

Unpalatability in anuran larvae as a defense against natural salamander predators

J.A. PETERSON and A.R. BLAUSTEIN¹

*Department of Zoology, Oregon State University, Cordley Hall 3029, Corvallis, Oregon
97331-2914, U.S.A.*

Received 23 February 1990, accepted 28 June 1990

Throughout the animal kingdom, there is a general correlation between conspicuousness and qualities that are aversive to predators. The larvae of certain species of anuran amphibians form extremely large, conspicuous, aggregations composed of thousands of individuals. Members of these aggregations are not overtly attacked or eaten by vertebrate predators. The larvae of other anuran species are cryptic, form small aggregations, disperse rapidly from and are readily eaten by vertebrate predators. In conjunction with forming large, conspicuous groups, unpalatability may be one means by which larvae in conspicuous groups avoid predation. Therefore, in the laboratory, we used natural salamanders as predators to investigate relative palatabilities of the larvae of three species of anurans that differ in their mode of aggregation. The larvae of the western toad (*Bufo boreas*) form large conspicuous aggregations and are not conspicuously attacked by most vertebrate predators. The larvae of the Cascades frog (*Rana cascadae*) and Pacific treefrog (*Hyla regilla*) form small aggregations and readily flee from and are taken by vertebrate predators. Proportionately fewer *Bufo* than *Rana* and *Hyla* tadpoles of similar size and same developmental stage were consumed by salamanders. Differential predation on *Bufo*, *Rana* and *Hyla* tadpoles was probably due to distasteful qualities of *Bufo* larvae as opposed to differences in prey size or escape ability. Most *Bufo* tadpoles captured by salamanders were rejected unharmed. *Rana* and *Hyla* tadpoles were palatable at all stages of development tested.

KEY WORDS: anurans, tadpoles, palatability, predator/prey.

Introduction	64
Methods	65
Results	67
Discussion	69
Acknowledgements	70
References	71

¹ Please address all correspondence to Andrew R. Blaustein, Department of Zoology, Oregon State University, Cordley Hall 3029, Corvallis, Oregon 97331-2914, U.S.A. Phone (503) 737-3705.

INTRODUCTION

Within the animal kingdom there is a general correlation between conspicuousness and noxiousness (see GUILFORD 1988 for a recent review). Both invertebrates and vertebrates display this relationship and the conspicuous qualities of an animal are often explained as warning coloration (e.g. DODSON & DODSON 1976; but see GUILFORD 1988 for alternative explanations). The relationship may be especially prevalent in larval anuran amphibians. The larvae of many species of anuran amphibians aggregate in nature. As in other animals, decreased risk of predation may be among one of the many benefits accrued by individual tadpoles within groups at this especially vulnerable stage (e.g. BEISWENGER 1975, WILBUR 1977, BRODIE & FORMANOWICZ 1987, BLAUSTEIN 1988). Indeed, it is well documented that anuran amphibian mortality is relatively high during the larval stages or during metamorphosis and much of this is due to predation (e.g. CALEF 1973, ARNOLD & WASSERSUG 1978, FORMANOWICZ & BRODIE 1982, CRUMP 1984).

Among group-forming tadpoles, there are species that are extremely conspicuous, whose aggregations may consist of millions of individuals stretching hundreds of meters and whose members do not conspicuously disperse from nor are attacked by large vertebrate predators (e.g. WASSERSUG 1971, BLAUSTEIN et al. 1987: 303). In contrast, there are other species of group-forming tadpoles whose aggregations are small, whose members are cryptic, and that disperse rapidly from and are taken readily by large vertebrate predators (see reviews in WASSERSUG 1973 and in DUELLMAN & TRUEB 1986, O'HARA & BLAUSTEIN 1981). In conjunction with conspicuous group formation, unpalatability may be one means by which amphibians avoid predation (e.g. VORIS & BACON 1966, WASSERSUG 1973, BRODIE et al. 1978, FORMANOWICZ & BRODIE 1982, KRUSE & STONE 1984, KATS et al. 1988). Unpalatability in larval anurans may be beneficial to an individual because a predator that tastes an unpalatable individual may not swallow it and the larva may escape. If, however, the larvae comprising an aggregation are mostly kin, and individuals are usually eaten rather than expelled by the predator, then the maintenance of noxiousness may be through kin selection (e.g. FISHER 1930, BENSON 1971, HARVEY & GREENWOOD 1978) if a predator who sampled a distasteful individual avoids the other members of the group (WASSERSUG 1973, WALDMAN & ADLER 1979).

