Abstract

Animals have many strategies to protect themselves against predators, such as avoidance and refuge-seeking behaviors. Animal personality, which is defined as a set of consistent behaviors, is a framework that has been used to categorize individuals as being "shy" or "bold". There are ecological costs and benefits to different personality types (e.g., predation risk, access to resources), and it is possible that personality determines which anti-predator strategy an animal will use. Our objectives were (1) to determine whether snails exhibit repeatable behaviors that can be classified as personality and (2) to determine the ecological significance of personality in coping with predators. We initially determined personality (i.e., shy vs. bold) by measuring latency to emerge. We then exposed both personality types to predator and no-predator environments. Throughout the experiment we collected weekly measurements of emergence time and avoidance behavior, and at the end we measured shell crush resistance. Our data suggest that latency to emerge is repeatable and indicative of personality type. Additionally, we found that, in the presence of a predator, "shy" snails invested greater resources in their shell, whereas "bold" snails exhibited avoidance behaviors. These results suggest that predator-defense strategies are linked to personality type.

Introduction

For centuries ecologists have been interested in the interactions between predators and prey. Predators are strong selective forces that, most obviously, have lethal effects on prey, but can also have non-lethal effects (Lima, 1998). For instance, non-lethal effects of predators can include shifts in prey habitat use, with prey opting for safer habitats even though they contain fewer necessary resources (e.g., food, shelter, nest sites) (Lima and Dill, 1989; Lima, 1998). Such shifts in habitat use can result in a change of food web dynamics (Turner, et al., 2000; Trussell, et. al, 2006). Indeed, many of the nonlethal effects of predators on prey are means of predator avoidance. Prey can adopt a wide array of defense strategies to protect themselves from predators (Lima, 1998). Anti-predator strategies may be physiological such as being brightly colored, morphological such as developing a more crush resistant shell, or behavioral such as avoidance of predators (Turner, et al., 1999; Turner, et al., 2006; Ahlgren et al., 2015). Recently researchers have begun investigating whether animal personality shapes behavioral responses of prey to predators (Ioannou, et al., 2008; Sih, et al., 2012). Animal personality is a set of behaviors consistent across context and time (Coleman, et al., 1998). For example, an individual that has a more aggressive personality type will not only be more aggressive in competitive situations, but also in foraging, mating, and anti-predator behaviors (Sih, et al., 2012). Given the consistency of personality across contexts, an animal's personality may not always be advantageous in every context leading some researchers to view animal personality as behavioral syndromes (Sih, et al., 2004), implying that there is a negative connotation to exhibiting consistent behaviors. For example, an individual consistently exhibiting more aggressive behavior demonstrates limited behavioral plasticity (Sih, et al., 2004). In some contexts, having more aggressive behavior may be beneficial, but in other contexts (e.g., in presence of a predator) this behavior may become costly (Sih, et al., 2004). Thus, each personality type is associated with differing costs and benefits across varying environmental contexts (Sih, et al., 2004); however, we know very little about how personality influences an individual's antipredator strategies.

To test whether personality influences individual antipredator strategies we used a snail-crayfish predator-prey model system. Previous studies have found the snail-crayfish system is a good model for studying the interactions between predator and prey (Dewitt, et al., 2000, Hoverman, et al. 2005, Salice and Plautz, 2011) because snails exhibit morphological and behavioral responses when exposed to crayfish predator cues, e.g., water from tanks housing crayfish and crushed conspecifics; Hoverman et al, 2005, Dalesman, et al., 2006). In this study, we exposed snails to predator cues to determine if snails exhibit repeatable, consistent behaviors (i.e., personality), and if personality influences anti-predator strategies (e.g., refuge seeking behavior, avoidance behavior).

Methods

2.1 Experimental Design

We haphazardly collected 80 snails (*Helisoma trivolvis*; 98.90 ± 34.57 mg) from an inbred laboratory population. Snails were housed individually in 400 mL glass jars containing 350 mL of decholorinated tap water. Prior to the experiment, we determined personality (shy vs. bold) according to how long it took snails to emerge from their shell (i.e., latency to emerge; see section 2.2). To test the effects of personality on antipredator responses, we exposed both bold and shy snails to 10 mL of either predator cue or dechlorinated tap water (control; n = 20 per group). The predator cue consisted of 5 crushed conspecifics and 500 mL of water from a tank containing 3 crayfish (*Procambarus spp.*), which has been previously shown to induce antipredator responses in *Helisoma* snails (Hoverman et al, 2005, Dalesman, et al., 2006). Predator treatment was maintained by adding freshly prepared predator cue every other day for 28 d- experiment was conducted from 24 September – 31 October, 2015. We measured latency to emerge from shell, crawl-out behavior, activity, and whole wet mass every 7 d. At the conclusion of the experiment, we photographed snails for morphometric analysis of shell shape and measured shell crush resistance. Throughout the experiment, snails were fed 5 mg of a 1:1 mixture spirulina (Spring Valley, Bentonville, AR) and TetraMin® (Tetra, Blacksberg, VA, USA).

2.2 Personality Determination

We assessed variation in risk-taking behavior (i.e., boldness) by measuring latency to emerge (Ahlgren, et al., 2014). To do so, we placed snails individually into a plastic petri dish filled with dechlorinated tap water and gave the snails 5 minutes to acclimate to the novel environment. After acclimation, we gently prodded the snails with forceps until they retreated into their shell; we then recorded the time it took for the snails to re-emerge from their shells. Trials were run in triplicate and latency to emerge values were averaged across trials. Snails were given a two-minute rest period between trials. We classified snails emerging in under 15 seconds as bold and over 20 seconds as shy (Fig. 1). We determined our shy and bold thresholds by initially testing the emergence time of 109 snails. Our bold and shy thresholds are consistent with a similar study examining snail personality (Ahlgren, et al., 2014). Although boldness is a continuous trait, we categorized snails as either bold or shy to facilitate effective assessment of the impact of boldness on antipredator responses in a factorial design (Hulthén et al., 2014).

2.3 Crawl-out Behavior

Previous studies have reported that snails exposed to alarm cues (i.e., crushed conspecifics) or crayfish predator cues will crawl out of the water column (DeWitt et al., 1999; Turner, et al., 1999). Therefore, we measured crawl-out behavior by scoring the position of snails in treatment jars 24 hours after we assessed latency to emerge and applied a fresh predator cue. Snail position within the jar was scored according to DeWitt et al. (1999): (1) snail was on the bottom of jar, (2) snail was on the jar wall below 3 cm of the water line, (3) snail was on the jar wall within 3 cm of the water line, (4) snail was at or above the water line. We considered snails receiving a score of a 4 as exhibiting complete predator avoidance.

