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"KIN RECOGNITION" AMONG SPADEFOOT TOAD TADPOLES: A SIDE-EFFECT OF HABITAT SELECTION?

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Abstract.—Many animals modify their behavior toward unfamiliar conspecifics as a function of their genetic relatedness. A fundamental problem of any kin recognition study is determining what is being recognized and why. For anuran tadpoles, the predominant view is that associating with relatives is kin-selected because these relatives may thereby accrue benefits through increased growth or predation avoidance. An alternative view is that kin associations are simply a side-effect of habitat selection and thus do not represent attempts to identify kin per se. In the laboratory, spadefoot toad tadpoles (*Scaphiopus multiplicatus*) preferentially associated with unfamiliar siblings over unfamiliar nonsiblings, as do other anurans. However, same age tadpoles also were more likely to orient toward unfamiliar nonsiblings reared on the same food (familiar food) than toward unfamiliar siblings that were reared on unfamiliar food. These results, together with the results of previous tadpole kin recognition studies, suggest that tadpoles orient toward cues learned early in ontogeny, regardless of the cues' source.

Tadpoles that preferentially associated with cues learned from their environment at birth would tend to be philopatric. Censuses of 14 natural ponds revealed that tadpole density remained greatest near oviposition sites until four days before metamorphosis. Tadpole philopatry may be advantageous: tadpoles restricted to their natal site had greater growth and survivorship than did their siblings restricted to randomly selected sites elsewhere within the same pond. Thus kin affiliative tendency observed in the laboratory in this and perhaps other species of anurans may be a by-product of habitat selection. Since kin discrimination in animals is most commonly assayed as orientation toward kin, it follows that many examples of "kin recognition" may not represent true attempts to identify kin as such, but rather may reflect some other recognition system that is under entirely different selective pressures.

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A cornerstone of behavioral ecology is that in certain situations individuals may increase their genetic fitness by modifying their behavior toward conspecifics according to their genetic relatedness. Animals as phylogenetically diverse as bryozoans and primates respond differentially toward conspecifics according to their genetic relatedness, a process termed kin recognition (reviewed in Fletcher and Michener, 1987). Despite the widespread occurrence of kin-biased behavior, in surprisingly few systems have investigators identified the selective factors responsible for its evolutionary maintenance (West-Eberhard, 1989). Indeed, Grafen (1990) recently suggested that most examples of kin recognition have nothing to do with the identification of kin per se.

The study of recognition behavior is confounded by the problem of determining which recognition system is being expressed. Many animals can discriminate between different classes of objects or locations, such as self and nonself (Scofield et al., 1982), kin and nonkin (Grosberg and Quinn, 1986), conspecific and nonconspecific (Paterson, 1982), host and nonhost (Jaenike, 1988), natal site and nonnatal site (Fisher, 1971). Recognition of novel objects or locations may be unlearned (as in many forms of self recognition) or learned. Learned recognition entails that an animal learns cues associated with itself, its conspecifics, or its environment and then matches the memory of the previously learned cues with cues associated with the novel object or location (Sherman and Holmes, 1985). The critical question is: if we observe recognition behavior, can we necessarily conclude that it is maintained evolutionarily because of the benefits of identifying that object per se? For kin recognition, many researchers answer yes because of the presumed advantages of dispensing altruism toward kin or of striking an optimal balance between inbreeding and outbreeding (e.g., Hepper, 1986; Wilson, 1987). But what if the kin-biased behavior simply involves animals preferen-

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tially orienting toward kin, as is most often the case? Animals may affiliate with kin because kin bear familiar cues; i.e., cues that correlate highly with those learned early in ontogeny. Without further information, however, we cannot conclude that associating with familiar cues has been selected because of the advantages of associating with familiar conspecifics (kin) any more than we could conclude that this behavior has been selected because of the advantages of associating with, for example, familiar habitat. To determine which recognition system is being expressed predominantly requires not only experimental manipulation of recognition cues but also a knowledge of the fitness consequences of recognition in the various recognition systems.

Here, I examine the adaptive significance of the well-documented tendency of anuran tadpoles to associate preferentially with kin both in the laboratory and in the wild (reviewed in Waldman, 1986; Blaustein et al., 1987*a*). Tadpoles have become a model organism for the study of vertebrate kin recognition. Recognition in tadpoles is assayed as a tendency to affiliate with kin (Table 1). While the mechanism of tadpole kin recognition is well understood (i.e., tadpole recognition involves matching), the adaptive significance of tadpole kin associations has eluded biologists (Blaustein et al., 1987*b*; Waldman et al., 1988; West-Eberhard, 1989). The predominant view is that consorting with conspecifics in general and kin in particular is selectively favored since group formation is thought to promote increased feeding efficiency (Bragg and King, 1961; Beiswenger, 1975), predator avoidance (Bragg, 1965; Black, 1970; Wassersug, 1973; Waldman and Adler, 1979; Brodie and Formanowicz, 1987; Hews, 1988), and enhanced development (Foster and McDiarmid, 1982; Blaustein, 1988; Waldman, 1988). An alternative view is that kin associations reflect selection to affiliate with a particular habitat or food type (O'Hara, 1981; O'Hara and Blaustein, 1982, 1985; Waldman et al., 1988). Conclusive support for either of these nonmutually exclusive hypotheses is lacking.

