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ABSTRACT: Individual size is an important determinant of the outcomes of inter- and intraspecific interactions. Different-sized members of a guild might represent prey, competitors, or predators. Although direct predation rates might be low, trait-mediated indirect effects of predators on prey can yield altered activity, microhabitat use, survival, and growth. If individuals respond to all sizes of a predator regardless of the predation threat, antipredator behaviors might incur costs for prey as they forgo foraging opportunities or experience predation by other predators. Accurate assessment of predation risk would minimize costs resulting from antipredator behavior. We evaluated the ability of larval salamanders to assess predation risk and alter their habitat selection in response to intraguild competitors and predators. Specifically, we assessed behavioral responses to the presence of a conspecific, a similarly sized heterospecific, and a small or large individual of a predatory species. We predicted that larval salamanders would select habitat differently in the presence of a large predatory heterospecific, but not in the presence of similarly sized heterospecifics or conspecifics. The focal species occupied habitat $29 \pm 0.02\%$ farther from a large heterospecific predator than from small heterospecifics, even if the heterospecifics were smaller individuals of the predatory species. The focal species also exhibited escape behaviors only in the presence of the large members of the predatory species. These data indicate that salamander larvae can assess size-specific predation threats, minimizing predation risk through use of antipredator behaviors.

Key words: *Desmognathus*; Intraguild predation; *Pseudotriton*; Threat sensitive; Trait-mediated indirect interactions

BODY SIZE is an important determinant of the outcomes of intraguild interactions (Wissinger 1992; Woodward and Hildrew 2002; Hartvig and Andersen 2013). Larger individuals can forage on a broader array of prey items and experience reduced predation risk from guild members relative to smaller individuals (Werner and Gilliam 1984; Polis et al. 1989; De Roos et al. 2003; Jonsson 2014). When guild members exhibit ontogenetic shifts from competitor to predator, population and community structure can shift as guild members both compete against small guild members and avoid predation by large guild members (Werner and Gilliam 1984; De Roos et al. 2003; Rudolf 2006, 2007).

Intraguild predators alter the behavior, microhabitat use, morphology, and life-history traits of their prey (Finke and Denno 2002; Werner and Peacor 2003; Schmitz et al. 2004; Rudolf 2008). These effects are known to have substantial influence on the distribution and abundance of intraguild prey (Gilliam and Fraser 1987; Gustafson 1994; Yurewicz 2004; Rudolf 2008). Behavioral adaptation by prey to reduce predation risk might facilitate coexistence and guild stability (Gilliam and Fraser 1987; Lima and Dill 1990). Although antipredator behaviors will improve the immediate survival of an organism, they often come at a cost as individuals forgo foraging or mating opportunities (Peacor and Werner 2001; Preisser et al. 2005). Threat-sensitive responses minimize opportunity costs when individuals allocate time to predator avoidance in proportion to predation threats (Helfman 1989; Domenici 2010; Crawford et al. 2011). For species experiencing size-dependent predation risk, it would be maladaptive to exhibit antipredator behaviors in the presence of individuals incapable of acting as predators (Helfman 1989).

Stream salamander assemblages are influenced by intraguild interactions because these species often have long

larval periods and life spans that allow for a variety of co-occurring sizes of individuals (reviewed by Hairston 1987). Because salamanders are gape limited, they often prey on smaller conspecifics and members of other guild species that also compete for invertebrate prey (Beachy 1994; Rudolf 2006). Presence of large predatory heterospecifics directly alters the survival of smaller guild members via predation, and indirectly via changes to nocturnal activity, microhabitat use, and growth (Southerland 1986; Roudebush and Taylor 1987; Formanowicz and Brodie 1993; Gustafson 1993; Rudolf 2008). Although different size classes represent varying levels of predation risk, it is unclear whether small guild members can evaluate predation risk. Furthermore, previous studies have identified long-term changes in survival and growth of intraguild prey, but limited data are available to indicate that short-term habitat selection behaviors change. Previously observed shifts in habitat selection include increased cover use and increased spatial and temporal distance from a potential predator (Gustafson 1993, 1994; Rudolf 2008). These indirect effects are hypothesized to result from predation threats (Rudolf 2008), but interference competition could produce similar patterns when large guild members force small individuals to alter their behavior through competitive rather than predatory interactions (Sih et al. 1992; Gustafson 1993).