2.4 Activity

After measuring latency to emerge, we placed the snails, 5 at a time, in a 9 x12 inch glass pan filled with 700 mL of dechlorinated tap water. We gave the snails five minutes to acclimate then recorded activity using Photo Booth application and a web camera (Logitech, Newark, CA, USA) for 5 minutes. We calculated average distance traveled by measuring total distance traveled using Tracker (Version 4.92) software (physlets.org/tracker) and dividing by duration of assay.

2.6 Crush Resistance

We measured snail crush resistance using previously established methods (Osenberg and Mittelbach, 1989; Beaty, et al, 2016). Briefly, we individually placed a snail on its right lateral side in a flat glass beaker and set a smaller flat glass beaker on top of the snail. We filled the smaller beaker with sand until the shell cracked. We then measured the mass of the beaker and sand and calculated the force required to crush each snail's shell.

Results

Growth Rate: We found that mass increased over the 28-day period for all snails (Fig. 1; Time: $F = 1793.4_{4, 283}$, p <.0001), regardless of personality or predator cue (predator x personality × Time: $F = 0.68_{4, 283}$, $p = 0.609$; Personality X Predator: $F = 1.04_{1, 283}$, p =0.31; Personality: $F = 0.11_{1, 283}$, $p = 0.744$; Predator: $F = 0.46_{1, 283}$, $p = 0.50$).
Latency to Emerge: We found that on average snails exposed to a predator cue emerged slower than snails not receiving a predator cue (Fig. 2; Predator: $F = 19.52_{1, 72}$, $p < .0001$), but this did not vary by time or personality (Personality × Predator: $F = .68_{1, 72}$, $p = .4117$; Predator × Time: $F = 2.37_{4, 287}$, $p = 0.7850$; Personality × Predator × Time: $F = 0.43_{4, 287}$, $p = 0.7850$). When looking at treatment groups we found that the bold snails initially emerged from their shells significantly faster than the shy snails, but over the course of the 28 days, the bold snails tend to emerge 50 % slower and the shy snails 50 % faster (Personality × Time $F = 25.70_{4,287}$; p <.0001) Post hoc analyses indicate that bold and shy snails differed in emergence time at each sample point (in all cases $p \leq 0.05$) except for day 28 ($p = 0.11$). Although all snails increased how quickly they re-merged from their shells over the course of the experiment, regression indicates that snails that emerged slower on day 0 also emerged slower on day 28 (Fig. 3; $R^2= 0.156$; p =.0002).

Crawl-Out Behavior: Snail crawl-out behavior varied over time depending on both predator cue and personality (Fig. 4b; Personality × Predator × Time: F value = $2.40_{4, 258}$, $p = 0.051$, Predator × Day: $F = 3.54_{4, 258}$; $P = 0.008$). We found that once exposed to a predator cue, bold snails increased their crawl-out score which remained elevated for the rest of the study. However, after exposure to predator cues, shy snails initially increased crawl-out behavior, but this effect lessened in a step-wise pattern with each additional exposure. Snails exposed to no predator cue exhibited similar crawl-out behavior regardless of personality throughout the course of the experiment.

Activity: We found an interactive effect of predator cue and time (Fig. 5. Predator × Time: $F = 3.83_{4, 275}$, $p = 0.005$) on snail activity. Before receiving a predator cue, all individuals exhibited similar activity, but by day 7 snails exposed to predator cues demonstrated more activity than control snails. Snails exposed to predator cues maintained higher activity throughout the experiment. Personality had no significant influence on activity (Personality: $F = 5.31_{1, 76}$, $p = 0.266$; Personality × Predator: $F = 1.05_{1, 76}$, $p = 0.309$; Personality × Time: $F = 0.98_{4, 275}$, $p = 0.419$; Personality × Predator × Time: $F = 0.78_{4, 275}$, $p = 0.537$).

Crush Resistance: Snails receiving a predator cue were significantly more crush resistant than control snails. (Fig. 6; Predator: $F = 6.97_{1}$, $p = 0.01$), but this did not vary by personality (Personality: $F = 1.77_{1}$, $p = .188$; Personality × Predator: $F = 2.13_{1}$, $p = 0.149$)

Discussion

The objectives of this project were to determine if snails exhibit repeatable, consistent behaviors and if personality influences anti-predator strategies. Based on our results we concluded that latency to emerge is a repeatable and consistent behavior, suggesting that latency to emerge may be indicative of personality type (Sih, et al., 2004). Our data also suggest that, in the presence of predators, bold individuals increase crawl-out behavior, whereas shy individuals have more crush resistance shells. Taken as a whole, these data suggest that bold and shy individuals employ different anti-predator strategies.

While personality has been vastly studied, there is not a consensus on the best way to determine personality (Algrehn, et al., 2015, Cole and Quinn, 2014). In this study, we focused on two behaviors, latency to emerge and activity. Previously, Algrehn, et al., categorized snails as having bold or shy personalities by latency to emerge, but they did not examine if latency to emerge was a repeatable behavior (Algrehn, et al., 2015). Our study, found that latency to emerge was repeatable over time. Even though shy individuals emerge quicker on day 28 compared to day 0, shy snails in a predator environment are slower to emerge from their shell. Therefore, since latency to emerge is consistent and repeatable within individuals, latency to emerge is indicative of personality type. Although we found a difference in latency to emerge prior to a predator cue, all snails expressed the same level of activity. Snails exposed to a predator cue expressed greater activity; however, we did not find evidence that personality influences activity in response to predators. Previous studies have found a correlation between boldness and activity (Dingemanse, et al., 2012). Yet, our results suggest that in snails, activity may not be correlated to personality.

In addition to avoidance and activity, previous studies have also examined crawl-out behavior and shell morphology in snails exposed to predators (DeWitt, et al., 1999, Beaty, et al., 2006). This is the first study to investigate whether personality influences the expression of crawl-out behavior and shell morphology in response to predators. By measuring multiple behavioral and morphological traits, we found that bold and shy individuals differed in their anti-predator strategies, which appear to result in tradeoffs. Shy individuals stay in the water and thus have greater access to resources (DeWitt, et al., 1999), but are more likely to encounter predators (Turner, 1996). To compensate for increased predation risk, shy individuals invest in shell maintenance (Dewitt, et al., 1999). Conversely, bold individuals are more likely to associate with the water line, and therefore have reduced investment in shell maintenance and probability of encountering predators, yet limit their access to resources by staying out of the water.

