

REACTIONS OF *Gammarus lacustris* TO CHEMICAL STIMULI FROM NATURAL PREDATORS AND INJURED CONSPECIFICS

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Abstract—We exposed the freshwater amphipod *Gammarus lacustris*, to chemical stimuli from injured conspecifics and to chemical stimuli from two types of natural predators: dragonfly larvae (*Aeshna eremita*) and northern pike (*Esox lucius*). Exposure to all three stimuli caused *G. lacustris* to reduce significantly its level of activity relative to activity recorded in response to a distilled water control. The similarity in responses to chemicals associated with predators and to injured conspecifics suggests the presence of an alarm pheromone within the body tissues of *G. lacustris*. In response to chemical stimuli from pike, *G. lacustris* tended to reduce its time in the water column and spend more time near the bottom of the test aquaria. However, no such trend was apparent in response to chemical stimuli from dragonfly larvae. The differences in response to chemical stimuli from pike and larval dragonflies suggest that *G. lacustris* does not have a rigid behavioral response to predation risk; instead, antipredator behavior may be modified to maximize avoidance of predators that are active in different microhabitats.

Key Words—*Gammarus lacustris*, alarm pheromone, kairomone, predator avoidance, antipredator behavior, *Esox lucius*, *Aeshna eremita*.

INTRODUCTION

Visibility in aquatic habitats is often limited due to low light levels, turbidity, and dense vegetation. Perhaps because of this, many aquatic organisms use chemical cues, such as alarm pheromones and/or kairomones to assess their risk of predation. Alarm pheromones from injured individuals are chemical signals

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which elicit the same, or a similar, response in conspecifics as stimuli associated with predators (Smith, 1992). Alarm pheromones have been identified in various groups of fish (see Smith, 1992 for a review) and numerous other aquatic organisms, including amphibians (e.g., Hews and Blaustein, 1985), gastropods (Snyder, 1967), echinoderms (e.g., Snyder and Snyder, 1970; Parker and Shulman, 1986), sea anemones (Howe and Sheikh, 1975), insect larvae (Sih, 1986; Scrimgeour et al., 1994; Chivers et al., 1996), crayfish (Hazlett, 1994), and one species of amphipod (Williams and Moore, 1985). Kairomones, however, are chemical signals that produce a behavioral change in heterospecific receivers (Brown et al., 1970). The ability to detect predator kairomones and respond in a way that reduces predator success has been studied in numerous and diverse aquatic organisms (see Weldon, 1990; and Dodson et al., 1994 for reviews).

The detection of an alarm pheromone by an individual indicates that a conspecific has recently been captured or injured by a predator in the immediate vicinity. Exposure to alarm pheromone can increase the probability of fathead minnows (*Pimephales promelas*) surviving an encounter with a northern pike (*Esox lucius*) by increasing the latency to capture (Mathis and Smith, 1993a). For larval western toads (*Bufo boreas*) an increase in activity in response to alarm pheromone decreases the capture efficiency of predatory larval dragonflies (*Aeshna umbrosa*) (Hews, 1988). Hews suggests the decrease in capture efficiency is possibly the result of an increase in the physical difficulty of prey capture, an increase in the confusion effect, or an increase in prey awareness and vigilance. Detection and avoidance of predator kairomones may increase prey survival simply by decreasing the probability an individual will occupy the foraging habitat of a potential predator (Brodie et al., 1991).

Previous work on gammarids (Crustacea: Amphipoda: Gammaridae), small freshwater and marine amphipods, has shown that *Gammarus pseudolimnaeus* respond to kairomones of fish predators by decreasing their activity and drift rate (Williams and Moore, 1982, 1985) and increasing the latency to precopulatory pair formation (Mathis and Hoback, 1997). *G. minus* decrease activity in response to chemical stimuli from green sunfish (*Lepomis cyanellus*) (Holomuzki and Hoyle, 1990). When Andersen et al. (1993) added predatory brown trout (*Salmo trutta*) to two previously fishless streams, they noted an immediate reduction in the nighttime drift rate of *G. pulex*. The authors attribute this reduction in activity to chemical detection of trout by the gammarid. *G. pulex* reduce activity in response to the presence of caged predatory sculpins (*Cottus gobio*), but do not react when the sculpins are visible in sealed glass jars (Andersson et al., 1986). This suggests that chemical, rather than visual cues, are important to gammarids for predator detection and, presumably, predator avoidance.

