a   **b**

FIG. 1. *Pleurodema brachyops* with (a) body inflated (at night in the field) and (b) body inflated, hindparts elevated, and displaying noxious glands, eyespots, and bright colored markings (by day in laboratory). Glands are black with small white markings; area surrounding glands is black; bright colored markings are stippled. Drawn from color diapositives.

Field observations were made in 1986 in temporary and permanent ponds in the savanna around Boa Vista (2°48'N, 60°12'W, 100 m elev.), Roraima, Brazil. More than ten *P. brachyops* males collected in these ponds at night were transported to the laboratory and tested separately in a plastic chamber (50 × 40 × 8 cm) the following morning. Each frog was tested just once. The tests consisted of inhibiting escape by the frog and stimulating it by tapping its back.

Pleurodema brachyops in Boa Vista has a reticulated, gray dorsum with smooth skin, lumbar glands black with small white markings, surrounded by an area of black. The inguinal region and hidden surfaces of the thighs are bright orange. In the field at night, *P. brachyops* males fled with a sequence of short jumps when approached. When caught and unable to jump, they inflated the body exposing only partially the lumbar glands and did not alter this posture when further stimulated (Fig. 1a). One juvenile exhibited the same behavior after several trials, and also remained immobile for a few seconds when I turned it upside down. I never found a *P. brachyops* by day in the field. In the laboratory, all *P. brachyops* males tested exhibited deimatic behavior when first stimulated (Fig. 1b). Their posture consisted of inflating the body and elevating the hindparts, thus displaying the lumbar glands, the orange spots of the inguinal region and posterior surfaces of the thighs. The head was lowered a little and the eyes were open. Glandular secretions were not observed. When re-stimulated, the posture was enhanced and when not, the posture was abandoned after a few seconds and the frog fled.

The deimatic behavior observed in *P. brachyops* consists of at least five types of displays: body inflation, hindparts elevation, noxious glands display, bright color display, and eyespots display. These displays are known in other frogs and are considered to be intimidating to potential predators (for a review, see Sazima and Caramaschi, 1986). *Physalaemus nattereri*,

P. deimaticus (Sazima and Caramaschi, 1986), *Pleurodema thaul* (Cei and Espina, 1957), and *P. bufonina* (Cei, 1962) exhibit all these displays, but they lack bright colored thighs, which are found in other frogs in which some of these displays occur (e.g., *Dendrobates flavopictus* and *Leptodactylus labyrinthicus*, I. Sazima, pers. comm.). *Pleurodema brachyops* is unique in presenting all of these displays. Although the deimatic behavior of these frogs can be considered a complex behavioral pattern, its evolution may have occurred in relatively simple steps (Sazima and Caramaschi, 1986) as each of its components alone or in combination is found in several frog families (Bufonidae, Dendrobatidae, Leptodactylidae, and Sooglossidae; Cott, 1940; Cei and Espina, 1957; Cei, 1962; Bajger, 1980; Sazima and Caramaschi, 1986; I. Sazima, pers. comm.; pers. obs.). The observations presented here and the visual nature of the deimatic displays observed in *P. brachyops* suggest that these displays occur only by day. This could explain the lack of observation of this behavior in natural field conditions (Duellman and Veloso, 1977; this paper). Although *P. brachyops* is a nocturnal breeding species (Staton and Dixon, 1977; Hoogmoed and Gorzula, 1979; pers. obs.), the combination of these five display components suggests that there is predation in possible diurnal activities and/or in its diurnal retreat.

Acknowledgments.—I thank C. Morato de Carvalho for the opportunity of working in Roraima, I. Sazima for discussion and valuable suggestions, J.-M. Hero for improving my English, and Convenio CNPq/ INPA/Governo de Roraima for financial support.

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Accepted: 3 February 1988.

Individual Variation in Antipredator Response of *Ambystoma jeffersonianum* to Snake Predators

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Salamanders are known to employ a wide variety of both morphological and behavioral antipredator mechanisms (Brodie, 1973, 1977). Several of these defensive mechanisms may occur in the repertoire of a single species, either simultaneously or alternatively (Dodd and Brodie, 1976; Brodie, 1977; Dodd, 1977; Arnold, 1982). A suite of antipredator characters may have additive (Arnold, 1982) or synergistic (Johnson and Brodie, 1972, 1975) effects. In some cases, salamanders respond with alternative mechanisms depending upon the predator species or upon the type of encounter (e.g., tongue-flick vs. body contact with a snake) (Dodd and Brodie, 1976; Ducey and Brodie, 1983). Ducey and Brodie (1983) have suggested that such intraspecific variation in defensive behavior is maintained by both the diversity of predators and the survival advantage to individuals that react appropriately to different types of encounters with the same predator.

