



Influence of physical stress, distress cues, and predator kairomones on the foraging behavior of Ozark zigzag salamanders, *Plethodon angusticlavius*

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Received 11 September 2003; received in revised form 11 September 2003; accepted 30 September 2003

Abstract

An animal's response to environmentally induced stress can have important fitness consequences. For example, an animal may reduce activity in response to stress related to increased predation risk, but this response carries the potential cost of missed foraging or mating opportunities. We used laboratory bioassays to determine whether Ozark zigzag salamanders, *Plethodon angusticlavius*, decreased their feeding behavior following increased levels of threat-related stress. Stress level was manipulated in three experiments where salamanders were exposed to direct or indirect indicators of stress. The direct cue was a physical attack. The indirect cues were chemical cues from distressed conspecifics and chemical cues ("kairomones") from predatory ringneck snakes, *Diadophis punctatus*. For all three cues, stressed salamanders showed lower foraging success than unstressed salamanders. The physical attack did not result in a more intense response than the other treatments, possibly because the attack occurred away from the foraging area. The intensity of the response to stress may depend more on the nature of the threat (identity and imminence) than the level of physical disturbance.

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Keywords: Chemical cues; Stress; Alarm; Predation; Antipredator; Salamander

1. Introduction

During normal daily activities, animals can be exposed to a wide range of biotic and abiotic environmental stresses, including changes to the habitat (Denver, 1997; Hoffman et al., 1999) and interactions with competitors, parasites, and predators (e.g. Lima, 1998). One of the most acute stresses that an animal can experience is the threat of immediate physical injury or death due to attack from competitors

or predators. Animals can decrease the probability of attack by decreasing behaviors that make them conspicuous and by increasing vigilance behaviors (Lima, 1987). However, increasing attack-avoidance behaviors carries the cost of decreasing the time allotted to activities such as foraging, territorial defense, or reproduction (Adams, 1990; Lima and Dill, 1990). Therefore, individuals can optimize their fitness benefits by adjusting the intensity of their attack-avoidance behavior to match the level of threat.

Threat can be assessed either directly via confrontation with the attacker or indirectly through the detection of cues such as scents or calls that indicate the presence of a potential attacker. For many vertebrates,

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chemical cues are a primary source of information. For example, identification of conspecifics and heterospecifics often is made based on chemicals released directly by the target animal (e.g. references in Mason et al., 1998). In this paper we use “kairomone” to describe chemical cues from heterospecifics such as predators (Weldon, 1980). Warning of the presence of an imminent threat also can be obtained from cues released by nearby conspecifics. Chemical warning cues may be released by prey when tissue is damaged by predatory attacks (fish: reviewed by Smith, 1992; amphibians: Hews and Blaustein, 1985; Luttershmidt et al., 1994) or by individuals that have been stressed but not mechanically damaged (fish: Wisenden et al., 1995; amphibians: Mathis and Lancaster, 1998; mammals: Vieuille-Thomas and Signoret, 1992). Increased levels of physiological stress can be associated with exposure to both predator kairomones (Rehnberg and Schreck, 1987) and conspecific alarm cues (Rehnberg et al., 1987).

Salamanders of the genus *Plethodon* (lungless salamanders) are an excellent model for the study of the influence of risk of attack on foraging behavior. Plethodontid salamanders respond both to chemical stimuli from predators (Cupp, 1994; Maerz et al., 2001) and to chemical cues from damaged or stressed conspecifics (Luttershmidt et al., 1994; Mathis and Lancaster, 1998; Graves and Quinn, 2000). They respond to these cues in ways that are consistent with antipredator behaviors, including avoidance and escape responses (Madison et al., 1999a; McDarby et al., 1999; Murray and Jenkins, 1999).

We examined whether the foraging behavior of Ozark zigzag salamanders, *Plethodon angusticlavius* (formerly *Plethodon dorsalis angusticlavius*; Highton, 1997) was affected by exposure to one direct and two indirect indicators of threat-related stress. First, we exposed salamanders to physical attack (direct threat) and comparing foraging behavior of salamanders that were attacked to the behavior of animals that were disturbed, but not attacked. We used chemical cues to provide focal individuals with indirect information about increased threat because salamanders rely heavily on their chemosensory systems. In a second experiment, we compared foraging behavior of salamanders exposed to secretions from highly stressed conspecifics to those exposed to secretions from salamanders experiencing lower levels of stress. The

stressed-conspecific treatment provided only information concerning a general disturbance in the area. In a final experiment, we compared foraging behavior of salamanders exposed to substrate-borne chemicals from a predatory snake (ringneck snake, *Diadophis punctatus*), a non-predatory snake (flathead snake, *Tantilla gracillis*), and a blank control. These cues provide information about both the presence and identity of the threat.

