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The alarm cue obstruction hypothesis: isopods respond to alarm cues, but do not respond to dietary chemical cues from predatory bluegill

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Abstract
Predator avoidance behaviours occur when prey detect a predator but the predator has not yet detected and identified prey. These defences are critical because they prevent predation at the earliest possible stages when prey have the best chance of escape. We tested for predator avoidance behaviours in an aquatic macroinvertebrate (*Caecidotea intermedius*; order Isopoda) in a series of three experiments. The first experiment attempted to determine if isopods possess alarm cues by exposing them to stimuli from macerated conspecifics. We then exposed isopods to kairomones from non-predatory tadpoles (*Rana catesbiana*) and predatory fish (*Lepomis macrochirus*) that had been fed a benign diet. Finally, we exposed isopods to kairomones of predatory fish that had been fed a diet exclusively of isopods. We found that isopods did not respond to any kairomone cues or dietary cues from any potential predator, but did reduce activity in response to alarm cues. These results suggest that isopods exhibit predator avoidance responses toward chemical cues in a limited setting (they do not respond unless the information suggests an attack has occurred in the immediate past) or that bluegill have the ability to modify or mask the alarm cues from their prey.

Keywords
antipredator, trade-off, alarm cues, kairomones, dietary cues.

1. Introduction

Predation is a strong driving force and provides a selective pressure that can dramatically modify prey behaviour (Lima & Dill, 1990; Brown, 2003; Ferrari et al., 2010). The ability of prey to assess the risk of predation is significant for decision-making and prey must balance trade-offs between responding to predators and increasing their fitness through alternative ac-

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tivities, such as foraging and mating (Lima & Dill, 1990). This trade-off between predator avoidance and fitness-enhancing behaviours creates a gradient of risk responsiveness that will differ for each species depending on their predator regime and life-history characteristics (Lima & Bednekoff, 1999).

Prey can respond to predators with a variety of behaviours. For example, anti-predator behaviours are used immediately after a predation event has been initiated and when the prey is in eminent threat of danger (Endler, 1986; Brodie et al., 1991). In comparison, predator avoidance behaviours occur before the prey has entered the perceptual field of the predator and provide the greatest reduction in predation risk because the interaction is terminated before an attack commences (Brodie et al., 1991). One type of predator avoidance strategy that is common in aquatic communities is the release and detection of species-specific alarm cues which are produced from injured tissues and function to signal to conspecifics and heterospecifics of the same prey guild that an active predator is in the area (Smith, 1977, 1992). After detecting these cues, prey can then take action through a variety of behaviours, such as seeking shelter or reducing activity (Ferrari et al., 2010). Once residual alarm cues are no longer present or are not as intense, prey can continue normal activities, such as foraging (Brown, 2003).

Another way prey can reduce their chance of being eaten is to utilise predator avoidance behaviours before an attack is made. Prey may be able to detect a nearby predator via its kairomones which are chemical cues unique to predatory species (Brown et al., 1970; Ferrari et al., 2010). After detecting predatory kairomones, prey often respond with similar behaviours as in response to alarm cues (Wooster & Sih, 1995; Kats & Dill, 1998). Unlike alarm cues, kairomones are more general signals and may not provide accurate information about current predation risk (Schoeppner & Relyea, 2005). Thus some prey may require additional chemical information other than kairomones before initializing predator avoidance behaviours (Schoeppner & Relyea, 2005). Dietary cues are post-digestive alarm cues in addition to kairomones which not only signal that a predator is nearby, but also that a predator has recently consumed conspecifics (Mirza & Chivers, 2003; Ferrari et al., 2010). Dietary cues should indicate to prey the dietary preference of the specific species of predator that is in the area (Howe & Harris, 1978; Crowl & Covich, 1990; Keefe, 1992; Wilson & Lefcort, 1993; Ferrari et al., 2010).

Although behaviours made in response to chemical signalling have been extensively studied in many aquatic organisms, it has yet to be fully documented in the order Isopoda, which are abundant consumers near the base of many aquatic food webs. We focused on behavioural changes made by aquatic isopods (*Caecidotea intermedius*) in response to various chemical stimuli in a series of three experiments. The first of these experiments tested for predator avoidance behaviours in response to alarm cues from macerated conspecifics. The second experiment tested the behaviour of isopods in response to predatory kairomones from bluegill that had not recently consumed isopods. The third experiment tested whether dietary cues (kairomone cues and post-digestive alarm cues) from bluegill elicited predator avoidance behaviours.