In this study, we examined the responses of intraguild prey to the predation threat of different-sized guild members in the absence of interference competition for either space or prey. We hypothesized that (1) intraguild prey would select habitat closer to similarly sized conspecific or heterospecific than to large, predatory heterospecifics and (2) intraguild prey would select habitat under cover more frequently in the presence of a large, predatory heterospecific. Finally, we predicted that habitat selection in response to a small member of a potential predator will be more similar to responses to conspecifics and similarly sized

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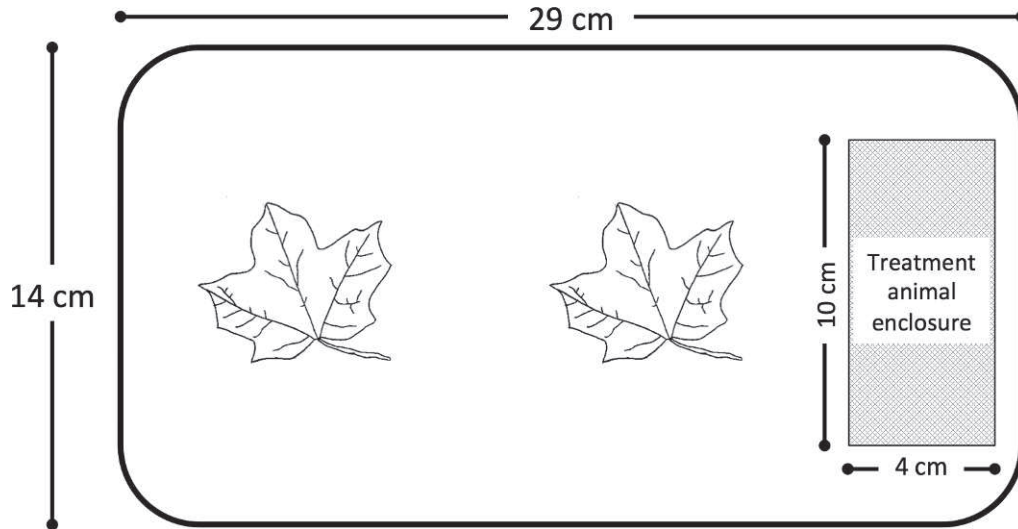


FIG. 1.—Diagram of enclosures for behavioral experiments involving different species of plethodontid salamanders. Leaf packs were constructed from leaves found on the same local stream bank from which sand substrate was collected. The substrate was 1 cm deep and 2 cm of water was added. A screen enclosure was used to contain treatment animals to prevent physical interaction between individuals but allow for the transfer of chemical and visual signals between subjects.

heterospecifics than responses to larger individuals of a predatory species.

MATERIALS AND METHODS

Study Community

Larval stream salamander communities in the eastern United States typically include species in the genera *Desmognathus* and *Eurycea* that transform at relatively small sizes after spending approximately 1–2 yr as larvae (e.g., *D. fuscus*, 15–20 mm snout–vent length [SVL]; *E. cirrigera*, 23–32 mm SVL; Petranka 1998). These communities also often harbor *Pseudotriton* spp. or *Gyrinophilus porphyriticus* that transform at large sizes after spending ≥ 2 yr as larvae (e.g., *P. ruber*, 44–52 mm SVL; *G. porphyriticus*, 55–65 mm SVL; Petranka 1998). *Gyrinophilus porphyriticus* is known to frequently consume other salamanders, and studies of *P. ruber* larvae indicate that they will also consume smaller salamanders (Cecala et al. 2007; Rudolf 2008). Because of high local abundances and small size, we used *D. fuscus* larvae as our intraguild prey member, *E. cirrigera* larvae as an example of a similarly sized guild member, and small and large *P. ruber* larvae as examples of an intraguild predator (Price et al. 2012).