2. Materials and methods

2.1. Collection and maintenance

We collected individuals of *P. angusticlavius* by hand in White County, central Arkansas. The salamanders were placed in zip-lock bags containing wet leaf litter and then were transported to Southwest Missouri State University (Springfield, MO, USA) in a cooler with ice. The salamanders were housed individually in clear, plastic petri dishes (14.6 cm diameter, 1.3 cm depth) lined with moist filter paper. Salamanders perform apparently normal behavioral patterns in these chambers (i.e. feeding, pheromonal marking, aggressive behavior, e.g. Mathis and Britzke, 1999; Mathis et al., 2000). Salamanders were maintained on a 12-h light:12-h dark cycle at $14 \pm 2^\circ\text{C}$ and fed *Drosophila hydei* ad libitum every 5–7 days until tested. Filter paper was changed every 20–30 days. Trials were conducted during the light portion of the cycle under fluorescent lighting; some salamanders are more sensitive to predatory stimuli under the diurnal portion of their activity cycle (Madison et al., 1999a,b).

Adult ringneck and flathead snakes were hand-caught in Christian and Taney counties in southwestern Missouri. Ringneck snakes are known to be predators of small salamanders (Blanchard et al., 1979), but flathead snakes feed strictly on invertebrate prey (Force, 1935). Both species co-occur with Ozark zigzag salamanders in Arkansas. The snakes were kept in separate plastic boxes (30 cm in length, 16.5 cm wide) on a 12-h light:12-h dark cycle at $20 \pm 4^\circ\text{C}$, with paper towel substrates and cover objects and with water continuously available. Both species of snakes were fed non-salamander prey (e.g. worms, *Lumbricus rubellus* and crickets) to rule out potential

effects of salamander diet on chemical stimuli (e.g. Madison et al., 1999a,b).

2.2. Influence of attack on foraging behavior of salamanders

We fed each salamander to satiation 4 days prior to testing to standardize hunger levels. We placed pairs of salamanders (mean SVL \pm S.D. = 36.54 \pm 4.59 mm, range 28.0–44.0 mm) in holding chambers (32.5 cm length, 18 cm width, 2.5 cm deep) that were each lined with a damp paper towel that was covered by two moist pieces of filter paper (15 cm diameter). Pairs remained together for 3 days prior to testing.

We stressed salamanders using the methods of Mathis and Lancaster (1998). Prior to each trial, we assigned one salamander of the pair to be the focal salamander for this experiment. This individual was removed from the chamber, placed into a clean petri dish, and randomly assigned it to either the “stress” or “non-stress” treatment. Each salamander in the “non-stress” treatment was left undisturbed for 2 min. Each salamander in the “stress” treatment was stressed for 2 min by grasping it around the pelvic-girdle region with a pair of forceps. By using this manipulation we mimicked an attack by a natural snake predator; ring-necked snakes subdue salamander prey in this manner (D. Lancaster, personal communication). Salamanders reacted to the attack by twisting their bodies and often biting at the forceps, and salamanders have been shown to respond similarly to predatory snakes (Brodie et al., 1989). In nature, salamanders also may suffer attacks from conspecific competitors (Maksimowich and Mathis, 2001; Mathis et al., 2000). In this species, conspecific bites typically are quick “nips” followed by immediate release (personal observations), and so our prolonged stress manipulation would not resemble a conspecific attack.

Each focal salamander (stressed or non-stressed) was then rinsed with 10 ml of dechlorinated water to obtain the stimuli for use in the following experiment (see the following). We left the other salamander of the pair in its chamber, placed an opaque cover (9.0 cm diameter, 1.5 cm deep; hereafter “habituation dishes”) over it, and set it aside for use as the focal animal in the following experiment.