In their review of 22 published studies of the antipredator behavior of stream prey in the presences of predators, Wooster and Sih (1995) found that, in general, prey increase drift in response to invertebrate predators and decrease

activity in response to vertebrate predators. In this study, we examined the response of *G. lacustris*, a common North American and European gammarid amphipod (Bousfield, 1958), to stimuli from injured conspecifics and to chemical stimuli (kairomones) from two natural predators that are active in different components of the *G. lacustris* habitat: benthic dragonfly larvae (*Aeshna eremita*), and an open-water predatory fish, the northern pike. Gammarids can compose a large portion of the diet of larval dragonflies (Pritchard, 1964) and pike (Chapman et al., 1989; Chapman and Mackay, 1990; Sammons et al., 1994), especially where gammarids are abundant and alternative invertebrate prey are scarce.

METHODS AND MATERIALS

Experimental Analysis. In May 1995, mature *G. lacustris* (mean = 0.071 g, SD = 0.007 g, $N = 25$) were collected from Pike Lake, Saskatchewan (51°54'N, 106°49'W), using dipnets, transferred to the laboratory and held in 175-liter aerated aquaria (22°C, 15.5L:8.5D photoperiod). Both northern pike and larval dragonflies occur naturally in Pike Lake; therefore, the test population of gammarids had previous experience with both experimental predators. The gammarids were identified using keys in Pennak (1978). In experiment 1, only male *G. lacustris* were used to avoid the possibility of sex differences in behavioral responses to predation risk during the breeding season (Boates et al., 1995; Mathis and Hoback, 1997). The breeding period of Canadian *G. lacustris* begins in April and continues into July (Bousfield, 1958; Clifford, 1969; De March, 1982), with maximal reproduction occurring when the water temperature reaches 18°C (Smith, 1973). No natural population of *G. lacustris* has been observed in precopula in late summer or autumn (De March, 1982), including the Pike Lake population (personal observation).

In August 1995, smaller, immature *G. lacustris* (mean = 0.026 g, SD = 0.004 g, $N = 25$) were collected from Pike Lake for use in experiment 2. These *G. lacustris* were immediately transferred to 37-liter study aquaria (room temperature of 22°C, 14L:10D photoperiod). The expected life-span of *G. lacustris* is about 15 months (Bousfield, 1958); the majority of mature individuals die in June or July after breeding (Hynes, 1955; Clifford, 1969; Menon, 1969). Menon (1969) estimated that in August, immatures compose 99% of the total *G. lacustris* population in Big Island Lake, Alberta. Since August is not the breeding season for *G. lacustris*, individuals of both sexes were tested.

Stimuli Preparation. Chemical stimuli from a single pike (fork length = 18.2 cm) were used in experiment 1. Use of multiple pike probably would not have affected the results, as several studies with fishes have shown that chemical stimuli from different individual pike elicit similar responses (Gelowitz et al.,

1993; Mathis and Smith, 1993b,c; Brown et al., 1995). Alarm pheromones of fathead minnows ingested by a pike can be released or excreted by the pike and detected by other prey (Mathis and Smith, 1993b,c; Brown et al., 1995). To ensure the pike stimulus contained only cues from the pike without residual alarm pheromones, the pike from which the stimulus was collected was maintained on a diet of mealworm larvae (*Tenebrio molitor*). Mealworms are terrestrial coleopteran larvae not normally encountered by pike or *G. lacustris*; therefore, even if *T. molitor* possesses an alarm pheromone, neither pike nor *G. lacustris* should recognize it. The pike received four mealworms per day for three days. Approximately 6 hr after the final feeding, the pike was rinsed in dechlorinated tap water and placed into an aerated, unfiltered collection chamber (26 × 8 × 8 cm) containing 1200 ml of dechlorinated water and held there for three days without food. The chamber was unfiltered to ensure that chemical stimuli produced by the pike were not removed from the water. The pike was then removed and the chamber water frozen at -20°C in 60-ml aliquots and thawed as required immediately prior to use.

