An Investigation of the Alarm Response in *Bufo boreas* and *Rana cascadae* Tadpoles

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Tadpoles of the western toad (*Bufo boreas*) and of the Cascades frog (*Rana cascadae*) show an alarm reaction to an extract containing chemical cues from damaged conspecifics. The mean time spent by individual *B. boreas* tadpoles in the half of the test tank to which the extract solution was added was significantly lower than expected by chance. Activity was also significantly greater in *Bufo* extract tests than in control tests. Tadpoles did not avoid an extract of another tadpole species (*Hyla regilla*). *Rana cascadae* tadpoles did not avoid areas containing *Rana* extract but did significantly increase their level of activity in response to the extract. These results suggest that the *R. cascadae* tadpole alarm reaction exists but differs from the *B. boreas* reaction. © 1985 Academic Press, Inc.

Chemoreception in vertebrates mediates diverse phenomena, including such behaviors as navigation and orientation to species recognition (see review in Stoddart, 1980). In amphibians, chemical cues may be important in navigating (Dole, 1972; Grubb, 1973), in finding food (Hemmer & Schopp, 1975; David & Jaeger, 1981; Dole, Rose, & Tachiki, 1981), and in indicating reproductive condition (Madison, 1977). Chemical cues are also important in individual, kin, sex, and species recognition (Twitty, 1955; Madison, 1975; Jaeger & Gergits, 1979; Blaustein & O'Hara, 1982a) and in intra- and interspecific social interactions (McGavin 1978; Jaeger & Gergits, 1979), and may play a role in defense against predators (Pfeiffer, 1974).

An alarm reaction to chemicals released from injured conspecifics occurs in a wide variety of aquatic animals, including various species of invertebrates (Howe & Sheikh, 1975; Snyder & Snyder, 1970; Stenzler & Atema, 1977) that move away from areas containing injured conspecifics,

and in fishes (Pfeiffer, 1974; Smith, 1977). In many fish species (Pfeiffer, 1974; Smith, 1977), the type of alarm response seems appropriate to the habitat it dwells in and the types of predators it has. Among fish, responses to alarm substances include resting on the bottom, remaining motionless, seeking cover in vegetation, leaping at the surface, or schooling more tightly (see reviews by Pfeiffer, 1974, 1977; Smith, 1977, 1982). Larval amphibians also display such responses, although they have not been as well studied as fish (Pfeiffer, 1974, 1977; Smith, 1977, 1982). The alarm response in amphibians may function as an antipredator defense mechanism (Pfeiffer, 1974; Smith, 1977) and individuals that respond in such a manner to chemicals released from damaged conspecifics may successfully avoid predation.

The taxonomic distribution of the alarm response in anuran larvae is not clear. Testing nine anuran species in five families (Bufonidae, Discoglossidae, Hylidae, Pipidae, and Ranidae), Pfeiffer (1966) found larval alarm reactions in only two species of bufonids. Pfeiffer (1966) speculated that the alarm reaction may be common in and unique to bufonids. Nonetheless, similar alarm responses have been reported for a pelobatid (Richmond, 1947) and a ranid (Altig and Christensen, 1981) and further research is needed to clarify the taxonomic distribution of the alarm response to help answer questions on its evolutionary and ecological significance.

This study investigated the response of larval Cascades frogs (*Rana cascadae*) and Western toads (*Bufo boreas*) to chemical cues from damaged and undamaged larvae of conspecifics and nonconspecifics. The larvae of these species were chosen because of their highly social behavior. Both species form conspicuous aggregations in nature and social cues are important in their formation (see O'Hara, 1981 for discussion; Blaustein & O'Hara, 1982b; O'Hara & Blaustein, 1982). Furthermore, it has been established that *R. cascadae* tadpoles display a well-developed ability to recognize kin based on chemical cues and they may form kin groups in nature (Blaustein & O'Hara, 1981, 1982a; O'Hara & Blaustein, 1981). Therefore, an alarm reaction could have been selected for this species (see Hamilton, 1964).

