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Antipredator Behavior in *Desmognathus ochrophaeus*: Threat-Specific Responses to Chemical Stimuli in a Foraging Context

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Abstract

Prey species may reduce the likelihood of injury or death by engaging in defensive behavior but often incur costs related to decreased foraging success or efficiency. To lessen these costs, prey may adjust the intensity or type of antipredator behavior according to the nature of the perceived threat. We evaluated the potential for threat-sensitive responses by Allegheny Mountain dusky salamanders (*Desmognathus ochrophaeus*) exposed to chemical stimuli associated with predation by asking three questions: (1) Do individual *D. ochrophaeus* respond to chemical cues in a threat-sensitive manner? (2) Do salamanders exhibit the same pattern of behavioral response while foraging? and (3) Is foraging efficiency reduced when focal individuals are exposed to stimuli from predators or predation events? In our first experiment, we evaluated salamander chemosensory movements (nose-taps), locomotor activity (steps), and edge behavior in response to chemical stimuli from disturbed and injured conspecifics as well as predatory *Gyrinophilus porphyriticus* and found that individual *D. ochrophaeus* show a significant graded increase in nose-taps when exposed to cues from conspecifics and a reduction in activity when exposed to the predator. In our second experiment, we again observed salamander responses to the same chemical stimuli but in this instance added five *Drosophila* prey to the test dishes. We found that salamanders exhibited a similar pattern of response to the chemical stimuli in the presence of prey, showing a graded increase in nose-taps to cues from conspecifics and a reduction in activity when exposed to the predator. However, foraging efficiency (i.e. the proportion of successful strikes) did not vary significantly among treatments. Our data show that individual *D. ochrophaeus* detect and differentially respond to chemical stimuli associated with predation, but do not significantly reduce foraging efficiency. Overall, the type and relative intensity of these responses is largely unaffected by the presence of potential prey.

Keywords: threat-sensitive, antipredator, foraging, chemical stimuli, *Desmognathus*

Introduction

Prey species must balance defensive behavior with other activities (Lima & Dill 1990; Brodie et al. 1991; Lima 1998; Richardson 2001). Although antipredator responses typically reduce the likelihood of injury or death during a predation event, they also may incur costs associated with a reduction in the time and energy devoted to mate search, courtship,

and foraging (Sih 1992; Candolin 1997; Polis et al. 1998). Depending on the species under consideration, these effects may have substantial consequences on fitness. For instance, the effects of decreased foraging activity as a result of antipredator responses may result in the reduction in rates of growth and development or fecundity in both vertebrate and invertebrate taxa (Skelly & Werner 1990; Peckarsky et al. 1993; Scrimgeour & Culp 1994).

Because individual prey must meet some minimum energetic requirement for growth and reproduction, responses to predators or predation events that result in decreased foraging may not be a viable strategy over long periods of time or where predators exist at relatively high densities (Sansom et al. 2009). This may be especially true in species that tend to respond to threat with a decrease in overall activity (Kohler & McPeck 1989; Madison et al. 1999a), movement between foraging patches (Roberts & Liebgold 2008; Sansom et al. 2009), or delayed emergence from refugia (Sullivan et al. 2002). Ultimately, prey that respond indiscriminately to every potential threat with antipredator behavior that limits foraging opportunities could greatly decrease energy available for other activities (Sih 1992).

Many species attempt to reduce the costs of antipredator behavior by adjusting the type, magnitude, or intensity of their response according to the level of threat perceived. The adjustment of prey responses to different threats is the primary tenet of the threat-sensitivity hypothesis (Helfman 1989) and is well documented, especially in aquatic systems. For example, the predator avoidance behavior of damselfish (*Stegastes planifrons*) exposed to model trumpetfish predators (*Aulostomus maculatus*) is positively correlated with the size and proximity of the model (Helfman 1989). In addition, Puttlitz et al. (1999) demonstrated size-specific responses by Pacific tree frog tadpoles (*Hyla regilla*) exposed to predatory salamander larvae (*Ambystoma gracile*) such that antipredator responses decreased as tadpoles increased in size, presumably because salamander larvae were no longer large enough to pose a significant risk. Chivers et al. (2001) report the use of threat-sensitive defensive behavior in slimy sculpin (*Cottus cognatus*) exposed to predatory brook char (*Salvelinus fontinalis*) that varied according to size. In one of the relatively few studies to evaluate threat sensitivity in terrestrial predator-prey contexts, Amo et al. (2004) show that the antipredator responses of wall lizards (*Podarcis muralis*) are greatest when lizards are exposed to both visual and chemical cues from smooth snakes (*Coronella austriaca*).

