INFORMATIONAL ENVIRONMENTS AND ANTI-PREDATOR BEHAVIOR IN *PHYSA ACUTA*

By

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INFORMATIONAL ENVIRONMENTS AND ANTI-PREDATOR BEHAVIOR IN *PHYSA ACUTA*

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Abstract:
Informational environments can alter how well predators and prey can find and avoid each other, and change how much certainty individuals experience. The impacts this has on ecological dynamics needs more investigation. Luttbeg and Trussell (2013) developed a mathematical model to describe predator-prey interactions when informational environments are unreliable. Their model predicted that an individual from an unreliable environment will not rely on alarm cues as much as individuals from reliable environments. Based on this model, I hypothesized that how individuals respond to the absence and presence of predator cues will be affected by the reliability of information in their ancestral environment. Within aquatic systems, cue disruption can be due to flow regime and flow magnitude. The rate and direction of water flow can disrupt the chemical cues prey use to detect predators. Using the freshwater snail, *Physa acuta*, and its crayfish predator, *Orconectes simulans,* I tested how responses of individuals to the absence and present of predator cues depended on whether their parents came from flowing or not flowing environments. Each individual was tested in a no flow environment with control (water) cue and a predator (crayfish odor) cue, they were then tested in a flow environment with only control cue. I found the type of environment that individuals came from did not affect their responses, but there were differences in correlated with the shape of individuals and the average shape of individuals from the collection location. This showed that ancestral environment plays a role in the offspring's ability to adapt to diverse informational environments. When I observed behavior without morphological shape, I found that the behavior of individuals differed among collection locations, no matter the type of informational environment they were from. The lack of behavioral differences could be explained by the differences of shell shape between reliable and unreliable environments. My findings do not completely validate the mathematical model predictions, but do confirm an interaction between informational reliability and individual ancestral environment.

TABLE OF CONTENTS

LIST OF TABLES

Table Page

LIST OF FIGURES

Figure Page

INTRODUCTION

Prey have to make a trade-off between finding food and avoiding predators. This trade-off can often cause prey to change their behavior or phenotype in the presence or the perceived presence of predators (Lima 1998). These changes in the behavior of prey can have large effects on population dynamics (Pressier et al. 2005) and lead to alterations of predator-prey population dynamics in direct and indirect ways not normally accounted for in simple predator-prey dynamics (Ives and Dobson 1987). The change in population dynamics from predator-prey interactions can alter the ecosystem and create a cascade of behavioral changes across multiple species and trophic levels (Beckerman et al. 1997; Schmitz 1998). An example of cascading behavioral changes is the lynx-hare system, where the presence of lynx cause hare to make trade-offs in foraging effort that might lead to the population having cyclic dynamics (Peckarsky et al. 2008). Another example is the presence of spiders can cause grasshoppers to shift their location and diet from grasses to forbs (Beckerman et al. 1997; Schmitz 1998).

One way for prey to more successfully reduce predation risk while still adequately foraging is to estimate current levels of predation risk, and to then change their foraging behavior based upon those estimates. If predation risk is estimated to be high and there is not a direct need to forage, prey are more likely to hide. When predation risk is

estimated to be low, prey will take advantage of foraging during these periods to increase their own fitness (Luttbeg 2017). To successfully do this prey have to accurately estimate levels of predation risk and use this information to shape their behavior. A prey's estimate of predation risk might be formed from a combination of information inherited from past generations and their own experience in the environment (Luttbeg and Trussell 2013; Dall, McNamara, and Leimar 2015). Their own experiences are more timely than the information they inherit, but is also less information and more prone to errors.

How well prey can estimate current levels of predation risk and thus how much they should vary their behavior in response to changing levels of predation risk depends on the reliability of available information about current predation risk levels. Individuals can gain information about their environments through acoustic, chemical, visual, and mechanosensory cues (Smee and Weissburg 2006; Lürling and Scheffer 2007; Kats and Dill 1997). The reliability of these cues can be disrupted by natural or anthropogenic changes in the environment, thus reducing their reliability (Wilder et al. 2005). Within terrestrial communities, disruption can occur in many ways such as wind direction changes that cause an individual to not be able to smell prey or predators (Fogarty et al. 2018) or when vegetation blocks sight lines thus disrupting the visual perception of prey and predator (Schmidt et al. 1998). Within aquatic systems, natural disruption can be due to flow regime and flow magnitude. The rate and direction of water flow can disrupt the chemical cues prey use to detect predators. For example, when dog whelks experience high flow environments they reduce their foraging behavior. This is compared to when they experience low to no flow environments where they increase foraging behavior (Smee and Weissburg 2006). A potential explanation is that cues about predation risk are