Behavioral Experiments

We conducted a laboratory study to examine the reactions of *D. fuscus* to intraguild members *E. cirrigera* and *P. ruber*. Twenty-five *D. fuscus* larvae (12–17 mm SVL), 10 *E. cirrigera* larvae (20–30 mm SVL), and 10 small (16–21 mm SVL) and 10 large (40–56 mm SVL) *P. ruber* larvae were collected from a 150-m stream in Cowan's Ford Wildlife Refuge, North Carolina in the spring of 2008. Individuals were selected such that all large *P. ruber* would be capable of consuming larval *D. fuscus* and all small *P. ruber* would be incapable of consuming larval *D. fuscus* (Gustafson 1994; Cecala et al. 2007). Larval *D. fuscus* in this region typically hatch in late fall, indicating that these individuals were all approximately 6 mo old and had experience with other guild members

abundant at this site (Petranka 1998; Cecala et al. 2009). Salamander larvae in this stream exhibit high frequencies of movement (Cecala et al. 2009), and we presume that individuals used in this study represent a well-mixed population.

Animals were collected 1 wk before testing and kept individually at 4°C in 13- × 13- × 5-cm plastic enclosures containing a paper towel and 2 cm of water collected from their capture location. Salamanders were fed thawed blood worms ad libitum until 3 d before trials began to eliminate diet odor cues (Katz and Dill 1998; Madison et al. 1999; Persons et al. 2001).

Experimental trials were conducted in a 29- × 14- × 12-cm enclosure where the responses of *D. fuscus* to the presence of other guild members were examined (Fig. 1). The enclosures consisted of a streambed sand substrate collected from a local stream and two leaf packs constructed with four to five leaves (*Acer rubrum*, *Fagus grandifolia*, and *Quercus* sp.) collected from local stream banks. Leaf packs were situated with one close to the predator and the other at the far end of the enclosure. Dechlorinated water was added to the enclosures at the beginning of the study and additional water was added as needed to maintain a depth of 2 cm, representative of local streams. All enclosures were kept at 24–26°C with a natural photoperiod during March and April (approximately 11 h of daylight) via an opaque skylight.

Individual *D. fuscus* were allowed to acclimate to the enclosures 24 h before trials began. Guild members were placed in a 10- × 4-cm treatment enclosure made of 1- × 1-mm screen mesh to allow for the transmission of visual and chemical cues, but prevent physical contact and predation. To test behavioral reactions of *D. fuscus* to larvae of other species, the behaviors of 25 individuals were measured in response to each of five treatments. The treatments included the presence of (1) an empty control; (2) a conspecific individual (an additional *D. fuscus* larva); (3) a similarly sized nonpredatory heterospecific (*E. cirrigera* larva); (4) a similarly sized individual of the predatory species (small *P. ruber* larva); and (5) a large, predatory heterospecific (a large

TABLE 1.—Effect sizes of response values in treatments relative to the control for interaction experiments involving different plethodontid salamanders. Positive values indicate increased movement away from the treatment, whereas negative values indicate movement toward the treatment. CI indicates the 95% confidence interval for the treatment. Values in bold are statistically significant.

	Parameter			
	Effect size	Standard error	Lower 95% CI	Upper 95% CI
<i>Desmognathus fuscus</i>	-2.24	0.61	-3.44	-1.04
<i>Eurycea cirrigera</i>	-0.22	0.91	-2.02	1.57
Small <i>Pseudotriton ruber</i>	0.32	1.00	-1.64	2.28
Large <i>P. ruber</i>	8.46	0.64	7.21	9.72

P. ruber larva). Each individual was tested in the presence of each of the treatments in a randomized order with 3-d intervals in between testing. Animals were placed in the center of the enclosure at the beginning of each 3-d trial. The location of the test subject (open, under cover, or out of water) and its distance from the smaller treatment enclosure were recorded every 6 h. Disturbance of trial animals was minimized during observations by using a flashlight with a light diffuser to detect individuals with the least amount of light possible.

