SIBLING ASSOCIATION AMONG SCHOOLING TOAD TADPOLES: FIELD EVIDENCE AND IMPLICATIONS

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Abstract. The results of recent laboratory studies suggest that the ability to recognize kin may be a widespread phenomenon among diverse animal groups, but the question of how such recognition abilities influence individuals' behaviour under natural conditions has not always been considered. As an assay for sibling recognition, I measured the sibship composition of experimental schools formed by tadpoles of the American toad (*Bufo americanus*) in their natural habitat. Sibling cohorts were obtained from amplectant pairs in the laboratory and reared in groups either (1) in separate tanks, apart from non-siblings; or (2) in a common tank, separated from non-siblings by a screen partition across which water could pass. Tadpoles were dye-marked to indicate sibship identity. Pairs of sibling groups were then mixed together in a bucket and released in natural outdoor ponds, where they formed schools. I found significant differences in sibship composition among schools in 79% of all sampling periods; overall, 64% of the schools sampled were significantly biased in favour of one or the other sibship. The formation of sibling schools appears to result from a behavioural recognition mechanism rather than from differential habitat selection. Tadpoles preferentially formed schools with familiar siblings over both familiar and unfamiliar non-siblings, suggesting that sibling discrimination is not based on familiarity alone. Although experience may affect the ontogeny of sibling recognition, sibling preferences are apparently formed early in development, perhaps prior to hatching. Grouped individuals may in some situations increase their inclusive fitness by associating with kin: aposematic advertisement, alarm signalling in response to predators' attacks, and kin-influenced growth regulation are suggested as three specific advantages conferred by the formation of sibling schools.

Tadpoles of many anuran amphibians aggregate in social groups generally similar in form to fish schools (reviewed in Wassersug 1973). Some aggregations may form as larvae individually respond to microclimatic gradients (Brattstrom 1962; Beiswenger 1977), but social factors probably are important for the maintenance of these aggregations (Beiswenger 1972; Waldman, unpublished data). Moreover, larvae of at least two anuran species preferentially associate with siblings in laboratory tests (*Bufo americanus* (Waldman & Adler 1979; Waldman 1981), *Rana cascadae* (Blaustein & O'Hara 1981)), suggesting that tadpole schools might consist of kin groups. In this paper, I present evidence that tadpoles of the American toad (*B. americanus*) do form sibling schools in the field, discuss the mechanism by which tadpoles recognize siblings, and suggest some factors that may favour schooling with one's siblings.

Tadpoles that school, whether with kin or non-kin, may gain many of the advantages conferred by group living (Alexander 1974; Bertram 1978). Increased feeding ability or decreased predation risk appear the most likely advantages for schooling tadpoles. Tadpoles can collectively stir food material from the substrate,

creating local areas of food abundance and thus facilitating feeding (Richmond 1947; Bragg 1965; Beiswenger 1972). Anti-predator advantages have not been as well documented for tadpoles, but several mechanisms are possible: schooling individuals may benefit by concealment from predators, increased capabilities to detect and evade predators, or by confusing or satiating predators (reviewed in Radakov 1973; Shaw 1978; Hobson 1979). Some schooling fishes suffer less predation than their solitary conspecifics (e.g. Neill & Cullen 1974; Seghers 1974; Major 1978); presumably other schooling organisms gain similar advantages.

Although the propensity to school, even with unrelated conspecifics, may thus be selectively advantageous, individuals that preferentially associate with kin might accrue additional benefits. For instance, if schooling has evolved in part as a 'selfish herd' response to predators (Williams 1964; Hamilton 1971), individuals consistently located at the edge of a school (perhaps because larger conspecifics displace them) might be more vulnerable to predation than they would be alone outside the school. Unless they are somehow compensated for their added risk, these peripheral individuals should

then leave the school to increase their direct (i.e. individual) fitness. However, if related to those in the centre that they shield, peripheral individuals might maximize their inclusive fitness by remaining in the school (see Alexander 1974; West Eberhard 1975). Kinship may thus be an important component of gregarious behaviour under some circumstances.

Other phenotypically 'altruistic' traits may also be favoured in individuals that associate with kin. The skin of *Bufo* tadpoles contains high concentrations of bufodienolides which may deter predators (Flier et al. 1980), and toad tadpoles are apparently distasteful to some potential predators (Voris & Bacon 1966; Heusser 1971; Cooke 1974). Toad tadpoles are coloured black, and form conspicuous, densely packed schools in open areas of ponds. Their gregariousness, distastefulness, and conspicuousness suggest that schooling may serve an aposematic function (Wassersug 1973). Because kin frequently share alleles, noxious chemicals or warning coloration, even if ineffective in causing a predator to release prey alive, can be selected for if as a consequence of taking prey, the predator develops an aversion to proximate conspecifics (or those similar in appearance to the distasteful prey) and then avoids taking the prey's kin (Fisher 1930; Hamilton 1964).

Generally, alleles encoding traits that do not enhance an individual's direct fitness but do increase its inclusive fitness should spread where kin groups exist, either as the result of highly structured populations or because individuals behaviourally discriminate between kin and non-kin. Although empirical work pertaining to how these factors operate in natural populations has been sparse, recent laboratory studies suggest that the ability to recognize kin may be a widespread phenomenon among diverse taxa (reviewed in Dawkins 1982; Holmes & Sherman 1982). This study was undertaken to investigate the sibship composition of toad tadpole schools in natural field conditions, as a basis for examining the possible adaptive value of kin association among tadpoles.

Methods
Study Animals
Fifteen pairs of *B. americanus* were collected in amplexus at three breeding ponds in Tompkins County, New York during May and June 1978 and 1979. Each pair spawned in a separate 10-litre plastic bucket, filled with 5 litres of dechlorinated tap water, in the laboratory.

