

There must be something in the water: assessing the behavioral responses of rusty crayfish (*Orconectes rusticus*) to fish and amphibian predator kairomones

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Abstract Animals use chemical cues to find food, locate mates, and detect potential predators. Detecting cues in a risky environment can induce behavioral changes to increase survival. Rusty crayfish (*Orconectes rusticus*) reduce activity, increase refuge use, and make defensive displays after detecting fish predator cues. However, no studies have introduced amphibian cues. We investigated crayfish responses to hellbender salamander (*Cryptobranchus alleganiensis*, a dominant predator of crayfish) cues and compared these to responses to largemouth bass (*Micropterus salmoides*) cues. Largemouth bass occur sympatrically with hellbenders and are known to induce distinct responses in rusty crayfish. We randomly assigned crayfish to predator cue and conspecific alarm cue combinations and recorded frozen behavior, appendage movement, locomotion, and refuge use. We found crayfish increased their proportion of time spent frozen and reduced their proportion of time spent active in the tank when exposed to either predator cue. Moreover, these responses were magnified when crayfish were exposed to predator cues in combination with conspecific alarm cues. Our experiment demonstrates evidence in support of the crayfish's ability to detect and appropriately respond to predator cues alone and in combination with conspecific alarm cues. Future work should investigate the effects of these behavioral changes on trophic dynamics in a natural system.

Keywords Hellbender salamander · *Cryptobranchus alleganiensis* · Predator detection · Largemouth bass · *Micropterus salmoides* · Conspecific alarm cue

Introduction

Animals use chemical, visual, and tactile senses to acquire information about their surrounding environment. Chemical cues provide a rich source of information compared to visual or tactile methods, especially in habitats with high levels of complexity, low light, and reduced visibility (Bryer et al. 2001; Ferrari et al. 2010). These cues are used to detect potential predators, find food, and recognize and locate potential mates (Hazlett 1985; Weissburg 2000; Acquista-pace et al. 2004; Kamio and Derby 2017). Semiochemicals, which are defined as chemical cues used for interactions between organisms, are divided into two broad classes: interspecific chemical cues known as kairomones and intraspecific chemical signaling known as conspecific alarm cues (Ferrari et al. 2010; Wyatt 2014). Kairomones are produced from one species and then received by a different species and are often adaptively beneficial to the receiver (Ferrari et al. 2010; Wyatt 2014). For example, kairomones that signal the presence of a predator induce behavioral, morphological, and/or life history changes of prey to reduce their risk of predation (Werner 1986; Hoverman et al. 2005; Brown et al. 2006).

Chemical signaling among conspecifics can include disturbance, defined as the release of chemical information by startled or disturbed prey prior to a predatory attack, or damage-released alarm cues, when an animal releases cues following a predator attack (Ferrari et al. 2010). Conspecific alarm cues are especially important for prey species because prey can acquire detailed information, including predator

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species, predator density, prey species being consumed, and level of risk (Larsson and Dodson 1993; Schoeppner and Relyea 2009). Moreover, these alarm cues warn others of an imminent risk or stressor and can induce behavioral responses that help reduce the probability of predation. For example, avoidance behaviors enable prey to quickly evade detection through crypsis, avoid attacks through escape, diminish capture by seeking shelter, or engage in defensive poses before predators strike (Lima and Dill 1990; Schoeppner and Relyea 2005; Ferrari et al. 2010). When individuals detect conspecific alarm cues in combination with predator kairomones, they often enhance the magnitude of their response as cue combinations indicate a higher degree of threat than either cue alone (Wilson and Lefcort 1993; Bryer et al. 2001; Schoeppner and Relyea 2005). Although the chemical cues may be complex, prey can best assess current and future risks when more detectable information is available (Bryer et al. 2001).

Antipredator responses to chemical cues are common among a diversity of aquatic organisms, including fishes, larval amphibians, and macroinvertebrates (Petranka et al. 1987; Hazlett 1994; Chivers and Smith 1998; Peckarsky et al. 2001). Crayfish can detect chemical cues released by food, predators, and disturbed or injured conspecifics (Blake and Hart 1993; Acquistapace et al. 2004; Breithaupt 2011). In response to predator cues, crayfish reduce activity, increase refuge use, and perform defensive chela displays (Stein and Magnuson 1976; Hamrin 1987; Blake and Hart 1993; Shave et al. 1994). These responses are even stronger among small crayfish, which lack the well-developed claws and carapace for protection against predators present in larger individuals (Clark et al. 2013).

