Fine-tuned responses to chemical landscapes: crayfish use predator odors to assess threats based on relative size ratios

Tyler C. Wood1,2 and Paul A. Moore1,2,3,

1Laboratory for Sensory Ecology, Department of Biological Sciences, Bowling Green State University, Bowling Green, Ohio 43402 USA
2University of Michigan Biological Station, 9133 Biological Road, Pellston, Michigan 49769 USA
3J.P. Scott Center for Neuroscience, Mind, and Behavior, Bowling Green State University, Bowling Green, Ohio 43402 USA

Citation: Wood, T. C., and P. A. Moore. 2020. Fine-tuned responses to chemical landscapes: crayfish use predator odors to assess threats based on relative size ratios. Ecosphere 11(9):e03188. 10.1002/ecs2.3188

Abstract. The threat-sensitive predator avoidance hypothesis suggests that prey animals should minimize the costs of antipredator behaviors by only responding to predators that pose a potentially lethal threat. Thus, prey must use risk assessment strategies to determine which predators present a great enough threat to merit a response. A rich literature demonstrates that chemical signals can communicate information about predator identity, diet, and size. However, the relationship between predator size and prey size has been largely overlooked. What remains unknown is how prey respond to odors from predators along a continuum of relative size. Here, we tested the responses of crayfish (prey) to odor cues from two species of predatory fish along a gradient of relative size relationships. Crayfish and fish were paired according to crayfish carapace width and the fish's gape width to represent different relative size pairings. Foraging and shelter use video assays were used to evaluate changes in crayfish behavior under the different levels of threat presented. The analysis revealed significant increases in macrophyte consumption, foraging effort, and overall activity among crayfish that were small relative to their predators, independent of the absolute size of fish or crayfish size. Crayfish that were small relative to predator size showed significantly less shelter use than crayfish that were large relative to predator gape size. The results demonstrate that the crayfish are assessing threat based on their size relative to the predator gape size solely using chemical signals. As a result of this assessment, crayfish are changing their resource use to potentially grow larger to limit future predatory threats. Overall, this research supports the threat-sensitive predator avoidance hypothesis and provides an opportunity to refine the landscape of fear concept to accommodate more detailed risk assessments by prey.

Key words: crayfish; gape ratio; Largemouth Bass; predator odor; Rainbow Trout; threat sensitive.

INTRODUCTION

Prey animals extract relevant information about predatory threats from the sensory landscape within their environment (Lima and Dill 1990, Wisenden 2000). This information is contained in a variety of sensory cues that are dispersed in a spatially and temporally heterogeneous fashion throughout their habitat (Brown et al. 1999, Laundré et al. 2001). The distribution of these sensory cues is a result of the movement of the predator and the physical processes that serve to move stimuli through habitats (Smee and Weissburg 2006). As a result of the detection of these stimuli, prey respond by altering their physiology, behavior, morphology, or life history (Lima and Dill...
1990). The information prey use to assess the level of threat posed by a predator includes factors beyond predator presence or absence like predator diet and size cues (Bishop and Brown 1992, Chivers and Mirza 2001, Henry et al. 2010).

Prey that can respond to gradients of risk are able to fine-tune their responses to only include predators that pose a potentially lethal threat. Since predator–prey encounters occur along a continuum of relative size, prey should only respond to predators that are potentially lethal, especially when predators have morphological features that limit the sizes of prey they can capture and consume. Hill et al. (2004) found that predatory fish like Largemouth Bass (Micropterus salmoides) and Peacock Cichlids (Cichla ocellaris) prefer prey that are smaller than 96% of their gape width. However, prey that are large enough to exceed the capture limits of the predator do not need to deploy their defensive mechanisms. In fact, both small Brook Sticklebacks (Culaea inconstans) and small Swordtails (Xiphophorus helleri) will alter their behavior in the presence of a predator, but large fish of either species do not modify their behavior for predators of the same size (Abrahams 1995, Di Sciullo and Basolo 2019).

However, we do not know whether prey animals are able to estimate the threat posed by a gape-limited predator relative to their own body size. The ability to identify and respond to threatening predators while ignoring those that do not pose a threat reduces the chance of unnecessary and costly antipredator responses in prey (Kats and Dill 1998).

Antipredator responses require that prey trade off time they could use to forage or find mates in favor of vigilance behaviors or maneuvers to avoid predator encounters (Laundré et al. 2001). Prey also expend energy resources to escape predators and through the development of defenses (Lima 1998). The benefits of safety lead to costs for prey including reduced growth or reproductive output and missed opportunities to access resources (Preisser and Bolnick 2008). Morphological defenses are costly to produce and maintain (Steiner and Pfeiffer 2006). In crucian carp (Carassius carassius), a shallow stream-lined body is the normal phenotype, while a deep body morphology confers a defense against gape-limited pike (Esox Lucius; Brönnmark and Miner 1992). However, under conditions of limited food availability, deep-bodied carp only gain half as much mass over time as their shallow-bodied competitors (Pettersson and Brönnmark 1997). Behavioral responses to predators are also costly for prey. Daphnia exposed to fish odors use diel vertical migration to avoid predation. However, migrating Daphnia only grow a third as much as non-migrating populations that are not exposed to fish odors (Dawidowicz and Loose 1992). Foraging activity is also frequently traded for increased vigilance to improve awareness of potential threats. Increased vigilance is known to reduce the feeding efficiencies of house sparrows (Passer domesticus), mallards (Anas platyrhynchos), and African ungulates among other species (Studd et al. 1983, Illius and Fitzgibbon 1994, Fritz et al. 2002).

Thus, animals should use costly defensive strategies only when the benefits of survival outweigh the costs of lost foraging or mating opportunities.

Temporal variation in cue availability arises from the activity patterns of predators (Palmer et al. 2017) and the persistence of cues (especially of odors) in the environment (Turner and Montgomery 2003). Some prey animals respond to temporal variation in predator cues by seeking shelter when the perceived risk of predation is high; meanwhile, prey take advantage of periods of relative safety to forage and be active (Lima and Bednekoff 1999). Under the risk allocation hypothesis, perceived risk is highest when the predator is present and able to hunt effectively. However, for most predators, there are times when the predator’s hunting effectiveness or activity is reduced in which prey can afford to take risks to access resources. Prey that use information extracted from predator odors can make detailed assessments of temporally dynamic predation risk.

