Kin recognition and cannibalism in polyphenic salamanders

We investigated kin discrimination among larvae of Arizona tiger salamanders (*Ambystoma tigrinum nebulosum*) which occur as "typical" morphs that feed mostly on invertebrate prey and occasionally on conspecifics, and as "cannibal" morphs that feed primarily on conspecifics. When housed with smaller larvae that differed in relatedness, both cannibals and typicals preferentially consumed less-related individuals. Cannibals ate typicals much quicker when the choice was between nonkin and siblings than when the choice was between nonkin and cousins, indicating that cannibals could distinguish different categories of relatives. Cannibals were less likely to eat a larval sibling that was a cannibal morph than a sibling that was a typical morph. Occluding animals' nares temporarily eliminated kin discrimination, implying that olfaction is important in recognition. Larvae from different sibships varied considerably in their ability to discriminate kin, and the greater the probability that a larva from a given sibship would develop into a cannibal morph, the more likely the members of that sibship were to discriminate kin. Our results enable us to infer the functional significance of kin recognition in this species and to develop an evolutionary model of the mechanisms underlying the joint control of kin recognition and cannibalistic polyphenism.

Key words: cannibalism, kin recognition, polyphenism, tiger salamanders. *[Behav Ecol 5:225–232 (1994)]*

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Many animals are potentially cannibalistic. Such individuals occasionally may have to choose between eating a relative or a nonrelative. Not surprisingly, parents of numerous species refrain from eating their own offspring (Dickinson, 1992; Elliott, 1973; FitzGerald and Whoriskey, 1992; Loekle et al., 1982; Nummelin, 1989; Sherman, 1981; Stanback and Koenig, 1992). In some species even collateral kin, such as siblings, are avoided (Pfennig et al., 1993).

Studies of how kinship affects cannibalism are potentially important for clarifying the functional significance of kin recognition, which is currently the focus of controversy (Barnard, 1991; Blaustein et al., 1991; Carlin, 1989; Grafen, 1990; Stuart, 1991). Contention arises in part because it is difficult to use most kin-recognition bioassays to infer adaptive significance (Barnard et al., 1991; Gamboa et al., 1991; Pfennig, 1990). For example, many anuran tadpoles associate preferentially with kin (Waldman, 1991) and this behavior is thought by some to reflect selection to recognize relatives and dispense nepotism (e.g., Blaustein and Waldman, 1992; Waldman, 1991). However, tadpoles may associate with any conspecifics that smell like "home" as an incidental effect of adaptive habitat selection (Pfennig, 1990). Therefore, although preferential association with relatives is technically kin recognition because it results in "the differential treatment of conspecifics as a function of their genetic relatedness" (Sherman and Holmes, 1985, p. 437; see also Gamboa et al., 1991), further information is necessary to decide why kin are discriminated.

The adaptive significance of kin recognition is clearer when the kin discrimination bioassay is cannibalism (Blaustein et al., 1987), because there are only two likely evolutionary reasons to expect cannibals to avoid preying on kin. First, eating relatives may reduce inclusive fitness. Second, deleterious pathogens can be contracted through cannibalism (Pfennig et al., 1991a; Polis, 1981) and pathogens may be especially transmissible among close relatives (Shykoff and Schmid-Hempel, 1991) because kin have similar immune systems (Bremermann, 1980; Hamilton, 1980; Rice, 1983). There have been only a few detailed investigations, however, of how kinship affects prey preferences (Elgar and Crespi, 1992). Such information could help clarify not only why certain animals recognize kin, but also why some species are cannibalistic in the first place (e.g., cannibalism may evolve more readily in species that encounter kin infrequently).

Cannibalistic polyphenism, in which a population contains distinct cannibalistic and noncannibalistic phenotypes (Polis, 1981), provides an ideal setting to study the functional significance of kin recognition. Such polyphenisms occur in protozoans (Waddell, 1992), planarians (Armstrong, 1964), rotifers (Gilbert, 1973), fish (Cuff, 1977), spadefoot toad tadpoles (Bragg, 1965), tiger salamander larvae (Powers, 1907), and gulls and skuas (Stanback and Koenig, 1992). Because eating a relative may have important fitness consequences for the cannibal, cannibalistic and noncannibalistic morphs should display different kin preferences. This prediction was recently confirmed for plains spadefoot toad tadpoles, which occur as alternative omnivore and carnivore morphs (Pfennig, 1992). In laboratory tests, omnivores preferentially associated with siblings, whereas cannibalistic carnivores from the same clutch preferentially associated with and ate nonsiblings (Pfennig et al., 1993).

