

Effects of competition and predation on the feeding rate of freshwater snails

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Abstract

Foraging behavior of snails is affected by competition and risk of predation, which can be detected by chemical cues in the water. Freshwater snails are able to detect and respond to kairomones, from predators, and chemical cues, such as alarm cues, from other snails. Invasive species, such as the Chinese mystery snail, are known to affect native species through processes such as competition and predation. This study examines the effects of different chemical cues on the feeding rate of *Helisoma trivolvis*. The different chemical cues involved in this study include kairomones, alarm cues from crushed conspecifics and from crushed invasive snails, and chemical cues from intraspecific and interspecific competitors. This study also looks at the effects of different densities of competitors and crushed snails on the feeding rate. Higher densities of competition cause the snails to increase their feeding rate compared to no competition and low densities. There is a trend for interspecific competition to cause higher feeding rates than intraspecific competition. Presence of crayfish causes the snails to decrease their feeding rate and it masks the effects on density and type of competition on the feeding rate. There is no significant difference in feeding rates for the different treatments between the predation and crushed snails experiments, suggesting kairomones are more influential than alarm cues in altering foraging behavior. Despite significant effects of Chinese mystery snails on the feeding rate of *H. trivolvis*, the invasion of Chinese mystery snails is likely to alter the community structure by consuming more algae and possibly increasing the feeding rate of native snails.

Introduction

Optimal foraging theory is based upon the idea that organisms make foraging decisions that maximize an individual's fitness by maximizing net energy gain (Pyke 1984). If simply presented with a variety of food resources, an organism will select an optimal diet based upon the nutritional value and energetic quality of the food. However, as costs become entangled in selecting an optimal diet, such as searching and handling time, it becomes more difficult for the organism to maximize benefits and reduce costs (Pyke 1984). Thus, identifying the benefits and costs that an organism must take into account and understanding how they alter the foraging behavior of an organism can be challenging. In the past optimal foraging theory was based upon the assumption that factors, other than qualities and location of food, affecting an individual's fitness did not affect optimal foraging strategy. However, more recently it is being recognized that other factors can affect the optimal foraging strategy (Sih 1990). Besides the qualities of food, interactions with other organisms, such as competition and predation, can also affect foraging behavior (Brown and Carman 1994, Lewis 2001, Sih 1990, Trussel et al. 2003).

Freshwater snails inhabit bottom substrates, such as sand, cobble, macrophytes and detritus. They graze upon algae and directly affect its abundance in an area (Weber and Lodge 1990). Because freshwater snails do not have image-forming eyes, chemical cues play important roles in their lives, conveying messages about the surrounding environment. Kairomones are chemicals produced by predators that convey information to and affect the behavior, morphology, or life history characteristics of prey species (Dodson et al. 1994). Freshwater snails can recognize and respond to kairomones from crayfish, one of their common predators. Some species also respond to chemical cues from crushed conspecifics, referred to as alarm cues (Dodson et al. 1994).

The feeding rate of snails upon algae has been shown to be affected by competition and the risk of predation. Feeding rates can be indicative of the developmental rate and future fecundity for snails because faster development and higher reproductive output require higher amounts of energy; thus higher feeding rates should help increase the snails' fitness (Schoener 1971, Sih 1990). Both intraspecific and interspecific competition may affect the feeding rate of snails. Brown and Carman (1994) observed that higher densities of conspecifics caused decreased feeding rates. This effect may be due to intraspecific interference, specifically behavioral interference. Interspecific competition of snails has been examined between native and invasive species to examine the capabilities of the invasive species to outcompete the native species. Riley et al. (2008) found that although the invasive species had higher growth rates, the native and invasive species did not differ in their feeding rate. This potentially indicates higher energy assimilation efficiency for the invasive species (Riley et al. 2008). Comparing intraspecific and interspecific competition between two snail species, Cross and Benke (2002) observed that snails respond similarly to both intraspecific and interspecific competition. They also found that high densities of competitors reduced snail growth rates.