Although it is often difficult to explain the evolutionary origins of conspicuousness and unpalatability, throughout the animal kingdom, there is a general correlation between conspicuous coloration and qualities that are aversive to predators (see discussion in GUILFORD 1988). To more fully understand the role of noxiousness as an antipredator defense in anuran larvae, we investigated the relative palatabilities of the larvae of three species of anurans to two natural salamander predators in choice tests. The larvae of one anuran we examined, the western toad (*Bufo boreas*), are conspicuously black in color, form enormous aggregations in nature composed of individuals from numerous clutches, and do not overtly disperse from their natural vertebrate predators (O'HARA 1981, O'HARA & BLAUSTEIN 1982, BLAUSTEIN et al. 1987, BLAUSTEIN 1988). Tadpoles of the second species we tested, the Cascades frog (*Rana cascadae*), are cryptically colored, form small cohesive groups of generally fewer than 100 individuals, and rapidly disperse from predators (O'HARA 1981, O'HARA &

BLAUSTEIN 1981, BLAUSTEIN & O'HARA 1987, BLAUSTEIN 1988). Tadpoles of the third species, the Pacific treefrog (*Hyla regilla*), are cryptic, intermittently form small, loose aggregations and are preyed upon by a wide range of large vertebrate predators (O'HARA 1981, NUSSBAUM et al. 1983).

As pointed out by BRODIE & FORMANOWICZ (1987; see also FORMANOWICZ & BRODIE 1982), the concept of prey palatability is most important in a relative sense and is probably contingent upon the availability of alternative prey. Based on larval ecology and behavior and on previous studies showing that tadpoles of some toad species may be noxious (e.g. FORMANOWICZ & BRODIE 1982, BRODIE & FORMANOWICZ 1987), we tested the hypothesis that *B. boreas* tadpoles would be less palatable to salamanders than are *R. cascadae* and *H. regilla* tadpoles. Because there may be ontogenetic changes in palatability and newly hatched tadpoles may be less palatable than other larval developmental stages (see BRODIE & FORMANOWICZ 1987), we evaluated tadpole palatability at two times in larval development.

METHODS

Anuran egg masses or tadpoles were collected from lakes and ponds in the Oregon Cascade Mountains and transported to our laboratory in Corvallis for rearing and testing. Roughskin Newts (*Taricha granulosa*) and Northwest Salamanders (*Ambystoma gracile*) were used as predators. Both salamanders are important predators of anuran larvae (e.g. CALEF 1973, LICHT 1974) and are frequently found in lakes and ponds with *R. cascadae*, *H. regilla*, and *B. boreas* tadpoles (personal observations). All of the *A. gracile* predators were captured from a lake in Linn County which is not used for breeding by *R. cascadae* or *B. boreas* (TAYLOR 1977, personal observations, R. O'HARA personal communication). Because we used aquatic *A. gracile* larvae and neotenic adults, which presumably have never left the confines of the lake, it is unlikely that any *A. gracile* used in this study had previously experienced either *R. cascadae* or *B. boreas* tadpoles. However, the *A. gracile* used in this study may have encountered *H. regilla* because *H. regilla* may breed at the lake from which *A. gracile* were captured. The *T. granulosa* predators used in one experiment (experiment 3; see below) were also captured from this lake and it is possible that these individuals had previously encountered all three tadpoles species because adults may leave the lake after breeding. However, the *T. granulosa* used in experiments 5 and 6 were taken from a lake in Benton County where neither *R. cascadae* or *B. boreas* occur and where *H. regilla* are rare (NUSSBAUM et al. 1983).

Tadpole palatability was evaluated using methods similar to those of BRODIE & FORMANOWICZ (1987). In each trial a starved salamander was offered 20 tadpoles, 10 of one species and 10 of another. In all experiments, tadpoles were matched as close as possible for size although it is difficult to control for size and developmental stage simultaneously. Because tadpole palatability may change with development and vulnerability to predation may change with growth (e.g. BRODIE & FORMANOWICZ 1983, 1987), a series of experiments that control precisely for developmental stage and size was carried out.

In experiments 1, 2, 3, and 4 (see below), tadpoles of each species were matched for developmental stage. In experiment 5, tadpoles of each species were carefully matched for size. Most of the matched-pairs offered to salamanders consisted of tadpoles that were from a species suspected as being distasteful and from a species thought to be palatable. However, we initially paired *B. boreas* (B), *R. cascadae* (R), and *H. regilla* (H) tadpoles (a known palatable species; unpublished data) in all possible combinations (B/H, B/R, R/H) and presented these matched-pairs to *A. gracile* larvae to evaluate the relative palatability of each species.

