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STUDY OF AGGREGATIVE BEHAVIOR OF *RHINOPHRYNUS DORSALIS* TADPOLES: DESIGN AND ANALYSIS

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ABSTRACT: We conducted experiments using the apparatus and design followed by Wassersug and Hessler (1971) and Wassersug (1973) to test the aggregative behavior of tadpoles of *Rhinophrynus dorsalis* in response to visual and olfactory stimuli. Results neither supported nor refuted the hypothesis that either stimulus is used as a mechanism for school formation. The exercise did lead to doubts about the experimental design. Some ambiguity resulted from the fact that the significance of the results depended upon the way in which the data were analyzed. Several alternative methods were considered. We also observed tadpoles reared in isolation to determine the effect of prior social conditioning on aggregative behavior. Isolates grew less than group-reared animals, were less active, and exhibited a strong avoidance reaction when subsequently exposed to conspecifics.

Key words: Amphibia; Salientia; Rhinophrynidae; *Rhinophrynus*; Growth; Schooling; Social conditioning; Tadpoles

ALTHOUGH schooling behavior is not as common among tadpoles as it is among fishes, it has been noted in a variety of species (e.g., Black, 1969; Bragg, 1948, 1968; Wassersug, 1973). Despite several hypotheses, however, its function remains unknown. Recent experimental work has focused on the mechanisms by which this behavior is accomplished, providing evidence that both visual and lateral line systems may be involved (e.g., Katz et al., 1981; Wassersug, 1973).

In one study, Wassersug and Hessler (1971) tested the response of *Xenopus laevis* (Pipidae) tadpoles to the visual presence of conspecifics to determine if aggregations of this species formed solely as a result of "the visual presence of other individuals." Generally, the experimental results supported this hypothesis. Wassersug and Hessler (1971) also tested other species and alluded to similar results obtained with tadpoles of *Rhinophrynus dorsalis* (Rhinophrynidae). Wassersug (1973) briefly considered these results in a later paper.

The observation of *R. dorsalis* was of particular interest to us. We studied larvae of this species in the field (Guanacaste Province, Costa Rica) for several months each year from 1971 to 1974, and our extensive observations suggest that their schools probably are not visually mediated. Although underwater visibility in ponds occupied by *R. dorsalis* varies greatly from year to year, it is generally very low (ca. 1–3 cm at the surface) because of high concentrations of suspended microorganisms and particulate matter. In addition, the tadpoles are often heavily pigmented with melanin over most of their dorsal and lateral surfaces, blending in with the dark color of the water. Given the apparent limitations to the use of vision in their natural habitat, we did not expect the tadpoles to depend on visual stimuli as a basis for aggregation. However, Wassersug and Hessler (1971) and Wassersug (1973) tested their tadpoles in clear water, and it is likely that schooling tadpoles use several sensory systems, the importance of which varies according to environmental conditions. Alternatives to vision are pressure-mediated perception through the lateral line system (Katz et al., 1981), which is highly developed in *Rhinophrynus* tadpoles (personal observation), and olfaction (Risser, 1914).

We attempted to reevaluate the use of vision for schooling in *R. dorsalis* and to determine the importance of a chemically-mediated system by conducting experiments on the aggregative behavior of tadpoles in response to visual or olfactory stimuli. The results of our tests were inconclusive, largely because of problems with the methodology which we copied from Wassersug and Hessler (1971) and Wassersug (1973). These problems led us to reexamine their methods of data analysis, which we now believe to have been inappropriate, and their data, which we find insufficient to support the conclusions they drew.

We also examined the effect of rearing *R. dorsalis* tadpoles in isolation on schooling. We reared tadpoles from eggs isolated within a few hours of oviposition and then observed the behavior of these larvae in isolation and when exposed to conspecifics. Recent work has shown that rearing conditions can influence the composition of schools (Blaustein and O'Hara, 1981; O'Hara and Blaustein, 1981; Waldman, 1980; Waldman and Adler, 1979). In addition, social interactions within aggregations may significantly influence metamorphic weight of tadpoles and number of days to metamorphosis (Breden and Kelly, 1982).