The use of chemical cues to evaluate levels of predation risk may be especially advantageous given the variety of possible sources and information conveyed (Kats & Dill 1998). The range of chemical stimuli that may be used by prey includes predator kairomones (produced by the predators themselves), disturbance cues (secreted or excreted by distressed or startled individuals), and injury-released cues (from physically damaged or injured individuals) (Wisenden 2000; Ferrari et al. 2010; Crawford et al. 2011). These

cues can relay information to prey regarding the proximity, intention, and recent foraging activity of a predator (Ferrari et al. 2010). For example, Kusch et al. (2004) manipulated the concentrations of chemical stimuli associated with predation and discovered that fathead minnow (*Pimephales promelas*) responses tended to be positively correlated with the concentration of the cue. Zhao and Chivers (2005) identified a similar trend in juvenile goldfish (*Carassius auratus*), as individuals exposed to higher concentrations of conspecific injury-released cues increased the intensity of their avoidance behaviors. In general, studies that examined threat sensitivity to chemical cues have documented similar behavioral patterns in a range of taxa including larval mosquitoes (Ferrari et al. 2008a), fish (Ferrari et al. 2005; Brown et al. 2006), and larval amphibians (Mirza et al. 2006; Ferrari et al. 2008b). However, evidence for graded or differential responses to chemical stimuli associated with predation by terrestrial organisms is somewhat lacking.

Plethodontid salamanders are good candidates for the investigation of chemically mediated antipredator behavior in terrestrial systems because they possess well-developed chemosensory organs (Dawley & Bass 1988) and rely on chemical stimuli for foraging (Placyk & Graves 2002), territory maintenance (Wise et al. 2004), and mate recognition (Roudebush & Taylor 1987). Furthermore, some species respond to predator kairomones (Madison et al. 1999b), 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). The purpose of this study is to evaluate the potential for threat-sensitive responses by Allegheny Mountain dusky salamanders (*Desmognathus ochrophaeus*) to chemical stimuli from disturbed and injured conspecifics as well as predatory northern spring salamanders (*Gyrinophilus porphyriticus*) and trade-offs between antipredator behavior and foraging. To this end, we attempted to answer three questions: (1) Do individual *D. ochrophaeus* respond to chemical cues associated with predation in a threat-sensitive manner? In this scenario, the cues from distressed conspecifics may represent the weakest threat as individuals may experience duress for a variety of reasons other than the presence of a predator whereas the injury-released cue may represent an intermediate threat as it could indicate a recent predation event, although it provides no indication regarding the proximity of a predator. We hypothesize that the chemical stimulus from

Gyrinophilus represents the greatest threat as it suggests a predator in the immediate vicinity. (2) Does the pattern of response exhibited by salamanders remain the same when exposed to a conflicting stimulus? In other words, will salamanders respond to the chemical stimuli associated with predation in the same manner when concurrently exposed to potential prey? and (3) Is foraging efficiency influenced by exposure to the chemical stimuli?

Methods

Collection and Maintenance of Animals

We collected 200 adult *D. ochrophaeus* (snout–vent length: \bar{x} = 3.71 cm) along the streamside of Houghton Creek, in Houghton, New York, USA (42°25'N, 78°9'W) from September 10 to October 03, 2012 for use in behavioral trials. Each salamander was housed individually in 15 cm diameter × 1.5 cm height petri dishes lined with acid-free paper towels saturated with distilled water. We maintained salamanders on a seasonal photoperiod (13:11 h light/dark, lights on at 0700 h E ST) with temperatures ranging from 18.3 to 12.8°C (night). Paper towels were moistened as needed and changed as they became soiled. Prior to use in behavioral trials, the salamanders were not fed, but were returned to the field within 10 d of capture. We collected four additional *D. ochrophaeus* (two males and two females) as well as three adult *G. porphyriticus* from our field site to serve as stimulus donor animals. The *D. ochrophaeus* were housed in the same manner as our test animals, whereas *G. porphyriticus* were housed together in a clear plastic bin (31 × 18 × 11 cm) with acid-free paper towels and 200 ml of distilled water. Spring salamanders were maintained in the laboratory at approximately 21°C, were not fed prior to the collection of the stimulus, and were returned to the field within 10 d of capture.