Before experiments began, predator hunger levels were standardized by placing a salamander in a 25 × 15 cm plastic test apparatus filled 5 cm deep with dechlorinated tapwater and allowing it to feed ad libitum on *Tubifex* worms for 24 hr. After this period, all food was removed, the water was changed, and predators were starved for various lengths of time.

Trial times were predetermined such that, on the average, a trial would last about 25% of one species had been consumed; thus, a predator's sample of prey items was never largely biased towards one species of tadpole. At the end of a trial we would record the number of tadpoles that survived and the number that was eaten.

Study animals were kept at 20-22 °C in a laboratory under a natural photoperiod. Tadpoles were maintained in 38-liter aquaria, with dechlorinated tapwater and an aeration stone. They were fed a diet of rabbit pellets daily and their water was changed as needed. Salamanders were held in 120×60 cm tanks filled 15 cm deep with dechlorinated tapwater. While in the laboratory, salamanders were maintained on *Tubifex* worms.

Before the experiments described below were conducted, 20-30 tadpoles of each species were randomly drawn and measured (so that body size matching could be precise; total length in mm), their developmental stage was determined (GOSNER 1960), and they were gently wiped dry with absorbent paper and weighed to the nearest centigram. Wet weights of predators were determined by wiping salamanders dry and weighing them to the nearest centigram. Upon completion of the study, surviving animals were released at their sites of capture.

Experiment 1. In this experiment, newly-hatched (stages 24-26) tadpoles were offered to larval *A. gracile* (total n = 15) that had been starved for 24 hr. Each category of matched-pair (B/R, B/H, R/H) had five replicates. Trials lasted for 7 hr.

Experiment 2. *A. gracile* larvae (total n = 15) were starved for 72 hr before being offered newly-hatched tadpoles (stages 25-26). A longer starvation period was used to determine whether the hunger level of a salamander has an effect on the acceptability of suspected distasteful tadpoles (KRUSE & STONE 1984). Five replicates of three categories of matched-pairs (B/R, B/H, R/H) were conducted. Trials lasted for 6 hr.

Experiment 3. Different natural predators may be more or less tolerant to tadpole chemical defenses. Therefore, newly-hatched *B. boreas* and *H. regilla* (B/H) tadpoles (stages 25-28) were offered to adults of another salamander predator, *T. granulosa* (total n = 7), that had been starved for 24 hr. Trials lasted for 24 hr.

Experiment 4. To evaluate the relative palatability of tadpoles in the middle stages of larval development (stages 34-41), large neotenic adult *A. gracile* (total n = 14) were starved for 72 hr and offered either a B/R matched-pair (n = 7) or a B/H pair using middle stage larvae for all tadpoles (n = 7). The results of preliminary experiments using large *A. gracile* as predators of mid-developmental tadpoles suggested that *R. cascadae* and *H. regilla* tadpoles were similar in palatability, but *B. boreas* tadpoles may be distasteful (unpublished data). Therefore, suspected unpalatable *B. boreas* were paired with both *R. cascadae* and *H. regilla* tadpoles. Trials lasted 24 hr.

Experiment 5. Tadpole vulnerability to predation may change with size. Therefore, we precisely controlled for between-species differences in tadpole size in this experiment. Adult *T. granulosa* (total n = 20) were starved for 52 hr and then offered *B. boreas* and *R. cascadae* (B/R) tadpoles (stages 27-31). Tadpoles of each species were weighed by gently blotting tadpoles dry with absorbent paper and then placing them in a cup of water on a balance (Mettler AC 100). Tadpoles of both species were matched for size. All tadpoles used in a trial weighed within 0.02 g of each other and tadpole weights ranged from 0.10 to 0.15 g. Trials lasted 12 hr.

Experiment 6. Rejection of tadpoles by adult *T. granulosa* (total n = 5) was quantified by starving salamanders for an extended period of time (70 hr) and recording the outcome of all attacks on tadpoles on a 10 min trial. *B. boreas* and *R. cascadae* tadpoles were weighed as in experiment 5 and matched for size. All tadpoles weighed 0.10-0.12 g. We recorded all captures (i.e. salamander engulfs at least head of tadpole and holds tadpole in buccal cavity) as either «rejected» (tadpole engulfed and subsequently released) or «swallowed» (tadpole engulfed and not released). We also noted whether «rejected» tadpoles survived or died.