less reliable in high water flow environments and prey cannot be as certain that a predator is not nearby making prey reduce foraging efforts (Weissburg et al. 2002). Turbidity can also be natural disruption within aquatic communities depending on the stream substrate and the flow magnitude.

There are also several sources of anthropogenic cue disruption such as habitat loss/fragmentation, various pollutants, and climate change (Sih et al. 2010; Cripps et al. 2011). Anthropogenic effects can alter information reliability on larger ecological scales and sometimes disable individuals in understanding the information they receive (Schmidt et al. 2010; Cripps et al. 2011). These can happen on a long-term or short-term scale, some being more permanent through habitat fragmentation and pollutants (Sih et al. 2010; Cripps et al. 2011).

To understand community dynamics, it is important to look at what cue types are used and how they are perceived. In aquatic communities individuals detect information mainly through waterborne chemical cues and are impacted by the hydrodynamics within the environment (Large et al. 2011). Though there are other risk cues that exist in aquatic environments besides chemical, not every individual can utilize them to gain information about the risk of the environment. Knowing the major cue detection for a particular system aids in understanding of how cue disruption can affect risk perception within an aquatic system. Thus, in order to understand risk detection in aquatic environments, the exploration of waterborne cues is necessary to understand the reliability of information.

Any type of disruption environment can cause individuals to mis-estimate the state of their environment and thus cause a decrease in their expected fitness (Lürling and Scheffer 2007). It has been shown that prey make mistakes in risk assessment due to

imperfect information from their environments (Luttbeg 2017; Schmidt et al. 2010). These effects are theorized to lead to ecological traps that turn reliable cues into unreliable ones (Schmidt et al. 2010). Through correlations between cue and habitat, fitness consequence of the decision, and commonness of the habitat, it is conceptualized that individuals and their ability to detect information within the environment are affected by their surroundings (Schmidt et al. 2010). This allows us to further examine the decision making process through what an individual has previously experienced and how that shapes their decision for an unknown or unreliable habitat choice. Leading to the concept that individuals that gain more information from their environment end up having a higher fitness than those that do not (Schmidt et al. 2010).

Previous studies have shown that prey change their responses to predator cues when the ability to detect cues is altered or less reliable to detect. However, less is known about how a population's history with reliable and unreliable environments should affect local adaptation. Luttbeg and Trussell (2013) used mathematical models to investigate how prey should change their behavior, fitness, and resource consumption as the reliability of the predator cue changes. They allowed prey within the model to estimate predation risk by either relying on the current information within the environment or relying on information (genetic) inherited from the experiences of past generations, and tested how reliance on predation cues depended on the reliability of cues in past and current environments (Luttbeg and Trussell 2013).

They predicted that when prey have evolved in environments where information is reliable, prey should increase foraging efforts when predators are not detected and produce increased levels of indirect non-consumptive effects. Prey that have evolved in

environments with unreliable information about current levels of predation risk should not strongly increase their foraging effort when predation risk is low, because they are not sure if their environment is devoid of predators (Luttbeg and Trussell 2013). This was due to prey being unable to accurately detect the level of risk within their environment while simultaneously foraging. Their model predicted that when prey come from an environment with less reliable information about predation risk that prey behavior would be shaped more by the genetic information inherited from the parents and that the non-consumptive effects of varying predation risk would be smaller (Luttbeg and Trussell 2013). Lastly, they predicted that a prey's ability to adapt to a new unreliable environment would also depend on the characteristics of the prey's native environment.