Larval dragonflies (*A. eremita*) (mean body length = 4.41 cm, SD = 0.37 cm, $N = 7$) were caught with a dipnet from Pike Lake in July 1995 for use in experiment 2. The larvae were identified using books by Merritt and Cummins (1984) and Walker (1958). Chemical stimuli from the larval dragonflies were collected in the same manner as the pike stimulus. However, prior to being placed in the collection chamber, all seven dragonflies were held in a 37-liter aquarium without food for one week to clear their digestive tract of residual alarm pheromones and prey consumed before capture. Dragonfly larvae can survive for extended periods without food, due to their low level of activity and low metabolic requirements (Corbet, 1962).

Experimental Protocols and Statistical Analysis. Thirty 37-liter study aquaria, with a substrate of silica sand 1 cm deep, were filled with dechlorinated water to a depth of 25 cm and aerated with a single airstone located at the back of each tank. A few strands of pondweed (*Potamogeton perfoliatus*), watermilfoil (*Myriophyllum*, spp.), and coontail (*Ceratophyllum demersum*), all collected from Pike Lake, were placed on the bottom of each tank such that the vegetation remained below a horizontal line drawn on the tank front 9 cm above the base of the aquarium's floor. The area above the horizontal line was designated as the "water column." The vegetation provided *G. lacustris* with both food and refuge during the experiments. Plastic airline tubing opening near the airstone served as a stimulus injection line. Each of the aquaria held a single, arbitrarily selected *G. lacustris*. Individuals were allowed 12–14 h to acclimate to laboratory conditions before data collection began.

In experiment 1, *G. lacustris* were exposed to one of three stimuli: (1) 20 ml of distilled water (control), (2) 20 ml of pike stimulus, or (3) 20 ml of distilled water containing two crushed mature *G. lacustris*. To test for an injury-

released alarm pheromone, *G. lacustris* were crushed using a mortar and pestle, similar to the way in which a predator might macerate its prey and release alarm pheromone.

In experiment 2, conducted in August, immature *G. lacustris* were exposed to one of three different stimuli: (1) 60 ml of distilled water (control), (2) 60 ml of larval dragonfly stimulus, or (3) 60 ml of distilled water containing three crushed immature *G. lacustris*. Experimental protocols and statistical analyses were identical to those used in experiment 1, except that in experiment 2 three *G. lacustris* were used to prepare the conspecific stimulus to compensate for the smaller size of the *G. lacustris* collected in August compared to those used in the conspecific stimulus of experiment 1.

To clear the stimulus injection line of any stagnant water, 60 ml of tank water was drawn through the line by a syringe just prior to testing and discarded. An additional 60 ml were then drawn and retained. Each experimental trial was composed of two 5-min observation periods separated by a 1-min interval. During the 1-min interval, the test stimulus was slowly injected into the injection line and then flushed into the tank using the previously collected 60 ml of tank water. Water currents created by the airstone quickly dispersed the stimulus throughout the aquaria. Dye tests conducted in previous experiments have shown that stimuli injected in this way are uniformly distributed throughout the tank in about 13 sec (Mathis and Smith, 1993b,c).

During each experimental trial, we quantified the total time each individual *G. lacustris* was active before and after the introduction of a stimulus. An individual was described as active if it was swimming through the water column, swimming or crawling among the vegetation, or crawling along the substratum. Change in activity was calculated by subtracting the time each individual spent active before stimulus injection from time spent active after injection. During each trial we also recorded the time spent above the horizontal line (i.e., in the water column) before and after stimulus injection and calculated the change in time spent in the water column in the same manner as for time active. A Kruskal-Wallis one-way analysis of variance test with nonparametric multiple comparisons (Siegel and Castellan, 1988) was used to test for significant differences in the change in total time active and the change in time spent in the water column in response to the three different chemical stimuli.