Tradeoffs in antipredator strategies are often found in other studies that have investigated the influence of predator cues on animal behavior (Lima, 1998). In our study, we found that tradeoffs and anti-predator strategies are explained by personality types (Wilson, et al., 1994, Smith and Blumstein, 2008, Sih, et al., 2012). The results of our study not only support what is already in the literature, but also link personality with behavioral and morphological antipredator defense strategies. This study provides further evidence that personality may influence a suite of ecological factors. To better understand the influence of personality on anti-predator responses, further studies could investigate the response of bold and shy individuals to multiple predator types or stressors.

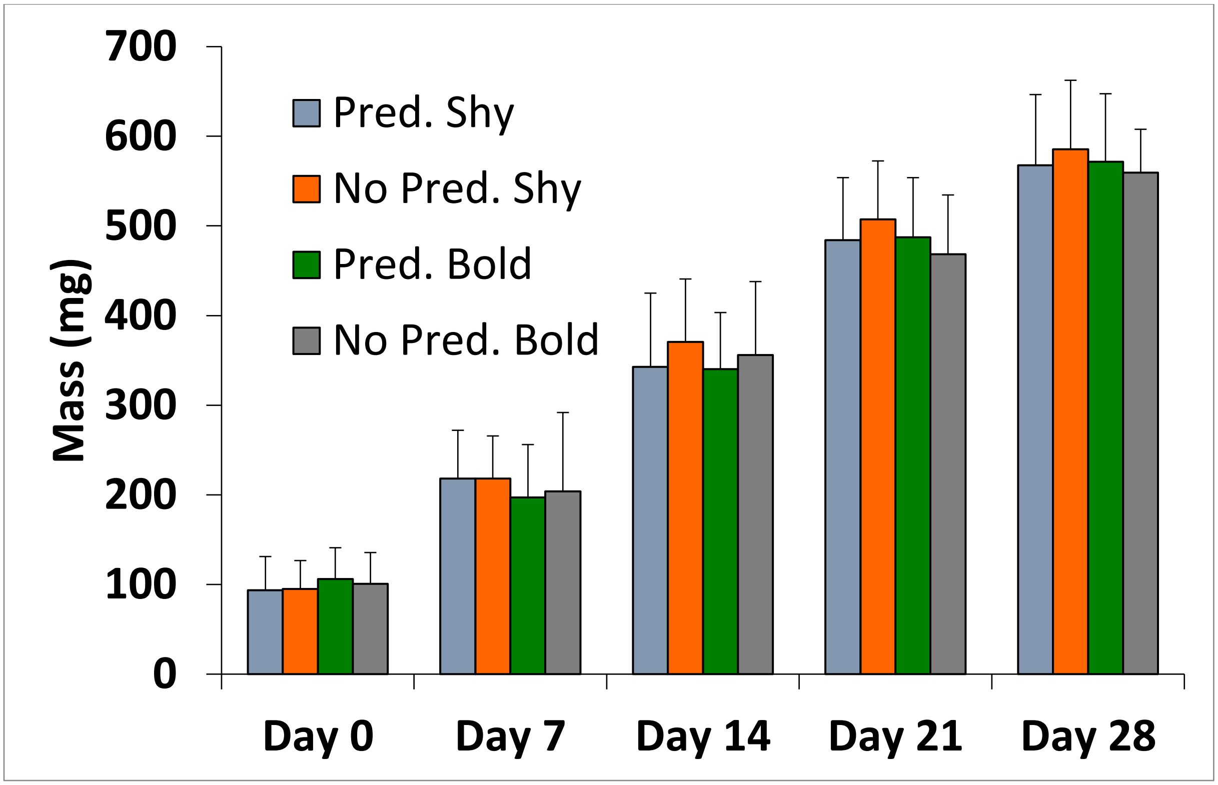

Figure 1: Mass (mean ± SE) of snails with shy or bold personalities that were either exposed or unexposed to a predator cue for 28 days.

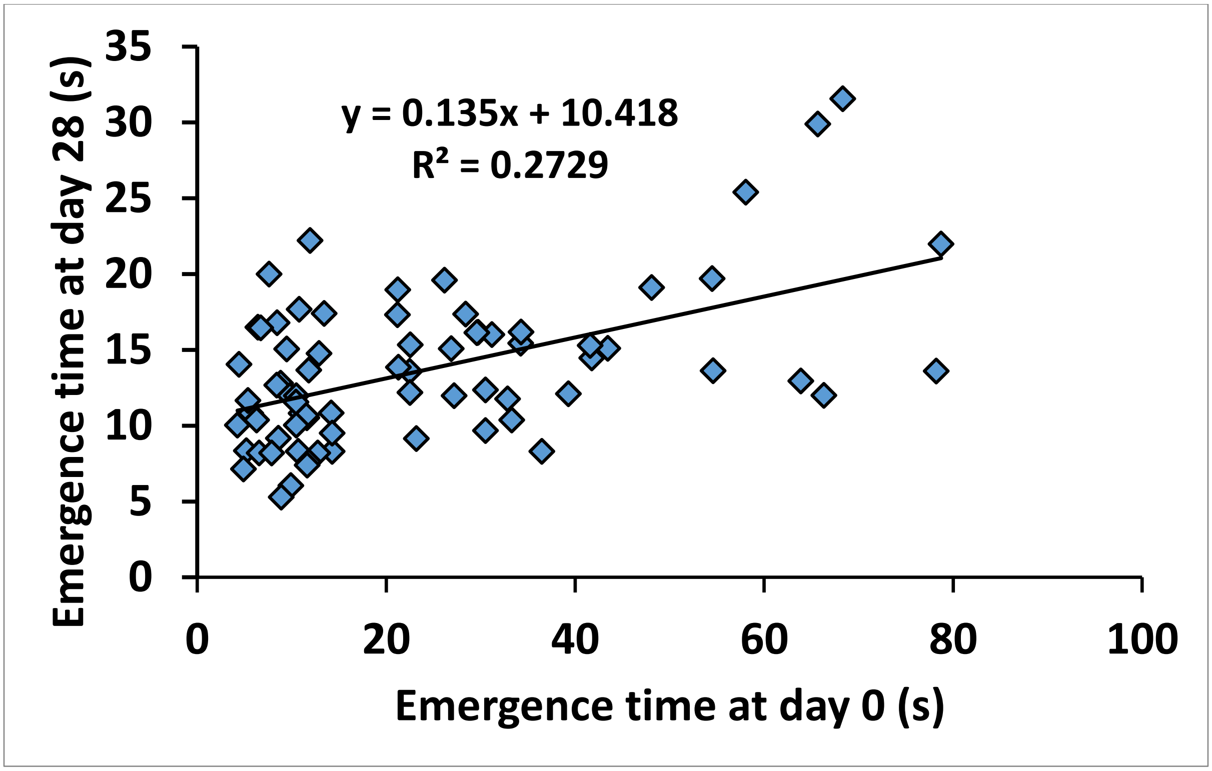

Figure 2: Correlation of emergence time at day 0 and day 28.

