HOW SHELL MORPHOLOGY MEDIATES PATCH USE IN RESPONSE TO PREDATION RISK IN FRESHWATER SNAILS

By

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Abstract: I examined how shell morphological defenses in freshwater snails (Physa sp.) influence patch choice and patch-use in response to predator cues. Behavioral responses were analyzed using a model comparison approach based on Akaike Information Criterion (AIC) to understand what morphological relationships and their interactions with predator cues best explained patch-use of the snails. I then tested alternative adaptive explanations for the morphological traits explaining patch-use by testing their effect on being killed by a predator in a no-choice predation study, as well as examining their influence on shell crush resistance. In this paper I also examined if the same type of cospecialization of complementary morphology and behavior found in earlier experiments occur between a behavior reducing the predator encounter rate, and morphological traits reducing the probability of surviving encounters with predators. I examined how shell morphology influences how physid snails use patches in the absence and presence of predator cues. I found that individuals with larger aperture lengths were more vulnerable to predators, and that more morphologically vulnerable individuals exhibited stronger antipredator behavior. Therefore, there is a compensatory relationship with an antipredator behavior and morphological defense that address different components of predation risk (i.e. reducing encounters with predators vs. increasing the probability of surviving such an encounter). I argue that separating predation risk into the two separate components of avoiding encounters and surviving encounters, can result in a better understanding of individual variation, and animal personalities in the context of predation risk.

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CHAPTER I

HOW SHELL MORPHOLOGY MEDIATES PATCH USE IN RESPONSE TO PREDATION RISK IN FRESHWATER SNAILS

Introduction

Predator-prey interactions influence many levels of ecology; from the behavior of individuals, to the life-history traits of populations, and even in some cases, trophic cascades determining community structure (Crowl and Covich 1990; DeWitt *et al.* 1999; Glinsky 1984; Schmitz et al. 1997). Predation risk is one of the most obvious and intuitive selection pressures in nature, often shaping both morphological and behavioral phenotypes (Endler 1991; Lima 1998; Lind and Cresswell 2005). It can be argued that natural selection should operate on antipredator behavior more than almost any other behavior; this is because only individuals that avoid predation early in life will even have a chance to perform other behaviors such as mate selection, or mate guarding (Westneat and Fox 2010).

Predation risk is made of two distinct risk components; the probability of encountering a predator, and the probability of surviving encounters (Lind and Cresswell 2005). Investing in predator defenses that reduce either of these risk components can sometimes be adaptive. Antipredator behaviors such as fleeing, hiding, or fighting to avoid being killed by a predator have a myriad of additional fitness consequences, often in the form of opportunity costs of not being able to perform other behaviors such as foraging or mating. Therefore morphological defenses that increase the probability of surviving encounters with predators may allow individuals to pursue other fitness increasing behaviors that they would otherwise avoid due to increased encounter rates with predators.

Some attention as of late has been given to the interplay between morphological defenses, and behavioral defenses against predators (Bibby 2007; DeWitt *et al.* 1999). Research on shell morphological defenses in gastropods has revealed two contrasting evolutionary outcomes. In the case of periwinkle sea snails, individuals in highly acidic conditions where shell morphological defenses are more costly to build and maintain, individuals exhibit higher avoidance responses to predator cues, suggesting morphological defenses and antipredator behavior compensate for one another (Bibby 2007). Alternatively, in physid freshwater snails, individuals have functionally complementary behavior and morphology, or what has been termed "cospecialization" (DeWitt *et al.* 1999). DeWitt *et al.* (1999) found that individuals with smaller aperture widths, that were presumed to be safer from predators that reach in shells to extract snails, exhibited more antipredator behavior (i.e. crawling above waterline). However, the antipredator behaviors correlated with the morphological defense, surviving encounters with predators, both reduce the second component of predation risk. Would one expect a similar complementary morphology and behavior if the antipredator behavior reduced the first component of predation risk, encounter rates with predators?

Positively correlated traits like aperture obstruction and crawling above water line, antipredator behavior, found by DeWitt *et al*. (1999) are important because they show that selection favoring suites of complementary morphological and behavioral defenses can give rise to consistent individual differences. Behavioral ecologists have largely considered behavior to be unlimitedly malleable (Sih *et al.* 2004). However, studies over the last quarter century have emphasized consistent variation among individuals that suggest that there is limited plasticity in behaviors that are not trivial and that demand an evolutionary explanation (Dingemanse and Wolf

2010; Sih *et al.* 2004; Van Doorn *et al.* 2009; Wolf *et al. 2008*). The study of so-called "behavioral syndromes" or "animal personality" has emerged as a modern attempt to provide an adaptive explanatory framework for consistent individual variation (Sih *et al*. 2004). Sih *et al*. (2004) have defined behavioral syndromes as "a suite of correlated behaviors reflecting between-individual consistency in behavior across multiple situations" (Bell 2006). Individuals within such a population should exhibit "behavioral types" (e.g., consistently aggressive to conspecifics across time or multiple contexts).

There are numerous explanations to account for the emergence of such syndromes, but most can be classified into just a few main categories. Correlational selection is a common adaptive explanation of behavioral types, the idea being that there are adaptive suites of behaviors that naturally complement each other and are driven by the same selection pressures (Bell 2007). For example, in a cricket species, a link between foraging effort and mating call intensity make up part of an adaptive suite where both appear to be driven by predation risk (Hedrick 2000). State-dependent behavior has also been a popular framework for explaining individual differences (Clark 1994; Clark and Mangel 2000). This framework posits that an individual's state determines their optimal behavioral response.

State-variables in ecology were first defined as "the physiological state of an organism", but have since been used more broadly, as anything about an organism that can change or differ between individuals (Clark and Mangel 2000). State-dependent behaviors are thought to create feedback loops between state and behavior, if an individual's behavior subsequently influences the individual's state (e.g., foraging behavior, and fat reserves). For example, the asset protection principle predicts that individuals with a higher state variable (e.g. size), would be more risk averse because they have more fitness assets built up that they could lose (Clark 1994; Clark and Mangel 2000). Recent theoretical analyses have shown that the asset protection principle is limited to explaining short-term consistency of behavior, and cannot account for stable long-term behavioral types (Luttbeg and Sih 2010). These models show that the asset protection principle is inherently a negative feedback loop, and that in general, any negative feedback loop cannot drive long-term behavioral types in a population because differing initial states and behaviors converge. However, a positive feedback loop such as state-dependent safety can lead to stable, long-term adaptive behavioral syndromes (Luttbeg and Sih 2010). The Luttbeg-Sih model suggests that when resources and predation risks are matched (e.g. low risk and low resources, or high risk and high resources), small differences in initial state can result in a positive feedback loop of state-dependency that results in diverging adaptive behavioral types (Clark and Mangel 2000). If there is state-dependent safety for larger individuals, then individuals that experienced early foraging success should be larger as a result. The relationship between early foraging success and subsequent foraging success is inherently a positive feedback loop, where individuals that experience early foraging success will be larger and experience lower predation risk in this model, which would allow them to forage even more without taking on additional risk.

Study System

Physid snails are common in lakes, ponds, and streams and play an important role in aquatic food webs, grazing on periphyton, and are known to be exposed to many aquatic predators such as crayfish, diving beetles, fish, flatworms, and birds (Bernot and Turner 2001; DeWitt *et al*. 1999, Snyder 1967;Taylor 2003). I chose this system because physid snails are known to respond behaviorally to chemical cues from crayfish and crushed conspecifics, and because it has been a common system for empirically testing many aspects of predator-prey relationships (Bernot and Whittinghill 2003; DeWitt 1996; DeWitt et al. 1999, 2003; Turner *et al*. 1999; 2000).

Predation risk is thought to be size-dependent for members of this genus, where larger (shell length ≥ 10mm) individuals have shells that are more difficult for predators to penetrate

(Alexander and Covich 1991). There is also research suggesting that individuals with smaller aperture widths sometimes show stronger antipredatory behavioral responses (DeWitt et al. 1999). This trade-off sets up an interesting opportunity to study how morphology influences predator-prey dynamics.