Each “stressed” and “non-stressed” salamander was then transferred to a new petri dish lined with

one piece of filter paper from its holding chamber so that the salamander would be exposed to the familiar substrate markings from its holding chamber. Focal salamanders ($n = 16$ per treatment) were covered with opaque habituation dishes for 5 min. We introduced five flies into the chamber via a hole in the center of the lid and removed the opaque dish. When a fly was consumed, it was immediately replaced to maintain a constant prey density of five prey items. Each trial ran for 10 min, with the following behavioral patterns recorded: (1) latency to first capture, and (2) total number of flies consumed. For each response variable, treatments were compared using one-tailed non-parametric Mann–Whitney U tests using the Minitab statistical program version 12.21. We used one-tailed tests because increased stress should result in decreased foraging activity (e.g. Jaeger, 1972). We also made descriptive notes about behavior of the focal salamanders (e.g. generally low activity, frequent edge behavior, etc.). Data were recorded by an individual who was not present during the stressing procedure and so was “blind” to treatment conditions.

2.3. Influence of chemicals from stressed conspecifics on foraging behavior of salamanders

Focal salamanders ($n = 16$ per treatment) were the salamanders that had been set aside in the previous experiment. Each focal salamander was randomly assigned to one of the following treatments: (1) chemicals from a stressed conspecific, (2) chemicals from a non-stressed conspecific, and (3) a blank control (10 ml of dechlorinated water). Conspecific stimuli were collected from the salamander that was paired with the focal animal in the previous experiment because salamanders often respond differently to chemical cues from familiar individuals and strangers (Jaeger, 1981; Guffey et al., 1998).

The individuals providing the stressed/non-stressed stimuli were the same individuals that were tested in the previous experiment. The rinse water from the non-stressed salamander was used as the “non-stress” treatment in this experiment and the rinse water from the stressed salamander was used as the “stress” treatment. Like many salamanders (Evans and Brodie, 1994), the stressed salamanders secreted a whitish substance when attacked. This secretion, which is the presumed

source of any alarm chemicals, occurs broadly over the surface of the skin and is not limited to areas of physical injury.

We placed the two pieces of filter paper from the home chamber (containing substrate markings from both salamanders) into a new experimental chamber, and saturated it with water from the “stress,” “non-stress,” or blank treatments. The focal salamander was then gently moved to the center of the new experimental chamber and covered with a habituation dish for 5 min.

This experiment used the same testing protocol and response variables as the previous experiment, and the observer was blind to treatment conditions. For each response variable (latency, number eaten), we compared the three treatments using non-parametric Kruskal–Wallis ANOVA tests followed by non-parametric multiple comparison tests (Zar, 1984).

2.4. Influence of predator kairomones on foraging behavior of salamanders

Each salamander was randomly assigned to one of the following treatments: (1) chemical stimuli from the predatory ringneck snake plus dechlorinated water, (2) chemical stimuli from a non-predatory flathead snake plus dechlorinated water, and (3) dechlorinated water (blank control). Each salamander was tested only once, and treatments were randomly assigned. Individual salamanders were tested in their home petri dishes.

Circles of filter paper (14 cm diameter) were placed on the substrates of the snakes’ home boxes at least 6 days prior to testing to allow the filter paper to absorb odors from the snakes. Salamanders were removed from their dishes immediately prior to the trials and placed in clean temporary holding chambers (petri dish) while the stimulus papers were added to their home chambers. Filter paper from one of the treatments (predatory snake, non-predatory snake, or blank) was saturated with approximately 10 ml of dechlorinated water and placed over the filter paper in the salamander’s dish, allowing the salamander to experience its own substrate markings in addition to the snake stimuli. The salamander was then returned to its home dish and covered with an opaque habituation dish for 5 min. Experimental protocols, response variables, and statistical anal-

yses were identical to those used in the previous experiment.

3. Results

3.1. Influence of attack on foraging behavior of salamanders

The latency to consume the first prey item was not significantly different among treatments ($W = 299.5$, $N = 16$, $P = 0.09$; Fig. 1A). However, salamanders that had been stressed by the simulated predator attack tended to show generally low levels of activity and ate significantly fewer flies than salamanders that were not stressed ($W = 209.5$, $N = 16$, $P = 0.02$; Fig. 1B).

