Journal of Herpetology, Vol. 29, No. 1, pp. 149-151, 1995
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A Novel Antipredator Mechanism in Salamanders: Rolling Escape in *Hydromantes platycephalus*

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Antipredator mechanisms in salamanders involve behavioral responses that are usually combined with aposematic coloration and skin toxicity (Brodie, 1970, 1977, 1983; Dodd and Brodie, 1976). Behavioral responses range from immobility to active escape, including the adoption of stereotyped postures (Brodie, 1983). Escape mechanisms involve active responses like rapid coiling and uncoiling movements which flip or propel the animal, tail lashing, lateral writhing, and locomotion (Duellman and Trueb, 1986). Although escape responses are usually followed by immobility, no escape mechanism involving passive transport has been reported.

Based on field observations, we document a novel antipredator mechanism in the salamander *Hydromantes platycephalus* that consists of body and tail coiling and limb tucking followed by passive rolling escape. Although coiling is widespread among salamanders, *H. platycephalus* performs it in the novel context of the steep slopes of the northern Sierra Nevada of California. This results in the peculiar antipredator mechanism of rolling escape.

We observed *Hydromantes platycephalus* at two localities in California, in the vicinity of Sonora Pass: (1) the slopes of Blue Canyon in Stanislaus National Forest, Tuolumne County, and (2) near the Pacific Crest Trail in Toyabee National Forest, Mono County. We found 19 individuals at the first locality on 21 August and 11 September, 1993 and two at the second locality on 11 September, 1993. We observed defensive behavior of 10 individuals from the first locality and two from the second.

We tested the repeatability of defensive behavior in the field on 12 specimens. We tested each individual twice for coiling by gently tapping it on the back and for rolling by dropping it onto a 25 cm long slope of exposed soil.

We first observed defensive behavior in *H. platycephalus* when we uncovered two individuals accidentally on a steep slope. The disturbed salamanders quickly assumed a coiled posture and rolled down the slope among dislodged stones. When they stopped rolling, ca. 0.5 m from their starting position, the salamanders uncoiled and assumed their normal stance. They remained stationary and inconspicuous on the substrate for approximately five sec before seeking shelter.

Tests performed in situ on 12 individuals of the repeatability of the coiling behavior revealed that *H. platycephalus* reacted to handling by stereotypically coiling the body and tail to form a spheroid (11 of 12 individuals handled). This stationary posture was maintained for three to 10 sec. The salamanders secreted a noxious, sticky skin fluid that burned severely when placed inadvertently in contact with the eyes. The spherical posture was achieved by curving the body laterally until the head was positioned over the pelvis, curving the tail laterally along the venter and tucking the limbs close to the body (Fig. 1).

TABLE 1. Results of laboratory tests indicating no (0), partial (*), or complete (1) body coiling, tail coiling, and rolling for each individual. See text for definitions of these responses and experimental conditions.

Species	N	Body coiling	Tail coiling	Rolling
Desmognathus quadramaculatus	3	0,0,0	0,0,0	0,0,0
D. santeetlah	3	0,0,0	0,0,0	0,0,0
Pseudotriton ruber	3	0,1,1	0,1,1	0,0,0
Gyrinophilus porphyriticus	3	1,1,1	0,*,0	0,0,0
Plethodon dunni	2	0,0	0,0	0,0
Aneides lugubris	2	0,0	0,0	0,0
A. flavipunctatus	2	0,0	0,0	0,0
Ensatina eschscholtzii	2	0,0	0,0	0,0
Batrachoseps attenuatus	2	1,1	1,1	0,0
B. nigriventris	3	1,1,1	0,0,0	0,0,0
B. pacificus	2	1,1	*,0	0,0
B. wrighti	2	1,1	0,0	0,*
Batrachoseps sp. (Kern Plateau)	3	1,1,1	0,0,*	0,*,0
Hydromantes shastae	3	0,0,0	0,0,0	0,0,0
Bolitoglossa subpalmata	3	0,0,0	0,0,0	0,0,0

Hydromantes platycephalus reacted to being dropped by rolling passively down the talus slope (100% of coiled individuals). The salamanders did not uncoil before stopping at the end of the slope.

To determine how widespread this antipredator mechanism is among plethodontids, we tested captive salamanders of 15 plethodontid species for body coiling behavior and rolling ability. We tested each individual twice for coiling by tapping it on the back and head and tested each twice for rolling by placing it on a 45° incline of moist paper towel. Responses were recorded for *Desmognathus quadramaculatus, D. santeetlah, Pseudotriton ruber, Gyrinophilus porphyriticus, Plethodon dunni, Aneides lugubris, A. flavipunctatus, Ensatina eschscholtzii, Batrachoseps attenuatus, B. nigriventris, B. pacificus, B. wrighti, Batrachoseps* sp. (Kern Plateau), *Hydromantes shastae,* and *Bolitoglossa subpalmata.* All animals were maintained at 13 C on a diet of crickets and fruitflies.