Several characteristics of odor cues make them useful in risk assessments. Olfactory cues persist in the environment for extended periods of time and offer detailed predator information long after the predator has moved off (Dusenbery 1992, Bradbury and Vehrencamp 1998). Variation in the mixture of chemicals in an odor cue can communicate information beyond predator presence (Wyatt 2010). For example, snails (Physella gyrina) can differentiate between predator species like sunfish (Lepomis gibbosus) and crayfish.
(Faxonius rusticus) using only odor cues (Turner et al. 1999). Predators of different sizes also smell different and larger predators are perceived as more threatening than small ones (Chivers et al. 2001). Cue concentration can also be an indicator of predator size (Hill and Weissburg 2014). Each of these types of predator information represents a gradient of threat posed by the predators that left them behind. Although many robust experiments have evaluated threat-specific responses in a variety of prey animals, few studies have considered the relationship that exists between gradients of prey size and predator size communicated through odor cues.

Therefore, we studied the effects of odor cues from two species of gape-limited predatory fishes on the macrophyte consumption, foraging behavior, shelter use, and activity of crayfish along a gradient of relative size relationships defined by fish gape width and crayfish carapace width. Largemouth Bass were chosen because they are a gape-limited predatory fish that occurs throughout much of North America and across the world via introductions for recreational fishing. Rainbow Trout (Oncorhynchus mykiss) were chosen as the second predatory fish species because their gape widths are smaller when compared to bass of the same total length. Using two different predatory fish species with different gape to total length ratios allowed us to eliminate the size of the predator as the only factor influencing the crayfish’s behavior. Rusty crayfish (F. rusticus) were selected as prey because they live throughout the bass's native range and are a preferred food for bass. Trout also consume crayfish, but the native ranges of O. mykiss and F. rusticus do not overlap. Crayfish range widely in size and grow in a stepwise manner by molting several times per year. Since crayfish often live in highly turbid flowing water or in the dark depths of lakes, they rely primarily on their extraordinary chemical sensitivity to detect predators. Under conditions where visual cues are unavailable, crayfish may be able to extract predator size information from olfactory cues to contrast with an estimate of their own size to determine the level of threat.

Previous studies of crayfish responses to bass odors found that crayfish increase their macrophyte consumption and nocturnal foraging effort under threat. This counterintuitive result could be driven by crayfish increasing their foraging activity at night to avoid exposure to diurnal predators (Lima and Bednekoff 1999). Crayfish exposed to bass odors consumed more biomass of Elodea canadensis and Chara spp. than crayfish that were not exposed (Wood et al. 2018). The predator exposed crayfish also increased the time that they spent foraging and reduced the time they spent in shelter. In a second experiment, crayfish were exposed to odors from bass of different sizes that were fed four different diets consisting of fish food pellets and three types of crayfish (Wood and Moore 2020). The responses of crayfish to the relative predator size gradient were dependent upon the predator’s diet. Overall, the combination of dietary cues and relative predator size significantly altered the macrophyte consumption, foraging effort, and shelter use behaviors of the exposed crayfish. Based on these prior results, we expected to find similar increases in macrophyte consumption and time spent foraging by the crayfish when predators are large relative to the size of the prey.

**Methods**

**Collection and housing of animals**

One hundred form II (non-reproductive) female rusty crayfish (F. rusticus) were captured from Maple Bay of Burt Lake in Cheboygan County, Michigan, USA (45.4873° N, 84.7065° W). The crayfish used had all their appendages intact. All F. rusticus were stored in a flow-through steel cattle tank (200 × 60 × 60 cm; l × w × d). Unfiltered water from the East Branch of the Maple River flowed into the tank from a PVC delivery pipe and exited the tank via a standpipe which kept the water depth at approximately 60 cm. Crayfish fed on natural detritus that was contained within the river water. Shelters made from clay pot halves were available in the storage tank. The post-orbital carapace length and maximum carapace width of each crayfish were measured to the nearest 0.5 mm before use in a trial. Crayfish were marked with a one square centimeter white patch on their carapace before each trial using a non-toxic correction pen (BIC Wite-Out 2 in 1 Correction Fluid, Shelton, Connecticut, USA) to improve visibility for tracking in video recordings. The behavior of crayfish is not altered by
the presence of Wite-Out application (Fero and Moore 2008, Martin and Moore 2008, Jurcak and Moore 2018). Each crayfish, used only once, was frozen after a successful trial (due to the non-native status of F. rusticus in Michigan).

Sixty Largemouth Bass (M. salmoides) and 60 Rainbow Trout (O. mykiss) served as sources of predatory fish odors. The fish were purchased from Harrietta Hills Trout Farm, Harrietta Michigan, USA. Thirty bass and 30 trout were stored singly in a large flow-through flume (1600 × 100 × 32 cm; 1 × w × d) constructed from cinderblocks and lined with plastic sheeting. The flume was filled with a mixture of water from the Maple River and well water. The addition of well water cooled the river water to approximately 11°C which was suitable for both bass and trout. Hardware cloth barricades divided the flume into 60 equal sections to provide each fish with its own space (25 × 100 × 32 cm; 1 × w × d). The large flume was covered with orange plastic snow fencing to filter the sunlight and provide protection from avian predators. Before being loaded into the flume, each fish was measured for total length to 0.1 mm, total weight, and the nearest millimeter on a scale. The prior width of each fish was recorded as an assessment of gape width (Lawrence 1958).

River water ran through steel cattle tanks (one for bass and one for trout: 200 × 60 × 60 cm; 1 × w × d each) were filled with 640 L of water from the East branch Maple River (for bass) and well water (for trout). The trout were kept in well water to reduce the temperature of their holding water. River water ranged from 12°C to 24°C, and well water was 9°C. The tanks were covered with 1 × 1 mm fiberglass mesh to protect the fish from avian predators, diffuse sunlight, and to filter the water to prevent the introduction of crayfish or other large invertebrates. The fish in the storage tanks were fed a diet of commercial fish food pellets (Sportsman’s Choice Trophy Fish Feed High Protein Multi-Species Fish Formula, Longs, South Carolina, USA).

**Diet production**

The F. rusticus crayfish used for food were frozen and then pulverized in a coffee grinder (Hamilton Beach, Model 80335R, Glen Allen, Virginia, USA) to produce a slurry. Pellets were made by freezing 0.5-mL portions of crayfish slurry. Each fish was fed a single pellet once per day. The fish were fed crayfish pellets in the holding flume for at least 48 h before use in any trials to flush any previous dietary cues from their system (Beattie and Moore 2018). Fish were never fed in the experimental mesocosms or during trials.