METHODS

Animals and Rearing Conditions

B. boreas tadpoles were collected in the Oregon Cascade Mountains (1219 m) from Lost Lake, Linn County, Oregon on 14 July 1982 and 28 July 1983. All *Bufo* tadpoles used in tests and extracts (see below) were at Gosner (1960) developmental stages 27–34 ($\bar{x} = 31$). *R. cascadae* egg masses were collected from a small pond (1290 m) in Marion County, Oregon on 20 July 1983. All *Rana* tadpoles used in tests and extracts were Gosner (1960) stages 33–38 ($\bar{x} = 35$). Tadpoles of the Pacific tree

frog (*Hyla regilla* were collected while in Gosner stages 27–35 ($\bar{x} = 32$) from a pond (1190 m) in Linn County. Tadpoles were maintained in 38-liter aquaria, in dechlorinated tap water with an aeration stone. Room temperature was 16–18°C, and the tadpoles were kept under a 16L:8D light cycle. The tadpoles were fed Purina Rabbit Chow daily and the water was changed every 3 days.

Apparatus and Testing Procedures

The protocol of von Frisch (1941) is generally used to study alarm reactions. When using this protocol individuals are trained to feed at a station and are then presented with an extract containing the supsected alarm substance and the behavioral reaction is recorded. This method has been recently criticized by Smith (1979) and Waldman (1982).

To quantify the potential alarm reaction in *B. boreas* and *R. cascadae* tadpoles we used procedures which avoided the "conditioning" method and its complications. We measured aspects of both spatial distribution and activity responses of individuals to the suspected alarm substance. In two experiments, we recorded responses of individual tadpoles to the presence of one of two types of stimulus solutions. In the first experiment using *Bufo* and *Rana* tadpoles, the stimulus solution contained chemical cues from damaged conspecifics to test the hypothesis that individuals would avoid areas containing cues emanating from damaged conspecifics. In the second experiment using both *Bufo* and *Rana* tadpoles, the stimulus solution contained chemical cues from damaged, nonconspecific tadpoles. In the control, the stimulus solution used was plain water. Twenty different test individuals were used to test reactions to the stimulus solutions and for the control solution, for each tadpole species.

The stimulus solutions used in the first experiment for *Bufo* and for *Rana* tadpoles will be referred to as "*Bufo* extract" and "*Rana* extract," respectively. Both extracts were made by macerating a known wet weight of tadpoles ($\bar{x} = 5.10$ g). After sacrificing the tadpoles, the viscera were removed. The remaining carcasses, consisting primarily of epidermal and dermal tissue layers, were then macerated. The resulting slurry was mixed with 200 ml of dechlorinated tap water and, after 20 min of agitation, the mixture was filtered through a Buchner funnel and brought to a 1-liter volume.

The stimulus solution for both *Bufo* and *Rana* tadpoles in the second experiment was a *Hyla* extract, made using the methods described above using *H. regilla* tadpoles. For the control tests, dechlorinated tap water was used as the stimulus solution. All stimulus solutions were stored on ice and used in tests within 1 week. Prior to use in a test, portions were removed from the stock stimulus solutions and allowed to reach room temperature (16–18°C).

Tests were conducted in an opaque plastic tub (28 × 18 × 12 cm)

with a line delineating two halves (14 × 19 cm) and filled to a depth of 4 cm with dechlorinated tap water. This tub, thoroughly rinsed between each test, was placed behind an opaque black plastic observation blind. Ten minutes prior to each test, one tadpole was released in the center of the tub and allowed to acclimate. Through a slit in the blind, 5 ml of the stimulus solution (control or experimental) was introduced, with a pipet, 1 cm below the surface of the water into both corners of one end of the tub. The side of stimulus introduction was alternated from left to right. The side of stimulus introduction was always the side in which the tadpole, at the beginning of the test, was not located. If, after the 10-min acclimation period, the tadpole was in the side designated to be the side of stimulus solution introduction, we waited (for no longer than 2 min; otherwise the trial was discarded) until the tadpole swam to the other side and then introduced the stimulus. Starting when the tadpole first swam to the stimulus side (waiting no longer than 2 min for this to occur), the time the tadpole spent (in seconds) in stimulus and nonstimulus halves of the tub was recorded during a 5-min observation period. One milliliter of stimulus solution was added to each stimulus-side corner at 1-min intervals. For *Rana* tadpoles, the time individuals spent swimming was recorded as a measure of activity. Pilot tests revealed, however, that individual *Bufo* tadpoles spent essentially the entire test period swimming. As a measure of *Bufo* activity, the number of times the center line was crossed during the 5-min observation period was recorded instead. Complete water mixing occurs in less than 16 min in 38-liter aquaria when vital dyes were used to test the diffusion rates of chemical substances in previous tests (O'Hara and Blaustein, 1981). In the plastic tubs used here, complete water mixing and diffusion of chemicals was much more rapid.