To test Luttbeg and Trussell's (2013) predictions, I gathered empirical data from individuals from locations that differ in their characteristic levels of water flow. I measured how prey change their behavior in reliable and less reliable informational environments using an aquatic system. I used *Physa acuta* and its crayfish predator, *Orconectes simulans*. *Physa acuta* is a freshwater snail found in the United States and has a short life span of approximately 20 weeks, reaching sexual maturity at about 5 weeks. It is an ideal study model because of the diverse environments they are found in and the simple husbandry requirements needed to lab rear them. My hypotheses are in alignment with Luttbeg and Trussell (2013); How individuals respond to the information in cues will depend on the reliability of the information they are receiving and the reliability of cues in their ancestral environment.

My predictions are that:

1. When snails are in a no flow environment (more reliable cues) and are exposed to a control (water) cue, that individuals from flow environments will show more anti-predator behavior than those from no flow environments.
2. When snails are in a no flow environment with a predator cue, that individuals from flow environments will exhibit lowers amounts of anti-predator behavior compared to snails from no flow environments.
3. When snails are in a flow environment with a control cue, that individuals from flow environments will exhibit less anti-predator behavior and more foraging behavior than those from no flow environments because they will be in an environment more similar to their native environment.

METHODS

Study Area

I collected *Physa acuta* from ten sites in Payne County, Oklahoma (Table 1). Five of the sites I classified as flow environments, meaning they had the physical appearance of moving water. Five of the sites I classified as no flow environments, meaning they had the physical appearance of still water. I selected sites so that each flow site was paired with a no flow site that was nearby. Each week for 5 weeks I collected snails from these paired sites.

Study Organism

Physa acuta are found throughout Oklahoma and found in a variety of habitat types. For the purpose of this study, I focused on two types of habitats, streams/creeks and ponds/lakes. From each of the 10 sites I collected at least 10 snails and group housed them in a Pyrex bowl in the lab. The day after collecting individuals (F_0) from the field, egg masses (F_1) were collected and placed into 500mL deli cups. Egg masses were observed after a week to check for hatchlings, if hatchlings were present the cup was given ~10mg piece of a Hikari algae wafer and left for an additional week. When snail hatchlings were a week old they were separated into individual deli cup housing for 4

weeks. Water was changed twice a week and individuals were given one ~20mg pieces of Hikari algae wafer each water change. At 5 weeks of age, individuals (F_1) were used in behavioral experiments. After behavioral experiments were done, individuals were euthanized in ethanol and stored in centrifuge tubes. Individuals were photographed approximately 5 months later for morphometric data analysis.

Experimental Setup

The experimental design imitated a flow and no flow environment. For both of these setups the experimental cup was a 500mL deli cup where individuals were observed. Each deli cup was marked in 4 spots along the height of the cup to classify snail locations during the trials. Starting from the bottom of the cup lines were marked 10.41mm from each other. Line markings were at 10.41mm, 20.82mm, 31.23mm, and 41.64mm (waterline). The scores of the cup were given a number from 1 to 8, 1 being the bottom of the cup and 8 being completely out of the water (Figure 1). Individuals from the pairs of sites (Table 1) were tested on the same day. This allowed for blind experiments with randomization of individuals between environment types.

Two types of cue were used for the behavioral experiment, a control (water) cue and a predator cue. Predator cue was made from crayfish water and crushed snail conspecifics using the methods and concentrations from Beaty et al. 2016 and was frozen. Control cue was made out of dechlorinated water and frozen within the same freezer space as the predator cue.

For the no flow behavioral testing, individuals were put into their own experimental cup. Experimental cups were clear plastic cups and contained ~300mL of dechlorinated water and ~50mg of algae wafer. At the start of the behavioral experiment a cue was deposited into each experimental cup. Every 5 minutes for an hour the location (using the 8 scores) of each snail was recorded.

For the flow behavioral testing I imitated a flow environment using, a 5 gallon bucket as an input chamber connected to the experimental cup and an output/drain connected to the bottom of the experimental cup to allow for an exit of the flowing water. The experimental cup was the same size and had the same behavioral markings as previously and was filled with ~300mL of water with a 5gal per hour flow rate. In addition, ~50mg of algae wafer was included within the experimental cup.

