

# Effectiveness and Ecological Implications of Anuran Defenses against Snake Predators

In-Ho Choi\*, Sung Ho Lee, and Robert E. Ricklefs<sup>1</sup>

Department of Life Science, College of Liberal Arts and Sciences, Yonsei University, Wonju 222-710, Korea:

<sup>1</sup>Department of Biology, University of Missouri-St. Louis, St. Louis, Missouri 63121, USA

Key Words:

Defense  
Frog  
Predation  
Snake

The aim of this study was to characterize antipredator tactics of anurans and to evaluate the effectiveness of these tactics for predator avoidance in real confrontations. Two types of experiments were conducted. In one experiment, one predator and one prey were placed together for one hour in a small confined space (one-to-one interaction). In another experiment, one predator and several prey were placed together for one day in a large enclosure in a field (field-based interaction). The prey consisted of three anuran species, *Rana nigromaculata*, *R. rugosa*, and *Bombina orientalis*; a snake species, *Rhabdophis tigrinus tigrinus*, was used as a predator. Results of both experiments demonstrated a range in antipredator responses of the frogs, from toxicity and warning coloration, coupled with slow responses in *Bombina* to little (or only slight) toxicity, crypsis, and fast take-off responses to the predator in the ranids. Both ranid species exhibited lower survival (57%) than *Bombina* (95%) in the field-based interaction, suggesting that motor responses of the palatable prey due to attacks of the predator ultimately limited their survival. The jumping of the ranids increased the activity of the predator, which became more likely to strike. Simple crouching (seen in *R. rugosa* and *B. orientalis*) and chemical defense (in *Bombina*) reduced predatory attacks.

Empirical studies of frog-snake interactions offer an opportunity to examine factors that contribute to the effectiveness of defense strategies of prey against predators. Anurans show diverse antipredator mechanisms, including take-off escape, crypsis, aposematic ('warning') coloration, toxin secretion, and various other morphological and behavioral attributes (e.g. Unken reflex posture, deceptive markings, mimicry) (Brodie and Tumbarello, 1978; Heinen, 1994; Daly, 1995; Choi and Park, 1996). Each prey species adopts only a limited set of these mechanisms because each exacts different costs and some mechanisms are intrinsically incompatible with others. From an energetic point of view, body coloration, chemical defense, and locomotory or behavioral performance all require the regulation of development and metabolism (e.g. production of chromophores for coloration, granular skin glands for toxin secretion, myofibers for contractility) (Duellman and Trueb, 1994; Marsh and John-Alder, 1994; Daly, 1995). Thus, within the limits of energetic and intrinsic constraints, each species may evolve a different suite

of antipredator mechanisms. For instance, frogs that can secrete toxin may be either brightly colored or cryptic, but also may be poor jumpers. Those with weakly developed chemical defenses are typically cryptic and exhibit quick reflexes for escape at critical moments. Skin toxicity would probably be the key mechanism that distinguishes the defensive strategies. Although a number of studies have shown interspecific variation in defensive responses (Duellman and Trueb, 1994), a few have systematically evaluated suites of defensive mechanisms in prey or their ecological significance (Ducey and Brodie, 1983; see Sih et al., 1985). How effectively does each type of strategy protect the prey from predation during a real encounter?

Choi and Park (1996) investigated variation in motor function of three anuran species, *Rana nigromaculata*, *R. rugosa*, and *Bombina orientalis*, finding that the two ranid species exhibited better-developed skeleto-muscular systems (e.g. longer hindlimbs, more massive thigh muscles, higher contraction rates of extensors) and significantly greater take-off speeds ( $2.4 \text{ m}\cdot\text{s}^{-1}$ ) than *Bombina* ( $1.7 \text{ m}\cdot\text{s}^{-1}$ ). Coloration and toxicity of the skin also differ among these species. *B. orientalis* secrete toxins and has bright, red-black patterns on its feet and ventral surface which is aposematic (Daly, 1995). The ranids are dull-colored, and *R. rugosa* has

\* To whom correspondence should be addressed.

Tel: 82-371-760-2244, Fax: 82-371-763-4323/760-2183

E-mail: ichoi@dragon.yonsei.ac.kr

numerous, tiny warts on the dorsal skin (Kang and Yoon, 1975), suggesting potential secretion of some noxious substance. Mori (1989) showed that one species of snake avoided feeding on *R. rugosa*. Considering these interspecific variations in the defense mechanisms, antipredator strategies of the three species seem to follow the aforementioned trend: *Bombina* is presumed to be the most toxic and *R. nigromaculata* the least.