2. Methods

2.1. Animal collection and maintenance

Aquatic isopods, *Caecidotea intermedius* (formerly *Asellus intermedius*), were collected by dip-net from small fishless pools near Hanover, IN, USA in the spring of 2013. For experiment 3, isopods were collected in January 2014 and wax worms (*Galleria mellonella*) were bought from a commercial supplier. After collection, isopods were placed in plastic tubs and transported to Hanover College. They were housed in 9.5-l tanks with deionized water, detritus from the site of collection, and an aerator. A 9.5-l tank with deionized water and an aerator was also set up and conditioned to the same temperature as the housing containers to serve as a source of clean water during the experiments; this water was used for all trials in each of the three experiments. Nonpredatory bullfrog tadpoles (*Rana catesbiana*) (mean mass ± SE 4.2 ± 1.5 g) and small predatory bluegill (*Lepomis macrochirus*) (11.1 ± 4.1 g) were collected by minnow-trap from a large lake adjacent to the fishless pools in February and January 2013, respectively. Tadpoles and fish were housed separately in 75-l tanks with gravel and a filter, and were fed flake and pelletized fish food for 2 months prior to stimulus collection. All animals were maintained at 21°C and kept on a natural light/dark cycle.

2.2. Experiment 1 — do isopods respond to chemical alarm cues?

Experiment 1 tested for the presence of alarm cues in isopods by examining their response to chemical stimuli from macerated conspecifics. The alarm stimulus was prepared by transferring three isopods with a pipette into a

1.5 ml microcentrifuge tube. Excess water was removed, isopods were macerated with a pestle, and then 1 ml of deionized water was added to the tube. The tube was then vortexed and frozen at −20°C. Control stimulus (1.5 ml of deionized water) was also frozen at −20°C. All trials were conducted inside an 8.5 mm petri dish. A circular piece of plastic mesh (1 mm square holes) was glued to the bottom of the petri dish to provide a substrate that the isopods could grasp to facilitate locomotion. Two lines were drawn perpendicularly on the bottom of the petri dish to create four equally-sized quadrants. During experimentation, 25 ml of conditioned water was placed inside the test chamber and an isopod was haphazardly selected from a holding tank and placed in the centre. After a 30-s acclimation period, a five minute pre-stimulus period was initiated and the number of times the isopod crossed a line was recorded. After the pre-stimulus period, 1.5 ml of either the control or alarm stimulus was added to the quadrant opposite the isopod; the stimulus tested was randomly determined with a random number generator and thawed at the start of a trial. A 30-s acclimation period was initiated, followed by a 5-min post-stimulus period where we recorded the number of times an isopod crossed a line; although measuring lines crossed in a circular arena can be an inconsistent measure of activity, isopods were generally observed on the outer edge of the dish and it is unlikely that individual variability between animals within the chamber can account for variation between treatments. Between each trial the petri dish was rinsed with warm tap water for 15 s followed by deionized water for 15 s.

For each trial we subtracted the number of lines crossed in the pre-stimulus period from the number of lines crossed in the post-stimulus period to get a change in activity following treatment introduction. We then compared the change in lines crossed between control and alarm cue treatments using Student's t-test ($\alpha = 0.05$).

2.3. *Experiment 2 — do isopods detect and avoid kairomones?*

Experiment 2 tested whether isopods respond to kairomones from a blank control, nonpredatory tadpoles (bullfrog), and predatory fish (bluegill). The chemical stimuli were prepared by placing three fish and two tadpoles individually in containers with 100 ml H_2O/g mass for 24 h. The tadpoles had been maintained in the lab on a non-isopod diet for four weeks prior to stimulus collection, whereas fish were maintained on a non-isopod diet for eight weeks prior to stimulus collection. Each of the five containers was supplied with an aerator. Control stimulus (1.5 ml of deionized water) was prepared in the same manner except no tadpole or fish was added to the container. Dividers were placed around the containers to reduce any external visual stimuli. After 24 h, the stimuli from individual fish or tadpoles were combined and mixed thoroughly to eliminate variation in individual kairomone cues, after which 1.5-ml aliquots were placed in 1.5-ml microcentrifuge tubes. After preparation, the tubes were coded so that the experimenter was blind to treatment and all tubes were frozen at −20°C. The experimental chamber and testing procedure was identical to that in experiment 1, except that 1.5 ml of either a control, tadpole, or fish stimulus was added after the pre-stimulus period. The change in lines crossed between isopods exposed to control, tadpole, and fish kairomones were analysed with a one-way ANOVA.

