and JM) examined 543 *A. stellio* (360 adults and 183 juveniles) from most of the range of the species (Greece, Turkey, Cyprus, Lebanon, Jordan, the Sinai, and the mesic portion of Israel [⅔ of the sample]), preserved in the Zoological Museum of the Hebrew University of Jerusalem. These had been collected without bias of tail condition. For the adult sample, 35% showed broken or regenerated tails, with no difference in frequency of injuries between sexes (χ^2, $P > 0.05$). Most of the tail injuries were fresh breaks, so only 27 broken tails were sufficiently regenerated to be scored for shape. Most of these were short, blunt structures, but one exceptionally long regenerated tail measured 39 mm (Fig. 1). In none of the tails was the regenerated portion significantly thicker than the stump. Although Arnold (1984) attributes considerable regenerative capacity to *A. stellio,* these data contradict this conclusion. The situation in *A. stellio* instead parallels that observed in the gecko *Stenodactylus sthenodactylus,* which also has a reduced autotomy system and regenerates only abbreviated nontapering blunt tails (Werner, 1961, 1965, 1968).

In summary, *Agama stellio* does not engage in tail whipping behavior and does not regenerate broken tails into clubbed shapes. *A. agama* males, in contrast, use the tail in social interactions, and males of this species are more likely to form clubbed regeneration. We have no data to support the proposal that clubbed tails are actually more effective during tail whipping bouts that are tapered tails. Clearly, experimental staged bouts between males with different tail forms is the only way to properly confirm our hypothesis. Even if such experiments demonstrate the value of clubbed tails during social interaction between males, this would not necessarily indicate that the tendency of male *A. agama* to produce clubbed tails is an adaptation. Perhaps clubbed regeneration is simply a developmental quirk that influenced selection leading to tail whipping behavior. Alternatively, the use of the tail in social contests may have antedated the origin of clubbed tail regeneration, and acted as the selective force that favored clubs over more tapered regenerated tissue. *A. agama* is a very wide ranging species (Harris, 1964), so this issue perhaps could be resolved through studies of the distribution of tail whipping behavior and club-forming tail regeneration among widely spaced populations.

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Deimatic Behavior in *Pleurodema brachyops*

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Deimatic behavior consists of intimidating postures or actions that occur in animals which cannot flee very fast, or which have been caught by a pursuing predator (Edmunds, 1981). Puffing up the body, elevating the hindparts, and displaying bright colored marks, glands and eyespots are known deimatic displays in frogs (Sazima and Caramaschi, 1988). *Physalaemus nattereri* and *Physalaemus deimaticus* puff up the body and display glands that resemble eyes when disturbed (Edmunds, 1981; Sazima and Caramaschi, 1988). Seven of 12 known species of *Pleurodema* have a pair of prominent lumbar glands; these glands are generally black with other contrasting colors (Duellman and Veloso, 1977). Cei and Espina (1957) reported on the deimatic behavior in *Pleurodema thaul* and Cei (1962, fig. 46) found it in *Pleurodema bufonina.* Duellman and Veloso (1977) did not observe this behavior in the other five species of *Pleurodema* having lumbar glands (including *P. brachyops*). During a study of the reproductive biology of frogs inhabiting the savanna in northern Brazil, I observed deimatic behavior in *Pleurodema brachyops* under laboratory conditions.
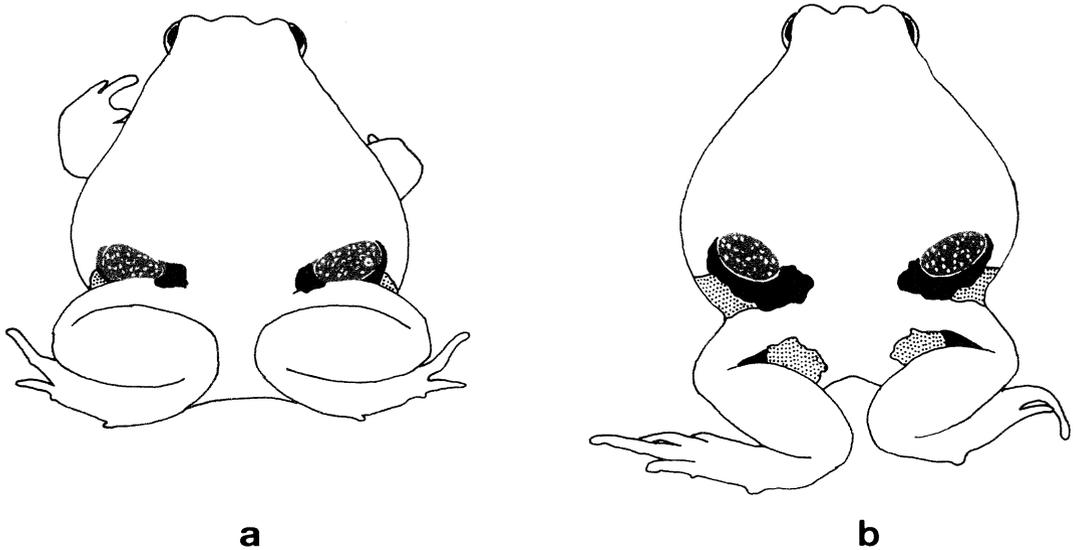
a   **b**

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.

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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 can 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-