METHODS

Visual orientation was tested in an apparatus roughly equivalent to that used by Wassersug and Hessler (1971). A glass tray was divided into four equal compartments with glass partitions held along the bottom and at each end by clear silicone seal. The tray was placed in a larger glass tank on top of a grid that effectively divided each compartment into four equal-sized, imaginary quadrants (designated by small letters in Fig. 1). Both containers were filled with water to the same depth to prevent reflections and refractions from the sides of the experimental tray. A movie camera mounted overhead and triggered by a remote release took single frame pictures. Lighting was arranged to minimize shadows.

Tests were run with tadpoles in two stages of development (Gosner, 1960) comparable to those of the *Rhinophrynus*

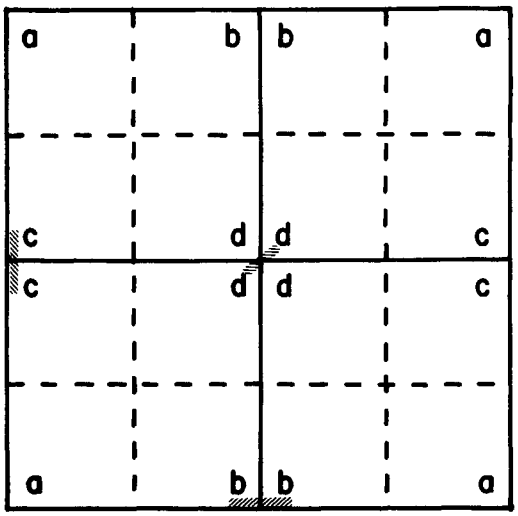

FIG. 1.—Design of experimental tray used in visual and olfactory experiments. Solid lines represent partitions dividing the tray into four equal-sized compartments. Dotted lines represent a grid lying beneath the tray and effectively dividing each compartment into four quadrants. Hatching indicates areas of silicone seal perforated for the olfactory experiments. As a result of the perforations, the chamber on the lower left communicated with the other three, which did not communicate with each other.

and *Xenopus laevis* tadpoles (Nieuwkoop and Faber, 1956) used by Wassersug and Hessler (1971) and Wassersug (1973). For the smaller ones (stages 26–29; body length = 10.9–13.0 mm; total length = 27.7–32.4 mm), the inner tray was 12 × 12 cm divided into compartments 6 cm on a side and filled to a depth of 3 cm. For the larger tadpoles (stages 33–36; body length = 14.0–17.2 mm; total length = 37.8–48.0 mm), the experimental tray was 25 cm on a side with compartments of 12.5 × 12.5 cm filled to a depth of 5 cm. Unless otherwise specified, untreated tapwater from a well was used in all experiments. Experiments were carried out at a room temperature of ca. 33 C, whereas Wassersug and Hessler (1971) carried out their experiments at 23 C. The higher temperature may have caused our tadpoles to be more active than theirs. It is unlikely, however, that the tadpoles experienced thermal stress, because water temperatures in ponds from which they were taken often exceeded 33 C on sunny days (Foster and McDiarmid, unpublished), with no apparent effects on the tadpoles.

During tests for visually mediated orientation, one tadpole was added to each compartment. Beginning 3 min after introduction, these individuals were photographed at 2-min intervals to record their positions within each quadrant and relative to each other. The water was stirred after each 10 exposures to insure uniform oxygen concentrations and water temperatures. Data were recorded for 40–50 min. Two trials with four different individuals each were conducted with the tadpoles in each stage of development. Following the procedure of Wassersug and Hessler (1971), we used single tadpoles as controls. Each was placed in a compartment and photographed at 2-min intervals for 40 min to determine its positions among quadrants. The other three compartments remained empty. Three individuals in each stage of development were tested. Data for individuals in each stage were combined for statistical analyses.

