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small Andean toads. Sympatry and call data require that no fewer than four taxa be recognized—one of the northern taxa (*maculosus* or *scoloblepharus*) may be conspecific with one of the southern taxa (*leptolophus* or *uranobates*). Because *E. peraticus* lacks a middle ear, it is thought not be conspecific with any other member of the group. Each of the five species has the "S" condition of the adductor muscles (Lynch, 1986).

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NOTES

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Differences in the Antipredator Behavior of Three Plethodontid Salamanders to Snake Attack

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Salamanders utilize various morphological and behavioral antipredator mechanisms including tail autotomy, repulsive or adhesive skin secretions, cryptic or aposematic coloration, tonic immobility, posturing, and biting (Brodie, 1977, 1983; Duellman and Trueb, 1986). While all of these defenses have been described for salamanders in the family Plethodontidae, there appears to be considerable interspecific variation in their relative importance, and intraspecific variation in the repertoire used against different types of predators (Brodie, 1977, 1983; Brodie et al., 1979; Arnold, 1982; Ducey and Brodie, 1983).

The type of antipredator response used by captured salamanders might depend on several factors, including body size, predator type, and body location of the capture. Location of the capture can be important because it limits the number of possible responses available to the salamander. For example, a salamander captured on the head can writhe but cannot bite or use tail autotomy. Salamanders captured

along the midsection of the body are able to bite and writhe, but cannot use tail autotomy. Salamanders captured on the tail can autotomize, bite, or writhe to escape. Thus, autotomy might be more frequent in one species than another because it is more prone to capture by the tail.

The plethodontids *Desmognathus ochrophaeus*, *D. fuscus*, and *Eurycea bislineata* are often found in the same stream habitats at low elevations in the northeastern United States (Behler and King, 1979), and thus probably encounter a similar array of predators. Because these three species differ morphologically and phylogenetically, we compared their antipredator responses to one of their major predators, garter snakes (*Thamnophis s. sirtalis*; see Fitch, 1965). Ducey and Brodie (1983) previously examined tail autotomy, antipredator behavior, and survival of *E. bislineata* during encounters with *T. sirtalis*, and Brodie et al. (1989) described biting and other defensive behaviors in *D. quadramaculatus* and *D. ochrophaeus*. However, no previous study has directly compared these species under the same conditions and with the same predators.

We specifically tested for the effect of capture location on type of antipredator response between these three species. Location of capture also affects tailless salamanders because they cannot rely on autotomy. We experimentally tested the hypothesis that tailless salamanders employ biting and writhing to escape predators more than tailed salamanders for all three salamander species.

The salamanders used in this study were collected from three sites in western Pennsylvania (Crawford, Forest, and Fulton counties). Salamanders were housed in an environmental chamber at 15 C and 12:12 h photoperiod, and fed redworms ad libitum. Individual salamanders were tested within one month of capture. Six eastern garter snakes (*Thamnophis s. sirtalis*) were captured locally, housed at 24 C, and fed

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goldfish daily prior to experimentation. Snakes were used in one predation trial per day. Although body sizes of each of the salamanders and snakes used in the experiments were not directly measured, the initial pool of experimental animals were chosen for their similarities in size. Snake predators were approximately 45 cm SVL.

Upon field capture, each salamander was scored for any indication of past autotomy such as a tail stub or evidence of regeneration. Both tailed and tailless salamanders were used in the snake predation experiments. We defined a tailless salamander as having no more than 5 mm of tail (measured distally from the cloaca). Tailless salamanders included both field-collected individuals and those which were autotomized in the lab during a padded forceps experiment that tested the economy of autotomy hypothesis (Whiteman, 1988). Previous work with *Eurycea bislineata* suggested that the pre-capture response (such as fleeing or immobility) to snake predators was not affected by the presence or absence of a tail (Ducey and Brodie, 1983); thus we assumed no differences in pre-capture response between tailed and tailless individuals.