The rusty crayfish (*Orconectes rusticus*) is native to the Ohio River basin, spanning across parts of Ohio, Kentucky, Tennessee, and most of Indiana (Hobbs 1974). Previous work has found that this species of crayfish can detect and respond to kairomones and alarm cues (Garvey et al. 1994; Willman et al. 1994; Hazlett and Schoolmaster 1998). For example, individuals respond to largemouth bass (*Micropterus salmoides*) cues with increased shelter use (Garvey et al. 1994). Moreover, rusty crayfish reduce movement when presented with a combination of predatory snapping turtle (*Chelydra serpentina*) cues and conspecific alarm cues (Hazlett and Schoolmaster 1998). However, no studies have used amphibian cues to elicit behavioral responses in rusty crayfish. Hellbender salamanders (*Cryptobranchus alleganiensis*; also referred to as hellbenders) are unique in that they are a predominant crayfish predator, overlap the native range of rusty crayfish, and occur sympatrically with largemouth bass in Indiana (Petranka 1998; Page and Burr 2011). Previous experiments have found distinct responses of crayfish to largemouth bass cues, which has provided researchers with a positive control for cue detection and behavioral change

(Garvey et al. 1994; Willman et al. 1994; Gherardi et al. 2011). However, no work has investigated crayfish responses to hellbenders or compared crayfish responses between two sympatric predator species.

In the study reported here, we examined and compared the behavioral responses of rusty crayfish to the chemical cues of hellbender salamanders and largemouth bass. Specifically, we investigated if crayfish perceive hellbender chemical cues as a threat, tested whether crayfish responses differ between hellbender and largemouth bass cues, estimated the relative frequency of varying crayfish avoidance behaviors following detection, and compared the type of behavior and magnitude of responses in the presence and absence of conspecific alarm cues. We predicted that crayfish would respond to both hellbender and largemouth bass cues with avoidance behaviors, primarily with reduced activity. However, crayfish would respond more strongly to largemouth bass cues as fish move more frequently through a river system than sedentary hellbenders, and the crayfish may have more experience detecting and responding to their cues. We also predicted crayfish would have heightened responses when predator cues were presented in combination with conspecific alarm cues.

Materials and methods

Using a combination of dipnets, seines, and hand-catching methods, we collected rusty crayfish on October 10 and 11, 2015 from the Blue River in southern Indiana where both predatory species coexist at equally low densities (Carnahan 2001; Burgmeier et al. 2011). We only collected crayfish with carapaces measuring < 25 mm as small crayfish are the most vulnerable to predation, are within the gape limitation of both largemouth bass and hellbenders, and often have stronger responses to predator cues (Clark et al. 2013). The caught crayfish were transported back to the Purdue University Aquaculture Research Laboratory and housed in a 40-gallon holding tank for 3 months prior to start of the trials. Water temperature was maintained at 14 °C, and the crayfish were fed fish food ad libitum.

We used a 2 × 2 factorial design with predator type and alarm cue combinations. Individual crayfish were randomly assigned to one of the following four treatments or control: (1) hellbender cues, (2) largemouth bass cues, (3) hellbender cues and crayfish alarm cues, (4) largemouth bass cues and crayfish alarm cues, or (5) no cues (control). We replicated each treatment 15 times ($n = 75$). The experimental trials were conducted in 3.8-L, flat-bottomed, drum fish bowls (diameter 21 cm, height 22 cm, depth 13 cm) containing 7-cm-long sections of halved 5-cm PVC pipe for refuge (Stauffer and Semlitsch 1993). We separated bowls by cardboard dividers to ensure crayfish could not see one another

during the trial (Hazlett 1994). We filled each bowl with 3 L of tap water and allowed the crayfish placed in the bowl 12 h to acclimate before testing. The bowls were covered with mesh to prevent escape, and each bowl was equipped with an airstone to oxygenate the water (Hazlett 1985).

