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THE DEVELOPMENT OF NOXIOUSNESS OF BUFO AMERICANUS TADPOLES TO AQUATIC INSECT PREDATORS

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ADULT toads (*Bufo* spp.) are well protected from vertebrate predators by the presence of noxious and toxic skin secretions produced and stored in granular glands of the skin. Apparently this toxin is secondarily deposited in the ova, and it is found also in the blood (Phisalix, 1922). This deposition of skin toxin in the ova probably accounts for the toxicity of the eggs of *Bufo* (Licht, 1967a, 1968, 1969), and a similar pattern of toxin production and deposition occurs in eggs of newts (Brodie et al., 1974a). In eggs of both *Taricha* (Twitty, 1937) and *Bufo* (Phisalix, 1922) the amount of toxin decreases as the fertilized eggs develop. This presence of toxin protects the eggs of *Bufo* from some predators. Licht (1968, 1969) established that ovarian eggs are avoided by leeches (*Batrachobdella* sp.), salamander larvae (*Ambystoma gracile*), and fish (*Gasterosteus aculeatus* and *Salmo clarkii*). Grubb (1972) observed that fish (*Gambusia affinis*) were not repulsed by pre-neural tube embryos of *Bufo*, and Huesser

(1970, 1971a) reared six species of anuran tadpoles on the "spawn" of *Bufo*. It appears from these studies that the protection enjoyed by the ova, and presumably therefore by the newly deposited fertilized eggs, is lost during development.

The greatest confusion is in regard to the palatability of tadpoles. Table 1 summarizes the interpretation of various authors in regard to the distastefulness of *Bufo* tadpoles. However, only Wassersug (1971) and Heyer et al. (1974) performed carefully controlled studies on tadpoles of known developmental stages. Wassersug (1971) determined that *B. marinus* tadpoles were distasteful to humans and that the noxiousness was concentrated in the skin. Wassersug (1973) later suggested that distasteful skin would not protect tadpoles from aquatic insect predators that suck body fluids. Heyer et al. (1975) suggested that noxiousness increases ontogenetically and assumed that the amount of toxin ingested probably would increase with increasing size of the larvae

TABLE 1.—Palatability of *Bufo* tadpoles.

Species	Gosner stage	Predator	Palatability	Reference
<i>B. americanus</i>	?	Bluegill (<i>Lepomis macrochirus</i>)	distasteful	Voris & Bacon, 1966
	?	Beetle larvae (<i>Dytiscus marginalis</i>)	palatable	Young, 1967
	?	Leech (<i>Batrachobdella picta</i>)	palatable	Brockelman, 1969
<i>B. bufo</i>	?	Odonata naiads	palatable	Brockelman, 1969
	25, 38-40	Newt (<i>Triturus cristatus</i>)	distasteful	Cooke, 1974
	25, 36-39	Newt (<i>Triturus vulgaris</i>)	distasteful	Cooke, 1974
	metamorphic	Newt (<i>T. cristatus</i>)	palatable	Huesser, 1971b
	metamorphic	Newts (<i>T. vulgaris</i> , <i>T. alpestris</i> , <i>T. helveticus</i>)	distasteful	Huesser, 1971b
<i>B. calamita</i>	metamorphic	Newt (<i>T. cristatus</i>)	palatable	Huesser, 1971b
	metamorphic	Newts (<i>T. vulgaris</i> , <i>T. alpestris</i> , <i>T. helveticus</i>)	distasteful	Huesser, 1971b
<i>B. cognatus</i>	?	Tadpoles (<i>Scaphiopus bombifrons</i>)	palatable	Bragg, 1940
<i>B. marinus</i>	30-32	<i>Homo sapiens</i>	distasteful	Wassersug, 1971
	20-27	Tadpoles (<i>Leptodactylus pentadactylus</i>)	palatable	Heyer et al., 1975
	28-29	Dragonfly naiads (<i>Pantala flavescens</i>)	palatable	Heyer et al., 1975
<i>B. speciosus</i>	premetamorphic	Tadpoles (<i>Scaphiopus bombifrons</i>)	not eaten	Bragg, 1960
	metamorphic	Tadpoles (<i>Scaphiopus bombifrons</i>)	eaten	Bragg & Nelson, 1966
<i>B. valliceps</i>	?	Beetle larvae (<i>Acilius semi-sulcatus</i>)	eaten	Neill, 1968
<i>B. sp.</i>	?	Fish and <i>Xenopus</i>	eaten	Wager, 1965

