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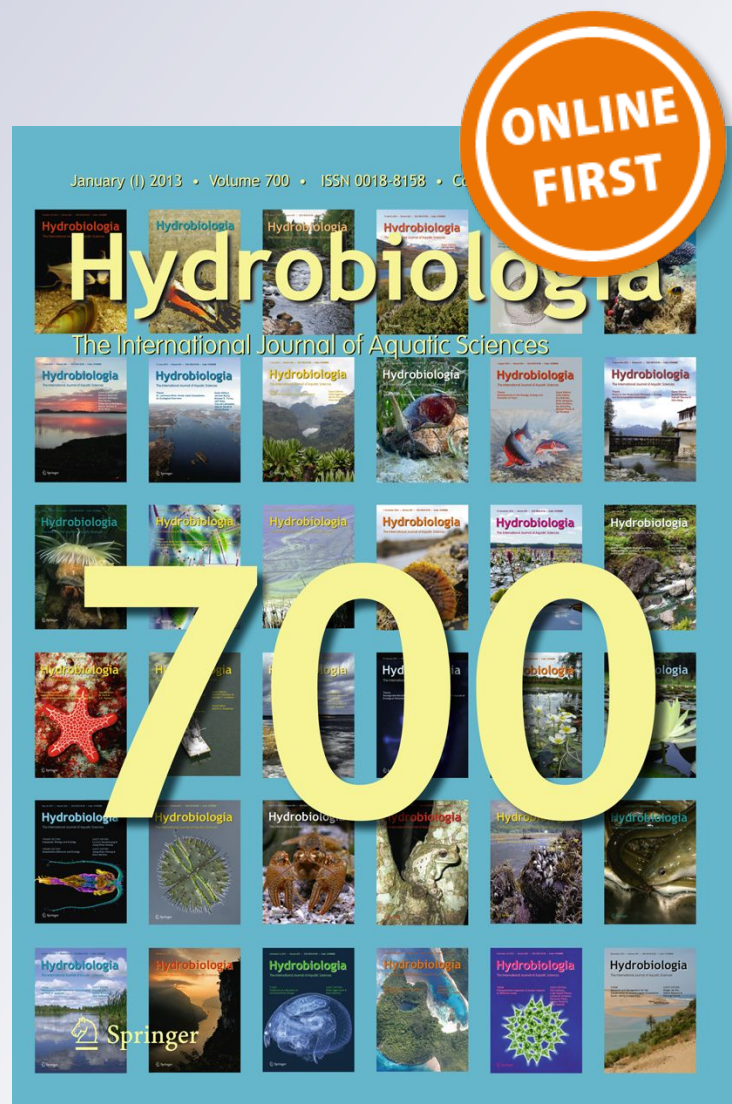
Hydrobiologia

The International Journal of Aquatic
Sciences

ISSN 0018-8158

Hydrobiologia

DOI 10.1007/s10750-017-3124-4



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Antipredator behavior of the Barton Springs salamander (*Eurycea sosorum*) in response to aquatic invertebrates: potential consequences of habitat restoration

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Received: 29 July 2016 / Revised: 16 February 2017 / Accepted: 16 February 2017
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Abstract The Barton Springs Salamander, *Eurycea sosorum*, is a fully aquatic salamander found in Barton Springs in Texas, USA, and has benefited from habitat restoration efforts. While important to improve overall habitat quality for this imperiled species, current management and restoration practices may also inadvertently increase the abundance of non-target organisms such as predatory invertebrates. Fish represent major predators of this species, but little is known about the role of invertebrates as potential predators. It is important to understand the role of these aquatic invertebrates as predators of *E. sosorum*, especially if habitat restoration also increases predator abundance. Using adult, predator-naïve salamanders, we examined the antipredator response of *E. sosorum* to chemical cues from the following treatments: crayfish,

dragonfly larvae, snails, and water. Salamanders decreased activity (antipredator behavior) only in response to the crayfish treatment. The responses to dragonfly larvae, snails, and water did not differ, suggesting that dragonfly larvae are not perceived as predators by these salamanders. Our study provides preliminary evidence suggesting that habitat restoration has unexpectedly increased crayfish abundance, which in turn may negatively affect *E. sosorum*, and that future management strategies should consider crayfish removal if salamander abundances decline with increasing crayfish abundance.