Procedures for the olfactory experiments were similar. Here, however, four openings, about 2 × 2 mm, were cut in each of the silicone seals supporting the partitions separating one of the chambers. As a result, this chamber (the "experimental chamber") communicated with the remaining three (Fig. 1). A single tadpole was placed in the experimental chamber; it and two other chambers were filled with tapwater while the holes communicating with the fourth chamber were blocked with plastic sheeting. The fourth chamber was filled with "tadpole water" taken from a 20-l tub in which ca. 300 *R. dorsalis* tadpoles had been held during the 36–48 h immediately prior to the experiment. The plastic sheet blocking the communicating holes was removed, and 3 min later we began to photograph the position of the tadpole at 2-min intervals for 40–42 min. The water

was not stirred during this period. After each trial, the experimental apparatus was emptied and cleaned. Six tadpoles in developmental stages 26–29 and six in stages 33–36 were tested, one at a time, all in the same experimental compartment. Each of the other three compartments was used for the tadpole water in two trials with the small individuals. For the larger tadpoles, one compartment was used for three trials, one for two, and one for one. Two tadpoles of each size class were used as controls. The control experiments were conducted in the same way, but all chambers were filled with tapwater. The data for each pair were combined for use in the analyses.

The positions of the tadpoles in each lettered quadrant (Fig. 1) were recorded from the photographs. A tadpole was considered to occupy the square in which its eyes were located.

Finally, we attempted to determine the importance of social conditioning on schooling behavior. Sibling tadpoles were reared from the egg in isolated, opaque chambers 5 cm in diameter and filled with water to a depth of 7 cm. We intended to repeat all the experiments outlined above using these tadpoles. However, the isolates did not grow as well as the tadpoles caught in the wild or reared in groups, and did not reach sizes and developmental stages comparable to those of the larvae used in the vision and olfactory tests. Thus, observations were confined to their behavior in isolation and when grouped with conspecifics. In two instances, single isolates were added to a large glass aquarium (75 × 35 cm, water depth 21 cm) containing 200 group-reared sibs associated in one or two schools and observed for 2 h. Two other isolates, added one at a time to small, opaque, plastic aquaria (19 × 12 cm, water depth 6 cm) containing 10 group-reared sibs, were observed, as were two groups of 10 isolates combined in the small plastic aquaria. In all instances, we used isolates (stage 35: body length = 12.9–13.1 mm; total length = 33.4–35.2 mm) most similar in size and developmental stage to the group-reared larvae (stages 34–36; body length = 11.2–13.4 mm; total length = 28.8–42.1 mm).

All tadpoles were fed ad libitum on Tetra Min Staple Food. Water in the containers was changed daily. The Chi-square Test for Goodness of Fit was used for the statistical analyses, which we describe below. Probabilities ≤ 0.05 were considered statistically significant.

Results

Experiments with Visual Stimuli

The results from the sight experiments in the compartmentalized test tray were analyzed in three ways. In the first, every possible combination of tadpole arrangements among the quadrants (when one tadpole was present in each chamber) was determined. Only a single arrangement could result in all four tadpoles being in close proximity (i.e., if each occupied quadrant *d*, Fig. 1). Twelve arrangements could result in three tadpoles being together (i.e., all three occupying quadrant *d*). Pairs could be formed in 111 arrangements (e.g., tadpoles occupying adjacent *b-b*, *c-c*, *d-d* quadrants); in six of these, two pairs could be formed. Aggregations were counted only once, in the category representing the largest grouping. In 132 possible arrangements, all tadpoles could occupy non-contiguous quadrants. These values were used to calculate the probabilities of any particular grouping occurring by chance. Although only 256 arrangements were possible, the six in which two pairs could occur simultaneously were counted twice, for a total of 262. Thus, given equiprobable positioning, the expected frequencies of four tadpoles occurring together, three together, two together, or all as singles, were 0.004, 0.046, 0.447, and 0.504, respectively. These values were used to calculate the numbers of each arrangement expected in the experiments, if positioning were random. These numbers were then compared with the observed distribution of

TABLE 1.—Results and chi-square analyses of tray experiments testing visual stimuli as a mechanism controlling aggregation in tadpoles of *Rhinophrynus dorsalis*.