**Plant collection and storage**

Samples of American waterweed (E. canadensis), muskgrass (Chara spp.), and northern watermilfoil (Myriophyllum exalbescens) were collected from North Fishtail Bay of Douglas Lake, in Cheboygan County, Michigan, USA (45.5618° N, 84.6762° W). A macrophyte sampling rake was cast into mats of submerged vegetation to collect the aquatic plants. The macrophyte species used were selected because their secondary metabolic contents and handling characteristics create a gradient of preference among crayfish (Lodge 1991, Cronin et al. 2002, Wood et al. 2018). Chara spp. is generally preferred by crayfish because of its fine texture, low buoyancy, and lack of noxious secondary metabolites. E. canadensis is more buoyant than Chara spp. and has slightly higher phenolic content. M. exalbescens should be the least preferred because it is buoyant enough to float and contains more secondary metabolic compounds (Wood et al. 2018). Previous studies have shown that crayfish choose macrophytes based primarily on their lack of chemical and structural defenses, not based on nutritional value (Bolser et al. 1998). The collected macrophytes were stored in three flow-through streams filled with water from the East branch of the Maple River. The plant storage streams were
lined with sand and located in open sunlight to mimic their natural environment. A surplus of plant samples was maintained from 18 June 2019 until all trials were complete on 12 August 2019.

**Experimental design**

Crayfish and fish were size-matched for each trial using the ratio between the crayfish’s carapace width and the fish’s gape width. To calculate the gape ratio, the carapace widths of the crayfish in a trial were divided by the gape width of the predator present in the trial. The influence of gape ratio was tested along a continuous gradient which ranged from 0.57 to 1.88. Crayfish ranged in carapace width from 0.90 to 2.40 cm. The gape width ranges of the bass (1.40–2.35 cm) and trout (1.15–1.75 cm) were different. The total length (distance from snout to tip of caudal fin with fin squeezed together) ranges were nearly identical for bass (16.8–23.1 cm) and trout (16.1–23.1 cm). A total of 90 trials were run consisting of 45 with bass and 45 with trout odor cues. Trials that were impacted by crayfish, escapes, molting, immigration, or deaths were discarded (19 trials were discarded).

**Experimental mesocosms**

Cinderblocks were used to frame eight flow-through stream mesocosms (160 × 40 × 24 cm; 1 × w × d) which were lined with 0.1 mm thick plastic sheeting (Fig. 1A). Each mesocosm had two sections. The predator section of each mesocosm measured 80 × 40 × 24 cm (1 × w × d), and the crayfish sections were the same size. The crayfish sections were lined with sand substrate which accumulated fine detrital material and provided a dark background against which the crayfish could be easily observed in video recordings. This same construction technique has been used successfully in previous experiments (Ludington and Moore 2017, Neal and Moore 2017, Wood et al. 2018). A pair of 208-l plastic drums served as constant head tanks for the eight mesocosms and were filled with water from the Maple River. The Maple River is part of a watershed that contains populations of both *M. salmoides* and *O. mykiss*. Each plastic drum fed four mesocosms with water from one 10 mm diameter garden hose per mesocosm (flow rate = 0.086 ± 0.003 l/s [mean ± SEM]). Water flowed into the upstream predator section of each mesocosm before overflowing through a screened opening (28 × 12 cm opening with 1 × 1 mm screening) in a partial wall into the downstream crayfish section. The water overflowing through the screened opening did not exceed 5 mm in depth, which is inadequate for crayfish to see into the predator section of the arena. The water would then exit from the downstream end of the mesocosm through another screened opening. A single PVC half-pipe shelter (10 × 8.5 × 4 cm; 1 × w × h) was placed near the down current end of the crayfish section.

A wooden frame held an infrared DVR camera (Zosi ZR08ZN10, Zhongshan City, Guongdon Province, China) 1.5 m above the water’s surface of each mesocosm to record the crayfish’s nocturnal behaviors. One low-intensity red light bulb (Great Value, Model A19045 LED Lamp, 9 W, 145 mA, 120 V, 60 Hz, RED) was used to illuminate each mesocosm from above. An awning made from a black utility tarp (9 × 6 m) covered all eight mesocosms to prevent weather and water damage to the electrical equipment. The awning also eliminated glare from moonlight and starlight from the recordings. Sunlight could enter the system through 1.5-m openings on the eastern and western ends of the mesocosms. Water flow through the mesocosms was slow enough that it did not produce any visible surface distortion in the video recordings.

**Experimental protocol**

Trials began 1 July 2019 and were concluded on 12 August 2019. Each trial was run for 24 hours. A trial cycle began at 08:30 with selection of plant samples from the plant storage streams. Single stems of each macrophyte species (weighing approximately 1 g) were selected for each trial. Excess surface water was removed from plant samples using a salad spinner (Farberware Basics, Item No. 5158683, Fairfiel, California, USA) before weighing to the nearest 0.001 g. The plant stems were then attached to glass rods (255 × 6 mm; 1 × OD) with 26-gauge green painted floral wire. The loaded rods were placed into a hardware cloth bracket (24 × 19 cm; 1 × w) which held the plant samples in position during the feeding trial (Fig. 1B). The arrangement of the three plant stems was rotated on the brackets across trials to prevent any selection bias caused by the location of plant samples.
in the mesocosm. After the plant samples were placed into the crayfish sections of the mesocosms, a single *F. rusticus* crayfish was selected for each stream. A single fish was placed into the predator section of each mesocosm at 11:00 each morning. After addition of the fish, the screened openings between the predator and crayfish section and at the outflow from the crayfish section were brushed to remove any debris that might inhibit water/odor flow.

Beginning at 23:00, an automatic light timer would activate the red lights illuminating the mesocosms. At 00:00, the cameras above each mesocosm would start recording the nocturnal behaviors of the crayfish. The cameras shut down at 04:00 when behavioral recordings were complete. All crayfish were removed from the mesocosms first on the following morning. The plant samples were then removed from each mesocosm and were surface dried in the salad spinner again before weighing a second time. After use in a trial, fish were replaced into their species-specific stock tanks. Once a trial cycle was complete, the mesocosms were flushed overnight (at least 12 h) before a new trial cycle began the following morning. The water in the mesocosms would be replaced approximately 24 times during the flush period.

**Data collection**

A viewer blind to treatment scored four hours of video per trial for the total time spent by each crayfish in the foraging and shelter zones of the mesocosm. Because the feeding appendages of crayfish are located on the underside of their bodies, it was not possible to determine when the crayfish were actually feeding. Thus, whenever the entire marker on the carapace was inside the foraging zone of the mesocosm, crayfish were scored as foraging (Fig. 1A). Similarly, crayfish were scored as using shelter whenever the entire marker on the animal’s carapace was within the shelter zone (Fig. 1A).

Foraging effort was calculated by dividing the time (s) that crayfish spent in the foraging zone of the mesocosm by 14,400 s (4 h in seconds); then, the quotient was multiplied by 100. The resulting percentage represents the percent of the four-hour video recording that was spent foraging. Shelter use was calculated the same way.
using time (s) spent in shelter as the numerator. The movements of crayfish into and out of the two resource zones were recorded as the number of transitions and used as a proxy for overall activity.