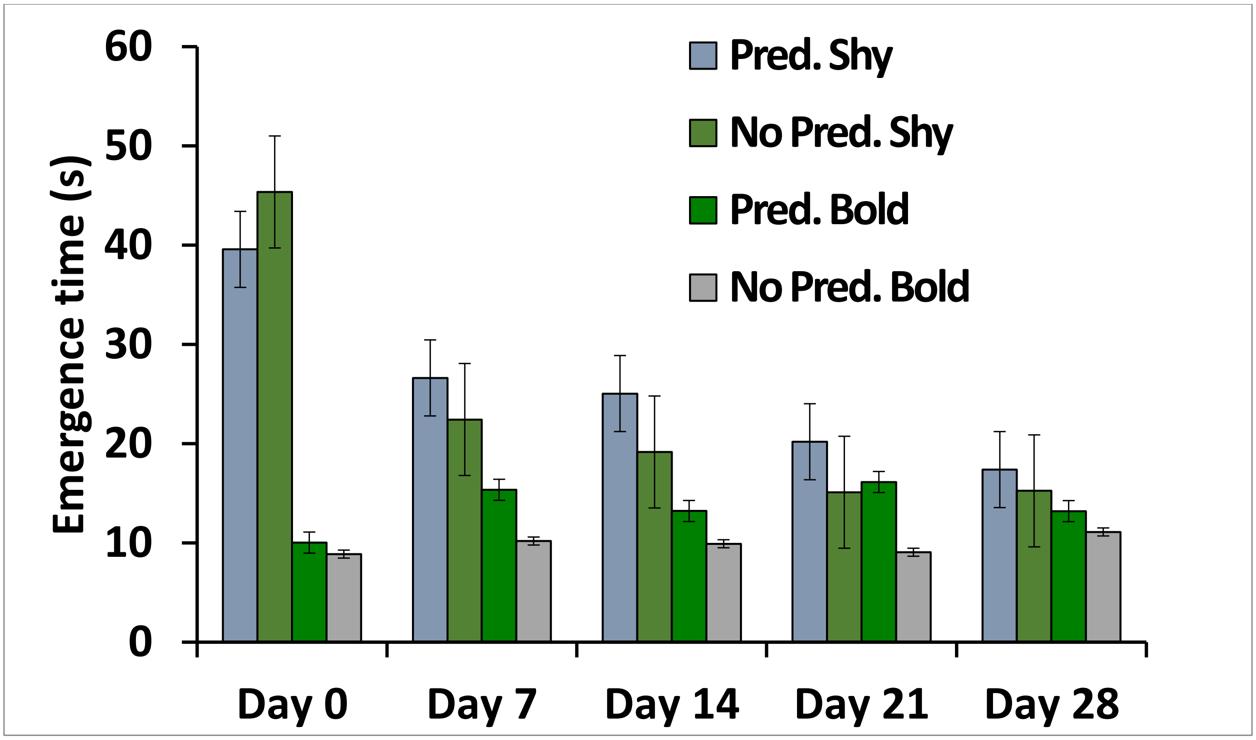

Figure 3: Emergence time (mean ± SE) of treatment groups over 28 days.

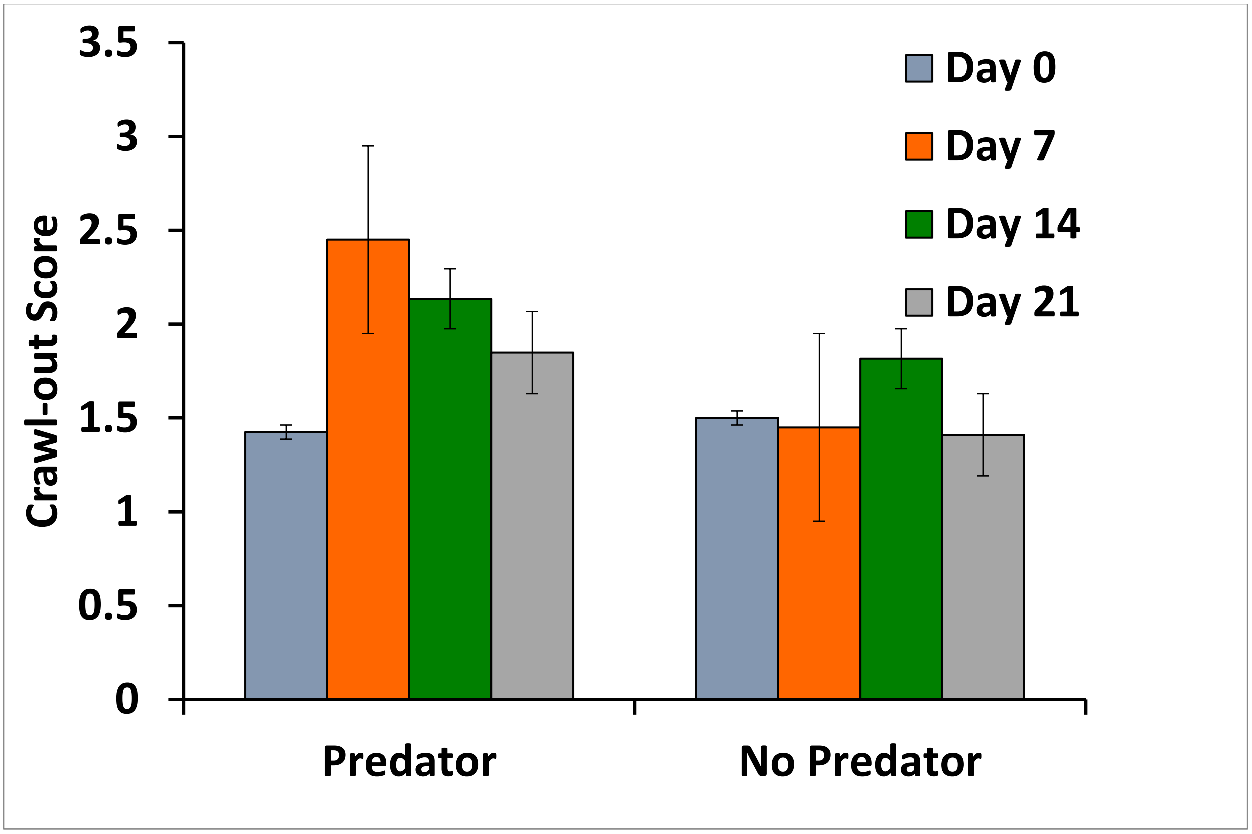

Figure 4a: Crawl-out behavior (mean ± SE) between predator and no predator treatment groups.