If antipredatory defenses are separated into the two categories mentioned before: reducing encounters with predators, and surviving encounters, climbing just out of the reach of predators could be viewed as surviving an encounter. I examined if the same type of cospecialization (i.e., complementary morphology and behavior) found by DeWitt *et al*. (1999) also exists between a behavior reducing the predator encounter rate, and morphological traits reducing the probability of surviving encounters with predators. I examined how the vulnerability of an individual's shell morphology to crayfish predators, and shell crush resistance influences the extent to which they avoid areas associated with crayfish predator cues. If there is cospecialization, I expect that individuals with "safer" morphologies should also show higher avoidance of predator cues.

Methods

Patch-Use Experiment

Approximately 200 adult physid snails were collected (shell length ≥ 4mm) from a local stream (Babcock Park, Stillwater, OK), and lab reared for approximately two generations before using the adults in my patch-use experiment (Tripet and Perrin 1994). Shell morphological measurements including: shell length, shell width, aperture length, and aperture width were recorded for 150 individuals (Figure 1.1.). A linear regression was performed for shell length versus aperture width and a line of best fit was produced (Figure 1.2). I classified individuals into one of two morphotypes (1. narrow aperture width, and 2. wide aperture width) by classifying individuals above the regression line as wide aperture width, and below the regression line as narrow aperture width. I then assigned three “narrow” aperture morphs and three “wide” aperture morphs to each of 15 experimental arenas. Individuals were marked with one of six different colors of enamel paint on their shell so that I could track each individual’s behavior throughout the experiment. Individuals were starved for 48 hours before being placed into 16” x 32” experiential arenas containing a low and high resource patch (Figure 1.3).

Periphyton grown on 2”x2” clay tiles under two different nutrient levels (low and high) served as the prey’s resource. The high resource patch periphyton was grown in the standard basal COMBO nutrient levels given by Kilham *et al*. (1998), and the low resource periphyton was given a solution that was 10% basal COMBO, and 90% reverse osmosis filtered H_2O, thus reducing the nutrients available to the periphyton (Jeyasingh et al. 2009; Kilham et al. 1998). Periphyton was collected from a local pond on campus at Oklahoma State University. To collect the periphyton, 2”x2” clay tiles were placed in shallow sections of the pond where periphyton were found growing on surrounding rocks. After one week the tiles were retrieved from the pond and brought into the lab to start the two different periphyton cultures. The low and high resource cultures were inoculated with the periphyton collected and the aforementioned growth mediums and kept under full spectrum growth lights at 20°C for 30 days before the patch-use experiment.

Individuals were placed into the experimental arenas and starved for two days (Figure 1.3.) On the third and fourth day, individuals were observed over 5 hour periods where they received 50cc of reagent water into the high resource patch at the beginning of the time period to serve as a control for the predator cues released in the second part of the experiment. After the two days of no predator cue trials individuals were again starved for 48 hours, followed by another 2 days of observation for 5 hours where they received 50cc of predator cues injected into the high resource patch, which consists of water from a tank containing a crayfish, paired with a crushed conspecific. Over each observational period I recorded which patch each individual was found in (low or high resource patch).

I used generalized linear mixed models to examine what factors influenced patch-use. This mixed model approach allowed me to treat the tank an individual was in, and the repeated measures of individuals as random variables. Thirty-one alternative models were constructed that included combinations of all morphological measurements, and ratios of measurements, and the presence or absence of the predator cue. All alternative models were analyzed using the Akaike information criterion (AIC) model selection approach to determine which morphological relationships, and their possible interactions with the presence of predator cues, best explained the use of the high resource patch. Models with ΔAIC scores greater than 7 were then removed from my analysis. To exclude models that have pretending variables, I only included more complex models if they had lower ΔAIC scores than their less complex versions (Richards 2008; Richards *et al*. 2011).

Crayfish Predation Experiment

I collected approximately 150 adult physid snails from two different collection sites, (1. Babcock Park, Stillwater, OK and 2. Teal Ridge, Stillwater, OK), and 50 crayfish from Teal Ridge. To collect crayfish, minnow traps containing approximately 150 grams of raw fish were placed at the two collection sites where the snails were collected. I placed three traps at Babcock Park, and three at Teal Ridge, and collected them 24 hours later. No crayfish were found in any of the three traps from Babcock Park, however a total of 125 crayfish were found in traps set at the Teal Ridge collection site, and 50 were brought back to the lab for the experiment.

The following morphological measurements were taken for each crayfish: claw length, dorsal length, dorsal width, and wet weight in grams. For snails I recorded shell length, shell width, aperture length, and aperture width (Figure 1.1.). Individual snails were marked with one of six different colors of enamel paint. Clear 1gallon Pyrex bowls served as the experimental arenas; they were filled to the maximum capacity with well water so that snails could not crawl out of the water as an escape response to predators. Six individuals were placed into each arena with a single crayfish predator. After one hour, I recorded which individuals were still alive. This would allow me to look for relationships between morphology and vulnerability to crayfish predation.

Statistical Analysis of Predation Experiment

I used generalized linear mixed models to examine what morphological traits make snails vulnerable to crayfish predation. I treated the bowl in which individuals were placed as a random variable. Thirty-six alternative models were constructed which included combinations of snail morphological measurements, and ratios of these measurements.. These alternative models were analyzed using model selection based on AIC to determine which morphological relationships best explained the probability of being killed by a predator. I again removed models with ΔAIC scores greater than 7 and excluded models that contained pretending variables by the method previously mentioned.

Shell Crushing Force Experiment

I performed a minimum force to crush experiment to examine what shell morphological characteristics influence crush resistance. Using 30 snails from each of the two collection sites, I took the same morphological measurements used in the previous experiments (Figure 1.1.). Individuals were placed in a glass jar, then a slightly smaller jar was placed on top of the snail. I proceeded to fill the small jar with sand until the shell was crushed. I then recorded the final weight of the jar filled with sand that crushed the snail’s shell. This allowed me to look for relationships between morphology and crush resistance of individuals.

Statistical Analysis of Shell Crushing Force Experiment

Using generalized linear models I produced similar models containing the morphological traits and their interactions as used in the crayfish predation experiment. I then performed the same AIC models selection approach previously mentioned. Again removing models with ΔAIC scores greater than 7, and excluding models that contained pretending variables by the methods previously mentioned.

Morphology Across All Experiments

To compare the importance of each morphological trait across all of the experiments I used the information theoretic approach (IT-AIC) of model averaging (Richards 2008; Richards *et al*. 2011). Using the AIC scores, ΔAIC scores, and AIC weights from each experiment, I identified the top candidate models by excluding all those with a ΔAIC s higher than seven. I excluded any models that have pretending variables by only including more complex models if they have lower ΔAIC scores than their more simple versions (Richards 2008; Richards *et al*. 2011). Each morphological trait was assigned an IT-AIC score that was the sum of the AIC weights for all models in which the variable is, divided by the sum of the AIC weights of all the remaining models used in the analysis.

Results

Patch-Use Experiment

The percent of snails in the high resource patch was 66% when no predator cue was present and 55% after the predator cue was added (Figure 1.4). The best supported model for use of the high resource patch included the presence or absence of predator cues, the ratio of an individual's aperture length to shell width, and their interaction (Table 1.1). This model shows that there is little to no effect on patch-use by an individual’s aperture length to shell width ratio on use of the high resource patch when predator cues were absent, but has a strong negative effect when predator cues were present (Figure 1.5). This means that the larger an individual’s aperture length to shell width ratio, the more likely they are to flee from the predator cue associated area. All three of the candidate models include aperture length in some form (i.e., in a ratio, or interacting with another morphological trait) with a interaction effect with predator cue (Table 1.1). The second best supported model included the presence and absence of predator cues, aperture length, and aperture width, and a three-way interaction between these variables (Table 1.1). This model shows that individuals with small aperture widths spend more time in the high resource patch in the absence of predator cues, however this affect of aperture width decreases as aperture length increases (Figure 1.6). In the presence of predator cues individuals with large aperture widths spend more time in the high resource patch, but again, this affect gets smaller as aperture length increases (Figure 1.6). Focusing on individuals with very small aperture lengths, predator cues have little affect on individuals with small aperture widths, but have a drastic impact on individuals with large aperture widths (Figure 1.6).

Crayfish Predation Experiment

All of the candidate models for explaining the probability of a snail being killed by a predator included site, from which they were collected from, and all include shell length (Table 1.2). Again, aperture length is important; it was included in three of the six candidate models (Table 1.2). These models show that individuals collected from Babcock Park (predator absent site), were much more likely to be killed by a predator than individuals collected from Teal Ridge (predator present site). In the one-hour predation experiment, the mortality for individuals collected from Babcock Park was approximately 84%, where in the Teal Ridge population it was approximately 30%. The mortality differences between these two populations led me to also analyze the data from these populations separately.