Consumption of *M. exalbescens* (g) was calculated by subtracting the mass of *M. exalbescens* remaining after the trial from the initial mass of *M. exalbescens* before the trial. The resulting difference was then divided by the initial mass *M. exalbescens* and multiplied by 100 to obtain the percent of *M. exalbescens* biomass that was either consumed or destroyed by the crayfishes' foraging activity, which we defined as *M. exalbescens* consumption.

Macrophyte consumption

\[
\text{Macrophyte consumption} = \left( \frac{(M_i - M_f)}{M_i} \right) \times 100
\]

This calculation was repeated for *E. canadensis* and *Chara* spp. as well to obtain the proportions of each of these species that were consumed. Since the plants are offered to the crayfish in approximately equal masses and at the same time, variation in consumption of each macrophyte species is a useful measure of choice under different threat conditions (Chambers et al. 1990, Lodge 1991). The goal of these measures is to assess the influence of foraging choices on the macrophyte community. Macrophyte consumption was not normalized against crayfish biomass, in alignment with the convention in this field (Feminella and Resh 1989, Cronin et al. 2002).

**Ethical approval**

Largemouth Bass were maintained and handled following established animal care and use procedures. The use of vertebrate animals was approved by the Institutional Care and Use Committee at University of Michigan (Protocol: PRO00008892).

**Relative size analysis**

Carapace widths of the crayfish were plotted against the gape widths of the fish used in each trial to check for possible trends as a result of the pairing fish and crayfish across a relative size gradient (Fig. 2). A linear model was run on the data using the lm function in the statistical program R to verify that there was no relationship between the crayfish carapace widths and the gape widths of each fish species (R Core Team 2019). Across all statistical tests, *P* values are significant at an alpha value of 0.05. No significant relationship was detected between crayfish carapace width and fish gape width (*F*<sub>1,68</sub> = 0.298, *P* = 0.587; Fig. 2) in the data. Due to the lack of a relationship between these two measures, further analysis is focused on gape ratio as the driving factor for the results.

The total lengths of the fish and gape ratios were not different between trials using bass and trout (*F*<sub>2,69</sub> = 2.579, *P* = 0.083; Fig. 3).

**Macrophyte consumption analysis**

The consumption of each macrophyte species was assessed using a linear mixed-effects model.
Fig. 3. Total lengths and gape ratios of fish used for odor generation. Boxes with red shading represent fish total lengths. Blue shading represents gape ratios. White filled circles indicate individual trials. Total length of the fish is measured as the distance from the end of the snout to the tip of the caudal fin with the caudal fin depressed. Gape ratio is equal to crayfish carapace width divided by the gape width of the fish in the trial. The bold lines indicate medians. The box indicates the interquartile range between the first quartile (bottom of box) and the third quartile (top of box). Whiskers indicate the overall ranges tested.

Comparison of gape ratio and total length models

It is possible that any behavioral or foraging changes could be a result of an increase in total chemical stimulus by using larger animals within a trial. To test for a simple size effect on the results, a second series of linear mixed-effects models were constructed using the same procedure described above which replaced gape ratio with predator total length. The Akaike information criterion was used to determine whether the linear mixed-effects models incorporating gape ratio or total length were better fit to each of the crayfish response variables.

RESULTS

Macrophyte consumption by crayfish

Crayfish significantly decreased their consumption of *M. exalbescens* as gape ratio increased ($F_{1,58.51} = 15.441, P < 0.001$; Table 1, Fig. 4A). Fish species had a marginally significant effect on *M. exalbescens* consumption ($F_{1,58.63} = 3.411, P = 0.070$). The interaction between gape ratio and fish species had a marginally significant effect on *M. exalbescens* consumption ($F_{1,59.09} = 3.731, P = 0.058$).

Crayfish consumption of *Chara* spp. was influenced significantly by gape ratio ($F_{1,64} = 7.100, P = 0.010$; Table 1, Fig. 4B). As gape ratio increased, the amount of *Chara* spp. consumed decreased. Fish species had no effect on *Chara* spp. consumption ($F_{1,64} = 0.666, P = 0.418$). There was no significant effect of the interaction between gape ratio and fish species on *Chara* spp. consumption ($F_{1,64} = 0.288, P = 0.593$).

The consumption of *E. canadensis* by crayfish was not significantly influenced by fish species or the gape ratio between prey body size and predator gape width.

Crayfish behavioral responses

The crayfish spent significantly less time foraging as gape ratio increased ($F_{1,64} = 18.334, P < 0.001$; Table 1, Fig. 5A). The species of fish did not influence foraging time ($F_{1,64} = 1.155$,
There was no interaction effect of gape ratio and fish species on the time crayfish spent foraging ($F_{1,64} = 0.522, P = 0.473$). The time crayfish spent in shelter increased significantly as gape ratio increased ($F_{1, 60.21} = 18.002, P < 0.001$; Table 1, Fig. 5B). There was no effect of fish species on shelter time ($F_{1, 60.59} = 0.068, P = 0.795$). Gape ratio and fish species did not have an interacting effect on the number of transitions made by the crayfish across the resource zone boundaries ($F_{1, 61.30} = 0.383, P = 0.538$).

The crayfish moved across the resource zone boundaries fewer times as gape ratio increased ($F_{1, 60.35} = 5.953, P = 0.018$; Table 1, Fig. 5C). Fish species did not affect the number of transitions ($F_{1, 60.57} = 0.097, P = 0.756$). There was no interaction effect of gape ratio and fish species on the number of transitions made by the crayfish across the resource zone boundaries ($F_{1, 61.11} = 0.184, P = 0.669$).

### Comparison of gape ratio and total length models

The fish total length showed no significant effects on any of the macrophyte consumption or crayfish behavior variables (Table 1). In addition, all models based on gape ratio produced lower AIC values (difference > 2) than models based on fish total length (Table 1).

### Discussion

Crayfish that were small relative to their predators consumed more macrophyte biomass (Fig. 4), spent more time foraging (Fig. 5A), decreased shelter use (Fig. 5B), and transitioned between sections more often (Fig. 5C) in the mesocosms than crayfish that were large relative to their predators. All these significant effects from gape ratio and the lack of fish species or general size effects support the hypothesis that crayfish use relative predator size to assess the threat posed by the predator and alter their behavior. Given the design of the experiment, these results support the conclusion that this measurement of threat as indicated by gape ratio comes solely from chemical cues. These results are consistent with findings from previous studies on predatory threat assessment in crayfish. The first demonstrated that crayfish increased macrophyte consumption and showed altered macrophyte species preferences in the presence of predatory fish odors (Wood et al. 2018). The other studies showed that crayfish could assess the threat posed by a predatory fish using dietary cues and size information extracted from the fish’s odor (Beattie and Moore 2018, Wood and Moore 2020). The current study demonstrates that individual crayfish assess threats posed by fish of different sizes relative to their own body size and alter their behavior accordingly. However, threat assessment is not a one-dimensional process. The crayfish are integrating multiple types of predator information including predator presence/absence, predator diet, predator species, and predator size while also considering their own size relative to the predator before making resource use decisions.