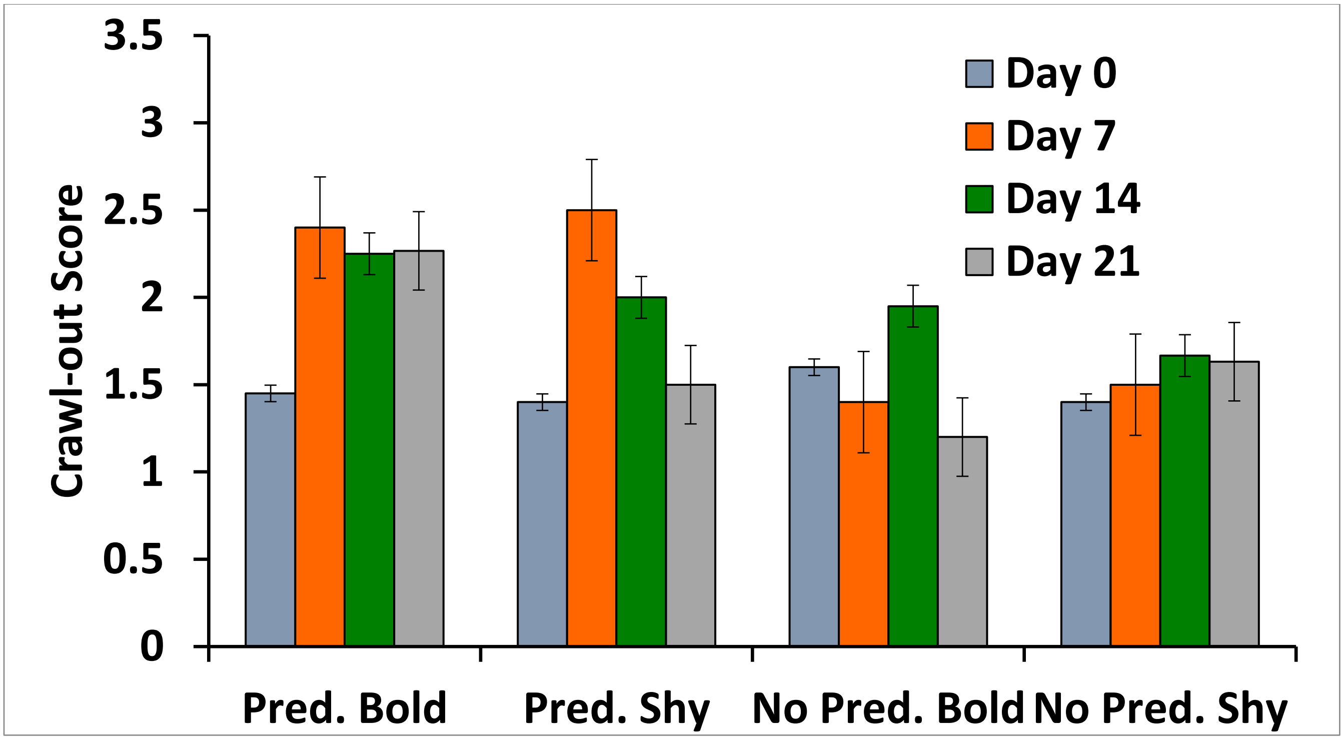

Figure 4b: Crawl-out behavior (mean ± SE) over the course of the experiment for all treatment groups.