Building upon these studies, we designed a frog-snake interaction experiment using the three frog species to explore the effectiveness of a range of defensive responses in predator avoidance. To approach the complex problem of prey-predator interaction in simple terms, we used only one snake species (*Rhabdophis tigrinus tigrinus*) as a representative predator. The study had two components. In the first, one predator and one prey were placed together for one hour in a small confined space ("one-to-one interaction"). In the second, one predator and several prey were placed together for one day in a large enclosure in a field ("field-based interaction", see below). We presumed that a period of one day was appropriate because the physiological performance of these animals would normally follow a circadian rhythm (Alcock, 1989). Both experiments provided information on the defense mechanisms used by individual frogs. In addition, the short encounters allowed us to test the potential of chemical defenses in the prey against the predator, and the longer encounters provided information on how well prey could survive repeated predator attacks.

## Materials and Methods

### Subjects

We collected frogs *R. nigromaculata*, *R. rugosa*, and *B. orientalis* from ponds or streams in Wonju, Korea, in July and August 1996 to 1997. We purchased three male *Rhabdophis* (two in 1996 and one in 1997) from a local animal farm. Populations of the three anuran species often occur sympatrically in shallow waterbeds of abandoned fields or along margins of waterways, although *R. nigromaculata* usually inhabits wet rice fields, *R. rugosa* is found in streams in areas of sandy soils, and *B. orientalis* occurs in small ponds or valley streams. *Rhabdophis* is known to include frogs as the major part of its diet and to occur sympatrically with the three frog species (Kang and Yoon, 1975). Frogs were caged in a circular terrarium (1 m diameter  $\times$  1 m high) placed at the edge of, and partly within, a stream near our field sites. They were able to feed freely on insects coming into the cage. Snakes were placed individually in several terrariums (0.5 m long  $\times$  0.3 m wide  $\times$  0.25 m high), and were provided water but no food during the pre-experimental periods of 3 to 4 d. The body masses of both frogs and snakes and the body lengths of snakes were measured before the experiments.

### Snake-frog one-to-one interactions

This experiment was conducted in 1996 with two snakes. We used an arena (1.2 m long  $\times$  1 m wide  $\times$  0.7 m high) of gray, plastic-coated (non-glare) wire mesh that was located in a natural field. The dimensions of the arena were similar to that of Mori (1989). A Sharp Slimcam VL-L50U video camera was set vertically about 2 m above the arena. The arena was divided into two compartments (1:3 ratio in area) by a removable transparent insert. A moistened piece of brown cardboard was nailed to the ground surface of the arena; the cardboard was replaced with a fresh piece before every trial. A small box was attached approximately 0.1 m above the ground on an outside wall of the larger compartment (the furthest side from the insert) to accommodate a frog. The bottom of the box was moistened and tilted down toward the arena so that the frog could be slipped into the compartment when a block between the wall and the box was removed.

Two experimental trials were conducted per day, one between 08:00 and 11:00 a.m. and a second between 15:00 and 18:00 p.m., and were made every other day. Each of the snakes was assigned to either the morning or the evening trial throughout the experiments. The three frog species were assigned sequentially to the trials, for example, species A to the morning, B to the evening, C to the following morning, and then species A to the following evening, and so on. This schedule resulted in each prey species being exposed to the predator alternately, resulting equally in four trials per prey species per snake. Each trial was conducted in the following sequence. A pre-assigned snake was placed in the small compartment; 90 min later a frog was put in the box; 10 min later the frog was slipped into the arena and the video camera turned on; after 20 min, the insert was removed, and the snake was allowed an hour to search for prey. Preliminary trials demonstrated an hour was sufficient for predation to occur. The experiment was terminated if the predator seized the prey within this period. Air temperature was monitored with a copper-constant thermocouple thermometer (Omega HH-73T) set approximately 5 cm above the bottom of the arena. The sensing tip of the thermocouple was painted white and shaded. All experimental operations (e.g., video powering, monitoring, removal of the block, and removal of the insert) were made from a blind installed 3 m from the arena. After completion of the experiments, we measured body mass and length of the snakes. The snakes and surviving frogs were freed to their natural habitat. For detailed analyses of anuran defensive responses as well as predatory behavior of snakes, recorded images (30 Hz) were sent frame by frame to a 586 IBM compatible computer via a Kasan WinX Perfect image grabber.