The design of the mesocosms used in this experiment limits the predatory stimuli available to the crayfish to only odor cues carried by the flowing water. So, the size information the crayfish are using to make resource use decisions must be extracted from the predator odor. These odor cues are a cocktail of many different chemicals released through the predator’s skin, gills, and excretory system (Brown et al. 1995, Evans

---

**Table 1. Comparison of gape ratio and fish total length effects on crayfish response variables.**

| Response variable | Gape ratio effects | Total length effects |
|-------------------|-------------------|---------------------|
|                   | $F$ value | $P$ value | Model AIC | $F$ value | $P$ value | Model AIC |
| Myriophyllum exalbescens consumption | 15.441      | <0.001    | −101.67   | 0.534    | 0.468    | −70.20 |
| Chara spp. consumption | 7.100      | 0.010     | 29.54     | 0.684    | 0.411    | 50.98 |
| Foraging time | 18.334     | <0.001    | 1196.57   | 1.029    | 0.314    | 1230.98 |
| Shelter time | 18.002     | <0.001    | 1247.39   | 0.076    | 0.784    | 1280.11 |
| Transitions | 5.953      | 0.018     | 569.16    | 1.446    | 0.234    | 590.34 |

Notes: Outputs are from linear mixed–effects models run independently on each response variable. Linear mixed–effects models incorporating gape ratio were run separately from models incorporating fish total length, and then, the two models for each response variable were compared using AIC.
et al. 2005, Glover et al. 2013). Although the mechanism by which crayfish determine the size of the predator from odor cues is not known, there are several possibilities that could provide an explanation. Larger predators have greater surface area, greater mass, and lower metabolic rates than smaller predators of the same species (Killen et al. 2010). The release of greater quantities of body odor and waste excretions, larger predators could be producing a more intense odor plume which reveals their size (Kusch et al. 2004, Hill and Weissburg 2013). The chemical composition of a predator’s odor could also change as they grow larger and age. Through ontogenetic effects on metabolism and physiology, larger predators could be releasing different chemical mixtures that prey can use to estimate size (Pilati and Vanni 2007). Possibly, the chemical cocktails released by predators of different sizes contain the same compounds but in different proportions or different concentrations (Pilati and Vanni 2007). Prey animals could then assess

---

**Fig. 4.** Influence of gape ratio on macrophyte consumption by crayfish. Panel (A) displays the consumption of *Myriophyllum exalbescens* by crayfish under threat. Panel (B) displays the consumption of *Chara* spp. by crayfish. In both panels, the red circles represent macrophyte consumption in the presence of bass odors. Pink shading represents a 95% confidence interval around the predicted response to bass odors. Blue triangles represent macrophyte consumption in the presence of trout odors. Light blue shading represents a 95% confidence interval around the predicted response to trout odors.

**Fig. 5.** Behavior of crayfish responding to gape ratio. Panel (A) displays the time crayfish spent foraging under threat. Panel (B) displays the time crayfish spent in shelter. Panel (C) displays the number of transitions crayfish made across the resource zone boundaries. In all three panels, red circles represent the time crayfish spent foraging in the presence of bass odors. Pink shading represents a 95% confidence interval around the predicted response to bass odors. Blue triangles represent the time crayfish spent foraging in the presence of trout odors. The light blue shading represents a 95% confidence interval around the predicted response to trout odors.
predator size using the relative concentrations of different chemicals in the predator’s odor plume. Whatever the mechanism of predator size recognition, our evidence shows that crayfish are comparing predator size information with an estimate of their own size to perform a risk assessment.

Crayfish may also be using chemical signals to gauge their own size against the size of the predator. The literature on social behavior in crayfish demonstrates that crayfish use urine-like excretions released from orifices on their heads called nephropores as a form of chemical communication during social interactions (Breithaupt 2010). These signals are used by crayfish to recognize previously encountered individuals and to discern the size of their opponents (Pavey and Fielder 1996, Seebacher and Wilson 2007). Previous work has suggested that crayfish may be sampling their own urinary signals as a measure of their own social status (Zulandt-Schneider et al. 2001). If so, some estimate of their own size may be contained within these signals. Comparing the information in the predatory odors with the information contained within urinary signals may provide crayfish with relative size estimates. While the relative size assessment mechanism in use remains unknown, future work aimed at testing this odor comparison strategy would be beneficial to our understanding of risk assessment and the exchange of information between predators and prey.

The behavioral responses of crayfish to the varying threats posed by predators of different relative sizes illustrate a non-consumptive effect of the predators on crayfish behavior. Crayfish in trials with small gape ratios consumed greater quantities of macrophytes and increased the time they spent foraging. This result seems counterintuitive considering that most prey animals decrease their foraging efforts when faced with predatory threats (Lima and Dill 1990, McMahon and Holanov 1995). The video recordings of crayfish behavior were only conducted at night from 00:00 to 04:00. During this dark period, the crayfish may perceive a reduction in predation risk from visually oriented predators. Thus, the videos may have captured the crayfish using a period of relative safety to forage more even though the odor of the predator was present. The behaviors of crayfish that were too large to be consumed by their predators are also consistent with the risk allocation hypothesis (Lima and Bednekoff 1999). The lack of nocturnal foraging effort and activity that was crayfish is not as plastic on a short temporal scale, crayfish could increase their overall body size through promoting faster growth between molts. By increasing their foraging effort, crayfish could be altering their growth rate to reach a size beyond the predator’s gape limitation.

Prey animals that can increase their growth rates have an advantage when faced with a threat from a gape-limited predator (Olson 1996). Under the paradigm of relative size effects, the goal for prey is not to reach a certain size which is safe from predators, but rather to outpace the size of the predatory size limitation. In bass and trout, this is their gape. For example, spot (Leiostomus xanthurus) that grow rapidly experience half as much mortality from southern flounder (Paralichthys lethostigma) predation compared to slow-growing spot populations (Craig et al. 2006). However, prey must consume greater quantities of resources in order to increase their growth rate. In the experiments by Craig et al. (2006), the accelerated growth rates of the spot fish in rapid growth treatments were achieved by increasing food availability. Thus, in natural systems, prey animals that are growing to outpace their predators size limitation need to seek additional food resources through increased foraging activity and greater food consumption. Threat assessment is important in this context because prey must expose themselves to predation risk in order to procure the additional resources they need for rapid growth.