For experiments 1, 2, and 4, a G-test of independence with Yates' correction for continuity (see SOKAL & ROHLF 1969) was used to test whether the proportion of *R. cascadae* tadpoles that survived in an experiment was different from the proportion of *H. regilla* tadpoles that survived. If

no difference was found, *R. cascadae* and *H. regilla* tadpoles were considered to be similar in palatability and were treated as «palatable control» tadpoles. A two-tailed Wilcoxon paired-sample test (ZAR 1984) was then used to test whether the number of *B. boreas* eaten by salamanders was different from the number of «control» (either *R. cascadae* or *H. regilla*) tadpoles eaten. For experiment 3, a two-tailed Wilcoxon paired-sample test was used to test whether the number of *B. boreas* tadpoles (suspected as being unpalatable) that survived a trial was greater than the number of *H. regilla* tadpoles (known to be palatable) that survived. A paired t test (SNEDECOR & COCHRAN 1980) was used to test whether the number of *B. boreas* surviving a trial differed from the number of similar sized *R. cascadae* tadpoles that survived in experiment 5.

RESULTS

Each experiment was designed with groups of palatable control tadpoles and suspected unpalatable tadpoles. Therefore, we make no direct, between experiment comparisons unless variables such as predator size, population of tadpole origin, starvation time or trial length were similar or controlled.

In all experiments, as has been observed in the field and in previous laboratory experiments (e.g. O'HARA 1981, O'HARA & BLAUSTEIN 1982, HEWS & BLAUSTEIN 1985), *B. boreas* tadpoles appeared more active than either *R. cascadae* or *H. regilla* tadpoles. *B. boreas* tadpoles continuously swam throughout the test container without overtly avoiding the predator whereas *R. cascadae* and *H. regilla* tadpoles tended to remain still, usually near the bottom of the container.

There was no significant difference between the proportion of *R. cascadae* tadpoles eaten by both larval and neotenic adult *A. gracile* and the proportion of *H. regilla* tadpoles eaten (Table 1). The relative palatability of *R. cascadae* and *H. regilla* tadpoles to *A. gracile* was similar in both early and mid-larval development (Table 1).

Larval *A. gracile* and adult *T. granulosa* consumed more newly-hatched *R. cascadae* and *H. regilla* tadpoles than *B. boreas* larvae of similar size and developmental stage (Table 2). Furthermore, neotenic adult *A. gracile* consumed more mid-develop-

Table 1.
Relative palatability of *Rana cascadae* and *Hyla regilla* tadpoles to *Ambystoma gracile* predators.

Experiment	Predator	Starve time (in hr)	Tadpoles				Adjusted G-statistic	Significance ($\alpha = 0.05$)
			<i>Rana</i>		<i>Hyla</i>			
			S	E	S	E		
1	<i>A. gracile</i> larvae	24	77	23	79	21	0.028	NS
2	<i>A. gracile</i> larvae	72	44	56	54	46	1.622	NS
4	<i>A. gracile</i> adults	72	58	12	60	10	0.052	NS

S = number that survived; E = number that were eaten.

Table 2.
Palatability of *Bufo boreas*, *Rana cascadae*, and *Hyla regilla* tadpoles to *Ambystoma gracile* and *Taricha granulosa*.

Experiment	Predator	Predator ^c weight		Tadpoles			P < (two-tailed)
					Control		
				<i>Bufo</i>	<i>Rana</i>	<i>Hyla</i>	
1 ^a	<i>A. gracile</i> larvae	3.81 ± 0.37 (n = 15)	Stages	25-26	25-26	24-25	0.05
			length ^d	13.9 ± 0.2 (n = 20)	16.9 ± 0.3 (n = 20)	14.2 ± 0.4 (n = 20)	
			% survived	100	77	79	
2 ^a	<i>A. gracile</i> larvae	4.97 ± 0.52 (n = 15)	Stages	25-26	25-26	25-26	0.01
			length ^d	14.3 ± 0.1 (n = 25)	17.4 ± 0.2 (n = 25)	15.5 ± 0.2 (n = 25)	
			% survived	94	44	54	
3 ^b	<i>T. granulosa</i> adults	10.70 ± 1.24 (n = 7)	Stages	25-27		25-28	0.05
			length ^d	15.1 ± 0.2 (n = 25)		17.9 ± 0.4 (n = 25)	
			% survived	89		50	
4 ^a	<i>A. gracile</i> adults	10.72 ± 1.11 (n = 14)	Stages	35-41	34-40	34-40	0.01
			length ^d	38.9 ± 0.5	50.2 ± 0.7	35.8 ± 0.8	
			weight ^c	0.51 ± 0.02 (n = 25)	0.90 ± 0.04 (n = 25)	0.64 ± 0.04 (n = 25)	
			% survived	99	83	86	