RESULTS

Experiment 1: Responses of Gammarus lacustris to Chemical Stimuli from Northern Pike and Injured Conspecifics. There was a significant overall difference in the change in time *G. lacustris* spent active among the three different treatment conditions ($KW = 8.86, P < 0.05$). In response to chemical stimuli

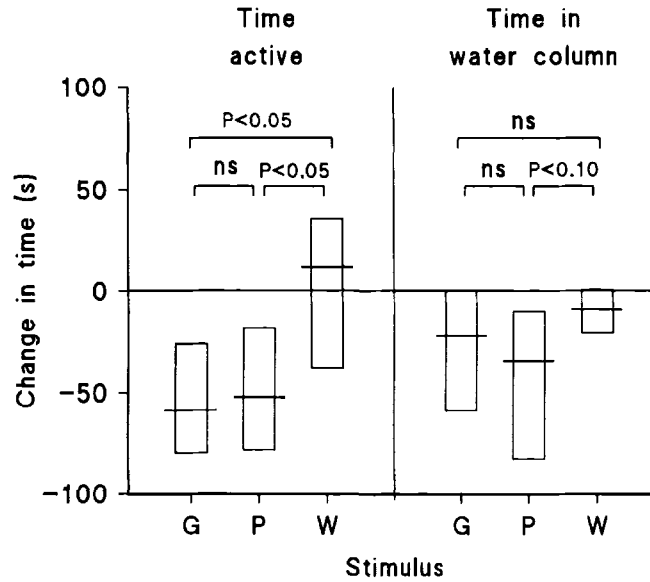


FIG. 1. Median values ($\pm 25\%$ quartiles) reflecting a change in the time *G. lacustris* spent active (swimming or crawling) and a change in the time spent in the water column before and after injection of various stimuli. Level of significance ($P < 0.05$, $P < 0.10$) calculated by post-hoc nonparametric multiple comparisons of a Kruskal-Wallis ANOVA (ns denotes $P > 0.10$). G = distilled water containing crushed conspecifics (*G. lacustris*), P = chemical stimuli from northern pike, W = distilled water control.

from injured conspecifics and from pike, *G. lacustris* significantly decreased their time spent active when compared to the distilled water control ($P < 0.05$ for both stimuli, Figure 1). There was no significant difference in the change in time spent active between the response of *G. lacustris* exposed to injured conspecifics and those exposed to chemical stimuli from pike ($P > 0.10$, Figure 1).

The overall difference among the treatment conditions in the change in time *G. lacustris* spent in the water column was not significant, although a trend was evident ($KW = 4.64$, $0.05 < P < 0.10$). *G. lacustris* tended to reduce the amount of time spent in the water column in response to the pike stimulus compared to distilled water (Figure 1).

Experiment 2: Responses of Gamma lacustris to Chemical Stimuli from Dragonfly Larvae and Injured Conspecifics. There was a significant overall difference in the change in time *G. lacustris* was active ($KW = 12.72$, $P < 0.05$). Compared to distilled water, *G. lacustris* significantly decreased activity

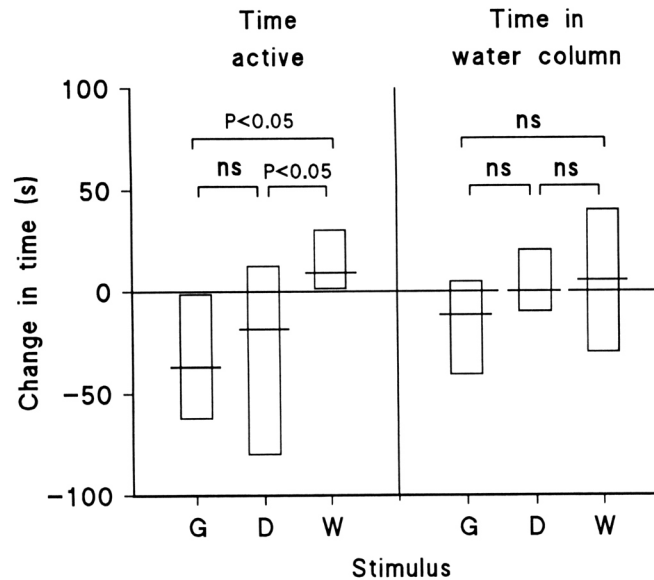


FIG. 2. Median values ($\pm 25\%$ quartiles) reflecting a change in the time *G. lacustris* spent active (swimming or crawling) and a change in the time spent in the water column before and after injection of various stimuli. Level of significance ($P < 0.05$) calculated by post-hoc nonparametric multiple comparisons of a Kruskal-Wallis ANOVA (ns denotes $P > 0.05$). G = distilled water containing crushed conspecifics (*G. lacustris*), D = chemical stimuli from dragonfly larvae (*Aeshna eremita*), W = distilled water control.

in response to stimuli from injured conspecifics and to stimuli from larval dragonflies ($P < 0.05$ for both stimuli, Figure 2). In terms of reduced time active, there was no significant difference between the response of *G. lacustris* exposed to injured conspecifics and those exposed to chemical stimuli from dragonfly larvae ($P > 0.10$, Figure 2). There was no overall significant difference among treatments in the time *G. lacustris* spent in the water column ($KW = 2.15$, $P > 0.10$, Figure 2).

