



Parasite-induced alteration of odour responses in an amphipod–acanthocephalan system



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ABSTRACT

Odour-related behaviours in aquatic invertebrates are important and effective anti-predator behaviours. Parasites often alter invertebrate host behaviours to increase transmission to hosts. This study investigated the responses of the amphipod *Hyaletta azteca* when presented with two predator chemical cues: (i) alarm pheromones produced by conspecifics and (ii) kairomones produced by a predatory Green Sunfish (*Lepomis cyanellus*). We compared the responses of amphipods uninfected and infected with the acanthocephalan parasite *Leptorhynchoides thecatus*. Uninfected amphipods reduced activity and increased refuge use after detecting both the alarm pheromones and predator kairomones. Infected amphipods spent significantly more time being active and less time on the refuge than uninfected amphipods, and behaved as if they had not detected the chemical stimulus. Therefore, *L. thecatus* infections disrupt the amphipods' anti-predator behaviours and likely make their hosts more susceptible to predation.

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1. Introduction

Many aquatic invertebrates rely heavily upon chemosensory perception for survival, particularly when in turbid and low-light environments. Ferrari et al. (2010) identify three categories of chemical cues that alert prey to the presence of predators: alarm pheromones, disturbance cues and kairomones (Wisenden, 2000). Prey species release alarm pheromones during or after predator attacks to alert conspecifics to impending danger (Chivers and Smith, 1998). Disturbance cues are released by disturbed or startled prey, and involve the release of a pulse of urinary ammonia (Kiesecker et al., 1999). Prey can also sense chemicals that predators unintentionally produce (kairomones) and alter their behaviour as they become aware of the threat. There is extensive literature on odour and predator-prey interactions and readers are recommended to see the reviews by Ferrari et al. (2010), Mathis (2009), and Wisenden and Chivers (2006), among others.

Freshwater amphipods (Crustacea) provide important systems for research on odours and associated anti-predator behaviour. Amphipods in the genus *Gammarus* (Gammaridae) are less active and less likely to drift in the water column in streams containing predatory fish kairomones than in streams without kairomones (Williams and Moore, 1985; Andersson et al., 1986; Holomuzki and Hoyle, 1990; Wudkevich et al., 1997). Fish kairomones also

cause amphipods to spend more time in refuges, to favour less exposed habitats, to swim down to substrates, to aggregate and to select smaller, less noticeable mates (Holomuzki and Hoyle, 1990; Mathis and Hoback, 1997; Wudkevich et al., 1997; Kullmann et al., 2008). Similar behaviours are observed in gammarids exposed to alarm pheromones (Wudkevich et al., 1997). These behaviours benefit amphipods by reducing predation rates. Amphipods previously exposed to either alarm pheromones or predator kairomones were less likely to be found and consumed by Green Sunfish (*Lepomis cyanellus* Rafinesque) than unexposed amphipods (Holomuzki and Hoyle, 1990; Wisenden et al., 2001). These studies demonstrate that decreased activity, increased refuge use and increased geotaxis by amphipods in response to alarm pheromones and kairomones are effective behaviours to reduce fish predation.

Many animals behave abnormally when infected with parasites and anti-predator behaviours are among those affected (see Moore, 2002). Parasites can benefit from altered host behaviour if the behavioural changes increase the parasite's transmission rates. These types of parasitic manipulations have been documented in a wide variety of host-parasite interactions (Poulin, 1994; Moore, 2002; Thomas et al., 2005). Aquatic arthropods serve as intermediate hosts for several parasite species (see review in Moore, 2002). Many of these parasites can only grow to adulthood after a predator consumes their intermediate host. Thus, interference in host anti-predator behaviours may be a parasite strategy to increase predation rates by suitable definitive hosts (Dianne et al., 2011).

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Amphipods feature prominently in manipulation research, particularly amphipods infected with worms from phylum Acanthocephala. These thorny-headed worms are known to alter activity (Thunken et al., 2010), orientation to light (Bethel and Holmes, 1973), drift rate (Dezfuli et al., 2003), and refuge use (Perrot-Minnot et al., 2007) in amphipods. This is not an exhaustive list of altered behaviours (see Moore, 2002), but this slate of behaviours is strikingly similar to those that influence predation rates and infected amphipods can be at greater risk of predation than uninfected amphipods (Bethel and Holmes, 1977).

Acanthocephalans also affect amphipod responses to odours. In choice experiments, uninfected amphipods avoided areas with high concentrations of predatory fish kairomones while amphipods infected with acanthocephalans did not. Similarly, given a choice between two water sources, one containing fish kairomones and one free of kairomones, uninfected amphipods avoided the stream containing fish kairomones, while infected amphipods did not discriminate between streams (Baldauf et al., 2007). Some amphipods aggregate when presented with predator kairomones (Kullmann et al., 2008), and certain parasites appear to negate this behaviour when they infect these amphipods (Durieux et al., 2012).