^a There were no trials where more *Bufo* were eaten than *Hyla* or *Rana* tadpoles. ^b In 1 of 7 trials more *Bufo* were eaten than *Hyla* tadpoles. ^c Mean weight (g) ± standard error of the mean. ^d Mean length (mm) ± standard error of the mean.

mental *R. cascadae* and *H. regilla* tadpoles than *B. boreas* tadpoles (Table 2). In experiments 1-4, *B. boreas* tadpoles were, on the average, slightly smaller than both the *R. cascadae* and *H. regilla* tadpoles that they were paired with. However, when tadpoles were carefully matched for size (experiment 5), adult *T. granulosa* consumed fewer *B. boreas* tadpoles than *R. cascadae* (Table 3). In all of the salamander experiments, regardless of whether tadpoles were newly-hatched or in mid-developmental stages, fewer *B. boreas* were eaten than either *R. cascadae* or *H. regilla*.

In experiment 6, *T. granulosa* (n = 5, mean wt = 10.91 g) rejected 57% of all *B. boreas* tadpoles captured during the trial (23 captured, 13 rejected). Only one *R. cascadae* tadpole captured was later rejected (18 captured, 17 swallowed). This individual was captured simultaneously with a *B. boreas* tadpole and was released when the *B. boreas* tadpole was released. *B. boreas* tadpoles were usually expelled within 60 sec of being captured, however, salamanders held some individuals in their buccal cavity for up to 3 min before releasing them. *B. boreas* tadpoles usually survived the process of being engulfed and expelled by salamanders with no apparent ill effects. In all of our experiments, only two newly-hatched *B. boreas* individuals were found dead and uneaten.

Table 3.
Palatability of 0.10-0.15 g *Rana cascadae* and *Bufo boreas* tadpoles to *Taricha granulosa*.

Experiment	Predator	Predator ^a weight		Tadpoles		Two-tailed paired t
				<i>Bufo</i>	<i>Rana</i>	
5	<i>T. granulosa</i> adults	10.83 ± 1.39 (n = 20)	Stages	27-31 (n = 30)	27-30 (n = 30)	t = 2.685*
			% survived	69.5	40.5	df = 19

* $P < 0.025$. ^a Mean weight (g) ± standard error of the mean.

The acceptability of newly-hatched *B. boreas* tadpoles relative to *R. cascadae* and *H. regilla* of similar size and developmental stage did not appreciably differ when *A. gracile* larvae were starved for 72 hr as opposed to 24 hr (Table 2).

DISCUSSION

The hypothesis that *B. boreas* tadpoles are less palatable to their natural salamander predators than are *R. cascadae* and *H. regilla* tadpoles is supported by our results. However, *R. cascadae* and *H. regilla* tadpoles were palatable at all stages of development tested. Therefore, the hypothesis that tadpoles display differential palatability at different stages of development was not supported by our results.

Proportionately fewer *B. boreas* tadpoles were consumed by *A. gracile* and *T. granulosa* predators than *R. cascadae* and *H. regilla* of similar size and same developmental stage, regardless of whether anuran larvae were newly-hatched or in mid-larval development. The proportion of *R. cascadae* tadpoles eaten by *A. gracile* did not significantly differ from the proportion of *H. regilla* tadpoles consumed.

Differential predation on *B. boreas*, *R. cascadae*, and *H. regilla* tadpoles by salamanders was likely due to distasteful qualities of *B. boreas* larvae as opposed to differences in prey size or escape ability. When tadpoles were carefully matched for size (experiment 5), *R. cascadae* tadpoles were selectively preyed upon over *B. boreas* tadpoles. In laboratory tests, *Bufo* and *Rana* tadpoles are about equal in their abilities to escape and out maneuver predators (K.S. HOFF pers. commun., HOFF 1986). However, in our experiments, *B. boreas* tadpoles constantly swam whereas *Rana* and *Hyla* tadpoles occasionally became inactive. Thus, *Bufo* tadpoles were frequently captured by salamanders which tend to focus their attacks on moving prey (WASSER-SUG & SPERRY 1977). Once *B. boreas* tadpoles were captured, they were usually held in the buccal cavity for several seconds and then expelled.

