

**Predator-prey Interactions Involving Chemical Stimuli in**

*Orconectes propinquus* and *Physa integra*

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## Abstract

Non-visual stimuli have recently been implicated in predator-prey interactions involving crayfish and snails. Chemical cues from actively foraging crayfish have been found to initiate avoidance response in a number of snail species. Avoidance behavior of the freshwater snail *Physa integra* in response to the crayfish *Orconectes propinquus* was examined in a series of experiments performed in a riffle of Tenderfoot Creek in the Upper Peninsula of Michigan. In laboratory experiments, snail avoidance response was found to be independent of dark conditions, which are normally associated with most active foraging. Laboratory experiments also demonstrated no significant difference in avoidance behavior between treatments with crayfish and those without crayfish, yet corresponding field experiments suggested a significant difference. In the second experiment, no significance was found between the three treatments: with crayfish, without crayfish, and "visual" crayfish. In the last experiment, *P. integra* was found to demonstrate avoidance behavior in the presence of actively foraging *O. propinquus*. Results demonstrate snail avoidance behavior in the form of crawl-out or burying under artificial substratum as a response to the active foraging of *O. propinquus* on *P. integra* conspecifics. It is thought this is an adaptive response to the shell architecture of *P. integra*. *P. integra* was only found to demonstrate an avoidance response without active foraging in the first field experiment, while other experiments showed no significant difference between the with crayfish and without crayfish treatments. From these results the possibility an avoidance response being elicited without active foraging remains inconclusive, yet data suggest stronger responses occur with predation.

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### Introduction

Benthic prey in aquatic ecosystems have been found to exhibit a wide variety of behavioral responses to invertebrate and vertebrate predators. Although a great number of behavioral observations have been made, the types of stimuli that cause these behaviors remain allusive in many cases. It is a current view that non-visual stimuli are an important component in many of these responses. Prey can use non-visual signals in detection and location of the predator, while predators have been found to use the signals to differentiate between prey. Results of recent studies suggest the area of non-visual communication to be of major ecological and evolutionary importance.

Four major types of chemicals used by aquatic prey to avoid predators have been identified (Dodson et al. 1994). They include kairomones, alarm substances, feeding deterrents, and chemicals used for habitat selection. Kairomones are chemicals that affect behavior, morphology and life history characteristics of prey. Alarm substances, produced by many species of fish, and in some invertebrates, are released by damaged conspecifics. Feeding deterrents are chemicals attached to the prey individual which are released after contact with the predator, therefore acting over a very small time and spatial scale. Habitat selection chemicals are emitted by predators and can be detected by prey if they are significantly stronger than the background signal.

Chemoreception has been shown to be extremely important to freshwater gastropods, specifically in the detection of predators. Most previous literature has focused on the interaction between the snail prey and the crayfish predator. Studies of gastropod-decapod interactions have shown that prey showed the strongest response when exposed not only to the predator, but also to injured conspecifics (Covich et al. 1994). Other studies have also found that both conspecific and predator signals are necessary for a response (Crowl and Covich 1990). Thus, a co-involvement of kairomones and alarm substances have been implicated in one of the major predator-prey interactions in streams, that of crayfish and snails.

One of the major effects of these chemicals is a change in life history characteristics of the prey. The snail *Physella virgata* has been observed to change its life history characteristics in response to chemicals stimuli released by the crayfish *Orconectes virilis* (Crowl and Covich 1990). The chemical is released when crayfish feed on snails. Snails in the presence of the cue exhibited rapid growth rate and minimal reproduction until they reached a size of about 10 mm in eight months, while without the cue, the snails grew to an average of 4 mm and then reproduced. It is believed that the increase in size and the delay of reproduction allows for coexistence with the predator, since crayfish prey selectively on smaller snails (Crowl 1990).

Alexander and Covich (1991b) further demonstrated this size-dependent avoidance response by measuring the frequency of crawl-out; the movement of the snail above the water line. Larger *Physella trivolis* did not exhibit a crawl-out response, but relied on a strong shell for defense. Smaller *P. trivolis* and *P. virgata* were found to exhibit crawl-out behavior in the presence of the crayfish. Further studies have attempted to determine if response is geographic or species specific. Responses of eight gastropod populations were exposed to predation by three species of crayfish to determine the importance of species or geography in the observed behavior. Pulmonate gastropod species were found to show similar responses to alarm signals, four of six populations demonstrated crawl-out. No crawl-out was observed in the Prosobranch species. Individual variations in responses to predators were also examined in differing snail species. Variation is thought to be a result of selection pressure of the varying costs and benefits associated with varying micro habitats (Covich et al. 1994).