We used six largemouth bass and six hellbenders to create predator cues. The largemouth bass (average length 20.5 cm) were obtained from Purdue's Aquaculture Research Laboratory where they were being reared for food sale. The captive hellbenders (average length 28 cm) were also being reared at the Purdue Aquaculture facility, but for ecological research. To collect predator kairomones, we housed each predator individually in 5-gallon buckets of water with an airstone for 40 h (Hazlett and Schoolmaster 1998). We never combined cue water among predators so that we could have replicated rather than repeated results on predators. To collect predator and conspecific alarm cues in combination, we presented predators with two crayfish to be eaten during the holding period. If a predator did not ingest all of the crayfish, we crushed both individuals in the water to ensure a mixture of crushed conspecific and predator cues. Crayfish release disturbance alarm cues while in the presence of predators, but we chose to crush crayfish to exaggerate these cues and strengthen any conspecific alarm signals (Hazlett 1985; Breithaupt 2011). We then collected and poured 10 mL of predator or predator/conspecific cue water directly into each of the appropriate treatment bowls. We also added 10 mL of filtered water to control bowls in order to account for changes in water level and disturbance (Acquistapace et al. 2004).

Immediately following the addition of the treatment water we observed, categorized, and recorded the behavior of crayfish at 1-min intervals for 20 min (Petranka et al. 1987). We focused our ethogram on frozen behavior, movement of appendages (i.e., chela, antennules, or fan organs), locomotion around the tank, and refuge use (Hazlett and Schoolmaster 1998). These four behaviors are comparable to those used in previous studies that have found shelter use, level of activity, and aggressive displays to be the most common crayfish responses to predator cues (Stein and Magnuson 1976; Garvey et al. 1994).

All analyses of the data were conducted in program R (3.3.2) and assigned an alpha level of 0.05. Our four behavioral responses were non-normally distributed; therefore, we ran non-parametric analyses. We combined proportion of time frozen, active in the tank, moving appendages, and using refuge as multivariate behavioral responses. These data were analyzed with multivariate analysis of variance (MANOVA; package 'stats') and the influence of predator type, the presence or absence of conspecific alarm cues, and any interactions between variables (predator \times alarm) were studied. We found no significant interaction between predator and alarm cues and

dropped it from our final model ($F = 0.397$, $P = 0.810$). We then conducted univariate ANOVA (package 'stats') for each of the four behaviors. Pairwise Wilcoxon tests (package 'multcompView') with a Bonferroni correction were used to detect significant differences among predator and between prey types. We constructed box and whisker plots and presented the median proportion of time spent exhibiting each behavior.

Results

No hellbenders consumed crayfish during the predator and crayfish cue collection periods, and only two largemouth bass consumed crayfish. Therefore, we crushed two crayfish in all of the hellbenders' containers and crushed crayfish in four of the six bass containers. For multivariate behavioral responses, we found significant differences among the predator treatments (Table 1). Separate, univariate comparisons showed that the proportion of time crayfish spent frozen, active in the tank, and moving appendages were all significantly different among predator treatments (Table 1). Post hoc, pairwise comparisons indicated that the median proportion of time spent frozen was greater for crayfish exposed to hellbender and largemouth bass cues than for control crayfish ($P < 0.001$; Fig. 1). In addition, the median proportion of time active in the tank was comparable among crayfish exposed to hellbender and bass cues, but crayfish exposed to hellbender and bass cues were 63% and 75% less likely to move, respectively, than control crayfish ($P < 0.050$; Fig. 1). The median proportion of time crayfish were moving appendages were similar between the bass cue and control treatments, but crayfish exposed to hellbender cues were 25% less likely to move their appendages ($P = 0.028$; Fig. 1). There were no differences in the median proportion of refuge use between the treatments or compared to the controls.

The presence or absence of alarm cues was found to be a significant predictor for all four behaviors (Table 1). Individual comparisons showed that the median proportion of time crayfish spent displaying frozen behavior and moving around the tank were significantly different when conspecific alarm cues were presented in conjunction with predator kairomones (Table 1). More specifically, the presence of conspecific alarm cues increased the median proportion of time crayfish spent frozen by 475% ($P < 0.001$; Fig. 2). Additionally, conspecific alarm cues significantly decreased the median proportion of time crayfish spent active in the tank by 25% compared to when alarm cues were absent ($P = 0.011$, Fig. 2). Crayfish refuge use and appendage movement were comparable regardless of whether conspecific cues were present (Fig. 2).