Keywords Chemical kairomone · Habitat restoration · Inadvertent restoration effects · Innate predator recognition · Invertebrate predator · Predator–prey interaction · *Procambarus clarkii*

Handling editor: Lee B. Kats

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Introduction

Habitat restoration has been instrumental in maintaining populations of imperiled or endangered species, often by increasing the amount and quality of critical habitat needed for a species to persist and recover (Bowles & Whelan, 1994; Dobson et al., 1997). In recent decades, conservation biologists have started to shift from single-species management to a more holistic, ecosystem management approach (Poiani et al., 2000). While some habitat restoration efforts

focus on maximizing the benefits to an entire community, this strategy can result in direct or indirect negative effects on particular species (Porej & Hetherington, 2005), which is especially of concern if this specifically results in negative effects on imperiled species (Casazza et al., 2016). For example, restoration of tidal marsh ecosystems, primarily achieved by the use of herbicides to remove invasive Atlantic Cordgrass (*Spartina alterniflora* Loisel), benefited many species of shorebirds and allowed normal ecosystem patterns to return (Casazza et al., 2016). However, the endangered California Rail (*Rallus obsoletus* Ridgway, 1874) was negatively affected by these habitat restoration efforts as it reduced the amount of usable habitat and cover, which increased predation rates (Harding et al., 2001; Casazza et al., 2016). Strategies to maximize success of both habitat restoration and endangered species recovery should be a priority, especially in regard to potential effects of increased predator abundance or increased predation rates on endangered prey species.

Predation is a strong selective pressure in most ecological systems, as predation should select for appropriate antipredator responses in prey populations (Kerfoot & Sih, 1987). While antipredator responses vary from plastic, rapidly changing behaviors to canalized, induced morphological traits, all increase the likelihood of surviving encounters with predators, but come at a cost to prey individuals (Lima & Dill, 1990). For behavioral antipredator responses, these costs often manifest as a reduction in time spent foraging or mating and have the potential to reduce individual fitness over prolonged periods of time. Therefore, it is predicted that prey species should exhibit threat-sensitive predator avoidance: efficient antipredator responses to specific predators that maximize survival and minimize fitness costs (Helfman, 1989; Mathis & Vincent, 2000; Chivers et al., 2001). Additionally, encounter frequency may also be an important factor influencing the antipredator response to particular predators (Lima & Bednekoff, 1999; Ferrari et al., 2009a), especially if habitat restoration may be inadvertently increasing the abundance of these predators.

Habitat restoration has played a critical role in the persistence of the Barton Springs Salamander, *Eurycea sosorum* Chippindale, Price, & Hillis, 1993 (Caudata: Plethodontidae). This small (adult SL = 23.5–36.5 mm), fully aquatic salamander is federally listed under the Endangered Species Act and is an IUCN Red List species

(IUCN, 2015) that is primarily found in Barton Springs in Austin, Texas, USA (Chippindale et al., 1993). Population sizes of *E. sosorum* across monitored sites vary through time, but Eliza Spring (Fig. 1a) consistently supports the largest number of individuals (N. Bendik, pers. comm.). Habitat restoration at Eliza Spring has included debris removal and lowering the water level, which helped flush out sediments, return natural spring flows, and assist in the establishment of aquatic macrophytes (Fig. 1a). This restoration process resulted in significant increases in *E. sosorum* abundance (compared to pre-restoration) and



Fig. 1 **a** Eliza Spring (September 2008) after habitat restoration efforts. While it remains a heavily modified site, water levels have been reduced, spring flow has improved, sedimentation rates have decreased, and aquatic macrophytes have become established. For scale, the long axis of Eliza Spring is ca. 12 m in length. Photograph by City of Austin. **b** Red Swamp Crayfish (*Procambarus clarkii*) consuming a Barton Springs Salamander (*Eurycea sosorum*) in Eliza Spring. Arrow points to the head of the salamander between the pair of crayfish chelipeds. Photograph by L. Colucci

additional restoration efforts at Eliza Spring and other sites are ongoing.