Toad eggs are externally fertilized; thus determination of parentage is unambiguous (see Waldman 1981).

After spawning was complete, clutches were reared either in separate 75-litre glass tanks (75 × 30 × 30 cm) in the laboratory or within 220-litre fibreglass screen enclosures (122 × 30 × 60 cm, 0.5 mm screen mesh) in larger outdoor wooden tanks (244 × 60 × 60 cm). Although all clutches were reared separately from one other, in the outdoor tanks water flowed between rearing compartments, allowing different sibships to have some exposure to each other. Under both rearing regimes, tadpoles were fed boiled spinach ad libitum daily. Tadpoles in the laboratory were kept on a L:D 14:10 photoperiod (overhead fluorescent lamps), and those reared outdoors were exposed to the natural photoperiod (approximately L:D 14:10).

Test Ponds
Eight natural ponds were used, ranging in area from 150 to 494 m², with a maximum depth of 0.5 m. These shallow pools were ephemeral, and during some periods many dried completely, causing several experimental tests to be terminated earlier than scheduled. Water was clear, and the substrate was of a light sand colour, making the tadpoles visually conspicuous. Potential predators present in the ponds (see Brockelman 1969) included newts (*Notophthalmus viridescens*), salamander larvae (*Ambystoma maculatum*), various water bugs and beetles (e.g. dytiscid larvae and adults), odonate nymphs, leeches, crayfish, snapping turtles, and small fish that had been trapped as flooding of a nearby creek subsided. Predation by avian or terrestrial predators was also possible (Beiswenger 1981), but never witnessed. Although clutches were not obtained from parents collected in test ponds, toads had bred in these ponds earlier during the season, thus ensuring that tadpoles were tested in natural habitat. However, most tadpoles present in these ponds had metamorphosed prior to experimental releases, and any remaining tadpoles were removed prior to the beginning of an experiment.

Testing Procedure
Six experimental tests were conducted, three with sibships reared in separate indoor laboratory tanks and three with sibships reared in separate compartments within a common outdoor tank. For each test, 2000 tadpoles (1000 belonging to each of two sibships) were marked to indicate

sibship identity, mixed thoroughly in a 50-litre bucket, and released together in the centre of a test pond. Three control tests were also conducted, in each of which 2000 tadpoles belonging to a single sibship reared together were randomly divided into two groups of 1000 tadpoles each, marked by group, and released. For all tests, tadpoles were marked immediately prior to release by placing them in 0.00025% aqueous solutions of either methylene blue or neutral red dye for 12 h. Dye solutions were freshly prepared for each test by mixing 0.05 g dye in 20 litres of dechlorinated tap water. Tadpoles belonging to one group were marked blue, and those of the other group were marked red. After marking, their group (sibship) identities were easily identifiable in the field for up to 4 weeks.

Each experimental test was conducted with a different pair of sibships, and consisted of a series of observations on the sibship composition of schools formed by these tadpoles over a 2 to 23 day period. Mean developmental stages of tadpoles introduced into the ponds ranged from 27 to 32 (Gosner 1960) for experimental and control tests. For each test, however, the different sibships used were matched for body length and developmental stage (i.e. means and variances of these parameters did not significantly differ between groups).

Data Collection and Analysis

Tadpoles released in the test ponds were monitored 24 h after their release and periodically thereafter. Observations were made between 1000 and 2000 hours in all weather conditions except heavy rain. Tadpoles formed schools virtually indistinguishable from natural schools in various areas of the ponds. Although somewhat variable in shape, all schools were characterized by definite boundaries and tadpoles within them were generally 2 cm or closer to one another. Typical schools, similar in form to the 'stationary feeding groups' described by Beiswenger (1975), are shown in Fig. 1 A, B (Plate I). Non-aggregated tadpoles (mean nearest-neighbour distance greater than 2 cm) and tadpoles aggregated in continuous narrow bands extending for several metres along a shoreline were also sometimes present in the ponds, but were not sampled.

To sample the sibship composition of each school, a wooden partition (0.5 × 0.5 m area) was quickly lowered around it before tadpoles scattered, and in most cases, more than 90% of the tadpoles in a school were trapped within the partition. All individuals contained within the partition were netted out, and their colours (sibship identities) were independently recorded by two observers. When observers disagreed on an individual's colour, e.g. because of an indistinct dye mark, that individual was not tallied (fewer than 5% of 6465 tadpoles sampled). Tadpoles were then released where they had been collected. Partitions were lowered around all schools in a pond simultaneously, and any given pond was sampled at most once daily. Thus, although schools sampled in any pond on one day contained different individuals, schools sampled in the same pond on subsequent days presumably contained some individuals that had been previously sampled.

To determine whether schools differed from one another in sibship composition, the proportions of school members belonging to each sibship were compared among schools sampled in a pond on each day. These data were treated as a $2 \times n$ contingency table, and were analysed by a model I two-way test of independence (Sokal & Rohlf 1969). Expected frequencies for each school were obtained as the products of the proportions of each of the two sibships represented in all schools sampled in the pond that day and the number of individuals in the school. Differences between observed and expected distributions were evaluated by a chi-square goodness of fit test, yielding the probability that sibships assorted similarly among schools. This analysis eliminates some possibly confounding factors. For instance, if members of only one of the two sibships in a pond showed a tendency to form schools, the null hypothesis that sibship composition was constant among schools generally would not be rejected, even though the schools sampled might differ in composition from the ratio of the two sibships present in the pond.