Using tadpoles of the Southern spadefoot toad (*Scaphiopus multiplicatus*), I tested the hypothesis that tadpole kin associations may reflect selection for tadpoles to orient toward their natal habitat and perhaps not necessarily toward kin per se. The rationale for the experiments is as follows. Kin association in tadpoles is mediated through chemical cues (Waldman, 1986). Thus, to determine what tadpoles are recognizing I modified the animal's chemical environment by feeding half the animals from each of several sibships two different diets, which presumably differed in their chemical properties: shrimp and a commercial tadpole chow. These two diets were selected to mimic the tadpoles' natural diet of freshwater shrimp (Eubranchipoda) and organic detritus, respectively. I tested kin affiliative tendencies by giving a test animal the choice between consorting with unfamiliar siblings (i.e., animals to which the test animal had not previously been exposed) that were reared on an unfamiliar diet versus unfamiliar nonsiblings that were reared on a familiar diet. This manipulation mirrored a situation that could occur in nature: spadefoot toads often oviposit both communally (i.e., separate pairs ovipositing at one site) and multiply (i.e., one pair ovipositing at more than one site in a pond) (Bragg, 1965). My null hypothesis was that modification of the habitat (i.e., diet) to which the animals were reared would not affect their ability to orient toward kin. Rejection of the null hypothesis would suggest need for an investigation into why tadpoles affiliate with cues learned from their environment early in ontogeny. Since tadpoles that associate with such cues in nature would tend to remain near their natal site, I was specifically interested in ascertaining whether tadpole philopatry is advantageous.

I found that tadpoles preferentially affiliated with cues associated with their natal (i.e., familiar) habitat, even if this meant affiliating with nonkin that had been reared in the familiar habitat over kin that had been reared in an unfamiliar habitat. Furthermore, I present evidence from a field study suggesting that tadpole philopatry is advantageous, which provides a possible selective agent promoting the tendency to affiliate with cues associated with the natal site. These findings, together with lack of empirical support for the kin selection hypothesis, suggest that tadpole kin recogni-

TABLE 1. Commonly referenced examples of kin recognition (data from Fletcher and Michener, 1987), listing the way in which recognition was assayed.

Organism	Manner in which kin recognition is expressed§	Reference
Mammals		
Yellow baboons (*Papio cynocephalus*)	1	Walters, 1981
Vervet monkeys (*Cercopithecus aethiops*)	1	Cheney and Seyfarth, 1982
Macaques (*Macaca nemestrina*)	0	Fredrickson and Sackett, 1984
Ground squirrels		
Arctic (*Spermophilus parryii*)	1	Holmes and Sherman, 1982
Belding's (*S. beldingi*)	1	Holmes and Sherman, 1982
Richardson's (*S. richardsonii*)	1	Davis, 1982
13-lined (*S. tridecemlineatus*)	0	Holmes, 1984
Mice		
Spiny (*Acromys caharinus*)	0	Porter and Wyrick, 1979
House (*Mus musculus*)	1	Yamazaki et al., 1976
White-footed (*Peromyscus leucopus*)	0	Grau, 1982
Norway rats (*Rattus norvegicus*)	0	Hepper, 1983
Birds		
Japanese quail (*Coturnix coturnix*)	0	Bateson, 1982
Bank swallows (*Riparia riparia*)	0	Beecher and Beecher, 1983
Canada geese (*Branta canadensis*)	0	Radesäter, 1976
Amphibians		
Cascades frogs tadpoles (*Rana cascadae*)	0	O'Hara and Blaustein, 1981
Red-legged frog tadpoles (*Rana aurora*)	0	Blaustein and O'Hara, 1986
Wood frog tadpoles (*Rana sylvatica*)	0	Waldman, 1984
American toad tadpoles (*Bufo americanus*)	0	Waldman and Adler, 1979
Western toad tadpoles (*Bufo boreas*)	0	O'Hara and Blaustein, 1982
Fish		
Guppies (*Poecilia reticulata*)	1	Loekle et al., 1982
Coho salmon (*Oncorhynchus kisutch*)	0	Quinn and Busack, 1985
Insects		
Honey bees (*Apis mellifera*)	1	Breed et al., 1985
Sweat bees (*Lasioglossum zephyrum*)	1	Greenberg, 1979
Paper wasps (*Polistes fuscatus*)	1	Pfennig et al., 1983
Ants (many species)	1	Breed and Bennett, 1987
Isopods (*Hemilepistus reaumuri*)	1	Linsenmair, 1987
Bryozoans (*Bugula neritina*)	0	Keough, 1984

§ 0 = kin bias is spatial proximity. 1 = kin bias in apportionment of aggressive or nepotunistic behavior.

tion may be an artifact. Tadpoles may orient toward familiar cues in nature because these cues correlate with their natal habitat; not because these cues correlate with kin per se.

MATERIALS AND METHODS

Test Animals and Rearing Procedures

Scaphiopus multiplicatus tadpoles occur as two discrete morphs: carnivores, which feed primarily on freshwater shrimp (Eubranchipoda), and omnivores, which feed on both shrimp and detritus (Pfennig, 1989). I used only omnivores in the present study.