Data Analysis

To examine whether or not *D. fuscus* accurately responded to the large intraguild predator, we used a linear mixed model to evaluate the effect of treatment on larval *D. fuscus* position and habitat selection. This mixed model is an alternative method to repeated-measures designs because it also accounts for potential influences of individual variation by including individual as a random factor (Bolker et al. 2009). This model was implemented using lmer in the add-on package lme4 in program R (Bates et al. 2011; R Core Development Team 2013). Significance of treatment was determined by using the lmerTest add-on package using the Kenward and Roger (1997) approximation of the *F*-ratios (Kuznetsova et al. 2014). We evaluated differences between

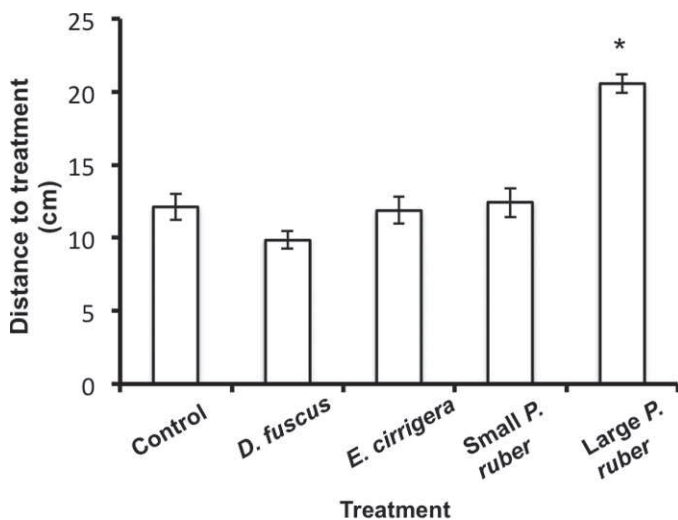


FIG. 2.—Distance that a larval *Desmognathus fuscus* was observed from a treatment enclosure as a function of the content of that enclosure (control, conspecific, or heterospecific individual). Values are depicted as means ± 1 SE; the asterisk denotes statistical significance (Table 1).

TABLE 2.—Effect sizes of response values for frequency of habitat use relative to the control for interaction experiments involving different plethodontid salamanders. Positive values indicate increases, whereas negative values indicate decreases in the frequency of habitat use. Values in bold are statistically significant.

	Behavior		
	Open	Under cover	Out of water
<i>Desmognathus fuscus</i>	-0.3%	4.7%	-1.3%
<i>Eurycea cirrigera</i>	4.3%	2.0%	-3.3%
Small <i>Pseudotriton ruber</i>	-5.0%	6.3%	0.7%
Large <i>P. ruber</i>	-23.7%	-8.3%	31.7%

treatments using post hoc Tukey contrasts among all treatments correcting for familywise error using glht in add-on package multcomp in program R (Hothorn et al. 2014).

RESULTS

We found that treatment influenced the distance that *D. fuscus* larvae located themselves away from the treatment individual ($F_{4,119} = 86.88, P < 0.001$; Table 1; Fig. 2). Treatments with a large *P. ruber* larva were different from all other treatments, with *D. fuscus* subjects located $29 \pm 0.02\%$