In addition, the numbers of members of each sibship in each school were statistically compared with those predicted by random association (binomial test, Siegel 1956), to provide an indication of which sampled schools departed from the sibship composition of the experimental population. Because equal numbers of tadpoles belonging to each sibship were released, the sibship composition of a school would not be expected to differ significantly from 50:50 if tadpoles associate indiscriminately with siblings and non-siblings, assuming equal mortality between sibships and simultaneous formation of all schools. To assess the validity of the as-

PLATE I

Fig. 1. Toad tadpole schools formed after an experimental release. Three schools of varied size along the edge of pond are shown (A), and the leftmost school is shown in greater detail (B).

sumption that different sibships suffered equal mortality, all tadpoles in the pond were collected at the conclusion of two tests, and the numbers of surviving individuals belonging to the two sibships were compared.

Data obtained from control tests were analysed in the same manner, but in each of these tests, all tadpoles belonged to a single sibship. Assortment based on mark-colour was not expected; the null hypotheses tested were (1) that proportions of red- and blue-marked siblings did not differ among schools, and (2) that each school consisted of equal numbers of red- and blue-marked siblings.

Sibship pairs used in each experimental test were obtained either from amplectant pairs collected from ponds located 6.0 or 13.2 km apart (tests 1–4) or from amplectant pairs collected from the same pond (tests 5–6). Field observations of adult *B. americanus* suggest that they move over distances of about 1 km during a season (Blair 1943; Oldham 1966; Ewert 1969). Although the movement patterns of juveniles are unknown, restricted dispersal may also be characteristic of newly metamorphosed toads (Ewert 1969). Moreover, data collected on other related species suggest that toads return with fidelity to a particular breeding pond (*B. bufo*: Heusser 1969), frequently their natal pond (*B. woodhousei fowleri*: F. Breden, unpublished data). As a result, toad pairs collected from separate, distant ponds probably are less closely related than those pairs obtained from the same pond. Thus distance between ponds of origin was also considered as a variable for analysis.

Results
Sibships Reared in Separate Tanks
In each of the three tests of sibships reared apart, the sibship composition of most schools (overall, 66%) differed significantly from that predicted by the null hypothesis of random association (Fig. 2). These 'sibling schools' appeared not to result from differential habitat preferences of the two groups, as a school's sibship composition was not predictable by the location in the pond in which it was found. In four of the six situations in which schools were directly adjacent to one another (i.e. less than 1.0 m apart measured from the centre of each school), these schools were composed largely of different sibships. For instance, in test 1, schools G (31% red, 69% blue) and I (72% red, 28% blue) were 0.7 m apart and schools J (37% red, 63% blue) and L (69% red, 31% blue) 0.5 m apart (Fig. 3).

Furthermore, two of the five schools found in approximately the same location in a pond on consecutive sampling periods were composed largely of different sibships. Thus, school B in test 1 consisted mostly of red-marked individuals, but school F sampled four days later in the same location had a preponderance of blue-marked individuals (Fig. 3). A collection of all tadpoles present in the pond on 13 July showed no significant difference in survivorship between the two sibships (310 versus 294, $P = 0.54$, binomial test, two-tailed).

Sibship composition significantly varied among schools on all sampling days of each test except the final two days of test 3 (Fig. 2). On both these days, all schools sampled departed from random in the direction of a single sibship, but towards a different sibship each day. In test 1, although sibship composition significantly differed among schools on each day, seven of the nine schools (78%) sampled on the first three sampling days but only two of the seven schools sampled (29%) on the final sampling day significantly departed from 50:50 in sibship composition. Moreover, three of the nine significant schools were biased in composition towards the sibship marked blue and the other six were biased towards the sibship marked red. Since the numbers of red- and blue-marked tadpoles remaining in the pond at the conclusion of the test did not significantly differ, individuals belonging to the sibship marked red may have had a greater tendency to school. In addition, the results of test 3 suggest that a sibship's schooling tendency might vary through time. Test 2 samples were conducted only on one day because the pond subsequently dried, causing the test to be terminated early.

