of normality (Sokal & Rohlf 1981).

RESULTS

Experiment 1

Omnivores spent significantly more time on the side of the test tank containing their siblings ($\bar{X} \pm \text{SD} = 0.597 \pm 0.119$) than expected if association were random with respect to kinship (Fig. 1; $N = 10$, $P = 0.035$). The omnivores' carnivorous siblings, by contrast, spent significantly less time

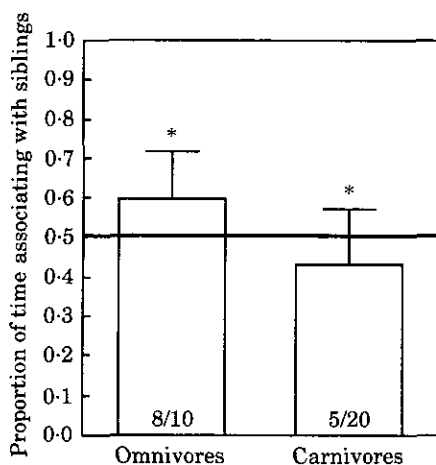


Figure 1. Mean (\pm SD) proportion of time carnivorous ($N=20$) and omnivorous ($N=10$) tadpoles spent nearer to a group of 16 unfamiliar siblings than to a group of 16 unfamiliar non-siblings in our test apparatus. The numbers in each bar are number of trials in which the test animal spent greater than 50% of a 10-min test period on the side of the test tray containing siblings/the total number of trials. The heavy, horizontal line is the value expected if the tadpoles' behaviour patterns were random with respect to kinship. * Indicates that the observed value was significantly ($0.01 < P < 0.05$) different from random expectation (i.e. 0.5).

with their siblings (0.432 ± 0.138) than random expectation (Fig. 1; $N=20$, $P=0.045$). The behaviour of omnivores and carnivores thus differed significantly from each other ($P=0.004$, two-tailed t -test): omnivores spent more time near their siblings, whereas carnivores spent more time near non-siblings.

Experiment 2

Carnivores were significantly more likely to consume non-siblings than siblings. In three trials involving five carnivores and 90 omnivores, carnivores ate 35 tadpoles. Of these, 27 (77%) were non-siblings. All five carnivores behaved similarly, cannibalizing far fewer of their siblings than non-siblings. The mean (\pm SD) number of siblings that they cannibalized was 1.6 ± 2.1 , versus 5.4 ± 1.5 non-siblings. The proportion of prey per carnivore that were siblings (0.175 ± 0.192) was significantly less than the value expected (0.5) if siblings and non-siblings were cannibalized randomly ($P=0.039$).

Carnivores apparently discriminated among prey through direct contact. Carnivores sucked

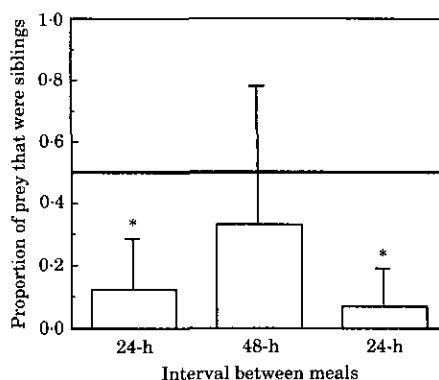


Figure 2. Mean (\pm SD) proportion of the prey of five carnivorous tadpoles that were siblings as a function of length of time between meals. The experiment was done sequentially over 96 h, with food withheld for 24 h, 48 h, and then 24 h again. At the end of each fasting period, the carnivore's consumption of kin and non-kin was assessed for 30 min. * Indicates that the observed value was significantly ($P < 0.02$) less than 0.5 (heavy, horizontal line), the value expected if cannibalism were random with respect to kinship.

non-siblings and siblings into their buccal cavity equally often (2.6 ± 1.8 and 3.2 ± 1.3 times/trial for siblings and non-siblings, respectively; $N=5$, $P=0.462$, two-tailed Wilcoxon matched-pairs signed-ranks test). Thereupon, non-siblings were frequently swallowed, whereas siblings were more likely to be released unharmed. Observations of tadpoles that had been engulfed and released proved that this oral contact was not fatal.