		Stage 26–29 tadpoles			Stage 33–36 tadpoles		
		Trial I	Trial II	Controls	Trial I	Trial II	Controls
Comparison of observed values with theoretical distributions expected on the basis of chance alone†							
		Observed (expected)					
No. assoc.	*n*:	27	21		24	24	
4		0 (0.1)	0 (0.1)	—	0 (0.1)	0 (0.1)	—
3		1 (1.2)	0 (1.0)	—	2 (1.1)	0 (1.1)	—
2		12 (12.1)	6 (9.4)	—	11 (10.7)	18 (10.7)	—
1		14 (13.6)	15 (10.6)	—	11 (12.1)	6 (12.1)	—
χ^2		0.146	4.156		0.944	9.255	
P		>0.5 (NS)	>0.1 (NS)		>0.5 (NS)	<0.05	
Comparison of experimental and control data with random, based on equal distribution of observations among all quadrants‡							
		Observed (expected)					
Quadrant	*n*:	100	84	62	84	84	60
a		26 (25)	26 (21)	14 (15.5)	13 (21)	10 (21)	13 (15)
b		28 (25)	12 (21)	21 (15.5)	20 (21)	16 (21)	14 (15)
c		15 (25)	27 (21)	9 (15.5)	23 (21)	34 (21)	23 (15)
d		31 (25)	19 (21)	18 (15.5)	28 (21)	24 (21)	10 (15)
χ^2		5.840	6.951	5.226	5.619	15.429	6.268
P		>0.1 (NS)	>0.05 (NS)	>0.1 (NS)	>0.1 (NS)	<0.005	>0.05 (NS)
Direct comparison of experimentals and controls§							
		Observed (expected)					
Quadrant	*n*:	100	84		84	84	
a		26 (22.6)	26 (19.0)	14	13 (18.2)	10 (18.2)	13
b		28 (33.9)	12 (28.5)	21	20 (19.6)	16 (19.6)	14
c		15 (14.5)	27 (12.2)	9	23 (32.2)	34 (32.2)	23
d		31 (29.0)	19 (24.4)	18	28 (14.0)	24 (14.0)	10
χ^2		1.694	31.281		18.123	11.600	
P		>0.5 (NS)	<0.005		<0.005	<0.025	

† Expected values for 4, 3, 2 and 1 calculated by multiplying total observations for each trial by 0.004, 0.046, 0.447 and 0.504, respectively; df = 3.

‡ Expected values for each quadrant calculated by dividing total n for each trial by 4; df = 3.

§ Expected values for each quadrant calculated by dividing control value by 62 (stage 26–29 tadpoles) or 60 (stage 33–36 tadpoles) and multiplying by total *n* for each trial; df = 3.

aggregations recorded from the photographs of the experimental animals. The two experimental groups of the tadpoles at stages 26–29 were compared separately, and neither differed significantly from the expected (Table 1). Even when the numbers for the two groups were combined, differences were not significant ($n = 48$, $\chi^2 = 2.377$, df = 3, $0.5 > P > 0.1$).

The results from the comparisons with the tadpoles at stages 33–36 were not as clear cut. Again, two groups were tested. In the first group, the number of aggregates of various sizes did not differ from the expected (Table 1). In the second group, however, significantly more pairs and fewer totally dispersed arrangements were observed than were expected (Table 1).

The second method of analysis was used to facilitate comparison with the results of Wassersug and Hessler (1971). Here, we also analyzed our experimental results against those obtained with the

controls in an indirect fashion, as did Wassersug and Hessler (1971). These authors reasoned that if the four experimental tadpoles exhibited some visually mediated aggregation, individuals would be found most frequently in quadrant *d*, followed by quadrants *c*, *b*, and then *a*. If there were an avoidance reaction, the reverse would be true. With no reaction, the quadrants would be occupied about equally. For the controls, where only a single tadpole was present, the tadpoles again would be expected to occupy all quadrants with about equal frequency. Wassersug and Hessler (1971) analyzed their data in two steps. They first considered the data from their controls and determined that these tadpoles were distributed equally among the quadrants. They then compared their experimental results with equal probability values. They did not directly compare control and experimental results. In our third method of data analysis, we made these direct comparisons.