Here we investigate the kin preferences of Arizona tiger salamander larvae (*Ambystoma tigrinum*

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nebulosum) which occur in nature as typical morphs that feed mostly on invertebrates and occasionally on other salamanders, and as physically distinctive cannibal morphs that prey mostly on conspecifics (Collins and Holomuzki, 1984). Cannibals are induced facultatively by high densities of conspecifics (Collins and Cheek, 1983; Pfennig et al., 1991a) and morph determination is reversible (up to a certain age) if conspecific density changes (Reilly et al., 1992).

The potential exists in nature for tiger salamander larvae to eat relatives. Cannibalistic individuals often consume conspecifics of their own size and smaller (Rose and Armentrout, 1976), and larvae may occur in a pond where the only prey available are kin, due to parental philopatry and a small number of adults breeding in the pond (Berna, 1990). In such situations, only refined kin discrimination abilities would enable individuals to avoid eating close relatives.

These considerations led us to design experiments to address three questions. First, do larval tiger salamanders refrain from cannibalizing kin, and if so, is the discrimination contingent upon the morphotype of the predator or that of its potential prey? Second, what is the sensory basis of the discrimination? Third, do members of different sibships vary in their abilities to recognize kin and, if so, why?

MATERIALS AND METHODS

Experimental animals

Arizona tiger salamanders occur in ephemeral and permanent ponds throughout montane Arizona, Utah, and western New Mexico and Colorado, USA. Adults breed in the spring and the eggs hatch into larvae that typically metamorphose in early autumn of the same year (Berna, 1990).

We studied *A. t. nebulosum* larvae from eight sibships whose parents or grandparents were captured in the White Mountains of Arizona, from five different ponds: Lower Cottonwood (LC), Snow (S), Old Apache (OA), South (So), and Wildcat Point (WP) (see the Appendix). Detailed descriptions of LC and S were provided by Collins and Holomuzki (1984). Three sibships were captive-bred offspring of pairs collected from OA, So, and WP. Two sibships were captive-bred offspring of pairs collected from S, but we assumed that they were unrelated to each other because of the large number of adults breeding in their parent's natal pond. The other three sibships were offspring of captive-bred animals whose grandparents had been collected from LC and whose mothers were sisters. Thus members of these three sibships were first cousins.

Each pair of adults was kept in a 120-l aquarium until the female laid eggs. Within two weeks after the eggs hatched, 10 groups of 16 larvae from each sibship were chosen randomly. Each group was placed into a separate aquarium (22 l) with 16 l of dechlorinated tap water from a common source. A total of 1280 larvae was used in this experiment: 16 individuals from each of the eight sibships, reared in 10 replicate aquaria. The rearing density was in the upper range of larval densities in natural ponds (Pfennig et al., 1991a).

Larvae were reared under identical conditions in the same aquarium room: 22°C–25°C water temperature and 14:10 h photoperiod; their water was changed weekly. During rearing and throughout our experiments, animals were fed ad libitum live brine shrimp (*Artemia*) daily (the hatch from 0.015 g of eggs per larva; this was the maximum amount that would not foul the water). At 7 weeks after hatching we scored larvae as being typical or cannibal morphotypes using criteria in Powers (1907) and Pedersen (1991). In particular, as illustrated by Lannoo and Bachmann (1984), cannibals possess an enlarged vomerine ridge and elongate teeth.

General experimental procedures

We tested the discrimination abilities of larvae 7–9 weeks after they had hatched. To start an experiment, we put 16 l of dechlorinated tap water into a 22-l aquarium and introduced one test animal (a cannibal or a typical morph) and either two or ten stimulus animals (all typical-morph larvae) that were matched for size. Half of the stimulus animals were from one sibship, and half were from another. Stimulus larvae were always smaller than the test animal (about half the snout–vent length, SVL). In all experiments stimulus animals had been separated and reared apart from test animals since they were ≤2 weeks old, so they had not been exposed to each other for 5–7 weeks; different sibships were completely unfamiliar with each other.