2.4. Experiment 3 — do isopods respond to dietary alarm cues?

Experiment 3 tested whether isopods respond to chemical cues from predatory fish that had consumed exclusively isopods in the lab. Four bluegill (the same fish used in experiment 2) were placed individually in 37-l tanks with gravel and an aerator. Two of the four fish were fed 30 isopods per day for 7 days prior to stimulus collection. The other two fish were fed 4 wax worms for 3 days prior to stimulus collection. Four wax worms equalled the average mass of 30 isopods (approximately 1 g). Approximately 4 h after the last feeding, all four fish were transferred to individual containers with 100 ml H_2O/g mass for 24 h. Each container was supplied with an aerator and dividers were placed around the containers. At the conclusion of 24 h, the stimuli from individual fish in each treatment were combined to reduce variation in individual cues and immediately used in the experiment. The experimental chamber and testing procedure was identical to that in experiment 1, except that 1.5 ml of either control, wax worm fed, or isopod fed chemical stimulus was added after the pre-stimulus period. The difference in the number of lines crossed between isopods exposed to a blank control and fish stimuli containing either wax worm fed or isopod fed cues were analysed with a one-way ANOVA.

3. Results

Isopods significantly decreased the number of lines crossed when exposed to a chemical alarm stimulus compared with the blank control (t-test, $t =$

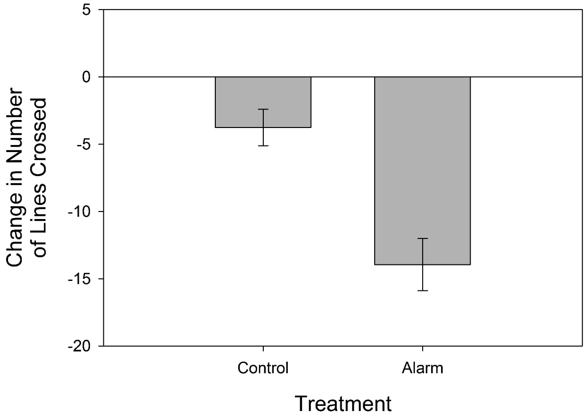

Figure 1. The mean (±SE) difference in the number of lines crossed between pre-stimulus and post-stimulus periods when isopods were exposed to either a blank control or alarm cues from macerated conspecifics. Isopods significantly decreased movement when exposed to alarm cues (t-test, $t = -3.84$, $N = 40$, $p < 0.001$).

-3.84, $N = 40$, $p < 0.001$, Figure 1). In experiment 2, there was not a significant difference in lines crossed between isopods exposed to a blank control or kairomones from nonpredatory tadpoles or predatory fish (one-way ANOVA, power = 0.111, $F_{2,73} = 1.41$, $p = 0.25$; Figure 2). There was

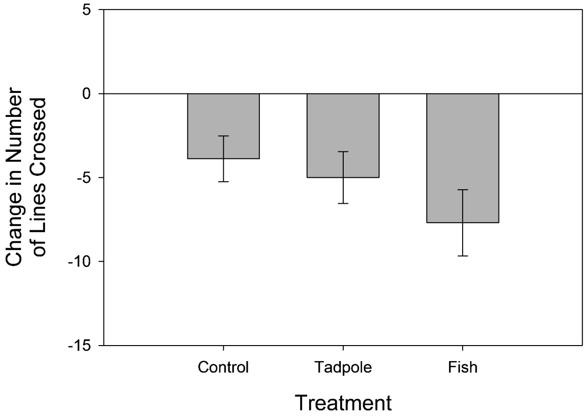

Figure 2. The mean (±SE) difference in the number of lines crossed between pre-stimulus and post-stimulus periods when isopods were exposed to either a blank control, nonpredatory tadpole kairomones, or predatory fish kairomones. Tadpoles and fish were maintained on a nonisopod diet. Isopods did not significantly change behaviour when exposed to any treatment (one-way ANOVA, $F_{2,73} = 1.41$, $p = 0.25$).

