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## KIN-MEDIATED MORPHOGENESIS IN FACULTATIVELY CANNIBALISTIC TADPOLES

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**Abstract.**—Inclusive fitness theory predicts that organisms can increase their fitness by helping or not harming relatives, and many animals modify their behavior toward kin in a manner consistent with this prediction. Morphogenesis also may be sensitive to kinship environment, particularly in species where certain individuals facultatively develop structures that can be used against conspecifics as weaponry. We tested this hypothesis by examining whether and how consanguinity affected the probability that a structurally distinctive carnivore phenotype, which is opportunistically cannibalistic, would be produced in plains spadefoot toad tadpoles (*Spea bombifrons*) and southern spadefoot toad tadpoles (*S. multiplicata*). For tadpoles of *S. multiplicata*, individuals were significantly more likely to express the carnivore phenotype in mixed sibship groups than in pure sibship groups. For tadpoles of *S. bombifrons*, individuals were significantly more likely to express the carnivore phenotype when reared alone than in pure sibship groups. Both outcomes were independent of food availability or sibship specific differences in size or growth rate, and waterborne chemical signals from nonkin were sufficient to trigger expression of the carnivore phenotype. Our results suggest that morphogenesis may be responsive to kinship environment in any species or population that occurs as multiple, environmentally induced forms (polyphenism) that differ in their ability to help or to harm others.

**Key words.**—Cannibalism, context-dependent morphogenesis, kin recognition, kin selection, polyphenism.

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The fundamental premise of inclusive fitness theory is that an individual can increase its genetic representation in the population by helping reproductive relatives, because relatives share copies of the individual's genes by descent (Hamilton 1964). Consistent with this theory, many organisms act altruistically toward kin, demonstrating that kinship environment can exert a profound influence on behavior (reviewed in Sherman et al. 1997).

Morphological development should be similarly responsive to kinship environment, because development—like behavior—is often context dependent (West-Eberhard 1992). In support of this prediction, some plants grow faster when potted with full or half siblings than when potted with nonrelatives (Willson et al. 1987; Tonsor 1989), and tadpoles of at least three frog species grow faster or larger when reared with kin as opposed to nonkin (Jasieński 1988; Smith 1990; Waldman 1991). While these studies illustrate that kinship environment can influence growth, the issue of whether and how consanguinity affects morphogenesis (the development of morphology) has been largely unexplored.

The best systems for examining the role of kinship environment in morphogenesis are those in which a single population occurs as multiple, environmentally induced forms (polyphenism) that differ in their ability to help or to harm others. Such systems are ideal, because quantifying the morphogenic response to environmental cues is unambiguous and the predictions regarding the conditions under which related individuals should assume the alternative phenotype are clear.

Species or populations that exhibit cannibalistic polyphenisms, where individuals express either a typical phenotype or an alternative, cannibal phenotype (Polis 1981), can be particularly informative for studies of kin-mediated developmental plasticity, because environmental cues largely

determine which phenotype an individual expresses. For example, starvation triggers the expression of large cannibalistic morphs in ciliates and cellular slime molds (reviewed in Waddell 1992); cannibalism and dietary vitamin E (tocopherol) together induce large cannibal morphotypes in rotifers (Gilbert 1973); certain diets trigger large-headed cannibal phenotypes in long-toed salamander larvae, *Ambystoma macrodactylum* (Walls et al. 1993); and crowding with conspecifics stimulates expression of similar cannibalistic forms in larvae of at least two salamanders (*A. tigrinum*: Collins and Cheek 1983; *Hynobius retardatus*: Nishihara 1996).

Kinship environment also appears to affect morphogenesis of certain cannibalistic forms, which is not surprising, given that cannibalism of kin can have a clear and direct effect on the cannibal's inclusive fitness (Hamilton 1964). However, proximate mechanisms mediating such responses are unclear. For instance, when reared in mixed sibship groups, larvae of *A. tigrinum* are more likely to transform into cannibals than when reared with siblings only (Pfennig and Collins 1993). Sibship specific olfactory signals, which are used in assessing whether to cannibalize more distant relatives in preference to close kin (Pfennig et al. 1994), may mediate larval development into a cannibal. Alternatively, the size distribution of larvae in a population may be the environmental cue that triggers development of cannibal morphs in mixed sibship groups, because relatives are often more similar in size than nonrelatives, and size disparities facilitate cannibalism (Polis 1981). Indeed, greater size variation among larvae of *A. tigrinum* stimulates expression of the cannibal phenotype (Maret and Collins 1994).