My laboratory experiments were conducted at the American Museum of Natural History's Southwestern Research Station near Portal, Arizona. On 4 August 1988 I collected 14 amplexed pairs of *S. multiplicatus* (species identified by electrophoresis [Simovich and Sassaman, 1986]) from a natural breeding congress 0.3 km SE of Rodeo, New Mexico. I then created 14 familial full-sibships of tadpoles by artificially fertilizing the eggs extracted from females with the sperm from one male each. I partitioned each clutch of fertilized eggs among six different trays and flooded them with spring

water from a common source. Thus siblings reared in separate trays were never exposed to each other. Fifty hours later, immediately before larval hatching (Gosner stages 18–19; Gosner, 1960), I randomly selected 8 embryos (with egg jelly) from each tray. I placed the eight embryos in each group (six groups per sibship) with their egg jelly into a 250-ml plastic cup and kept them at 30°C. I fed the three groups from each sibship twice daily 0.20 g of frozen Bay Area® brine shrimp (*Artemia*). I fed the other three groups twice daily 0.20 g of Carolina Biological Supply® *Xenopus* tadpole chow. I exposed the tadpoles to a natural photoperiod and replaced their water every third day.

Laboratory Experimental Procedures

Three laboratory experiments were begun when most tadpoles had reached Gosner stage 34 (10 days old). The basic protocol was modified from previous tadpole kin recognition studies (Blaustein and O'Hara, 1981; Cornell et al., 1989). The three experiments were aimed at determining the probable role of the environment on recognition cue learning.

I designed Experiment 1 to ascertain whether *S. multiplicatus* tadpoles preferentially associated with unfamiliar siblings over unfamiliar nonsiblings as do tadpoles of at least five other anuran species. I used unfamiliar stimulus animals to obviate effects due to prior exposure. I divided a plastic tray (38 × 15 × 5 cm) into three, equal-sized sectors with vertical 80 μm nylon mesh and flooded the tray with 750 ml of spring water. The nylon mesh separated stimulus animals from the test animal while allowing visual, olfactory, and limited tactile exchange. I removed eight stimulus animals from separate sibships from their rearing cups, thoroughly rinsed each with spring water, and placed them into each end compartment. Ten minutes later, I placed a test animal at the center of the tray and allowed the tadpole to acclimate for 10 minutes. The test animal was an unfamiliar sibling of one group of stimulus animals (i.e., they were reared in a different cup) and an unfamiliar nonsibling of the other group (Fig. 1A). Test animals and stimulus animals were matched for diet, snout–vent length, developmental stage (Gosner stages 33–36), and age (10–16 days old). Following acclimation, I continuously recorded the test animal's position for 10 minutes. The bioassay of association was the proportion of time the test animals spent on either side of the center line. All tests were blind; i.e., the observer did not know which end compartment contained the test animal's siblings. I used test animals once only. I used stimulus animals multiple times, though only once per day and only after they had been rinsed thoroughly with spring water and left overnight in their rearing cups. I used animals from all 14 sibships in the experiments. I rinsed the test trays with water after each trial and rotated them to obviate effects due to lighting or temperature differences. I conducted 20 trails from 24–29 August 1988 between 0900 h and 1700 h under natural photoperiod.

In Experiment 2, I was interested in ascertaining whether tadpoles would learn to associate with whatever cues to which they were exposed early in ontogeny, regardless of whether the cues were genetically or environmentally derived. My procedures for this experiment were the same as those used in Experiment 1 with the following modifications. I replaced stimulus animals with water that had been "treated" with either tadpole chow or *Artemia*. I obtained treated water by placing 10 g of either food type in 2.5 liters of spring water for 10 minutes and then filtering this water through a 120 μm mesh net. I poured the treated water into one of two 250 ml cups positioned at each end of the test tray. I placed one end of a flexible plastic tube inside both cups. I placed the other (distal) end into one of the two end compartments of the test tray. I capped the distal end with a hypodermic needle protective cover that had a 1 mm hole punched in it. Creating a vacuum on the distal end caused water to drain from the cups into the test tray at approximately 60 ml/min. I then placed a test animal in the center of the test tray (Fig. 1B). Test animals in this experiment, as in all three laboratory experiments, were fed the morning of the test. Thus, different satiation levels could not account for differences between the results of the first two experiments. I allowed