and may account for the apparent ontogenetic change in taste."

Our purpose was to determine if *Bufo americanus* tadpoles of different developmental stages and newly-metamorphosed juveniles are palatable to aquatic insects. Aquatic insects are among the most important predators on anuran larvae (Brockelman, 1969; Heyer and Belin, 1973; Heyer et al., 1975).

METHODS

The invertebrate predators used were 122 larvae of the predaceous diving beetle *Dytiscus verticalis* (average volume = 0.55 cm³, range = 0.1-1.8) and 21 nymphs of the giant water bug *Lethocerus americanus* (average volume = 1.05 cm³, range = 0.4-2.2). Average sizes (Tables 2, 3) were also determined for the tadpole prey

(staged following Gosner, 1960); sizes were determined as volume rather than length in order to minimize handling of predators and prey. Water temperature at time of testing was 17.8-21.0°C.

The prey (184 *Bufo americanus* and 234 *Hyla crucifer*) were offered to predators in paired trials in which two anurans were offered in random order to the same individual predator for a 3-h period each, with 1 h between trials. All trials were in round (150 mm diam.) plastic containers filled to a depth of 35 mm with filtered pond water. Numbers of prey surviving versus number killed (those killed but not eaten and those eaten were combined) were compared by a chi-square test.

All specimens were collected on or near the E. N. Huyck Preserve, Rensselaerville, Albany County, New York.

TABLE 2.—Palatability of *Bufo americanus* and *Hyla crucifer* tadpoles, and of newly-metamorphosed juveniles, to larvae of the predaceous diving beetle *Dytiscus verticalis*.

Prey species	Gosner stage	Mean size (cm ²)	Predator response		
			Killed & eaten	Killed/not eaten	Survived
Experiment #1					
<i>B. americanus</i>	38-39	0.1	47	2	0
Experiment #2					
<i>B. americanus</i>	41	0.2	30	0	0
<i>H. crucifer</i>	38-39	0.25	29	0	1
Experiment #3					
<i>B. americanus</i>	46	0.2	20	9	23
<i>H. crucifer</i>	38-42	0.31	50	0	2
Experiment #4					
<i>H. crucifer</i>	46	0.2	50	0	0
<i>H. crucifer</i>	38-39	0.25	50	0	0

RESULTS AND DISCUSSION

Tadpoles, stages 38-41, of both *Bufo americanus* and *Hyla crucifer* were fully palatable to both *Dytiscus* (Table 2) and *Lethocerus* (Table 3). The same predator species avoided ($P < .005$) stage 46 *Bufo* which had metamorphosed less than 24 h prior to testing, whereas they continued to eat *Hyla* tadpoles (stages 38-42). To determine if this avoidance was the result of unpalatability of metamorphosed *Bufo* or a reduced propensity of these aquatic insects to feed on the water surface where metamorphosed anurans positioned themselves, we offered them newly-metamorphosed *Hyla crucifer* (Expt. 4, Table 2). The 50 stage 46 *Hyla* and the 50 stage 38-39 *Hyla* were all eaten. This establishes that newly-metamorphosed anurans are acceptable prey to these predators, but that *Bufo americanus* at this stage are distasteful even though they are fully palatable at earlier stages (38-41).