3.2. Influence of chemicals from stressed conspecifics on foraging behavior of salamanders

The latency to consume the first prey item was significantly different among treatments ($H = 10.50$, $d.f. = 2$, $P = 0.005$; Fig. 2A). Salamanders exposed

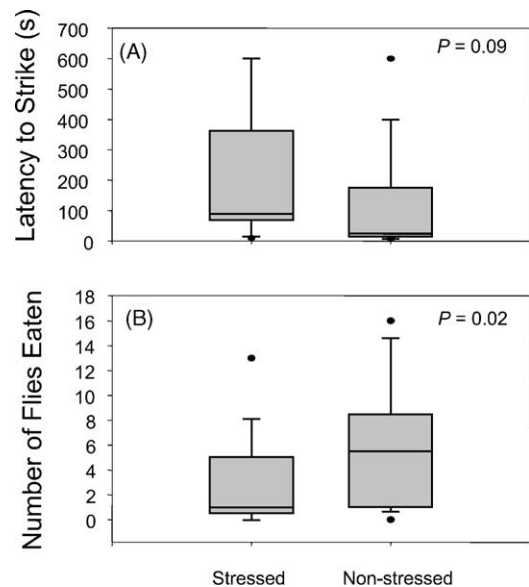


Fig. 1. Foraging responses of salamanders that either were stressed by a physical attack or were disturbed but not attacked (“non-stress”). Responses are (A) latency to strike at fruitfly prey, and (B) number of flies eaten in a 10-min trial. P -values are for non-parametric Mann–Whitney U-tests. Boxplots present medians with interquartile ranges and circles indicate outliers.

to stimuli from distressed conspecifics showed generally low levels of activity and took significantly longer to consume the first prey than in the other two treatments (stress versus non-stress, $Q = 2.5$, $0.02 < P < 0.05$ and stress versus blank, $Q = 4.82$, $P < 0.001$). The non-stress treatment was not significantly different from the blank treatment ($Q = 2.32$, $0.05 < P < 0.10$).

Salamanders also showed a significant difference in the number of flies eaten per treatment ($H = 8.03$, d.f. = 2, $P = 0.018$; Fig. 2B). Salamanders ate significantly fewer flies when exposed to chemical stimuli from stressed conspecifics than when exposed to the blank treatment ($Q = 4.19$, $P < 0.001$). Salamanders exposed to the non-stress stimuli did not differ significantly from either the stress ($Q = 1.8$, $0.10 < P < 0.20$) or the blank ($Q = 2.35$, $0.05 < P < 0.10$) treatments.

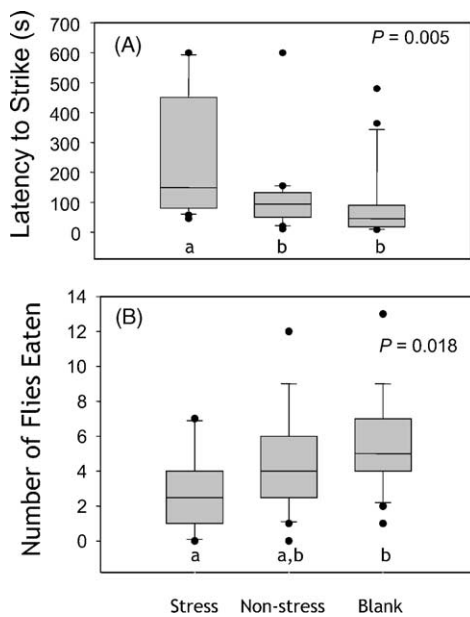


Fig. 2. Foraging responses of salamanders exposed to chemical stimuli from stressed and non-stressed conspecifics. Stimuli were collected as water rinsed over salamanders that were either stressed by a simulated predator attack or not stressed. Responses are (A) latency to strike at prey (fruitfly), and (B) number of flies eaten during a 10-min trial. P -values are for non-parametric Kruskal–Wallis ANOVA's and different letters indicate significant differences according to non-parametric multiple comparison tests. Boxplots present medians with interquartile ranges and circles indicate outliers.

3.3. Influence of predator kairomones on foraging behavior of salamanders

Salamanders exposed to chemical stimuli from predatory snakes exhibited frequent edge behavior, often pressing their snouts against the crevice between the sides and lids of the testing chambers, whereas salamanders in the other two treatments appeared to be more focused on foraging activity. Consequently, the latency to consume the first prey item was significantly different among treatments ($H = 10.73$, d.f. = 2, $P = 0.004$), and salamanders exposed to stimuli from predatory snakes took the longest time to consume their first prey (Fig. 3A). Latency for the predatory snake treatment was significantly longer than the other two treatments (predatory snake versus non-predatory snake, $Q = 2.60$, $0.02 < P < 0.05$, and predatory snake versus blank, $Q = 3.04$, $0.005 < P < 0.01$). The non-predatory snake treatment was