Experiment 3

Carnivores preyed more on their siblings when they were hungry. The mean (\pm SD) proportion of siblings cannibalized by five carnivores after they had not eaten for 24 h was 0.116 ± 0.161 (Fig. 2). This value was significantly less than expected (0.5) if cannibalism were random with respect to kinship ($P=0.016$). However, after these same carnivores had been deprived of food for 48 h, the proportion of siblings consumed (0.334 ± 0.472) increased markedly; indeed it was not significantly less than 0.5 ($P=0.438$). The change in behaviour was more likely due to differences in hunger levels than to habituation or ageing, because after these same carnivores had not fed for another 24 h, the proportion of siblings cannibalized again dropped to a value (0.066 ± 0.148) that was significantly less than 0.5

(Fig. 2). Thus, carnivores became less selective when their own survival was potentially threatened.

DISCUSSION

Why do *S. bombifrons* tadpoles recognize their siblings? For omnivores, there are at least two possible reasons to associate with relatives. First, tadpoles that remain near their oviposition site grow faster (Pfennig 1990a). Because a female's eggs often are laid in groups, siblings tend to smell like the oviposition site. Thus, tadpoles may associate preferentially with conspecifics that smell like 'home' (i.e. siblings) as a manifestation of adaptive habitat selection (philopatry; see Pfennig 1990a). Second, affiliating with relatives may also be an outcome of kin selection. Associating with conspecifics in general and kin in particular may be selectively favoured if schooling promotes increased feeding efficiency (Bragg & King 1961; Beiswenger 1975), predator avoidance (Bragg 1965; Black 1970; Wassersug 1973; Brodie & Formanowicz 1987; Hews 1988), enhanced development (Waldman 1991), or optimal thermoregulatory performance (Brattstrom 1962). However, none of these putative kin-selected benefits has been tested rigorously for *S. bombifrons*, nor indeed for any other larval anuran (Waldman 1991).

For carnivores, there are at least three possible reasons to avoid relatives. The first and most likely possibility is that foraging preferences have been moulded by kin selection. All else being equal, eating siblings decreases inclusive fitness more than eating non-kin.

A second hypothesis is that cannibalizing siblings is dangerous; for example, siblings may be more likely to carry contagious, debilitating pathogens than non-siblings. This hypothesis is suggested by the report (Pfennig et al. 1991a) that cannibalistic, larval tiger salamanders, *Ambystoma tigrinum*, can acquire deadly pathogens from diseased conspecifics. Such lethal pathogens are especially transmissible among phenotypically similar organisms (Anderson & May 1982).

The disease hypothesis seems an unlikely explanation for the avoidance of kin in *S. bombifrons* for three reasons. First, extensive surveys of tadpoles in 37 ponds in Arizona and New Mexico during 1986–1988 (Pfennig 1990b) revealed no evidence of disease epidemics in *S. bombifrons* similar to those occurring in *A. tigrinum* (Worthylake & Hovingh 1989; Pfennig et al. 1991a). Second, the disease

hypothesis requires that pathogens be highly sibship-specific, and that siblings be especially susceptible to their sibship-specific pathogens. We do not know if pathogens are so family-specific that it is much safer to eat non-siblings than siblings. Finally, the hypothetical pathogen would be more dangerous to carnivores if there were nothing to eat but conspecifics (because they would probably carry deleterious pathogens) than if there were a mixture of prey species available. Therefore, carnivores should occur less frequently in natural ponds containing only conspecifics. Contrary to this prediction, carnivores were found more frequently in ponds containing conspecifics only than in ponds containing multiple tadpole species (i.e. possible alternative prey). Surveys in 1987 revealed that seven ponds in southeastern Arizona and southwestern New Mexico in which only one species was present contained $74 \pm 22\%$ carnivores, whereas 19 ponds in the same area in which more than one species was present contained $18 \pm 23\%$ carnivores ($P = 0.001$, two-tailed Mann–Whitney U -test; for a description of surveying technique, see Pfennig 1990b).