Babcock Park Population Predation Experiment

The best supported model for the Babcock Park population shows that the probability of being killed by a predator was higher for individuals with larger aperture lengths, but only ranged from 91% to 99%, suggesting almost no individuals were safe from predators in this population (Figure 1.7). Shell length was included, in some form, in four of the nine candidate models, suggesting it was also important in determining an individual's predation risk (Table 1.3).

Teal Ridge Population Predation Experiment

In contrast to the Babcock Park population, over 70% of individuals collected from Teal Ridge survived the one-hour experiment. The best supported model for the Teal Ridge population for the probability of being killed by a crayfish included the aperture and shell lengths of individuals (Table 1.4) (Figure 1.8). In this model, an individual's probability of being killed was lower for individuals with larger shell lengths, but like the Babcock Park population, increased with aperture length. However, this affect of shell length decreases as aperture length increases. Shell length was included in three of the four candidate models for Teal Ridge individuals. Therefore, the apertural opening was important, as well as the overall size of the individual (Table 1.4).

Shell Crush Resistance

The mean weight needed to crush an individual's shell from Babcock Park was 507.76g, while it was 1379.98g for individuals from the Teal Ridge population (Figure 1.9). The best supported model for the combined data set of both populations included the site from which individuals were collected and shell length (Table 1.5). This model showed that the amount of force needed to crush a shell increased with larger shell lengths. This was also true for larger shell widths. To compare these results to the predation experiment I again analyzed the two populations separately.

Babcock Park Population Shell Crush Resistance

The best supported model for the Babcock Park population included both shell length and shell width, as well as the interaction between the two (Table 1.6.). Crush resistance increased with shell length for individuals with larger shell widths, but shell length led to lower crush resistance for individuals with small to medium shell widths (Figure 1.10). This result is puzzling because the medium shell width had a lower crush resistance than small shell widths, yet the large shell width had higher crush resistance, as expected.

Teal Ridge Population Shell Crush Resistance

Similar to the combined analysis, the best supported model for individual's collected from Teal Ridge included shell length, and was closely followed by shell width as the second best model, and moderate support for aperture length as the third candidate model (Table 1.7). Crush resistance of Teal Ridge individuals was highly positively correlated with shell length (Figure 1.11).

Morphology Across All Experiments

In order to compare the importance of each morphological trait across all of the experiments I used the information theoretic approach (IT-AIC) of model averaging (Richards 2008; Richards *et al*. 2011). Using the AIC scores, ΔAIC scores, and AIC weights from each experiment, I first identified the top candidate models by excluding all those with a ΔAIC s higher than seven. I then excluded any models that have pretending variables by only including more complex models if they have lower ΔAIC scores than their more simple versions (Richards 2008; Richards *et al*. 2011). Each morphological trait was assigned an IT-AIC score that was the sum of the AIC weights for all models the morphological trait was in, divided by the sum of the AIC weights of all the remaining models used in the analysis (Table 1.8). This table shows that the only ratio with a noteworthy IT-AIC score was the aperture length to shell length ratio in the patch-use experiment. To break the results down into each standard measurement, I show the proportion of the IT-AIC explained by shell length, shell width, aperture length, and aperture width for each of the experiments (Figure 1.12). This shows that aperture length plays a significant role in all the experiments, supporting why it may be a good predictor of patch-use.

Discussion

I examined how shell morphology of freshwater snails mediates patch-use in response to predator cues, and also performed additional experiments testing adaptive explanations for the effects of these morphological traits on behavior. My findings suggest that shell morphology does indeed influence the patch-use response of individuals. All models explaining patch-use that did better than an AIC weight of 0.001 included the presence and absence of predator cues interacting with morphological characteristics, but the model containing only predator cue did poorly. Individuals with higher aperture length to shell width ratios showed a more drastic fleeing response when predator cues were present.

DeWitt *et al*. (1999) observed contrasting results with aperture width, where individuals that were more morphologically protected, exhibited more antipredator behavior. They concluded that since it was reported that crayfish are “reach-in predators”, meaning they pull snails out of their shells rather than crushing their shells, that their results represented a “double-defense”. They termed this behavioral response complementing a morphological defense, cospecialization; meaning that the behavior and the morphology functionally have the same goal (DeWitt *et al*. 1999). This is in contrast to compensatory behavior, where the behavioral response is meant to make up for less effective morphological defenses.

I also examined if the same type of cospecialization of complementary morphology and behavior found by DeWitt *et al*. (1999) occur between these morphological defenses, and a behavior reducing the predator encounter rate. I found that individuals with larger aperture lengths were more vulnerable to predators, and that more morphologically vulnerable individuals exhibited more antipredator behavior. Therefore, there is a compensatory relationship with an antipredator behavior and morphological defense that address different components of predation risk (i.e., reducing encounters with predators vs. increasing the probability of surviving such an encounter). I compared the IT-AIC scores from all of the experiments and look for common explanatory factors (Figure 1.12). The only ratio that was more informative than the standard measurements (i.e., SL, SW, AL, AW) was the aperture length to shell width ratio in the patch-use experiment. If there were cospecialization, I would expect to see that this ratio also played a major role in the predation experiment, but it did not. The only factor that does tie to all the experiments in any meaningful way is aperture length. DeWitt *et al*. (1999) make the claim that individuals with wider apertures are more vulnerable to crayfish because they are reach in predators, and a larger aperture would allow easier access to the soft body parts of snails. The crayfish predation data partially conflicts with this claim; while individuals with larger apertures were at more risk to crayfish, nearly all snails killed in the no-choice predation experiment were crushed, meaning their shells were not left intact.

If the reach-in predator safety effect is not the adaptive explanation for this positive correlation between aperture length and predation risk, what is? Alternative explanations for this outcome could be that while *P. simulans* may not be a reach-in predator, most crayfish are, and have evolved to use a general cue that happens to also be an adaptive response to the crushing methods used by the species of crayfish in my experiment. Aperture length best explained the probability of being killed by a crayfish for the Babcock population, however the effectiveness of this morphological defense was very small. Even individuals with small aperture lengths still had more than a 90% chance of being killed during the one-hour experiment. If these individuals are not morphologically safe, then why do they seem to base their behavior on these traits as if they were? This could be because these same morphological traits protect them from other predators in their environment, such as diving beetles, and they were responding to the crushed conspecific cues, rather than the crayfish cues. Lind and Cresswell (2005) have also pointed out that laboratory predation studies may deprive animals of many compensatory behaviors that could normally be performed in nature. For example, individuals in the predation experiment were not able to climb out of the water to avoid being eaten, which could lead to misleading predation risk estimates.

Shell length played a major role in explaining both the predation risk and shell crush resistance, but explained very little about patch-use. This is very interesting because shell length, for snails, is the most well documented morphological defense against predators of all kinds (Alexander and Covich 1991; DeWitt *et al* 1999; Tripet and Perrin 1994). Indeed, my data supports this notion as well. Regardless of whether the crayfish is reaching in or crushing the snails, shell length also explained a large proportion of the variance in crush resistance, especially in the population that was exposed to predator cues in their environment. This suggests that something more complex is going on between traits addressing these two different components of predation risk. It could also be argued that perhaps I would have seen cospecialization if I tested patch-use with individuals that were from the crayfish present collection site, rather than lab reared individuals originally from a more crayfish free environment.