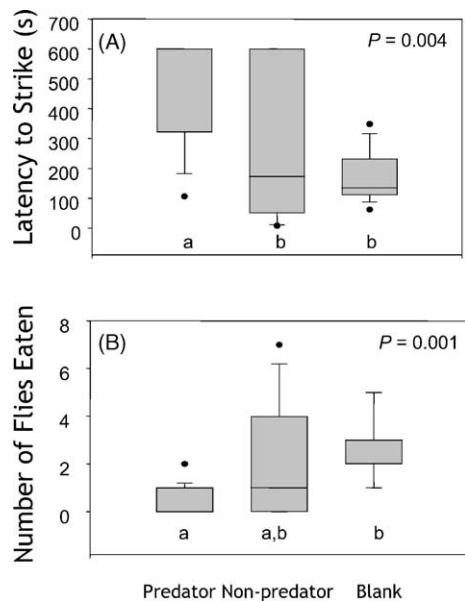


Fig. 3. Foraging responses of salamanders exposed to chemical stimuli from predatory (*Diadophis punctatus*) and non-predatory (*T. gracillis*) snakes and to a blank control. Responses are (A) latency to strike at prey (fruitfly), and (B) number of flies eaten during a 10-min trial. P -values are for non-parametric Kruskal–Wallis ANOVA's and different letters indicate significant differences according to non-parametric multiple comparison tests. Boxplots present medians with interquartile ranges and circles indicate outliers.

not significantly different from the blank ($Q = 0.45$, $P > 0.50$).

Salamanders also showed a significant difference in the number of flies eaten per treatment ($H = 13.15$, d.f. = 2, $P = 0.001$; Fig. 3B). Salamanders ate fewer flies when in the presence of chemical stimuli from snakes. Fewer flies were eaten in the predatory snake treatment than in the blank treatment (predatory snake versus blank, $Q = 3.60$, $P < 0.001$). The number of flies eaten in the non-predatory snake treatment was not significantly different from the other two treatments (non-predatory snake versus predatory snake, $Q = 2.12$, $0.10 < P < 0.20$; non-predatory snake versus blank, $Q = 1.45$, $0.20 < P < 0.50$).

4. Discussion

4.1. Effects of attack on foraging behavior

As predicted, salamanders that were stressed by an attack ate fewer flies than those that were not stressed. Qualitatively, decreased foraging success seemed to be related to an overall decrease in activity. Decreased activity is a common response to increased predation risk (e.g. Van Damme et al., 1990; Mathis and Vincent, 2000; Sullivan et al., 2002), and two hypotheses have been suggested to explain the antipredator benefits of this reduction. First, reduced activity can lead to lower rates of detection by visually oriented predators and, subsequently, increased survival of prey (Azevedo-Ramos et al., 1992; Skelly, 1994). Second, decreased activity may allow the prey to devote more time to vigilance behavior. Reduced foraging due to increased vigilance for predators has been reported for a number of taxa, including fishes (Magnhagen, 1988; Angradi, 1992), birds (Lima, 1987), and mammals (Wawra, 1988).

In this experiment, salamanders resumed foraging relatively quickly and there was no significant difference between attack latency for “stressed” versus “non-stressed” individuals. This result contrasts with the results of the other two experiments where latency to resume foraging was significantly affected by exposure to both conspecific distress chemicals and kairomones from predatory snakes (see the following). This difference between experiments was surprising because we initially considered “attack” to be

the strongest stressor of those used in the three experiments. One possible explanation for the relative weakness of the latency response was that the attack occurred away from the foraging area. Once removed from the area where the attack had occurred, the salamanders may have felt safe enough to cautiously begin foraging, albeit at a relatively slow rate. The cost of missed foraging opportunities for terrestrial salamanders may be substantial. Jaeger (1980) found that on most sampling days, most red-backed salamanders, *Plethodon cinereus*, were on negative energy budgets.

4.2. Effects of chemicals from stressed conspecifics on foraging behavior

Salamander foraging behavior was depressed by distress cues from conspecifics. Salamanders exposed to stimuli from stressed conspecifics were slower to begin foraging than those exposed to stimuli from non-stressed conspecifics and to a blank control. The salamanders exposed to stimuli from stressed conspecifics consumed fewer prey than those exposed to a blank control. Some fishes also have been shown to lower their feeding rates in the presence of alarm chemicals in experiments under both laboratory (Fricke, 1987; Rehnberg and Smith, 1988; Jakobsen and Johnsen, 1989) and semi-natural (Irving and Magurran, 1997) conditions.