To keep track of kinship identities, we cut a small hole (2–3 mm) in either the dorsal or ventral half of each stimulus animal's fin. To control for effects of these marks, in half the aquaria the test animal's closer kin (i.e., siblings or cousins) were marked dorsally, and in the other half they were marked ventrally. These marks did not affect larval mortality.

An observer who was unaware of the sibship identities of the stimulus animals checked each aquarium at least once every hour between 0800 h and 2000 h and noted when cannibalism had occurred (i.e., when a tank mate was consumed) and the tail mark(s) of the surviving stimulus animal(s). Nonlethal attacks were not recorded. Throughout all experiments, larvae were fed the standard ration of live *Artemia* daily. Unless otherwise noted, test and stimulus animals were used only once.

Experiments 1a–c: do tiger salamander larvae avoid consuming relatives?

We investigated whether larvae avoid consuming relatives and if an individual's morphotype or that of its potential prey influence the probability that it would eat kin.

Experiment 1a: cannibal–typical discrimination

To determine whether cannibal-morph larvae avoid consuming related typicals, we placed one cannibal, 4.72 ± 0.32 cm (mean ± SD) in SVL, in a 16-l tank with 10 similarly sized (2.74 ± 0.21 cm, SVL) typical-morph larvae. Thirty-six cannibals from eight different sibships were tested. Of these, 13 cannibals were housed with typicals, half of which were their siblings and half of which were their nonrelatives; 15 cannibals were housed with typicals that were their cousins and nonrelatives; and 8 cannibals were housed with typicals that were their siblings and cousins. We decided a priori to end the experiment after five of the typicals were consumed (i.e., half of them). A Wilcoxon matched-pairs, signed-rank test was used to compare the numbers of closely and distantly related typical-morph larvae consumed.

Experiment 1b: cannibal–cannibal discrimination
To see whether cannibal-morph larvae discriminate among cannibals based on relatedness, we placed two similarly sized cannibals (differing in SVL by no more than 2 mm) in each of 25 aquaria (16 l). In 10 aquaria, the two cannibals were siblings, and in 15 aquaria they were cousins. After one week, the fraction of tanks containing just one larva was recorded. The proportions of sibling and cousin pairs that had engaged in cannibalism were compared using a chi-square test.

Experiment 1c: typical–typical discrimination
Typical-morph larvae also occasionally eat conspecifics. To see whether typicals avoid consuming related typicals, we studied 75 typical-morph larvae from six different sibships. To create small stimulus animals within a sibship of typicals, we slowed the growth of some by rearing them for nine weeks at 18°C. In each experimental trial, a test larva (2.74 ± 0.21 cm, SVL) was placed in a 16-l aquarium with two similarly sized, smaller typicals (1.8 ± 0.20 cm, SVL). For 43 trials, the test typical was housed with a sibling and a nonrelative; and for 32 trials, with a cousin and a nonrelative. Each experimental trial was terminated when one larva was eaten. We used a chi-square test to compare the proportion of the more closely related individuals consumed with the proportion expected (0.5) if cannibalism were random with respect to kinship.

Experiment 2: do tiger salamander larvae use olfaction to discriminate kin?

Kin recognition in many larval anurans is mediated by olfactory cues (e.g., *Bufo americanus* tadpoles: Waldman, 1986; omnivorous *Scaphiopus multiplicatus* tadpoles: Pfennig, 1990; carnivorous *S. bombifrons* tadpoles: Pfennig et al., 1993). To see whether tiger salamander larvae also use their well-developed sense of smell (Arzt et al., 1986) in this context, we covered the nares of test animals, both cannibals and typicals, with Vetbond (3M Animal Care Products), an *n*-butyl cyanoacrylate tissue adhesive. This material temporarily occluded the nares, thus blocking passage of water over the nasal epithelium; within a few days the Vetbond fell off.