While habitat restoration is critical to maintaining *E. sosorum* in these highly developed and modified sites, the process of habitat restoration also benefits other sympatric species, including potential predators. The restoration of Eliza Spring to a more natural site prevents many large fish (i.e., centrarchids) from being able to survive due to significantly lower water levels; however, invertebrate predators may benefit from restoration aimed at increasing habitat quality for *E. sosorum*. These benefits to invertebrate predators include the elimination of large predatory fish, the establishment of aquatic macrophytes, and increased habitat by reducing sediment accumulation among cobble substrates. Since 2003, City of Austin biologists have conducted consistent surveys for salamanders and aquatic invertebrates at Barton Springs. Preliminary data from these surveys suggest that the abundance of native Red Swamp Crayfish [*Procambarus clarkii* (Girard, 1852)] is greater in Eliza Spring, which has been restored as high quality salamander habitat, than in Zenobia Spring, which remains unrestored (Wilcoxon Signed-Rank Test: $Z = -88.5$, $P = 0.0214$; Siegel, 1956). These crayfish, while native to Barton Springs, are highly invasive outside their native range and have been found to consume and negatively impact many amphibian species (Gamradt & Kats, 1996; Gamradt et al., 1997; Cruz & Rebelo, 2005). Within these springs, niche overlap between crayfish and *E. sosorum* has the potential to be high, further increasing potential predation rates. Other aquatic invertebrates such as dragonfly larvae are known predators of amphibians, and extensive literature exists documenting strong predatory interactions with anurans (increased tail fin depth: Van Buskirk & Relyea, 1998; Lardner, 2000; increased pigmentation: Caldwell, 1982; McIntyre et al., 2004); however, fewer studies have examined interactions between invertebrate predators and aquatic salamander prey (Yurewicz, 2004; Drake et al., 2014; Vollmer & Gall, 2014).

Here we investigate the antipredator response of *E. sosorum* to sympatric aquatic invertebrates. Of special interest is the antipredator response to crayfish given that restoration efforts may be simultaneously increasing crayfish abundance. Field observations of interactions between *E. sosorum* and invertebrate predators are extremely limited given the habitats that *E.*

sosorum occupies (aquatic macrophytes, cobble substrates) and their largely nocturnal activity patterns, and therefore, laboratory investigation into antipredator responses of *E. sosorum* can provide information on potential interactions between species in the field. Here, we exposed adult, predator-naïve (captive-hatched) *E. sosorum* to chemical stimuli from crayfish (Red Swamp Crayfish [*P. clarkii*]), dragonfly larvae [Common Green Darner: *Anax junius* (Drury, 1773)], non-predatory planorbid snails, and water. Investigating these interactions will provide insight to better understand predator–prey interactions involving the federally endangered *E. sosorum*. Furthermore, in the context of ongoing habitat restoration efforts at Barton Springs, an increased understanding of the interactions between *E. sosorum* and invertebrates is particularly important if the unexpected increase in crayfish abundance needs to be addressed.

Materials and methods

Experimental treatments

To investigate interactions between invertebrates and *Eurycea sosorum*, we collected three locally abundant invertebrates: the Red Swamp Crayfish (Malacostraca: Decapoda: Cambaridae: *Procambarus clarkii*), Common Green Darner larvae (Hexapoda: Odonata: Aeshnidae: *Anax junius*), and planorbid snails (Gastropoda: Pulmonata: Planorbidae). These invertebrates are all sympatric with *E. sosorum* and native to Barton Springs (DRD, pers. obs.). Planorbid snails represent a non-predatory invertebrate treatment as these snails consume algae, macrophytes, and other decomposing organic material (Callow, 1974; Strong et al., 2008), and are not predators of salamanders. Aeshnid dragonfly larvae are generalist predators (Pritchard, 1964, 1965; Folsom & Collins, 1984) and have long been known to induce phenotypic defenses in amphibians, particularly larval anurans (McCollum & Leimberger, 1997; Van Buskirk et al., 2003). Less is known about interactions between dragonfly larvae and aquatic salamanders, but experimental studies have shown predation on eggs, larvae, and adults (Yurewicz, 2004; Drake et al., 2014; Vollmer & Gall, 2014) as well as behavioral antipredator responses to predator stimuli (Storfer & White, 2004; Crane et al., 2012). Similar to most other crayfish, *P. clarkii* is an