Cues from distressed conspecifics provide a relatively low level of information. Salamanders are warned of a general disturbance but are unaware of the specific nature of the threat. The best strategy in such cases may be to minimize the probability of being detected and maximize vigilance behavior, resulting in the overall low levels of activity that we observed for salamanders in this treatment.

We follow the terminology of Mathis and Lancaster (1998) in using the term “stress” or “distress” cues to distinguish the stimuli in our study from the damage-released chemicals referred to in other studies as “alarm” cues (e.g. Luttershmidt et al., 1994; Marvin and Hutchison, 1995; Chivers and Smith, 1998). The stimuli used in these other studies were homogenates of skin tissue whereas our stimuli were apparently from voluntarily released secretions. Although no tissue damage was apparent in our study, we cannot completely rule out the possibility that there may have been some slight damage to epithelial cells as a

result of our forceps technique. We feel that any tissue damage would have been minor and so it is unlikely that injury was the source of the warning chemicals. Some other species (reviewed in Wisenden, 2003) also voluntarily release warning chemicals without damage, but these “disturbance” chemicals typically are released without actual contact with the predator. The active components of our “distress” stimuli may or may not be the same as those of damage-released or, possibly, disturbance-released stimuli, but this hypothesis remains to be tested.

4.3. Effects of predator kairomones on foraging behavior of salamanders

Responses to predator kairomones were similar to responses to conspecific distress chemicals in that salamanders exposed to snake cues resumed foraging more slowly and consumed fewer prey than those exposed to the control treatments. Depressed foraging in the presence of kairomones from predatory garter snakes, *Thamnophis sirtalis*, also has been reported for *P. cinereus* (Maerz et al., 2001).

In contrast to the previous experiment with distress chemicals, the decrease in foraging behavior did not appear to be due to a general decrease in activity. Qualitatively, salamanders in the predatory snake treatment typically showed accelerated activity, often pressing their snouts against spaces between the sides and the lid of the chamber (“escape” behavior: Mathis and Lancaster, 1998). Similarly, *P. cinereus* exposed to water soiled by garter snakes showed increased non-foraging activity, perhaps indicating hyperactive search for refuges (Madison et al., 1999b). The presence of snake kairomones indicates that a snake is or has recently been in the immediate vicinity and the most effective response for salamanders may be to seek shelter (Sullivan et al., 2002) or to avoid the area (Cupp, 1994).

Salamanders in our study were able to distinguish between predatory and non-predatory snakes at least with respect to foraging latency. Some salamanders can use short-term diet-based cues in assessment of predation (Madison et al., 1999a,b; Murray and Jenkins, 1999). In our study, discrimination between predatory and non-predatory snakes was not based on recent diet because both species of snakes had consumed only invertebrate prey for several weeks prior

to stimulus collection. Discrimination was thus based either on long-term dietary cues (from salamanders eaten prior to our capture of the snakes) or cues independent of diet. The ability of salamanders to discriminate between the two species could be based either on innate recognition or learning; both snake species co-occur with salamanders in our Arkansas population.

4.4. Conclusions

When stressed by attack, exposure to conspecific distress cues, or exposure to predator kairomones, Ozark zigzag salamanders responded with reduced foraging activity. The degree of the response appeared to depend more on the nature of the threat rather than the intensity of the stress. Salamanders experiencing the most intense physical disturbance (attack) generally reduced activity, including foraging, but did not show a more intense response than salamanders that were exposed to more indirect indicators of threat. When the identity of the threat was known (predator kairomones) and the threat was in the immediate vicinity, salamanders reduced foraging and appeared to focus more time on searching for a hiding place. When the threat was only of a general nature (distress cues from conspecifics), salamanders reduced foraging, decreased activity and appeared to focus primarily on vigilance behavior. In all stress treatments, many salamanders continued to forage, although at reduced levels, indicating a high cost to missed foraging opportunities.

Acknowledgements

We thank the Graduate College and Biology Department at Southwest Missouri State University for funding. This research protocol was approved by SMSU IACUC #98H. Collection permits were provided by Arkansas Game and Fish and the Missouri Department of Conservation.

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