Thus, the benefits of becoming a cannibal might be greater in mixed sibship groups—and decreased consanguinity may serve as a proximate cue to trigger cannibal morphs—for two separate reasons. First, kin selection may favor suppression of cannibal morph production in the presence of kin to max-

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imize inclusive fitness by reducing the risk of harming relatives. Second, cannibalism may be favored in the presence of nonkin, if these individuals are less similar in size than are kin, and if size disparities facilitate cannibalism. It is important to distinguish between these two proximate mechanisms, because kinship environment per se is critical only for the first mechanism of context-dependent morphogenesis.

It is also unknown if kin-mediated morphogenesis is dependent on the internal state of the decision maker. Such plasticity in expression of kin-mediated morphogenesis might be expected, because kin discrimination often varies according to its fitness consequences in different ecological contexts (Waldman 1988; Reeve 1989; Sherman et al. 1997). One such context is an animal's hunger state. For example, facultatively cannibalistic spadefoot toad tadpoles (*Spea bombifrons*) ingest nonkin in preference to kin when the cannibal is satiated, but these tadpoles become less selective when food is limited (Pfennig et al. 1993). Presumably, hungrier tadpoles are less discriminating of kin than satiated tadpoles because the former are at greater risk of dying in a deteriorating larval environment, and cannibalism hastens metamorphosis (Crump 1992). Satiated tadpoles can afford to be choosier when selecting prey if the benefits of cannibalism are less important than are the inclusive fitness costs of eating a relative.

We examined the proximate basis of kin-mediated morphogenesis in spadefoot toad tadpoles. Spadefoot tadpoles often occur in nature as either an omnivore morph or as a larger, physically distinctive carnivore morph that has specialized oral structures to facilitate the ingestion of large prey (including conspecifics; Bragg 1965; for illustrations of both morphs see Pfennig 1992a). The carnivore phenotype is induced facultatively when tadpoles ingest macroscopic animal food, such as fairy shrimp (Pfennig 1990a).

We designed a series of field and laboratory experiments to test the role of kinship environment, larval size distribution, and food availability on induction of the cannibalistic morphology in plains spadefoot toad tadpoles (*S. bombifrons*) and southern spadefoot toad tadpoles (*S. multiplicata*). Specifically, we asked four questions. (1) Are carnivores more cannibalistic than omnivores, and thus do carnivores pose a greater potential threat to eat kin than do omnivores? (2) If so, is the probability of producing the carnivorous phenotype influenced by the kinship environment in which tadpoles develop? (3) What are the roles of larval size distribution and chemical cues emanating from kin in mediating the expression of the cannibalistic phenotype? (4) Is the expression of kin-mediated morphogenesis dependent on the animal's hunger state?

## MATERIALS AND METHODS

### *Study Species*

Spadefoot toads (Anura: Pelobatidae) are desert dwellers occurring primarily in western North America (Stebbins 1985). Adults breed in one night in small pools that form after summer rainstorms. Eggs hatch within 42 h, and tadpoles can metamorphose as soon as 12 to 16 days later (Pfennig 1992a). Despite this rapid developmental rate, many ponds dry before any tadpoles metamorphose (Newman 1987; Pfennig 1990a). Tadpoles of at least three species, *S.*

*bombifrons*, *S. intermontana*, and *S. multiplicata*, possess a unique means of acquiring extra nourishment, thereby hastening development (Pfennig 1992a). Following ingestion of fairy shrimp or other tadpoles, typical omnivorous tadpoles may alter behavioral and morphological development to assume a carnivore phenotype, which confers an accelerated development rate, hastening metamorphosis (Pfennig 1990a). Production of the carnivorous phenotype is adaptive, because it is induced in highly ephemeral pools where rapid growth and development are favored (Pfennig 1990a); in longer lasting pools, tadpoles retain the omnivorous phenotype and metamorphose later than carnivores but in better condition (Pfennig 1992a). Compared to omnivores, carnivores have shorter intestines, better developed keratinized mouthparts, and an enlarged jaw hyoidean muscle group resulting in a more massive head (Pfennig 1992b). Finally, these morphs differ dramatically in behavior; omnivores are gregarious detritivores that dwell along pond margins, whereas carnivores are solitary, patrolling hunter/scavengers that pursue shrimp schools at the pool surface (Pomeroy 1981).