We studied 19 cannibals and 18 typicals that had consumed more nonkin than kin in Experiments 1a and 1c. These animals were immobilized by immersion for 1–2 min in a 1:2000 solution of tricaine methanesulfonate, then rinsed thoroughly in dechlorinated tap water to remove the anesthetic. One drop (0.02 ml) of tissue adhesive was placed on each naris of treatment animals. Control animals received an equal total amount of adhesive (0.04 ml) between the nares. Each test animal was placed in a tank with a cousin and a nonrelative that were about half its size. The number of cousins consumed by 16 treatment animals (9 cannibals and 7 typicals) and 21 control animals (8 cannibals and 13 typicals) was recorded hourly. Differences from random consumption of kin were tested using a chi-square test. Data for cannibals and typicals were pooled because the two morphs did not differ significantly in discrimination (see Results; Figure 1).

Experiment 3: do larvae from different sibships differ in kin recognition abilities?

We investigated whether larvae from different sibships were equally likely to prey on relatives and then examined the possible basis of any such variation. We used data from the six sibships for which more than two animals were tested in Experiments 1a–c, again combining data for cannibals and typicals. To see whether different sibships varied in the frequency with which they produced cannibal-morph larvae, we used a *G* test to evaluate heterogeneity in the proportion of aquaria containing each sibship that produced a cannibal-morph larva. We then checked for any correlation between kin discrimination ability and the propensity to produce a cannibal morph.

Laboratory estimates of the frequency with which different sibships produced cannibal morphs are not artifactual: the proportion of larvae that developed into cannibals from eggs collected in ten different ponds and reared in the laboratory was significantly positively correlated (Spearman's $r = .82$, $p = .002$) with the proportion of cannibals among free-living larvae from those ponds (Pfennig DW and Collins JP, unpublished data).

RESULTS

Experiments 1a–c: do tiger salamander larvae avoid consuming relatives?

Experiment 1a: cannibal–typical discrimination
Cannibal-morph larvae ($N = 36$) ate significantly more distant relatives or nonrelatives (2.83 ± 0.7 larvae) than close kin (2.17 ± 0.7 related larvae; $p = .013$; two-tailed Wilcoxon matched-pairs signed-rank test) when housed with five of each. For 26 cannibals, the identity of the first prey was known, and of these, 22 (85%) first ate one of the less related typicals; this proportion differed significantly from random expectation (i.e., 0.5; $\chi^2 = 12.46$, df = 1, $p = .0004$).

Despite the difference in relatedness between siblings and cousins, cannibals ate cousins and siblings equally rarely when there was a choice between them and nonrelatives ($H_{\text{adj}} = 0.55$, df = 2,

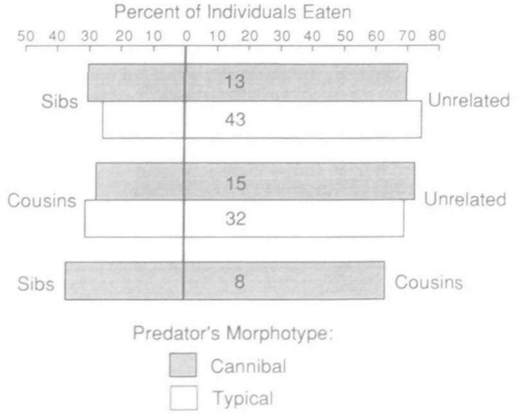

Figure 1
Comparison of the percentage of individuals eaten from different classes of relatedness by cannibal (shaded bars) and typical (unshaded bars) morph Arizona tiger salamander larvae in experiments in which larvae were given a choice (i.e., Experiments 1a and 1c). Relationship of test animal to the two groups of stimulus animals is indicated on either end of the bars. Sample sizes for each category are shown.

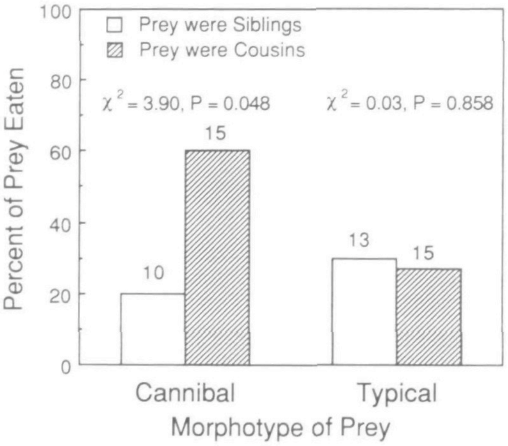

Figure 2
Prey preferences of cannibal-morph larvae as indicated by the ratio of the number of siblings eaten to the number of cousins eaten when both were cannibal-morph larvae or when both were typical-morph larvae. Sample sizes for each category are shown.