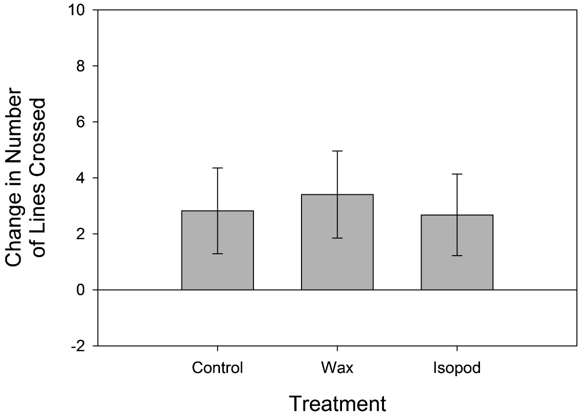

Figure 3. The mean (±SE) difference in the number of lines crossed between pre-stimulus and post-stimulus periods when isopods were exposed to either a blank control or cues from fish that had been wax worms or isopods. Isopods did not change behaviour when exposed to any treatment (one-way ANOVA, $F_{2,94} = 0.063$, $p = 0.94$).

no significant difference in movement between isopods exposed to chemical stimuli from a blank control, cues from fish fed wax-worms, or cues from fish fed isopods (one-way ANOVA, power = 0.049, $F_{2,94} = 0.063$, $p = 0.94$, Figure 3).

4. Discussion

Isopods significantly decreased their overall activity when exposed to alarm cues released from injured conspecifics, indicating that isopods possess and respond to alarm cues. This is not surprising given the immense number of species that have already been shown to possess and respond to alarm cues (Chivers & Smith, 1998; Wisenden et al., 1999, 2009; Ferrari et al., 2010). These cues are functionally important for prey to assess the threat of predation and to respond with appropriate anti-predator or predator avoidance behaviours (Wisenden et al., 1999; Brown, 2003; Schoeppner & Relyea, 2005). These results are further supported by a study by Wisenden et al. (1999), in which macerated isopods (*Lirceus fontinalis*) were used to determine if amphipods (*Gammarus minus*) exhibited cross-species recognition of alarm cues. Nevertheless, this study focused solely on the behaviour of amphipods. Our results show that freshwater isopods, specifically *C. intermedius*, possess and respond to alarm cues, thereby expanding our knowledge of chemical alarm cues within aquatic taxa.

Chemical alarm cues inform aquatic taxa of a recent and possible impending predatory attack, yet some prey can recognize their predator before it attacks (Ferrari et al., 2010). These prey could maximise their chance of survival because the interaction is halted at the earliest possible phase and when the chance of escape is greatest (Endler, 1986; Hopkins et al., 2011). Early predator detection can be made through the use of kairomones (Ferrari et al., 2010). We hypothesized that if isopods employed alarm cues then they might also respond to kairomones from a potential predator. Despite a slight trend for avoiding predatory kairomones, isopods did not significantly alter their behaviour in the presence of kairomone cues from predatory fish. Previous studies on responses of isopods to chemical stimuli from predators have yielded mixed results. A series of papers looking at the behaviour of a stream-dwelling isopod (*Lirceus fontinalis*) in the laboratory and field found a general reduction of activity in response to chemical cues from predatory fish (Holomuzki & Short, 1988, 1990; Short & Holomuzki, 1992; Holomuzki & Hatchett, 1994). However, in another study, isopods that had prior experience with predatory crayfish did not respond to crayfish kairomones, despite being extremely susceptible to predation (Vollmer & Gall, 2014). The isopods used in our study were collected from fishless pools to control for any learned predator-recognition. This has important implications for predator avoidance behaviour and may be one of the reasons isopods did not respond to predator kairomones in our study. A recent study by Harris et al. (2013) on a closely related isopod (*Caecidotea aquaticus*) found that prior experience with predators is critical to the initiation of predator avoidance behaviour. In this case, individual isopods responded strongly to chemical cues from predatory fish (*Perca fluviatilis*), but only when they were collected from a habitat that contained this predator.

Bluegill are major predators that have a generalized diet which consists of a wide array of macroinvertebrates (Keast, 1970; Schramm Jr. & Jirka, 1989). The fish used in this study were fed a benign diet that excluded isopods, and in addition to kairomones, many prey species require post-digestion alarm signals in the predator's diet to modify behaviour (Ferrari et al., 2010). For example, Jacobsen & Stabell (2004) found that a marine snail (*Tegula funebralis*) exhibits predator avoidance behaviour in response to crabs that have recently fed on conspecifics, but do not modify behaviour in response to chemical stimuli from non-feeding crabs or crabs that have been feeding on other gastropod species. Since isopods did not respond to non-specific kairomone cues alone, we hypothesized that isopods might need additional information (post-digestion alarm cues in addition to the kairomones) in order to recognize and respond to these cues with predator avoidance behaviours. Surprisingly, isopods did not respond to dietary cues from bluegill that had been fed isopods exclusively for 7 days prior to testing; we replicated this experiment and got identical results.