After starving *T. granulosa* for an extended period of time (70 hr), we found that 57% of all *B. boreas* captured were released unharmed. Those *B. boreas* tadpoles that were captured and rejected survived with no apparent ill-effects for at least several days. None of the tadpoles we observed being rejected died. Both newly-hatched and mid-developmental *B. boreas* tadpoles were captured and rejected by salamanders. KRUSE & STONE (1984) reported that largemouth bass (*Micropterus salmoides*) rejected

B. americanus and *B. woodhousei* tadpoles in a similar way and that only 0.7% of the tadpoles rejected by bass died. Salamanders that ate *Bufo* tadpoles showed no ill effects but they were monitored carefully for only several hours after they had eaten a tadpole.

Bufo tadpoles are distasteful to both vertebrates (humans: WASSERSUG 1971; fish: VORIS & BACON 1966, KRUSE & STONE 1984, KATS et al. 1988; salamanders: HEUSSER 1971, COOKE 1974, WALTERS 1975; BRODIE & FORMANOWICZ 1987) and invertebrates (e.g. diving beetle larvae, water bug nymphs and dragonfly naiads: BRODIE et al. 1978, BRODIE & FORMANOWICZ 1987). However, many species of natural predators apparently find *Bufo* larvae palatable (salamanders: HEUSSER 1971, MORIN 1983; diving beetle larvae: YOUNG 1967, NEILL 1968, BRODIE et al. 1978, KRUSE 1983; water bugs: BRODIE et al. 1978, HEWS 1988; dragonfly naiads: BROCKELMAN 1969, HEYER & BELLIN 1973, HEYER et al. 1975, HEWS 1988; birds: BEISWENGER 1981; snakes: ARNOLD & WASSERSUG 1978).

Several factors may be responsible for the differences found in *Bufo* tadpole palatability. For example, it is possible that some predators find certain stages of tadpoles unpalatable whereas other predators may find the same stage palatable. Importantly, the experimental protocol for measuring tadpole palatability differs between studies. Many early studies were not carefully controlled because the developmental stages of the tadpoles being tested were not determined, predator hunger levels were not known, previous experience of predators was not known or predators were not offered a choice between *Bufo* larvae, suspected as being unpalatable and alternative palatable prey (for discussions see BRODIE et al. 1978, BRODIE & FORMANOWICZ 1987).

In natural situations the acceptability of a prey item is probably dependent on the availability of alternative palatable prey. Therefore, the concept of prey palatability should be interpreted in a relative sense (BRODIE & FORMANOWICZ 1987; see also PETERSON & RENAUD 1989). Similarly, the acceptability of relatively unpalatable prey may be correlated with predator hunger levels (KRUSE & STONE 1984). It is possible that there are significant interspecific and intraspecific differences in both *Bufo* tadpole chemical defenses and predator tolerance of tadpole distasteful qualities (WASSERSUG 1973). Adults of different *Bufo* species differ in the amount and type of toxins found in the skin (DALY & WITKOP 1971). If larval *Bufo* vary in a similar way, it may be expected that a given predator would find some species unpalatable, but others palatable.

Both experimental work (e.g. GITTLEMAN & HARVEY 1980, GUILFORD 1986) and theory (see for example reviews in KREBS & DAVIES 1987, GUILFORD 1988) suggest that there are benefits for distasteful prey to be conspicuous. Predators may learn to avoid conspicuously colored prey more easily and after they learn to avoid such prey, they may be less likely to attack these prey if they are conspicuous (GUILFORD 1986).

ACKNOWLEDGEMENTS

We thank N. Anderson, J. Beatty, E. Brodie Jr, T. Farrell, D. Formanowicz Jr, R. O'Hara, D. Olson, B. Tissot, T. Halliday and two anonymous reviewers for reading the manuscript. We thank V. Boggs for assistance in the laboratory and field and K. Chang, R. Harryhausen, and O'Brien for their usual tremendous help. Discussions with B. Menge, R. O'Hara, K.S. Hoff, and C.S. Peterson

were extremely helpful. This research was supported by Oregon State University Zoology grants, a grant from the Northwest Scientific Association to Jeffrey A. Peterson and National Science Foundation (U.S.A.) grants BNS-8406256 and BNS-8718536 to Andrew R. Blaustein.