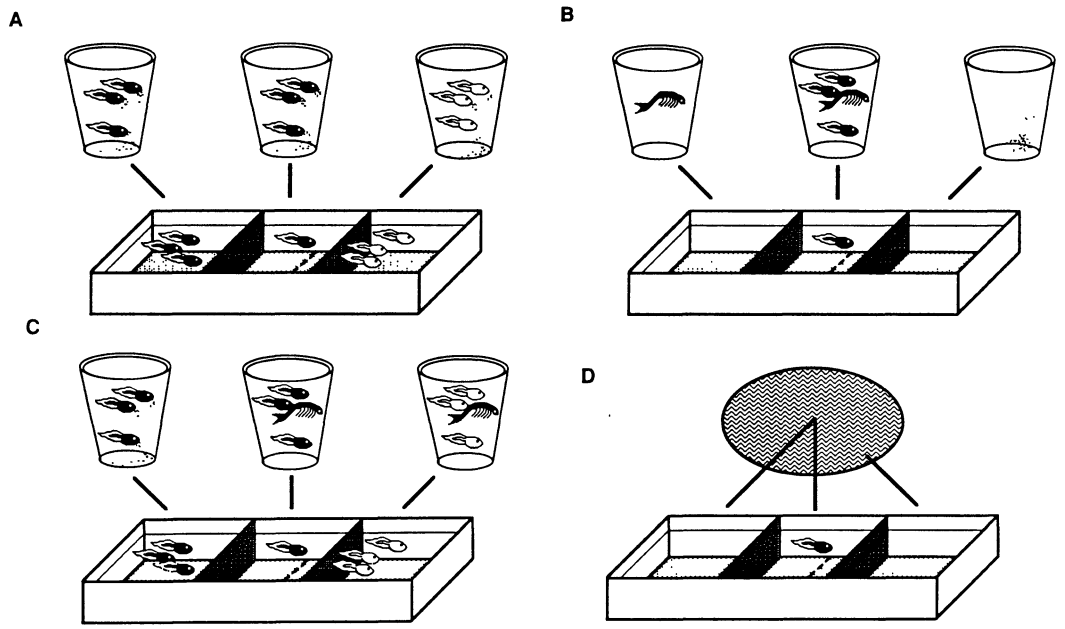

FIG. 1. Diagrammatic representations of the experimental setups used to assay tadpole associational behavior in Experiments 1–4. The basic apparatus consisted of a plastic tray divided into three, equal-sized compartments by nylon mesh. The test animal was placed in the center compartment. The bioassay of association was the proportion of time the test animal spent on either side of center. A) In Experiment 1 eight animals (one group of which were unfamiliar siblings of the test animal, the other of which were unfamiliar nonsiblings of the test animal) were placed in each end compartment. In half the trials, all animals had been reared on tadpole chow; in the other half all had been reared on shrimp. B) In Experiment 2 stimulus water (one type of which was familiar to the test animal, the other type of which was unfamiliar to the test animal) was drained from the cups into each end compartment. C) In Experiment 3 the setup was the same as Experiment 1 except the test animal had been reared on the same diet as the unfamiliar nonsiblings, but on the opposite diet as its unfamiliar siblings. In half the trials the test animal and nonsiblings were reared on tadpole chow; in the other they were reared on shrimp. D) In Experiment 4 the setup was the same as Experiment 2 except the test animal was given a choice between associating with water from its capture site and water from elsewhere within the same pond. Trials were run simultaneously in pairs such that the familiar water for one member of the pair was the unfamiliar water for the other.

the test animal 10 minutes to acclimate before continuously observing its position for 10 minutes. I conducted 20 trials from 25–30 August 1988 between 0900 h and 1700 h under natural photoperiod.

In Experiment 3, I mimicked the situation in which a tadpole (the "discriminator") was faced with the choice of joining an aggregation composed of one of two different types of tadpoles: (1) unfamiliar siblings that had been exposed to a habitat unfamiliar to the discriminator (simulating an instance in which some of the discriminator's siblings were oviposited in a different area of the pond than was the discriminator), and (2) unfamiliar nonsiblings that had been exposed to a habitat familiar to the discriminator (simulating an instance in which the nonsiblings were oviposited near the discriminator's egg mass). The purpose of this experiment was to determine if environmentally derived recognition cues were transferrable to nonrelated conspecifics. Procedures for Experiment 3 were the same as those for Experiment 1 with the following exception. The test animal had been reared on the opposite diet of the unfamiliar siblings in the stimulus compartment but on the same diet as the unfamiliar nonsiblings in the opposite stimulus compartment (Fig. 1C). I conducted 16 trials from 31 August to 4 September 1988 between 0900 h and 1700 h under natural photoperiod.

Field Experimental Procedures

I conducted field experiments in two ephemeral ponds: a natural playa lake 27 km west of Lordsburg, New Mexico (ele-

vation ~1,000 m) and a manmade cattle tank 3 km east of Portal, Arizona (elevation ~1,500 m). The playa lake was roughly circular (~40 m diameter) with a maximum depth of 21 cm. The playa's clay and silt substrate was coated with a thin layer of bacteria and algae. *Scaphiopus multiplicatus* oviposited on emergent twigs at both the playa's edge and center. The playa supported a large population of fairy shrimp. The cattle tank was shaped roughly like an equilateral triangle (7 m on a side) with a maximum depth of 16 cm. The pond's sand and gravel substrate was covered in places by dense masses of filamentous algae. On 8 August 1988 a rainstorm filled the previously dry cattle tank, and a single pair of *S. multipicatus* spawned at this site. I observed no other anurans breeding in the pond on this or on the subsequent night.

I designed Experiment 4 to ascertain whether tadpoles in the wild preferentially associated with water from their capture site (familiar water) over water from elsewhere within the same pond (unfamiliar water), implying that the laboratory experiments could be extrapolated to the field. On 4 September 1988, I placed next to the playa two of the experimental apparati described in Experiment 2. From the center of the playa I collected a solitary omnivore (Gosner stages 34–37) and two liters of water. I then collected a solitary omnivore of the same developmental stage and approximate size as the first tadpole and 2 liters of water from the playa's edge. Within 10 minutes of capture I placed the two tadpoles into separate test trays with 250 ml of spring water. While the animal was acclimating to the test tray, I used a 120 μm mesh net to filter the water from each of the two capture sites. Ten minutes after placing the tadpoles in the test trays, I filled a plastic cup on both ends of each test tray with 250 ml of filtered water from each of the two capture sites. As in Experiment 2, I used a tube to drain water slowly from the two cups into the end compartments of each test tray (Fig. 1D). I arranged the trays facing in opposite directions so that if both tadpoles associated with familiar water, they would swim to opposite ends. I conducted each pair of trials simultaneously and gave the two tadpoles a choice between water from the same two sites (i.e., edge and center). I recorded the tadpoles' positions continuously for 10 minutes. I rinsed the test trays with water after each trial and rotated them to obviate effects due to lighting or temperature differences. I conducted 17 trials from 4–5 September 1988 between 1000 h and 1700 h.

