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# Effects of size, caudal autotomy, and predator kairomones on the foraging behavior of Allegheny Mountain dusky salamanders (*Desmognathus ochrophaeus*)

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**Abstract** Prey must balance the conflicting demands of foraging and defensive behavior. Foraging under the threat of predation may be further complicated among species that engage in caudal autotomy, the loss of a portion of the tail at preformed breakage planes, because the tail may serve as an important energy storage organ and contribute to motility, culminating in a trade-off between foraging and predator avoidance. As a result of the advantages conferred by the presence of a tail, individuals that have recently undergone autotomy may be more motivated to forage despite elevated levels of threat indicated by predator kairomones. We used a full factorial design to evaluate the combined effects of body size, exposure to predator kairomones, and experience with autotomy on the latency to strike at *Drosophila* prey, number of strikes, and prey captured per strike by Allegheny Mountain dusky salamanders (*Desmognathus ochrophaeus*). In our study, caudal autotomy was the only significant main effect and influenced both the latency to attack prey and the number of strikes attempted. In terms of latency to attack prey, there was a significant interaction between body size and autotomy such that “small” salamanders ( $\leq 3.2$  cm SVL) without tails delayed their foraging behavior. In terms of the number of strikes toward prey, there was a significant interaction between autotomy and exposure to predator kairomones such that individuals with intact tails exhibited a greater number of strikes, with the exception of the “large” ( $> 3.2$  cm SVL) salamanders, which performed

fewer strikes when exposed to the snake kairomones. There was no significant effect on foraging efficiency, although the trend in the data suggests that autotomized individuals forage more efficiently. This study was designed to evaluate the confluence of factors related to size, caudal autotomy, and exposure to stimuli from predators and hints at the magnitude of caudal autotomy on antipredator decision-making. Our data suggest that despite the importance of tail tissue for energy storage, locomotion, and mating, salamanders without tails are cautious when foraging under elevated risk.

**Keywords** Autotomy · Foraging behavior · Kairomones · Predation risk · Size

## Introduction

The complex nature of predator–prey interactions in the natural environment forces species to balance the conflicting demands of defense, mate search, courtship, and foraging (Lima and Dill 1990; Brodie et al. 1991; Sih 1992; Candolin 1997; Lima 1998; Polis et al. 1998). Although antipredator behavior and predator avoidance can reduce the likelihood of injury, death, or detection by predators, they often impose some cost on other aspects of the fitness of individuals. These compromises may be most pronounced in prey that respond to threat with a decrease in overall activity (e.g., Kohler and McPeck 1989; Madison et al. 1999), altered movement between foraging patches (e.g., Roberts and Liebgold 2008; Sansom et al. 2009), or delayed emergence from refugia (e.g., Sullivan et al. 2002). In each of these scenarios, the decrease in foraging opportunity or success may be accompanied by reduced rates of growth and development, as well as fecundity (Skelly and Werner 1990; Peckarsky et al. 1993; Scrimgeour and Culp 1994).

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Refinement of predator avoidance strategies may be further complicated in species that concurrently engage in both predator avoidance and antipredator behavior, such as autotomy. Caudal autotomy is utilized by a number of vertebrate species and involves the loss or shedding of a portion of the tail at preformed breakage planes (Stebbins and Cohen 1995; Downes and Shine 2001; Bateman and Fleming 2009; Marvin 2010). Previous studies suggest that the shedding of the tail when grasped by a predator can increase the likelihood of prey escape or serve as a distraction to the predator (Ducey and Brodie 1983; Maginnis 2006; Arnold 2007). However, this defense mechanism includes a substantial cost as the tail often plays a role in energy storage, balance, climbing, and locomotion (Jamison and Harris 1992; Maginnis 2006). As a result, individuals with autotomized tails may exhibit decreased locomotor ability and speed (e.g., Cooper et al. 2004; Marvin 2010), which may lead to fewer prey encountered or captured.