DISCUSSION

G. lacustris displayed the ability to detect and respond to predator kairomones from pike and from a larval dragonfly. In response to kairomones from both predators, *G. lacustris* significantly decreased activity. Both larval dragonflies (Corbet, 1962; Pritchard, 1965) and pike (Savino and Stein, 1989) are visually oriented, ambush predators, remaining immobile until they perceive

movement by a prey organism. By reducing activity, *G. lacustris* can possibly reduce visual detection and avoid attack, especially from larval dragonflies, which can perceive moving prey at distances of up to 20 cm; however, motionless prey can only be detected at distances of up to 5 cm (Corbet, 1962). Motion has also been shown to increase the distance at which fish (Wright and O'Brien, 1982) and bird (Martel and Dill, 1995) predators can detect their potential prey. The ability to detect and respond adaptively to kairomones from predatory invertebrates and fish has also been found in *G. pseudolimnaeus* (Williams and Moore, 1982, 1985; Mathis and Hoback, 1997), *G. minus* (Holomuzki and Hoyle, 1990), and *G. pulex* (Andersson et al., 1986; Andersen et al., 1993).

The reduction in activity displayed by *G. lacustris* when exposed to crushed conspecifics was similar to its response to chemical stimuli from both predators. This indicates that some component of the body tissues of *G. lacustris* alerts conspecifics to respond in the same manner as to chemicals associated with danger from predators. Therefore, *G. lacustris* possesses an alarm pheromone.

Wooster and Sih (1995) found that, in general, prey increase drift in response to invertebrate predators and decrease activity in response to vertebrate predators. *G. lacustris* tended to move out of the water column towards the bottom of the test aquaria in response to chemical stimuli from pike, predators that remain in or near the shallow vegetated regions of the littoral zone (Chapman and Mackay, 1984). However, there was no such tendency in response to chemical stimuli from larval dragonflies, benthic predators that live among submerged vegetation (Pritchard, 1965). This qualitative difference in antipredator response suggests that *G. lacustris* is capable of recognizing and reacting with variable antipredator behavior to stimuli from different types of predators. Variable antipredator behavior has previously been observed in *G. pseudolimnaeus* (Williams and Moore, 1985). In response to the slow-moving, tactile, benthic, predatory stonefly larvae, *Phasganophora capitata*, *G. pseudolimnaeus* increases activity and drift; however, to visually oriented predators, such as the crayfish, *Cambarus robustus*, *G. pseudolimnaeus* significantly reduce their activity level.

Mature individuals of a closely related species, *G. pseudolimnaeus*, react to the non-contact presence of numerous fish and invertebrate predators regardless of season (Williams and Moore, 1985). All sizes of *G. pseudolimnaeus* respond to trichopteran predators, which only prey on very small amphipods (Williams and Moore, 1985). In both experiments, *G. lacustris* decreased activity in response to conspecific cues (a general antipredator response) independent of the time of year and the age class of test gammarids. Therefore, it is unlikely that the different times of season and age classes of test animals used in this study are responsible for the variation in antipredator behavior of *G. lacustris*. Besides fish and dragonfly larvae, amphipods are potential prey to many other predators, such as ducks (Winfield and Winfield, 1994), shorebirds (Boates et

al., 1995), crayfish (Williams and Moore, 1985), and numerous small predatory invertebrates (e.g., Dytiscidae, Notonectidae). Being vulnerable to so many different types of predators, each with its own unique hunting style, possession of variable antipredator behavior that allows individuals to react to each potential threat as it occurs would be of great benefit to *G. lacustris*. Variability in antipredator behavior allows prey individuals an opportunity to maximize survival against multiple predators that are active in different microhabitats or that possess different hunting styles.

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