CHEMICALLY MEDIATED PREDATOR AVOIDANCE IN THE BARTON SPRINGS SALAMANDER (*EURYCEA SOSORUM*)

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ABSTRACT: Predation is a dominant and influential factor in most ecological communities. However, little is known about how the federally endangered Barton Springs Salamander, *Eurycea sosorum*, responds to predators. Using captive-hatched (predator-naïve) salamanders, we examined the antipredator response of *E. sosorum* to chemical cues from (1) native Western Mosquitofish (*Gambusia affinis*), (2) introduced Redbreast Sunfish (*Lepomis auritus*), (3) native Largemouth Bass (*Micropterus salmoides*), and (4) a blank water control. Salamanders decreased activity (antipredator behavior) in response to all fish treatments but not to the blank water control. There was no difference between the response to the *G. affinis* and *L. auritus*, but salamanders responded less to these treatments than to *M. salmoides*. The antipredator response to *G. affinis* may be an ontogenetic hold over as *G. affinis* has been found to consume amphibian larvae and eggs. In an additional study to test whether antipredator behavior was a generalized response to all fish species, we found that *E. sosorum* did not respond to small, nonnative, nonpredatory Guppies (*Poecilia reticulata*). This suggests that the observed behavior in our first experiment represents antipredator behavior specific to the species tested. Overall, these results indicate that *E. sosorum* has innate recognition of predatory fish, and that the stronger antipredator response to *M. salmoides* over the other fish species may be an outcome of risk assessment. The antipredator response to *G. affinis* has management implications as *G. affinis* is sympatric with the largest population of *E. sosorum*, and may be consuming both eggs and larvae of these salamanders.

Key words: Antipredator behavior; Chemosensory; *Gambusia affinis*; Innate recognition; Kairomone; Predator–prey interaction

DECLINES in amphibian populations represent a global biodiversity crisis and can be attributed to factors such as habitat destruction, ultraviolet radiation, pathogens, and introduced predators (reviewed by Alford and Richards, 1999; Sodhi et al., 2008; Wake and Vrendenburg, 2008). The introduction of predatory fish species into amphibian environments has been particularly problematic and has led to declines in amphibian populations (Knapp and Matthews, 2000; reviewed by Kats and Ferrer, 2003; Gall and Mathis, 2009). Predation represents a strong selective force, as an incorrect response to predators typically results in the death of prey individuals. However, there are costs associated with predator avoidance. Time spent responding to predators is time not spent foraging or mating (Lima and Dill, 1990). Prey can optimize their responses to predators, and minimize the costs, by differentially responding to low- and high-risk predators (Helfman, 1989; Chivers et al., 2001). Additionally, prey should be able to differentiate their responses based upon risk and encounter frequencies associated with particular predators (Lima and Bednekoff, 1999).

Prey species typically recognize predators through learned or innate recognition (Wisenden, 2003). Individuals that have learned predator recognition initially require potentially dangerous encounters with predators in order to recognize them in the future. Innate predator recognition does not require prey individuals to have these initial encounters with predators to achieve recognition, as recognition is genetically inherited. In environments that have dynamic predator composition or low-risk predators, learned predator recognition may be advantageous, whereas in environments that have static predator composition or high-risk predators, innate predator recognition may be advantageous (Wisenden, 2003). In amphibians, both learned (Suboski, 1992; Woody and Mathis, 1998; Wildy and Blaustein, 2001) and innate (Mathis et al., 2003; Epp and Gabor, 2008) predator recognition have been documented. Additionally, certain amphibian species have been documented to generalize their response

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to predators (Ferrari et al., 2009; Davis et al., 2012). Predator generalization is based on similarities between recognized predators and novel predators, generally of the same species or higher taxa, based on chemical cues that can be detected by prey species (Ferrari et al., 2007).

Among amphibians, chemical stimuli are important for the detection of predators (Woody and Mathis, 1998; Sullivan et al., 2000; Hickman et al., 2004). In aquatic systems, these predator–prey interactions are mediated through a variety of chemical cues, including alarm cues, diet cues, and kairomones (reviewed by Ferrari et al., 2010). For our purposes, we focus on the detection of chemical kairomones emitted by predators. Chemical kairomones are compounds emitted by one species that can be detected by another species (Brown et al., 1970), and are considered to be complex blends of metabolic wastes and hormones (Mathis et al., 2003). These substances are known to elicit an antipredator response in many aquatic amphibians (Mathis et al., 2003; Epp and Gabor, 2008; Davis et al., 2012).