Sibships Reared in a Common Tank
The sibship composition of the majority of schools sampled (overall, 62%) significantly differed from 50:50 in each of the tests of sibships reared in a common tank (Fig. 4), as in the tests of sibships reared in separate tanks. Of three cases in which schools were less than 1.0 m apart, in two these adjacent schools were composed largely of different sibships; e.g. schools T (75% red, 25% blue) and U (27% red, 73% blue) in test 4 (Fig. 5). Three of the six schools found in approximately the same location on consecutive sampling periods were composed largely of different sibships. After the last sample in test 4 (July 26), all tadpoles present in the pond were collected and their sibship
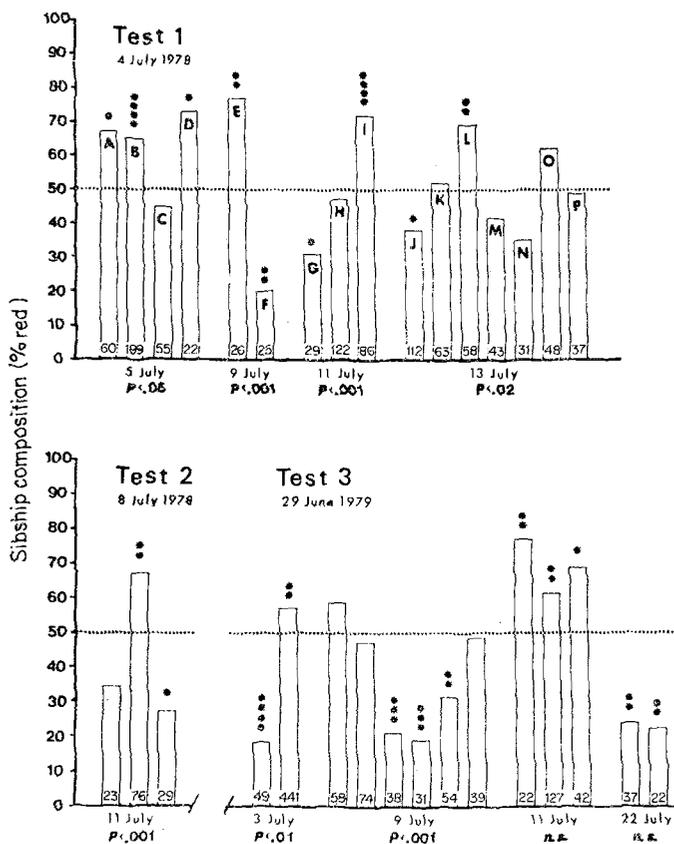
Fig. 2. Results from tests in which two sibships reared apart were released together in a pond. For each test, 1000 tadpoles belonging to each sibship were dye-marked and then released on the date indicated beneath the test number. Schools were sampled on subsequent dates (abscissa). Each school is represented by a bar, and the sibship composition of the school is indicated by the proportion of red-marked individuals in the school, individuals from one sibship having been marked red and those from the other sibship blue. The total number of tadpoles in the school is given at the base of the bar. Thus in test 1, a total of 60 tadpoles were counted in the first school sampled (labelled 'A') of which 67% were marked red (and thus 33% were marked blue). These proportions significantly differ from the 50:50 ratio expected if schools formed randomly. Proportions were tested with the binomial test, two-tailed (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$). Below each sampling date, the result of a chi-square analysis examining whether sibship composition significantly varied among schools on that date is shown.

identities recorded. No significant difference in survivorship between the two sibships was found (350 versus 378, $P = 0.32$, binomial test, two-tailed).

Sibship composition significantly varied among schools on all sampling days of each test except the final two days of test 4 (Fig. 4). In both tests 4 and 5, as in test 1, the data show some trend for fewer significant schools to be present in the pond on later sampling days. Between these two tests, nine of the 10 schools (90%) sampled on the first two days after release significantly departed from random sibship composition, but only two of the nine (22%) sampled on the final two days were significantly different from random. Samples were conducted
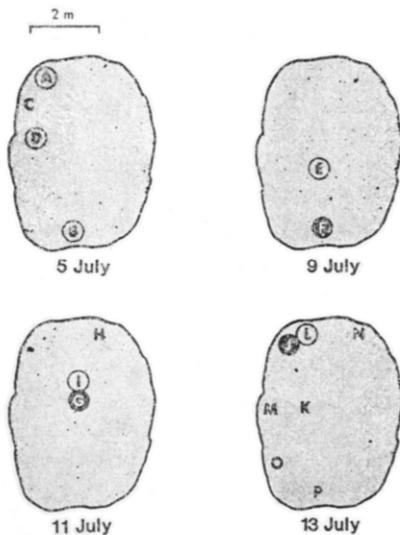
Fig. 3. The locations in the pond of all schools sampled in test 1. Each school is identified by a letter, which corresponds to that used in presenting sibship composition data shown in Fig. 2. Schools denoted by open circles were significantly biased towards one sibship, marked red; those denoted by filled circles were significantly biased towards the other sibship, marked blue.

for only two days in test 6, again because the pond dried.

Effect of Distance between 'Home' Ponds

In each of the three tests of sibships reared in separate tanks, tadpoles were obtained from amplectant pairs collected in different ponds (distance between ponds for test 1 and test 2 was 6.0 km, and for test 3 was 13.2 km). Among these tests, the sibship composition of 66% of the schools sampled significantly differed from random (Table I). Of those tests of sibships reared in a common outdoor tank, test 4 was conducted with clutches of amplectant pairs collected from ponds 6.0 km apart, and sibships tested in test 5 and test 6 were each obtained from parents collected in the same pond. Fifty-six per cent of the schools formed in test 4 significantly differed from random sibship composition, while 67% of those formed in tests 5 and 6 significantly differed from random (Table I). Overall, 63% of 32 schools sampled in the four tests of sibships with 'home' ponds at least 6 km apart, and 67% of 15 schools sampled in the two tests of sibships with the same 'home' pond, significantly differed from random sibship composition. Although these data are

partially confounded by rearing regime and reflect only two tests with sibships obtained from the same 'home' pond, they suggest that the sibship association effect is apparent regardless of the distance between the sibships' home ponds.

Controls

In three control tests of individuals belonging to single sibships but marked different colours, tadpoles formed schools as in the experimental tests. Mark-colour composition of schools did not significantly vary among schools on any sampling day, and none of the schools showed significant bias in favour of either mark-colour (Fig. 6). These results suggest that neither the marking nor testing procedures effected the results obtained in the experimental tests. No notable differences are apparent among sampling days in any control test.

Discussion

In 64% of the experimental schools but in none of the control schools sampled, sibship (mark-colour) composition departed significantly from that expected if individuals formed schools indiscriminately by group. Overall, significant differences in sibship composition among schools were found in 79% of all experimental sample periods but in none of the control sample periods. This non-random association suggests that toad tadpoles recognize their siblings under natural conditions, as has been demonstrated in laboratory tests (Waldman & Adler 1979; Waldman 1981), and that these results are not due to the marking or testing procedures. Sibling preferences may thus play an important role in the schooling behaviour of toad tadpoles. I now consider the proximate factors leading to the formation of sibling schools and suggest some ultimate factors that may favour this behaviour.

Differential Habitat Selection or Sibling Recognition?