### Snake-frog field-based interaction

This experiment was conducted in the summer of 1997, with one snake and several frogs released in a large enclosure (7.3 m long × 5.2 m wide × 1.2 m high) in a natural field. The enclosure was surrounded completely by a non-glare, wire-mesh fence. The top of the enclosure was left open and the fence was high enough to prevent small animals (snakes, frogs, mammals) from entering or leaving. The area of the enclosure was large enough for frogs to complete three or more long jumps from the center to the fence. A pond (ca. 10% of the ground surface of the cage) and two rocks (25% of the surface) located in the middle of the enclosure were provided as shelters. The rocks and several young pine trees around the cage provided shade for protection from the midday sun. A low blind near the enclosure and two dim lights beside the fence were placed for close observations and night watches. The video camera was used to record behavior. Air temperature was monitored as in the one-to-one interaction trials.

Experiments lasted for 24 h and were conducted on every third day. Three fresh frogs of each species (totaling nine frogs per one-day trial) were released in the enclosure for every new experiment, resulting in a predator to prey ratio of 1:9 and a density of 0.26 individuals m<sup>-2</sup> in the enclosure. The ratio and the density were arbitrary inasmuch as local population densities of prey differed greatly. Thin colored threads attached to one toe web of a forelimb allowed us to identify individual prey before and after each experiment. We tested this method twice (each for 24 h) in the enclosure without the predator to determine that the ringed tags did not interfere with the free movement of the prey. At the end of each experiment, the snake was put aside temporarily in a small cage, and the remaining frogs were collected and identified. After the completion of seven trials, we determined the percent of each species that survived the trials.

### Statistical analysis

Predator preference for specific prey species in both one-to-one interactions and field-based interactions was tested by Fisher's exact test. The effect of prey mass on predation in both experiments was tested by logistic regression using maximum likelihood. Difference in predatory success between two snakes in one-to-

**Table 1.** Body sizes of snakes and frogs used in interaction studies

Species	N	Body mass (g, $\bar{x} \pm SD$ ) (range)	Total body length (m) (range)
One-to-one interaction			
<i>Rana nigromaculata</i>	8	7.0 ± 4.03 (3.3 - 15.9)	
<i>R. rugosa</i>	8	6.00 ± 1.90 (3.2 - 8.1)	
<i>Bombina orientalis</i>	8	6.6 ± 1.61 (5.0 - 8.7)	
<i>Rhabdophis tigrinus tigrinus</i>	2	(100 - 120)*	(0.90-0.95)*
Field-based interaction			
<i>Rana nigromaculata</i>	21	17.78 ± 8.51 (4.2 - 29.5)	
<i>R. rugosa</i>	21	8.32 ± 4.32 (3.0 - 18.5)	
<i>Bombina orientalis</i>	21	6.43 ± 1.21 (4.5 - 8.6)	
<i>Rhabdophis tigrinus tigrinus</i>	1	100.20*	0.85*

\*Body weight and length of snakes changed little before and after experiments of one-to-one interaction (1996) and field-based interaction (1997), and were averaged in each season.

one interactions was examined by G-test adjusted with William's correction. Trends of predatory success over repeated trials in field-based interactions were examined by run tests on the numbers of frogs killed in each trial. Procedures followed Sokal and Rohlf (1998), and were performed using Statistical Analysis System (SAS).

## Results

### Defense mechanisms of prey

Body sizes of frogs and snakes used in this study are given in Table 1. Results of the one-to-one and field-based trials to determine defensive responses of the three anuran species are summarized in Table 2. From video analyses of one-to-one interactions, further information on responses of anurans and snakes to each other are presented in Table 3. The ranids were cryptic against the wet, vegetated background, whereas the *Bombina* were aposematic with their bright, red-black patterns on the feet and the ventral surface. When threatened, *R. nigromaculata* always jumped immediately, while *R. rugosa* jumped or crouched motionlessly (see definition of terms in Tables 2 and 3). *Bombina* responded primarily by crouching, but mucus

**Table 2.** Contrasts in behavioral and physiological responses of three anuran species for antipredator defense

Species	Take-off	Crouch <sup>1</sup>	Crypsis	Aposematic coloration	Toxic skin	Unken reflex <sup>4</sup>
<i>Rana nigromaculata</i>	+	-	+	-	-	-
<i>R. rugosa</i>	+	+	+	-	- <sup>2</sup>	-
<i>Bombina orientalis</i>	+ <sup>3</sup>	+	-	+	+	+

+ = present; - = absent; <sup>1</sup>The motionless posture with the head lowered and the four limbs compressed (after Heinen 1994); <sup>2</sup>Toxicity of the frog skin was not apparent to *Rhabdophis tigrinus tigrinus*; <sup>3</sup>Hopping rather than jumping; <sup>4</sup>A postural response of prey with the ventral surface elevated to display its bright coloration to predator.