Central Texas, USA, is home to a diverse group of salamanders in the genus *Eurycea* (Chippindale et al., 2000). These salamanders are neotenic and fully aquatic, inhabiting spring and karst environments along and throughout the Edwards Plateau. The Barton Springs Salamander, *Eurycea sosorum*, is a federally endangered, International Union for Conservation of Nature Red List species, endemic to Barton Springs, Travis County, Texas (Chippindale et al., 1993; IUCN, 2013). Labay et al. (2011) found that Western Mosquitofish (*Gambusia affinis*), Redbreast Sunfish (*Lepomis auritus*), and Largemouth Bass (*Micropterus salmoides*) were among the most widespread fish species present in the Barton Creek watershed and that *L. auritus* and *G. affinis* were also the most abundant across sampled locations. Both *G. affinis* and *M. salmoides* are native to Barton Creek whereas *L. auritus* was likely introduced in the early 1950s. Studies examining the diets of *L. auritus* and *M. salmoides* suggest that both are generalists, often consuming aquatic invertebrates and small fish (Cooner and Bayne, 1982; Matthews et al., 1992). Even

though potential predation pressure is high, little is known about the predator–prey interactions of *E. sosorum*.

Here we propose to examine the antipredator response of *E. sosorum* to chemical kairomones of native and introduced predatory fish. We tested the antipredator response of salamanders to two native species, *G. affinis* and *M. salmoides* (Jordan and Gilbert, 1886), and an introduced species, *L. auritus*. *Gambusia affinis* is a small native fish that is not large enough to consume adult salamanders; however, *G. affinis* is known to consume amphibian larvae and eggs (Grubb, 1972; Gamradt and Kats, 1996; Baber and Babbitt, 2004; Zeiber et al., 2008) and thus may only represent a threat to immature salamanders. Both *M. salmoides* and *L. auritus* are benthic and limnetic foragers that have been observed feeding on *Eurycea* (Tupa and Davis, 1976; Epp and Gabor, 2008), and allow for a comparison of antipredator behavior in response to native and introduced predators. Examining the differential response to these potential predators might help inform future management decisions. Additionally, by testing the response of predator-naïve (captive-hatched) individuals, we can assess whether these salamanders demonstrate innate or learned predator recognition.

Materials and Methods
Experimental Protocol

We used adult, predator-naïve (captive-hatched) *E. sosorum* from the San Marcos Aquatic Resources Center, San Marcos, Texas. These salamanders were hatched from eggs produced by wild-caught adults from Eliza Spring, Travis County, Texas (30.26428°N, 97.77014°W; datum = WGS84). Through the use of predator-naïve salamanders, we avoided confounding effects of learning from experienced individuals (Epp and Gabor, 2008). 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*) ad libitum.

We tested salamanders individually in 9.5-L glass aquaria (covered on three sides to

minimize visual distraction) containing 4.5 L of well water. We conducted tests during peak activity times for *E. sosorum*, beginning 2 h after sunset and lasting for up to 4 h. We used low-level red lighting (25 W) during observations. After we placed salamanders into the testing aquaria, we allowed individuals to acclimate for 20 min. Once acclimated, we recorded the amount of time spent moving for 8 min. Active behavior included swimming or walking, but did not include buccal pumping or gill movement that was not accompanied by other movements of the body. These data constitute the baseline (prestimulus) activity level for each individual. Afterwards, we exposed each individual to 50 mL of water containing chemical stimuli from one of the following treatments: (1) native Western Mosquitofish (*G. affinis*; $n = 19$), (2) introduced Redbreast Sunfish (*L. auritus*; $n = 19$), (3) native Largemouth Bass (*M. salmoides*; $n = 19$), or (4) only water (a blank control; $n = 19$). We randomized the order of treatments and coded them to control for observer bias. We injected chemical stimuli at a rate of 2 mL/s into the aquarium through a plastic tube attached to the center of one side of the testing chamber. We placed the end of the introduction tube approximately 2 cm below the surface of the water to reduce disturbance during treatment introduction. After introduction of the stimulus, we observed and recorded the activity level of the salamander for another 8 min as an indication of potential antipredator response (poststimulus). We exposed each individual to a single treatment to eliminate any effects of habituation to stimuli. Following completion of each trial, we recorded the sex and snout–vent length (SVL; distance from the tip of the snout to the anterior edge of the vent) for each individual, and we washed all equipment with 3% hydrogen peroxide solution to remove any remaining chemical stimuli.