Experiments were performed in a 75 × 78 × 60 cm wooden chamber with a plexiglass pane on one side to permit behavioral observations. Prior to each trial the floor of the predation arena was moistened with water and preheated to 25 C with a heat lamp to facilitate snake and salamander movement. Salamanders did not appear to be adversely affected by this temperature, even though it is higher than what they normally experience in nature. Similar temperatures have been used in other *Thamnophis*-salamander predation experiments (see Arnold, 1982).

A single salamander was introduced into the chamber and allowed to acclimate for several minutes before a garter snake was introduced. Data recorded from the subsequent encounter included where the salamander was captured (head, body, tail), occurrence and location of autotomy, and occurrence of antipredator behaviors such as writhing and biting. Escapes from capture were followed by subsequent stalk, strike, and capture (or miss) sequences until the salamander was ingested. Thus, we obtained two parameters of survival; escape from the first capture, and total number of escapes.

Data for *D. ochrophaeus* and *D. fuscus* were combined in some instances for comparison with *E. bislineata* because these congeners showed similar antipredator behavior patterns. Because behaviors did not differ between individuals from different locations, we combined results from all localities. Data were analyzed by t-tests and multivariate ANOVA and chi-square analysis using the SAS Statistical Package (SAS Institute).

During field collection all three salamanders exhibited evidence of tail autotomy. Although *E. bislineata* showed a slightly higher frequency of autotomy (32%, 12 of 39) than either *D. ochrophaeus* (19%, 15 of 80) or *D. fuscus* (23%, 9 of 39), the differences were not significant ($\chi^2 = 2.67$, $P = 0.26$, $N = 156$). In addition, there was no species-specific pattern to the location of the break point in field-caught salamanders.

The location of the first capture did not vary significantly among the three species (Table 1). Moreover, the presence/absence of a complete tail also did

TABLE 1. Body location of the first capture on *Desmognathus ochrophaeus*, *D. fuscus*, and *Eurycea bislineata* during encounters with snake predators ($\chi^2 = 0.36$, $P = 0.99$, $N = 116$).

Species	Number of first captures			
	Head	Body	Tail	Total
<i>D. ochrophaeus</i>	10	31	17	58
<i>D. fuscus</i>	6	14	9	29
<i>E. bislineata</i>	6	14	9	29

not affect the location of the first capture, except that tailless individuals could not be attacked on the tail. Tailless salamanders were attacked no more frequently on the head (21%, 8 of 39) than tailed salamanders (18%, 14 of 77), ($\chi^2 = 0.09$, $P = 0.76$, $N = 116$). In *Desmognathus* the point of capture influenced which defense mechanism was used. Biting occurred only when individuals were attacked on the body or tail, and autotomy occurred only when attacked on the tail. The combined effects of these two escape tactics in *Desmognathus* resulted in more frequent escapes from the first capture when attacked on the body or tail (67%, 33 of 49) than when attacked on the head (10%, 1 of 11) ($\chi^2 = 9.00$, $P = 0.01$, $N = 60$).

Autotomy during the predation experiments was almost twice as frequent in *E. bislineata* (59%, 10 of 17) trials as in *D. fuscus* (24%, 5 of 21) and *D. ochrophaeus* (28%, 12 of 43) trials (Fisher's exact test, $P < 0.03$, $N = 81$). *Eurycea bislineata* used autotomy to escape in 47% (8 of 17) of first captures, and this was their only mode of escape. The *Desmognathus* species, in contrast, used autotomy for only 22% (14 of 64) of the first capture escapes (Table 2). For all species combined, autotomizing individuals escaped the first capture more frequently (88%, 22 of 25) than those that did not (48%, 28 of 58; $\chi^2 = 19.65$, $P < 0.001$, $N = 83$). The few cases in which autotomy did not result in escape occurred when snakes simultaneously grasped the tail and another body part, or when the salamander was trapped and immediately fled back into the snake's mouth after the snake swallowed the tail.