opportunistic omnivore, consuming microbe-enriched plant detritus, macrophytes, and benthic invertebrates (Huner & Naqvi, 1984; Brown et al., 1992). The significant role of *P. clarkii* as a predator on amphibians has also been recognized, with studies documenting decreased individual survival and reduced population sizes in amphibians following the introduction of *P. clarkii* (Gamradt & Kats, 1996; Gamradt et al., 1997; Cruz & Rebelo, 2005). Additionally, *P. clarkii* has been observed to consume *E. sosorum* (Owen et al., 2016; Fig. 1b), though the frequency of predation events is unknown. Both the dragonfly larvae and crayfish treatments represent predatory invertebrate treatments.

Stimulus acquisition

We collected all invertebrates from the San Marcos Aquatic Resources Center (SMARC) in San Marcos, Texas, USA in July 2012. These invertebrates were collected from various sites at the SMARC including flow-through systems (snails), dugout ponds (dragonfly larvae), and drainage ditches (crayfish). Because these predators were collected from outdoor ponds at the SMARC, they had no prior interactions with *E. sosorum* or other salamanders, however, planorbid snails are often kept in the flow-through systems with salamanders to help minimize algal growth in aquaria. Predators were not fed for 7 days before the collection of chemical cues (kairomones) to eliminate any effects of prior diet. The volume of each stimulus animal was determined via water displacement. To maintain similar chemical concentrations between treatments, we used 230 ml of well water per 1 ml of stimulus animal in the collecting chamber, similar to concentrations used by previous studies (i.e., Mathis et al., 2003). We then placed stimulus animals (2 crayfish, 10 dragonfly larvae, 10 snails) into glass aquaria containing the appropriate volume of aerated well water for 24 h. Individual crayfish were housed in separate aquaria, while dragonfly larvae and snails were each kept in single aquaria during chemical cue collection so that a sufficient volume of water would be present in the aquarium. Before acquisition of the chemical cues, we removed the stimulus animals from the aquaria, stirred the water (mixing equal parts water from the two crayfish), and froze 50-ml aliquots of each cue in plastic bags (-20°C).

Experimental protocol

We used 80 adult ($n = 40$ male, $n = 40$ female), predator-naïve (captive-hatched) *E. sosorum* from the SMARC. These salamanders were hatched from eggs produced by wild-caught adults from Eliza Spring in Austin, Texas, USA. We used predator-naïve salamanders to avoid confounding effects of learning from experienced individuals. Prior to testing, we maintained salamanders on a 12:12 h light:dark cycle in large fiberglass flow-through tanks maintained at 21°C and fed them blackworms [*Lumbriculus variegatus* (Müller, 1774)] ad libitum. We tested salamanders individually in 9.5-l glass aquaria, which were covered on three sides to reduce any background disturbance and contained 4.5 l of well water. Given that activity levels for *E. sosorum* increase beginning at dusk and continuing through the night (DRD, pers. obs.), we conducted all experimental trials 2–4 h after lights were turned off. All observations were conducted under low-level red lighting (25 W). Plethodontid salamanders have retinas that are dominated by rods that are relatively insensitive to long-wavelength colors (i.e., red; Linke et al., 1986), and therefore, the use of low-level red lighting allowed us to observe salamanders without disrupting nocturnal behaviors. After we placed salamanders into the testing aquaria, individuals were allowed to habituate for 20 min, after which they resumed normal activity (i.e., normal movement patterns around the experimental aquaria). Once habituated, we recorded the total time spent moving (in seconds) for 8 min (following Davis et al., 2012). Active behavior included swimming or walking, but did not include head or gill movement that was not accompanied by other movements of the body. These data constitute the baseline activity level for each individual (pre-stimulus activity). Afterwards, we exposed each individual ($n = 20/\text{treatment}$) to 50 ml of chemical kairomones from one of following four treatments: (1) Red Swamp Crayfish (*P. clarkii*), (2) Common Green Darner larvae (*A. junius*), (3) planorbid snail (Planorbidae), or (4) water only. We randomized the order of treatments and coded them to control for observer bias and all experimental trials were conducted individually. We injected chemical stimuli at a rate of 2 ml/s into the aquarium through a 60-ml syringe connected to plastic tubing that was attached to the center of one side of the testing chamber. We placed the end of the introduction tube