Preparation of Chemical Stimuli

To collect the disturbance and injury-released cues from the *D. ochrophaeus*, we transferred the four stimulus donors (3.7–4.6 cm snout–vent length) to a clear plastic bin (31 × 18 × 11 cm) filled with 200 ml of distilled water. To prepare the disturbance cue, we used blunt forceps to repeatedly grasp each salamander for 1 min to simulate predator attack. After the four salamanders had been agitated, the solution was filtered through glass wool to remove debris (e.g. dirt and fecal pellets). Next, we prepared the

injury-released cue by forcing the four stimulus donor animals described above to autotomize their tails by grasping them with forceps 1 cm posterior to the cloacal vent. Previous studies suggest that the chemical stimulus from the autotomized tails of salamanders may indicate areas of elevated predation risk to conspecifics (Arnold 1982; Labanick 1984; Hucko & Cupp 2001). Each autotomized tail was weighed (0.7 g total tail tissue), homogenized in a blender with 200 ml of distilled water for 5 min, and filtered through glass wool to remove large particles. The disturbance and injury-released treatments were then divided into eight 25-ml aliquots in conical-bottom centrifuge tubes, rapidly frozen using liquid nitrogen, and stored in a freezer until use.

To collect the predator cue, we transferred all *G. porphyriticus* to a clear plastic bin (31 × 18 × 11 cm) containing 200 ml of distilled water for 28 h. At the end of this period, we removed the salamanders, filtered the solution through glass wool, divided it into eight 25-ml portions in conical-bottom centrifuge tubes, and froze with liquid nitrogen and stored in a freezer until needed.

Threat-Sensitive Responses to Chemical Stimuli

We examined the responses of *D. ochrophaeus* to the four chemical stimuli in order to determine whether members of this species engage in threat-sensitive behavior. Salamanders were transferred to the laboratory 30 min prior to the commencement of trials to allow acclimation to room temperature (approx. 21°C) and ambient light levels as a 25-watt red bulb lighted the laboratory. We observed 25 different individuals in each treatment group and tested each salamander once prior to release. We implemented a stratified design such that an equivalent number of salamanders was tested in each treatment group each evening. All trials were performed between 1915 and 2230 h over eight consecutive nights beginning on October 01, 2012.

To observe salamander behavioral responses, we used 15-cm-diameter petri dishes lined with filter paper and saturated with 3 ml of either one of our prepared cues or a distilled water control. To begin each trial, we transferred one salamander from its home dish to the center of a test dish using a cotton swab. After a 2-min acclimation period, we recorded the following behaviors for 10 min: nose-taps, steps, and edge behaviors. Nose-tapping behavior among plethodontid salamanders serves to bring the nasolabial grooves into contact with the substrate that then facilitates the transfer of chemicals from the substrate

to the vomeronasal organ (Dawley & Bass 1989). For the purpose of our study, we defined a nose-tap as any time a stationary salamander quickly touched the base of the nasolabial grooves to the substrate (Jaeger 1984). Steps, as a measure of locomotor activity, were counted as movements of individual forelimbs that resulted in the forward movement of the body. Edge behavior, as an estimate of escape behavior, included the amount of time that salamanders spent with their head or body (excluding tail or legs) in contact with the side of the petri dish. A paper divider was placed between the observer and the test dish to reduce the likelihood that observer movements would influence salamander behavior. At the completion of each trial, salamanders were removed from test dishes and returned to home dishes until their release at the site of capture.

Threat-Sensitive Responses While Foraging

In the second experiment, we examined the responses of foraging dusky salamanders to the chemical stimuli associated with predation and evaluated the effects of predation-related cues on foraging efficiency. To accomplish this, we utilized the bioassay described above with the following exceptions: after the 2-min acclimation period, we added five wingless *Drosophila* sp. to each test dish and recorded the number of strikes, flies successfully captured, nose-taps, steps, and edge behaviors. Strikes are rapid movements of the salamander in the direction of the prey with mouth open or tongue extended, and successful captures are instances when flies were ingested (Jaeger & Rubin 1982; Maerz et al. 2001).