p =.761, Kruskal-Wallis test; Figure 1). Two lines of evidence demonstrated that cannibals could distinguish siblings from cousins, however. First, cannibals ate significantly more cousins when the choice was between cousins and siblings (Figure 1). Second, cannibals ate five typicals quicker when the choice was between nonrelatives and siblings (26.5 ± 18.1 h) than when the choice was between nonrelatives and cousins (63.5 ± 31.7; p =.0005; Mann-Whitney test).

Experiment 1b: cannibal–cannibal discrimination
Cannibals preyed on their cannibal-morph cousins significantly more often than on their cannibal-morph siblings. One larva was eaten in 9 of 15 tanks (60%) containing pairs of cannibals that were cousins, but among pairs of siblings, cannibalism occurred in only 2 of 10 tanks (20%; χ^2 = 3.90, df = 1, p =.048).

Although cannibals in this experiment ate siblings significantly less often than cousins when prey were similarly sized cannibal-morph larvae, cannibals in Experiment 1a did not eat smaller siblings (4 of 13 cases) significantly less often than smaller cousins (4 of 15 cases) when the prey were typical-morph larvae. Because the design of Experiments 1a and 1b differed (the former matched a cannibal with two sets of typicals, whereas the latter matched two cannibals), the rate at which cannibal-morph siblings were consumed could not be compared directly with that for typical-morph siblings. Using the frequency of cousin cannibalism as a standard for comparison, however, revealed that cannibal-morph larvae were less likely to eat a larval sibling that was a cannibal morph than a sibling that was a typical morph (Figure 2).

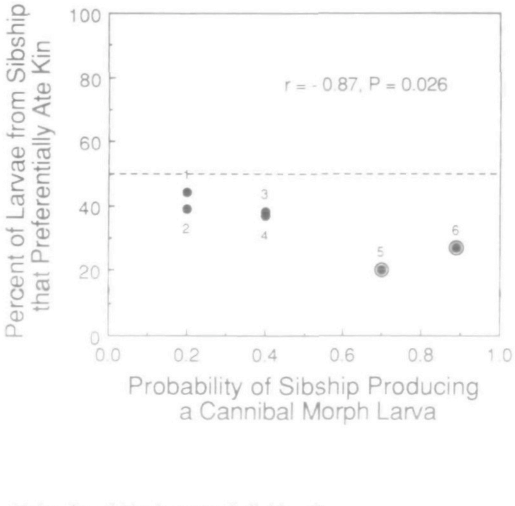

Figure 3
Relationship between the proportion of larvae from each of six sibships (1–6) that ate more kin than nonkin and the proportion of cannibals produced by that sibship. The latter was determined by the fraction of aquaria containing each sibship that produced a single cannibal-morph larva (results of Experiment 3). Sibship designation and sample size (N = number of individuals tested) for each data point are as follows: 1: WP, N = 9; 2: LC-16, N = 28; 3: So, N = 13; 4: OA, N = 13; 5: LC-23, N = 35; 6: LC-21, N = 22. The three LC sibships were cousins. Significantly fewer larvae in sibships 5 and 6 (circled) ate kin than nonkin; i.e., less than 50% (dashed horizontal line), the value expected if cannibalism were random with respect to kinship.

Experiment 1c: typical–typical discrimination
Typicals also preferentially ate nonrelatives. In 32 of 43 trials (74%) in which a typical was housed with two smaller, similarly sized typicals, a sibling and an unrelated larva, the typical ate the nonrelative (χ^2 = 10.26, df = 1, p =.001). In 22 of 32 trials (69%) in which a typical was housed with a cousin and an unrelated larva, the typical ate the nonrelative (χ^2 = 4.5, df = 1, p =.034).

Comparing these results with those of Experiment 1a reveals that typicals were no more likely than cannibals to eat nonrelatives, regardless of whether choosing between siblings and nonrelatives (χ^2 = 0.02, df = 1, p =.881; Figure 1) or between cousins and nonrelatives (χ^2 = 0.0004, df = 1, p =.983). Therefore, for all subsequent analyses we combine data from cannibals and typicals.