Gastropod-decapod interactions were explored in a stream in the Upper Peninsula of Michigan, to expand on previous work. Predator-prey interactions between the crayfish species *Orconectes propinquus* and the snail species *Physa integra* were examined in this study. Objectives were to (1) investigate the difference in avoidance behavior in the day vs the night, (2) determine if snails of this species would demonstrate an avoidance response without active foraging, (3) explore the influence of a visual predator in order to enforce the idea of chemical cues, and (4) to determine if avoidance response existed with active foraging, and if it elicited the greatest response. Avoidance response, defined as crawl-out or hiding under the substrata was used to determine prey response.

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### Materials and Methods

Field experiments were performed in a riffle area of Tenderfoot Creek located in the Western half of the upper peninsula of Michigan on the UNDERC property. They were conducted from early to mid-summer (May to mid-July). Laboratory experiments were performed in the wet lab on the UNDERC property.

In order to measure the response of snails to the crayfish predator in the field, predation cages were built and placed in a riffle of Tenderfoot Creek, oriented parallel to the current (Figure 1). The cages consisted of 1 m long plastic gutters, measuring three inches at the base and five inches at the top. Chicken wire (1/8") was cut to cover both ends and to create a middle division. Wire size prohibited the movement of organisms out of the cage or their respective halves, while minimally affecting the flow rate of the water within the cage. Holes were drilled on either end and in the middle of the gutter to attach the wire screens. Clear plexiglass was placed on top of each of the gutters, and attached on one side to allow for opening during the experiment. Wire screens and the plexiglass covers were both attached using fishing line. Two holes were also drilled in the bottom of the cages approximately 1 inch from the end. Small rope was strung through the two holes and tied to the top of two bricks to prevent movement downstream and to allow for positioning in the water column. A piece of chicken wire was cut to cover the bottom of the upstream half of the cages so the crayfish had more stability and freedom of movement in the flowing water. Four 3" X 3" tiles were placed in the downstream end of the gutters to simulate natural hiding substrate for the snails. Tiles were placed in the stream at least 2 weeks prior to the beginning of the experiment to ensure a significant source of phytoplankton for the snails. The tiles were elevated slightly with small rocks from the stream (1-2 per tile) to allow for snail movement underneath the tiles. Snails were collected from Tenderfoot Creek by hand from stones, cobble or decaying wood. Crayfish were collected by a combination of trapping and snorkeling in various lakes on the UNDERC property (primarily Tenderfoot Lake). Three separate experiments were performed to examine the effect of chemical stimuli released from crayfish on prey behavior.

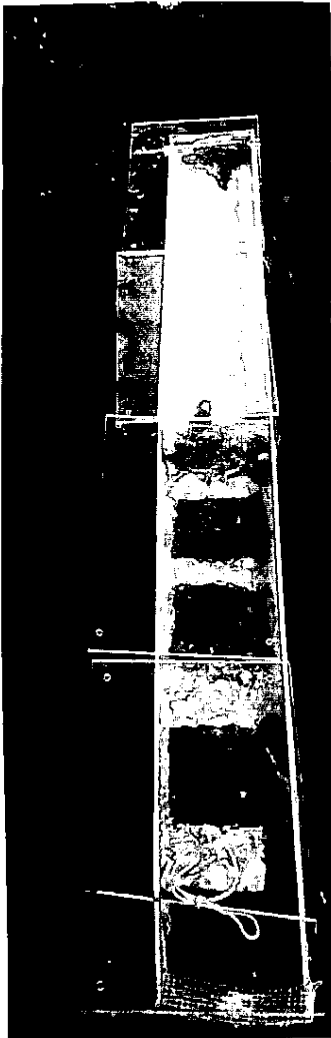
#### *Experiment 1a: Predator avoidance in light and dark and crayfish presence under controlled lab conditions*

The laboratory experiment was conducted to determine if (1) a significant difference existed between avoidance behavior in the night and day and (2) to determine if predation avoidance was affected by crayfish presence. Chicken wire (1/8") was used to divide large(10 gall.) aquaria in half. A wire top was also constructed for the crayfish side to prevent climb out, creating what looked like an upside down L' in the tank. Aquaria were filled with water from Tenderfoot Lake, and maintained at a temperature of 12 ° C by placing the aquaria in cool ground water which was run over a lab bench (about 1" deep). The lab bench had been constructed with two faucets at one end and a drainage pipe at the other end, allowing constant flow to be maintained. The top of the bench had a plastic top and sides that prohibited water loss from the sides and bottom of the structure. Bubbler were placed at both ends of the tank. Four 3" X 3" tiles were each placed on top of a small rock in the snail half of the tank to provide a place for refuge. Ten snails were placed in one half of all four tanks, in the middle of the four tiles, so the relative positions in the replicates would be the same at the beginning of the experiment. Two of the tanks remained empty on one side, while the other two had 2 crayfish in each. Organisms were given an hour to acclimate before observations were begun. Avoidance behavior was defined as crawl-out or hiding underneath the tiles (substrata). It was measured by counting the number of snails that were visible in the cages that had not moved above the water line. This number was subtracted from ten to determine the number under the substrate, and the percent avoidance behavior was calculated. Observations were recorded every hour for the next six hours, and four replicates were performed. Night observations were taken using a red headlamp, since the crayfish are sensitive to white light. Snails could only be kept alive for a maximum of 48 hours in the lab, and the cause of the death could not be determined. Because of this problem, the other two experiments were not performed in the lab.