Captured *D. ochrophaeus* and *D. fuscus* bit garter snakes much more frequently (37%, 30 of 87) than did *E. bislineata* (3%, 1 of 29; $\chi^2 = 8.78$, $P = 0.01$). Biting in *Desmognathus* was most effective when salamanders were attacked on the body or tail. Salamanders turned and aggressively bit at the snake's face and mouth and frequently clamped onto the snake's upper lip. The snake responded to this biting by whipping its head and body from side to side, and/or coiling to rub the salamander against the arena wall.

Biting behavior in *Desmognathus* was an effective escape strategy. The occurrence of biting had a positive effect on the total number of times *D. ochrophaeus* and *D. fuscus* escaped capture (Fig. 1). Overall, *Desmognathus* that bit snakes escaped significantly more frequently than those that did not ($F = 15.69$, $P < 0.001$, $N = 87$).

Frequency of salamanders biting snakes was not affected by the presence/absence of a tail ($\chi^2 = 0.05$, $P = 0.82$, $N = 103$). The presence of a tail had no effect on escape for *D. ochrophaeus*. Tailed individuals escaped a mean 0.78 times per trial compared to 1.56

TABLE 2. Comparison of the antipredator mechanisms of *Desmognathus ochrophaeus*, *D. fuscus*, and *Eurycea bislineata* during encounters with snake predators.

Species	N	Percent escaping first capture by:		
		Autotomy	Other behaviors: (biting or writhing)	Total % escape first capture
<i>E. bislineata</i>				
Tailed	17	47	0	47
Tailless	12	0	0	0
<i>D. ochrophaeus</i> and <i>D. fuscus</i>				
Tailed	64	22	36	58
Tailless	23	0	39	39

times per trial for tailless individuals, but did not differ significantly ($t = 1.43$, $P = 0.17$, $N = 58$). However, our qualitative observation was that tailless *D. ochrophaeus* ran faster and were more agile than conspecifics with tails. Tailed *D. fuscus* escaped about the same mean number of times (1.85 per trial) as did tailless individuals (1.33 per trial; $t = 0.64$, $P = 0.53$, $N = 29$). In contrast, the presence of a tail had a positive effect on *E. bislineata* (0.53 escapes per trial by tailed individuals compared to no escapes by tailless individuals, $N = 29$). Thus, the three species varied in the degree to which presence or absence of a tail affected escape success.

Our results suggest that *Desmognathus* and *Eurycea* differ in their relative use of tail autotomy and biting as escape tactics when attacked by garter snakes. Tail autotomy was an important first defense for all three salamander species tested, and as in previous studies occurred only when salamanders were attacked on the tail (Arnold, 1982; Ducey and Brodie, 1983; Labanick, 1984; Beneski, 1989). However, autotomy in our study was almost always a first response tactic for these species. This result is in contrast to the findings of Brodie et al. (1989) in which tail autotomy occurred later in the capture sequence for *D. ochrophaeus*. In Brodie et al. (1989), *D. ochrophaeus* used tail autotomy both as an early response to attack on the tail, and after capture a last resort if biting failed to elicit escape. We rarely observed autotomy as a last resort tactic for the *D. ochrophaeus* in our study. Similar interpopulational differences in escape behavior from the same type of predator have been observed in lizards (Schall and Pianka, 1980) and salamanders (Ducey and Brodie, 1983; Dowdey and Brodie, 1989).

It is also possible that predator size may have affected which behavior a salamander used. Although our salamanders were of the same general size as the *D. ochrophaeus* used by Brodie et al. (1989), the snakes we used were much larger. Salamanders might autotomize less often when attacked by a smaller predator because biting may be sufficient for escape. Beneski (1989) suggested that tail autotomy may only occur under life-threatening situations when escape through other defensive mechanisms seems improbable. Because large snakes may be more life-threatening than small snakes, and because behaviors such as biting and writhing may not result in a high probability of escape with large snakes, selection may favor the use of tail autotomy.

Individual *Desmognathus fuscus* and *D. ochrophaeus*

that did not escape by autotomy often escaped by biting. The biting behavior observed in this study was nearly identical to that reported by Brodie et al. (1989), except that the biting we observed was always restricted to the snake's face. The total number of escapes that accompanied biting emphasizes the importance of this behavior for these *Desmognathus* species.