A large percentage of newly-metamorphosed *Bufo* that were killed were not eaten (Table 2, 3) by either *Lethocerus* (78.6%) or *Dytiscus* (31.0%). Additionally 2 of the 3 *Lethocerus* that ate stage 46 *Bufo* died soon after feeding (37 min, and 3 h 40 min). These observations support our interpretation that newly metamor-

phosed *Bufo* are unpalatable. We assume that this development of unpalatability is correlated with the maturation of the skin and the activity of the granular glands. Dense aggregations of granular glands are not apparent in the parotoid region until 3-4 weeks after metamorphosis (Licht, 1967b), but the skin changes visibly in the few days during which metamorphosis takes place. An increase in noxiousness as the result of larger size (therefore more toxin ingested) as suggested by Heyer et al. (1975) can be ruled out in this case because stage 41 and stage 46 *Bufo* were equal in size. The noxiousness must therefore be accounted for by changes in the skin. Much more work must be done before the interspecific differences in palatability of *Bufo* larvae reflected by Table 1 will be understood.

Our findings suggest that the noxious substance in stage 46 *Bufo* (which we presume to be the skin secretion found in adult toads) is found both in and beneath the skin. *Dytiscus* feeds on surface tissues as well as body fluids, but *Lethocerus* appears to feed only on internal tissues.

The behavior of toadlets enhances the survival value of the noxious skin secretions. These toads became immobile immediately when seized or touched by either of the predators used. This often resulted

TABLE 3.—Palatability of *Bufo americanus* and *Hyla crucifer* tadpoles, and of newly-metamorphosed juveniles, to nymphs of the giant water bug *Lethocerus americanus*.

Prey species	Gosner stage	Mean size (cm ²)	Predator response		
			Killed & eaten	Killed/not eaten	Survived
Experiment #5					
<i>B. americanus</i>	41	0.1	29	0	1
<i>H. crucifer</i>	38-39	0.1	30	0	0
Experiment #6					
<i>B. americanus</i>	46	0.2	3*	11	9
<i>H. crucifer</i>	38-42	0.27	22	0	0

* Two bugs died (37 min, and 3 h 40 min) after eating *Bufo*.

in a seizure and subsequent release of a *Bufo* without injury. Immobility in toads has been reported (Dickerson, 1906; McNicholl, 1972; Nero, 1967) but is exhibited more readily by newly-metamorphosed individuals than by adults. Because each contact with a predator entails a risk even for distasteful species (e.g., the large percentage of *Bufo* killed but not eaten), reducing the intensity of predator attack would (and did in these experiments) greatly enhance survival. This same correlation of immobility behavior and noxiousness has been noted for many salamanders (Brodie, 1977; Brodie et al., 1974b).

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HABITAT USE BY FIVE SYMPATRIC WATER SNAKES IN A LOUISIANA SWAMP

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ABSTRACT: Five sympatric species of water snakes were studied along the shorelines of two swamp waterways. All species were sighted most frequently in or over water, seldom on land. Snakes of all species were most frequently observed lying on emergent objects, swimming, or lying immobile in the water. *Nerodia erythrogaster* were seldom seen lying on branches or logs, whereas *Regina grahamii* were frequently seen doing so. *Nerodia cycloption*, *Nerodia fasciata*, and *Nerodia rhombifera* exhibited similar behavior patterns, but *N. cycloption* were observed basking more frequently than the other species during the day, and *N. fasciata* and *N. rhombifera* were more common on emergent objects at night. Microhabitat preferences of *N. cycloption*, *N. rhombifera*, and *N. erythrogaster* were similar, these species being found most frequently along gently sloping shorelines essentially devoid of vegetation. *Regina grahamii* was most common in areas of intermediate vegetation density, and *N. fasciata* was common in all microhabitat types.