REFERENCES

- ARNOLD S.J. & WASSERSUG R.J. 1978. Differential predation on metamorphic anurans by garter snakes (*Thamnophis*): social behavior as a possible defense. *Ecology* 52: 1014-1022.
- BEISWENGER R.E. 1975. Structure and function in aggregations of tadpoles of the American toad, *Bufo americanus*. *Herpetologica* 31: 222-233.
- BEISWENGER R.E. 1981. Predation by gray jays on aggregating tadpoles of the boreal toad (*Bufo boreas*). *Copeia*: 459-460.
- BENSON W.W. 1971. Evidence for the evolution of unpalatability through kin selection in the Heliconiinae (Lepidoptera). *American Naturalist* 105: 213-226.
- BLAUSTEIN A.R. 1988. Ecological correlates and potential functions of kin recognition and kin association in anuran larvae. *Behavior Genetics* 18: 449-464.
- BLAUSTEIN A.R., BEKOFF M. & DANIELS T.J. 1987. Kin recognition in vertebrates (excluding primates): empirical evidence, pp. 287-331. In: Fletcher D.J.C. & Michener C.D., Edits. Kin recognition in animals. London: John Wiley and Sons.
- BLAUSTEIN A.R. & O'HARA R.K. 1987. Aggregation behaviour in *Rana cascadae* tadpoles: association preferences among wild aggregations and responses to non-kin. *Animal Behaviour* 35: 1549-1555.
- BROCKELMAN W.Y. 1969. An analysis of density effects and predation in *Bufo americanus* tadpoles. *Ecology* 50: 632-644.
- BRODIE E.D. JR & FORMANOWICZ D.R. JR 1983. Prey size preference of predators: differential vulnerability of larval anurans. *Herpetologica* 39: 67-75.
- BRODIE E.D. JR & FORMANOWICZ D.R. JR 1987. Antipredator mechanisms of larval anurans: protection of palatable individuals. *Herpetologica* 43: 369-373.
- BRODIE E.D. JR, FORMANOWICZ D.R. JR & BRODIE E.D. III 1978. The development of noxiousness of *Bufo americanus* tadpoles to aquatic insect predators. *Herpetologica* 34: 302-306.
- CALEF G.W. 1973. Natural mortality of tadpoles in a population of *Rana aurora*. *Ecology* 54: 741-758.
- COOKE A.S. 1974. Differential predation by newts on anuran tadpoles. *British Journal of Herpetology* 5: 386-390.
- CRUMP M.L. 1984. Ontogenetic changes in vulnerability to predation in tadpoles of *Hyla pseudopuma*. *Herpetologica* 40: 265-271.
- DALY J.W. & WITKOP B. 1971. Chemistry and pharmacology of frog venoms, pp. 497-519. In: Bucherl W. & Buckley E.E., Edits. Venomous animals and their venoms. Vol. II. Venomous vertebrates. New York: Academic Press.
- DODSON E.O. & DODSON P. 1976. Evolution: process and product. New York: D. Van Nostrand Company.
- DUELLMAN W.E. & TRUEB L. 1986. Biology of amphibians. New York: McGraw-Hill.
- FISHER R.A. 1930. The genetical theory of natural selection. Oxford: Clarendon Press.
- FORMANOWICZ D.R. JR & BRODIE E.D. JR 1982. Relative palatabilities of members of a larval amphibian community. *Copeia*: 91-97.
- GITTLEMAN J.L. & HARVEY P.H. 1980. Why are distasteful prey not cryptic? *Nature* 286: 149-150.
- GOSNER K.L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16: 183-190.
- GUILFORD T. 1986. How do warning colours work? Conspicuousness may reduce recognition errors in experienced predators. *Animal Behaviour* 34: 286-288.
- GUILFORD T. 1988. The evolution of conspicuous coloration. *American Naturalist* 131S: S7-S21.
- HARVEY P.H. & GREENWOOD P.J. 1978. Anti-predator defence strategies: some evolutionary problems, pp. 129-151. In: Krebs J.R. & Davies N.B., Edits. Behavioural ecology: an evolutionary approach. Sunderland, Mass.: Sinauer Associates.
- HEUSSER H. 1971. Differenzierendes Kaulquappen-Fressen durch Molche. *Experientia* 27: 475-476.