#### *Experiment 1b: Predator avoidance under field conditions*

In the field portion of the first experiment, four cages were set up in the stream as described above. Two crayfish were placed into the upstream half of two of the gutters, while the other two remained empty in the

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**Figure 1.** Experimental enclosures. Upstream halves contain the crayfish, downstream halves contain the snails.

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upstream half. Ten snails were placed in the middle of the downstream halves of all four cages. After a one hour acclimation period, the prey behavior was observed. Behaviors were recorded every hour for the next 6 hours. The experiment was replicated a total of 4 times.

### *Experiment 2: Predator avoidance in response to visual stimulus*

The second experiment was designed to determine if the prey behavior was a response to visual or chemical stimuli. Two crayfish were frozen and then dried for several hours before being placed in the stream to ensure that they were not emitting any kind of chemicals. The design consisted of 3 cages, again only varying the upstream halves. These "visual" crayfish were placed in one of the cages, two live crayfish in the second cage, and no crayfish in the third cage. Avoidance behavior was determined for each hour of the 4 hour experimental period in the same manner as the first experiment, by counting the number of visible snails in the cage and subtracting this from ten in order to determine percent avoidance behavior. The experiment was replicated seven times.

### *Experiment 3: Predator avoidance in response to active foraging of conspecifics*

The third experiment examined the difference in behavioral responses of prey in the presence of only the predator and in the presence of the predator actively preying on conspecifics. Four cages were set up in the stream. All four contained 10 snails in the downstream half. Four different treatments were applied to the upstream component: crayfish, crayfish and snails together, snails, and a control with no organisms. To ensure the crayfish preyed on the snails in the second treatment, live snails were superglued to each tile, and then their shells were crushed just before placement in the stream. This prevented drift of the snails downstream, while allowing the crayfish to easily consume the prey. The organisms were allowed a one hour acclimation period, and then observations were recorded every hour for four hours. This procedure was performed six times.

### *Statistical Procedure*

One-way ANOVA was used to determine if a significant difference existed between night and day. Separate ANOVA's were performed for the with crayfish and without crayfish treatments. Two-way ANOVA was used to determine if differences existed between the treatments. Significance values were obtained for treatment and hour effect, and interaction. Tukey's HSD test was used to determine where specific differences among treatments and time resided in experiments. An alpha level of 0.05 was applied to all experiments. Graphs of the results showing percent avoidance behavior per hour were also created.