Given the complex relationship between antipredator behavior, predator avoidance, and foraging behavior, selection should favor sensory mechanisms that allow prey to optimize their defensive strategies. Many prey use disturbance cues (from distressed or startled individuals), injury-released cues (from physically damaged individuals), and predator kairomones (emitted directly from predators) to evaluate predation risk (Wisenden 2000; Ferrari et al. 2010; Crawford et al. 2011). These stimuli can relay information to individuals regarding the proximity and recent foraging activity of a predator or predation event (Ferrari et al. 2010). In addition, the recognition of these chemical stimuli to assess risk has advantages in many environmental contexts because they can be detected in the dark and around obstacles (Smith 1992; Dodson et al. 1994). Kairomones from predators can persist in the environment and convey information to prey species even after the predator has left an area, which may be especially beneficial if predators show fidelity to foraging sites (Bradbury and Vehrencamp 1998).

We studied Allegheny Mountain dusky salamanders (*Desmognathus ochrophaeus*, Plethodontidae) to examine the influence of multiple factors related to predation (e.g., body size, tail autotomy, presence of predator kairomones) on foraging behavior in a terrestrial system. Plethodontid salamanders possess well-developed chemosensory organs (Dawley and Bass 1988) and rely on chemical stimuli for foraging (Placyk and Graves 2002), territory maintenance (Mathis 1990; Wise et al. 2004), and mate recognition (Marco et al. 1998). Furthermore, some species respond to predator kairomones (Madison et al. 1999), predator diet cues (Sullivan et al. 2002, 2004, 2005), disturbance cues (Lutterschmidt et al. 1994), and injury-released cues from conspecifics, as well as heterospecifics belonging to the same prey guild (Sullivan et al. 2003). Individual *D. ochrophaeus* exhibit threat-sensitive changes in foraging behavior and activity when

exposed to predator kairomones as a means of refining their defensive strategy (Johnson and Sullivan 2014). In addition, desmognathine salamanders autotomize their tails during encounters with predators and tend to exhibit decreased locomotor speeds as a result (Labanick 1984; Marvin 2010).

The purpose of this study was to use a factorial design to evaluate the combined effects of individual body size, exposure to predator kairomones, and experience with caudal autotomy on the latency to strike at prey, number of strikes made, and prey captured per strike by Allegheny Mountain dusky salamanders (*Desmognathus ochrophaeus*). We hypothesized that these metrics of foraging behavior would be generally suppressed by the presence of predator kairomones and experience with caudal autotomy because each may indicate the recent presence of a predator. We predicted that (1) “small” individuals would be more likely to forage sooner, exhibit a greater number of strikes toward prey, and forage with greater efficiency in order to maximize growth and attain a refuge body size; (2) autotomized individuals in both size categories would tend to exhibit a greater latency to strike, exhibit fewer strikes, but forage more efficiently when exposed to kairomones because they can no longer employ caudal autotomy if attacked by a predator; and (3) exposure to kairomones from predators will cause “large” salamanders to exhibit a greater latency to strike, exhibit fewer strikes, but forage more efficiently because they can afford to be cautious due to higher energy stores.

## Methods and materials

### Collection and maintenance

We collected 120 individuals of *D. ochrophaeus* from the campus of Houghton College (Allegheny Co., NY) between 17 and 23 June 2015 for use in behavioral trials. Each salamander was brought into the laboratory and transferred individually to 15-cm-diameter × 1.5-cm-height Petri dishes lined with acid-free paper toweling saturated with reverse-osmosis (RO) water. Paper towel substrates were moistened as needed with additional RO water and changed as they became soiled. We maintained all test salamanders in a climate-controlled chamber on a 14:10 h light/dark (lights on at 0600 h E ST) photoperiod with temperatures ranging from 12.8 °C (night) to 15.5 °C (day). Within 5 days of capture, each individual was provided five apterous *Drosophila* sp. in an attempt to standardize the date of the last successful foraging event, although some salamanders failed to consume all flies. During this period, we also collected two adult eastern garter snakes (*Thamnophis sirtalis*, Colubridae) from our field site to serve as the donors of the predator kairomone (SVL > 40 cm; snout-vent length was measured from the tip of the snout to the posterior margin of the cloacal vent). These two snakes were

housed separately in 22.7-l glass aquaria with crumpled paper towels provided for substrate and cover. Snakes were maintained in the laboratory at the photoperiod described above but at approximately 20 °C. We provided water for the snakes in 5-cm-diameter glass petri dishes, as well as two dusky salamanders (SVL > 3.3 cm) as prey immediately before kairomones were collected. All surviving salamanders and snakes were returned to the point of their capture within 25 days of capture.