**Table 3.** Responses of frogs and snakes to each other in one-to-one interaction

Snake response	Responses of frogs at snake's action (N)		
	<i>R. nigromaculata</i>	<i>R. rugosa</i>	<i>B. orientalis</i>
Attack <sup>1</sup>			
Seize-ingest	jump (8)	jump (5)	hop (1)
Seize-release	-	-	hop/mucous*(1)
Avoidance <sup>2</sup>	-	-	crouch (3)
Unresponsiveness <sup>3</sup>	-	crouch (3)	crouch (1), ignoring <sup>4</sup> (2)
Total numbers of prey	8	8	8

<sup>1</sup>Actions including chasing and/or striking; <sup>2</sup>Retraction before approaching to prey; <sup>3</sup>No specific response to presence of prey; <sup>4</sup>Free movements of frogs irrespective of the snake's behavior. \*Mucous secretion was checked after experiment.

secretion and probably the ventral color patterns (at Unken posture) also seemed to discourage the predator effectively. When a predator bit a *Bombina* (1 case, Table 3), the frog quickly released a volatile agent (stinging to human noses) and coated itself with a thick mucous secreted from the skin, which was strong enough to irritate the observer's hands when touched. In two cases of interaction with *Bombina*, a snake was unresponsive even when the prey touched the snake's mouth or head (Table 3).

#### Survival of prey from one-to-one interaction

Air temperature ranged between 22° and 32°C for the experimental period. We used frogs of similar masses to reduce the effect of prey size on the predatory response (Table 1). There was no statistical evidence that predation was biased with respect to prey size (logistic regression,  $P > 0.5$ ). Because the two *Rhabdophis* individuals killed frogs of each species with similar rates ( $G_{adj}=1.164$  for the two ranid species,  $df=1$ ,  $P > 0.05$ ), data from both snakes were pooled. For the hour-long interaction, survival was 0% for *R. nigromaculata*, 37% for *R. rugosa*, and 87% for *Bombina*. Interspecific differences in the survival rates were statistically significant, indicating that predation was heterogeneous with respect to anuran species (Fisher's exact test,  $P < 0.001$ ). Time interval (mean  $\pm$  1 SD) from initiation of interaction to the moment of seizure by the predator was  $5.9 \pm 7.9$  min in *R. nigromaculata*,  $28.4 \pm 27.7$  min in *R. rugosa*, and  $53.1 \pm 19.6$  min in the *Bombina*. These response delays differed significantly between prey species (one-way ANOVA,  $F_{2,21}=11.0$ ,  $P < 0.001$ ).

#### Survival of prey from field-based interaction

During the two-months of experimental trials, no frog or snake entered or left the fenced enclosure. No animals other than the study subjects were observed in the enclosure. Air temperatures ranged between 17° and 31 °C during the period. After a one-day exposure to one *Rhabdophis*, survival was 57% for both ranid species but 95% for *Bombina*. No trend in predation

rates across trials was apparent (runs tests,  $t_s=0.380$  for *R. nigromaculata* and  $t_s=0.00$  for *R. rugosa*,  $P > 0.05$  for both species). Predation bias with respect to anuran species was statistically significant (Fisher's exact test,  $P=0.043$ ). We could not maintain a consistent prey size in this experiment because of difficulty in capturing large numbers (21 per species) of similar-sized frogs within one season. However, there was no evidence of a predation bias based on prey size (logistic regression,  $P > 0.1$ ), and survival rates did not differ between the two ranid species despite a more than 2-fold difference in mass between them (Table 1).

#### Discussion

Our results demonstrate that defensive responses of frogs represent several different functional suites. The two ranid species had a crypsis-escape strategy, whereas *Bombina* used an aposematism-toxin secretion strategy against the *Rhabdophis*. The predators evidently considered all the ranids, but only some *Bombina* to be edible. There were also differences between the two ranid species. *R. rugosa* displayed a crouching behavior that resembled that of *Bombina*. Potential secretion of noxious substance from numerous dorsal warts in *R. rugosa* might also be effective against other types of predators, as in Mori's (1989) finding that young Japanese striped snakes (*Elaphe quadrivirgata*) avoided feeding on frogs of this species. Our study produced no evidence that *Rhabdophis* avoided *R. rugosa*.