### *Experiment 1: Cannibalism Rates of Carnivores and Omnivores*

We first examined whether carnivores pose a greater threat to kin than omnivores by assaying cannibalistic tendencies for each morph. We constructed a floating raft of cups to contain tadpoles within treatments in a natural pond. The raft was constructed by attaching 10 250-ml opaque plastic cups (perforated on the sides and bottom with 1-mm diameter holes) to a 1-m board such that the rim of each cup was flush with the upper surface of the board. The holes in each cup were small enough (1 mm) to retain the tadpoles, but large enough to admit plankton and detritus, and mesh was tacked over the top of each cup to prevent tadpoles from swimming out of the large opening. The raft was floated on the surface of a pond near Portal, Arizona, that contained both morphs. One-hundred carnivore-morph and 100 omnivore-morph *S. bombifrons* tadpoles of approximately the same size and developmental stage (Gosner stage 32) were captured, and 20 individuals of each morph were placed into separate cups (i.e., five cups contained 20 carnivores and five cups contained 20 omnivores). Numbers of tadpoles in each cup were censused daily over a two week interval. We inferred that cannibalism had occurred if a tadpole was missing or if a partially consumed tadpole was found in the cup. Morph-specific cannibalism rates were contrasted using a two-way analysis of variance.

### *Experiment 2: The Role of Kinship Environment in the Morphogenesis of Cannibalistic Tadpoles*

We tested the hypothesis that kinship environment influences the probability of tadpoles developing the carnivore phenotype by comparing the likelihood of tadpoles assuming the cannibalistic phenotype when raised alone, in kin groups, or in nonkin groups. To do this, we collected four amplexant pairs each of *S. bombifrons* and *S. multiplicata* during July 1995 at a pond near Portal, Arizona. Pairs spawned in separate 14-L buckets filled with pond water. One week after the tadpoles hatched, we randomly assigned similarly sized

larvae from each sibship to one of three treatment categories: (1) tadpoles reared in isolation; (2) tadpoles reared in groups of eight with full siblings only; or (3) tadpoles reared in groups of eight with one full sibling and two larvae from each of the three other conspecific sibships. Treatment category (2) reflected the situation where tadpoles are surrounded solely or primarily by siblings in ponds in which only a few females oviposit, whereas treatment category (3) mimicked the situation where tadpoles are surrounded primarily by nonrelatives in ponds in which numerous females oviposit. Tank mates differed in snout-vent length by no more than 5%.

Tadpoles were reared in the same room in clear plastic tanks (28 × 18 × 10 cm) filled with 6 L of dechlorinated tap water. Tanks were cleaned once a week, and tadpoles were provided with rabbit chow and live fairy shrimp (*Thamnocephalus* and *Streptocephalus* spp.) ad libitum. The experiment was ended 25 days posthatching, because carnivores are unlikely to be produced after this time (Pfennig 1992a). Tanks were coded by number, and, without knowledge of which treatment group was in a tank, one person scored each animal as being of the omnivore or carnivore morphotype using criteria in Pfennig (1990a). Morph assignments were always unambiguous.

The expected probability that a larva in each mixed sibship group would become a carnivore morph was calculated from the observed probabilities in the constituent pure sibship groups (see Pfennig and Collins 1993). The observed probability that any given larva from a sibship would become a carnivore morph when reared with siblings only was:

$$O_i = 1 - \sqrt[S]{1 - p_i}, \quad (1)$$

where  $p_j$  = the observed probability in Table 1 of sibship  $j$  producing a carnivore morph (e.g., the observed probability of any given larva from sibship Q producing a carnivore =  $1 - [1 - 0.4]^{1/8} = 0.062$ ). The expected probability of a carnivore morph developing in each mixed sibship group was:

$$E = 1 - \prod_{j=1}^S (1 - O_j)^{N_j}, \quad (2)$$

where  $O_j$  = observed probability that a larva from sibship  $j$  would become a carnivore morph when reared with siblings only,  $S$  = number of sibships per tank (= 4), and  $N_j$  = number of larvae from sibship  $j$  per tank (= 2). Because no more than one carnivore was produced per tank in this experiment, we derived the expected probability that a carnivore morph would be produced in  $S$  sibships (each containing  $N$  larvae) by subtracting from one the expected probability that those  $S$  sibships would not produce a carnivore morph (=  $[1 - O_1]^{N_1} * [1 - O_2]^{N_2} * \dots * [1 - O_S]^{N_S}$ ). The observed and expected number of mixed sibship tanks in which a carnivore morph developed were then compared with a one-sample chi-square test.