Two hypotheses exist to explain the failure of isopods to respond to dietary alarm cues from bluegill. The first is that these isopods may have limited exposure to potential predation, and therefore they may curtail predator avoidance behaviour until their risk of death is maximized. For most organisms, a balance must be achieved between responding to potential predators, meeting daily energetic requirements, and producing offspring or mating (Lima & Dill, 1990; Brown, 2003). For many species, these trade-offs have been documented and these studies often indicate that given certain conditions the value of risk they perceive from predators does not exceed the value of the alternative behaviour (Lima & Bednekoff, 1999). In these cases, anti-predator behaviours should only be exhibited under high-risk situations that are relatively infrequent and under low-risk situations feeding and other activities will occur normally (Lima & Bednekoff, 1999). For example, Rohr & Madison (2001) exposed male newts in reproductive condition to alarm cues and pheromones from female newts. The authors found that males were attracted to pheromones from females but ignored alarm cues. In this case, the benefits of mating exceeded the potential risk of death and the prey chose to ignore the predatory stimulus. In our study, isopods responded to predation risk when the cues indicated a predator was actively foraging in the immediate vicinity. Although additional research is needed to determine the role learning plays in this species, isopods only modified their behaviour when the risk of predation was at its highest, further supporting the predation risk allocation hypothesis (Lima & Bednekoff, 1999). Isopods (including *Caecidotea intermedius*) are extremely abundant in small temporary pools where they forage on decaying vegetation, fungi, and algae (Moore, 1975; Graca et al., 1993). These pools are often void of other aquatic organisms (BG personal observation) and predation risk may be minimal. Given the typical habitat and life-history patterns for this species, responding to these alternative cues from predators, such as predatory kairomones and post-digestive alarm cues, may unnecessarily decrease time spent on alternate activities. Only exhibiting anti-predator behaviours when the risk of predation is at its greatest may allow isopods to balance these trade-offs.

Given the survival benefits that accrue to prey by recognizing and responding to alarm cues (Mathis & Smith, 1993), as well as the often intense co-evolution between predators and their prey (Brodie & Brodie, 1999), there may be strong selection on predators to reduce or eliminate the alarm cues from their prey during digestion. The second hypothesis for the failure of isopods to respond to dietary alarm cues is that bluegill possess the ability to either mask the alarm cue (possibly with a binding protein) or break the alarm compound into smaller components that are unrecognizable to the prey. Although isopods collected for this study were taken from predator-free pools, the same isopod species co-occurs with bluegill in a large lake less than 15 m away from these pools (the same lake from which bluegill were collected for this study). These predator-exposed isopods are found in the margins and benthic regions of the lake and are likely subject to predation from bluegill, which may have facilitated selective pressure for the ability to obstruct the alarm cues from their prey during digestion. Previous research has found very limited support for the alarm cue obstruction hypothesis. To our knowledge, only one other study has demonstrated a failure of a prey species to respond to dietary alarm cues (Feminella & Hawkins, 1994). In this study, tailed-frog tadpoles (*Ascaphus truei*) were unable to detect dietary alarm cues from shorthead sculpins (*Cottus confusus*), but did respond to dietary alarm cues from three other predators (Feminella & Hawkins, 1994). Subsequent authors proposed that these sculpin evolved the ability to mask or break down the alarm cues released from the tadpoles (Chivers & Smith, 1998; Ferrari et al., 2008; Wisenden et al., 2009). In contrast, a recent study by Sutrisno et al. (2014) did not find support for the alarm cue obstruction hypothesis, specifically in bluegill. In this study, fathead minnows (*Pimephales promelas*) responded to dietary alarm cues from bluegill with the same intensity as they did to dietary alarm cues processed by a distantly related fish, indicating that the more phylogenetically derived bluegill do not chemically alter the alarm cue from fathead minnows. Different prey species (vertebrate vs. invertebrate) were used in our study and that by Sutrisno et al. (2014), which may account for the differing results. Nevertheless, additional research, especially related to the chemical composition of alarm cues in different taxa, is necessary to determine whether bluegill have the capacity to modify the alarm cue from at least some prey to facilitate prey capture.

The results of our study indicate that at least one species of aquatic isopods possess alarm cues and is the second known study to demonstrate a failure by a prey organism to respond to dietary alarm cues from a predator. Whether isopods ignore dietary alarm cues to optimize fitness or the alarm cue is modified by the predator during digestion remains to be determined.

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