### Simulated attack and stimulus preparation

To determine the impact of a predator encounter on salamander foraging behavior under the threat of predation, we simulated an attack by a snake predator on half of our study population ( $n = 60$ ) 17 days before they were tested in our bioassay. Our simulated attack was based on the methods of Mathis and Lancaster (1998) and Watson et al. (2004) with the exception that we firmly grasped individual salamanders with fine-tipped forceps approximately 1 cm posterior to the cloacal vent and applied pressure until tails were autotomized at the point where the force was applied. Autotomized tails were removed from the home dishes and animals were returned to the climate-controlled chamber. To minimize the confounding variable related to additional handling time or disturbance in our treatment group, we removed the remaining 60 individuals with intact tails from the climate-controlled chamber and performed a sham procedure designed to replicate the general disturbance of handling home dishes. In this procedure, we placed the forceps approximately 1 cm posterior to the cloacal vent without the application of pressure or induction of caudal autotomy.

We collected the predator kairomone by way of a RO-water rinse of the captive *T. sirtalis*. Each of the captive snakes was transferred to a clean 4-l beaker that was subsequently covered with cheesecloth and placed on the counter in our laboratory. After 72 h, we carefully removed the snakes and returned them to their home aquaria and then rinsed each beaker with 200 ml of RO water. We filtered this rinse through glass wool to remove large solids (e.g., waste, bits of shed skin) then divided the filtrate into four 50-ml aliquots to be rapidly frozen in liquid nitrogen and stored in a freezer until use. It is possible that this filtrate also contained disturbance cues from the prey salamanders, as well as the predator kairomones (Madison et al. 2002).

### Behavioral assay

We evaluated the foraging behavior of salamanders under the threat of predation through a series of behavioral trials conducted between 1915 and 2230 h. We transferred salamanders to the laboratory 30 min prior to the commencement of observations to allow adjustment to room temperature and ambient light levels provided by two 13-watt red compact fluorescent bulbs. Over the course of the experiments, we observed 30 different

individuals in each of four treatment groups: autotomized tail exposed to water, autotomized tail exposed to snake kairomone, intact tail exposed to water, and intact tail exposed to snake kairomone. Each of the 120 salamanders was tested once prior to their release and we implemented a bioassay with a stratified design such that an equivalent number of the treatment groups listed above were tested each night.

We observed salamander behavior within 15-cm-diameter petri dishes lined with filter paper and saturated with 3 ml of a distilled water control or predator kairomone. Next, we transferred one salamander from its home dish to the center of a test dish using a cotton swab. After a 2-min adjustment period, we added 10 apterous *Drosophila* sp. to the test dish and determined the (1) latency to first strike, (2) total number of strikes, and (3) foraging efficiency for the 10-min trial period. For the purpose of our study, latency to strike was defined as the amount of time elapsed from the beginning of each trial to the first strike toward *Drosophila* prey. A salamander that did not strike was assigned a latency of 600 s. Strikes are rapid movements or lunges of a salamander toward the prey with mouth open or tongue extended (Jaeger and Rubin 1982; Maerz et al. 2001; Johnson and Sullivan 2014; Ryerson 2013). Foraging efficiency is the number of prey captured per strike and was calculated for individuals with at least one strike directed toward prey.

### Statistical analyses

Because data related to salamander foraging behavior did not fit the assumptions of normality, we used the non-parametric generalized linear model (GZLM) to test the full factorial model with categorical factors: body size (small, large), autotomy (intact, autotomized), and stimulus exposure (water, snake kairomone). We used a factorial ANOVA with a log-link function in Statistica's (Statsoft, Inc., 2001, version 6.0) GZLM because, unlike most non-parametric tests, it allows for an examination of the interactions between main effects, autotomy, exposure, and size. We designated individuals as "small" (SVL < 3.3 cm,  $n = 52$ ,  $\bar{x} \pm SE = 2.94 \pm 0.04$ , range = 2.2–3.2 cm) or "large" (SVL  $\geq$  3.3 cm,  $n = 68$ ,  $\bar{x} \pm SE = 3.68 \pm 0.03$ , range = 3.3–4.3 cm) based on the bimodal frequency distribution of the SVL of our test subjects and the fact that "small" salamanders are significantly smaller than "large" salamanders ( $t$  test,  $t_{118} = 15.235$ ;  $p < 0.001$ ).