Statistical Analyses

Because our data violated the assumption of homoscedasticity, we utilized Kruskal–Wallis one-way analyses of variance to evaluate differences in nose-taps, steps, edge behaviors and foraging efficiency among our treatment groups as the sampling distribution of the Kruskal–Wallis test statistic is less affected by the violation of this assumption, especially when sample sizes between groups are equal (Sheskin 2007). When the main effect was significant, we performed post hoc comparisons with Mann–Whitney *U*-tests and adjusted the experimentwise error rate using the Dunn–Šidák method. Lastly, we used a Pearson's product-moment correlation analysis in an effort to detect a relationship between salamander foraging efficiency and movement (which could influence prey encounter rates).

Results

Threat-Sensitive Responses to Chemical Stimuli

The chemical stimulus to which salamanders were exposed significantly influenced chemosensory behavior ($H = 43.89$, $p < 0.001$) with salamanders performing more nose-taps in response to disturbed and injured conspecifics than to control and predator treatments (Mann–Whitney *U*-test: control vs. disturbed $p < 0.001$, control vs. injury-released $p < 0.001$, control vs. predator $p = 0.121$, disturbed vs. injury-released $p = 0.010$, disturbed vs. predator $p = 0.004$, injury-released vs. predator $p < 0.001$, Fig. 1). In addition, the chemical stimulus significantly affected locomotor activity ($H = 19.12$, $p < 0.001$) with salamanders reducing the number of steps when exposed to the predator cue (Mann–Whitney *U*-test: control vs. disturbed $p = 0.168$, control vs. injury-released $p = 0.040$, control vs. predator $p = 0.037$, disturbed vs. injury-released $p = 0.400$, disturbed vs. predator $p \leq 0.001$, injury-released vs. predator $p < 0.001$, Fig. 1). Lastly, the average duration of edge time by salamanders varied according to treatment ($H = 10.97$, $p < 0.012$) as salamanders exposed to injured conspecifics increased contact with the edge of the test dish compared with the control (Mann–Whitney *U*-test: control vs. disturbed $p = 0.101$, control vs. injury-released $p \leq 0.001$, control vs. predator $p = 0.085$, disturbed vs. injury-released $p = 0.041$, disturbed vs. predator $p \leq 0.484$, injury-released vs. predator $p = 0.430$, Fig. 1).

Threat-Sensitive Responses While Foraging

While foraging on *Drosophila* sp., salamander chemosensory behavior significantly differed among treatment groups ($H = 8.40$, $p = 0.038$) with salamanders performing more nose-taps in response to injured conspecifics compared with the control (Mann–Whitney *U*-test: control vs. disturbed $p = 0.008$, control vs. injury-released $p = 0.075$, control vs. predator $p = 0.497$, disturbed vs. injury-released $p = 0.834$, disturbed vs. predator $p = 0.097$, injury-released vs. predator $p = 0.156$, Fig. 2). Likewise, the chemical stimulus significantly affected locomotor activity ($H = 10.05$, $p = 0.018$) with salamanders performing the fewest steps when exposed to the predator cue compared with the disturbed conspecific (Mann–Whitney *U*-test: control vs. disturbed $p = 0.472$, control vs. injury-released $p = 0.992$, control vs. predator $p = 0.028$, disturbed vs. injury-released $p = 0.447$, disturbed vs. predator $p = 0.002$, injury-released vs.