However, the behavioral patterns of crayfish in the current study could be further explained by temporal variation in the crayfish’s perception of risk. Both predator species used in this study (M. salmoides and O. mykiss) are visually oriented, diurnal foragers (Angradi and Griffith 1990, McMahon and Holanov 1995). The video recordings of crayfish behavior were only conducted at night from 00:00 to 04:00. During this dark period, the crayfish may perceive a reduction in predation risk from visually oriented predators. Thus, the videos may have captured the crayfish using a period of relative safety to forage more even though the odor of the predator was present. The behaviors of crayfish that were too large to be consumed by their predators are also consistent with the risk allocation hypothesis (Lima and Bednekoff 1999). The lack of nocturnal foraging effort and activity that was
observed in the crayfish that were large relative to their predators makes sense considering that the predators pose no real threat. Thus, the crayfish can spread their activity throughout the day. There is also no urgency to increase growth if the crayfish are already too large to be consumed, which helps explain their low macrophyte consumption. Crayfish of all sizes exhibited differences in their responses to predators dependent on the size ratio between predator and prey. A similar behavior has been observed in the elk (Cervus canadensis) in Yellowstone National Park, responding to temporal variation in wolf predation risk. The elk in the park are more vigilant and occupy safer regions during the crepuscular periods of the day when wolves tend to hunt, and are more active and occupy riskier areas during the daylight hours when wolves are less active (Kohl et al. 2018).

In the current study, the relationship between crayfish size and predator size should not be viewed as a cutoff where some individuals that are small are vulnerable while other bigger crayfish are invulnerable to specific predators. While this mechanism seems tidy, a bimodal distribution of responses on either side of a relative size threat threshold would be needed to support this conclusion. However, the data show here present a smooth, albeit variable, gradient of responses to differences in the ratio between predator gape width and prey body size. Thus, the responses of prey to variation in threats presented by predators of different relative sizes are well described as a continuous phenomenon. While there is some possibility that crayfish which are relatively large show an increased fear response to predators because they make them more conspicuous, and this would not be very advantageous from a resource allocation perspective. Following this idea, large crayfish who show fear responses to predators across the relative size spectrum would incur considerable costs in lost opportunities to access resources, during the time when they are most reproductively viable. Thus, the best response is one that is fine-tuned to allow prey to only respond to predators that present a real threat under current conditions.

Threat assessment allows prey to fine tune the landscape of fear and minimize the impact of non-consumptive predator effects. Under classical landscape of fear theory, prey animals reduce encounters with predators by detecting predator cues in the environment and avoiding areas where predators are or have been in the past (Laundré et al. 2001, 2010). The perceived risk in these locations comes from the predator’s current or past presence at a specific locale. Prey animals incorporate information about more than just predator presence as they move through the landscape. Factors like predator identity, dietary components, satiation state, and activity patterns are known to influence prey responses (Turner et al. 1999, Chivers and Mirza 2001, Bell et al. 2006, Kohl et al. 2018). Prey use this additional information about their predators to decide if a predator poses a real threat to them (Ferrari et al. 2010). The literature is rich with information about the size-dependent prey selection by predators, but comparatively little is known about the size-dependent avoidance of predators by prey. Until now, the field has largely overlooked the influence of predator size relative to prey size in size-limited predators as sources of information that could be used in risk assessment.

In situations where predator–prey size ratios favor the prey, the perceived risk is lower, while size ratios that favor the predator heighten the perception of risk (Puttlitz et al. 1999). Thus, predator–prey relative size as opposed to predator size provides a refined landscape of fear concept. Prey can ignore cues from juvenile predators or relatively small individuals because these predators do not pose a threat, while respecting their antipredator strategies for potentially lethal predators that need to be avoided (Helfman 1989). Wahl (1992) showed that small lobsters (Homarus americanus) spent more time in shelter in the presence of predatory sculpins (Myoxocephalus anaeus), while large lobsters confronted the predator with aggressive displays. Thus, prey animals are sensitive to the predatory limitations of their predators. However, previous studies have only tested the responses of prey along a size gradient to a few predators of very similar sizes. The conclusion that prey are sensitive to predator size cannot be reached without considering relative sizes of the predator and prey. Thus, prey may be responding to the ratio of size in addition to or instead of just size of the predator.

The crayfish responded to the relative size ratio between their carapace width and the gape of their predators and adjusted their resource use...
behaviors to set themselves on a growth trajectory to get beyond the predator’s gape limitation. Considering Helfman’s (1989) threat-sensitive predator avoidance hypothesis in light of the current study, we see that prey can determine the level of threat posed by the predator and use this information to make resource use decisions. Incorporating the threat sensitivity of prey to relative predator size into the background level of risk refines the landscape of fear concept (Brown et al. 2006). The numerous species interactions that occur within an ecosystem are governed by a highly complex system of risk assessments and decisions made by individuals within a spatially and temporally dynamic landscape of predatory cues (Ferrari et al. 2009, Gaynor et al. 2019). The fully integrated landscape of fear would involve prey assessing multiple aspects of predator cues beyond their presence in the landscape to determine which predators present a legitimate threat. A deeper understanding of risk assessments in prey reveals how altered prey behavior impacts biological communities and informs our perspective on the top-down influence of predators.

ACKNOWLEDGMENTS

We thank the members of the Laboratory for Sensory Ecology for their help with experimental setup, collection of crayfish, and comments on the manuscript. We also thank the University of Michigan Biological Station for the use of facilities and funding through the Marlan P. and David M. Gates Graduate Student Endowment Fund to T.C.W. Funds were also generously provided by the Bowling Green State University Department of Biological Sciences through the Barbara Long Masters Research Award presented to T.C.W. Lastly, we thank the Bowling Green State University Faculty Research Committee for a Building Strength Award and the Fullbright Fellowship to P.A.M. for help in funding this research.

LITERATURE CITED

Abrahams, M. V. 1995. The interaction between antipredator behaviour and antipredator morphology: experiments with fathead minnows and brook sticklebacks. Canadian Journal of Zoology 73:2209–2215.

Angradi, T. R., and J. S. Griffith. 1990. Diel feeding chronology and diet selection of rainbow trout (Oncorhynchus mykiss) in the Henry’s Fork of the Snake River, Idaho. Canadian Journal of Fisheries and Aquatic Sciences 47:199–209.

Beattie, M. C., and P. A. Moore. 2018. Predator recognition of chemical cues in crayfish: Diet and experience influence the ability to detect predation threats. Behaviour 155:505–530.