It is interesting to note that simple behavior such as crouching could make a large difference in survival over a relatively short period of interaction within a small confined space. By employing this behavior, *R. rugosa* increased its survival rate by 37% and delayed the time of predation by 23 min, compared with *R. nigromaculata*, which never crouched (Table 3). A motionless crouch may be adaptive if it actually reduces the frequency of strikes by predators, because many species of snakes use visual information as well as vomerolfactory stimuli to orient to potential prey (Duellman and Trueb, 1994, Heinen, 1994). A prey species that is palatable to predators could use crouching to gain time to escape from a confined area if the predator were to move away. According to Heinen (1994), 60 to 80% of newly metamorphosed American toads (*Bufo americanus*) tended to crouch when threatened by their natural predators, garter snakes (*Thamnophis sirtalis*), and thereby increased survival more than 2-fold during 10 min of interaction. In this study, however, *R. nigromaculata* jumped away immediately when threatened, which excited the predator and decreased the time to predation. Like juvenile American toads, the toxic *Bombina* primarily crouched in response to predator threat.

Initially we asked whether the alternative defensive tactics of weakly toxic prey would protect a frog well

from snake predation as toxicity. The field-based interaction study showed substantially lower survival rates in the former (57% versus 95%). The relatively low survival may result from an intrinsic limit to the motor capacity of the palatable prey. Our video analyses of one-to-one interactions indicated that the ranid and the snake moved with comparable speed: for example, ranid take-off ranged between 2.1 and 3.3 m s<sup>-1</sup> and the snake struck out at up to 2.4 m s<sup>-1</sup> (Choi and Park, 1996; I. Choi, unpublished data). However, as the frogs required a response time (latency) of 70-100 ms before take-off was initiated, the snake could successfully hunt them if it attacked within the response time. The video analyses showed that the *Rhabdophis* struck the prey at a distance of 0.10-0.25 m, which was covered in about 42-104 ms (I. Choi, unpublished data), and often struck the prey before it could escape. Although this scenario of attack-and-response has been recognized in the past, the interaction is quantitatively poorly understood. In our 2-month study of field-based interactions, the snake apparently did not habituate to the enclosure as the probability of ranid survival did not change over time. Some reports suggest that snakes may habituate to places where frogs aggregate in a certain period (e.g. the time of transformation; Licht, 1974; Arnold and Wassersug, 1978).

The survival rate of toxic prey in our experiment cannot be extrapolated to other predator-prey relations because of individual variability in toxicity, variation in toxicity to different predators, and the potential for coevolution between prey and predators (Brodie and Brodie, 1990). As found in this study, toxic prey tend to be slow to escape and would therefore be vulnerable to attacks by inexperienced predators (Duellman and Trueb, 1994). Attacks could be repeated if prey individuals varied in toxicity and palatable individuals were occasionally consumed (Dowdey and Brodie, 1989; Brodie and Brodie, 1990). A few cases in this study in which *Bombina* were eaten by the *Rhabdophis* might reflect this possibility. Toxic species can be more easily captured by predators that do not react to their toxins. For instance, several colubrid snakes in the genera *Heterodon* and *Xenodon*, as well as *Thamnophis sirtalis*, can feed on highly toxic amphibians, including *Bufo*, *Atelopus*, *Dendrobates* and *Taricha* without significant ill effect (Brodie, 1968; Myers et al., 1978; Brodie and Brodie, 1990). Some recent articles have postulated that such immunity by predators may present a strong selective pressure on prey, resulting in a co-evolutionary arms race between prey and predators (Brodie and Brodie, 1990).

In conclusion, the weakly toxic prey showed substantially low survival rates compared to highly toxic ones, and this result seemed to arise from the intrinsic limit of motor responses (reaction time) of the palatable prey used in escape. Clearly, predator-prey interactions and survival rates obtained in short-term field experiments do not accurately portray the long-term,

diverse ecological interactions of predators and their prey in natural habitats. Nevertheless, this study may provide an initial step in addressing the fundamental question of how an organism's physiological capacities affect its ecological performance (Feder, 1987; Losos, 1990).

#### Acknowledgements

We thank Dr. Jonathan Losos of the Department of Biology, Washington University (St. Louis, Missouri, USA) for his special concerns and support in this study. Drs. A. S. Rand and K. Park provided useful comments for this project. Ms. Y. M. Cho and Mr. J. W. Choi gratefully assisted in the collection of study subjects and analyses of video tapes. This study was supported by a grant from the Non-Directed Research Fund, Korea Research Foundation, to I. Choi in 1996.