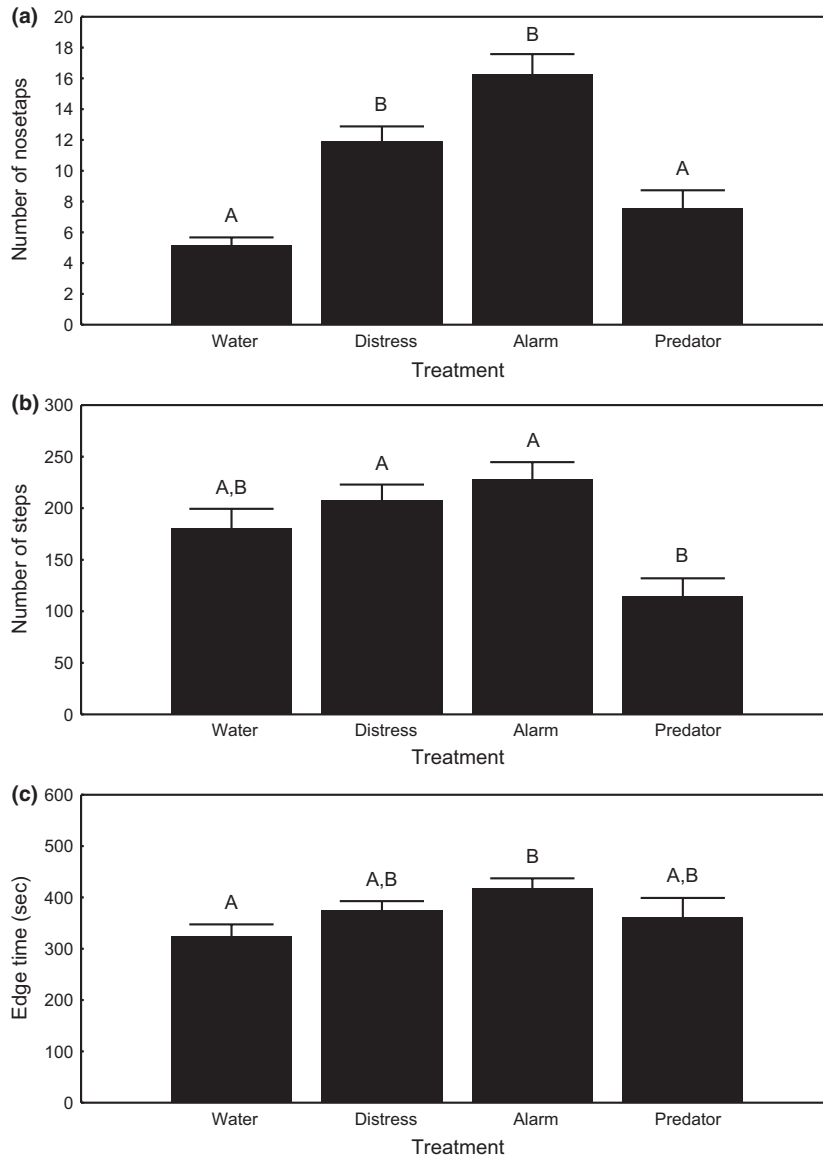


Fig. 1: The mean \pm SEM (a) number of nosetaps, (b) number of steps, and (c) duration of edge time (seconds) exhibited by non-foraging *Desmognathus ochrophaeus* exposed to four chemical stimuli: distilled water (Control), chemical secretions from disturbed conspecifics (Disturbance), a rinse prepared from the damaged skin tissue from conspecifics (Injured), and an aqueous rinse from *Gyrinoophilus porphyriticus* (Predator). Bars capped with different letters indicate significant differences among treatments.

predator $p = 0.034$, Fig. 2). The average duration of edge time by salamanders did not vary according to chemical treatment ($H = 2.90$, $p = 0.406$). Lastly, salamander foraging efficiency, as defined by the number of prey successfully captured per strike, did not significantly differ among treatment groups ($H = 6.76$, $p = 0.080$, Fig. 3), and there was no significant correlation between foraging efficiency and activity ($r = -0.126$; $p = 0.212$).

Discussion

Our results show that individual *D. ochrophaeus* tend to exhibit different behavioral responses to the variety of chemical stimuli associated with predation used in

our study. Furthermore, salamanders exhibit a similar pattern of response when provided with a conflicting stimulus in the form of *Drosophila* prey. For instance, individuals tended to elevate levels of their chemosensory behavior when exposed to the stimuli collected from conspecifics, showing a significant increase in nose-tapping, showing a significant increase in nose-tapping to both distressed and injury-released stimuli in the first experiment and a significant increase when exposed to the distress stimulus in the presence of prey. However, the response to most threatening stimulus (stimuli from predatory *G. porphyriticus*) involved a significant reduction in movement relative to the conspecific treatments (with the control serving as a statistical intermediate). These results suggest that salamanders differentially respond