The distribution of the controls of the stage 26–29 tadpoles did not differ significantly from random (Table 1), nor did the distributions of the experimental groups in trials I and II (Table 1). When the distributions of these experimentals were compared with expected distributions based on those of the controls, the distributions in trial I did not differ significantly, but trial II distributions differed to a highly significant degree (Table 1). The occurrence of tadpoles in quadrants *a* and especially *c* was higher than expected.

The results for the stage 33–36 tadpoles were similar. Again, the distribution of the controls did not differ significantly from random, nor did that of the trial I group of experimentals (Table 1). However, when compared with the controls, the difference was highly significant (Table I), primarily because of an increased occurrence of tadpoles in quadrant *d*. The results for the experimental trial II group differed significantly from both random and from the controls (Table 1), again because of a surprisingly high occupancy of quadrant *d*.

Experiments wtih Olfactory Stimuli

Six replicates of the olfactory experiments were run with tadpoles of each size. Results of these trials were tested only against the distribution of the controls when all chambers contained clean water. The stage 26–29 tadpoles in two trials showed a strong positive attraction to the opening communicating with the "tadpole water" (Table 2). In three other trials, the experimentals did not differ significantly from the controls (Table 2). The distribution of the tadpole in the remaining trial differed significantly from the controls but did not favor the quadrant with openings communicating with the chamber containing the tadpole water (Table 2).

The distributions of the large tadpoles differed significantly from that of the controls in all six trials. However, in three trials the tadpoles showed a positive attraction to the opening communicating with the "tadpole water", and in three they were attracted elsewhere (Table 2).

Experiments with Social Conditioning

Tadpoles reared in isolation behaved differently from those reared in groups. Within 24 h after hatching, the tadpoles reared in groups swam actively, though intermittently. The periods of activity increased so that 2–3 days after hatching, swimming was nearly continuous. By 4–6 days after hatching, the tadpoles exhibited well-defined schooling behavior and remained in schools through metamorphosis.

In contrast, tadpoles reared in isolation lay on the bottom of the container nearly all the time, often on one side, only occasionally surfacing to gulp air. When disturbed, they swam rapidly about their containers for a few seconds and then settled back on the bottom. Isolated tadpoles did not grow as quickly or as large as those reared in groups, apparently because of a reduced feeding rate, although

TABLE 2.—Results and chi-square analyses of experiments testing olfactory stimuli as a mechanism controlling aggregation in tadpoles of *Rhinophrynus dorsalis*.

	Stage 26–29 tadpoles: observed (expected)†						
Trial:	I	II	III	IV	V	VI	Controls
n:	21	20	22	21	20	20	41
Quadrant							
a	3 (3.6)	3 (3.4)	5 (3.8)	1 (3.6)	7 (3.4)	1 (3.4)	7
b	2 (5.6)	0 (5.4)	3 (5.9)	10 (5.6)	3 (5.4)	3 (5.4)	11
c	12 (3.6)	17 (3.4)	7 (3.8)	4 (3.6)	2 (3.4)	8 (3.4)	7
d	4 (8.2)	0 (7.8)	7 (8.6)	6 (8.2)	8 (7.8)	8 (7.8)	16
χ^2	24.165	67.647	4.797	5.969	5.460	9.082	
P	<0.005	<0.005	>0.1 (NS)	>0.1 (NS)	>0.1 (NS)	<0.05	
Cue quadrant‡	*c*	*c*	*b*	*b*	*d*	*d**	
	Stage 33–36 tadpoles: observed (expected)†						
Trial:	I	II	III	IV	V	VI	Controls
n:	20	21	20	21	20	21	40
Quadrant							
a	0 (2.0)	0 (2.1)	2 (2.0)	1 (2.1)	1 (2.0)	0 (2.1)	4
b	12 (3.0)	3 (3.2)	2 (3.0)	12 (3.2)	3 (3.0)	7 (3.2)	6
c	0 (10.5)	7 (11.0)	3 (10.5)	3 (11.0)	0 (10.5)	1 (11.0)	21
d	8 (4.5)	11 (4.7)	13 (4.5)	5 (4.7)	16 (4.5)	13 (4.7)	9
χ^2	42.222	12.013	21.746	30.613	40.389	30.361	
P	<0.005	<0.01	<0.005	<0.005	<0.005	<0.005	
Cue quadrant‡	*b*	*c**	*c**	*c**	*d*	*d*	

† Expected values for each trial calculated by dividing controls by 41 (stage 26–29 tadpoles) or 40 (stage 33–36 tadpoles) and multiplying by total *n* for each trial. For all values, df = 3.