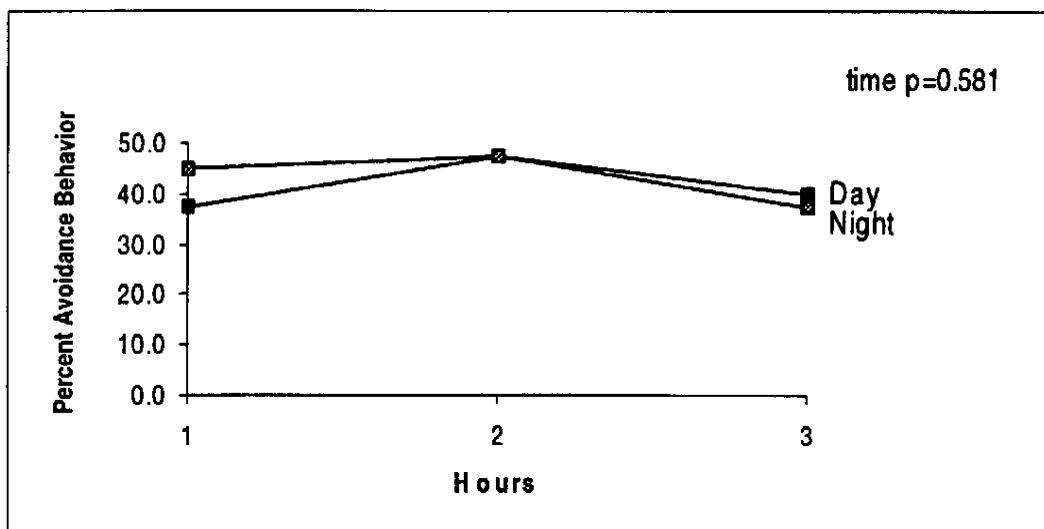
## Results

### *Experiment 1a: Predator avoidance in light and dark and crayfish presence under controlled lab conditions*

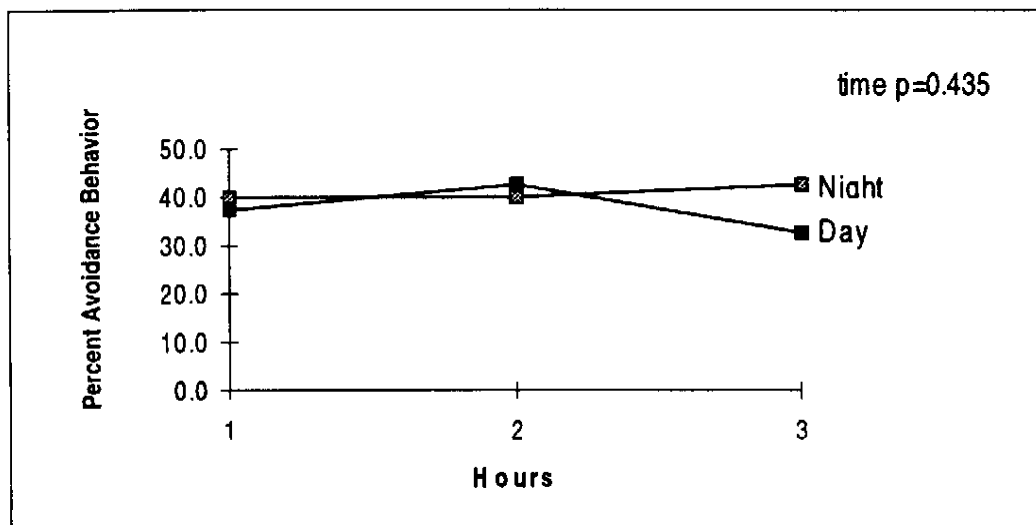
The four replicates were averaged to create a percent avoidance behavior for hours one, two and three in the light, and for hours one through three in the dark. The with crayfish and without crayfish treatments were separated for statistical and graphing procedures. In the presence of the crayfish, the snails exhibited an average of 37.5% avoidance for hour 1, 47.5% avoidance for hour 2, and 40.0% avoidance for hour three in the light. In the dark with crayfish, the snails showed 45.0% avoidance hour 1, 47.5% avoidance hour 2, and 37.5% avoidance hour 3. There was no significant difference between light and dark (One-way ANOVA,  $F_{1,22}=.314$ ,  $p=.581$ ). In the treatment without crayfish in the light, snails exhibited an average of 37.5% avoidance for hour 1, 42.5% avoidance for hour 2, and 32.5% avoidance for hour 3. The dark values were 40.0% avoidance for hour 1, 40.0% avoidance for hour 2, and 42.5% avoidance for hour 3. There was also no significant difference between light and dark in this treatment (one-way ANOVA,  $F_{1,22}=.633$ ,  $p=.435$ ) (Figures 2a & b).

To determine the effect of the treatment on the avoidance behavior, the four replicates were averaged to obtain percent avoidance behavior for each of the six hours for the two treatments with crayfish and without crayfish. In the presence of crayfish, percent avoidance behavior ranged from 37.5% for hour six to 47.5% for hour

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**Figure 2a.** Laboratory experiment 1. Percent avoidance behavior during day and night conditions in the with crayfish treatment. No significant difference was found in behavior between the night and day.



**Figure 2b.** Laboratory experiment 1. Percent avoidance behaviors during day and night conditions in the without crayfish treatment. No significant difference was found in behavior between the night and day.

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five. Without the crayfish, percent avoidance behaviors ranged from 32.5% for hour three to 42.5% for hour three. The interaction term was not significant (two way ANOVA,  $F_{5,36}=0.276$ ,  $p=0.923$ ). No significant difference was observed between the two treatments (two-way ANOVA,  $F_{1,36}=0.762$ ,  $p=0.389$ ). A significant difference was not observed between hours (two-way ANOVA,  $F_{5,36}=0.562$ ,  $p=0.728$ ) (Figure 3).

### *Experiment 1b: Predator avoidance under field conditions*

Like the laboratory experiment, four replicates were averaged to determine average percent avoidance behavior for each of the six hours. The values ranged from 20.0% avoidance for hour six to 47.5% avoidance for hour 2 with the crayfish. Without the crayfish, the values ranged from 10% avoidance for hour 6 to 32.5% avoidance for hour 1. The interaction term was not significant (two-way ANOVA,  $F_{5,36}=0.628$ ,  $p=0.680$ ) A significant difference exists between the two treatments (two-way ANOVA,  $F_{1,36}=6.153$ ,  $p=0.018$ ). A significant difference was also found in the hours (two-way ANOVA,  $F_{5,36}=3.664$ ,  $p=0.009$ ). Tukey's LSD showed a significant difference between hours one and six ( $p=0.043$ ) and between hours two and six ( $p=0.009$ ) (Figure 4).