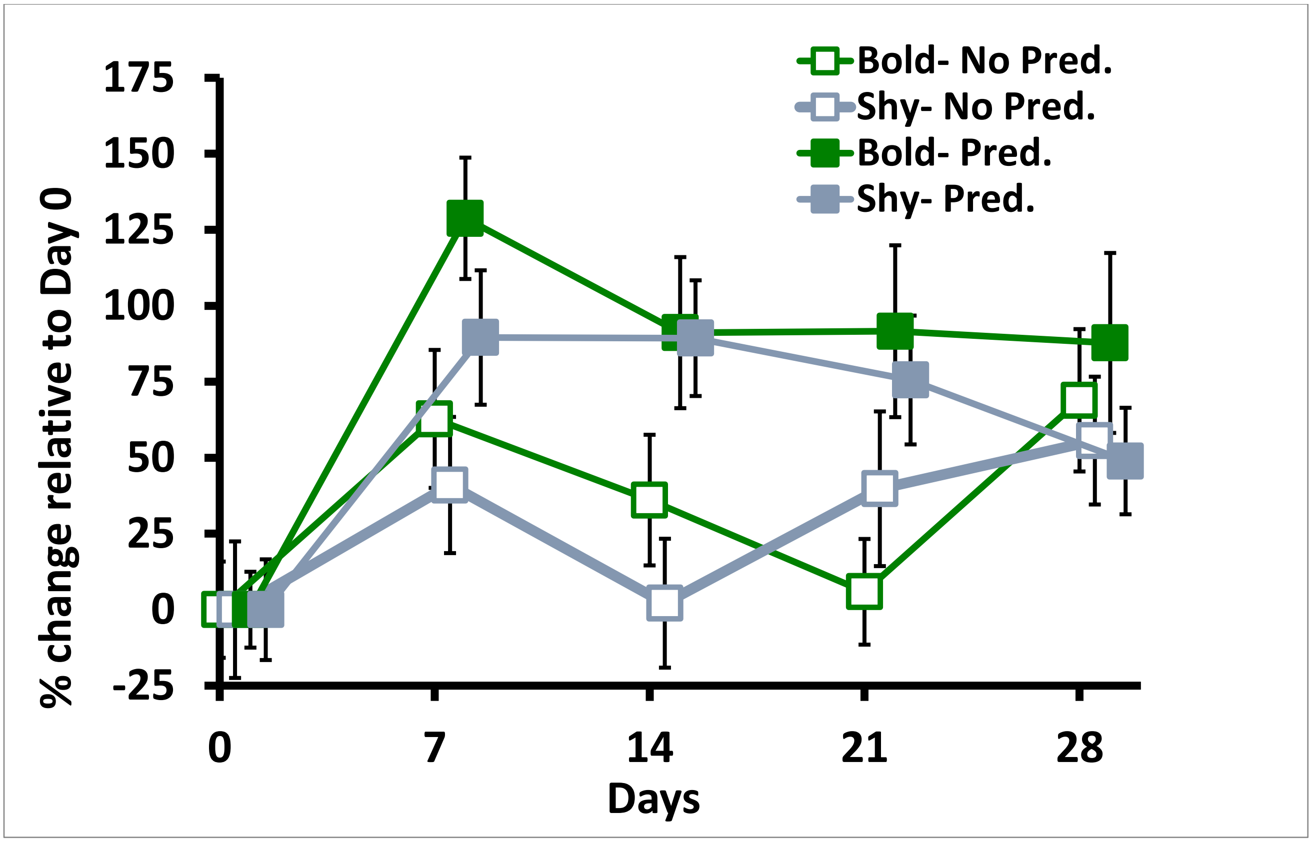

Figure 5: Percent change (mean ± SE) in active over 28 days for all treatment groups.

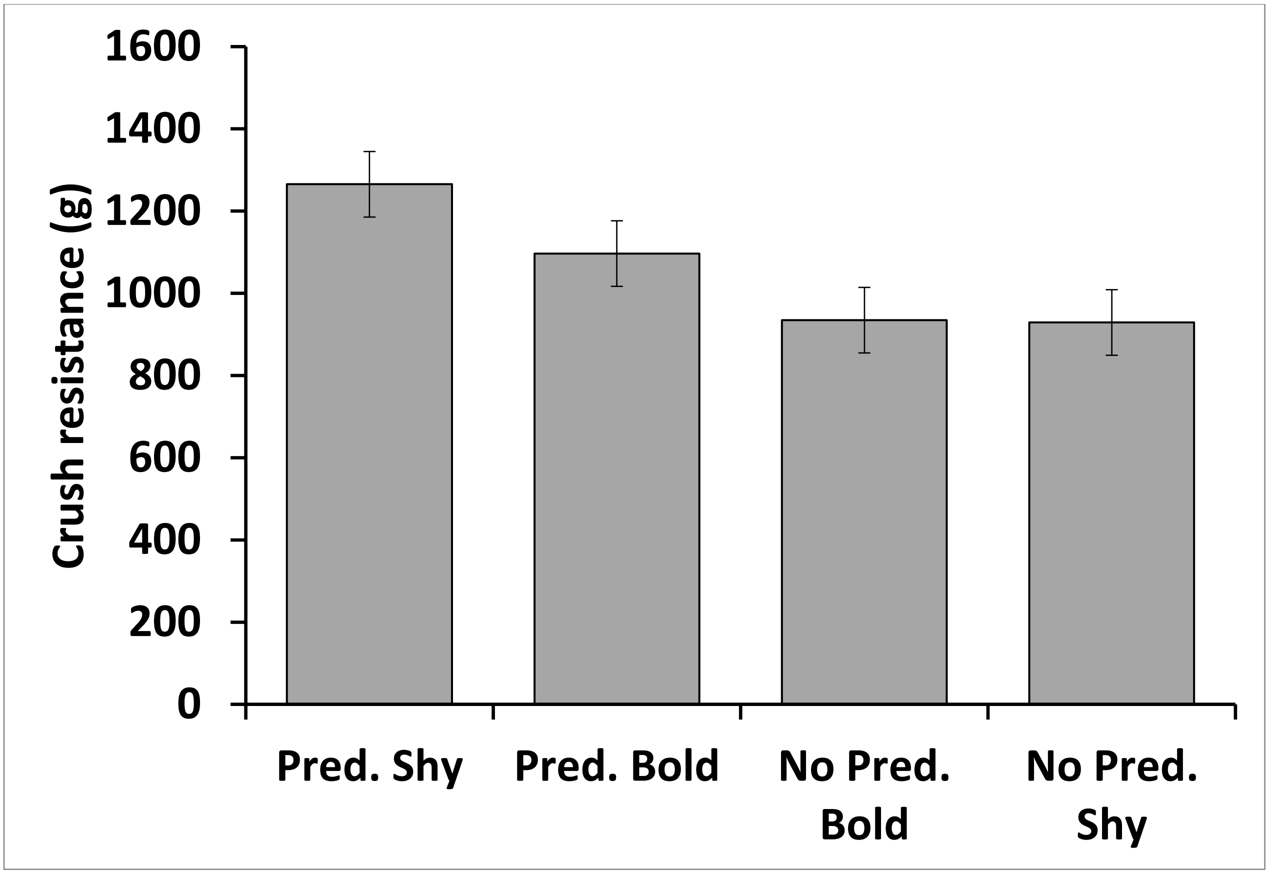

Figure 6: Mass to crush snail's shells for all treatment groups.

Annotated Bibliography

Ahlgren, Johan, Chapman, Ben B., Nilsson, P. Anders, J., Bronmark, Christer. (2015). Individual boldness is linked to protective shell shape in aquatic snails. *Biology Letters*, 11, 20150029.

- Study suggesting bold snails compensate for increased predation by changing shell morphology.
- Determined snail's personalities solely using emergence time, which my study used as a starting point in determining personality.
- Found that bold individuals have more morphological defenses than shy individuals.

Coleman, Kristine, Wilson, David Sloan. (1998). Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Animal Behaviour*, 56, 927-936.

- Observational study that looked at how shyness or boldness affected juvenile pumpkinseed sunfish's reactions to a threatening object and a novel food source.
- Two measures of personality were used. The first was the introduction of a meter stick and the second was the introduction of a net with aquatic vegetation tied to it. The researchers determined personality based on whether the fish approached or fled from the meter stick and net. This was done before and after exposure to a predator.
- Determined that shyness and boldness is context related and suggests that shyness and boldness could be a two dimensional continuum.

Wilson, David Sloan, Clark, Anne B., Coleman, Kristine, Dearstyne, Ted. (1994). Shyness and boldness in humans and other animals. *Tree*, 9, 442-445.