The experimental timeline was staggered by group to allow consistent testing age. Each week for 5 weeks straight, individuals from a pair of sites were subjected to three types of behavioral trials over two days. During the first day I did no flow behavioral trials. Individuals were starved prior to the first day and placed into experimental cups with ~50mg of algae wafer. I put ~1mL of control cue into the experimental cup using a 10mL syringe and recorded the location of the snail every five minutes for one hour. When the trial was over I transferred the individuals into fresh deli cups without algae wafers and allowed to rest for 2 hours. I then moved the individuals into another fresh experimental cup and observed behavior with predator cue, putting ~1mL of predator cue with a 10mL syringe, and recorded the location of the snail every five minutes for one hour. After the predator cue trial, I placed individuals into fresh deli cups without algae wafers for the remainder of the day. On day 2 individuals were placed into experimental

cups with flowing water (described above) and were exposed to control cue. I put ~1mL of control cue into the input chamber of the flow environment using a 10mL syringe and recorded the location of each snail every five minutes for one hour.

Morphemetrics

I photographed individuals who were euthanized in ethanol immediately following behavioral trials. I used the program tpsUtil64 to randomize the images and TPSDig232 to landmark them for morphometric analysis. Each photograph was scaled to create uniformity in image size during landmarking. In addition, 11 landmarks were made along the shell shape as well as 4 lines to compare shapes and size of shells across the dataset. Once landmarking was complete, individuals were returned to correct order in tpsUtil64. Using the same software image list, centroid size, relative warps, links, and sliders were pulled from the landmark data. The documents that included the image list, centroid size, and relative warps were combined into a single file for analysis. I also calculated individual divergence vectors (dv_indiv) from the relative warps by taking the average relative warp across the entire sample size subtracting the individual's relative warp (Average Sample Size Relative Warp – Individual Relative Warp) and used the values in behavioral analysis. From the individual divergence vector I calculated the average divergence vector calculated previously and averaged it per site (dv_site) to use in behavioral analysis. The documents links and sliders were used to create images of morphological change in tpsRegr32.

Statistical Analyses

To test how the location of individuals in cups during trials were affected by what site they were collected from, the type of location it was, and the time in the trial I used R (version 3.5.2) and the lme4 linear mixed model function. My random effects used were the individual ID (Indiv_ID), site an individual came from (SITE), or individual ID nested within Sites. I used model comparison approach based on Akaike information criterion to quantify the evidence the data gave to alternative models. The response variable was the individual's location in the cup (Figure 1). When testing the effects of whether individuals came from a Flow or No Flow environment, I had models that used all combinations of Time (time step in the trial), LOC (whether the individuals descended from individuals collected at Flow or No Flow sites), and the interaction of Time and LOC. When testing how the site at which F_0 were collected, I had models that used all combinations of Time (time step in the trial), SITE (which of the 10 collection sites F_0 were collected), and the interaction of Time and SITE.

When I found that the model with Site as an explanatory variable was my top model, I used pairwise Tukey's Honestly Significant Difference tests to test for significant differences between pairs of sites. For testing the effect location type had on the size of F_1 individuals I used Centroid (size) as the response variable and LOC as my explanatory variable in linear mixed model and SITE as a random effect. I calculated a p-value from the model in order to determine if location affected centroid of individuals. For testing the effect site of F_0 collection had on the size of F_1 individuals I used Centroid (size) as the response variable and Site as my explanatory variable in a linear model.

For the morphometric analyses I used SAS (version 9.4) and the Kenward-Roger method for group effect and fixed effect. I used a mixed MANCOVA to test whether F_1 individuals descended from F_0 individuals from Flow or No Flow environment differed in morphology. The LOC*VAR term reporting whether shape varied between the two location types. I did the same to test if shape differed between sites and the SITE*VAR term reports on this effect.

RESULTS

Behavioral Trials

I found no evidence that whether a snail came from a flow or no flow environment had any effect on their locations in cups during behavioral trials. When the snails were exposed to control cue in no flow treatments, the best supported model had the location of snails depending on the time step of observation (Time; Table 2) with them tending to go lower in the experimental cup as time increased (Figure 2). When the snails were exposed to a predator cue in no flow treatments, the best supported model had the location of snails depending on the time step of observation (Time; Table 3) with them tending to go higher in their cup as time increased in the trials (Figure 3). Finally, when the snails were exposed to control cue in flow treatments, again the best supported model had the location of snails depending on time (Time; Table 4) with them tending to go lower in their cup as time increased in the trials (Figure 4).