In some circumstances, animals might be found in sibling groups even though they have not evolved a mechanism to identify siblings. Of course, the advantages of kin-directed behaviours accrue to members of kin groups regardless of how such groups are formed. As an example, a brood of individuals that recognized and stayed close to their parents would thereby be associating with their siblings, although they might not recognize these siblings in other social
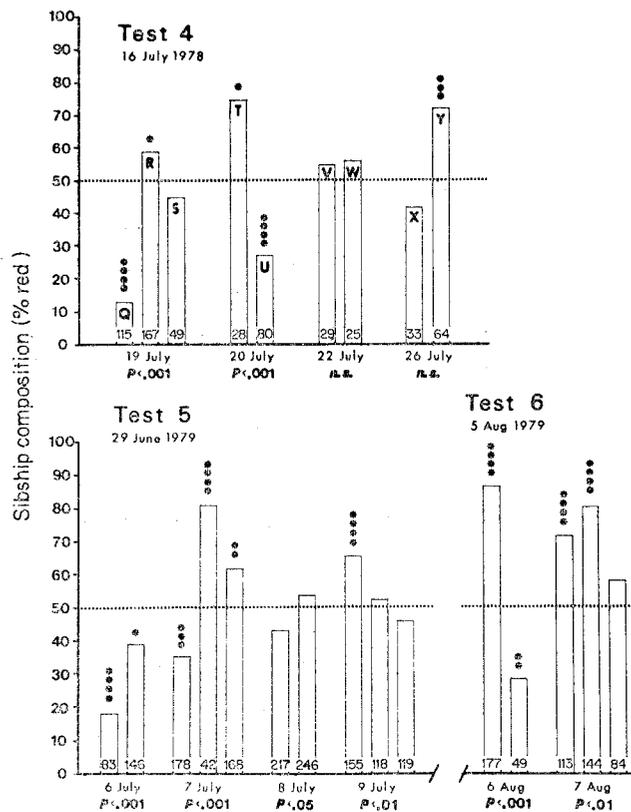
Fig. 4. Results from tests in which two sibships reared in a common tank separated by a fibreglass screen partition were released together in a pond. Data are presented as in Fig. 2.

contexts. Alternatively, sibling cohorts might express different habitat preferences so that siblings oriented similarly with respect to environmental cues (e.g. topographic landmarks). For instance, tadpoles might form sibling groups if they all returned to their hatching site. Clearly, sibling association need not imply behavioural recognition of siblings.

Previously, tadpoles were tested under relatively uniform conditions in a laboratory pool, and analyses of the positions of sibling groups through time suggest that sibling association is not accomplished by differential responses of the two sibships to possible micro-environmental gradients (Waldman & Adler 1979). However, gradients in natural ponds are more pronounced than those in a laboratory test pool, perhaps providing more opportunity for habitat selection to be important (e.g. Wiens 1970, 1972). Nevertheless, I was unable to

discern any consistent pattern of habitat selection by tadpoles belonging to particular sibships. If habitat selection were important in effecting sibling association, one would expect most adjacent schools in environmentally similar areas of a pond to have approximately the same sibship composition; yet schools less than 1 m apart were often composed predominantly of different sibships. Furthermore, schools consisting mostly of tadpoles belonging to a single sibship were simultaneously found in shaded and well-illuminated, deep and shallow areas of a pond (e.g. Fig. 3, Fig. 5). Because of the apparent lack of differential habitat selection by the sibship pairs tested, I suggest these data provide evidence that tadpoles have evolved some mechanism for the recognition of kin.

Mechanism of Sibling Recognition

Until recently, discussions of inclusive fitness and behaviours favoured by kin selection have
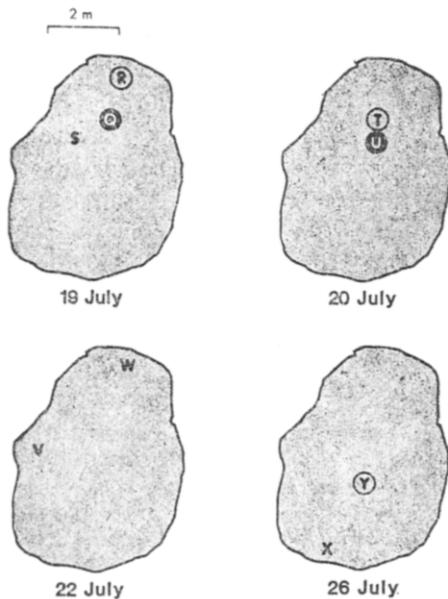
Fig. 5. The locations in the pond of all schools sampled in test 4. Each school is identified by a letter, which corresponds to that used in presenting sibship composition data shown in Fig. 4. Open and filled circles denote schools whose composition is significantly biased towards a particular sibship, as in Fig. 3.

generally not considered the mechanisms used to identify kin, perhaps implicitly assuming that recognition is based on familiarity (see Bekoff 1981). Indeed, when an individual's familiarity with its conspecifics is an accurate indicator of its relatedness to them, the simplest rule for

kin discrimination would seem to be to treat familiar individuals as kin and unfamiliar individuals as non-kin. Many animals appear to follow this rule. Spiny mice preferentially touch conspecifics with which they have been reared regardless of their relatedness (Porter et al. 1981). Moreover, after an 8-day separation period, they seemingly lose this littermate preference (Porter & Wyrick 1979). Similarly, sweat bees recognize nestmates whether related or not (Buckle & Greenberg 1981) presumably by learning their odours, but after one to twelve days of separation from nestmates, recognition of them (as assayed by whether or not they are allowed entry into the nest) wanes (Kukuk et al. 1977).