Intraspecific variation in salamander antipredator mechanisms has been observed in different contexts,

TABLE 1. Results of analysis of variance of duration of tail undulation. Significant effects are in bold type.

Source	Degrees of freedom	F	P
Snake species	2,102	1.54	0.220
Stimulus area	2,102	0.91	0.405
Order of trial	8,96	1.25	0.277
Individual	**12,92**	**2.16**	**0.015**

whereas no attempts have been made to quantify individual variation in response to a single stimulus or to determine whether salamanders respond differently to contact with predatory and non-predatory species of similar taxa (i.e., snakes). In light of the specificity of stimulus–response relationships already demonstrated for some salamanders (Dodd and Brodie, 1976; Ducey and Brodie, 1983), this latter problem is especially important since some studies of antipredator behavior have been conducted using non-predatory snake species as a stimulus (Dodd, 1977; for *Coleonyx variegatus* Johnson and Brodie, 1974).

The antipredator repertoire of *Ambystoma jeffersonianum* is known to include the production of noxious skin secretions from glands concentrated in the tail and tail undulating behavior presumably intended to draw a predator's attention to this area (Brodie, 1977). When harassed, small and medium-sized individuals raise the tail vertically and begin a rapid (but not violent) undulation. Larger individuals hold the tail straight out behind them or arched over so that the tip touches the ground. During this display, the tail is covered with a sticky white substance secreted from the skin glands. This behavior has been observed in response to attacks by snakes (Dodd, 1977; Ducey and Brodie, 1983), shrews (Brodie, 1977) and humans (Rand, 1954). In this paper, I examine *A. jeffersonianum* for individual variation in antipredator response to predatory and non-predatory snakes. Individual variation is one of the necessary conditions for any phenotypic trait to exhibit an evolutionary response to selection (Arnold and Bennett, 1984).

Thirteen adult *Ambystoma jeffersonianum* were collected near the E. N. Huyck Preserve in Albany Co., New York in early April 1982. The subjects were housed individually in plastic containers 7 cm deep × 15 cm in diameter and maintained on a 12L:12D photoperiod at 23–25°C for the duration of the study. Testing was conducted in the housing chambers.

Salamander responses to snake tongue-flicks were examined using three snakes (all long-term captives): one common garter snake (*Thamnophis sirtalis*), a known amphibian predator, and one corn snake (*Elaphe guttata*) and one rosy boa (*Lichanura trivirgata*), neither of which is known to prey on amphibians (Wright and Wright, 1957). To avoid incidental body contacts, snakes were hand held and allowed to tongue-flick a salamander only once per trial.

Response to tongue-flicks by each of the three species of snakes were observed for contacts to the head, body and tail, yielding a total of nine trials for each salamander. Trials were conducted each day for nine consecutive days. The order of testing was randomized using a random numbers table (Wonnacott and Wonnacott, 1984).

A response to a tongue-flick was classified as pos-

TABLE 2. Individual responses to snake tongue-flicks. The percentage of positive responses refers to the proportion of tail undulations elicited out of nine trials. The mean duration of tail undulation is calculated over all positive responses for each individual.

	Salamander												
	1	2	3	4	5	6	7	8	9	10	11	12	13
% positive response	67	100	56	89	67	100	78	67	100	89	89	89	100
Duration of undulation (mean ± SE)	32.8 ±37	62.5 ±28	46.1 ±78	82.0 ±70	20.2 ±19	63.8 ±66	54.6 ±53	58.4 ±65	101.0 ±51	76.8 ±50	185.4 ±130	129.9 ±108	84.0 ±31

itive if the tail was undulated for more than ten seconds (no undulations lasting less than ten seconds were observed). Snake and stimulus effects on frequency of response were analyzed using a Friedman Two-way Analysis of Variance (Siegel, 1956). Order effects and individual differences in frequency of response were examined using a Cochran Q-test (Siegel, 1956). Data on duration of undulation for positive responses were natural-log transformed to achieve normality and subjected to Analysis of Variance. *Ambystoma jeffersonianum* responded with the previously described tail undulation behavior in 84% (N = 98 of 117) of the trials. The duration of the behavior averaged 77 seconds (SE = 77 sec; range: 10–350 sec).

Salamanders showed no evidence of habituation to the threat stimulus during the course of the study. The order of the trial did not affect the number of positive responses ($Q_8 = 13.24$, NS) or the duration of the tail undulation (Table 1).

Antipredator response of the salamanders was not affected by the type of snake making contact. Neither the number of positive responses ($\chi_{r2} = 3.53$, NS) nor the duration of tail undulation (Table 1) showed any effect of snake species.