### Results

Our analysis of body size, tail autotomy, and exposure to predator kairomones on the latency to strike at prey reveals a significant main effect of autotomy, as well as a size  $\times$  autotomy interaction (Table 1). Salamanders with autotomized tails tended to delay foraging behavior after the adjustment period

but the effect is most pronounced in “small” individuals (Fig. 1). We also identified a significant main effect of autotomy and a size  $\times$  exposure interaction on the number of strikes directed toward prey (Table 1). In general, salamanders with intact tails tended to perform more predatory strikes, with the exception of “large” salamanders foraging in the presence of snake kairomones (Fig. 2). Lastly, we detected no significant main effect or interaction related to prey captured per strike for “large” or “small” salamanders (Table 1, Fig. 3).

## Discussion

The body size of the individual, induction of tail autotomy, and exposure to predator kairomones each exerted some effect on foraging in *D. ochrophaeus*. Our data suggest that the forfeiture of the tail had the most important effect on behavioral responses in our study, as autotomized salamanders tended toward a significantly greater latency to strike at prey and fewer predatory strikes. Foraging efficiency, indicated by the number of prey captured per strike, by autotomized individuals was not statistically different from intact individuals ( $p = 0.06$ ), but the trend in the data suggests an increase regardless of the chemical stimulus. This is consistent with the other foraging behavior observed in the current study despite the lack of statistical significance. However, the effect of autotomy on the latency to strike and number of strikes revealed a significant interaction with size and exposure, respectively. Small salamanders with autotomized tails exhibited the greatest latency to strike at prey regardless of their exposure to snake kairomone or the control. The effect of autotomy on the number of strikes by foraging salamanders was affected by the exposure to predator kairomones as autotomized individuals exposed to predator stimuli tended to strike less frequently than intact salamanders, especially in the control treatment. These results are generally consistent with our hypotheses that an overall decrease in foraging behavior would be observed in

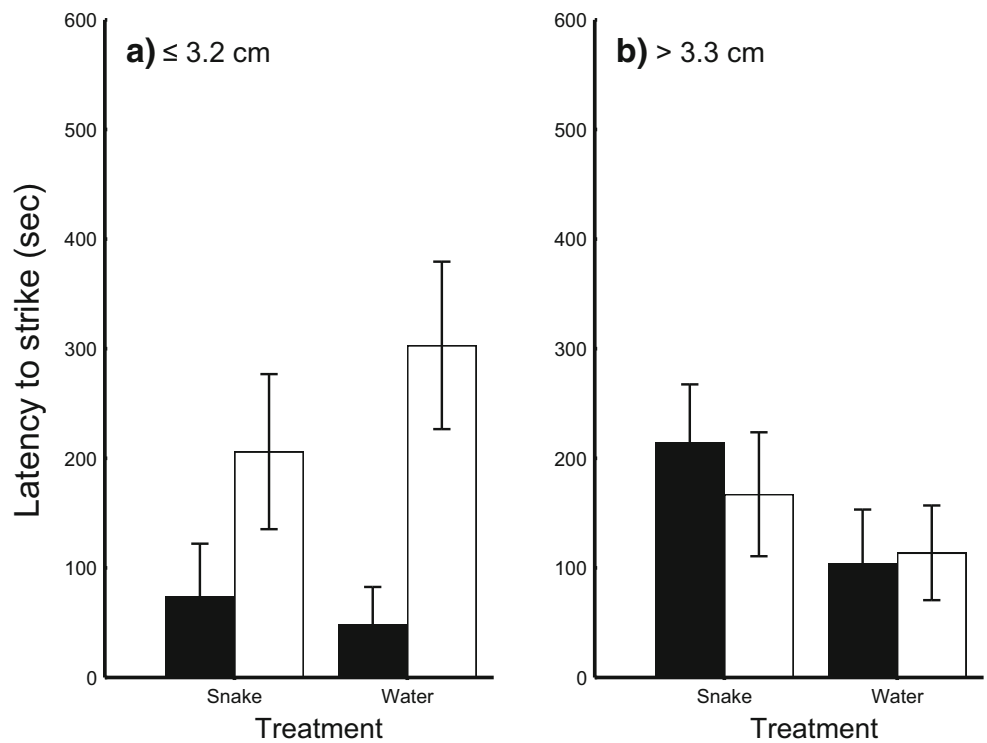
salamanders exposed to predator kairomones and induced autotomy. Conversely, the prediction that “small” salamanders would be more likely to maintain high levels of foraging following autotomy or exposure was not supported as “small” individuals exhibited some of the greatest latency scores and lowest number of strikes toward prey, especially after experiencing autotomy.