‡ Quadrant the tadpole was expected to occupy if responding to olfactory cues. * indicates tadpole distribution differs significantly from the controls but not in favor of the quadrant expected.

water conditions and feeding regimes were the same. In fact, we were unable to rear isolates through to metamorphosis.

To determine if the lack of activity of the isolates was due only to a lack of stimulation from conspecifics, we combined isolates with other individuals of about the same stage and observed their behavior. The behavior patterns of two isolates added (separately) to the large aquarium containing 200 other tadpoles were the same. During the first 10 min, the lone tadpole lay on the bottom, only occasionally surfacing to gulp air. Whenever it was approached by other tadpoles, it immediately turned and swam away. This initial strong avoidance reaction gradually diminished, so that for about the next 5 min, the tadpole merely turned away when approached. It still remained motionless on the bottom, except when avoiding other tadpoles. Eventually, the tadpole allowed itself to be engulfed by schools as they swam over it. For the rest of the 2-h observation period, the isolate tadpole was intermittently surrounded by a passing school. It did not try to escape the school, but never moved with it, and usually remained motionless or swam slowly in the opposite direction.

The behavior patterns of two other isolates added to separate, small aquaria containing only 10 group-reared conspecifics was essentially the same as that outlined above, although these isolates, without any apparent stimulus, also engaged in occasional frenzied, undirected swimming bouts lasting several seconds. The tadpoles never appeared to "join" the others present. The 10 social tadpoles tended to remain near one another even in these small containers.

The isolates, combined 10 each in two

of these small containers, remained dispersed and moved randomly without apparent regard for the movement of the other tadpoles.

Discussion

Before the results of the vision experiments can be evaluated, the most appropriate statistical treatment must be determined because the different tests resulted in different levels of statistical significance. We believe that the analyses used by Wassersug and Hessler (1971) and Wassersug (1973) are inappropriate. The independent comparison of experimentals and controls to random masks differences or similarities that may exist between the experimentals and controls themselves. For example, direct comparison of the distributions of the controls and experimentals in Fig. 2 of Wassersug and Hessler (1971) showed that the stage 48 tadpoles in tray 1 and the stage 53 tadpoles did differ significantly from expected values calculated on the basis of the controls ($\chi^2 = 9.035$, df = 3, $P < 0.025$; and $\chi^2 = 92.333$, df = 3, $P < 0.005$, respectively), as they indicated. In contrast to their assertion, however, the tadpoles in tray 2 did not differ significantly ($\chi^2 = 6.683$, df = 3, $P > 0.05$).

Even the direct comparison of the distribution of the controls among the quadrants *a* through *d* does not reveal much about aggregation in these tadpoles, because a tadpole may occupy square *d* or *c* or *b* without another tadpole lying in an adjacent chamber. Thus, a high proportion of occurrence of tadpoles in any of these squares does not necessarily imply association, as demonstrated by consideration of the distribution of our stage 33–36 tadpoles in response to visual stimuli. When the occurrence of tadpoles in the various quadrants was compared to the controls, both trials I and II differed significantly, a higher than expected number of tadpoles occurring in square *d* (Table 1). However, when the actual number of associations was determined, the numbers of pairs, trios and quartets in trial I did not differ from the expected (i.e., there was no positive visual response) though in trial II, the number of pairs was significantly greater than expected. Thus, the analysis considering only the distribution among quadrants, instead of numbers of associations, was biased in favor of visual aggregation. Unfortunately, Wassersug and Hessler (1971) did not provide data on the actual numbers of aggregations they observed.