The risk of predation by crayfish, recognized by kairomones, may alter the cost of foraging (Kotler and Holt 1989). In the presence of crayfish, snails face a trade-off between foraging optimally and reducing their risk of predation (Lewis 2001). Snails may alter their foraging behavior by changing where they forage or their feeding rate. Weber and Lodge (1990) found that snails forego their preferred rock substrate with high periphyton abundance for less desirable macrophytes in the presence of crayfish. Both Lewis (2001) and Trussel et al. (2003) observed that snails show a decrease in their feeding rate in the presence of crayfish kairomones.

The hypothesis being tested is whether competition and risk of predation, in terms of just a predator present and crushed prey, will cause native snails to alter their foraging behavior, in terms of their feeding rate. Based upon other studies, both competition and the risk of predation, in terms of just predator presence and crushed prey, will cause a change in the feeding rate of snails. There will be no difference in the amount of change caused between interspecific and intraspecific competition, and risk of predation will cause a larger amount of change in feeding rate than competition alone.

Materials and Methods

Organisms

Native snails (*Helisoma trivolvis*, Planorbidae) were collected from Tenderfoot Lake. Chinese mystery snails (*Cipangopaludina chinensis*, Viviparidae), an invasive species, were collected from Brown Creek. Collected native and invasive snails were housed in separate aerated aquaria throughout the duration of the experiments. Water from Tenderfoot Lake was used for housing the snails. Snails were provided algae covered rocks and natural muck collected from Tenderfoot Lake. Crayfish (*Orconectes propinquus*) collected from Tenderfoot Lake were used as predators.

Experimental Design

Twelve hours prior to running experiments, snails were removed from their housing aquarium and placed into an experimental aquarium with domestic water, no sediment and no food. Experimental aquaria were set up with a small corner (15 ½ by 15 ½ cm) sectioned off for the feeding snail and an algae covered tile. Two Plexiglas sheets were connected to partition the corner off, and holes were drilled through the Plexiglas to allow movement of water and

chemical cues. Outside of the sectioned off corner, two Ziploc plastic containers, with holes cut into their sides and lids, were placed into the aquarium to hold either crayfish or other snails. Tiles (7 ½ cm by 7 ½ cm) used for the experiments were set on the bottom of a shallow northern portion of Tenderfoot Creek for at least a week until they were covered with algae.

The feeding rate of snails was measured by counting the number of grids exposed during the allowed foraging time. Two sets of experiments were run: the competition experiment and the predation experiment. The competition experiment had 4 treatments and 1 control. The control had one native snail feeding for the duration of the experiment. The 4 treatments were (1) low intraspecific competition (one native snail feeding and one native snail caged), (2) high intraspecific competition (one native snail feeding and five native snails caged), (3) low interspecific competition (one native snail feeding and one invasive snail caged), and (4) high interspecific competition (one native snail feeding and five invasive snails caged). The predation experiment had the same control and the same 4 treatments, except a caged crayfish was also present in the aquarium, mimicking a predation risk to the snails.

A third set of experiments, the crushed snails experiment, was also run. The crushed snails experiment had 4 treatments that all had a crayfish present. The 4 treatments were (1) low intraspecific crushed (one native snail feeding and one native snail crushed), (2) high intraspecific crushed (one native snail feeding and five native snails crushed), (3) low interspecific crushed (one native snail feeding and one invasive snail crushed), and (4) high interspecific crushed (one native snail feeding and five invasive snails crushed).

Each treatment and control for the competition and predation experiments was replicated 10 times throughout the summer. Each treatment of the crushed snails experiment was replicated 5 times. Experimental treatments were run randomly, and tiles and snails were randomly

assigned to a treatment insuring that time of day, time of season, amount of algae on the tile and the size of the snail did not bias the feeding rate.