In a second study to test whether salamanders exhibited an antipredator response to all fish, we exposed adult, captive-hatched *E. sosorum* to one of two treatments: (1) a small, nonnative Guppies (*P. reticulata*; $n = 20$), or (2) only water (a blank control; $n = 20$). We used identical methods for both the initial and follow-up studies. Although both *G. affinis*

and *P. reticulata* are small, live-bearing fish, the latter are not known to prey on amphibian eggs or larvae.

Stimulus Acquisition

We collected adult *L. auritus* ($n = 2$) and *M. salmoides* ($n = 2$) from Spring Lake, Hays County, Texas (29.89321°N, 97.93148°W; datum = WGS84) and *G. affinis* ($n = 35$) from the Blanco River, Hays County, Texas (29.91297°N, 97.89938°W; datum = WGS84). For the follow-up study, we used captive-raised *P. reticulata* ($n = 16$) from Texas State University. To minimize the effects of prior diet, we fed the fish a neutral diet of earthworms (*L. auritus* and *M. salmoides*) or commercial fish food (*G. affinis* and *P. reticulata*) for 5 d before the collection of chemical cues. We determined the volume of each stimulus animal by displacement. To maintain similar chemical concentrations between treatments, we used approximately 230 mL of dechlorinated tap water per 1 mL of stimulus animal in the cue-collecting chamber. Before acquisition of the stimulus water, we removed animals from the tanks and thoroughly stirred the water. We mixed equal proportions of water from a minimum of two fish before freezing individual 50-mL aliquots. We used dechlorinated tap water for the blank water control treatments. This method has been used successfully in previous studies (Mathis et al., 2003; Epp and Gabor, 2008; Davis et al., 2012).

Statistical Analysis

Analysis of the behavioral data included the calculation of an activity index (poststimulus activity − prestimulus activity). Positive indices indicate increased activity and negative activity indices indicate decreased activity in response to the stimulus. To examine differences among treatments, we performed an analysis of variance (ANOVA) followed by subsequent multiple comparisons (Tukey's HSD; $\alpha = 0.05$). For the second study, we performed a Student's *t*-test ($\alpha = 0.05$) to examine any differences between treatments. All data met the assumptions of parametric analyses (i.e., normality, homoscedasticity, and independence). We conducted statistical
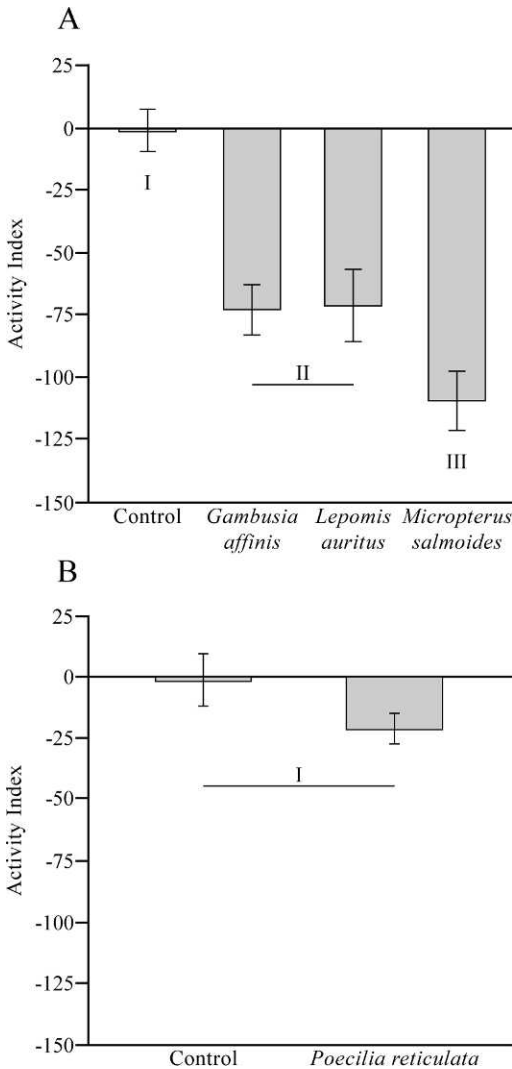
A