Table 1 Multivariate and univariate analysis of variance tests comparing the effects of predator treatments and the presence/absence of conspecific alarm cues on crayfish behavior

Multivariate analysis of variance	<i>df</i>	<i>F</i>	<i>P</i>	
Predator	2, 71	3.76	< 0.001*	
Alarm cue	1, 71	2.73	0.039*	
Univariate analysis of variance	Behavioral response ^a			
	Frozen	Active	Appendages	Refuge
Predator				
<i>F</i> value	14.84	5.46	3.94	0.01
<i>P</i>	< 0.001*	0.006*	0.024*	0.985
Alarm cue				
<i>F</i> value	12.75	4.78	0.36	0.01
<i>P</i>	< 0.001*	0.032*	0.553	0.918

Predator treatments included exposure to largemouth bass (*Micropterus salmoides*) cues, hellbender (*Cryptobranchus alleganiensis*) cues, and no cues

*Significant differences at $P < 0.05$

^aBehavioral responses were measured as the proportion of time spent frozen, active in the tank, moving appendages, or using refuge. Seventy-five rusty crayfish (*Orconectes rusticus*) were tested in November of 2015, without repeated trials

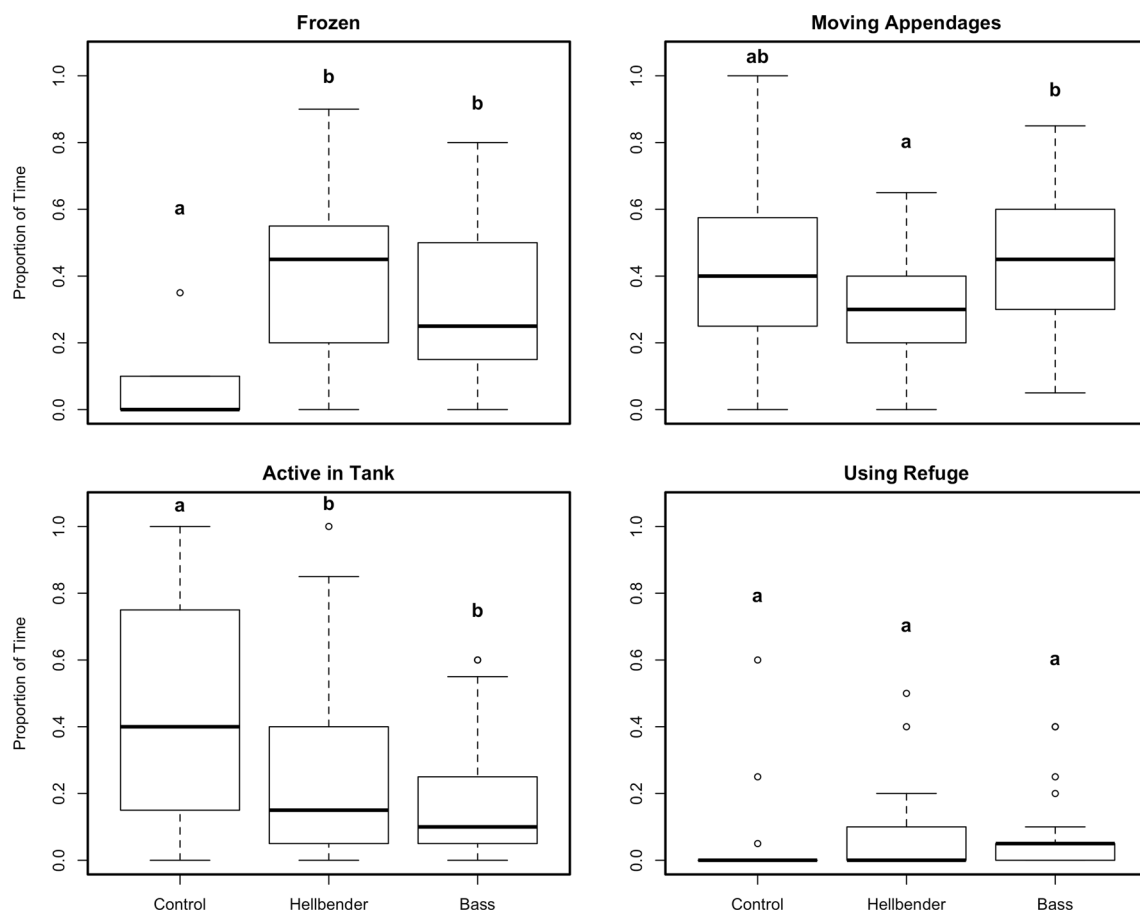


Fig. 1 Pairwise, Wilcoxon test comparisons across predator treatment groups for each of the four, recorded behaviors. Black lines indicate median values with surrounding upper and lower quartiles at

the box edges; white dots mark potential outliers. Lowercase letters indicate significant differences between groups at $P < 0.05$