Bell, R. D., A. L. Rypstra, and M. H. Persons. 2006. The effect of predator hunger on chemically mediated antipredator responses and survival in the wolf spider Pardosa milieina (Araneae: Lycosidae). Ethology 112:903–910.

Bishop, T. D., and J. A. Brown. 1992. Threat-sensitive foraging by larval threespine sticklebacks (Gasterosteus aculeatus). Behavioral Ecology and Sociobiology 31:133–138.

Bolser, R. C., M. E. Hay, N. Lindquist, W. Fenical, and D. Wilson. 1998. Chemical defenses of freshwater macrophytes against crayfish herbivory. Journal of Chemical Ecology 24:1639–1658.

Bradbury, J. W., and S. L. Vehrencamp. 1998. Principles of animal communication. Sinauer, Sunderland, Massachusetts, USA.

Breithaupt, T. 2010. Chemical communication in crayfish. Pages 257–276 in T. Breithaupt, and M. Thié, editors. Chemical Communication in Crustaceans. Springer, New York, New York, USA.

Brönnmark, C., and J. G. Miner. 1992. Predator-induced phenotypical change in body morphology in crucian carp. Science 258:1348–1350.

Brown, G. E., D. P. Chivers, and R. J. F. Smith. 1995. Localized defecation by pike: A response to labelling by cyprinid alarm pheromone? Behavioral Ecology and Sociobiology 36:105–110.

Brown, G. E., A. C. Rive, M. C. Ferrari, and D. P. Chivers. 2006. The dynamic nature of antipredator behavior: Prey fish integrate threat-sensitive antipredator responses within background levels of predation risk. Behavioral Ecology and Sociobiology 61:9–16.

Brown, J. S., J. W. Laundré, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80:385–399.

Chambers, P. A., J. M. Hanson, J. M. Burke, and E. E. Prepas. 1990. The impact of the crayfish Orconectes virilis on aquatic macrophytes. Freshwater Biology 24:81–91.

Chivers, D. P., and R. S. Mirza. 2001. Predator diet cues and the assessment of predation risk by aquatic vertebrates: a review and prospectus. Pages 277–284 in A. Marchlewksa-Koj, J. J. Lepri, and D. Müller-Schwarze, editors. Chemical Signals in Vertebrates 9. Springer, Boston, Massachusetts, USA.

Chivers, D. P., R. S. Mirza, P. J. Bryer, and J. M. Kiesecker. 2001. Threat-sensitive predator avoidance
by slimy sculpins: understanding the importance of visual versus chemical information. Canadian Journal of Zoology 79:867.

Craig, J. K., B. J. Burke, L. B. Crowder, and J. A. Rice. 2006. Prey growth and size-dependent predation in juvenile estuarine fishes: experimental and model analyses. Ecology 87:2366–2377.

Cronin, G., D. M. Lodge, M. E. Hay, M. Miller, A. M. DiSciullo, R. A., and A. L. Basolo. 2019. Body size, but not age-at-maturation or context, affects the expression of predator-induced behavioural plasticity in female green swordtails (Xiphophorus hemilus). Ethology 126:320–332.

Dawidowicz, P., and C. J. Loose. 1992. Metabolic costs during predator-induced diel vertical migration of Daphnia. Limnology and Oceanography 37:1589–1595.

Dijkstra, R. A., and A. L. Basolo. 2019. Body size, but not age-at-maturation or context, affects the expression of predator-induced behavioural plasticity in female green swordtails (Xiphophorus hemilus). Ethology 126:320–332.

Dusenbery, D. B. 1992. Sensory ecology: How organisms acquire and respond to information. WH Freeman, New York, New York, USA.

Evans, D. H., P. M. Piermarini, and K. P. Choe. 2005. The multifunctional fish gill: dominant site of gas exchange, osmoregulation, acid-base regulation, and excretion of nitrogenous waste. Physiological Reviews 85:97–177.

Feminella, J. W., and V. H. Resh. 1989. Submersed macrophytes and grazing crayfish: an experimental study of herbivory in a California freshwater marsh. Ecography 12:1–8.

Fero, K., and P. A. Moore. 2008. Social spacing of crayfish in natural habitats: What role does dominance play? Behavioral Ecology and Sociobiology 62:1119–1125.

Ferrari, M. C., A. Sih, and D. P. Chivers. 2009. The paradox of risk allocation: a review and prospectus. Animal Behaviour 78:579–585.

Ferrari, M. C., B. D. Wisenden, and D. P. Chivers. 2010. Chemical ecology of predator–prey interactions in aquatic ecosystems: a review and prospectus. Canadian Journal of Zoology 88:698–724.

Fox, J., and S. Weisberg. 2019. An R companion to applied regression. Third edition. Sage, Thousand Oaks, California, USA.

Fritz, H., M. Guillemaud, and D. Durant. 2002. The cost of vigilance for intake rate in the mallard (Anas platyrhynchos): an approach through foraging experiments. Ethology Ecology and Evolution 14:91–97.

Gaynor, K. M., J. S. Brown, A. D. Middleton, M. E. Power, and J. S. Brashares. 2019. Landscapes of fear: spatial patterns of risk perception and response. Trends in Ecology and Evolution 34:355–368.

Glover, C. N., C. Bucking, and C. M. Wood. 2013. The skin of fish as a transport epithelium: a review. Journal of Comparative Physiology B 183:877–891.

Helfman, G. S. 1989. Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. Behavioral Ecology and Sociobiology 24:47–58.

Henry, L. M., J. A. Bannerman, D. R. Gillespie, and B. D. Roitberg. 2010. Predator identity and the nature and strength of food web interactions. Journal of Animal Ecology 79:1164–1171.

Hill, J. E., L. G. Nico, C. E. Cichra, and C. R. Gilbert. 2004. Prey vulnerability to peacock cichlids and largemouth bass based on predator gape and prey body depth. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 58:47–56.

Hill, J. M., and M. J. Weissburg. 2013. Predator biomass determines the magnitude of non-consumptive effects (NCEs) in both laboratory and field environments. Oecologia 172:79–91.

Hill, J. M., and M. J. Weissburg. 2014. Crabs interpret the threat of predator body size and biomass via cue concentration and diet. Animal Behaviour 92:117–123.

Huskey, S. H., and R. G. Turingan. 2001. Variation in prey-resource utilization and oral jaw gape between two populations of largemouth bass, Micropterus salmoides. Environmental Biology of Fishes 61:185–194.

Illius, A. W., and C. Fitzgibbon. 1994. Costs of vigilance in foraging ungulates. Animal Behaviour 47:481–484.