B

FIG. 1.—(A) Mean activity indices (±1 SE) of *Eurycea sosorum* in response to four treatments: (1) blank water control, (2) native Western Mosquitofish (*Gambusia affinis*), (3) introduced Redbreast Sunfish (*Lepomis auritus*), and (4) native Largemouth Bass (*Micropterus salmoides*). Numerals indicate groups from Tukey's HSD multiple comparisons ($\alpha = 0.05$). (B) Mean activity indices (±1 SE) of *E. sosorum* in response to two treatments: (1) blank water control, and (2) nonnative, nonpredatory Guppy (*Poecilia reticulata*). The response to each treatment was similar (Student's *t*-test; $\alpha = 0.05$). Activity indices > 0 indicate increased activity and < 0 indicate decreased activity in response to stimuli.

analyses using JMP 9.0 (SAS Institute Inc., Cary, NC, USA) software.

RESULTS

In our initial experiment, there was a significant difference in the activity indices among the four treatments (ANOVA: $F_{3,72} = 20.94$, $P < 0.0001$; Fig. 1A). The mean activity index for the blank water control was greater than that of *G. affinis* (Tukey's HSD: $P < 0.0001$), *L. auritus* ($P < 0.0001$), and *M. salmoides* ($P < 0.0001$). The activity index for *M. salmoides* was lower than the activity index for *G. affinis* ($P = 0.019$) and *L. auritus* ($P = 0.015$). Additionally, the activity index did not differ between *G. affinis* and *L. auritus* ($P = 0.999$). We found no significant difference between the mean activity indices for *P. reticulata* and blank water control treatments ($t_{38} = -1.624$, $P = 0.113$; Fig. 1B).

DISCUSSION

Predator-naïve *E. sosorum* decreased activity (antipredator behavior) in response to chemical stimuli from native Western Mosquitofish (*G. affinis*), introduced Redbreast Sunfish (*L. auritus*), and native Largemouth Bass (*M. salmoides*), but not to nonnative Guppies (*P. reticulata*) or the blank water control. There was no difference between the response of *E. sosorum* to *G. affinis* and *L. auritus*. Additionally, salamanders showed stronger antipredator behavior in response to *M. salmoides* than to both *G. affinis* and *L. auritus*. Because we tested predator-naïve individuals, the antipredator responses to all of the fish treatments indicate that *E. sosorum* innately recognize fish predators through detection of chemical stimuli. Similarly, Epp and Gabor (2008) found that predator-naïve *Eurycea nana* also exhibited innate predator recognition when exposed to chemical stimuli from fish predators.

An alternative hypothesis for why *E. sosorum* showed decreased activity in response to the chemical cues of *G. affinis*, *L. auritus*, and *M. salmoides* is that they were showing a generalized response to all fish rather than a response to specific predatory fish. To evaluate this hypothesis, we tested the response of *E. sosorum* to *P. reticulata*, another small,

gape-limited, nonpredatory fish. We found that chemical stimuli from *P. reticulata* did not elicit antipredator behavior in *E. sosorum*. This supports the hypothesis that the responses to *G. affinis*, *L. auritus*, and *M. salmoides* represent an antipredator response specific to each species instead of a generalized response to all fish species.

The similar response of *E. sosorum* to both *G. affinis* and *L. auritus* is interesting. Although *G. affinis* is not large enough to consume adult *Eurycea*, it is possible that *Gambusia* consume eggs or larval *Eurycea* (Wood, 1953). Previously, Epp and Gabor (2008) tested the response of *E. nana* to *Gambusia geiseri* (a native mosquitofish sympatric with *E. nana*), showing that, in contrast to the blank water control, *E. nana* decreased its activity in response to *G. geiseri*; however, the responses were statistically similar. As with our results, Epp and Gabor (2008) also found that the antipredator responses to *G. geiseri* and *L. auritus* did not differ. Little work has been done on the foraging preferences of *G. geiseri*, so it is unknown whether this species consumes amphibian larvae and eggs (but see Rehage et al., 2005). *Gambusia affinis*, on the other hand, is considered a generalist forager and is known to consume larval amphibians (Gamradt and Kats, 1996; Zeiber et al., 2008), but direct consumption of eggs or larval *E. sosorum* is unknown and warrants investigation. If there is selection on *E. sosorum* as a result of predation pressure by *Gambusia* on larval salamanders, then it is possible that the antipredator response is maintained as an ontogenetic hold over in adults. Additionally, because we tested predator-naïve individuals, it may also be possible that antipredator behavior has not been modified through learning and might represent a stronger response than may be seen in predator-experienced salamanders.