There was no significant difference in the frequency of response due to stimulus area ($\chi_{r2} = 4.26$, NS). However, tongue-flicks to the tail and body elicited more positive responses (94% and 92%, respectively) than tongue-flicks to the head (78%). Stimulus area also had no significant effect on duration of the tail undulation behavior (Table 1).

Analysis of individual response frequencies reveals a significant difference in number of positive responses among individual salamanders ($Q_{12} = 21.07$, $P < 0.05$; Table 2).

Individual variation in duration of undulation was also apparent (Tables 1, 2). Linear regressions reveal no significant relationship between the duration of the behavior and snout–vent length ($F_{1,93} = 0.39$, NS) or tail length ($F_{1,93} = 1.33$, NS).

Although salamanders can respond alternatively to specific cues from a single predator (Ducey and Brodie, 1983), the data presented here indicate that *A. jeffersonianum* cannot distinguish between the tongue-flicks of predatory and non-predatory species of snakes. Whether this is due to an inability to perceive differences in the stimulus or whether there is no stimulus-difference between tongue-flicks of predatory and non-predatory snakes is unknown. The alternative responses to different types of contact by a predatory snake have been shown to be adaptive (Ducey and Brodie, 1983). However, unless there is a significant energetic cost associated with tail undulation, it is unlikely that there is ever a disadvantage to responding to a tongue-flick, regardless of the snake species. A non-predatory snake poses no threat to survival so there has probably been no selection to recognize and respond only to predatory species.

The failure to detect differences in response to the three species of snakes and three stimulus areas could alternatively be explained as an artifact of design. Because snakes were hand-held in all trials, there may be a human component to the stimulus perceived by the salamander. If responses to a "human-plus-snake" stimulus are greater (in duration or frequency) than to a snake alone, small differences in response attributable to the type of snake or stimulus area may not

be detectable. Nonetheless, salamanders do not react differently to hand-held predatory and non-predatory snakes, so behaviors observed in response to non-predatory snakes in this context probably represent actual antipredator mechanisms.

Previous studies of intrapopulational variation in salamander antipredator mechanisms have shown alternative responses to several stimuli, either different predators (Brodie, 1977) or different types of contact with the same predator (Ducey and Brodie, 1983). The present study is the first demonstration that salamanders from the same population react differently to a single stimulus. Rand (1954) suggested that the differences in the vigor of the display of *A. jeffersonianum* were due to the size of the tail, a larger tail being more difficult to undulate. The lack of a relationship between duration of tail undulation and body or tail size indicates that the individual variation observed is not an indirect result of a morphological constraint.

Selection can only occur if variation is present. If such variation is heritable, then evolution also may occur. Arnold and Bennett (1985) established a genetic basis for antipredator behavior in neonatal garter snakes. The data presented in this paper cannot reveal whether there is a genetic component to individual variation in salamander defensive display, but differences in individual response frequency and duration of tail undulation do indicate potential for selection on antipredator behavior in *A. jeffersonianum*.

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Feeding Habits and Behavior of the Whiptail Lizard, *Cnemidophorus tigris tigris*

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The western whiptail lizard, *Cnemidophorus tigris tigris*, is an active diurnal animal found in semi-arid, sparsely vegetated habitats with open areas. Twelve subspecies, three of which are endemic, occur in Baja California and the adjacent islands in the Gulf of California (Zwiefel, 1962; Stebbins, 1966).

Studies of *C. tigris* have included data on feeding habits and behavior (Milstead, 1957a, b, 1965; Asplund, 1964; Johnson, 1966; Maya, 1968; Pianka, 1970); however, of these workers, only Maya indicated that *C. t. tigris* is a predator on petrel eggs. A study to determine the pattern of predation was conducted from 25 May to 23 July 1977 on Isla Partida (28°53' north latitude, 113° west longitude) in the Gulf of California. The main study area was a talus-sided valley 250 m long, with walls that slope upwards at a 45° angle for 50 m. The rock slides where the animals live have a sandy base, and vary in depth to a maximum of 1 m.

Foraging lizards were collected with slingshots and snaptraps. Stomachs were removed; frequency of families in contents were recorded.

The black storm-petrel, *Oceanodroma melania*, the least storm-petrel, *Oceanodroma microsoma*, and the fish-eating bat, *Myotis vivesi*, are found together in the same roosts in the talus during the summer months. The bats were usually positioned vertically in any of numerable cracks; the petrels are always on the floor of the roost. The population ratio in the talus of bat to least storm-petrel to black storm-petrel is 3:3:1 (Maya, 1968). Petrels are migratory, arriving in late