### *Experiment 2: Predator avoidance in response to visual stimulus*

Experiment 2 consisted of three treatments: with crayfish, without crayfish and "visual" crayfish. Values for the seven replicates were averaged for each of the four hours. For the without crayfish treatment, the values ranged from 21.4% for hour 2 to 22.9% for hours 1, 3, and 4. The with crayfish treatment exhibited values from 25.7% for hours 2 and 4 to 30.0% for hour 3. The "visual" crayfish treatment values ranged from 20.0% to 27.1% for hours 2 and 4. Interaction was not significant (two-way ANOVA,  $F_{6,72}=0.282$ ,  $p=0.944$ ). There was no significant difference between the treatments (two-way ANOVA,  $F_{2,72}=0.775$ ,  $p=0.465$ ). There was also not a significant hour difference (two-way ANOVA,  $F_{3,72}=0.161$ ,  $p=0.922$ ) (Figure 5).

### *Experiment 3: Predator avoidance in response to active foraging of conspecifics*

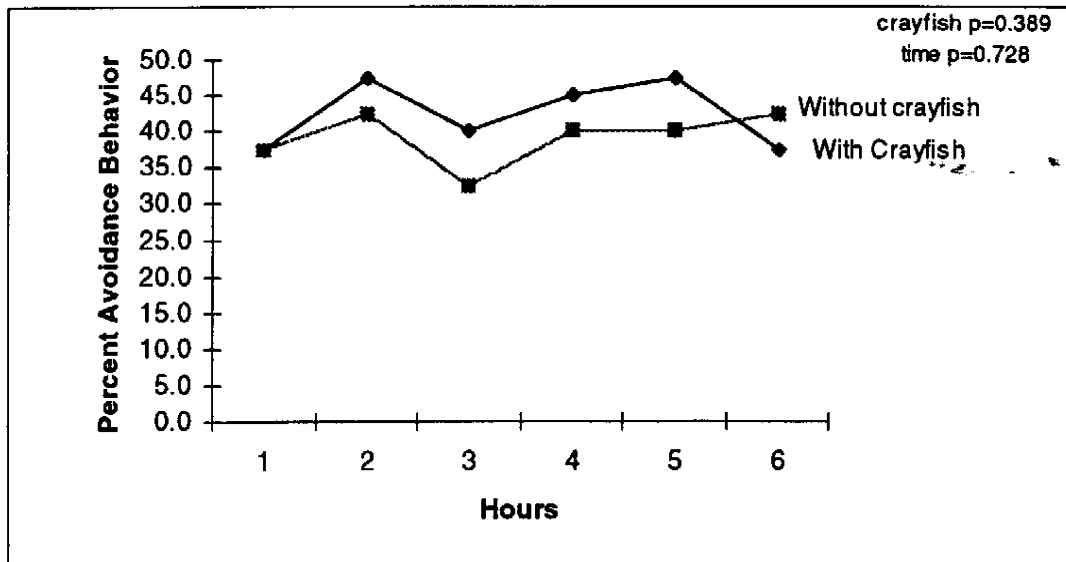
Four upstream treatments were used; without crayfish, with crayfish, crayfish and snails, and snails. Six replicates were averaged for the each of the four hours to determine percent avoidance behavior. For the without crayfish treatment, values ranged from 17.0% for hour four to 22% for hours one, two and three. The with crayfish treatment showed values from 27.0% for hour four to 35% for hour three. Values ranged from 25.0% to 45.0% for the crayfish and snails treatment. For the snails treatment, values were observed from 20% at hour three to 25% at hour two. The interaction term was not significant (two way ANOVA,  $F_{9,80}=0.821$ ,  $p=0.599$ ) No significant difference was observed between the hours (two way ANOVA,  $F_{3,80}=0.297$ ,  $p=0.827$ ). A significant difference was demonstrated between the treatments (two way ANOVA,  $F_{3,80}=4.152$ ,  $p=0.009$ ). Tukey's HSD Multiple Comparison's Test was used to determine a significant difference between the crayfish and snails treatment and the snails treatment ( $p=.033$ ), and between the crayfish and snails treatment and the without crayfish treatment ( $p=.007$ ) (Figure 6).