The total amount of time spent on stimulus and nonstimulus halves of the tank was used as a measure of tadpole preference (or aversion). The Wilcoxon signed-ranks test (Sokal and Rohlf, 1969) was used to test whether the time tadpoles spent on the stimulus half was significantly different from random expectation. To conduct this analysis, 150 s (the expected time out of a possible 300 s tadpoles would spend on each tank side if choice behavior was random) was subtracted from the total time spent by each tadpole on the stimulus side. In addition, the number of individuals spending the majority of their time (>150 s) on the stimulus side was compared to random expectation using the binomial test (Siegel, 1956) with a null hypothesis of no difference.

For both species, the activities of tadpoles in response to the experimental stimulus solutions were compared to the activities observed in response to the control stimulus solution. Comparisons were made using the Mann-Whitney U test (Sokal and Rohlf, 1969). Statistical comparisons involving results from the first experiment were one-tailed based on the predictions

that tadpoles would avoid the side containing chemical cues from damaged conspecifics and would increase their activity in response to these cues. Statistical tests for the second experiment and for the control were two-tailed because of no a priori expectations. A significance level of $p <$ .05 was used in all statistical tests.

RESULTS

Bufo Experiments

Results of the *Bufo* extract experiment suggest that this species has an alarm response. Individuals avoided the side of the tank to which an extract solution was introduced (Table 1). The time spent in the stimulus half in the first experiment differed significantly from random, and only 3 of 20 tadpoles spent the majority of their time on the stimulus half. In addition, activity was greater in Experiment 1 compared to the control; the number of times test tadpoles crossed the center line was significantly higher than in the control.

Bufo tadpoles did not respond to chemical cues from damaged non-conspecific tadpoles (Table 1). In the second experiment, which used *Hyla* extract, neither the amount of time spent on the stimulus side nor the number of individuals spending the majority of their time on the stimulus side differed from random expectation. Activity in the second experiment also did not differ from activity observed in the control. These results suggest that the observed alarm response to *Bufo* extract is not simply a general response to injured tadpoles. Tadpoles exhibited no side preferences in control tests and there were no biases in the testing procedures

Rana Experiments

Although *Rana* did not exhibit as distinctive a response to damaged conspecifics as did *Bufo*, results suggest they also have an alarm response (Table 1). Individual *Rana* tadpoles did not avoid the half of the tank that contained chemical cues from damaged conspecifics (Experiment 1, Table 1). Neither the time spent on the stimulus half nor the number of individuals spending the majority of their time in the stimulus half differed from random in the first experiment. However, *Rana* activity increased significantly in response to the extract of damaged conspecifics. Tadpoles spent significantly more time swimming in the first experiment than in the control. Results from the second experiment suggest that *Rana* was not affected by chemical cues from damaged *Hyla* tadpoles (Table 1). Tadpoles exhibited no side preferences in control tests.

DISCUSSION

The results of this study suggest that larval *B. boreas* have an alarm response. *B. boreas* tadpoles avoided an area containing chemicals from

TABLE 1

Association Preferences and Activities of Larval *B. boreas* and *R. cascadae* in Response to Stimulus Solutions

Experiment	Species tested	Stimulus solution	No. spending majority of time[a]		Seconds, out of 300 spent on stimulus half (mean ± SE)	Wilcoxon t	No. times individual crossed center line (mean ± SE)	Mann–Whitney[b] U
			Toward stimulus	Toward nonstimulus				
1	*Bufo*	Extract	3	17*	125.4 ± 5.9	15.5*	47.7 ± 3.3	363*
	Rana	Extract	10	9**	147.4 ± 12.7	96.5**	54.9 ± 9.3	292*
2	*Bufo* response to *Hyla*	Extract	11	9**	159.5 ± 1.3	99**	28.1 ± 3.1	228**
	Rana response to *Hyla*	Extract	14	6**	182.3 ± 17.4	57**	29.5 ± 6.2	206**
Control	*Bufo*	Water	11	9**	152.8 ± 10.6	85.5**	26.2 ± 2.1	
Control	*Rana*	Water	10	10**	146.4 ± 16.1	94.5**	29.0 ± 4.8	

Note. $N = 20$ for each experiment.
[a] Compared using binomial test.
[b] Values compared to control.
* $p < 0.01$.
** $p > 0.05$.

injured conspecifics and increased their activity but neither avoided the stimulus side nor increased their activity in response to an extract of nonconspecific (*Hyla*) tadpoles. These results suggest that avoidance and activity changes are in response to chemical cues that occur in conspecifics and are not a general response to injured tadpoles.