Implications and Future Directions

I believe that separating predation risk into the two separate components of predation risk, avoiding encounters and surviving encounters, can provide a better understanding of individual variation, and animal personalities in the context of predation risk. Stevison and Luttbeg (in prep) have attempted to form a theoretical framework that integrates both the asset protection principle by Clark (1994), and the size-dependent safety principle, by Luttbeg and Sih

(2010). Snails are an ideal system that meet both of the main assumptions of these models (Stevison and Luttbeg in prep; Clark 1994; Luttbeg and Sih 2010). Snails have size-dependent assets (e.g., fecundity), related to body mass, and size-dependent predation risk, related to shell morphology (Alexander and Covich 1991). A theoretical analysis addressing the link between investment in morphological defenses and a predator encounter rate related behavior show that a compensatory relationship should occur when the probability of surviving an attack and the resource availability are balanced (Stevison and Luttbeg in prep). Therefore, when the probability of surviving an encounter is low and moderate resource levels, there should be cospecialization between the defense and antipredator behavior. This model also explored the link between fecundity and this antipredator behavior. Again, when the probability of surviving encounters was somewhat balanced with resource levels, individuals that had higher fecundity performed more antipredator behavior. This could explain why the ratio of aperture length to shell width best predicted the patch-use of individuals. The predation experiments show that aperture length largely determines an individual's predation risk, especially in the Babcock Park population (Table 1.2) (Table 1.3) (Figure 1.7) (Table 1.4) (Figure 1.8). Shell width is also known to be a good predictor of fecundity (Alexander and Covich 1991). Therefore I could think of the ratio between these two traits essentially as the probability of the individual dying in an encounter, divided by the reproductive value of the individual.

The theoretical work by Stevison and Luttbeg (in prep) could be tested more comprehensively in this system by rearing snails in different environments in the lab, manipulating the perceived predation risk, and resource availability. Further research needs to address the heritability of these correlated traits, to see if they are separately plastic, or if only the morphology is plastic to best match the innate behavior of individuals. There may be many aspects of ecology involved in the onset of these behavior matching morphology, as experiments comparing wild-caught vs. lab reared individuals suggests (DeWitt and Langerhans 2003).

Understanding how these traits are inherited is key in understanding how selection can operate on them as suites, rather then separate traits. Future studies need to be performed that manipulate early life exposure to different levels of risk and resources to see how developmental plasticity can shape morphology and behavior, in hope that the gene, and environment, interaction can be understood.

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TABLES AND FIGURES

Figure 1.1 Shell morphological measurements used in all experiments: SL, shell length; SW, shell width; AL, aperture length; AW, aperture width.

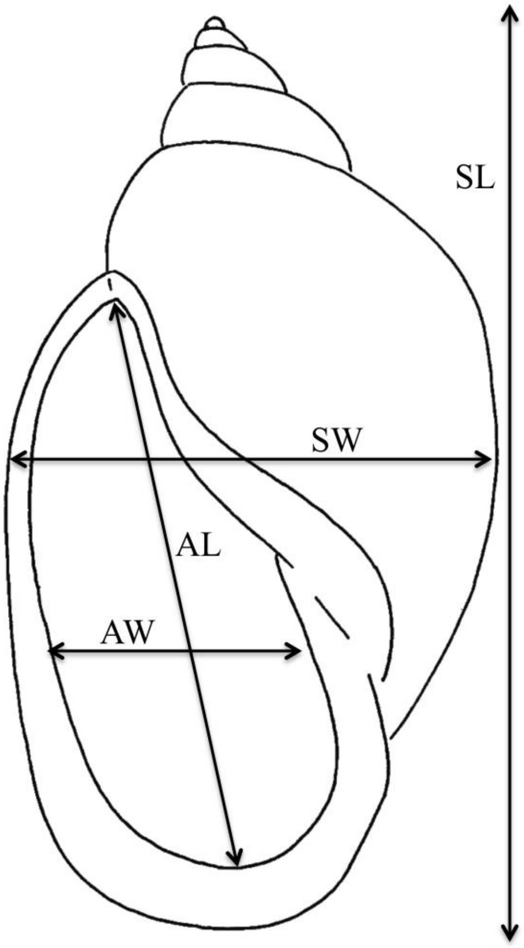


Figure 1.2 Linear regression for shell length (mm) and aperture width (mm) used to designate aperture width: shell length morphotypes, the equation of this line is (0.4156*SL-2.5982). Individuals above the regression line were classified, as wide aperture morphotype, and individuals bellow the line were designated narrow aperture morphotype.

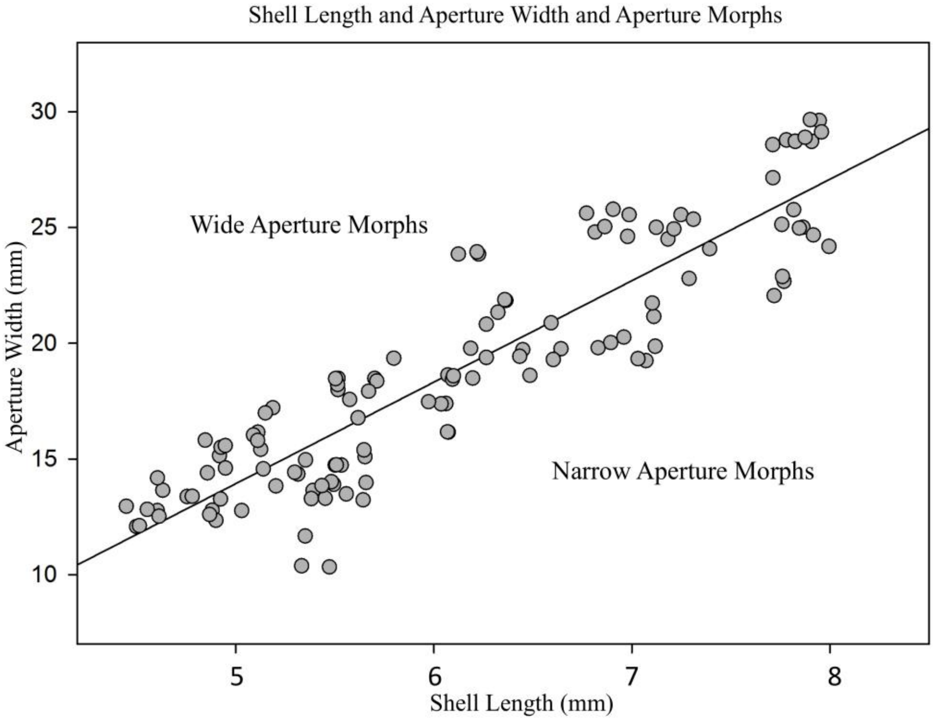


Figure 1.3 Experimental arenas 16" x 36", used in patch-use experiment, consisting of a low and high resource patch that contained three 2" x 2" clay tiles covered in periphyton grown in different nutrient level growth mediums.

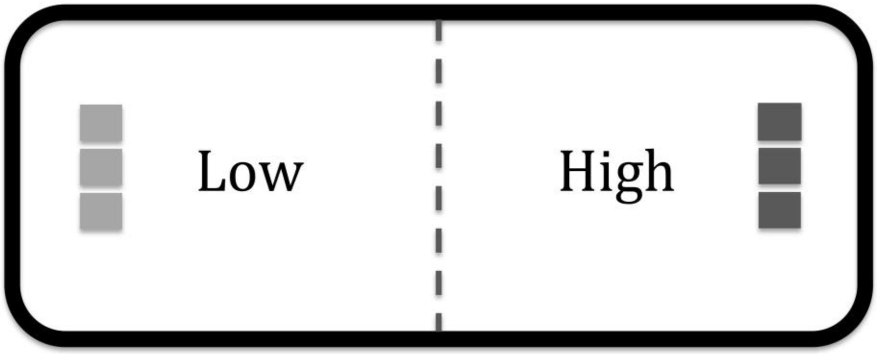


Figure 1.4 Mean and standard errors for use of the high resource patch for the patch-use experiment in the presence 66%, and absence 55%, of predator cues.