Jurcak, A. M., and P. A. Moore. 2018. Sensory signals and the reaction space in predator–prey interactions. Hydrobiologia 816:137–152.

Kats, L. B., and L. M. Dill. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. Ecoscience 5:361–394.

Killen, S. S., D. Atkinson, and D. S. Glazier. 2010. The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. Ecology Letters 13:184–193.

Kohl, M. T., D. R. Stahler, M. C. Metz, J. D. Forester, M. J. Kauffman, N. Varley, P. J. White, D. W. Smith, and D. R. MacNulty. 2018. Diel predator activity drives a dynamic landscape of fear. Ecological Monographs 88:638–652.

Kusch, R. C., R. S. Mirza, and D. P. Chivers. 2004. Making sense of predator scents: investigating the sophistication of predator assessment abilities of fathead minnows. Behavioral Ecology and Sociobiology 55:551–555.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. ImerTest package: tests in linear
mixed effects models. Journal of Statistical Software 82, 1–26.
Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the ‘landscape of fear’ in Yellowstone National Park, USA. Canadian Journal of Zoology 79:1401–1409.
Laundré, J. W., L. Hernández, and W. J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. Open Ecology Journal 3:1–7.
Lawrence, J. M. 1958. Estimated sizes of various forage fishes largemouth bass can swallow. Proceedings of the Southeastern Association of Game and Fish Commissioners 11:220–225.
Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. BioScience 48:25–34.
Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. The American Naturalist 153:649–659.
Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619–640.
Lodge, D. M. 1991. Herbivory on freshwater macrophytes. Aquatic Botany 41:195–224.
Ludington, T. S., and P. A. Moore. 2017. The degree of impairment of foraging in crayfish (Orconectes virilis) due to insecticide exposure is dependent upon turbulence dispersion. Archives of Environmental Contamination and Toxicology 72:281–293.
Martin, A. L. III, and P. A. Moore. 2008. The influence of dominance on shelter preference and eviction rates in the crayfish, Orconectes rusticus. Ethology 114:351–360.
McMahon, T. E., and S. H. Holanov. 1995. Foraging success of largemouth bass at different light intensities: implications for time and depth of feeding. Journal of Fish Biology 46:759–767.
Neal, A. E., and P. A. Moore. 2017. Mimicking natural systems: changes in behavior as a result of dynamic exposure to naproxen. Ecotoxicology and Environmental Safety 135:347–357.
Olson, M. H. 1996. Predator-prey interactions in size-structured fish communities: implications of prey growth. Oecologia 108:757–763.
Palmer, M. S., J. Fieberg, A. Swanson, M. Kosmala, and C. Packer. 2017. A ‘dynamic’ landscape of fear: prey responses to spatiotemporal variations in predation risk across the lunar cycle. Ecology Letters 20:1364–1373.
Pavey, C. R., and D. R. Fielder. 1996. The influence of size differential on agonistic behaviour in the freshwater crayfish, Cherax cuscipulatus (Decapoda: Parastacidae). Journal of Zoology 238:445–457.
Peckarsky, B. L., P. A. Abrams, D. I. Bolnick, L. M. Dill, J. H. Grabowski, B. Luttbeg, J. L. Orrock, S. D. Peacoer, E. L. Preisser, O. J. Schmitz, and G. C. Trussell. 2008. Revisiting the classics: considering nonconsumptive effects in textbook examples of predator–prey interactions. Ecology 89:2416–2425.
Pettersson, L. B., and C. Brönmark. 1997. Density-dependent costs of an inducible morphological defense in crucian carp. Ecology 78:1805.
Pilati, A., and M. J. Vanni. 2007. Ontogeny, diet shifts, and nutrient stoichiometry in fish. Oikos 116:1663–1674.
Preisser, E. L., and D. I. Bolnick. 2008. The many faces of fear: comparing the pathways and impacts of nonconsumptive predator effects on prey populations. PLOS ONE 3:e2465.
Puttlitz, M. H., D. P. Chivers, J. M. Kiesecker, and A. R. Blaustein. 1999. Threat-sensitive predator avoidance by larval Pacific treefrogs (Amphibia, Hyliidae). Ethology 105:449–456.
R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Seebacher, F., and R. S. Wilson. 2007. Individual recognition in crayfish (Cherax destructor): the roles of strength and experience in deciding aggressive encounters. Biology Letters 3:471–474.
Shave, C. R., C. R. Townsend, and T. A. Crowl. 1994. Anti-predator behaviours of a freshwater crayfish (Paranephrops zealandicus) to a native and an introduced predator. New Zealand Journal of Ecology 18:1–10.
Smee, D. L., and M. J. Weissburg. 2006. Clamping up: Environmental forces diminish the perceptive ability of bivalve prey. Ecology 87:1587–1598.
Steiner, U. K., and T. Pfeiffer. 2006. Optimizing time and resource allocation trade-offs for investment into morphological and behavioral defense. American Naturalist 169:118–129.
Studd, M., R. D. Montgomery, and R. J. Robertson. 1983. Group size and predator surveillance in foraging house sparrows (Passer domesticus). Canadian Journal of Zoology 61:226–231.
Turner, A. M., S. A. Fetterolf, and R. J. Bernot. 1999. Predator identity and consumer behavior: differential effects of fish and crayfish on the habitat use of a freshwater snail. Oecologia 118:242–247.
Turner, A. M., and S. L. Montgomery. 2003. Spatial and temporal scales of predator avoidance: experiments with fish and snails. Ecology 84:616–622.
Wahle, R. A. 1992. Body-size dependent anti-predator mechanisms of the American lobster. Oikos 65:52.
Weiss, L. C. 2019. Sensory ecology of predator-induced phenotypic plasticity. Frontiers in Behavioral Neuroscience 12:330.
Wisenden, B. D. 2000. Olfactory assessment of predation risk in the aquatic environment. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 355:1205.

Wood, T. C., R. E. Kelley, and P. A. Moore. 2018. Feeding in fear: indirect effects of predatory fish on macrophyte communities mediated by altered crayfish foraging behaviour. Freshwater Biology 63:1523–1533.

Wood, T. C., and P. A. Moore. 2020. Big and bad: How relative predator size and dietary information influence crayfish (Faxonius rusticus) behavior and resource use decisions. Canadian Journal of Zoology 98:62–72.

Wyatt, T. D. 2010. Pheromones and signature mixtures: defining species-wide signals and variable cues for identity in both invertebrates and vertebrates. Journal of Comparative Physiology A 196:685–700.

Zulanft-Schneider, R. A., R. Huber, and P. A. Moore. 2001. Individual and status recognition in the crayfish, Orconectes rusticus: the effects of urine release on fight dynamics. Behaviour 138: 137–153.