This study asks whether the acanthocephalan *Leptorhynchoides thecatus* (Kostylev) alters its amphipod host's odour-related anti-predator behaviour. *Leptorhynchoides thecatus* is a common fish parasite found in eastern and central North America. It uses a single amphipod species, *Hyalella azteca* (Saussure), as an intermediate host and a broad range of centrarchid fish as definitive hosts. The amphipod is infected when it consumes the parasite egg, which hatches and then develops in the amphipod's haemocoel from a non-infective acanthella stage into an infective cystacanth. A fish acquires the parasite when it consumes an amphipod hosting a cystacanth. The acanthocephalan establishes in the fish's intestinal ceca, matures, finds a mate and produces eggs that pass with the fish's faeces to continue the life cycle.

We hypothesised that *L. thecatus* would alter host amphipod odour responses to alarm cues from *H. azteca* and predator kairomones from *L. cyanellus*. To our knowledge, altered odour behaviour had not been previously investigated in this host-parasite system, and this was one of the first studies to address parasite-altered responses to alarm cues in amphipods. For this *L. thecatus* population it was also found that infected amphipods exhibit altered photophilia, geotaxis and activity, behaviours that may reasonably be thought to influence the likelihood of encountering predators (C.F. Stone and J. Moore, unpublished data). We wished to determine whether *L. thecatus* altered *H. azteca* behaviours directly implicated in predation and transmission rates, that is, anti-predator behaviours. Because dissection is required to reliably determine amphipod infection, it was not easy to conduct predation experiments to determine whether a fish captured infected amphipods at a higher rate than uninfected amphipods.

2. Materials and methods

2.1. Collection of organisms

All organisms used in this study were collected from Atkinson Reservoir, Holt County, Nebraska, USA (42° 32' 36" N, 98° 58' 22" W). This population of *L. thecatus* appears unique in its host use patterns with Green Sunfish (*L. cyanellus*) providing the primary definitive host in this location (Ashley and Nickol, 1989). Capture, collection and culture of animals were carried out under Colorado State University, USA Animal Care and Use protocol 11-2590A and Nebraska Game and Parks Commission scientific collection permits. Green Sunfish (*L. cyanellus*), Pumpkinseed Sunfish (*Lepomis gibbosus* Linnaeus), and Bluegill (*Lepomis machrochirus* Rafinesque)

were captured by seine net on the littoral portion of the lake. On the day of capture, fish were dissected and adult *L. thecatus* worms were removed from each host's alimentary tract, placed in aged tap water and stored at 4 °C. Three juvenile *L. cyanellus* sunfish were captured and transported to the laboratory at Colorado State University, Fort Collins, CO, USA where they served as kairomone sources. Amphipods were also collected from aquatic vegetation found in the same littoral zone as fish sampling and transported to the laboratory.

2.2. Culturing of organisms

Fish captured and transported to the laboratory were cultured in individual 37.85 L aquaria with a hang-on-the-back filtration system. The fish were fed to satiety on Tetramin® tropical fish food once per day and water was changed once every 2 weeks. Because the carbon component of the filtration system removes the organic compounds including fish kairomones sensed by amphipods, the carbon filter was removed from the culture tanks 24 h before behavioural tests.

Amphipods were cultured in 27 L and 30 L Sterilite® plastic storage containers with 1.25 cm of sand substrate and approximately 20 L of culture water. Culture water was formulated from deionised water according to the Moderately Hard Water formula (see U.S. Environmental Protection Agency, 1994). Cultures were given Tetramin® tropical fish food three times per week and water changed weekly. All animals were kept in a climate-controlled room a 23 °C, on a 15:9 light–dark (LD) cycle.

2.3. Infection of amphipods

Eggs were harvested from gravid female worms dissected in several millilitres of tap water. The resulting egg suspension was standardised so that an average of 1.5 fully-embryonated eggs was present per field of view in 0.05 ml of suspension at 100× (Barger and Nickol, 1998). Fifty *H. azteca* were placed in wide-mouthed glass 0.95 L jars containing 800 ml of culture water, 50 g of gravel and 4 g of filamentous green algae (*Pithophora* spp.). Amphipods were exposed to 1 ml of the egg suspension, which was pipetted over the algae. The amphipods foraged for 24–72 h and were then transferred to 4.5 L Rubbermaid® plastic containers, where they were maintained for 32–40 days at 23 °C.

2.4. Test apparatus

A single unframed 18.93 L aquarium (40 cm × 20 cm × 25 cm) was ideal for observing amphipod behaviour, but it had two drawbacks: (i) the volume of water was too large, compared with previous studies (Wisenden et al., 1999), and (ii) the single apparatus was difficult to clean and prepare quickly, given the large number of behavioural tests required. These inadequacies were addressed by inserting a single clear glass partition that separated the aquarium into two equal halves. Silicone sealant was used to line joints to completely separate the two halves, thus creating the functional equivalent of two aquaria. Either half of the aquarium could be filled without water flowing into the other half; each half was similar in size to that used by Wisenden et al. (1999) in their study. A single preparation of this divided aquarium allowed two amphipods to be tested. Detailed behavioural data in both halves of the aquarium could not be recorded simultaneously, so both halves were prepared, two amphipods selected, one amphipod randomly chosen and observed, and the second amphipod observed after the completion the first test. Two potential consequences of this set-up were identified: test order and potential visual interaction of the amphipods during tests. Both of these were statistically eliminated as confounding factors in methods.

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