ca. 2 cm below the surface of the water to reduce disturbance during treatment introduction. After introduction of the stimulus, we observed and recorded the total time the salamander spent moving for another 8 min as an indication of potential antipredator response (post-stimulus activity). Similar methods have been used successfully in previous studies to study aquatic salamander antipredator behavior (i.e., Mathis & Vincent, 2000; Mathis et al., 2003; Davis & Gabor, 2015). We exposed each individual to a single treatment to eliminate any effects of habituation to stimuli (Hazlett, 2003). Following completion of each trial, we recorded the sex and snout–vent length (SVL) of each individual and washed all equipment with a 3% hydrogen peroxide solution.

Statistical analyses

Analysis of the behavioral data included the calculation of an activity index (post-stimulus activity–pre-stimulus activity). Positive indices indicate increases in activity and negative indices indicate decreases in activity in response to a stimulus. All data met the assumptions of parametric data (independent observations, normality, and homoscedasticity). To examine for differences between treatments, we performed an ANOVA followed by subsequent multiple comparisons (Tukey's HSD; $\alpha = 0.05$). We conducted statistical analyses using JMP v12.0 (SAS Institute, Cary, NC, USA) software.

Results

We did not find a statistical difference in activity times between male ($\bar{x} = 37.43$ mm SVL) and female ($\bar{x} = 38.65$ mm SVL) salamanders, and therefore, data from male and female trials were combined. Mean activity times decreased from pre-stimulus to post-stimulus for all treatments (Table 1). There was a statistical difference in the activity indices among the four treatments (ANOVA: $F_{3,76} = 5.10$, $P = 0.003$; Fig. 2). The mean activity index for the crayfish treatment was statistically lower than that of the water (Tukey's HSD: $P = 0.001$), snail ($P = 0.001$), and dragonfly larvae treatments ($P = 0.03$). There was no statistical difference between the water and both the snail ($P = 1.0$) and dragonfly larvae treatments ($P = 0.96$); additionally, there was no statistical

difference between the snail and dragonfly larvae treatments ($P = 0.96$).

Discussion

Eurycea sosorum decreased activity (antipredator behavior) in response to chemical stimuli from only the crayfish treatment and not to the water, snail, or dragonfly larvae treatments. Additionally, there was no significant difference in the response of *E. sosorum* to water, snail, and dragonfly larvae treatments. Many studies have shown that the reduction in activity is an effective antipredator response in aquatic amphibians (Mathis & Vincent, 2000; Mathis et al., 2003; Mathis et al., 2003) as it decreases the probability of detection, and therefore, reduces subsequent predation rates (Azevedo-Ramos et al., 1992; Skelly, 1994). Because we tested predator-naïve individuals, the antipredator response to crayfish suggests that *E. sosorum* innately recognizes these invertebrates as predators through detection of kairomones. Innate predator recognition has been found in both *E. sosorum* (DeSantis et al., 2013) and *E. nana* Bishop, 1941 (Epp & Gabor, 2008; Davis et al., 2012; Davis & Gabor, 2015) and appears to be the major form of predator recognition in many aquatic amphibians (Ferrari et al., 2010). Our results differ from those of Gillespie (2011) who did not find an antipredator response by *E. sosorum* to chemical cues from crayfish and our differing results are likely due to major differences in stimulus collection and experimental methods.