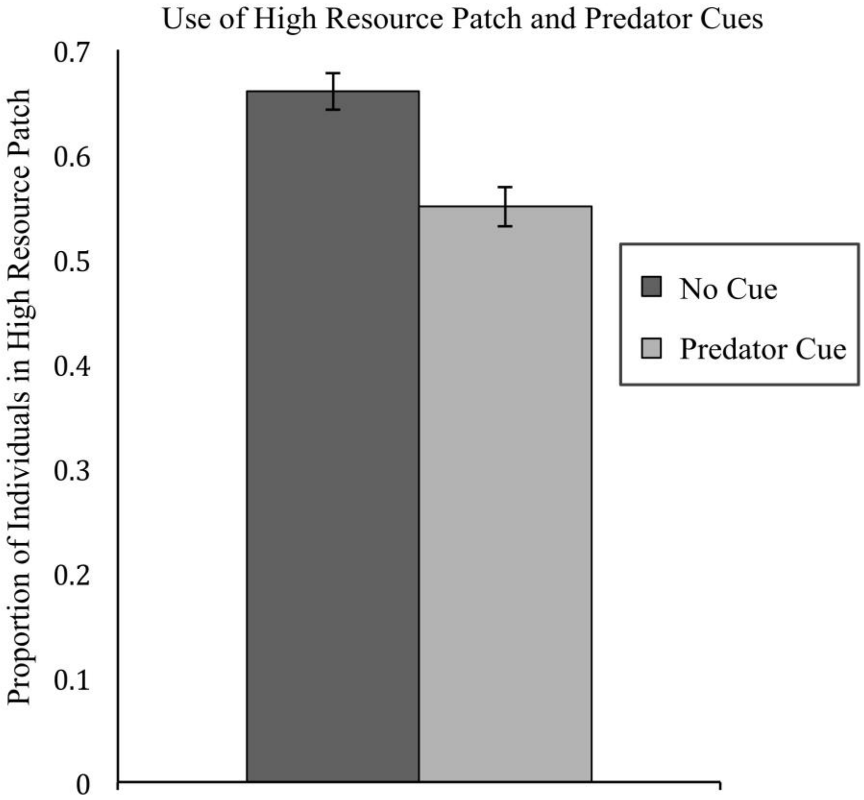
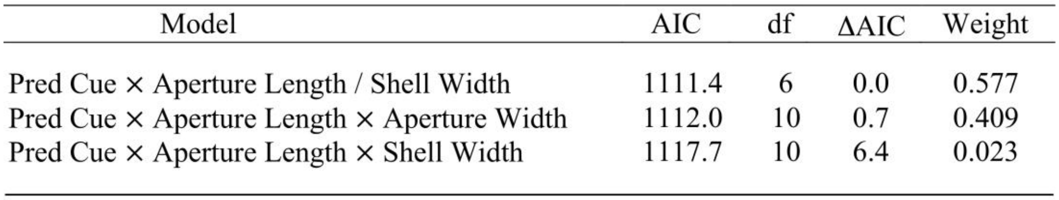


Table 1.1 AIC analysis of alternative models explaining use of the high resource patch in the presence and absence of predator cues after removing models with ΔAIC scores greater than 7, and excluding models that contained pretending variables.



Model	AIC	df	ΔAIC	Weight
Pred Cue × Aperture Length / Shell Width	1111.4	6	0.0	0.577
Pred Cue × Aperture Length × Aperture Width	1112.0	10	0.7	0.409
Pred Cue × Aperture Length × Shell Width	1117.7	10	6.4	0.023

Figure 1.5 Probability of using the high resource patch in the presence and absence of predator cues for a range of aperture length to shell width ratios, based on the top model from the AIC analysis. The equation for the no cue line is exp(1.6211 - 0.4916*AL/SW) / (1+(exp(1.6211 - 0.4916*AL/SW))), and the equation for the predator cue line is exp(1.6211 + 8.0246*AL/SW - 7.6253*AL/SW) / (1 + (exp(1.6211 + 8.0246*AL/SW - 7.6253*AL/SW)).

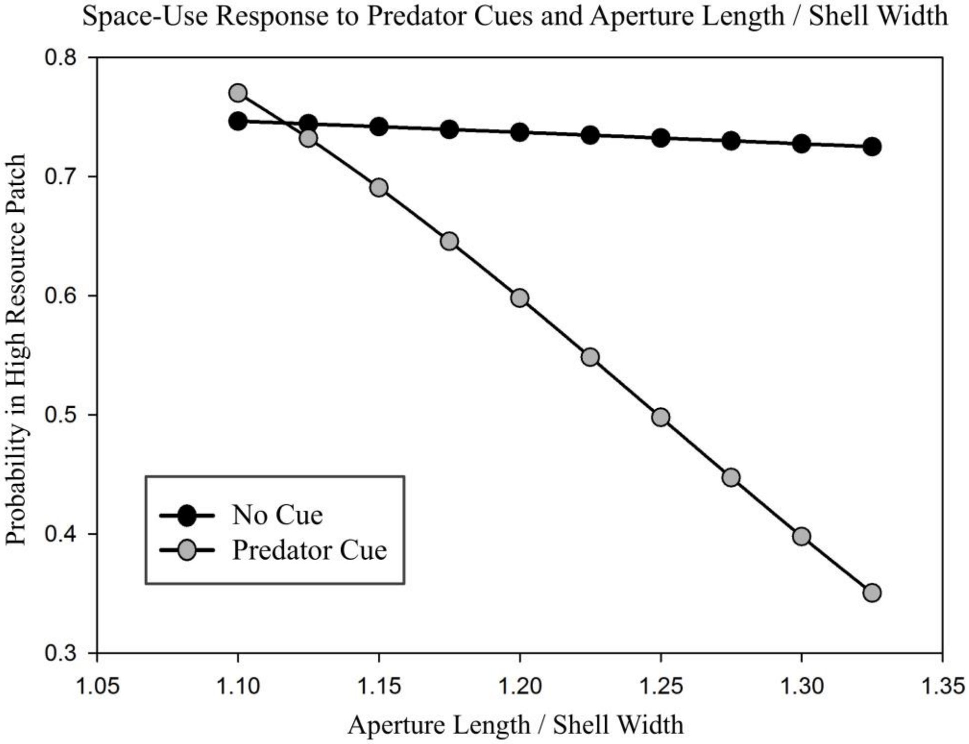


Figure 1.6 Probability of using the high resource patch in the presence and absence of predator cues for a range of aperture length (mm) and two sizes of aperture width (mm), based on the second best model from the AIC analysis. The equation for the no cue lines are exp(0.5729 + 0.068055*AL -0.19208*AW + 0.00229*AL*AW) / (1 + exp(0.5729 + 0.068055*AL - 0.19208*AW + 0.00229*AL*AW). The equation for the predator cue present lines are exp(0.5729 + 0.068055*AL -0.19208*AW + 0.00229*AL*AW -0.254427*AL + 0.472351*AW - 0.001625*AL*AW)/1 + exp(0.5729 + 0.068055*AL -0.19208*AW + 0.00229*AL*AW - 0.254427*AL + 0.472351*AW -0.001625*AL*AW); where small and large aperture widths were 1.75 mm, and 3 mm respectively.

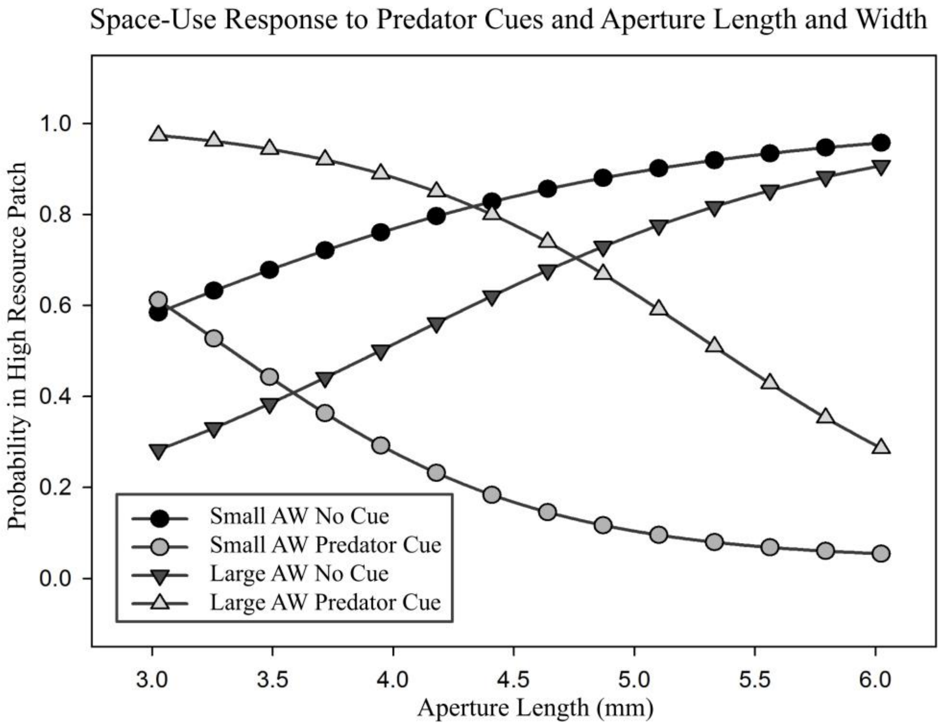
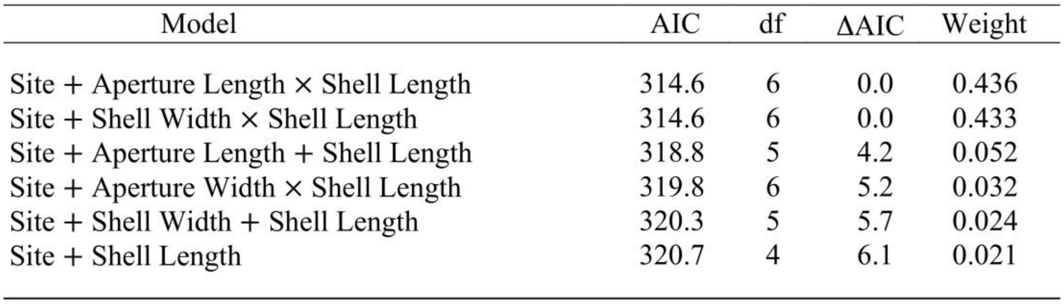