Responses of each individual for each of the two trials were identical unless noted. Lateral body coiling with complete tail coiling was observed in two individuals of *P. ruber,* and both *B. attenuatus* (Table 1). Lateral body coiling with partial tail coiling (i.e., part of the tail not included in the coil) was observed in one *G. porphyriticus,* one *B. pacificus,* and one *Batrachoseps* sp. (Kern Plateau). Lateral body coiling with no tail coiling (i.e., tail extended and not part of coil) was observed in two *G. porphyriticus,* all three *B. nigriventris,* one *B. pacificus,* two *B. wrighti,* and two *Batrachoseps* sp. (Kern Plateau). Animals that did not

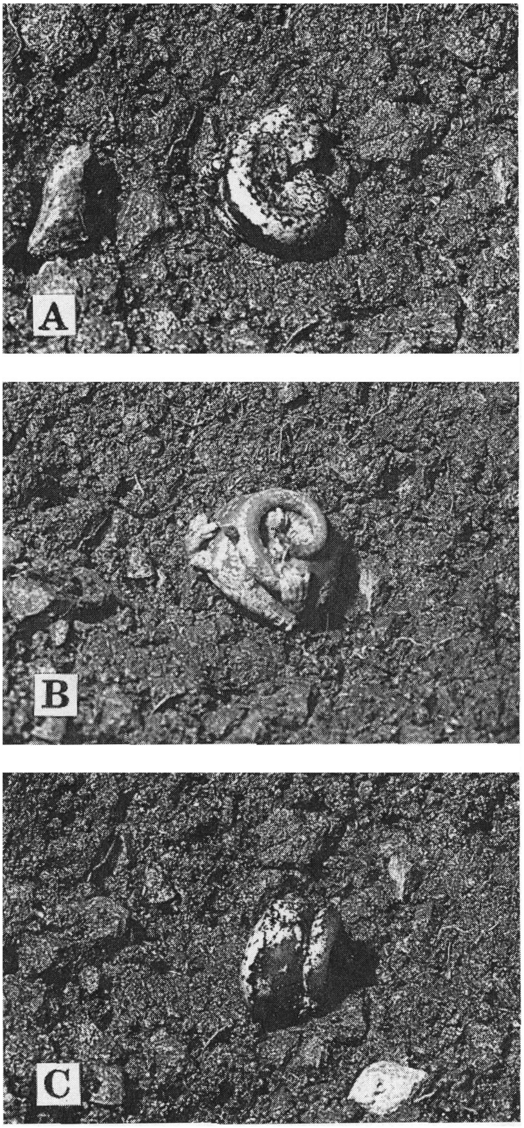

FIG. 1. *Hydromantes platycephalus* in the posture assumed during rolling behavior. The animal was photographed in the field immediately after rolling stopped. Photos are dorsal (A), ventral (B) and lateral (C) views. Note the tucked limbs and coiled tail in B.

coil either the body or tail in the laboratory include: all three *D. quadramaculatus,* all three *D. santeetlah,* one *P. ruber,* both *P. dunni,* both *A. lugubris,* both *A. flavipunctatus,* both *E. eschscholtzii,* all three *H. shastae,* and all three *B. subpalmata.*

Batrachoseps wrighti and *Batrachoseps* sp. (Kern Plateau) were the only species that rolled part of the way down a 45° incline (i.e., partial rolling) in one of the two trials, despite the extended tail and limbs. Neither species exhibited rolling in the second trial, and none of the other species we examined exhibited rolling. *Gyrinophilus porphyriticus* and *P. ruber* appeared to actively prevent rolling while coiled by extending the limbs, unlike *H. platycephalus,* which tucked the limbs close to the body. None of the species tested in the laboratory exhibited the tight coiling or the high tendency to roll that we observed in *H. platycephalus* in the field.

Immobility and body coiling are widespread defensive responses of salamanders (Brodie, 1977,1983). Often these are accompanied by tail extension and undulation and secretion of noxious compounds. Static body coiling has been reported for the plethodontid genera *Aneides, Batrachoseps, Bolitoglossa, Chiropterotriton, Eurycea, Gyrinophilus, Hemidactylium, Hydromantes, Plethodon, Pseudoeurycea, Pseudotriton, Thorius,* and *Typhlotriton* (Brame et al., 1973; Brodie, 1983; Stebbins, 1985; Duellman and Trueb, 1986).

Complete coiling of the body and tail has been observed in the plethodontid species *H. platycephalus, B. attenuatus* (this paper), a Oaxacan species of *Thorius* (D. B. Wake, pers. comm.), *P. ruber* (Brandon et al., 1979), and *Plethodon larselli* (Brodie, 1970). Complete body and tail coiling may represent derivations of the more widespread body coiling behavior seen among salamanders, possibly by the addition of a modified tail-lashing behavior.

In all salamanders that exhibit the behavior, static body coiling is a defense, but not an escape mechanism. In *H. platycephalus,* however, when this generalized static defensive behavior is performed with the addition of tail coiling and limb tucking on steep slopes, a novel antipredator mechanism results: rolling escape. This escape method differs from the rapid coiling-uncoiling escape movements described for tropical bolitoglossines (Dodd and Brodie, 1976; Brodie, 1977).

Hydromantes platycephalus is unique among congenerics in occupying exclusively volcanic and granitic substrates at high elevation. The remaining *Hydromantes* are found mainly on limestone substrates at lower elevations (Bruno, 1973; Stebbins, 1985). The volcanic substrates of the Sierra Nevada form the talus slopes where *H. platycephalus* displays rolling behavior. The combination of steep slopes and abundant small stones makes the rolling behavior an effective escape mechanism. The cryptic coloration helps to conceal the coiled salamander among the rolling stones. Members of the anuran genus *Oreophrynella* display similar rolling escape while on an incline by a combination of limb and head tucking (McDiarmid and Gorzula, 1989). The presence of convergent limb tucking behavior and rolling escape in distantly related taxa that occur on rocky slopes, such as *Oreophrynella* and *H. platycephalus* suggests that natural selection plays an active role in maintaining this defense.

Acknowledgments.—We thank D. Wake, A. Graybeal and two anonymous reviewers for helpful suggestions. This work has been partially supported by a postdoctoral fellowship (FPPI EXT) of the Ministerio de Educación y Ciencia of Spain to MGP.

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Accepted: 30 October 1994.