In laboratory studies, toad tadpoles preferentially associate with siblings with which they have been reared over unfamiliar non-siblings, but tadpoles continuously exposed to siblings and non-siblings throughout development do not discriminate familiar siblings from familiar non-siblings (Waldman 1981). Since siblings develop within a continuous jelly mass prior to hatching, and in natural conditions remain aggregated around the jelly mass remnants for several days after hatching, tadpoles might 'learn' traits of individuals around them during these early periods. Indeed, this hypothesis is supported by the finding that toad tadpoles reared in sibling groups during their first 18 days of development, and then exposed to siblings and non-siblings in mixed group tanks for periods of several weeks, subsequently associate with familiar siblings over familiar non-siblings (Waldman 1981). During an early sensitive

Table I. Summary of Sibling Association Results

| Test no.	Rearing conditions	Mean developmental stage (Gosner 1960)	Distance between ponds of origin (km)	No. of schools sampled	No. of schools significantly different from random ($P < 0.05$)	No. of sampling days	No. of days with significant differences among schools ($P < 0.05$)
1	Separate tanks	27	6.0	16	9 (56%)	4	4 (100%)
2	Separate tanks	30	6.0	3	2 (67%)	1	1 (100%)
3	Separate tanks	30	13.2	13	10 (77%)	4	2 (50%)
4	Same tank	31	6.0	9	5 (56%)	4	2 (50%)
5	Same tank	30	0.0	10	6 (60%)	4	4 (100%)
6	Same tank	32	0.0	5	4 (80%)	2	2 (100%)
7	Same tank—control	30	—	6	0 (0%)	2	0 (0%)
8	Same tank—control	32	—	7	0 (0%)	3	0 (0%)
9	Same tank—control	32	—	5	0 (0%)	2	0 (0%)
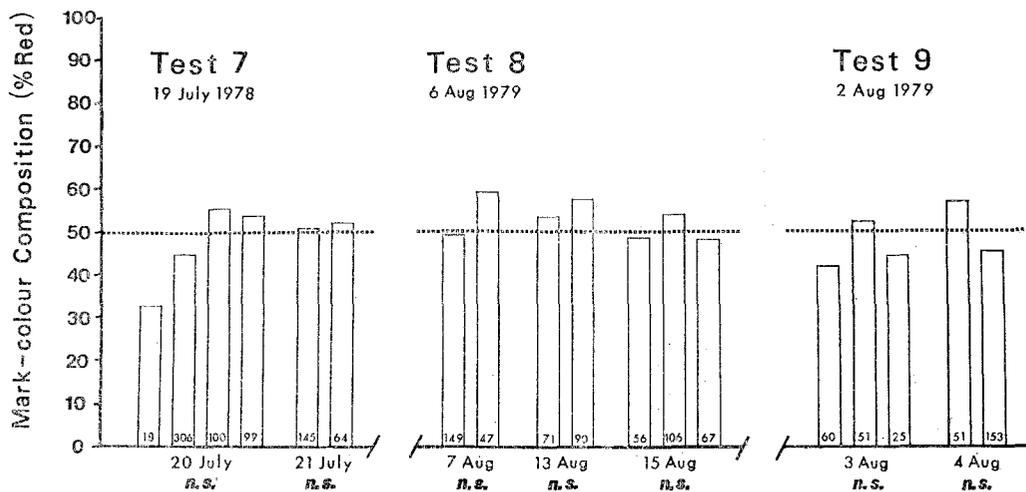
Fig. 6. Results from control tests in which 2000 siblings reared together were divided into two groups; 1000 were marked red and 1000 were marked blue. Data are presented as in Fig. 2.

period, individuals may form a recognition 'template' of traits upon which later sibling identifications can be based.

In the field experiments reported here, 66% of the schools formed by tadpoles belonging to sibships reared in separate tanks significantly departed from random sibship composition. By comparison, 62% of the schools formed by tadpoles belonging to sibships reared in a common tank were significantly different from random. Thus, unlike in laboratory tests, tadpoles discriminated familiar siblings from both familiar and unfamiliar non-siblings. The discrepancy between field and laboratory results might be due to either differences in rearing or testing procedures. Tadpoles used in laboratory tests were reared in a tank containing eight different sibships, each confined to a separate screen compartment. Water was actively circulated among all compartments by means of a motorized pump, so that dye placed into a tank was distributed uniformly among all compartments within 5 min (see Waldman 1981 for details). For field experiments, four sibships were reared in a larger outdoor tank in which water flow between compartments was passive; complete dispersion of dye introduced into a single compartment required up to 90 min. Consequently, during rearing, contact between different sibships was probably less complete in field than in laboratory tests, but perhaps more like the natural environment in which larvae

develop (particularly during early development). Tadpoles may thus have recognized siblings because they were 'more familiar' than non-siblings. Aside from this possibility, field tests seem to represent a more sensitive assay of sibling recognition than laboratory tests. Many more individuals were simultaneously tested in field tests than in laboratory tests, and schools sampled in the field were much more cohesive and well-defined than those measured in the laboratory.

Other results suggest that sibling preferences cannot be completely explained by a familiarity-based recognition system. In laboratory tests, tadpoles reared in sibling groups show stronger association with siblings over non-siblings if the two sibships are obtained from pairs collected in distant ponds than if they are obtained from pairs collected in the same pond (Waldman 1981). If individuals can gauge their genetic relatedness to conspecifics (e.g. Greenberg 1979), they might be expected to show lesser preference for siblings over related non-siblings (e.g. cousins) obtained from the same 'home' pond than for siblings over unrelated individuals obtained from a distant pond. In contrast to the laboratory findings, results from the field tests presented here do not provide evidence of this effect; overall, 63% of the schools sampled in tests of sibships with different 'home' ponds and 67% of those sampled in tests of sibships with the same 'home' pond significantly differed from

random sibship composition. Many more sibship pairs were tested in laboratory than in field tests, however, so these data do not provide grounds for discounting the importance of the laboratory results. Rather, I suggest that the laboratory testing paradigm is a more conservative indicator of sibling preferences than the field experiments, so that sibling preferences that may appear weak in laboratory tests are more readily apparent in field tests.