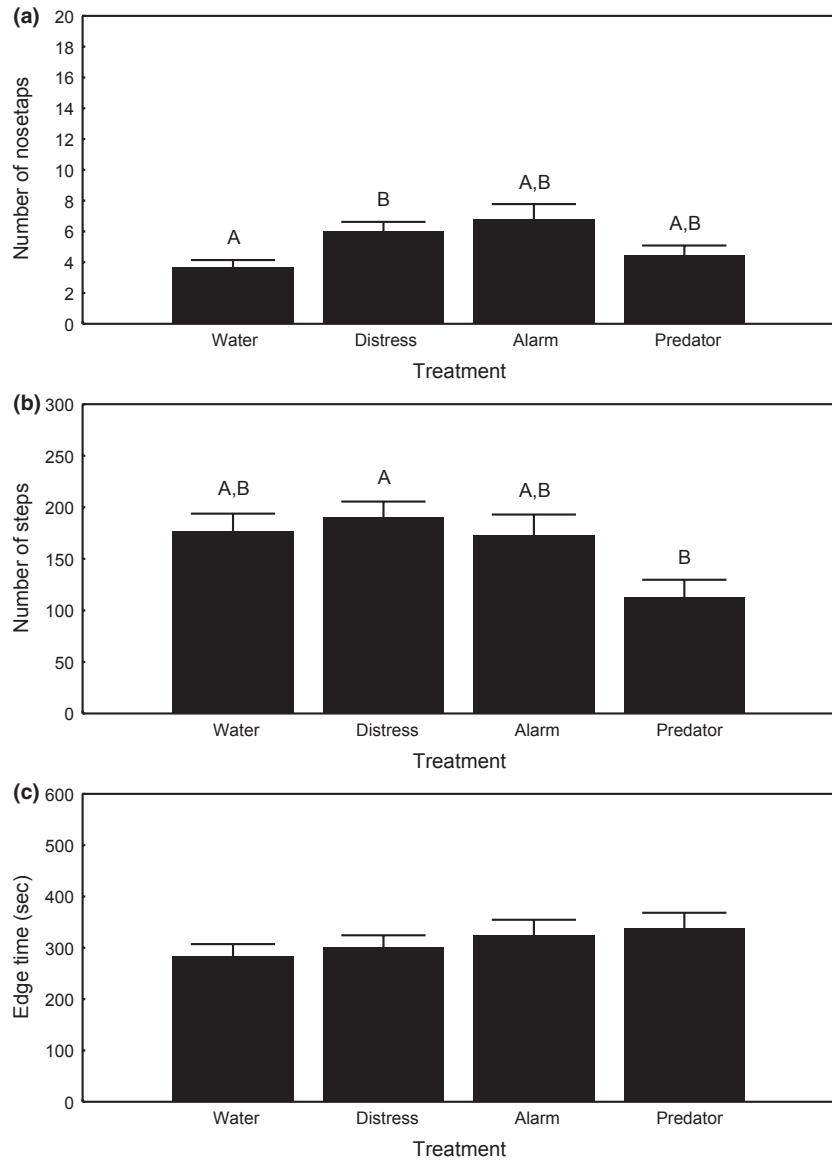


Fig. 2: The mean \pm SEM (a) number of nose-taps, (b) number of steps, and (c) duration of edge time (seconds) exhibited by foraging *Desmognathus ochrophaeus* exposed to four chemical stimuli: distilled water (Control), chemical secretions from disturbed conspecifics (Disturbance), a rinse prepared from the damaged skin tissue from conspecifics (Injured), and an aqueous rinse from *Gyrino-phillus porphyriticus* (Predator). Bars capped with different letters indicate significant differences among treatments.

to a range of stimuli associated with predation with behaviors that seem to be consistent regardless of whether prey are present, although the magnitude of those responses seems to decrease with the addition of prey. Our results regarding foraging behavior under the threat of predation provide preliminary data that suggest that the detection of predator stimuli has the potential to incur a cost related to feeding as salamanders that cannot be explained by the overall reduction in locomotor activity.

Many prey species adjust their behavioral response to cues associated with predation based on the type of threat perceived (e.g. Puttlitz et al. 1999; Mirza et al. 2006; Ferrari et al. 2008b; Crawford et al. 2011). The variety of responses observed is

likely due to the complex nature of the interactions with different predators and the conflicting demands that such exposure may place on the prey (Kotler et al. 1992; Matsuda et al. 1993). In the case of our study, the predator stimulus elicited a significant decrease in activity, which is a common predator avoidance mechanism in response to visually oriented predators (Brodie et al. 1974; Chelini et al. 2009). On the other hand, chemical stimuli from injured and disturbed conspecifics caused an increase in chemosensory behavior, which may represent an increase in vigilance as these cues may convey information about a recent predation event in the vicinity (Kiesecker et al. 1999). The flexibility to respond differentially to different sources of