- Models of optimal risk, density- or frequency dependent selection, and phenotypic plasticity can help us learn about shyness and boldness as a result of natural selection.
- The shy-bold continuum has been identified in humans and a few other species. It is possible that this same continuum could be seen across many taxa.
- Like my study, other studies have shown that there are ecological costs of shyness and boldness. One studied identified three axes of behavioral variation which are "approach", "avoidance", and "sociability".

Ioannou, C. C., Payne, M., Krause, J. (2008). Ecological consequences of the bold-shy continuum: the effect of predator boldness on prey risk. *Oecologia,* 157, 177-188

- Study that investigated if the risk influenced by the prey is related to the boldness of the predator.
- Individuals were found to accept more risk when situations favored a larger foraging reward, and larger individuals were more likely to take foraging risk than smaller individuals.
- Found that risk experienced by prey is determined by risk perceived by predators.

Sih, Andrew, Bell, Alison, Johnson, J. Chadwick. (2004). Behavioral syndromes: an ecological and evolutionary overview, *Trends in Ecology and Evolution*. 19, 372-377.

- Review paper that defines behavioral syndromes as sets of correlated behaviors.

- States behavioral syndromes are important because they imply that there is limited plasticity in behavior, that an individual's behavior and performance are correlated, and that there is individual variation in behavior.
- Different types of behavioral syndromes include activity, aggression, boldness, and the proactive-reactive axis.
- Behavioral syndromes can help explain suboptimal behaviors.

Sih, Andrew, Cote, Julien, Evans, Mara, Fogarty, Sean, Pruitt, Johnathan. (2012). Ecological implications of behavioral syndromes. *Ecology Letters*, 15, 278-289.

- Behavioral syndromes play an important role in an individual's fitness; bold individuals may be more likely to take risks that result in death.
- Individuals will continue to exhibit their behavioral type in situations that are suboptimal. Hence, fish of high activity in no predator waters will continue to be of high activity in predator waters even though such behavior is not appropriate.
- Behavioral types affect interactions between predator and prey through consumptive v. non-consumptive effects of predators on prey. My study looked at the non-consumptive effects of predation on snails in relation to boldness.
- Human induced rapid environmental change elicits 3 responses: managing novel enemies and stressors, use of novel resources, and adjustment of time or space use.

Bell, Alison M., Sih, Andrew. (2007). Exposure to predation generates personality in threespined sticklebakcs (*Gasterosteus aculeatus). Ecology Letters,* 10, 828-834.

- Study exposing sticklebacks, that showed no correlation between boldness and aggression, to predators.
- Before exposure to predator's boldness and aggression were not correlated but a positive correlation was found after exposure.
- Author's state this correlation is the result of natural selection and plasticity. Bold and unaggressive individuals suffered higher mortality suggesting that being bold and aggressive is more fit.
- Suggests that there are different strategies for coping with predators. Some sticklebacks will school while others will inspect the predator. Schooling individuals may be more shy whereas predator inspectors may be bold. My study found two different strategies of anti-predator behavior in snails. Bold snails had high levels of predator avoidance whereas shy snails developed more crush resistant shells.

Salice, Christopher J., Plautz, Stephanie C. (2011). Predator-induced defences in offspring of laboratory and wild-caught snails: prey history impacts prey response, *Evolutionary Ecology Research.* 13, 373-386.

- Study that looked at how predators effect defences of physid snails. The authors hypothesized that wild-caught snails would have stronger predator-induced defences compared to laboratory raised snails but that both would have reduced predator avoidance.
- Exposed snails to crayfish and crushed snails to elicit a predator response. Crawl out behavior and shell length, height, and thickness were measured.
- Observed diminished predator avoidance towards the end of the experiment, found that lab raised snails and wild caught snails had thicker, rounder shells with narrower

apertures than control snails, and that reproduction was lower in snails exposed to predators.

Dewitt, Thomas J. (1998). Costs and limits of phenotypic plasticity: Tests with predator-induced morphology and life history in a freshwater snail. *Journal of Evolutionary Biology*, 11, 465-480.

- This study tested for energetic costs, developmental instability costs, and developmental range limits using snails raised with pumpkinseed sunfish, crayfish, or without predators.
- Found that energetic costs were equal for snails with rotund and elongate shells, developmental instability was not an effect of phenotypic plasticity, and high plasticity did not have less of a developmental range.
- Believe that constraints on plasticity may be difficult to detect in nature.

Smith, Brian R., Blumstein, Daniel T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology,* 19, 448-455.

- Meta-analysis that looked at the single dimensions of animal personality on fitness correlates; looked at boldness, exploration, and aggression on correlates of reproduction and survival.
- Found that bolder individuals reproduced more than shyer individuals, and bolder individuals had shorter life spans than shyer individuals.
- Discovered that there is no relationship between avoidance and reproduction, a small effect of avoidance on survival, and that aggression had only a small effect on both reproduction and survival.
- The results of this study indicate the overall trends of personality and suggests that boldness may follow the trade-off hypothesis.

Dewitt, Thomas J., Sih, Andrew, Hucko, Jeffrey A. (1999). Trait compensation and cospecialization in a freshwater snail: size, shape and anti-predator behavior. *Animal Behaviour,* 58, 397-407.

- Study using physid snails that quantified behavior with and without a refuge, repeatability of avoidance behavior, and relationship of anti-predator response to morphology.
- Snails with a refuge will either crawl out of the water to avoid predators or seek refuge, but snails without a refuge exhibit significantly more crawl out behavior.
- Found a correlation between snail's size and strength of anti-predator response.

Lima, Steven L. (1998). Nonlethal Effects in the Ecology of Predator-Prey Interactions, *Bioscience.* 48, 25-34.

- Review stating that non-lethal effects of predators on populations can be of equally important as lethal effects of predation.
- There are tradeoffs between how much an individual can find resources without facing predation. The benefit of anti-predator decision making is a reduced risk in predation, yet the cost is lower energy intake which can lead to less reproduction and even death.
- Non-lethal effects have been shown to greatly impact the larger ecosystem. For example, non-lethal effects can affect the result of competition between two prey species for a limited resource.

DeWitt, Thomas, J., Robinson, Beren W., Wilson, David Sloan. (2000). Functional diversity among predators of a freshwater snail imposes an adaptive trade-off for shell morphology. *Evolutionary Ecology Research,* 2, 129-148.

- Different types of predators create a trade-off in snail's shell morphology.
- Snails can have either a narrower aperture which protects from entry of a predator or they can have a rounder shell which is more crush resistant.
- Snails with narrow apertures were found to live in areas absent of fish and snails with rounder shells were found to live in areas that contained fish.
- A trade off exists where snails with narrow apertures are less susceptible to predation by crayfish yet more susceptible to predation by fish, and snails with round shells are more susceptible to predation by crayfish yet less susceptible to predation by fish.