Even in the absence of post-embryonic experience with conspecifics, *B. americanus* tadpoles reared in isolation (beginning prior to neural plate formation) discriminate unfamiliar siblings from unfamiliar non-siblings in laboratory tests, forming sibling groups just as well-defined as those formed by familiar siblings (Waldman 1981). However, the embryonic environment may play an important role in the formation of sibling preferences. Toad tadpoles reared in isolation discriminate full-siblings from paternal half-siblings but not from maternal half-siblings, suggesting that some factor contributed by the mother is important in the ontogeny of sibling recognition (Waldman 1981). The factor might be either genetically or environmentally determined, and present in the cytoplasm of the egg cell or possibly in the egg jelly. A mechanism by which recognition specificity is determined prior to hatching could provide a sufficient basis for later sibling recognition even when clutches from several parental pairs have been deposited at one site within a pond. Whatever its ontogenetic basis, tadpoles apparently discriminate siblings from non-siblings based on waterborne cues that are probably detected through olfaction (Waldman, unpublished data).

Why are Sibling Schools Not 'Pure'?
Although the data presented here support the hypothesis that tadpoles recognize and preferentially associate with siblings in natural conditions, the sibship composition of every school sampled did not significantly differ from random, and even those that were significantly biased toward one or the other sibship were not 'pure' sibling schools. By demonstrating that tadpoles associate with siblings, I infer that they possess recognition abilities. However, the failure to measure kin association does not imply the absence of recognition abilities; an individual that recognizes its kin need not necessarily behaviourally discriminate among kin and non-kin. Perhaps tadpoles can recognize siblings, but association with them is not always advantageous,

and thus they do not continuously school with siblings. Sibling schools might form only under particular conditions, e.g. when the probability of predation by certain types of predators is high. *Bufo* tadpoles apparently are distasteful to vertebrate, but not invertebrate, predators (Wassersug 1973; Brodie et al. 1978); thus if sibship schooling has evolved in tandem with noxious taste and aposematic coloration (Waldman & Adler 1979), the formation of sibling schools might not be adaptive in situations in which predation by vertebrates is unlikely. Schooling may have several functions, and in some circumstances the direct benefits to individuals forming large schools, perhaps composed of non-siblings, may outweigh advantages to their inclusive fitness gained by kin-directed behaviours. Frequently in the field, *Bufo* tadpoles swarm together in large schools which appear to consist of more individuals than could possibly hatch from a single clutch, but at other times these large schools subdivide into smaller schools that might indeed represent sibling cohorts (Beiswenger 1972, 1975; Samollow 1980; personal observations). Presumably traits such as distastefulness or aposematic coloration are most advantageous when tadpoles are aggregated in sibling groups.

When circumstances favour schooling with siblings, 'pure' sibling schools would still not necessarily be expected for two reasons. First, sibling recognition might not be error-free. Assessment of relatedness is inherently probabilistic if based on trait overlap among related and unrelated conspecifics (see Getz 1981). Errors in assessment might also occur if identifiable labels were transferred among members of a kin group (e.g. Crozier & Dix's (1979) 'Gestalt model') and non-siblings that came into contact exchanged these recognition labels (Linsenmair 1972). Second, if predators avoid a school because they have learned that its members are distasteful, any palatable individual would presumably benefit by joining that school. Therefore, although distasteful tadpoles should seek to school only with kin, non-kin would benefit by schooling with distasteful individuals regardless of their relatedness. 'Pure' sibling schools might then be invaded by non-siblings unless they were somehow repelled from joining the school. Few data exist on antagonistic interactions among *Bufo* tadpoles. Beiswenger (1975, page 224) described 'butting' behaviour in *B. americanus* tadpoles, in which '...one tadpole swims forward and butts against another, some-

times continuing to lash its tail and push'. I have observed similar behaviour. Perhaps one function of it is the maintenance of sibling schools.

In addition, my sampling procedure provides only a 'grainy' indication of sibship composition. The 0.5 × 0.5 m partition used to capture tadpoles in a school frequently also enclosed non-schooling individuals outside the school, and sometimes might have included two or more adjacent clumps of tadpoles. Moreover, tadpoles within a school might segregate by sibship, forming subgroups consisting predominantly of single sibships. Such possible differential sibship composition among subgroups within a school would be masked by my data collection method. However, in analogous laboratory experiments, data collection procedures allowed for precise analysis of positions of all tadpoles, and yet, as in the field tests reported here, significant sibling association was not found in all samples (Waldman & Adler 1979).

Possible Advantages of Sibling Schools
Previous studies have demonstrated that toad tadpoles are distasteful to a variety of vertebrate predators (Voris & Bacon 1966; Heusser 1971; Wassersug 1971; Cooke 1974). Nevertheless, vertebrates do sometimes prey upon toad tadpoles (e.g. Walters 1975), and although toad tadpoles may have chemical defences against predators (Flier et al. 1980), these substances appear not to be acutely toxic to them (but substances in toad eggs may be (Licht 1967a, 1968)). After discovering a distasteful individual in an aggregation, a predator may learn that tadpoles are distasteful (e.g. Brodie & Formanowicz 1981) and then skip over the other individuals in that aggregation (Arnold 1978 and references therein). Thus prey can increase their inclusive fitness by clumping with kin. Individual prey need not be extremely unpalatable to effect a predator's aversion; indeed, some predators might be deterred by noxious properties of prey only after sampling many prey (Matthews 1977), or after a delayed period in which slow-acting effects of the toxin are experienced. In these cases, individuals should be increasingly selected to become more gregarious as a means of providing an effective signal to the predator (e.g. Pough et al. 1973). The expression of aposematic coloration or conspicuous behaviours may further serve to deter experienced predators (e.g. Gittleman & Harvey 1980; Gittleman et al. 1980), and thus these traits should also spread among distasteful prey.