Table 1.2 AIC analysis of alternative models explaining survival of the crayfish predation experiment for both the Babcock park and Teal Ridge populations. The table includes remaining models after removing models with ΔAIC scores greater than 7, and excluding models that contained pretending variables.



Model	AIC	df	ΔAIC	Weight
Site + Aperture Length × Shell Length	314.6	6	0.0	0.436
Site + Shell Width × Shell Length	314.6	6	0.0	0.433
Site + Aperture Length + Shell Length	318.8	5	4.2	0.052
Site + Aperture Width × Shell Length	319.8	6	5.2	0.032
Site + Shell Width + Shell Length	320.3	5	5.7	0.024
Site + Shell Length	320.7	4	6.1	0.021

Table 1.3 AIC analysis of alternative models explaining survival of the crayfish predation experiment for the Babcock park population. The table includes remaining models after removing models with ΔAIC scores greater than 7, and excluding models that contained pretending variables (Crayfish Absent Site).

Model	AIC	df	ΔAIC	Weight
Aperture Length	124.1	3	0.0	0.202
Shell Length	124.6	3	0.5	0.155
Aperture Length / Shell Width	125.0	3	0.9	0.127
Shell Width	125.4	3	1.3	0.103
Shell Width / Shell Length	125.5	3	1.4	0.101
Aperture Width	125.5	3	1.4	0.098
Aperture Width / Shell Length	126.2	3	2.1	0.071
Aperture Length / Shell Length	126.2	3	2.1	0.071
Aperture Width / Shell Width	126.2	3	2.1	0.069

Figure 1.7 The probability of being killed by a predator over a range of aperture lengths for individuals from Babcock Park, the predator absent collection site; based on the top model from the AIC analysis. The equation for the line is 1 - (exp(-0.3918 + (-0.5058*AL))) / (1 + (exp(-0.3918 + (-0.5058*AL))))).

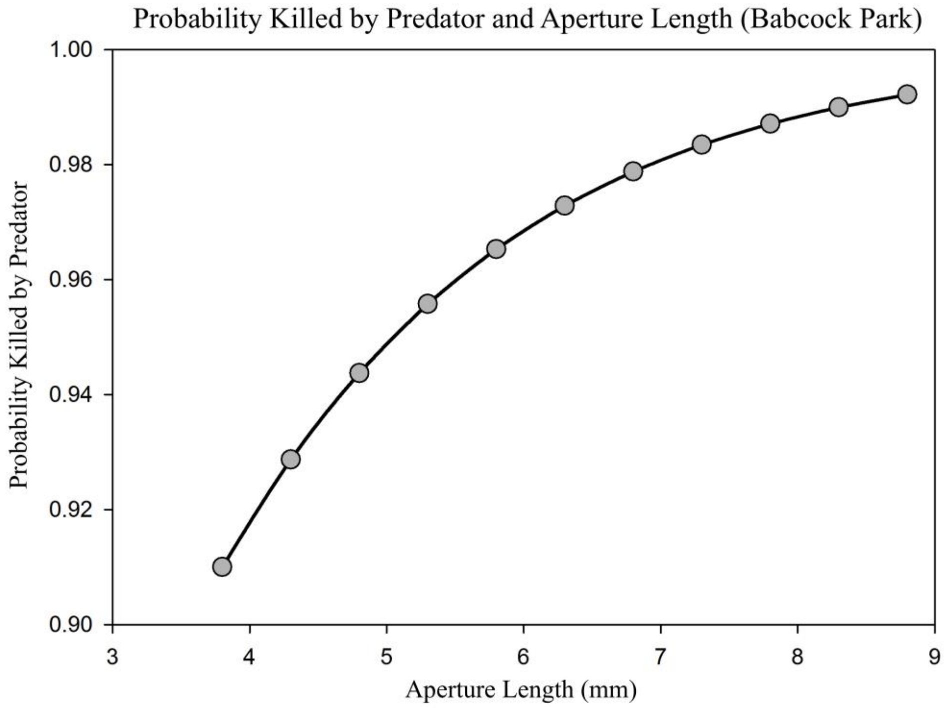
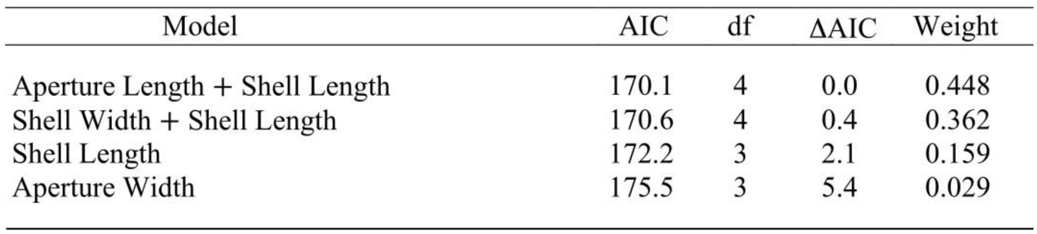


Table 1.4 AIC analysis of alternative models explaining survival of the crayfish predation experiment for the Teal Ridge population. The table includes remaining models after removing models with ΔAIC scores greater than 7, and excluding models that contained pretending variables (Crayfish Present Site).



Model	AIC	df	ΔAIC	Weight
Aperture Length + Shell Length	170.1	4	0.0	0.448
Shell Width + Shell Length	170.6	4	0.4	0.362
Shell Length	172.2	3	2.1	0.159
Aperture Width	175.5	3	5.4	0.029

Figure 1.8 The probability of being killed by a predator for different levels of aperture length (mm) and for three shell length sizes (mm), based on the top model selected in the AIC analysis for individuals from Teal Ridge, the crayfish present collection site. The equation for these lines is 1-(exp(-3.74 – 0.93222*AL + 1.0576*SL) / exp(-3.74 – 0.93222*AL + 1.0576*SL)+1)), where SL was 8 mm, 10 mm, and 12 mm for small, medium, and large shell lengths respectively.