Due to the potential fitness costs associated with antipredator behaviors (Lima & Dill, 1990), we predicted that salamanders would show threat-sensitive predator avoidance: efficient behavioral responses specific to different levels of perceived threat (high-risk, low-risk) rather than responding to all predators similarly (Helfman, 1989; Chivers et al., 2001). For example, in amphibians, antipredator behaviors are known to shift in response to the size of predators (Puttlitz et al., 1999), relatedness to known predators (Ferrari et al., 2009b; Davis et al., 2012), or based on the foraging mode of predators (e.g., specialist vs. generalist; Crawford et al., 2012). While we are unable to directly test for differences in threat or risk among predator species (given the sole response to crayfish), other studies suggest the role of threat-sensitive predator avoidance in *Eurycea*. Such studies have

Table 1 Mean \pm 1 SE activity times (s) of Barton Springs Salamanders (*Eurycea sosorum*) during pre- and post-stimulus behavioral trials for each experimental treatment

Treatment	Pre-stimulus activity (s)	Post-stimulus activity (s)
Water	118.5 \pm 6.6	101.8 \pm 8.9
Planorbid snail	139.7 \pm 12.6	123.5 \pm 10.5
Dragonfly larvae	134.8 \pm 9.6	112.0 \pm 9.9
Crayfish	123.6 \pm 9.1	66.1 \pm 9.3

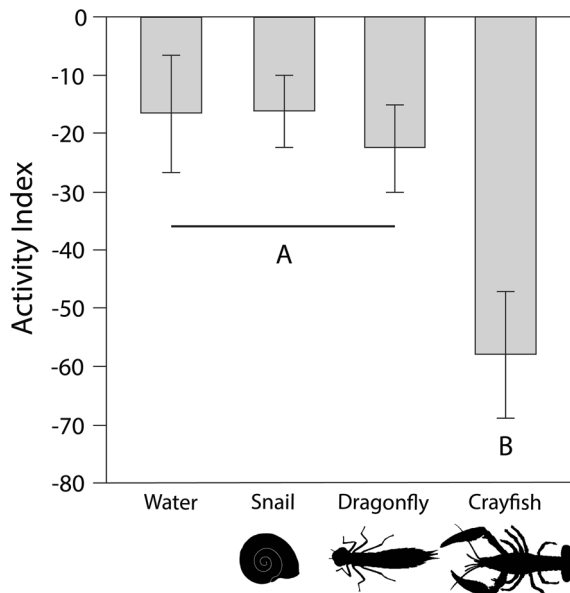


Fig. 2 Mean activity index (\pm 1 SE) of Barton Springs Salamanders (*Eurycea sosorum*) in response to four experimental treatments: water, planorbid snails, dragonfly larvae, and crayfish. Letters indicate groupings from Tukey's HSD mean comparisons ($\alpha = 0.05$)

found that stimuli from *Lepomis auritus* (Linnaeus, 1758) (Redbreast Sunfish) elicit weaker antipredator behaviors (low-risk) than stimuli from *Micropterus salmoides* (Lacepède, 1802) (Largemouth Bass; high-risk) in both *E. sosorum* (DeSantis et al., 2013) and *E. nana* (Davis & Gabor, 2015). Even though our ability to understand if crayfish are low- or high-risk predators from this study is limited, the effect size of the crayfish treatment (Cohen's $d = 0.98$) is similar to that from the low-risk predator *L. auritus* as previously examined by both DeSantis et al. (2013; Cohen's $d = 1.15$) and Davis & Gabor (2015; Cohen's $d = 1.02$). While crayfish abundance appears to have increased due to habitat restoration, the coinciding increase in *E. sosorum* abundance may be partially attributed to appropriate antipredator behavior. If

crayfish abundance continues to increase, elevated predation pressure on *E. sosorum* is likely to occur, and as a result, antipredator behavior may shift so that individuals continue to efficiently match the intensity of antipredator responses to the threat of crayfish predation. Additionally, increased costs associated with elevated antipredator behaviors may decrease individual fitness and result in population-level declines. Future studies should monitor these interactions and empirically test if antipredator behaviors of *E. sosorum* are sufficient under increasing levels of risk and predator abundance.