Plausible explanations for the perceived priority of caudal autotomy on changes in foraging while under the threat of predation include the increased susceptibility of autotomized individuals to predators and distinctive energetic requirements related to sex and sexual maturity. It is conceivable that the observed responses by “small” autotomized salamanders result from increased susceptibility to gape-limited predators, as well as the temporary loss of an effective antipredator mechanism (until substantial caudal regeneration). Prey vulnerability is a function of their size relative to the gape of a predator such that any factor that affects the relative size of the prey could influence their vulnerability to a particular predator (e.g., Hambright 1991; Ovadia and Schmitz 2002). Arnold (1982) showed that body size and tail length can have a significant impact on the predation of red-backed salamanders (*Plethodon cinereus*, Plethodontidae) by the garter snake *T. elegans*. In his study, salamanders responded to contact with snakes by writhing and thrashing their tail. These tail movements significantly delayed ingestion due, in part, to the formation of loops around the head of the snake and the deposition of adhesive skin secretions. Furthermore, he showed that larger individuals (by mass) with intact tails experienced the lowest rates of ingestion. Because caudal autotomy by *D. ochrophaeus* decreases the overall length of an individual, removes constraints related to the gape of some predators, and the ability to apply defensive skin secretions, it may increase the perceived level of predation risk (Hambright 1991; Ovadia and Schmitz 2002; Urban 2007). An additional explanation for the prioritization of autotomy in shaping behavior may be that once caudal autotomy has occurred there is an increased reliance on predator avoidance mechanisms such as a reduction in overall activity or immobility (Brodie et al. 1974; Brodie 1977;

**Table 1** Results of the factorial ANOVA in the generalized linear model for the effects of size (small  $\leq 3.2$  cm SVL versus large  $> 3.2$  cm SVL), autotomy (autotomized versus intact tails), and exposure (control versus kairomone from *Thamnophis sirtalis*) on the latency to strike, number of strikes and foraging efficiency (i.e., number of prey captured per strike) exhibited by *Desmognathus ochrophaeus*

	df	Latency		Strikes		Efficiency	
		Wald	<i>p</i>	Wald	<i>p</i>	Wald	<i>p</i>
Size	1	0.278	0.598	0.169	0.666	0.408	0.523
Autotomy	1	4.791	0.029	6.606	0.010	3.539	0.060
Exposure	1	0.860	0.354	0.500	0.480	0.768	0.381
Size $\times$ autotomy	1	5.990	0.014	2.721	0.099	1.109	0.292
Size $\times$ exposure	1	0.742	0.389	5.103	0.024	0.020	0.887
Autotomy $\times$ exposure	1	0.861	0.354	2.570	0.109	0.314	0.575
Size $\times$ autotomy $\times$ exposure	1	0.147	0.701	0.235	0.628	0.138	0.710

**Fig. 1** Mean  $\pm$  SE latency to strike at prey by **a** “small” (SVL  $\leq$  3.2 cm) or **b** “large” (SVL  $>$  3.2 cm) *Desmognathus ochrophaeus* exposed to kairomones from predatory snakes (*Thamnophis sirtalis*) or a water control. *Solid bars* (■) are individuals with intact tails; *open bars* (□) are individuals with autotomized tails