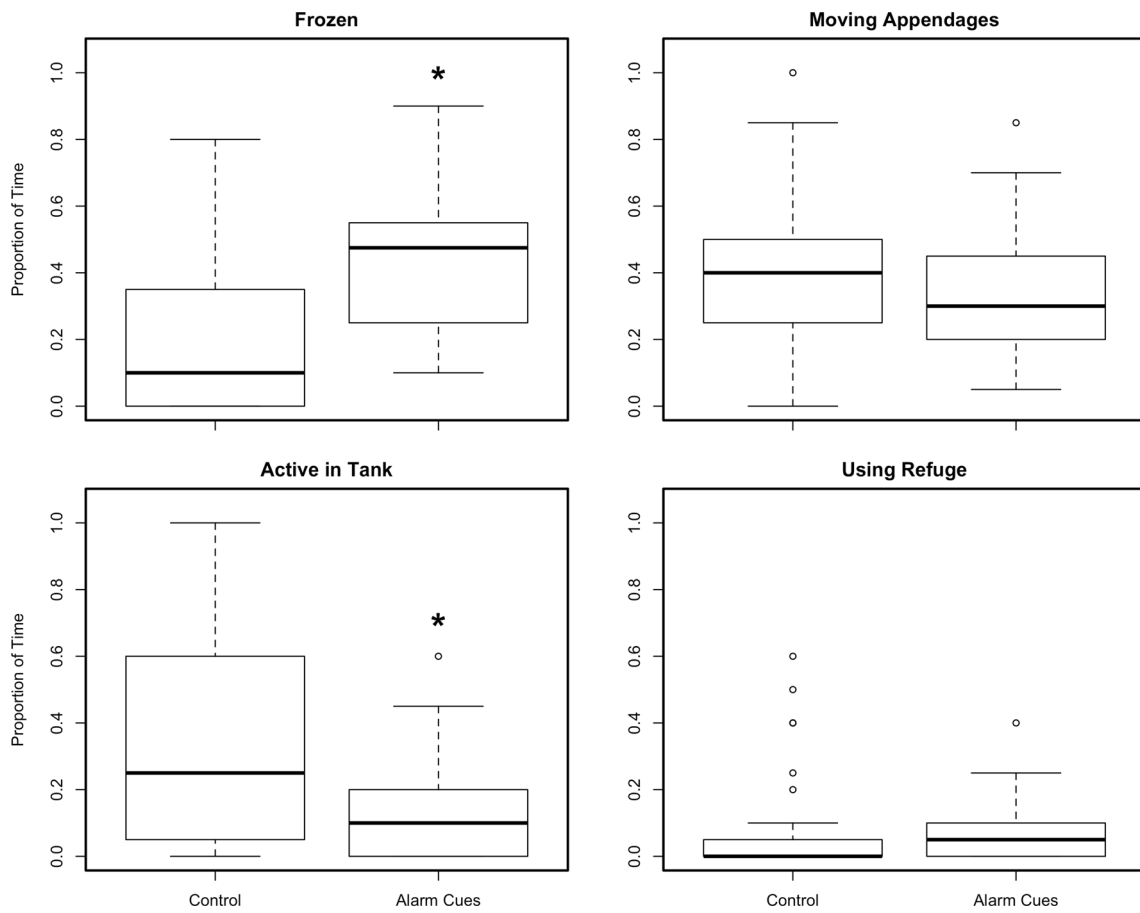


Fig. 2 Wilcoxon test comparisons between control and alarm cue treatments for all four behavioral responses. Black lines indicate median values with surrounding upper and lower quartiles at the box

edges; white dots mark potential outliers. Asterisks denote significant differences between groups at $P < 0.05$