#### Experiment 3: The Role of Tadpole Size Distribution and Kinship Environment in the Morphogenesis of Cannibalistic Tadpoles

This experiment was designed to elucidate the proximate mechanism by which decreased consanguinity triggers de-

velopment of the carnivore morph. We hypothesized that kinship environment may affect tadpole developmental tactic choice in one of two ways. First, siblings may be more similar in size than nonsiblings, and greater variation in tadpole size among nonsiblings may lead to increased production of carnivorous morphs (see Introduction). Alternatively, tadpoles may use chemical cues to assess their relatedness to neighbors (e.g., see Blaustein and Waldman 1992) and respond with an enhanced likelihood of expressing the carnivore phenotype in mixed sibship groups. To tease apart these two proximate mechanisms, we varied the size distribution and sibship environment of focal tadpoles in the laboratory.

We examined the relative roles of among-tadpole size variation and kinship environment in the morphogenesis of cannibalistic tadpoles by employing a full 2 × 2 factorial design with eight randomized blocks. Four sibships of *S. multiplicata* tadpoles were collected as in experiment 2. One week after hatching, tadpoles were randomly assigned in groups of eight to one of four treatment groups: (1) high size variation, high kinship environment; (2) high size variation, low kinship environment; (3) low size variation, high kinship environment; or (4) low size variation, low kinship environment.

Manipulation of tadpole size distributions was accomplished by making use of naturally occurring variation among tadpoles in body size. Tadpoles were reared in groups of eight where individuals were (1) similarly sized (= low size variation treatment); or (2) disparately sized (= high size variation treatment). The variance in body size differed significantly between the two groups (mean ± SD variance in snout-vent length for the two high size variation treatments =  $1.9 \pm 0.17$  and  $1.85 \pm 0.07$  and for the two low size variation treatments =  $0.34 \pm 0.13$  and  $0.36 \pm 0.16$ ; ANOVA:  $F_{3,28} = 85.5$ ,  $P < 0.0001$ ). However, the mean body sizes did not differ (mean ± SD mean snout-vent length for the two high size variation treatments =  $5.63 \pm 0.20$  mm and  $5.51 \pm 0.15$  mm and for the two low size variation treatments =  $5.57 \pm 0.11$  mm and  $5.47 \pm 0.12$ ; ANOVA:  $F_{3,28} = 1.97$ , NS).

Kinship environment was manipulated by rearing tadpoles in groups of eight with (1) siblings only (= high kinship environment treatment); or (2) one sibling and two larvae from each of the three other sibships (= low kinship environment treatment). Tadpoles were reared and scored for morphology as in experiment 2. An analysis of variance was used to examine the effects of tadpole size variation and kinship environment and their interactions on the response variable, the number of carnivores produced per tank.

Because propensity to develop the carnivorous phenotype was only affected by sibship environment (see Results), we conducted a separate experiment to determine whether sibship-specific chemical factors are used by tadpoles as the proximate environmental cue to become carnivorous.

#### Experiment 4: The Role of Waterborne Cues from Kin in the Morphogenesis of Cannibalistic Tadpoles

The goal of this experiment was to determine if tadpoles exposed to waterborne cues emanating from nonsiblings would express the carnivore phenotype at a higher rate than tadpoles exposed to waterborne cues emanating from sib-

lings. Four amplexant pairs of *S. multiplicata* were collected and treated as in Experiment 2. One week after tadpoles hatched, groups of eight similarly sized siblings were transferred to fiberglass screen enclosures (12 × 12 × 12 cm), which were placed in groups of four inside a 11.3-L rearing tank (38 × 25 × 15 cm). The enclosure's mesh size (0.5 mm) was small enough to contain larvae. To ensure equal exposure of all tadpoles to any chemical cues in the water, a small pump circulated water continuously (20 L/min) through all enclosures within a tank.