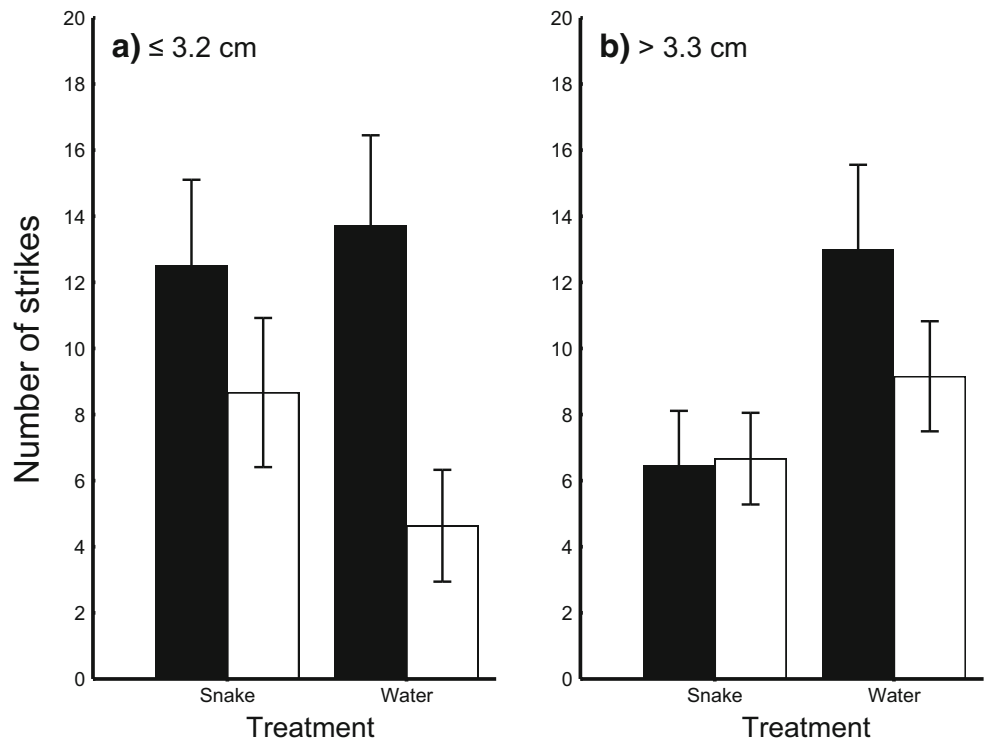


Madison et al. 1999). As a result, small individuals may be even more inclined to employ immobility or cryptic behavior after autotomy (Martin and Avery 1998; Cooper 2003; Cooper 2007; Bateman and Fleming 2009; McElroy and Bergmann 2013).

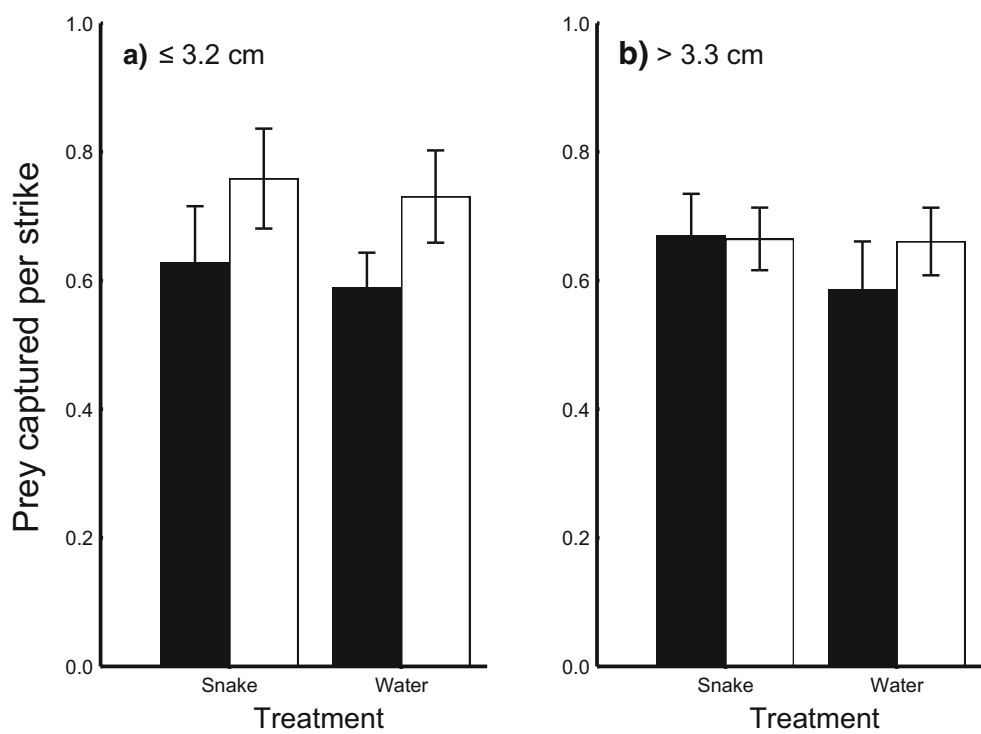
The patterns of foraging behavior exhibited by *D. ochrophaeus* in our study could be related to energetic

requirements that differ with sex and sexual maturity. The bimodal distribution of SVL that led to the use of “small” and “large” size categories may indicate the relative abundance of juvenile to sexually mature individuals as Keen and Orr (1980) found that female *D. ochrophaeus* in an Ohio population oviposit when between 3.0–3.4 cm SVL.