Experiment 2: do tiger salamander larvae use olfaction to discriminate kin?

Of 16 individuals whose nares were blocked, six (38%) consumed a cousin and 10 consumed a nonrelative, a ratio not different from random expectation (χ^2 = 1.00, df = 1, p =.317). By contrast, of 21 control larvae, only four (19%) consumed a cousin and 17 consumed a nonrelative, a ratio that differed significantly from random expectation (χ^2 = 8.05, df = 1, p =.004). Individuals whose nares were occluded were thus less discriminating of kin than were control animals (χ^2 = 3.88, df = 1, p =.048).

Experiment 3: do larvae from different sibships differ in kin recognition abilities?

Larvae from six sibships in which numerous individuals were tested (Experiments 1a–c) differed significantly in their propensity to discriminate kin. Larvae ate significantly (p <.01; χ^2 test) more nonkin than kin in 2 of the 6 sibships (points 5 and 6 in Figure 3).

Larvae from different sibships also differed significantly in their propensity to develop alternative cannibalistic and noncannibalistic phenotypes when 16 larvae from each sibship were reared in separate 16-l aquaria (G = 15.934, df = 5, p =.0116; Figure 3).The probability that an individual from a particular sibship would eat a relative was inversely correlated with the probability that its sibship would produce a cannibal morph (Figure 3).

Variation in larval size might be the proximate cause of variation among sibships in their tendency to produce cannibals. In particular, sibships with pronounced variation among individuals in size might be more likely to contain a larva large enough to cannibalize a tankmate and thereby produce a cannibal morph. Contrary to this prediction, the proportion of cannibal morphs that a sibship produced did not correlate significantly with either the mean mass of individual larvae from the sibship (r = −.412, N = 6 sibships, p >.05) or the variance in mass among individual larvae within the sibship (r =.240, N = 6 sibships, p >.05). Mean mass of individual larvae for a sibship was, however, significantly inversely correlated with the sibship's propensity to produce cannibal morphs, after the percent of cannibals and typicals from that sibship that preferentially ate kin was taken into account (partial $r = -.957$, $N = 6$ sibships, $p < .05$). Similarly, mean mass of larvae in a sibship was significantly inversely correlated with the propensity of its larvae to eat relatives, after the tendency of that sibship to produce cannibal morphs was taken into account (partial $r = -.948$, $N = 6$ sibships, $p < .05$).

DISCUSSION

Cannibalistic Arizona tiger salamander larvae have well-developed kin recognition abilities, and olfaction plays an important role in mediating such recognition. The effects of kinship in modulating cannibalism are remarkably precise: cannibals discriminated between different levels of kinship and even between first cousins (coefficient of relatedness [r] =.125) and nonrelatives ($r = 0$). To our knowledge, such fine-scale kin discrimination has not been reported previously in amphibians. The presence of refined kin discrimination abilities implies that in this species the fitness costs of eating even a distant relative are greater than the costs of passing up a meal.

The larvae in our experiments were exposed to siblings for the first two weeks after hatching, and it is possible that they avoided eating anyone they were reared with, as opposed to kin per se. This seems unlikely, however, given that both morphs were just as effective in discriminating between first cousins and nonrelatives as they were in discriminating between siblings and nonrelatives (Figure 1), despite their never having been exposed to cousins.

Why, in an ultimate sense, do larval *A. t. nebulosum* refrain from eating kin? Grafen (1990) suggested that many putative examples of kin discrimination are artifacts of species recognition. That is, larvae might learn their species recognition "template" early in life from nearby associates, which are usually siblings. Thus a preference for eating nonrelatives might actually reflect selection to prefer heterospecifics. For our results, this scenario is unlikely: *A. t. nebulosum* is the only species of salamander endemic to Arizona (Stebbins, 1985), probably since the last Pleistocene glaciation (Porter 1972: 255). Thus, there apparently has been no selection for *A. t. nebulosum* larvae to prefer heterospecifics, at least for the past 10,000 years.