- HEWS D.K. 1988. Alarm response in larval western toads, *Bufo boreas*: release of larval chemicals by a natural predator and its effect on predator capture efficiency. *Animal Behaviour* 36: 125-133.
- HEWS D.K. & BLAUSTEIN A.R. 1985. An investigation of the alarm response in *Bufo boreas* and *Rana cascadae* tadpoles. *Behavioral & Neural Biology* 43: 47-57.
- HEYER W.R. & BELLIN M.S. 1973. Ecological notes on five sympatric *Leptodactylus* (Amphibia, Leptodactylidae) from Ecuador. *Herpetologica* 29: 66-72.
- HEYER W.R., McDIARMID R.W. & WEIGMANN D.L. 1975. Tadpoles, predation and pond habitats in the tropics. *Biotropica* 7: 100-111.
- HOFF K. 1986. Morphological correlates of fast start performance in anuran larvae. *American Zoologist* 26: 132A.
- KATS L.B., PETRANKA J.W. & SIH A. 1988. Antipredator defenses and the persistence of amphibian larvae with fishes. *Ecology* 69: 1865-1870.
- KREBS J.R. & DAVIES N.B. (Edits). 1987. An introduction to behavioural ecology. *Sunderland, Mass.: Sinauer Associates*.
- KRUSE K.C. 1983. Optimal foraging by predaceous diving beetle larvae on toad tadpoles. *Oecologia* 58: 383-388.
- KRUSE K.C. & STONE B.M. 1984. Largemouth bass (*Micropterus salmoides*) learn to avoid feeding on toad (*Bufo*) tadpoles. *Animal Behaviour* 32: 1035-1039.
- LICHT L.E. 1974. Survival of embryos, tadpoles, and adults of the frogs *Rana aurora aurora* and *Rana pretiosa pretiosa* sympatric in southwestern British Columbia. *Canadian Journal of Zoology* 52: 613-627.
- MORIN P.J. 1983. Predation, competition, and the composition of larval anuran guilds. *Ecological Monographs* 53: 119-138.
- NEILL W.E. 1968. Predation on *Bufo valliceps* tadpoles by the predaceous diving beetle *Acilus semisulcatus*. *Bulletin of the Ecological Society of America* 49: 169.
- NUSSBAUM R.A., BRODIE E.D. JR & STORM R.M. 1983. Amphibians and reptiles of the Pacific Northwest. *Moscow, Idaho: University Press of Idaho*.
- O'HARA R.K. 1981. Habitat selection behavior in three species of anuran larvae: environmental cues, ontogeny and adaptive significance. *Ph.D. Thesis, Oregon State University*.
- O'HARA R.K. & BLAUSTEIN A.R. 1981. An investigation of sibling recognition in *Rana cascadae* tadpoles. *Animal Behaviour* 29: 1121-1126.
- O'HARA R.K. & BLAUSTEIN A.R. 1982. Kin preference behavior in *Bufo boreas* tadpoles. *Behavioral Ecology and Sociobiology* 11: 43-49.
- PETERSON C.H. & RENAUD P.E. 1989. Analysis of feeding preference experiments. *Oecologia* 80: 82-86.
- SNEDECOR G.W. & COCHRAN W.G. 1980. Statistical methods. *Ames, Iowa: The Iowa State University Press*.
- SOKAL R.R. & ROHLF R.J. 1969. Biometry: the principles and practice of statistics in biological research. *San Francisco: Freeman*.
- TAYLOR J.T. 1977. The behavioral ecology of larval and neotenic northwestern salamanders (*Ambystoma gracile*). *Ph.D. Thesis, Oregon State University*.
- VORIS H.K. & BACON J.P. 1966. Differential predation on tadpoles. *Copeia*: 594-598.
- WALDMAN B. & ADLER K. 1979. Toad tadpoles associate preferentially with siblings. *Nature* 282: 611-613.
- WALTERS B. 1975. Studies of interspecific predation within an amphibian community. *Journal of Herpetology* 9: 267-279.
- WASSERSUG R.J. 1971. On the comparative palatability of some dry-season tadpoles from Costa Rica. *American Midland Naturalist* 86: 101-109.
- WASSERSUG R.J. 1973. Aspects of social behavior in anuran larvae, pp. 273-297. In: Vial J.L., Edit. *Evolutionary biology of the anurans. Columbia: University of Missouri Press*.
- WASSERSUG R.J. & SPERRY D.G. 1977. The relationship of locomotion to differential predation on *Pseudacris triseriata* (Anura: Hylidae). *Ecology* 58: 830-839.
- WILBUR H.M. 1977. Density-dependent aspects of growth and metamorphosis in *Bufo americanus*. *Ecology* 58: 196-200.
- YOUNG A.M. 1967. Predation in the larvae of *Dytiscus marginalis* Linnaeus (Coleoptera: Dytiscidae). *Pan-Pacific Entomologist* 43: 113-117.
- ZAR J.H. 1984. Biostatistical analysis. *Englewood Cliffs, New Jersey: Prentice Hall, Inc.*