The fact that *Eurycea bislineata* infrequently bit to escape snake capture is not surprising, given the fragile jaws of this species in comparison with *Desmognathus*, and the fact that biting is an uncommon defense among plethodontid salamanders (Brodie, 1977). It is surprising, however, that *E. bislineata* did not exhibit a writhing response, which is one of the more common antipredator mechanisms among the Plethodontidae (Brodie, 1983). Selection for this behavior may be weak, given that this species has other effective antipredator traits, including (1) tail undulation to effectively attract predators (Brodie, 1977, although not for snake predators, see Ducey and Brodie, 1983); (2) high frequency and effectiveness of autotomy (Ducey and Brodie, 1983; this study); and (3) speed and agility when escaping (Ducey and Brodie, 1983; Dowdey and Brodie, 1989; pers. obs.). Such traits may allow salamanders to escape before a second capture.

Differences in escape behavior are summarized in Table 2, which compares the frequency of escaping the first capture between *E. bislineata* and the *Desmognathus* species. *Eurycea bislineata* escaped the first capture less frequently than *D. ochrophaeus* or *D. fuscus*, and autotomy was its only defense mechanism. In contrast, the *Desmognathus* species used autotomy less frequently than *E. bislineata*, but had a similar total escape frequency because of the use of biting and/or writhing. Overall, tailless salamanders escaped less frequently than tailed salamanders because of the lack of autotomy. However, tailless *Desmognathus* had a higher escape frequency than tailless *E. bislineata* because of the added effectiveness of biting and writhing.

The effect of presence/absence of a tail on survival is obvious for *E. bislineata* but it is less so for *D. ochrophaeus* and *D. fuscus*. The absence of a tail in *Desmognathus* does reduce the chance of escape by autotomy after capture, but does not change the effectiveness of biting and writhing. In addition, our qualitative data suggest that in *D. ochrophaeus* the absence of a tail may increase the chance of escaping an attack. This suggests a tradeoff similar to that described for

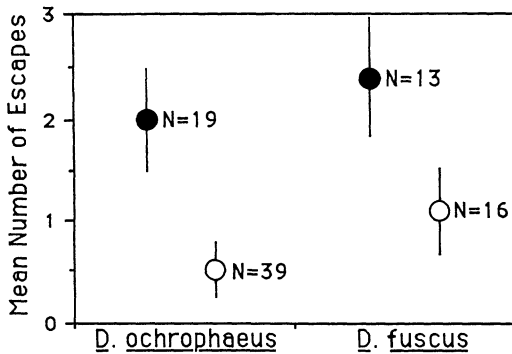


FIG. 1. The effect of biting on total escapes from garter snakes for *Desmognathus ochrophaeus* and *D. fuscus*. Closed symbols denote biting individuals, open symbols non-biting. Vertical bars represent two standard errors of the mean.

a number of lizard species in which increased speed without a tail offsets the value of the tail of autotomy (Daniels, 1985).

In summary, we suggest tail autotomy is more important for *E. bislineata* escape from garter snakes than it is for *D. ochrophaeus* or *D. fuscus*. The higher (though non-significantly) proportion of autotomy observed in the field for *E. bislineata* compared to either *Desmognathus* species is consistent with this conclusion. Finally, this study emphasizes that *Desmognathus* escape from garter snakes involves a combination of tactics that vary in importance depending on the location of attack and initial presence or absence of a tail.

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Relationship Between Cover Availability and Larval Pacific Giant Salamander Density

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Substrate composition and the availability of suitable cover are known to strongly influence salamander distribution and abundance. Experimental additions of cover objects, resulting in increased salamander densities, demonstrate that cover objects may be a limiting resource in a variety of habitats (Kleeberger, 1985; Southerland, 1986; Davic and Orr, 1987). Here I describe the relationship between cover density and the density of stream-dwelling larvae of the pacific giant salamander, *Dicamptodon tenebrosus* (formerly *D. ensatus* [Good, 1989]), in a headwater stream in NW California.

The genus *Dicamptodon* is a prominent member of