Key words: Colubridae; Ecology; Habitat; Squamata

THE most thorough study to date of habitat partitioning in snakes is that of Carpenter (1952) on three sympatric species of garter snakes (*Thamnophis*). He found that each species prefers certain elements of the structural habitat (e.g., bushes, margins of marshes), and that the

species are absent from areas lacking these elements.

Habitat partitioning of sympatric water snakes (*Nerodia*¹ and *Regina*) has not been studied in such detail. Diener (1957)

¹ Our generic usage follows Rossman and Eberle (1977).

and Preston (1970) reported on microhabitat preferences of water snakes in communities of 2-3 species. Observations by Clark (1949) on snakes collected in northern Louisiana indicate that *Nerodia fasciata* and *Nerodia erythrogaster* are found in a broad range of macrohabitats, each occupying 6 of the 7 types of habitats listed. *Nerodia rhombifera* occurs in three of the habitat types, *Regina grahamii* in two, and *Regina rigida* and *Nerodia cycloption* in one each. In another study performed in Louisiana, Tinkle (1959) reported that *N. cycloption* occupies a narrower range of microhabitats than sympatric *N. fasciata*.

What follows is an evaluation of habitat use in a community comprised of five species of snakes: *N. cycloption*, *N. rhombifera*, *N. erythrogaster*, *N. fasciata*, and *R. grahamii*. *Regina rigida* was extremely rare in the study area and is not included in most of the following analyses. Major emphasis is on interspecific comparisons of behavior and habitat preferences that could be important in allowing coexistence of these five semiaquatic snakes.

STUDY AREA AND METHODS

Description of study area.—The study area was situated in Alligator Bayou swamp in Ascension Parish, Louisiana. The forest in this swamp is partly cypress (or cypress-tupelogum) swamp and partly bottomland hardwood forest (see Penfound and Hathaway, 1938). Major bodies of water include Spanish Lake, Alligator Bayou, and Bayou Braud.

Study area A was in Bayou Braud, a straight, man-made canal about 25 m wide and usually less than 4 m deep. The eastern shore of this canal is bounded largely by a 25-yr-old spoil levee in an advanced stage of succession. Trees on this levee include hackberry (*Celtis laevigata*), boxelder (*Acer negundo*), Nuttall oak (*Quercus nuttalli*), haw (*Crataegus* sp.) willow (*Salix* sp.), live oak (*Quercus virginiana*), and cypress (*Taxodium distichum*). Fallen

trees are common where the bank has eroded. There are five gaps in the spoil bank in area A that provide connections between Bayou Braud and the backswamp during high water. A section along this eastern shore of Bayou Braud measuring two kilometers in length was marked off at 25-m intervals using numbered aluminum markers. The markers were visible at night with headlamps, and enabled us to determine our position within the study area at any given time.

Study area B was situated in Alligator Bayou, a natural, meandering stream similar in depth and width to Bayou Braud. This stream has been dredged, and as a result there is a spoil levee on the south shore with plant species similar to those in area A. A 1-km stretch of shoreline along this southern shore of the bayou was marked off in a manner identical to that used in area A. A portion of the spoil bank at meter 425 B collapsed in early August 1975, and water drained rapidly from the impounded area into the non-impounded swamp. This flow continued until the break was repaired in mid-October.

Habitat classification.—To facilitate quantitative analysis of snake distribution in relation to littoral microhabitats, the shoreline was characterized in terms of the slope of the bank and the density of overhanging or emergent vegetation. Slope of the shoreline was expressed as "1" (0-45°) or "2" (46-90°), using the lowest point on the bank supporting terrestrial vegetation as a point of reference. Density of overhanging or emergent vegetation was coded as "A," "B," or "C," corresponding to sparse, patchy, and dense, respectively. Areas classified as sparse had only occasional emergent trees and branches, providing very few basking sites for snakes. Areas of moderate vegetation density were characterized by occasional patches of dense vegetation separated by stretches of relatively bare shoreline. Overhanging or emergent vegetation was virtually continuous along shorelines classified as dense.