The antipredator response to *M. salmoides* was stronger than the response to the blank water control and the other two fish treatments. The difference between the response to *L. auritus* and *M. salmoides* might indicate that *E. sosorum* is differentiating between low- and high-risk predators. Alternatively, the differences in response might be attributed to differences in coevolutionary histories,

as *L. auritus* is introduced and *M. salmoides* is not. Epp and Gabor (2008) found that predator-experienced (wild-caught) *E. nana* showed a stronger antipredator response to *M. salmoides* as compared to *L. auritus*, and hypothesized that this was caused by either the difference in risk, with *M. salmoides* being a high-risk predator and *L. auritus* being a low-risk predator, or by a shorter coevolutionary history with *L. auritus*. Differential responses to low- and high-risk predators might minimize the costs attributed to responding to predators (Lima and Dill, 1990), but the actual risk of each predator species is still unknown.

The ability of predator-naïve salamanders to recognize an introduced predator, *L. auritus*, might be the result of predator generalization. Ferrari et al. (2007) suggested that prey species might generalize novel predators based on similarities to native predators. Prey species capable of predator generalization might be at a selective advantage over those prey species that are not capable. Within Barton Springs there are several native *Lepomis* (Labay et al., 2011) that might share physiological and ecological traits with *L. auritus*, thus allowing salamanders to generalize their response. Davis et al. (2012) found that *E. nana* generalize among *Lepomis* fish predators and between perciform families (Centrarchidae and Cichlidae). Introduced fish predators have been linked to declines in amphibian populations (reviewed by Kats and Ferrer, 2003), but predator generalization might reduce the negative impacts of introduced predators.

Our assessment of antipredator behavior by predator-naïve *E. sosorum* differs from the results of Gillespie (2011) who found that predator-experienced (wild-caught) *E. sosorum* did not decrease activity in response to chemical stimuli from the same predator, *M. salmoides*. Gillespie (2011) observed antipredator behavior under high-light conditions and attributed the lack of response to chemical stimuli to sensory compensation. Sensory compensation suggests that, in high-light environments, visual systems can override olfactory systems, resulting in decreased responses to chemical stimuli (Roth, 1987). In our study, we tested salamanders in the

dark. Additionally, Gillespie (2011) observed antipredator behaviors in predator-experienced salamanders, and experience is known to influence antipredator behaviors in a congener (Epp and Gabor, 2008). In sum, the differences between what we observed in our results versus Gillespie's (2011) observations are likely caused by our testing at night and using predator-naïve salamanders.

Our results provide useful information for management efforts of *E. sosorum*. Similar to a congener, *E. sosorum* demonstrated innate predator recognition, and because of this no associative conditioning or training to respond to predators is necessary before possible reintroduction of captive individuals. The lack of an antipredator response to *P. reticulata* suggests that antipredator behavior might be specific to individual fish species rather than a generalized response to all fish. The largest population of *E. sosorum* occurs at Eliza Spring, where *G. affinis* are abundant. Interestingly, salamanders responded to *G. affinis,* which suggests that these small fish may represent a greater threat than previously considered. Future studies on the interactions between *Eurycea* and *Gambusia* are needed to elucidate whether the antipredator response is retained from earlier in ontogeny. Because we tested predator-naïve salamanders that have not experienced *G. affinis*, it is possible that they have not had the opportunity to further modify their antipredator response (i.e., decrease it). Additionally, the response of *E. sosorum* to *L. auritus* indicates that this salamander might be capable of predator generalization. Therefore, if further introductions of novel predators into Barton Springs occur, the salamanders might respond appropriately if these species are similar enough to native predators. Overall, our results provide important management implications pertaining to native and introduced predators and indicate that further action is needed to evaluate the immediate impact *Gambusia* may have on *E. sosorum* egg and larval survival.

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