Tadpoles were assigned randomly to one of two different treatment tanks: (1) mixed sibship tanks containing one sibship per mesh enclosure (four sibships per tank); or (2) pure sibship tanks containing only one sibship (all four enclosures in the same rearing tank held the tadpoles from a single sibship). Thus, in the mixed sibship tanks, tadpoles were exposed to chemical cues of nonsiblings and siblings, whereas in the pure sibship tanks, tadpoles were exposed to chemical cues of siblings only.

Each treatment group contained 256 tadpoles equally divided among four tanks (8 tadpoles/enclosure × 4 enclosures/tank × 4 tank replicates/treatment). All tanks were kept in the same room, and tadpoles were provided with rabbit chow and live fairy shrimp ad libitum. The experiment was ended 25 days posthatching, at which time we scored each animal as being of the omnivore or carnivore morphotype using criteria in Pfennig (1990a).

#### Experiment 5: The Effect of Hunger State on the Expression of Kin-Mediated Morphogenesis

This experiment was designed to determine whether the carnivore phenotype was more likely to be expressed in the presence of kin when tadpoles were food deprived, and presumably hungry, than when satiated (i.e., when the focal animal's own survival was at risk). Such plasticity in the expression of kin-mediated morphogenesis might be expected, because kin discrimination often varies according to its fitness consequences in different ecological contexts, and one such context is an animal's hunger state.

We used tadpoles from the same eight sibships (four each of *S. bombifrons* and *S. multiplicata*) used in experiment 2. As before, tadpoles were reared in groups of eight with siblings only (10 replicate groups per sibship). However, half of the tadpoles from each sibship were fed live fairy shrimp daily ad libitum (= satiated tadpoles treatment), and the other half were fed a restricted diet of live fairy shrimp (as much shrimp as the tadpoles could consume in an hour = hungry tadpoles treatment). We scored each tadpole's morphology as described in experiment 2 and compared the proportion of hungry tadpoles that developed into carnivores with that for satiated tadpoles using a chi-square test.

## RESULTS

#### Experiment 1: Cannibalism Rates of Carnivores and Omnivores

Carnivore morph tadpoles were much more likely to eat conspecifics than were omnivores (Fig. 1; ANOVA:  $F_{1,8} =$

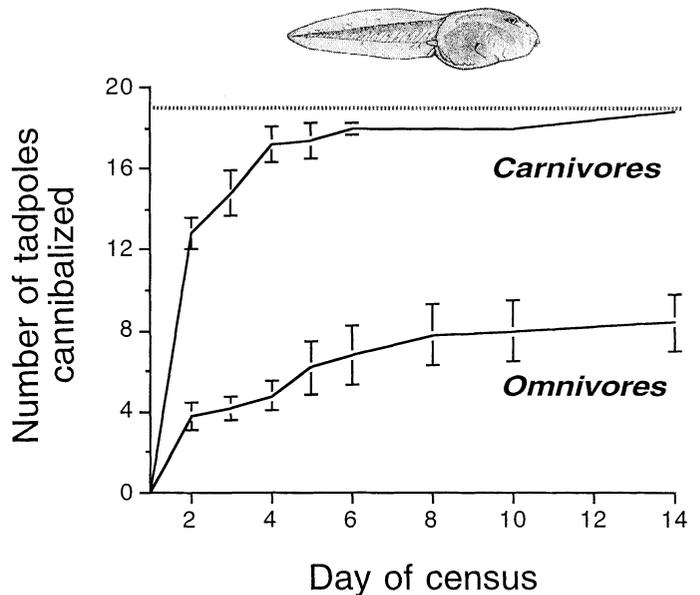


FIG. 1. Comparison of cannibalism rates in the wild of carnivore and omnivore-morph spadefoot toad tadpoles, *S. bombifrons*. Each line represents the mean cumulative number of tadpoles cannibalized in five small enclosures positioned in a breeding pond, where each enclosure initially contained either 20 carnivores or 20 omnivores (all of the same approximate size and developmental stage). Dashed line: maximum possible number of tadpoles cannibalized; vertical lines:  $\pm 1$  SEM.