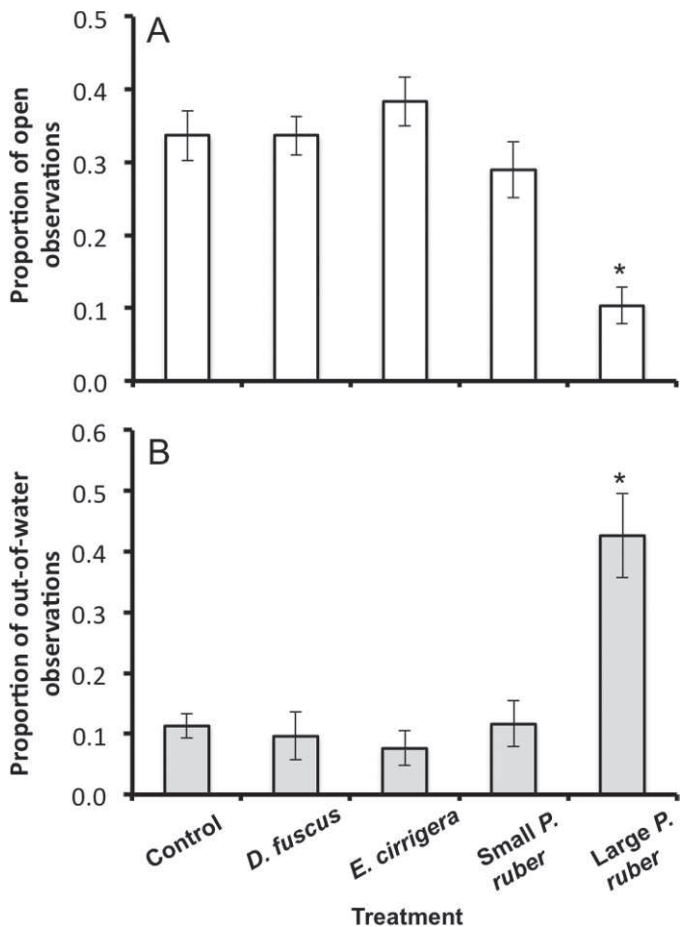


FIG. 3.—Behavior of larval *Desmognathus fuscus* as a function of the content of a treatment enclosure (control, conspecific, or heterospecific individual). Response variables are the proportion of observations that the test subject was (A) in open water or (B) out of the water on the wall of the test chamber. Values are depicted as means ± 1 SE; the asterisk denotes statistical significance (Table 2).

TABLE 3.—Bonferroni-adjusted P -values for Tukey post hoc contrasts of response values assessing different behaviors of larval *Desmognathus fuscus* presented with different treatments in experimental enclosures. Bold values represent significant differences between treatments.

	Treatment				
	Control	<i>D. fuscus</i>	<i>Eurycea cirrigera</i>	Small <i>Pseudotriton. ruber</i>	Large <i>P. ruber</i>
Distance from treatment					
Control	—	0.306	0.999	0.999	<0.001
<i>D. fuscus</i>		—	0.416	0.186	<0.001
<i>E. cirrigera</i>			—	0.990	<0.001
Small <i>P. ruber</i>				—	<0.001
Large <i>P. ruber</i>					—
Frequency found in open habitat					
Control	—	0.966	0.994	0.488	<0.001
<i>D. fuscus</i>		—	0.831	0.868	<0.001
<i>E. cirrigera</i>			—	0.262	<0.001
Small <i>P. ruber</i>				—	0.002
Large <i>P. ruber</i>					—
Frequency found out of the water					
Control	—	0.997	0.972	0.999	<0.001
<i>D. fuscus</i>		—	0.998	0.997	<0.001
<i>E. cirrigera</i>			—	0.972	<0.001
Small <i>P. ruber</i>				—	<0.001
Large <i>P. ruber</i>					—

(mean \pm 1 SE) farther from the treatment individual (Tables 2, 3; $P < 0.001$). Treatment also influenced the frequency with which larval *D. fuscus* used open habitats ($F_{4,119} = 11.31$, $P < 0.001$; Table 1; Fig. 3). Specifically, presence of a large *P. ruber* larva induced habitat selection changes that were different from all other treatment types, the latter of which were all similar to one another (Table 3; $P < 0.001$). Individuals were 24% less likely to be found away from cover in the presence of a large *P. ruber* larva than in the presence of any similarly sized larvae. Likewise, the expression of an escape behavior—where individuals were found on the sides of the enclosures, with all but their head and gills located out of the water—was influenced by treatment ($F_{4,119} = 12.27$, $P < 0.001$). Individuals were found out of the water 31% more frequently in the presence of a large *P. ruber* larva than in all other treatments (Table 3; Fig. 3).