Both the laboratory and field experiments suggested that tadpoles orient toward familiar cures, regardless of the cues' origin (see Results). Since tadpoles that associate with cues learned in their environment at birth would tend to remain at their natal site I investigated the advantages, if any, of philopatry. Within 12 hours of when the single pair of *S. multiplicatus* had oviposited in the cattle tank, I transferred the eggs to the laboratory and placed them in a 5-liter container filled with aerated spring water. I fed the tadpoles a commercial tadpole chow ad libitum for one week and exposed them to a natural photoperiod and temperature (range = 19°C at night and 27–31°C at midday). Rearing tadpoles in the laboratory for one week allowed me to create randomly 12 different groups of 20 tadpoles that had roughly the same snout–vent lengths and developmental stages (Gosner stages 29–31) for release into their natal pond.

I created twelve field enclosures by cutting out the bottoms of 39 × 27 × 14 cm clear plastic Rubbermaid® storage boxes. I punched holes (~1 mm diameter) in all sides to allow water exchange. I arranged six enclosures radially such that one end of each was within 10 cm of the oviposition site (50–150 cm from shore, water depth = 10–12 cm). Using a random number generator, I deployed randomly the remaining six enclosures at nonoviposition sites (20–250 cm from shore, water depth = 5–14 cm) (Fig. 2). I randomly assigned each group of 20 tadpoles to one of the enclosures and released them into the enclosure at a density that fell within the range of tadpole densities found in the field (Pfennig, 1989). An opaque plastic cover moderated interior temperature and excluded predators (In a sympatric congener, *S. couchii,* predation was the primary cause of tadpole mortality in only 16 of 82 natural ponds examined [Newman, 1987]). After three weeks (the time at which the first metamorphs were expected) I removed the survivors and immediately

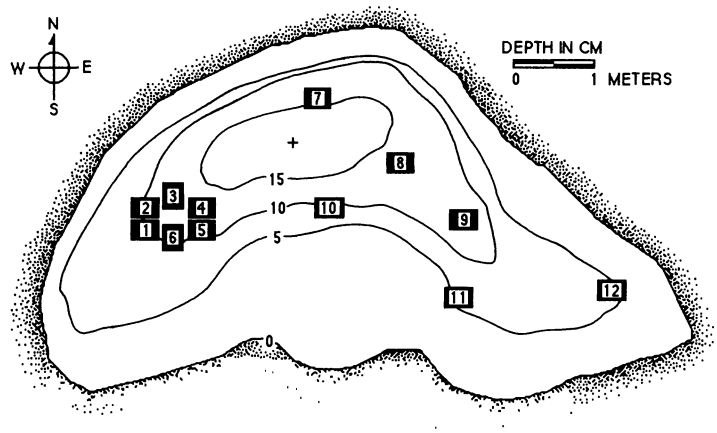

FIG. 2. Bathymetric map (depth contours in centimeters) of pond in which 12 field enclosures (black rectangles), each containing 20 tadpoles, were placed to investigate the advantages of tadpole philopatry. Six enclosures (nos. 1–6) were placed within 10 cm of their oviposition site; the other six (nos. 7–12) were dispersed at randomly selected sites.

weighed them (live wet weight) and recorded their developmental stages.

Field Censusing Procedures

To determine if tadpoles are philopatric, I censused 14 natural ponds near Portal, Arizona to compare tadpole density at oviposition sites and at randomly selected nonoviposition sites within each pond. Although sibship identities were unknown, high tadpole density near oviposition sites for weeks following hatching was taken as circumstantial evidence of tadpole philopatry. All ponds surveyed were cattle tanks similar to the pond described above. I identified oviposition sites by mapping locations of egg masses within two days after *S. multiplicatus* had bred in a pond. I chose nonoviposition sites by randomly selecting a number between 0–360 and, with a compass oriented toward the pond's center, walking around the pond's periphery until the compass direction matched the random number. The nonoviposition site sample was the point at which the water depth was equal to that at the oviposition site. I conducted censuses by tossing into the pond at the predetermined site a portable 0.6 × 0.6 × 0.3 m quadrat sampler. The sampler, which had an open top and bottom, sank quickly, trapping any tadpoles within its confines. I then used a net to sweep out all tadpoles. I alternated the order of sampling so that oviposition sites were sampled first at one census and second at the next. I sampled the 14 ponds every 4 days, up to day 20 (when metamorphosis began).