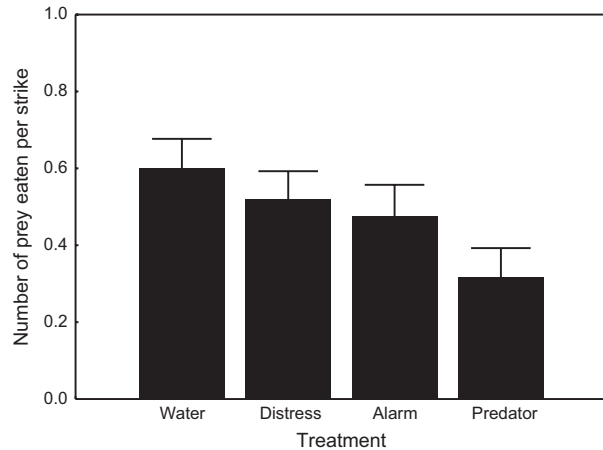


Fig. 3: The mean \pm SEM number of flies ingested per strike by foraging *Desmognathus ochrophaeus* exposed to four chemical stimuli: distilled water (Control), chemical secretions from disturbed conspecifics (Disturbance), a rinse prepared from the damaged skin tissue from conspecifics (Injured), and an aqueous rinse from *Gyrinophilus porphyriticus* (Predator).

threat may allow individual *D. ochrophaeus* to balance the costs and benefits of defensive behavior.

It is worth noting the general decrease in chemosensory behavior exhibited by *D. ochrophaeus* in the second experiment, especially noticeable when exposed to the disturbance and injury-released cues from conspecifics. This suppression of chemosensory investigation may be related to the visual stimuli provided by the movement of *Drosophila* in test dishes. Terrestrial salamanders, including plethodontids, may utilize chemical cues to orient toward prey (e.g. Placyk & Graves 2002), but they seem to prioritize visual stimuli when available (Wake & Deban 2000). This is supported by previous work suggesting that salamanders tend to ignore motionless live prey as well as odoriferous dead prey at low ambient light levels (Roth 1987). Furthermore, some salamanders engage in feeding behavior when exposed to an inedible object in motion (Lindquist & Bachmann 1982). In the current study, the existence of a visual stimulus related to foraging appears to suppress the motivation to explore the environment via nose-tapping when exposed to chemical stimuli from disturbed and injured conspecifics.

The capacity to engage predators in a threat-sensitive or threat-specific manner while foraging may be particularly advantageous for prey. Responding to relatively low levels of threat or 'false alarms' with an unnecessary decrease in foraging activity may incur a cost related to fitness. This may be especially true among salamanders that tend to reduce rates of food

consumption or decrease attempts to capture prey when exposed to stimuli from predators (Whitham & Mathis 2000; Maerz et al. 2001). Our data suggest that dusky salamanders adjust the form of their behavioral response to the source of the stimulus to which they are exposed, pairing their costliest response (decreased locomotor activity) to the most threatening stimulus. This ability to differentially respond to cues related to predation may allow individuals to maintain relatively high levels of food intake when the level of perceived threat is relatively low. Our data, although marginally significant ($p = 0.080$), support this hypothesis, as foraging efficiency is lowest for *D. ochrophaeus* exposed to stimuli from predators. These data suggest that behavioral responses to chemical stimuli associated with predation may carry with them a cost with regards to foraging ability or potential.

In conclusion, threat-sensitive or threat-specific responses may be advantageous for organisms because they increase the likelihood of surviving predation but help to minimize the costs associated with defensive behavior. Individual *D. ochrophaeus* utilize threat-specific behavior by engaging in elevated chemosensory behavior in the presence of stimuli from disturbed and injured conspecifics but decreased locomotor activity only when exposed to chemical stimuli from the predator. By detecting and differentially responding to the variety of cues associated with predation events, *D. ochrophaeus* may minimize costs such as reduced foraging efficiency unless facing a genuine threat such as a predator foraging in the same microhabitat. Although the decrease in foraging efficiency was not statistically significant over the course of our study, our data do suggest that over a different temporal scale, or when food availability varies, the impact on salamander fitness could be substantial. This study identifies a pattern of threat-specific responses by individual *D. ochrophaeus* to three stimuli associated with predation and shows the presence of prey does not alter the general behavioral response. It also suggests that this pattern of response may benefit individual salamanders as it may allow for higher rates of foraging efficiency in this species.

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