Another problem is that this method of analysis artificially inflates sample size even if successive photographs are independent. For example, in the vision experiments with the stage 26–29 tadpoles, we used four tadpoles in each of two trials, taking 25 and 21 photographs of those tadpoles, respectively. If we analyzed our data as Wassersug and Hessler (1971) did, by means of total number of tadpoles occupying each quadrant, our sample sizes were 100 and 84 for the two trials. However, even if the successive photographs were independent, we tested the behavior of only eight tadpoles, and in only two trials.

That the successive photographs were independent may be questioned also. Wassersug and Hessler (1971) pointed out that two tadpoles making visual contact and then rarely moving for the rest of the experiment would inflate *n* for use in the Chi-square Test. They noted, however, that only very rarely did all four tadpoles occupy the same position in successive photographs, and that eliminating duplicates from the analysis did not change the results. Our photographs included only five duplicates, in three of which tadpoles did not occupy adjacent squares. When we reanalyzed our data omitting the duplicates, in only one test did the significance of the result change. Results of that trial, which included two duplicates with no paired tadpoles, changed from nonsignificant to significant. Even so, we believe it inappropriate to assume independence of successive photographs simply because one tadpole changes position. A more reliable way to insure in-

dependence, and one that has been adopted in recent studies (Katz et al., 1981; Wassersug et al., 1981), is to disturb the tadpoles between each photograph.

Because of problems with methodology, we believe that conclusions on aggregation behavior drawn by Wassersug and Hessler (1971) and Wassersug (1973) on the basis of their experiments must be reexamined. Our attempt to do this, however, was less than satisfactory. Our results are somewhat contradictory and depend upon the way in which the data are analyzed. As a result, no clear evidence emerges either for or against the two proposed mechanisms of aggregation in tadpoles of *Rhinophrynus dorsalis*. The inconsistencies in our results may be due to our small sample sizes. When we conducted our experiments, we planned to analyze our results in the manner of Wassersug and Hessler (1971). As discussed above, if analyzed in that manner, our sample sizes would be 10 to 12 times larger. We should, of course, have recognized the shortcomings of this method beforehand, and now, unfortunately, we are not in a position to perform additional experiments. However, we hope this discussion will serve to alert other researchers to the problem.

Although the data are too few to allow for firm conclusions, both growth and schooling behavior appear to be influenced by social conditioning. Previous studies (e.g., Brockelman, 1969; Collins, 1979; Wilbur, 1976) have shown that weight at metamorphosis is negatively correlated with the density at which tadpoles are reared, at least at high densities. Thus, *R. dorsalis* reared in isolation might be expected to grow more quickly than their group-reared sibs. Ours did not. However, *Bufo americanus* tadpoles experience an Allee effect (i.e., at low densities, growth is positively correlated with increasing density; Wilbur, 1977). It may be that growth is not affected by density per se, but by amount of social interaction (Breden and Kelly, 1982). Similar findings have been obtained with schooling fishes (Shaw, 1960, 1961). As *Rhinophrynus* larvae school in nature, it would not be surprising if such social stimulation had a positive effect on growth.

The lack of schooling behavior in the *Rhinophrynus* larvae reared in isolation contrasts sharply with observations on other species with social larvae. *Rana cascadae* tadpoles reared in isolation subsequently associated with conspecifics, but preferred sibs to non-sibs (Blaustein and O'Hara, 1981; O'Hara and Blaustein, 1981), as did *Bufo americanus* tadpoles (Waldman, 1980). The conspecifics to which the *R. dorsalis* isolates were exposed were their sibs. The initial, strong aversion and subsequent passive responses of the isolates may imply an inability to school with tadpoles (including sibs) to whom they have not been exposed during some critical stage of development. Shaw (1960, 1961), however, working with two species of schooling fishes, described a latency period between initial exposure to conspecifics of fishes reared in isolation, and development of schooling behavior. During this period, the "isolate fishes" passed through several transient stages of increasing sociability. *Rhinophrynus* tadpoles reared in isolation may pass through a similar period, but of a duration longer than our period of observation.

An equally interesting hypothesis to explain the lack of schooling by isolates suggests that the absence of early social experience prevented them from expressing later social behavior in the expected fashion.

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