Statistical Analyses

In Experiments 1–4, which were designed to examine associational preferences, my null hypothesis was that the test animal would move about the test tray randomly, spending half the time orienting toward either end compartment. I compared the proportion of time (out of 10 minutes) the test animal spent on the side of the test tray closer to the end compartment that contained its unfamiliar siblings/familiar water with 0.50, the value expected under the null hypothesis. Since the data were appropriately distributed for a parametric test, I employed a one-sample t-test. The P values in Experiments 1–3 were based on a two-tailed test. The P value in Experiment 4 was based on a one-tailed test since I made the a priori prediction (based on the results of the previously completed laboratory experiments) that wild-caught tadpoles would favor familiar water. In the field censuses, I treated data from the two sample sites within each pond (oviposition and nonoviposition sites) independently for statistical analysis since the total numbers of tadpoles in each pond (~9,000–14,000 tadpoles) were large relative to the numbers of tadpoles actually cen-

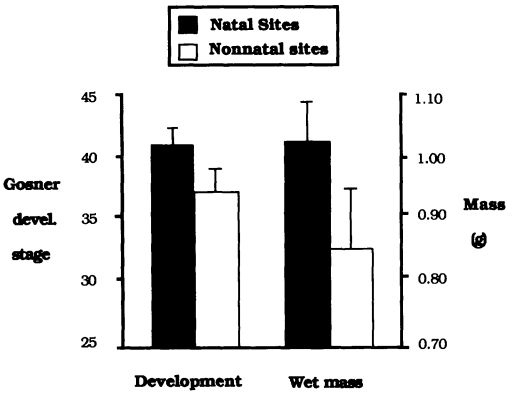

FIG. 3. Mean (±1 SEM) development and growth rates of tadpoles restricted to their natal site compared with that of their siblings restricted to nonnatal sites within the same pond. Development and growth rates at the two types of sites differed significantly at $P < 0.05$ (two-tailed paired-comparisons t-test, $N = 6$ for each pair of bars).

TABLE 3. Analysis of variance of tadpole development (Gosner developmental stage) and growth (wet weight of Gosner stage 39 animals) by rearing location (natal or nonnatal site) and water depth (shallow or deep). Water depth was classified acccording to whether the initial water depth at the center of the 12 enclosures shown in Fig. 2 was shallow (≤10 cm, $N = 6$ enclosures) or deep (>10 cm, where 10 cm was the mean water depth of all 12 enclosures).

Source of variation	*d.f.*	MS	*F*	*P*
Gosner developmental stage				
Location	1	24.368	22.738	0.001
Water depth	1	0.241	0.225	0.648
Location × water depth	1	2.707	2.526	0.151
Residual	8	1.072		
Wet weight				
Location	1	0.06	6.272	0.037
Water depth	1	0.013	1.32	0.284
Location × water depth	1	0.002	0.251	0.63
Residual	8	0.01		

sused. To compare the numbers of tadpoles at each type of site within 14 different ponds, I used a two-tailed paired comparison t-test.

RESULTS

As shown in Table 2, *S. multiplicatus* tadpoles displayed a greater tendency to associate with unfamiliar siblings over unfamiliar nonsiblings. However, these tadpoles also favored unfamiliar nonsiblings that were reared on familiar food over unfamiliar siblings that were reared on unfamiliar food (Table 2). In fact, test animals spent a significantly greater proportion of time on the side of familiar food (0.81 ± 0.24, mean, SD) than on the side of unfamiliar siblings (0.67 ± 0.19; $P < 0.05$, two-tailed t-test, $N = 20$ trials each). Similar associations were observed in the field: wild-caught tadpoles favored water from their capture site over water from elsewhere in the same pond (Table 2).

Tadpoles restricted to their natal site developed and grew a significantly greater amount than their siblings restricted elsewhere within the same pond (Fig. 3). Twenty-two of the 120 tadpoles restricted to their natal site metamorphosed by the end of the experiment; none of the tadpoles limited to nonnatal sites had yet metamorphosed. Moreover, all 120 tadpoles restricted to their natal site were alive when the experiment was terminated whereas only 102 of 120 tadpoles restricted to nonnatal sites were alive.

One possible explanation for the observed differences in tadpole growth and survivorship between the two types of location (natal and nonnatal sites) was that there was greater variation in water depth among enclosures at nonnatal sites than among enclosures at natal sites. This potentially could have contributed to differences

TABLE 2. Tadpole preferences in experiments 1–4.

Exper. no.	No. of trials	Mean proportion of time test animal spent on each side ±1 SD	
1	20	unfam. sibs (0.67 ± 0.19)**	unfam. nonsibs (0.33 ± 0.19)
2	20	famil. water (0.81 ± 0.24)***	unfam. water (0.19 ± 0.24)
3	16	unfam. sibs/unfam. water (0.38 ± 0.12)	unfam. nonsibs/fam. water (0.62 ± 0.12)**
4	17	water from capture site (0.59 ± 0.18)*	water from noncapt. site (0.41 ± 0.18)

*** $P < 0.0001$, two-tailed t-test; ** $P < 0.001$, two-tailed t-test; * $P < 0.03$, one-tailed t-test (values indicated by asterisks significantly >0.5, value expected under random movement).

between the different locations since tadpole growth and survivorship correlate with water temperature (which, in turn, correlates with water depth). However, as shown in Table 3, variation in water depth between natal and nonnatal sites did not account for the variation in tadpole growth and survivorship at the two locations. Differences in algal abundance between sites was a more likely cause of these differences. Benthic algae was markedly denser at the natal site than at the nonnatal sites.