Schooling with siblings might result in other anti-predator benefits as well. *Bufo* tadpoles injured by a predator may warn surrounding individuals of the predator's presence. Tadpoles of many bufonids have a chemical contained in their epidermis that, when released, provokes a fleeing alarm reaction in nearby conspecifics (Hrbacek 1950; Kulzer 1954; Pfeiffer 1966, 1974). This 'alarm substance' cannot be actively secreted into the water; release is dependent on an individual's skin being broken, presumably in natural conditions by a predator. As in the apparently analogous alarm behaviour system of many ostariophysean fishes (von Frisch 1941; Pfeiffer 1974, 1977), the signalling individual usually does not survive. Unless the behavioural response represents a secondary adaptation to a chemical that serves some other function (Williams 1964), alleles for the warning chemical presumably have spread through kin selection (Hamilton 1964; Maynard Smith 1965). Thus release of this pheromone would increase an individual's inclusive fitness only when kin benefit disproportionately, as when individuals associate in kin groups. Smith (1977), following West Eberhard (1975), argues that schooling fish need not be closely related for this trait to evolve, but the spread of alleles encoding the pheromone would be quicker if kin groups existed. Although generally considered to be limited to bufonid species among anuran larvae (Pfeiffer 1966, 1974), similar alarm behaviour systems may occur in other species. For example, tadpoles of the eastern spadefoot toad (*Scaphiopus holbrooki*) sometimes respond to crushed conspecifics with typical alarm behaviour (see Richmond 1947).

Social behaviour may influence growth of anuran larvae, and growth regulation may be another factor favouring the formation of sibling schools. Large, growing tadpoles can effectively reduce the growth rate of smaller conspecifics by releasing growth inhibiting factors into the water (e.g. Richards 1958, 1962; Rose 1960; Licht 1967b) or through behavioural interactions (Gromko et al. 1973; John & Fenster 1975). The relatedness of individuals releasing and responding to the inhibitors may be important. Substances released by large *Rana arvalis* tadpoles have a greater inhibitory effect on the growth of smaller siblings than on that of smaller non-siblings (Shvarts & Pyastolova 1970a). Many temperate zone anurans deposit

large clutches in ephemeral habitats, and under these conditions individuals should be selected to grow quickly to gain an early size refuge from predators and to metamorphose before the pond dries. If critical resources are limiting, robust individuals might benefit by suppressing the growth of conspecifics. Although inclusive fitness would presumably be maximized by directing growth inhibition effects toward non-kin rather than toward kin, selection may be acting on the specificity with which individuals respond to the regulatory substance. Smaller larvae, if their probability of successfully completing metamorphosis is low, might have more to gain indirectly by allowing themselves to be stunted (and perhaps under extreme conditions to be cannibalized by larger more vigorous kin) than they could potentially gain by directly competing with these kin. Consistent with a kin selection model, factors released by small larvae may actually increase the rate of growth of their larger kin (Shvarts & Pyastolova 1970b; also see Steinwascher 1979), and at metamorphosis these larger tadpoles may release chemicals that accelerate, rather than inhibit, the growth of less developed individuals (Licht 1967b). By schooling with siblings, individuals can presumably maximize their exposure to growth regulators of kin.

Although most studies of growth regulation have been conducted on frog larvae, the growth of toad tadpoles may also be affected by water-borne regulators. Licht (1967b) found that the growth of three *Bufo* species was inhibited by exposure to water in which other tadpoles had been reared, but growth of *Bufo woodhousei* tadpoles was actually accelerated by such treatment. Preliminary data I recently collected suggest that the growth of *B. americanus* tadpoles may be either inhibited or accelerated when they are exposed to water in which conspecifics have been reared. Moreover, like *R. arvalis* tadpoles, under some conditions *B. americanus* tadpoles may respond differentially to substances released by siblings and non-siblings. An individual's responsiveness to growth regulating factors might be influenced by its stage of development and likelihood of survival to metamorphosis. Although the mechanism of action is unclear, specificity of growth regulators may provide another clue as to the adaptive advantage of forming sibling schools. Whether the physiological 'recognition' mechanism underlying such a system of growth regulation is related to the behavioural kin recognition mechanism

demonstrated in this study requires further investigation.

Conclusion
The larval period represents a short but critical phase in the toad's life history (see Wassersug 1975; Wilbur 1980). Toads deposit large clutches (2000 to 13 000 eggs), usually in transient environments, and cohorts suffer enormous mortality, particularly during larval and early post-metamorphic stages. Although tadpoles appear well-adapted for exploiting available food resources, these resources may sometimes be limiting, and larval competition consequently may be intense. In addition, predation pressures can be substantial (see Brockelman 1969). The field data presented here suggest that the ability to form sibling schools may represent an important adaptation to these problems. Further study is required to delineate the ecological and evolutionary factors that favour kin association, the mechanism by which sibling schools increase larval (and perhaps indirectly, post-metamorphic) survivorship, and the possibility that kin recognition abilities are retained after metamorphosis and play some role in adult behaviour.

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