Numerous studies have highlighted the importance of dragonfly larvae as predators of aquatic amphibians, particularly anurans (Caldwell, 1982; McCollum & Leimberger, 1997; reviewed by Alford, 1999), though fewer studies have examined the response of salamanders to these predators (Yurewicz, 2004; Drake et al., 2014; Vollmer & Gall, 2014). The lack of a response to dragonfly larvae may be due to several different ecological factors including encounter frequency, predator abundance, microhabitat selection, and activity times. It is possible that dragonfly larvae represent a low predatory threat because dragonflies have a life-history shift from aquatic larvae to terrestrial adults, unlike crayfish that remain fully aquatic. Moreover, though dragonfly larvae may be present throughout the year due to a multi-year larval stage, densities of most Odonata can vary seasonally and appear to be greatest from late May–September (Montgomery, 1947). Aeshnid dragonfly larvae typically forage among aquatic macrophytes and structure (Pritchard, 1965; Tarr & Babbitt, 2002) while crayfish forage among benthic substrates and cobble (Nyström, 2002). *Eurycea sosorum* is typically found among cobble and rock substrates and therefore, may be less likely to experience predation by dragonfly larvae than by crayfish. Additionally, *E. sosorum* is primarily nocturnal (DRD, pers. obs.), and therefore, predation by dragonflies, which are primarily visual, diurnal

predators, may be minimal (D. Soluk, unpubl. data; Corbet, 1980; Folsom & Collins, 1984). Conversely, crayfish are primarily crepuscular and nocturnal (Gherardi, 2002) and would be active when salamanders are active. As a result, interactions between salamanders and crayfish may be more likely to occur or occur more frequently than interactions between salamanders and dragonfly larvae. Given these factors, there may have been less selection on innate predator recognition of dragonfly larvae as compared to crayfish.

Given that *E. sosorum* is a closely monitored endangered species persisting in a highly modified landscape surrounded by urban development, there is a clear need to understand and monitor both natural and anthropogenic threats to this species. Both the United States Fish and Wildlife Service and the City of Austin maintain captive populations of *E. sosorum* and should the need for future reintroduction of individuals arise, our results may help to inform management strategies. Similar to a previous study, antipredator behaviors were observed in predator-naïve *E. sosorum* indicating the role of innate predator recognition. Unlike other species of amphibians, if reintroduction of individuals is necessary, associative conditioning or training with the predators examined herein may not be warranted (see Woody & Mathis, 1998, Crane & Mathis, 2010); however, should crayfish abundance continue to increase at these sites, associative conditioning may help increase post-release survival of individuals.

Studies that increase our understanding of behavior are critical to the conservation of imperiled species (Caro, 1998), and information from these studies can directly influence management practices and decisions (Berger-Tal et al., 2011). This study adds to the understanding of predator–prey interactions in a group of endangered aquatic salamanders, and is the first to suggest the potential role of crayfish as more prominent predators on *E. sosorum* than commonly perceived, which may also be true for many other aquatic salamanders. Additionally, preliminary data indicate that crayfish may benefit from habitat restoration efforts targeted at *E. sosorum*, and therefore, our results are an important first step towards better understanding how restoration efforts may influence predator–prey interactions in this system.

Acknowledgements We thank T. Brandt, J. Fries, V. Cantu, and the San Marcos Aquatic Resources Center (SMARC) for logistical support and use of both facilities and experimental animals. We also thank the City of Austin and L. Colucci for generously providing permission to use photographs, N. Bendik for providing crayfish abundance data, K. Pitcher for helpful discussion on invertebrates, and M. Dixon for statistical advice. Funding for this study was provided by the Texas Academy of Science and the Texas State University Undergraduate Research Initiative. Helpful comments on this manuscript were provided by J. Farkas, the GrEBE Discussion Group at the University of South Dakota, and two anonymous reviewers. This experiment was conducted under an approved Texas State University IACUC protocol (#01-039-028) and permits for captive salamanders are maintained by the SMARC (TPWD SPR-0390-045; USFWS TE676811-2).

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