Finally, mean tadpole density was significantly greater at oviposition sites than at randomly chosen nonoviposition sites within the same pond for up to 12 days after oviposition (Fig. 4).

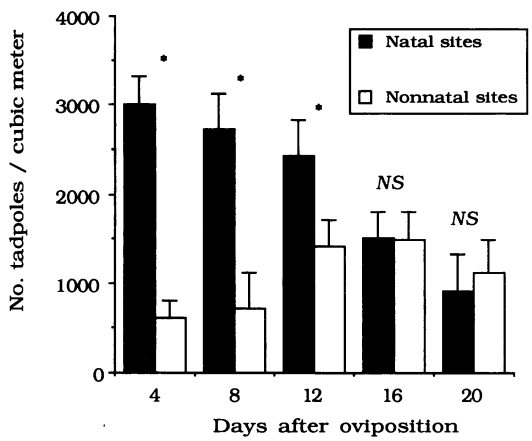

FIG. 4. Mean (±1 SD) tadpole densities at oviposition sites and at nonoviposition sites in 14 natural ponds. Asterisks indicate that mean tadpole densities at the two types of sites differed significantly at $P < 0.05$ (two-tailed paired-comparisons t-test, N = 14 for each pair of bars) up to day 12. The first metamorphs began appearing by day 20.

DISCUSSION

Experiments that document kin affiliative behavior, whether conducted in the laboratory or in the field, may reflect the test animals' preference for specific food or habitat types and not for kin per se. *Scaphiopus multipicatus* tadpoles displayed stronger spatial association with water strained through food on which they were reared (familiar food) than they did with unfamiliar siblings reared on the same food. Tadpoles even preferred unfamiliar nonsiblings reared on familiar food over unfamiliar siblings reared on unfamiliar food. The field results suggested that these laboratory preferences were not artifacts: wild-caught, solitary tadpoles favored water from their capture site over water from elsewhere within their pond. It is unlikely that these wild-caught animals were orienting toward recognition cues produced by conspecifics. Test animals were not in aggregations when captured, and recognition cues emanating from conspecifics do not persist in the absence of tadpoles producing such cues (Dawson, 1982; Waldman, 1985).

Scaphiopus multiplicatus tadpoles, as do many other animals (Sherman and Holmes, 1985), apparently *learn* recognition cues early in ontogeny since these tadpoles showed the strongest association toward familiar environmental cues to which they were exposed only after hatching. Tadpoles that associate with cues learned in the environment at hatching would tend to remain near their natal (oviposition) site even it they occasionally drifted away because of floods, predators, or foraging. Such behavior would be advantageous if breeding adults assess larval environment quality as suggested by the finding that natal sites in some anurans contain fewer predators (Howard, 1978, 1980), more suitable water temperature (Seale, 1982), and more suitable water pH (Gascon and Planas, 1986) than do nonnatal sites in the same pond.

As illustrated in Figure 3, tadpoles restricted to their natal site developed and grew a significantly greater amount than their siblings restricted elsewhere within the same pond. Thus, tadpole philopatry may be advantageous. This finding, together with the laboratory results (Table 2) indicating that tadpoles would likely prefer their natal site, suggest that selection favoring philopatry could account for tadpole kin association.

Why do tadpoles not respond directly to environmental cues that promote growth and development rather than to secondary factors such as philopatry that may be correlated with these cues? In other words, if high algal counts, high temperatures, and high oxygen levels, and so on are important, why do tadpoles not respond to these factors directly? First, there may be a cost of assessment. Tadpoles may operate according to the rule of thumb: swim back to the natal

site if swept away in a flood or if chased by a predator because the natal site is the one location that the tadpole "knows" contains more food, etc. It may take the tadpole longer to assess different regions of the pond. Second, this sort of rule of thumb would not require the tadpole to assess each important ecological factor separately. Third, factors such as predation pressure may not be assessable (or not before it is too late, anyway).

Are Tadpoles Philopatric?

One prediction of the philopatry hypothesis is that aggregations should be restricted to oviposition sites. *Scaphiopus multiplicatus* schools tended to remain near oviposition sites: mean tadpole density was significantly greater at oviposition sites than at randomly chosen nonoviposition sites of similar water depth within the same pond (Fig. 4). Unfortunately, sibship identities of these tadpoles were unknown, so it is unclear if these tadpoles were philopatric or if different sibships moved from one preferred location to another. Interestingly, the tendency to associate with oviposition sites diminished with time (Fig. 4), as does the tendency to associate with kin in the laboratory in *Rana aurora* tadpoles (Blaustein and O'Hara, 1986). Perhaps natal habitats become less desirable with time because of food depletion or predator accumulation.