288,  $P < 0.0001$ ). Thus, carnivores pose a greater potential threat to kin than do omnivores.

#### Experiment 2: The Role of Kinship Environment in the Morphogenesis of Cannibalistic Tadpoles

Carnivore morph tadpoles were significantly more likely to be produced in mixed sibship groups than in pure sibship groups of *S. multiplicata* tadpoles but not of *S. bombifrons* tadpoles (Table 1). For *S. multiplicata*, three of 20 (15%) pure sibship tanks produced a carnivore morph as opposed to 11 of 20 (55%) mixed sibship tanks. For *S. bombifrons*, six of 20 (30%) pure sibship tanks produced a carnivore morph as opposed to 11 of 20 (55%) mixed sibship tanks. After we had controlled statistically for differences among sibships in the probability of producing a carnivore morph (see Methods), we found that larvae in the mixed sibship treatments were significantly more likely to express the carnivore phenotype than were their siblings that were reared in pure sibship treatments for *S. multiplicata* tadpoles but not for *S. bombifrons* tadpoles (Table 1).

Interestingly, *S. bombifrons* were significantly more likely to express the carnivore phenotype when tadpoles were reared alone (mean  $\pm$  SD proportion of carnivores =  $0.19 \pm 0.1$ ) than when tadpoles from the same sibships were reared in groups with siblings (the mean  $\pm$  SD expected probability that any one tadpole from each of the four *S. bombifrons* sibships would develop into a carnivore when reared in groups of eight siblings =  $0.06 \pm 0.08$ ; two-tailed paired  $t$ -test:  $t_4 = 7.82$ ,  $P < 0.01$ ; Table 1). However, *S. multiplicata* were not significantly more likely to develop into carnivores

TABLE 1. Effect of consanguinity on expression of the carnivore phenotype in spadefoot toad tadpoles, *S. multiplicata* and *S. bombifrons*.

Treatment group	Sibship(s)	n	Number of carnivores:		
			Observed	Expected	P
Tadpoles reared alone					
<i>S. multiplicata</i>	K	5	1 (20%)		
	N	9	0		
	P	7	0		
<i>S. bombifrons</i>	Q	10	0		
	J	8	1 (12.5%)		
	L	10	1 (10%)		
	M	10	2 (20%)		
	O	9	3 (33%)		
Tadpoles reared in groups of eight					
One sibship	K	5	0		
<i>S. multiplicata</i>	N	5	0		
	P	5	1		
	Q	5	2		
Tadpoles reared in groups of eight					
One sibship	J	5	0		
<i>S. bombifrons</i>	L	5	1		
	M	5	1		
	O	5	4		
Four sibships	K, N	20	11	3.36	0.0009
<i>S. multiplicata</i>	P, Q				
	J, L	20	11	8.05	0.19
<i>S. bombifrons</i>	M, O				

when tadpoles were reared alone (mean  $\pm$  SD proportion of carnivores =  $0.05 \pm 0.1$ ) than when tadpoles from the same sibships were reared in groups with siblings (the mean  $\pm$  SD expected probability that any one tadpole from each of the four *S. multiplicata* sibships would develop into a carnivore when reared in groups of eight siblings =  $0.02 \pm 0.03$ ; two-tailed paired *t*-test:  $t_3 = 0.47$ , NS; Table 1). This suggests that *S. bombifrons* were sensitive to kinship environment in a way different from that of *S. multiplicata*: namely, tadpoles of *S. bombifrons*, but not of *S. multiplicata*, were less likely to develop into carnivores in the presence of kin than when reared alone.

#### Experiment 3: The Role of Tadpole Size Distribution and Kinship Environment in the Morphogenesis of Cannibalistic Tadpoles

Kinship environment had a significant effect on a tadpole's propensity to develop into a carnivore, but variation in the size distribution among larvae and the interaction between kinship environment and tadpole size variation did not (Table 2). Thus, some aspect of kinship environment per se other than tadpole size distribution is responsible for the greater production of carnivores in mixed brood groups.