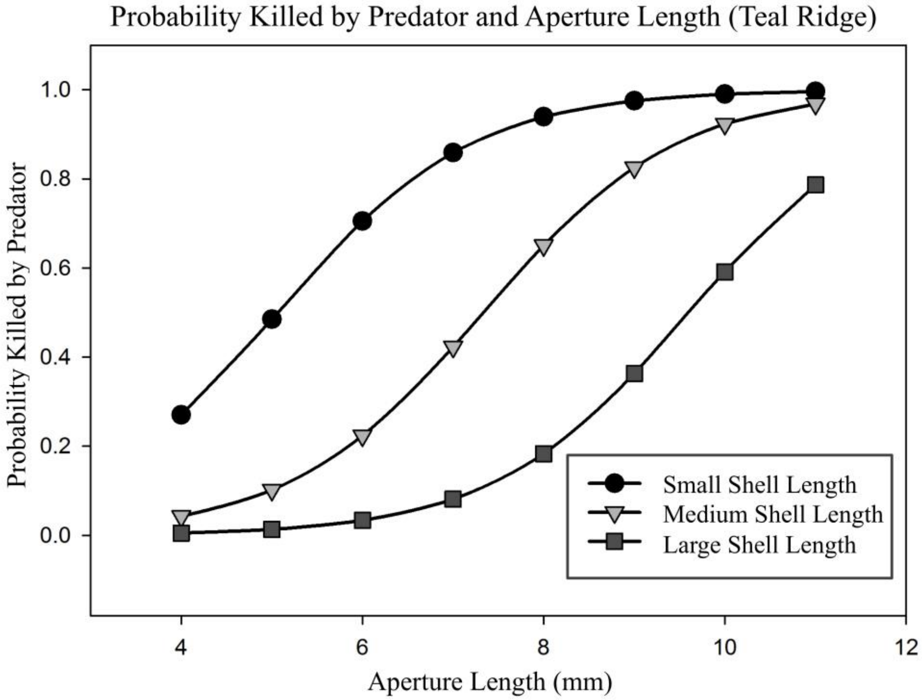
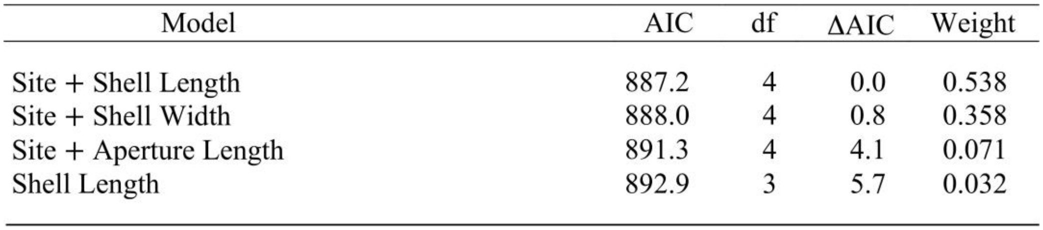


Table 1.5 AIC analysis of alternative models explaining the amount of weight needed to crush the shell of individuals from both the Babcock Park, and Teal Ridge populations. The table includes remaining models after removing models with ΔAIC scores greater than 7, and excluding models that contained pretending variables.



Model	AIC	df	ΔAIC	Weight
Site + Shell Length	887.2	4	0.0	0.538
Site + Shell Width	888.0	4	0.8	0.358
Site + Aperture Length	891.3	4	4.1	0.071
Shell Length	892.9	3	5.7	0.032

Figure 1.9 The mean weight in grams needed to crush an individual’s shell from the two populations**.**

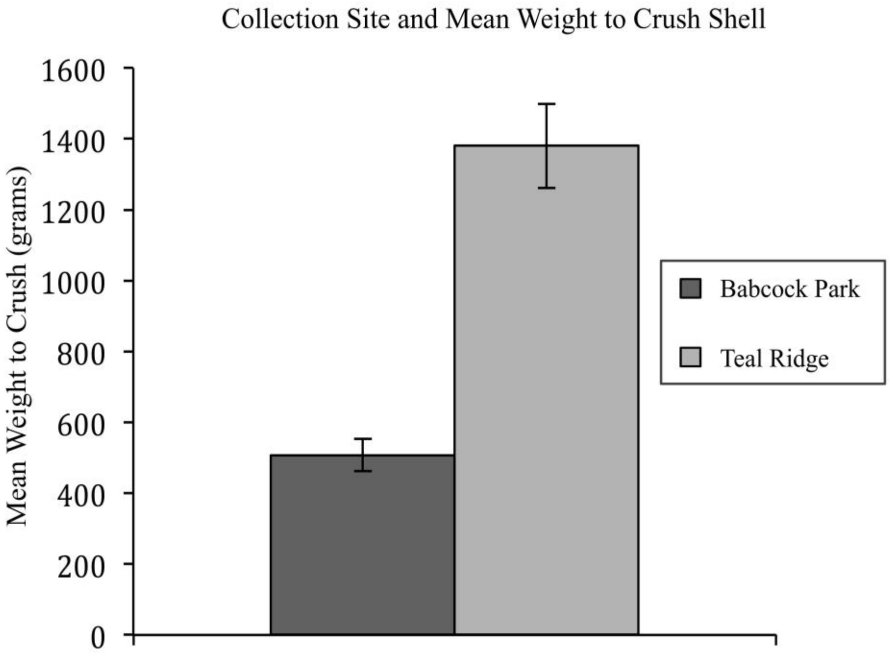
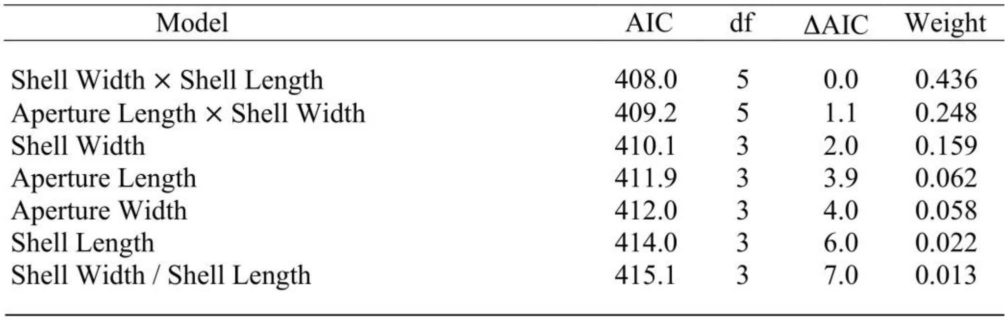


Table 1.6 AIC analysis of alternative models explaining the amount of weight needed to crush the shell of individuals from the Babcock park population. The table includes remaining models after removing models with ΔAIC scores greater than 7, and excluding models that contained pretending variables (Crayfish Absent Site).



Model	AIC	df	ΔAIC	Weight
Shell Width × Shell Length	408.0	5	0.0	0.436
Aperture Length × Shell Width	409.2	5	1.1	0.248
Shell Width	410.1	3	2.0	0.159
Aperture Length	411.9	3	3.9	0.062
Aperture Width	412.0	3	4.0	0.058
Shell Length	414.0	3	6.0	0.022
Shell Width / Shell Length	415.1	3	7.0	0.013

Figure 1.10 Predicted weight (grams) needed to crush the shell of individuals with different shell widths, and three sizes of shell length (mm) for Babcock Park population (crayfish absent site), based on the top model from the AIC analysis. The equation for these lines is (2390 -414.4*SL - 165.1*SW + 56.43*SL*SW), where shell width was 5 mm, 7 mm, and 9 mm, for small, medium, and large shell widths respectively.

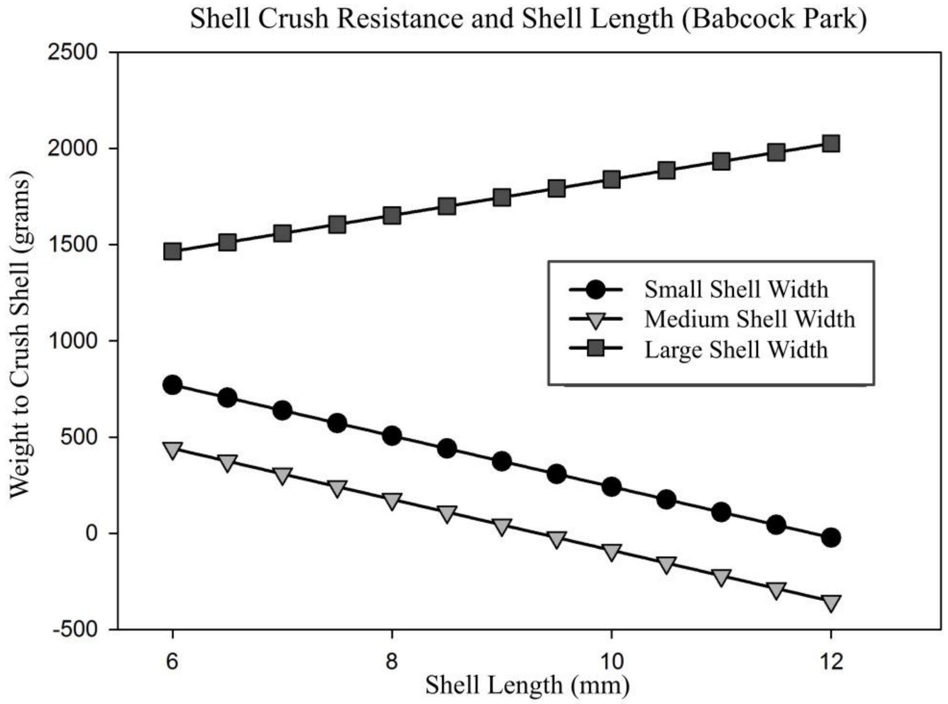
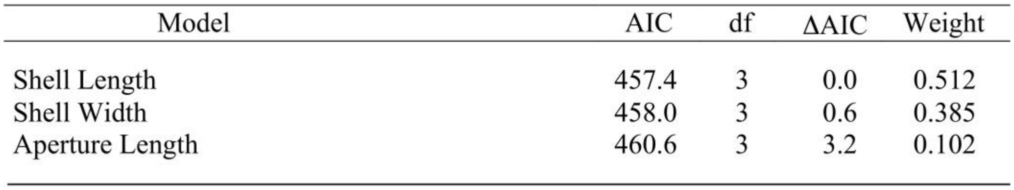


Table 1.7 AIC analysis of alternative models explaining the amount of weight needed to crush the shell of individuals from both the Teal Ridge population. The table includes remaining models after removing models with ΔAIC scores greater than 7, and excluding models that contained pretending variables (Crayfish Present Site).