Data from previous experiments where sibships were marked and released in the field do not suggest philopatry. Waldman (1982) found that sibling schools of *Bufo americanus* moved throughout test ponds. O'Hara and Blaustein (1985) found that while *Rana cascadae* aggregations occurred repeatedly in the same area of the pond, there was no significant correlation between pond location and aggregation identity. However, in both experiments young tadpoles were reared under uniform environmental conditions in the laboratory. Thus, test animals had no opportunity to learn about and hence develop preferences for slightly disparate environmentally-based cues associated with different pond regions. That sufficient intrapond variation in recognition cues exists to permit discrimination of different pond regions was demonstrated in Experiment 4 of this investigation. Results of experiments controlling for differences in environment simply imply that tadpoles prefer whatever cues they encounter early in ontogeny, regardless of whether these cues are environmentally or genetically based. Thus, while tadpoles reared under common laboratory conditions would be expected to associate with genetically similar (hence familiar) siblings, they would not be expected to prefer any region of a pond over another. Tadpoles prefer recognition cues learned early in ontogeny, regardless of the cues' origin, either from themselves (in the absence of external cues) or from egg jelly. This finding is consistent with results of experiments demonstrating full or paternal half sibling recognition in tadpoles reared in social isolation (Blaustein and O'Hara, 1981; O'Hara and Blaustein, 1981; Waldman, 1981) and full sibling recognition in tadpoles with switched egg jelly (Blaustein and O'Hara, 1982).

The Probable Role of Kin Selection in Shaping Tadpole Kin Association

Kin selection is often implicated as the primary selective force shaping tadpole kin association behavior. The present study does not demonstrate that kin selection is not important in maintaining tadpole kin aggregations. In fact, the kin selection hypothesis has not even been tested for tadpoles. The present study does, however, provide support for a nonmutually exclusive alternative explanation (i.e., selection favoring philopatry) that can account for the same phenomenon.

Selection favoring philopatry may be a more critical factor than kin selection for the evolutionary maintenance of kin associations in species such as *S. multiplicatus* for the following reasons. These tadpoles showed a stronger preference for familiar environmental cues than for familiar genetic cues, and environmental cues may be unreliable predictors of genetic relatedness in anurans such as *S. multiplicatus* that oviposit both communally and at multiple sites (Bragg, 1965; pers. obs.). Because siblings often occur separately and are exposed to different environments, tadpoles may fail to associate with some siblings (thereby committing a rejection error; Reeve, 1989). More importantly, the present investigation dem-

onstrates that tadpoles would favor any conspecific that had been exposed to common environmental cues (thereby committing an acceptance error; ibid.). The probability of committing a recognition error increases concomitantly with both the number of sites at which each female oviposits and the number of sibships deposited at each site. To take an extreme case, suppose that the number of sites at which each female oviposits is equal to her clutch size, such that each female oviposits one egg per oviposition site. If females oviposit communally (and if self learning or recognition alleles are not present or are overriden by the learning of environmental cues) individuals will preferentially associate with the nonsiblings with whom they are reared. Another reason for doubting kin selection as the primary agent favoring kin associations among *S. multiplicatus* tadpoles is that omnivores cannibalize siblings and nonsiblings at an equal rate in the laboratory, even when well-fed (Pfennig, unpubl.). Kin selection should favor reduction in sibling cannibalism if the sensory machinery to discriminate siblings were present.

Once kin are brought together at their natal site kin selection may favor schooling. Some tadpoles possess a lateral line system, which they use to form cohesive aggregations with conspecifics (Wassersug, 1973; Katz et al., 1981). Schooling is maintained by visual cues in light and by lateral line input in darkness, with vision as the primary mechanism (Wassersug, 1973; Katz et al., 1981). Visual cues may provide additional input into recognition of the natal site. Substrate preference has been documented in tadpoles of *Rana aurora, R. cascadae* (Wiens, 1970) and in *Kaloula pulchra* (Punzo, 1976, cited in Duellman and Trueb, 1986 p. 170). Substrate patterns are learned early in life (Wiens, 1970).

Do Tadpoles and Other Gregarious Animals Recognize Kin?

The theoretical framework provided by kin selection theory has motivated the discovery of numerous examples of surprisingly sophisticated kin-biased behavior (reviewed in Fletcher and Michener, 1987). However, the fact that animals have extremely refined abilities to discriminate among different classes of conspecifics based on relatedness should not be construed as evidence that the kin-biased behavior arose and is being maintained evolutionarily as a mechanism for discriminating kin. As evidenced by the results of the present study, many examples of "kin" recognition (e.g., see Table 1) may be partially or entirely a manifestation of some other recognition system (Grafen, 1990).

For example, as in tadpoles, the ability of newly metamorphosed laboratory-reared anurans to associate with familiar odors borne by kin (Blaustein et al., 1984; Cornell et al., 1989) many reflect selection for philopatry. In newly metamorphosed anurans, orienting toward familiar cues may lessen the risk of desiccation, since familiar cues correlate with the natal pond. Creusere and Whitford (1976) found that recently metamorphosed *Scaphiopus* remained near their natal pond for up to 55 days after metamorphosis. In older adults, orienting toward familiar cues may help locate breeding sites. Adult anurans have well-developed olfactory discriminatory abilities (Grubb, 1971 and references therein), and there is evidence of philopatry among adult anurans (*Bufo bufo*: Heusser, 1969; *B. valliceps, B. woodhousei fowleri, Pseudacris clarki, P. streckeri*: Grubb, 1971; *Rana sylvatica*: Berven, 1981; *B. w. fowleri*: Breden, 1987).

The use of spatial association to assess kin recognition—and to then infer a selective basis for identifying kin—is not restricted to anurans (e.g., see Table 1). Ascertaining whether kin-biased behavior is maintained selectively to direct altruism toward kin or whether it is a fortuitous outgrowth of a different adaptation is critical for understanding the evolution of social behavior. A complete understanding of the adaptive significance of recognition behavior entails resolving the fitness consequences of the behavior.

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