Discussion

The results of this experiment provide evidence in support of two ecological themes: behavioral changes mediated by predator kairomones and heightened responses when predator cues are presented in combination with conspecific alarm cues. Moreover, we report here the first experimental evidence which clearly shows predator-induced avoidance behaviors of rusty crayfish exposed to amphibian cues. Our experiment was limited to 20 min of observation time without measures of weight loss, changes in foraging time, or evidence of stress responses; therefore, we cannot provide evidence for predatory avoidance trade-offs or long-term effects on crayfish individuals or populations. Along this same line, we did not incorporate physical interactions between predators and prey to test the effectiveness of prey defensive behaviors. However, this simplified experiment strongly demonstrates evidence of predator-mediated behaviors in crayfish, indicating the importance of kairomones and conspecific alarm cues in crayfish risk assessment, and can be applied in future work

investigating trait-mediated trophic cascades within river systems (Creed 1994).

We observed crayfish freezing in place and reducing locomotion when exposed to hellbender or largemouth bass cues. Such behavior is common among many other prey species that become more cautious and alter their vigilance, refuge use, or locomotion in an attempt to reduce their risk of predation (Petranka et al. 1987; Sih et al. 1988). In order to avoid predation, prey must be able to recognize the presence of predators and appropriately respond with effective avoidance tactics (Sih et al. 1988; Epp and Gabor 2008). Movement is especially dangerous to prey because it can increase encounter rates with predators and provides opportunity for prey detection (Werner and Anholt 1993). Hellbenders and largemouth bass both rely on a lateral line system to detect stimuli in the water (Nyberg 1971; Bishop 1994). Therefore, decreasing movement is most likely to reduce the crayfish’s likelihood of being detected and is, consequently, an advantageous response.

Crayfish also reduced their appendage movement in response to hellbender cues. Chela movement is often

used in defensive behavior to attack or intimidate predators (Bovbjerg 1953). However, chela movement is likely to be ineffective in deterring hellbender predation because hellbenders are primarily sit-and-wait predators which quickly capture crayfish before they can defend themselves. We did observe greater chela movement in the presence of bass cues, which is similar to the observations by Shave et al. (1994) and led these authors to suspect that chela movement was a way to deter trout. Crayfish are capable of detecting, differentiating, and selectively responding to predatory species; however, chela movement in lobsters and crabs is also used to better assess the aquatic environment (Weissburg 2000, 2011). Crayfish may have increased the use of fan organs, antennae, and chela movement to help move water and better detect, assess, and interpret the chemical information that was available in the fish bowls (Bruski and Dunham 1987; Breithaupt 2001, 2011). We found no difference between chela movement in the bass and control treatments, which makes it difficult to argue that increased chela movement with bass cues was a predator-specific response.

We did not detect any differences in the amount of time crayfish spent in refuge across treatments, and the time they did spend in refuge was far less than the time they spent on the other three behaviors, respectively. This is contrary to observations reported in previous studies where crayfish, including rusty crayfish, were found to commonly increase their shelter use in response to predator cues in order to minimize their chances of being detected (Stein and Magnuson 1976; Blake and Hart 1993; Garvey et al. 1994). Blake and Hart (1993) found that the probability of crayfish seeking shelter and the amount of time under a shelter were positively correlated with the availability of sensory information, such that the behavioral responses of crayfish were most marked when the crayfish could see and smell the predators (Blake and Hart 1993). We did observe our crayfish entering and using our PVC pipe hides; however, if they had been able to view predators they may have responded differently and used shelter objects more frequently. Alternatively, as our experimental tanks were 1.4- to 3.6-fold smaller than those used in previous studies (e.g., Blake and Hart 1993; Willman et al. 1994; Hazlett and Schoolmaster 1998; Acquistapace et al. 2004; Gherardi et al. 2011), the cue-treated water may have been quickly distributed throughout the fish bowl, leaving the refuge areas seemingly unsafe and perhaps deterring crayfish from entering.