Model	AIC	df	ΔAIC	Weight
Shell Length	457.4	3	0.0	0.512
Shell Width	458.0	3	0.6	0.385
Aperture Length	460.6	3	3.2	0.102

Figure 1.11 Predicted weight (grams) needed to crush the shell of individuals with different shell lengths (mm) for Teal Ridge population (crayfish present site) using a generalized linear model. The equation for this line was (-1530.47+(236.62*SL)).

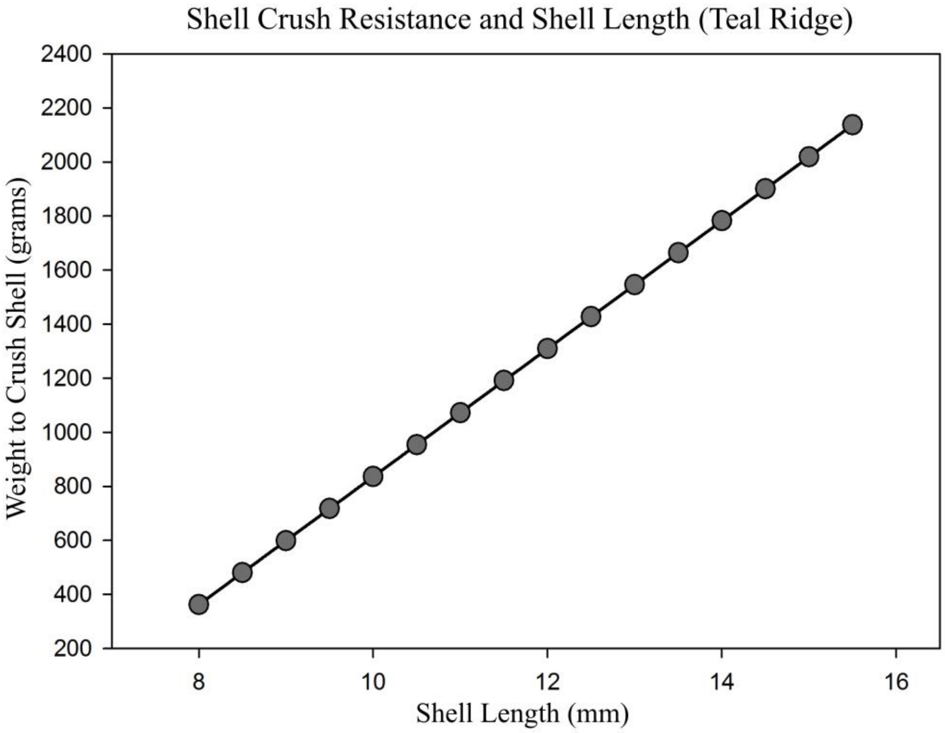
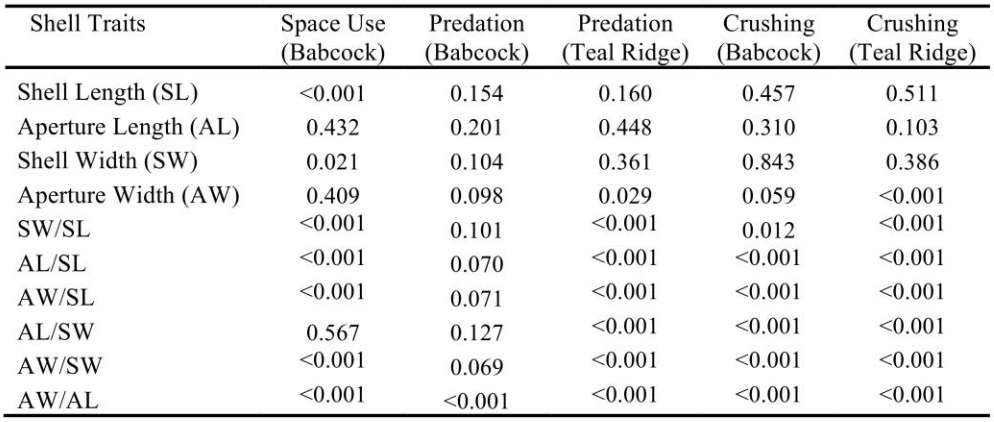
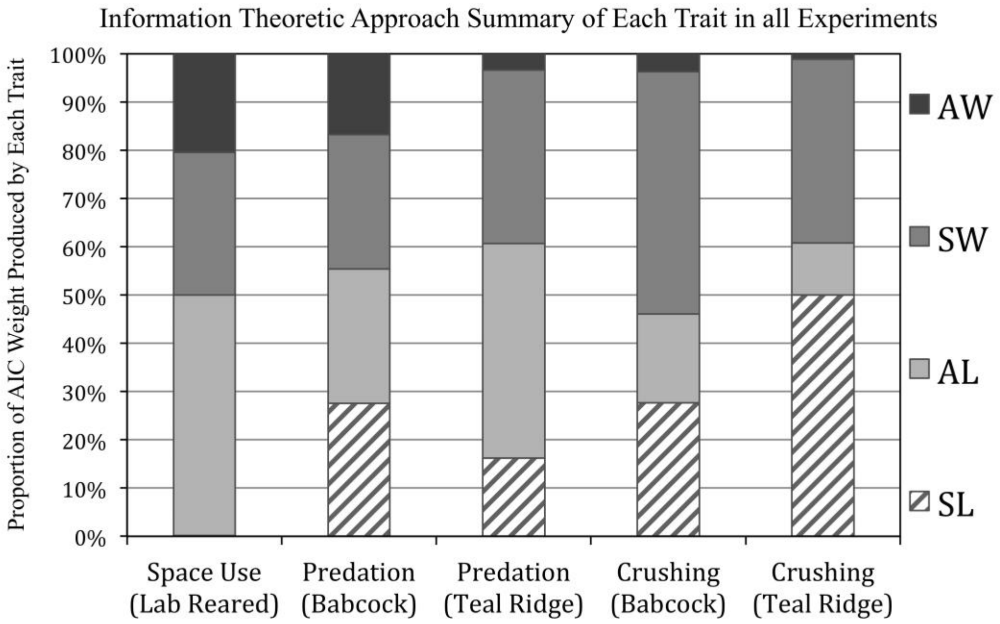


Table 1.8 IT-AIC scores from model averaging analysis showing relative importance of each morphological trait in each of the experiments (see text for details of analysis).



Shell Traits	Space Use (Babcock)	Predation (Babcock)	Predation (Teal Ridge)	Crushing (Babcock)	Crushing (Teal Ridge)
Shell Length (SL)	<0.001	0.154	0.160	0.457	0.511
Aperture Length (AL)	0.432	0.201	0.448	0.310	0.103
Shell Width (SW)	0.021	0.104	0.361	0.843	0.386
Aperture Width (AW)	0.409	0.098	0.029	0.059	<0.001
SW/SL	<0.001	0.101	<0.001	0.012	<0.001
AL/SL	<0.001	0.070	<0.001	<0.001	<0.001
AW/SL	<0.001	0.071	<0.001	<0.001	<0.001
AL/SW	0.567	0.127	<0.001	<0.001	<0.001
AW/SW	<0.001	0.069	<0.001	<0.001	<0.001
AW/AL	<0.001	<0.001	<0.001	<0.001	<0.001

Figure 1.12 Information theoretic approach AIC weight summary for the four standard morphological measurements for each of the experiments.



VITA

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