#### Experiment 4: The Role of Waterborne Cues from Kin in the Morphogenesis of Cannibalistic Tadpoles

Significantly more tadpoles developed into carnivores in the mixed sibship treatment than in the pure sibship treatment. Six of 128 (4.7%) tadpoles in the pure sibship treatment developed into carnivores, compared with 18 of 128 (14%) tadpoles in the mixed sibship treatment (chi-square test:  $\chi^2_1$

TABLE 2. Two-way ANOVA of consanguinity and tadpole size distribution on expression of the carnivore phenotype in spadefoot toad tadpoles, *S. multiplicata*.

Source of variance	n	Number of carnivores	df	F	P
Consanguinity			1	6.018	0.021
high (one sibship)	8	3			
low (four sibships)	8	10			
Size variation			1	3.070	0.091
high size variation	8	9			
low size variation	8	4			
Consanguinity $\times$ size variation			1	1.105	0.302

= 5.56,  $P < 0.02$ ). Thus, waterborne cues emanating from nonkin stimulate the expression of carnivores, or alternatively, waterborne cues emanating from kin suppress the expression of carnivores.

#### Experiment 5: The Effect of Hunger State on the Expression of Kin-Mediated Morphogenesis

Food-limited tadpoles were no more likely to develop into carnivores in the presence of kin than were satiated tadpoles. Five of 30 (16.7%) hungry tadpoles developed into carnivores compared with three of 36 (8.3%) satiated tadpoles (chi-square test:  $\chi^2_1 = 1.07$ , NS). Thus, there is no evidence that expression of kin mediated morphogenesis is dependent on the hunger state of cannibals.

## DISCUSSION

This study clarifies some of the proximate mechanisms involved in kin-mediated morphogenesis in facultatively cannibalistic spadefoot toad tadpoles. We predicted that tadpoles would be less likely to express the carnivore morphology and more likely to express the omnivore morphology when surrounded by kin as opposed to nonkin, because carnivores are more cannibalistic than omnivores (Fig. 1). Indeed, the carnivore phenotype was less likely to be induced in the presence of kin than in the presence of nonkin (for *S. multiplicata*) or when tadpoles were reared in sib groups rather than alone (for *S. bombifrons*). Thus, spadefoot toad tadpoles modify morphogenesis in response to kinship environment, as has been shown for facultatively cannibalistic tiger salamanders (Pfennig and Collins 1993).

Contrary to our expectation, we found no evidence of a statistically significant effect of hunger on expression of kin mediated morphogenesis. Although satiated tadpoles were half as likely as food limited tadpoles to express the carnivore phenotype in the presence of kin, these differences were not statistically significant. This lack of a statistically significant effect of hunger on expression of kin-mediated morphogenesis may suggest that there is strong selection on these tadpoles to avoid developing into carnivores in the presence of kin, even when the tadpoles' own survival is at risk. Alternatively, our diet manipulation may not have been stressful enough (i.e., it did not produce sufficiently "hungry" tadpoles) to alter the cost/benefit relationship associated with consuming kin.

It might be contended that decreased consanguinity per se may not serve as the proximate cue to trigger production of the carnivore morph. Instead, cannibalism may be favored in the presence of nonkin, if these individuals are less similar in size than are kin and if size disparities facilitate cannibalism. Thus, increased variation among tadpoles in size, and not decreased consanguinity per se, may stimulate the production of carnivores.

Three lines of evidence argue against the size variation hypothesis. First, we found no evidence of a statistically significant effect of increased size variation on expression of carnivores (Table 2). Although there was a statistically non-significant trend ( $P = 0.09$ ) of increased size variation on the development of the carnivore morph, there was nevertheless a significant effect of kinship that was independent of any effects of size variation (Table 2). Second, the size variation hypothesis does not explain why tadpoles of *S. bombifrons* were more likely to develop the carnivorous phenotype when reared alone than when reared with kin (Table 1). Third, the results of experiment 4 demonstrate that the presence of chemical cues alone from kin mediates expression of cannibalistic tadpoles.

It appears that the production of carnivores is influenced in part by sibship-distinctive chemical signals that carnivore morph tadpoles of *S. bombifrons* and *S. multiplicata* use to associate with and cannibalize unrelated individuals in preference to siblings (Pfennig 1990b; Pfennig et al. 1993). Sibship-specific chemical cues are similarly thought to enable kin recognition in various larval anurans (reviewed in Blaustein and Waldman 1992), and chemical cues alone have been shown to influence growth rates of anuran larvae differentially by kinship (Waldman 1986). More generally, chemical cues emanating from heterospecific predators have long been known to have pronounced effects on morphogenesis in many organisms (reviewed in Dobson 1989).