Our study animals may have avoided ingesting relatives for at least two adaptive reasons. First, all else being equal, eating kin diminishes inclusive fitness more than eating nonkin. Second, cannibalizing close relatives may jeopardize the cannibal's own survival if close kin are more likely than nonrelatives to carry contagious, debilitating pathogens. In nature, *A. t. nebulosum* larvae are afflicted by a deadly bacterium that can decimate entire populations (Pfennig et al., 1991a; Worthylake and Hovingh, 1989), and cannibalistic larvae can acquire these pathogens by ingesting diseased conspecifics (Pfennig et al., 1991a). Moreover, sibships differ in their susceptibility to this bacterium (Pfennig and Collins, unpublished data).

At present, we do not know if our study animals recognized their kin solely to avoid diminishing inclusive fitness or to avoid disease as well. Indeed, perhaps both are important. Because the pathogen hypothesis specifically predicts that cannibalizing close kin increases a cannibal's chances of dying, the most direct test would be to offer some cannibals diseased relatives and others diseased nonrelatives. Under the disease avoidance hypothesis, cannibals in the former group should be more likely to die of the disease.

Is kin recognition in larval tiger salamanders context dependent?

Kin discrimination should vary according to its fitness consequences in different ecological contexts (Reeve, 1989). One such context is an animal's morphology. Omnivore-morph plains spadefoot toad tadpoles preferentially associated with siblings, whereas carnivores from the same clutch preferentially associated with and ate nonsiblings (Pfennig et al., 1993). Based on this, we had expected that cannibal and typical-morph Arizona tiger salamander larvae also would differ in their kin preferences. The two morphs were, however, equally unlikely to eat relatives (Figure 1), probably because both morphs are predacious (Reilly et al., 1992).

We also anticipated that when given a choice between eating prey that differed in relatedness, a salamander would be less likely to eat kin when the prey was a cannibal-morph larva than when the prey was a typical-morph larva, and this was confirmed (Figure 2). There are two likely reasons for this result. First, cannibalistic larvae may value most highly, in terms of inclusive fitness potential, any relative that is close to metamorphosis because slowly developing larvae become increasingly subject to desiccation, predation, and disease (Berna, 1990; Pfennig et al., 1991a; Worthylake and Hovingh, 1989). Cannibals typically transform at an earlier age (Lannoo and Bachmann, 1984) and therefore should be more likely to escape these conditions. Second, the ingestion of a cannibal-morph relative may threaten a cannibalistic larva's own survival. Pathogens may be especially transmissible among kin, and cannibal-morph larvae are more infested with deleterious pathogens that can be acquired through cannibalism (Pfennig et al., 1991a). Thus, eating a close cannibal-morph relative may be more dangerous than eating a close typical-morph relative.

The connection between kin recognition and cannibalistic polyphenism

There was apparently a linkage between kin discrimination and the probability a larva would develop into a cannibal morph (Figure 3). Significant variation among sibships in the likelihood of producing cannibal morphs exists both between (Pfennig et al., 1991a) and within populations (Experiment 3), and individuals from sibships that were most likely to produce cannibals were best able to discriminate kin (Figure 3). Our data suggest that larval size and an opposing factor—perhaps the individual's genotype—influence the probabilities of ingesting kin and of becoming a cannibal morph. Figure 4 summarizes what we currently know about the joint control of kin recognition and cannibal-

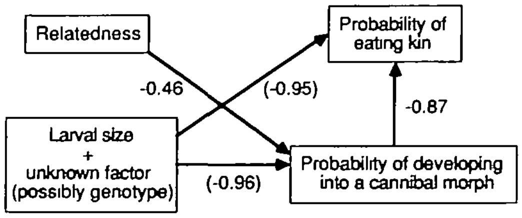

Figure 4
Diagrammatic representation of the hypothesized link between kin recognition and cannibalistic polyphenism in larval Arizona tiger salamanders. The numbers beside the arrows are correlation coefficients and the numbers in parentheses are partial correlation coefficients. The direction of an arrow indicates the hypothesized direction of causality.

istic polyphenism in larval tiger salamanders. There are four key correlations:

(1) Associations with kin during rearing affect the expression of the cannibal morphology. Increased consanguinity in the larval environment decreases a larva's probability of becoming a cannibal ($r = -.46$; Pfennig and Collins, 1993). From an ultimate perspective, this may reflect that cannibal-morph larvae are more likely to engage in cannibalism than typicals (Collins and Holomuzki, 1984), and cannibals that eat relatives may experience reduced inclusive fitness and, perhaps, also survival (due to disease).