DISCUSSION

Our results indicate that salamanders are capable of responding to predation risk in a threat-sensitive manner. The prey species exhibited an escape behavior and located themselves farther from the larger heterospecifics capable of preying on them. Species identity did not affect behavioral responses as long as they were of similar size to the prey individual. By caging potential predators, we have demonstrated that indirect effects attributable to predator presence can be induced in the absence of interference competition. Despite observations that indicate that *P. ruber* will prey on small guild members (Rudolf 2008), predation by *P. ruber* on *D. fuscus* is rare in natural environments (Cecala et al. 2007). We suggest that accurate assessment of size-dependent predation threats may be one mechanism that facilitates coexistence of stream salamanders.

Studies that have observed trait-mediated indirect effects have identified interference competition as a mechanism driving these indirect effects (Gustafson 1994; Rudolf 2008). Our study eliminated the potential for interference competition by preventing physical interactions and demonstrated that intraguild prey exhibit behavioral avoidance of only heterospecifics capable of consuming them. We predicted that, to effectively compete with small members of a predatory species, larval *D. fuscus* would exhibit threat-sensitive behavioral avoidance using visual or chemical cues. Because of high organic loads and siltation of many undisturbed streams, visual cues may be ineffective. Alternately, salamanders are widely known to use olfaction to detect chemical stimuli and respond appropriately to generalist versus specialist predator odors, making it likely that individuals in our study also used olfaction (Mathis and Vincent 2000; Hickman et al. 2004; Crawford et al. 2011). Because we ensured that salamanders used as treatment individuals had not been fed before their use as a treatment, we eliminated the availability of cues related to the diet of the treatment individual. This suggests that salamanders might exude different types or concentrations of chemicals or kairomones as they grow or supplement olfactory cues with visual cues (Laurila et al. 1997; Persons et al. 2001; Hickman et al. 2004).

Behavioral changes in the presence of a predator may force *D. fuscus* to use less productive microhabitats in these natural environments. Because larval stream salamanders require aquatic habitats for survival to metamorphosis, leaving the stream to avoid a predator has consequences including potential desiccation or increased predation rates by non-guild predators, ultimately reducing survival to adulthood (Bruce 1978; Semlitsch et al. 1988; Scott 1994). Furthermore, larval *Desmognathus* spp. are suction feeders until metamorphosis and likely to be inefficient foragers if they spend significant time out of water (Deban and Marks 2002). Limited foraging success by *D. fuscus* could also reduce larval growth rate and body size, and lower survival (Gilliam and Fraser 1987; Skelly 1992; Bernardo and Agosta 2003).

More research is needed to understand how amphibians distribute themselves in streams relative to other individuals. Although not significant in our mixed model, evaluation of the conspecific effect size and its 95% confidence interval might indicate that larval *D. fuscus* are found closer to conspecifics than similarly sized heterospecifics (Table 1). Because these results lack statistical support, additional research is needed to evaluate the potential for conspecific cue use in larval salamander habitat selection. Similarly, because tested *D. fuscus* larvae likely had prior experience with other guild members, we cannot determine if the observed behavioral differences are innate, learned, or represent a response to selection (Borenstein et al. 2008). For example, if they do not respond to potential predators, they are likely to be depredated; or if they respond negatively to all individuals of a predatory species despite their size, they might be outcompeted by similarly sized individuals for prey (Schmitz et al. 2004; Preisser et al. 2005; Rudolf 2008).

Trait-mediated indirect effects likely reduce predation rates on intraguild prey but might also generate costs for avoiding predation (Gustafson 1993; Peacor and Werner 2001; Preisser et al. 2005; Rudolf 2008). Salamanders that fail to respond to heterospecifics in a threat-sensitive manner

may be less competitive than individuals that can accurately assess the predation risk posed by an individual of a predatory species. This sensitivity in predator detection is one possible mechanism that facilitates coexistence of stream salamander intraguild predators and prey.

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