## Discussion

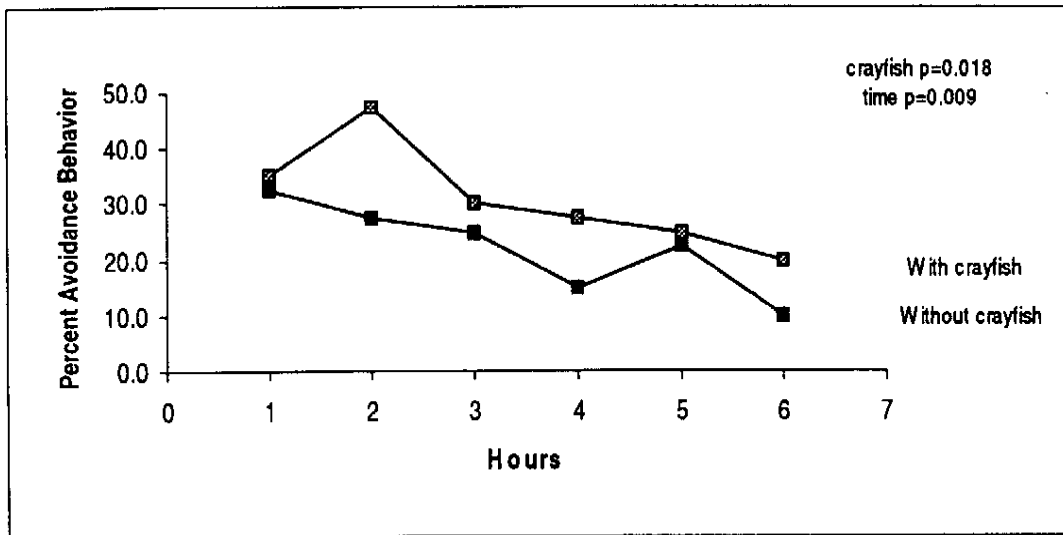
Previous studies exploring the predator prey interactions of snails and crayfish have been conducted at night to stimulate natural conditions under which crayfish are the most active. (Alexander and Covich 1991b, Crowl and Covich 1990). Experimental results demonstrate no significant difference between night and day for the snail avoidance behavior. *O. propinquus* may exhibit the same amount of activity during the night as in the day, perhaps demonstrating some sort of species-specific effect. Or, greater crayfish activity during the night could have occurred, but may have had a minimal effect on the snail avoidance behavior. Further experimentation would be needed to determine the reason conclusively, specifically experiments conducted in natural conditions to support or refute what was found in the laboratory.

Because there was significant difficulty keeping the experimental organisms alive in the laboratory set-up, this could have had some effect on the data generated. When the laboratory data for the first experiment are compared with the field data for the first experiment, the results are conflicting. The data from the lab experiment shows no significant difference in the two treatments. Data from field experiments show differing results, and

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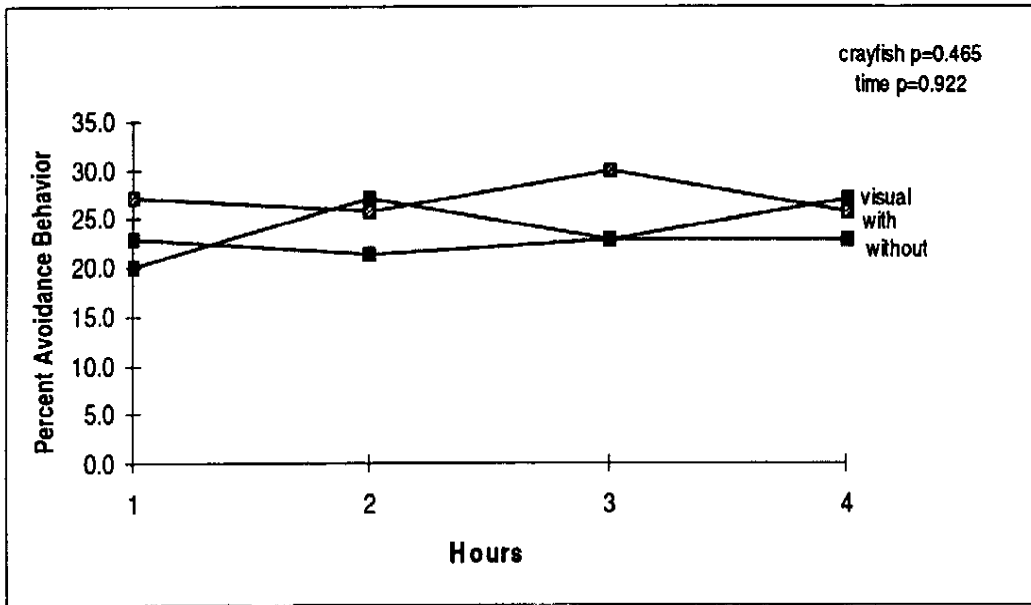


**Figure 3.** Laboratory experiment 1. Percent avoidance behavior under controlled laboratory conditions for with crayfish and without crayfish treatments. No significant difference was found between the treatments or the hours. The interaction term was not significant.