Hoverman, Jason T., Auld, Josh R., Relyea, Rick A. (2005). Putting prey back together again: integrating predator-induced behavior, morphology, and life history. *Oecologia,* 144, 481-491.

- Study that exposed snails to three resource levels and five predators to determine relationships between traits, limits on phenotypic responses, and costs and benefits of different phenotypes.
- The type of predator (water bug vs. crayfish) determined the snail's location and shell morphology, but both predators caused a delay in reproduction. Resource levels affected snail's reproduction and morphology.
- Concluded that there is a trade off in shell morphology based on the type of predator and that plasticity is an environment dependent response.

Hoverman, Jason T., Relyea, Rick A. (2016) Prey responses to fine-scale variation in predation risk from combined predators. *Oikos,* 125, 254-261.

- Study that investigated how prey react to multiple risks of predation by exposing snails to both water bugs and crayfish at the same time.
- Found that snails had a reduced response to one predator when in the presences of another.
- Determined that individuals can combine information from their environment to make phenotypic decisions.

Pruitt, Jonathan N., Stachowicz, John J., and Sih, Andrew. (2012). Behavioral types of predator and prey jointly determine prey survival: potential implications for the maintenance of within-species behavioral variation. *The American Naturalist,* 179, 217-227.

- Tested the behavioral types of both the predator and the prey in order to determine the impact on interactions with one another
- The effects of predator avoidance and maximum shell diameter were dependent on the predator's behavioral type. Snails with high predator avoidance were more likely to survive with active prey and snails with low predator avoidance survived better with inactive prey.
- State that interactions between different species could be important in maintaining variation within populations.

Osenberg, Craig W., Mittelbach, Gary G. (1989). Effects of body size on the predator-prey interaction between pumpkinseed sunfish and gastropods. *Ecological Monograph,* 5 405-432.

- The diets of pumpkinseed sunfish are primarily snails, but there is lots of variation between snail taxa and size among locations.
- This study measured the effects of snail size on encounter rates, attack probabilities, and capture success.
- Concluded that the effects of predator-prey interactions in size-structured populations is complicated, but understanding prey distributions can help this variation be understood.

Rundle, Simon D., Bronmark, Christer. (2001). Inter-and intraspecific trait compensation of defence mechanisms in freshwater snails. *Proceedings: Biological Sciences*, 268, 1463-1468.

- Study that demonstrates trait compensation in response to predators across multiple species of snails.
- Different species demonstrate different avoidance responses. Species with thinner shells were more likely to move out of the water while thicker shelled species tended to hide.
- Found an overall negative correlation between crush resistance and avoidance behavior.

Turner, Andrew M., Fetterolf, Shelley A., Bernot, Randall J. (1999). Predator identity and consumer behavior: differential effects of fish and crayfish on the habitat use of a freshwater snail. *Oecologia,* 2, 242-247.

- Study that compared snail's behavior to two different predators: crayfish and fish.
- Found that snails exposed to fish hid while snails exposed to crayfish moved out of the water.
- Concluded that different species of predators induce different behavioral responses, which could affect snail's availability of resources.

Turner, Andrew M. (1996). Freshwater snails alter habitat use in response to predation. *Animal Behaviour*, 51, 747-756.

- Contrasted how snails used habitats in lakes that contained pumpkinseed sunfish with snails in lakes that did not have pumpkinseed sunfish.
- Snails in water that had been exposed to pumpkinseed sunfish doubled their use of refuges. When refuges were unavailable snails would move to the surface of the water.
- Determines that snails have behavioral flexibility that allows them to decrease the cost of predation.

Turner, Andrew M., Turner, Sarah E., Lappi, Heidi M. (2006). Learning, memory and predator avoidance by freshwater snails: effects of experience on predator recognition and defensive strategy. *Animal Behaviour,* 6, 1443-1450.

- Study that examined if experiences influence perception of risk and defensive strategy.
- Compared responses of wild caught snails and lab raised snails. Found that wild caught snails showed a stronger predator response then the lab raised snails.
- Performed a second experiment comparing snails raised with and without crayfish. Found that defense strategy was dependent of experience; snails raised without the

crayfish responded to fish cues by hiding but snails raised with crayfish moved out of the water in response to fish cues
- Concluded that there are some effects of experience but antipredator responses are mostly innate.

Turner, Andrew M., Bernot, Randall J., Boes, Christina M. (2000). Chemical cues modify species interactions: the ecological consequences of predator avoidance by freshwater snails. *Oikos*, 88, 148-158.
- Observed snails increasing use of covered habitats with increasing depth. Hypothesized that changing habitat use was due to changes in predation risk and that these habitat shifts affect snail's interactions with food resources.
- In the presences of fish snails moved under cover and in the presence of crayfish snails avoided the predator by moving out of the water; these predator responses were shown to affect snails interactions with resources.
- The results indicate that predator cues could have a large impact in shaping food webs.

Trussell, Geoffrey C., Nicklin Matthew O. (2002). Cue sensitivity, inducible defense, and trade-offs in a marine snail. *Ecology*, 83, 1635-1647.
- Study that looked at defenses induced in the snail, Littorina obtusata, by a crab predator.
- Found that cues from crab and crushed snails resulted in thicker snail shells than just exposure to crab.
- Conclude that costs of having a thick shell is outweighed by reduced risk of predation.

Brookes, J. I., Rochette, Remy. Mechanism of a plastic phenotypic response: predator-induced shell thickening in the intertidal gastropod Litorina obtusata. *Journal of Evolutionary Biology*, 3, 1015-1027.
- Study that examined if phenotypically plastic predator responses, such as increased shell thickness, are physiological or product of reduced feeding due to predation.
- Snails exposed to crabs feeding on snails produced 91% more shell material than snails not exposed to predators.
- Found that snails exposed to predation increase calcification rates, but snails feeding behavior has little influence this physiological change.
- Discuss developmental and energetic costs required for increased shell thickness.

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- Examined how consumptive and non-consumptive effects of predators influenced prey foraging rates and occurrence of trait- and density-mediated trophic cascades in a three level food chain consisting of crab, snail, and barnacle.
- Trait-mediated cascades were as strong or stronger than density mediated- cascades.
- Size of predator effects depended on whether they were in a risky or refuge habitat. In risky habitats snails foraging was strongly suppressed, but predation risk had no effect in the refuge habitat.

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