The experimental snail was placed into an empty aquarium and allowed to acclimate for 5 minutes before the treatment containers were placed into the aquarium and then another 5 minutes before the tile was placed into the aquarium. The snail was allowed to feed for 1 ½ hours before the tile was removed. A picture was taken of the tiles with a gridded (0.5 by 0.5 cm) transparency placed on top, both before and after the experiment was run. Sets of before and after pictures for each tile were compared and the number of grids fed upon was recorded. The number of grids fed upon was converted to area fed upon during the feeding time to determine the feeding rate.

Statistics

All statistical tests were run with MYSTAT with $\alpha = 0.05$. The original data was log transformed because it violated the assumption of normality but not homogeneity.

The competition and predation controls were compared using a one-way ANOVA. For both the competition and predation experiments, a one-way ANOVA was then used to compare the feeding rate between the control and all treatments (low intra, high intra, low inter, high inter). The crushed snails experiment data was compared to the mean of the competition control with a one-sample t-test. The treatments of the crushed snails experiment were compared to the predation control with a one-way ANOVA. A 2² factorial ANOVA was run on the competition, predation and crushed snails experiments with density (low vs. high) and competition type (intraspecific vs. interspecific) as factors. A multiway ANOVA was run on the crushed snails and predation experiments with experiment (predation vs. crushed snail), density (low vs. high) and competition type (intraspecific vs. interspecific) as factors.

Results

The original data for the competition, predation and crushed snails experiments violated the assumption of normality (Shapiro-Wilk test, $p < 0.0001$), but not homogeneity (Levene's test, $p = 0.5262$). A log transformation normalized the data (Shapiro-Wilk test, $p = 0.2835$) and maintained homogeneity (Levene's test, $p = 0.4886$). Competition control feeding rates were 31.6% higher than predation control feeding rates ($F_{1,18} = 5.6568$, $p = 0.0287$, Figure 1).

In the competition experiment, there was no significant difference between the different treatments and the control ($F_{4,45} = 1.8681$, $p = 0.1326$). Also in the competition experiment, there was no significant difference between the intraspecific and interspecific treatments ($F_{1,36} = 0.8776$, $p = 0.3551$). However, the high density treatments had feeding rates 36.5 % higher than the low density treatments in the competition experiment ($F_{1,36} = 4.8392$, $p = 0.0343$, Figure 2). The interaction between density and competition type was not significant ($F_{1,36} = 0.1492$, $p = 0.7016$).

In the predation experiment (Figure 3), there was no significant difference between the different treatments and the control ($F_{4,45} = 0.5997$, $p = 0.6648$). Also, there was no significant difference between high and low densities ($F_{1,36} = 1.1247$, $p = 0.2960$), intraspecific and interspecific competition ($F_{1,36} = 0.0097$, $p = 0.9223$), or for the interaction between density and competition type ($F_{1,36} = 1.0247$, $p = 0.3182$).

The crushed snails experiment data was significantly different from the mean of the competition control ($t = -4.6434$, $df = 19$, $p = 0.0002$, Figure 4). However, the different treatments of the crushed snails experiment were not significantly different from the predation control ($F_{4,25} = 0.1361$, $p = 0.9674$). For the crushed snails experiment there was no significant difference between high and low densities ($F_{1,16} = 0.0506$, $p = 0.8249$), intraspecific and

interspecific competition ($F_{1,16}=0.0331$, $p = 0.8579$), or for the interaction between density and competition type ($F_{1,16}=0.0810$, $p = 0.7796$). None of the factors or interactions were significant for the crushed snails and predation experiments (Table 1).