A third hypothesis for kin discrimination by carnivores is that it is an epiphenomenon of species recognition (Grafen 1990). Because carnivores were raised only with siblings, they might have learned their species recognition cues or 'template' from siblings. If so, their avoidance of siblings might actually represent attempts to consume heterospecifics. This seems unlikely for two reasons. First, spadefoot toad tadpoles (Pfennig 1990a) and many other anurans (e.g. Waldman 1981) learn the template for kin recognition from cues in their nearby environment shortly after hatching, when individuals are surrounded solely or primarily by kin. If tadpoles were using only nearby conspecifics to form their species recognition template, many unrelated conspecifics would be misidentified as heterospecifics; i.e. such a recognition system would be extremely error-prone. Second, it is unclear why heterospecifics would be more valuable as prey. Indeed in some species, there is evidence that individuals who prey on conspecifics obtain a better balance of nutrients, necessary for growth and body maintenance, than individuals who prey on heterospecifics (Crump 1986, 1991). For example, treefrog tadpoles, *Hyla pseudopuma*, reared exclusively on conspecifics grow larger than those reared exclusively on heterospecifics (Crump 1990).

For these reasons, the best interpretation of our results is that the behaviour of carnivorous *S. bombifrons* tadpoles is the product of kin selection. Kin recognition in carnivores enables them to obtain nourishment without killing relatives. The opposite kin preferences for omnivores and carnivores as well as the low rate of sibling consumption by all but hungry carnivores support the kin selection hypothesis. Kin selection undoubtedly also explains why parents generally avoid killing and eating their offspring in various species, including waterstriders (Nummelin 1989), certain fish (Loekle et al. 1982), birds, and mammals (e.g. Sherman 1981; Hausfater & Hrdy 1984).

Carnivorous *S. bombifrons* tadpoles apparently use chemical cues to discriminate kin, as do omnivorous *S. multiplicatus* tadpoles (Pfennig 1990a) and *Bufo americanus* tadpoles (Waldman 1986). By using these chemical cues, a carnivore may 'taste test' each tadpole it engulfs before either eating it (non-siblings) or releasing it (siblings). The much larger carnivore is clearly better able than the engulfed tadpole to determine whether or not the latter is swallowed. It seems unlikely that the victims were sacrificing themselves given that non-siblings were eaten more often than siblings.

Few studies have examined whether potentially cannibalistic animals discriminate non-descendant kin. In field experiments in which foundresses of social wasps, *Polistes fuscatus*, were given a choice between eating the brood of a sister or that of a non-sister, they were more likely to cannibalize the latter (Klahn & Gamboa 1983). In laboratory tests, Walls & Roudebush (1991) found that larval salamanders, *Ambystoma opacum*, were less aggressive and more submissive to siblings than to non-siblings. They suggested that such behaviour might function to minimize harmful acts of aggression against relatives.

Walls & Roudebush (1991, page 1027) proposed that, 'avoidance of siblings in larval salamanders, in contrast to the preferential aggregation of siblings in larval anurans, suggests a divergence in the possible function of kin recognition among amphibians'. Our results do not support this hypothesis. Rather, we suggest that divergence in the functions of kin recognition can occur between cannibalistic and non-cannibalistic morphs in any species. The manner in which kin recognition is expressed (e.g. as aversion or as affinity for kin) should vary with the animal's morphology and ecological context. Such shifts in kin preference are

predicted by a general, quantitative model of context-dependent kin recognition (Reeve 1989).

For *S. bombifrons*, the fitness consequences of kin recognition clearly differ for carnivorous and omnivorous morphs. For omnivores, the advantage probably lies in remaining near the natal site or in helping kin to avoid predators, feed more efficiently, or grow faster. For carnivores, the advantage probably lies in obtaining sustenance without reducing inclusive fitness. Because morph determination in *Scaphiopus* is reversible (Pomeroy 1981; Pfennig 1992a, b), it is even possible that kin recognition plays different roles at various points in the ontogeny of an individual tadpole.

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