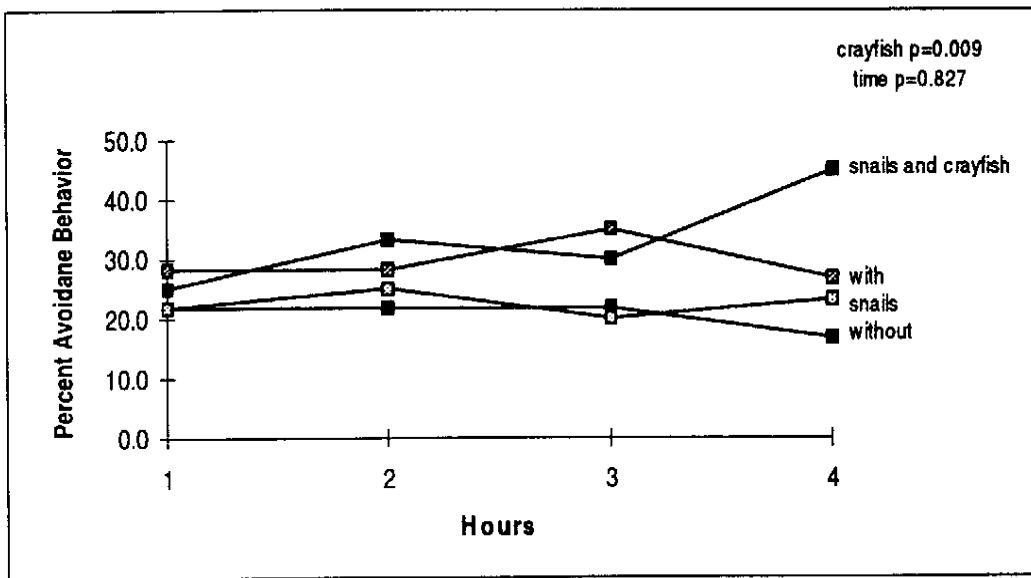


**Figure 4.** Field experiment 1. Percent avoidance behavior of snails under field conditions for with crayfish and without crayfish treatments. A significant difference was found between the treatments and the hours. Tukey's LSD showed a significant difference between hours one and six ( $p=0.043$ ) and hours two and six (0.009). The interaction term was not significant.

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**Figure 5.** Experiment 2. Percent avoidance behavior of snails to the presence of "visual" crayfish, with crayfish and without crayfish treatments. No significant difference was found between the treatments or the hours. The interaction term was not significant.



**Figure 6.** Experiment 3. Percent avoidance behavior of snails to crayfish and snails, snails, with crayfish, and without crayfish treatments. A significant difference was found between the treatments. Tukey's LSD showed a significant difference between the snails and crayfish and the snails treatment ( $p=.033$ ) and the crayfish and snails and the without crayfish treatment ( $p=.007$ ). The interaction term was not significant.

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demonstrate a significant difference in avoidance behavior in the presence of the crayfish. Neither of the experiments had a significant interaction term, demonstrating that the hour has no effect on the treatment, and vice versa. This held true for all the other experiments that were performed also; no interaction terms were found to be significant.

Perhaps the artificial conditions in the laboratory differed too greatly from the natural conditions the crayfish and snails are accustomed to. The differences could have an effect on the crayfish or snail behavior separately or in combination, generating different results than were seen in the field. Because of the high mortality rate, it is unclear how much the lab data can be interpreted. Snail mortality was extremely high in the laboratory experiments. Many adjustments were made to the water, oxygen, and temperature conditions before the snails would survive for an entire experimental period. The cause of the high mortality could not be determined even after several of these adjustments. It is thought that running water may have been the needed environmental factor, since this is the only measure that could not be changed to make the lab conditions resemble the field conditions. Snails used to acquire data for these experiments survived a maximum of forty-eight hours after the observations were taken. For this reason, and reasons mentioned above, the field data is most likely more representative of natural behavior. Therefore, accompanying laboratory experiments were discontinued for the remainder of the experiments.

Although the laboratory data showed no significant hour effect, the field data did show some significant differences between hours. The data for the first experiment in the field demonstrate a greater amount of avoidance behavior during the beginning hours of the experiment, with an average decrease as time went on (Figure 4). Tukey's LSD test conducted on the hour data demonstrated significant differences between hours 1 and 6 and hours 2 and 6. Alexander and Covich (1991a) have found a decrease in crawl-out response 3 hours after the onset of avoidance response. Findings indicate support to a 2-4 hour period of alarm behavior that has been shown for most snails, because avoidance behavior is significantly lower in the last hour than the first two.

The "visual" crayfish experiment was designed to enforce the idea of a strictly chemical cue acting as the catalyst of avoidance behavior. Yet, results demonstrated no significant difference in the avoidance behavior of the snails in the three treatments. Several reasons have been hypothesized for these results. Although the crayfish was dried after freezing, the drying time may have been too short. Crayfish still may have been emitting smell, or chemicals that could have had an effect on snail behavior. Also, some crayfish decomposition occurred during the course of the experiment. By the last replication, they were obviously emitting odor, yet it is unclear if this could have had an effect on response. It is interesting to note that all averages for the with crayfish treatment were higher than the without treatment (though not significant), but the visual treatment fluctuated between the two, showing no real pattern. Data suggest a re-examination of the data from the first field experiment, which suggested a significant difference between the with crayfish and without crayfish treatments, which is not supported here. None of the ANOVA terms were significant which suggests that active foraging may be necessary to elicit snails avoidance response. From these results, in light of those in field experiment 1, it is not conclusive if a chemical released by the crayfish without predation is responsible for avoidance behavior. From these results, it can not be inferred that the cue is strictly chemical.