Discussion

For the competition experiment, density had a significant effect on the feeding rate of the native snails; higher densities of competitors caused higher feeding rates. This result was opposite of Brown and Carman (1994), which observed that higher densities of snails caused decreased feeding rates. However, because this study only involved chemical cues, exploitative competition instead of interference competition was a factor. Exploitative competition reduces the amount of resources available for an individual because competitors are consuming the resource before the focal individual can access the resource. But in this study competitors were not allowed to feed on the algal tiles, allowing the focal individual more algae to feed upon. It is beneficial to have a higher feeding rate in the presence of many competitors to insure enough food is acquired. Although competition type (intraspecific vs. interspecific) did not have a significant effect on the feeding rate, there was a trend of higher feeding rates when interspecific competitors were present instead of intraspecific competitors (Figure 2). Cross and Benke (2002) also found no significant difference between intraspecific and interspecific competition; however, in contrast to this study, they observed intraspecific competition to be slightly stronger than interspecific competition.

Also, the Chinese mystery snails are much larger than the *H. trivolvis*, they most likely need to consume more food than an equal number of *H. trivolvis* and it benefits *H. trivolvis* to have higher feeding rates in the presence of Chinese mystery snails. This study cannot conclude

whether *H. trivolvis* increased their feeding rate because interspecific competitors instead of intraspecific competitors were present or whether it was just because the large size of the Chinese mystery snails caused them to release larger amounts of chemical cues, mimicking a higher density.

The results indicate the presence of crayfish, as detected by chemical cues, causes the native snails to decrease their feeding rate relative to the absence of crayfish (Figure 1), which was expected based upon previous studies (Lewis 2001 and Trussel 2003). Decreasing their feeding rate is costly to the snails because their metabolism, growth and reproduction depend upon the amount of energy they assimilate (Studier et al. 1975). A decrease in feeding rate likely arises from defensive behaviors, such as moving to the surface of the water, which inhibits the snail from feeding but protects the snail from predation. Also a reduced feeding rate may reflect a reduced activity level, which will also protect snails from visual predators, such as crayfish.

There was no significant difference in feeding rates between low and high densities or between intraspecific and interspecific competition for the predation experiment (Figure 3). For both intraspecific and interspecific competition in the presence of crayfish, there was a trend for higher densities to have a lower feeding rate than lower densities. However, the lower density interspecific competition value was quite high. This treatment showed a feeding rate higher than the average of the competition control, which is a baseline-feeding rate with *H. trivolvis* feeding on a tile (Figure 3). There was one data point, not detected as an outlier, that had a high feeding rate, which may have driven the high average of the low density interspecific competition treatment. There is no ecological basis for this result and needs more investigation. But for the predation experiment, it seems the presence of the crayfish overpowers the differences in feeding rates that were observed for the competition experiment.

Studies have examined the responses invoked in snails by the mere presence of a predator, predators feeding upon unrelated prey, and predators feeding on conspecifics (Turner 2008, Turner et al. 2006, Yamada et al. 1998). Turner et al. (2006) found that exposure to unfed predators and to predators feeding upon unrelated prey caused a weak response in snails relative to the response caused by predators feeding upon conspecifics. For an intertidal snail, Yamada et al. (1998) found that the mere presence of a crab predator did not cause the snails to alter their behavior; the crab had to be actively feeding in order to elicit a response from the snails. Because *H. trivolvis* can distinguish among predator diets of closely related prey and more distantly related prey, predator diet has an effect on both the behavioral responses and growth of *H. trivolvis* (Turner 2008). *H. trivolvis* exhibited behavioral changes only when the predators fed upon conspecifics and congeners (Turner 2008).

Crushed conspecifics and Chinese mystery snails were used to examine possible different effects between kairomones, from just the predator, and alarm cues, from crushed prey. The feeding rates for the crushed snails experiment were significantly different from the competition control, but not from the predation control (Figure 4). The mere presence of the predator, detected by kairomones, is enough to cause the snails to alter their feeding rate; the alarm cues from crushed snails do not elicit a significant decrease in the feeding rate compared to just having kairomones. Although it was not significant, there is a trend for higher densities of crushed conspecifics to cause lower feeding rates than high densities of living conspecifics in the presence of a predator. This suggests an effect of alarm cues from crushed conspecifics because if alarm cues were not having an effect, the feeding rate would be the same as the living conspecifics. There was no difference between crushed conspecifics and crushed Chinese mystery snails on the feeding rate of the native snails. It cannot be concluded that *H. trivolvis*