(2) Larvae that were most likely to develop into cannibals were also best able to discriminate kin ($r = -.87$; Figure 3), again because cannibal-morph larvae that eat relatives diminish their own inclusive fitness and, perhaps, survival.

(3) The mean size of individual larvae in a sibship was inversely correlated with that sibship's probability of producing cannibals (partial r controlling for the sibship's probability of eating kin $= -.96$). We hypothesize the following evolutionary explanation for this correlation. In many amphibians, size at metamorphosis correlates positively with adult fitness (Berven, 1990; Pfennig et al., 1991b; Semlitsch et al., 1988; Smith, 1987). Smaller, slower-developing larvae also are more likely to succumb to predation, desiccation, and disease (Berna, 1990; Pfennig et al., 1991a; Worthylake and Hovingh, 1989). Through cannibalism, larvae can increase their size at metamorphosis and hasten their development. Even a single cannibalistic event can shorten the time to metamorphosis significantly (Lannoo et al., 1989). As a result, selection may favor a greater propensity to become a cannibal in sibships containing smaller, more slowly developing larvae than in those containing larger, more rapidly developing larvae. It might not pay for a larger larva that is close to metamorphosis to assume the time and developmental costs of changing into a cannibal.

(4) The mean size of individual larvae in a sibship was inversely correlated with that sibship's probability of eating kin (partial r controlling for the sibship's probability of becoming a cannibal morph $= -.95$). Perhaps smaller larvae are less discriminating of kin than larger larvae because the former are at greater risk of dying in a deteriorating larval environment, and cannibalism hastens metamorphosis. Even cannibalism of close kin can be favored if it sufficiently increases the cannibal's survival (Eickwort, 1973). Larger, rapidly developing larvae can be more choosy when selecting prey if the nutrients in a conspecific's body are less important than are the inclusive fitness costs of eating a relative.

The control of kin recognition in *A. t. nebulosum* is thus complex. Kinship environment, larval size, and perhaps genotype affect the probability of becoming a cannibal morph, and larval morphology and size affect the probability of eating kin. This complexity may help us reconstruct four steps in the evolution of cannibalistic polyphenism. We hypothesize that over evolutionary time (1) a larva in a deteriorating environment (e.g., a drying pond) that underwent behavioral and structural modification enabling cannibalism could take advantage of highly nutritious prey, thereby hastening its development (Crump, 1990) and decreasing the number of competitors. As cannibalistic and noncannibalistic phenotypes diverged, (2) factors modifying the frequency of becoming a cannibal morph (e.g., kinship environment, size) attained increased importance. Those sibships that developed greater tendencies than others to produce cannibals, (3) increased their chances of eating relatives. Finally, (4) kin recognition was favored in these lineages as a mechanism to enable cannibals to obtain sustenance without diminishing inclusive fitness and/or acquiring lethal pathogens.

It is currently unknown whether such richness and complexity govern kin recognition in other species that produce alternative cannibalistic and noncannibalistic morphs, but we predict that at least three links in the above hypothetical chain will occur generally. First, kinship environment should affect the tendency to become a cannibal morph. Second, individuals that prey mostly on conspecifics should avoid eating kin. Third, variation among lineages in their potential to cannibalize or otherwise harm relatives should correlate with variation in kin recognition abilities. Testing these predictions may help explain why ceratin species recognize kin and why these species are cannibalistic in the first place.

APPENDIX

Locality data for populations used in this study
Lower Cottonwood Pond: 14.3 km SW of Show Low, AZ, 34°08′32″ N, 110°07′33″ W, elevation = 1860 m; Old Apache Pond: 32 km W of Alpine, AZ, 33°49′37″ N, 109°28′43″ W, elevation = 2731 m; South Pond: 15.2 km W of Alpine, AZ, 33°55′01″ N, 109°16′53″ W, elevation = 2707 m; Snow Pond: 3.6 km SSW of Indian Pine, AZ, 34°03′07″ N, 109°55′39″ W, elevation = 2134 m; Wildcat Point Pond: 15.3 km NW of Hannigan Meadow, AZ, 33°42′50″ N, 109°27′32″ W, elevation = 2316 m.

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