The avoidance behavior was the greatest when crayfish were actively foraging on the snails, supporting the literature (Alexander and Covich 1991a; Alexander and Covich 1991b; Crowl and Covich 1990; Crowl 1990). Avoidance averages were greatest for this treatment, with the crayfish treatment showing similar but slightly lower averages (Figure 6). Tukey's HSD test results demonstrate a significant difference between (1) the crayfish and snails treatment and the snails treatment and (2) the crayfish and snails treatment and the without crayfish treatment. No significant difference was found between the crayfish and without crayfish treatments, supporting the results of experiment two. This seems to further the evidence that a significant avoidance response is most obviously demonstrated with active foraging on conspecifics.

The release of the chemical with active foraging supports the behaviors that have been previously observed in snail and crayfish interactions. *Physella virgata* has been found to react to chemical signals given off by crayfish actively foraging on conspecific snails; they do not react to inactive crayfish (Alexander and Covich 1991). These findings correspond to recent studies which have also found avoidance behavior occurs in the

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presence of crayfish actively foraging on snails. Responses of delayed age and size of maturity and increased longevity in *Physella virgata virgata* were only elicited in the treatment with crayfish actively preying on snails. Crayfish only and snails only treatments did not result in any response (Crowl and Covich 1990).

Experimental evidence supports Covich and Crowl's (1994) conclusion that crawl-out behavior is widespread in populations of thin-shelled Physids and Lymnaeids. Alexander and Covich (1991) also demonstrated avoidance response in the presence of active foraging. When crayfish were feeding, small *P. trivolis* and all *P. virgata* showed crawl-out behavior. *P. integra* has a similar shell architecture to *P. virgata*: a thinner, elongate spiral shell. Because this shell can be easily manipulated and crushed by the crayfish, *P. integra* is vulnerable to crayfish predation. This increased vulnerability provides a possible explanation for the experimental behavior observed. As a result of the of this vulnerability, the avoidance behavior demonstrates an adaptive advantage since crawl-out and burying behavior of snails acts minimizes the possibility of an encounter with the crayfish predator. Also, the need for oxygen in this species is not limiting. This offers supporting evidence that the observed snail response was due to predation threats and not other factors. It also indicates that other possible factors that might elicit avoidance response should be examined in further studies.

It is evident from the results that crawl-out behavior in *P. integra* is advantageous. Although crawl-out behavior has been demonstrated as adaptively advantageous, it is important to note that avoidance behavior, specifically crawl-out has associated costs. These include increased risk of terrestrial predation, decreased foraging time, and the risk of desiccation (Alexander and Covich 1991b). The presence of these risks has specific effects on the amount of avoidance behavior exhibited by the snails. This difference in environmental factors may be a possible explanation for the differences in avoidance response between the experiments. Depending on other environmental factors, avoidance behavior will show fluctuation.

Along with differing environmental factors, the nature of the chemical cue may cause a difference in the level of response. Because the exact chemical has not yet been identified, it is unclear what these mechanisms may be. There are two possible sources of the chemical borne cue. Either one of two types of chemical cues are involved—a combination of a kairomones emitted from the crayfish and an alarm substance emitted from the snails or the crayfish must consume the conspecific prey and secrete or release a partially digested snail extract modified by crayfish enzymes (Covich and Crowl 1994). Both of these hypotheses suggest a need for the active foraging to elicit a response, which was indicated in all but one experiment.

Results indicate an agreement with past conclusions on the effect of crayfish actively foraging on snails on avoidance behavior. Yet, findings also may indicate some avoidance behavior without active foraging. Reasons for these differences are inconclusive, yet the positive avoidance response without active predation can not be ignored. Uncaged conspecifics in the stream were also likely to be emitting kairomones and/or alarm substances, which may have had an effect on experimental results. Yet, the effect of these chemicals can not be determined, since very little is known about the persistence of chemical signals in the aquatic environment. In streams, this would decrease the possibility of influence from non-experimental organisms. Turbulence can also distribute chemicals much faster than diffusion kinetics, so chemicals may be very short lived. There is also the possibility of a threshold for chemical signals. If this threshold is exceeded, then a behavioral response will be observed, independent of gradient. (Dodson et al. 1994) Perhaps such a threshold could vary between the experimental time (month and time of day), the weather, or other non-static factors, which were all differences between the experiments.

Considering these factors, it seems possible that the results of field experiment 1 demonstrating avoidance response without active predation can not be considered completely incorrect. Therefore, while it seems unlikely from other results that only presence caused avoidance response, this can not be concluded from the experimental evidence. The results do point to an increased percentage of avoidance behavior in the presence of active foraging. *P. integra* most likely exhibits this behavior as an adaptive response to its shell architecture. *Physa integra* does exhibit avoidance response in the presence of *Orconectes propinquus* actively foraging on snail conspecifics, yet it remains unclear what the effect of the crayfish is on avoidance behavior without active predation. Future research is needed to determine the exact nature of the avoidance response, and if it can actually be elicited without the active foraging of *O. propinquus*.

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