There are at least three evolutionary hypotheses to explain the existence of kin mediated morphogenesis in these and perhaps other species exhibiting cannibalistic polyphenism. The first possibility is that morphogenesis of inducible carnivore morphs has been molded by kin selection (Hamilton 1964). All else being equal, developing into a carnivore in the presence of kin decreases inclusive fitness more than developing into an omnivore, because carnivores pose a greater threat to kin (Fig. 1).

A second hypothesis to explain kin mediated morphogenesis is that developing into a carnivore and cannibalizing close relatives is dangerous to the carnivore, because kin may be more likely than nonkin to transmit contagious, debilitating pathogens to each other. Cannibalistic animals can acquire deadly pathogens from diseased conspecifics (e.g., see Pfennig et al. 1991, in press). Such pathogens may be especially transmissible among kin (Shykoff and Schmid-Hempel 1991; Black 1994), because related individuals have similar immune systems, and the population of pathogens has been recently selected in a genetically similar environment (Pfennig 1997). We currently lack the data to test this hypothesis for spadefoots, but in facultatively cannibalistic salamander larvae, pathogens are no more likely to be transmitted among kin than among nonkin (D. Pfennig, unpubl. data).

Finally, kin-mediated morphogenesis may reflect manipulation (Alexander 1974) by individuals to prevent kin from developing into carnivores in their presence. For example, sibship-specific chemical cues may be produced by tadpoles to prevent siblings from developing into carnivores, even though developing into a carnivore may be in the focal animal's own best interest. This hypothesis seems implausible, however, because selection should favor individuals to overcome chemical suppression by simply ignoring the signal if responding to it does not benefit that individual (Seeley 1985). Thus, it seems most likely that kin-mediated morphogenesis reflects kin selected nepotism.

Kin-mediated morphogenesis provides an alternative proximate mechanism for identifying relatives. In general, organisms discriminate kin through the use of labels that are produced by another organism ("phenotypic recognition"), or alternatively, by clues related to time or place and without reference to recipient phenotypes ("nonphenotypic recognition"; Waldman et al. 1988; Sherman et al. 1997). The latter works only when relatives occur predictably in time or space. Spadefoots employ both phenotypic and nonphenotypic cues to identify relatives. First, carnivores are less likely to be produced in the presence of kin than in the presence of nonkin (a form of phenotypic recognition). Second, females exert some control over the kinship environment of their tadpoles by ovipositing portions of each sibship in different areas of the pond (a form of nonphenotypic recognition). Third, carnivores disperse from those areas of the pond where they were born (Pfennig 1990b), and, finally, failing all else, carnivores use taste to distinguish kin from nonkin (Pfennig et al. 1993). One explanation for why carnivores use so many different mechanisms to identify kin is that failure for a cannibalistic animal to recognize its kin means the death of a relative, and, consequently a decrement in the cannibal's inclusive fitness. Thus, it may be necessary for such animals to employ a variety of mechanisms to identify kin.

The role of kinship environment in influencing morphogenesis is just beginning to be explored (Pfennig and Collins 1993; Passera et al. 1996). Systems in which individuals differ in their ability to help or to harm others offer an excellent opportunity for studying kin-mediated morphogenesis. All else being equal, individuals that preferentially help or avoid harming kin should be favored over those that help or harm others indiscriminately (Hamilton 1964). Thus far, the only systems in which kin-mediated morphogenesis has been documented are species that exhibit cannibalistic polyphenism. It is currently unknown whether kinship also influences morphogenesis in species that produce alternative "fighter" and "nonfighter" morphs (Hamilton 1979), but there are some promising possibilities. For instance, different species of similarly sized parasitic wasps may attack the same caterpillar. Larvae of species in which each female typically lays a single egg per host tend to develop formidable mandibles, whereas larvae of species in which each female typically lays many eggs per host—and whose larvae therefore share their host with many siblings—lack these structures (Godfray 1994, see also Wilson 1987). Thus, although lethal rivalry can arise among close relatives (Grbic et al. 1992),

kin-mediated morphogenesis may provide a general mechanism to reduce this conflict.

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