The crayfish used in this experiment were not trained with predator cues prior to the experimental trials, and yet these cues still elicited behavioral responses. Our observations suggest that either the crayfish used in the experiments have previously detected and avoided these predatory species in the wild or they have innate responses to predator kairomones; based on our experimental set-up and results we cannot distinguish between the two possibilities. Crayfish,

hellbenders, and largemouth bass reside in habitats that closely overlap in a riverine system, which could facilitate learning. However, cues are continually being moved downstream and diluted in a lotic system and, therefore, crayfish would have to be exceptionally sensitive to predator kairomones. Rusty crayfish collected from lakes where largemouth bass co-occur respond with increased time outside of refuge even though the two species likely use varying habitat types (littoral vs. limnetic zones) and may have limited interactions (Creed 1994; Willman et al. 1994). We housed crayfish in the laboratory for 3 months prior to the trials, which may have been sufficient time for crayfish to regain naïveté, but still the crayfish responded to both largemouth bass and hellbender cues. However, previous experiments showed rusty crayfish only exhibiting behavioral responses to predatory snapping turtles when they were trained with predator cues in conjunction with conspecific alarm cues (Hazlett and Schoolmaster 1998). Nevertheless, the crayfish still detected predators, perceived them to be a threat, and responded cautiously to the combination of predator and conspecific alarm cues regardless of whether the responses were learned or innate.

We observed a stronger response from crayfish when they were provided with predator and conspecific cues in combination. Prey responses are strongly related to predator diet and are magnified when predators are able to attack, eat, and digest prey in the presence of their conspecifics (Schoepner and Relyea 2009; Weissburg et al. 2016). Even though some conspecifics were crushed rather than eaten, we still observed evidence for predator detection, elevated risk, and appropriate avoidance behaviors. Crayfish release alarm cues when they are consumed by a predator, manually crushed, and experiencing stress (Hazlett 1985). These various forms of chemical cues provide reliable information to prey species about their level of risk and allow a more appropriate response to be induced (Chivers and Smith 1998; Gherardi et al. 2011). Moreover, during the cue collection procedure, crayfish likely released disturbance cues from the stress of being housed with a predator, as well as additional cues when they were crushed in the container (Gherardi et al. 2011). This combination of cues may have increased the magnitude of the conspecific chemical cues present and were sufficient to signal danger to other individuals (Smith 1992). Similarly, *Daphnia magna* alter their position in the water column, aggregate into groups and, subsequently, experience lowered predation rates when presented with crushed conspecifics (Pijanowska 1997).

We found crayfish became stationary when exposed to predator cues alone or in combination with conspecific alarm cues. In a natural system, predator-mediated behavior can influence interactions between predators and prey, it but can also affect additional levels within a trophic system (Peacor and Werner 2001; Werner and Peacor 2003).

For example, the time crayfish spend frozen could reduce time spent foraging, which in turn could affect primary production and nutrient cycling (Stein and Magnuson 1976; Creed 1994). Predator-induced changes are examples of trait-mediated indirect effects, which occur when one species indirectly influences a third species by altering the behavior of a second. These indirect, behavioral changes are speculated to be as important, if not more so, than direct consumptive effects (Grabowski and Kimbro 2005).

Crayfish have been identified as keystone consumers in natural systems because they regulate periphyton growth and alter the distribution of lower trophic macroinvertebrates (Creed 1994). However, hellbenders are termed keystone species because they regulate crayfish populations and maintain equilibrium among freshwater communities and food-web dynamics (Paine 1980). Therefore, the interactions of these two species could have pivotal effects on the ecosystem. Previous surveys have found that intermediate densities of crayfish enhance periphyton productivity through grazing. However, high, unregulated densities cause overgrazing which, in turn, reduces primary production (Stein and Magnuson 1976). Unfortunately, hellbenders have experienced precipitous declines over the past few decades, which could leave crayfish abundance and grazing intensity unchecked (Wheeler et al. 2003). Yager et al. (unpublished results) verified that rivers with declining hellbender populations have elevated crayfish densities compared to rivers that support healthy populations of the former. However, it is currently unknown how hellbender extirpation could affect primary production, trophic stability, and ecosystem health as no research has verified the strength of hellbender interactions in riverine food webs. Our data provide evidence of altered crayfish behavior in the presence of hellbender cues. Furthermore, this project provides important insight into the predator-induced behavioral changes that could indirectly have top-down effects on a natural system. If crayfish become more active in the absence of hellbenders, they have the opportunity to increase foraging and mating opportunities, and there may be cascading effects on the river system. Future work should investigate the potential for trophic cascades and the importance of predator-mediated behavioral change in riverine systems.

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

Informed consent For this type of study formal consent is not required.

Ethical approval This article does not contain any studies with human participants performed by any of the authors. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted; PACUC #1406001094314.

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