#### References

- Alcock J (1989) *Animal Behavior: an Evolutionary Approach*, 4th Ed. Sinauer Associates Inc. Publishers, Sunderland.
- Arnold SJ and Wassersug RJ (1978) Differential predation on metamorphic anurans by garter snakes (*Thamnophis*): social behavior as a possible defense. *Ecology* 59: 1014-1022.
- Brodie ED, Jr (1968) Investigations on the skin toxin of the adult rough-skinned newt, *Taricha granulosa*. *Copeia* 1968: 307-313.
- Brodie ED, Jr and Tumbarello MS (1978) The antipredator functions of *Dendrobates auratus* (Amphibia, Anura, Dendrobatidae) skin secretion in regard to a snake predator (*Thamnophis*). *J Herpetol* 12: 264-265.
- Brodie ED, III and Brodie ED (1990) Tetrodotoxin resistance in garter snakes: an evolutionary response of predators to dangerous prey. *Evolution* 44: 651-659.
- Choi I and Park K (1996) Variations in take-off velocity of anuran amphibians: relation to morphology, muscle contractile function and enzyme activity. *Comp Biochem Physiol* 113A: 393-400.
- Daly JW (1995) The chemistry of poisons in amphibian skin. *Proc Natl Acad Sci USA* 92: 9-13.
- Dowdey TG and Brodie ED, Jr (1989) Antipredator strategies of salamanders: individual and geographical variation in responses of *Eurycea bislineata* to snakes. *Anim Behav* 38: 707-711.
- Ducey PK and Brodie ED, Jr (1983) Salamanders respond selectively to contacts with snakes: survival advantage of alternative antipredator strategies. *Copeia* 1983: 1036-1041.
- Duellman WE and Trueb L (1994) *Biology of Amphibians*. Johns Hopkins University Press, Baltimore.
- Feder ME (1987) The analysis of physiological diversity: the prospects for pattern documentation and general questions in ecological physiology. In: Feder ME, Bennett AF, Burggren WW, and Huey RB (eds), *New Directions in Ecological Physiology*, Cambridge University Press, Cambridge, pp 38-75.
- Heinen JT (1994) Antipredator behavior of newly metamorphosed American toads (*Bufo americanus americanus*), and mechanisms of hunting by eastern garter snakes (*Thamnophis s. sirtalis*). *Herpetologica* 50: 137-145.
- Kang YS and Yoon B (1975) *Illustrated Encyclopedia of Fauna and Flora of Korea*. Vol 17. Amphibia and Reptilia. Korean Ministry of Education, Seoul.
- Licht LE (1974) Survival of embryos, tadpoles, and adults of the frogs *Rana aurora aurora* and *Rana pretiosa pretiosa* sympatric in southwestern British Columbia. *Can J Zool* 52: 613-627.
- Losos JB (1990) Ecomorphology, performance capability, and scaling of west Indian *Anolis* lizards: an evolutionary analysis. *Ecol Monogr* 60: 369-388.
- Marsh RL and John-Alder HB (1994) Jumping performance of

*Defense Strategies of Anurans against Snakes*

- hylid frogs measured with high-speed cine film. *J Exp Biol* 188: 131-141.
- Mori A (1989) Behavioral responses to an unpalatable prey, *Rana rugosa* (Anura: Amphibia), by newborn Japanese striped snakes, *Elaphe quadrivirgata*. *Curr Herpetol East Asia* 459-471.
- Myers CW, Daly JW, and Malkin B (1978) A dangerously toxic new frog (*Phyllorbates*) used by Embera Indians of western Colombia, with discussion of blowgun fabrication and dart poisoning. *Bull Am Mus Nat Hist* 161: 307-366.
- Sih A, Crowley P, McPeck M, Petranka J, and Strohmeier K (1985) Predation, competition, and prey communities: a review of field experiments. *Annu Rev Ecol Syst* 16: 269-311.
- Sokal RR and Rohlf FJ (1998) *Biometry: the Principles and Practice of Statistics in Biological Research*, 3rd Ed. W. H. Freeman and Company, New York.
- Turner FB (1960) Population structure and dynamics of the western spotted frog, *Rana p. pretiosa* Baird & Girard, in Yellowstone Park, Wyoming. *Ecol Monogr* 30: 251-278.
- Turner FB (1962) The demography of frogs and toads. *Quart Rev Biol* 37: 303-314.

[Received May 20, 1999; accepted June 18, 1999]