**Fig. 2** Mean  $\pm$  SE number of strikes toward prey by **a** “small” (SVL  $\leq$  3.2 cm) or **b** “large” (SVL  $>$  3.2 cm) *Desmognathus ochrophaeus* exposed to kairomones from predatory snakes (*Thamnophis sirtalis*) or a water control. *Solid bars* (■) are individuals with intact tails; *open bars* (□) are individuals with autotomized tails



**Fig. 3** Mean  $\pm$  SE number of prey captured per strike at prey by **a** “small” (SVL  $\leq$  3.2 cm) or **b** “large” (SVL  $>$  3.2 cm) *Desmognathus ochrophaeus* exposed to kairomones from predatory snakes (*Thamnophis sirtalis*) or a water control. *Solid bars* (■) are individuals with intact tails; *open bars* (□) are individuals with autotomized tails



Unfortunately, we lack data regarding the sex of the individuals tested so definitive statements about sex-specific patterns of foraging are impossible but such data would be insightful as the reproductive needs of mature females may be met by higher foraging rates. For instance, Ryan and Hopkins (2000) demonstrated that the metabolic rates of mole salamanders (*Ambystoma talpoideum*, Ambystomatidae) were affected by an interaction between sex and body size, likely a result of the different physiological requirements related to the production of gametes. A similar pattern was reported in gravid *A. texanum* that exhibited higher rates of  $O_2$  consumption than males or non-gravid females (despite a lack of difference in SVL between the sexes), which may necessitate higher energy consumption (Finkler and Cullum 2002). An additional factor that could influence patterns of foraging that is related to sex and sexual maturity is the variation in body mass and fat storage among individuals. Unfortunately, we lack data on the masses of individuals tested and therefore cannot speak toward the impact of this factor on our study. While our data suggest that size can play a significant role in foraging under an elevated threat of predation, the influence of sex, reproductive needs, and fat stores on these responses represent an area for future research.

The general tendency to increase the latency to strike at prey, reduce the number of strikes, and forage more efficiently by salamanders who have experienced autotomy is consistent with other studies that show suppression of foraging behavior during periods of elevated threat (Whitham and Mathis 2000; Sullivan et al. 2002; Epp and Gabor 2008; Sullivan and Jensen

2013). The significant effect of size on foraging by *D. ochrophaeus* in our study likely reflect key differences in predation pressure that changes ontogenetically as seen in studies of aquatic vertebrates and invertebrates (e.g., Holomuzki and Short 1990; Wahle 1992; Kats et al. 1994). For Allegheny Mountain dusky salamanders, larger individuals implement a wider array of effective antipredator mechanisms such as biting, writhing, and secreting noxious and adhesive secretions (e.g., Arnold 1982; Brodie et al. 1989). Marvin (2010) suggested that biting by *Desmognathus* might be more effective at deterring predation when performed by larger, and likely more powerful, individuals. Additionally, a combination of defenses (e.g., autotomy, glutinous secretions, and writhing) may be more efficacious in larger salamanders during a single predator encounter (Beneski 1989).

Prey must balance the conflicting demands of foraging and defensive behavior, which can be complicated among species that engage in caudal autotomy because the tail serves as an energy storage organ and antipredator device. With this study, we attempted to untangle the combined effects of individual size, exposure to predator kairomones, and caudal autotomy on foraging. Overall, we found that levels of foraging by “small” animals were highly contingent on their experience with tail autotomy as intact individuals tended to forage faster and more frequent. Autotomized individuals tended to be less inclined to perform predatory movements but also tended to be more efficient. Lastly, predator kairomones were less suppressive to large salamanders than expected, except for the number of strikes toward prey. To develop a more complete

picture of how selection shapes complex defensive strategies of prey, future studies should consider ontogenetic changes in susceptibility to predation, environmental factors shaping responses to threat, as well as the size-, sex-, or age-specific trade-offs between foraging and predator avoidance behavior.

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