responds the same to both conspecifics and the Chinese mystery snails, however, because the feeding rates for crushed snails were not different from the feeding rates for the predation experiment. Again, it appears the mere presence of the crayfish is overpowering different feeding rates due to other factors. The experiment using crushed snails had a smaller sample size, so it would be beneficial to repeat the experiment with more replicates, higher densities of crushed snails, and to possibly allow a longer feeding time.

When comparing the predation and crushed snails experiments, there is an interesting result in regards to the Chinese mystery snails when comparing the predation and crushed snails experiments. The high density of Chinese mystery snails showed a much lower feeding rate than any other treatment, including the high density of crushed Chinese mystery snails (Figures 3 & 4). Because the Chinese mystery snails are large, they cast large shadows when they were attached to the sides of their holding containers. During the duration of the predation experiment, *H. trivolvis* received kairomones and chemical cues from the Chinese mystery snails. Since *H. trivolvis* has not encountered the Chinese mystery snails before, it is possible visual cues were playing a role and *H. trivolvis* was interpreting the large shadows of the Chinese mystery snails as the crayfish. For other treatments of the predation experiment and for the crushed snails experiment, nothing else caused a shadow that could be interpreted as a nearby crayfish form which kairomones were being released. Five large Chinese mystery snails during the predation experiment may have been interpreted as a nearby crayfish, representing a more immediate threat of predation to *H. trivolvis*, causing a major decrease in the feeding rate.

Chinese mystery snails are found at very high densities naturally, and when they invade the habitat of *H. trivolvis* they may cause much lower feeding rates initially, especially when crayfish predators are present. After the native snails become accustomed to their presence, they

may cause feeding rates higher than what is natural for the native snails. The alteration of the feeding rates of *H. trivolvis* may have far reaching effects on the whole community. Snail grazing on algae plays important roles on the community food web dynamics. Bertness (1984) removed an invasive snail species from an area, monitored the community structure, and found a huge increase in the amount of algae and sediment. Thus, the Chinese mystery snails may directly affect the community structure by decreasing the amount of algae and sediment present. This change may affect the rest of the food web because different organisms survive better in different amounts of algae and sediment accumulation (Bertness 1984). The Chinese mystery snails may also indirectly affect community structure by its effects on the native snails. The invasion of the Chinese mystery snails may cause *H. trivolvis* to alter its foraging behavior, which in turn may affect the growth rate, metabolism, and reproductive output of the native snails since these things depend upon energy assimilated (Studier et al. 1975). Alterations in the life history of *H. trivolvis* could affect population dynamics and be transferred throughout the community. Future experiments could more directly measure affects of Chinese mystery snails on *H. trivolvis*, such as examining growth of *H. trivolvis* overtime with and without Chinese mystery snails present. Also, amount of food ingested by *H. trivolvis* was found to be directly related to the weight of the snail (Studier et al. 1975). Thus, future experiments should control the weight of the snails feeding upon the tiles.

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Tables

Table 1. Statistical results from a multiway ANOVA of the crushed snails and predation experiments with competition type, density and experiment as factors.		
Factor	F-statistic	p-value
Competition Type	$F_{1,52} = 0.0021$	0.9633
Density	$F_{1,52} = 0.2901$	0.5924
Experiment	$F_{1,52} = 0.0666$	0.7974
Treatment*Density	$F_{1,52} = 0.2231$	0.6386
Treatment*Experiment	$F_{1,52} = 0.0292$	0.8650
Density*Experiment	$F_{1,52} = 0.6511$	0.4234
Treatment*Density*Experiment	$F_{1,52} = 0.6592$	0.4205

Figures