R. cascadae tadpoles also seem to have an alarm response. *R. cascadae* did not avoid the *Rana* extract but activity did increase significantly over control levels in response to the extract. *Rana* tadpoles did not avoid chemicals from injured nonconspecifics. The increased activity in response to *Rana* extract could be interpreted as an alarm response and not a feeding response, because *Rana* extract did not attract *Rana*. Our laboratory results showing increased activity of *R. cascadae* tadpoles in response to conspecific extract are consistent with field observations. In the field, *R. cascadae* tadpoles, when alarmed by predators, quick movement of water, or by an approaching human, respond with an explosive burst of swimming in which individuals of a group disperse rapidly (up to 10 m away), sink to the bottom, and remain motionless (personal observations; O'Hara, 1981). Frequently, (although this was not quantified) the increase in activity in *Rana* extract tests was due to chaotic spurts of activity; the test tadpole swam around the tank several times before stopping on one side or the other, apparently at random. The alarm response to *Rana* extract reported here could be a similar response constricted by the test tank.

Larval predation defenses. Larval anuran amphibians may be more vulnerable to predation than other phases in the anuran life-cycle (Savage, 1952; Turner, 1962; Herreid & Kinney, 1966; Calef, 1973; Heyer, 1976) and predation may influence the distribution and abundance of tadpole populations (Brockelman, 1969; Licht, 1974; Heyer, McDiarmid, & Weigmann, 1975; Heyer, 1976; Heyer & Muedeking, 1976; Cecil & Just, 1979; Caldwell, Thorp, & Jervey, 1980; Wilbur, Morin, & Harris, 1983). The effects of predation, however, can be modified by a variety of morphological, physiological, and behavioral factors (Wassersug, 1971, discussed below).

Bufonid larvae possess several traits that may reduce predation. Larval bufonids aggregate and many of the hypothetical antipredator advantages of aggregating (Alexander, 1974; Bertram, 1978) could apply to tadpoles. In addition, larval bufonids, like the adults, are toxic or unpalatable to many predators (Voris & Bacon, 1966; Wassersug, 1971; Cooke, 1974; Hews, unpublished data), although this distastefulness may vary with larval stage (Formanowicz & Brodie, 1982) and may be ineffective against certain predators (Cooke, 1974; Walters, 1975; Arnold & Wassersug, 1978; Beiswenger, 1981; Morin, 1981, 1983; Hews, unpublished data). Toad tadpole aggregations may function aposematically and warn wouldbe predators, as suggested by the gregariousness, distastefulness, and

conspicuousness of these tadpoles (Wassersug, 1971, 1973). Many bufonid tadpole aggregations are highly visible aggregations of hundreds to thousands of individuals (Wassersug, 1973; O'Hara, 1981; O'Hara & Blaustein, 1982), which are all the more conspicuous because of their black coloration (Wassersug, 1973). Any benefits of distastefulness could be augmented by aposematic coloration or conspicuous behaviors, because visual predators may more readily learn to avoid such distasteful prey (Gittleman, Harvey, & Greenwood, 1980).

Ranid larvae also have characteristics that may lessen the impact of predation. Antipredation benefits of aggregating (Alexander, 1974; Bertram, 1978) may also apply to ranid larvae that aggregate. Like bufonids, some ranid larvae are not preferred prey, compared to other anuran larvae, or are completely rejected by predators, probably because of distastefulness (Lewis, Gunning, Lyles & Bridges, 1961; Liem, 1961; Walters, 1975; Kruse & Francis, 1977; Morin, 1981). Moreover, *R. cascadae* tadpoles are sensitive to visual and physical disturbances of the water and have an explosive escape response when startled by an approaching human (personal observations; O'Hara & Blaustein, 1981). Also like bufonids, some unpalatable ranids form conspicuous aggregations that may function aposematically (Wassersug, 1973). Furthermore, the ability of *R. cascadae* tadpoles to recognize kin could help ensure against recognition errors if warning behavior is an important function of the alarm response when mixing of kin and nonkin occurs in nature due to disturbances. Individuals that warn others in groups of many relatives could increase their inclusive fitness through kin selection by warning members of their group, compared to those individuals giving a similar warning in groups of fewer or no kin (Blaustein & O'Hara, 1982b; O'Hara & Blaustein, 1981). The chemical cues examined in this study may trigger an alarm response that could deter predation. This alarm reaction is an example of how group-living animals such as larval *R. cascadae* and *B. boreas* may increase their ability to detect and avoid predators.

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