I also found no evidence that whether snails were collected from flow or no flow environments affected the change in their average locations between exposure to control and predator cues during no flow treatments. The null model was better at predicting the

change in average locations during no flow treatments between control cues and predator cues than the model that included the type of location where snails were collected (Null; Table 5). I found that there was an average increase of 1.23 in the location within the cup from control cue exposure to predator cue exposure (Figure 5).

I did find that the site at which snails were collected affected their locations in cups during trials. For all three types of behavioral trials, the model that was best supported by the data was (Site * Time; Tables 6, 7, and 8). Pairwise Tukey's HSD tests showed that for control cue in no flow treatments, there were mixed significant outcomes depending on the site (Figure 6). I found that Boomer Creek and Brush Creek were considered statistically the same, but significantly different than the rest of the sites. When looking at other sites, Cow Creek and Stillwater Creek were considered statistically the same but significantly different from the rest of the sites. For the majority of the sites, there was a statistical similarity between sites that were from similar environments. This excludes Dugout Creek and Hinrich Lake which showed statistical similarities between a flow and no flow site. Pairwise tests for predator cue in no flow treatments show there were significant differences across all of the sites except for Dugout Creek and Experimental Ponds (Figure 7). Lastly, when looking at pairwise tests for control cue with flow treatments, there were more sites that were similar than significantly different (Figure 8). I found that Boomer Creek, Brush Creek, and Cow Creek were considered statistically similar. In addition, I found that Hinrich Lake, Meridian Pond, and Whittenberg Lake were statistically similar as well. There were a pair of sites that showed statistical similarities between flow and no flow sites, Dugout Creek and Experimental Ponds.

Morphometric Analysis

I found that environment type (flow or no flow) affected the shapes of shells (LOC*VAR: $p = 0.0001$, Table 8). I also found that site affected the shape of the shell (SITE*VAR: $p < 0.001$, Table 9). There was no evidence environment type affected size of shell ($p = 0.604$), but the site of F_0 collection did affect the size of shell ($p < 2.26e\text{-}16$).

Behavior explained by Morphometrics

I analyzed how the shell shapes of individuals (using the individual divergence vector calculated from across the entire sample size, dv_indiv) affected their location during behavioral trials. When I looked at how individual divergence vectors affected the location of a snail during behavioral trials with control cues in no flow treatments, the best supported model had the location of snails depending on the time step of observations (Time; Table 11, Figure 2). When they were exposed to predator cue with no flow treatments, I found the best supported model had their location depending on time and on the individual divergence vector (dv_indiv) (dv_indiv + Time; Table 12). Individuals with higher dv_indiv values, which means those individuals had larger apertures and shorter spires (Figure 9), tended to be at higher locations within the cup than individuals with lower dv_indiv values. There was an overall increase in location over time with all types of individuals (Figure 10). When they were exposed to control cue in flow treatments, the best supported model had the location of snails depending on the time step of observations (Time; Table 13, Figure 4).

When I used the average divergence vector for a site (dv_site), based on the average dv_indiv for individuals from a site, I found that when exposed to control cue with no flow treatment, the best supported model had their location depending on time, dv_site, and their interaction (dv_site * Time; Table 14). Individuals from sites with higher dv_site values, which means larger apertures and shorter spires, had higher locations in cups early in trials and location decreased over time (Figure 11).

When exposed to predator cue with no flow treatment, the best supported model again had the location of snails being affected by dv_site, time, and their interaction (dv_site * Time; Table 15). Individuals with higher dv_site values had higher locations and were unaffected by time, while individuals with lower dv_site values were lower in their cup and moved higher in the cups as the time of the trial increased (Figure 12). However, when snails were exposed to control cue in flow treatment the best supported model had their location being only affected by time (Time; Table 16, Figure 4).

DISCUSSION

I found that the type of environment, defined as flow or no flow, that a snail's parents came from had no detectable effect on how they responded to the absence or presence of predator cues or to flowing water, but that the individual's shell shape and the average shell shape of individuals from a site both affected their responses. The effects shell shape had on how individuals responded to the absence and presence of predator cues demonstrated with cup location depended on whether shell shape of individuals was used or the average shell shape of individuals from a site was used. The type of shell shape morphology used showed differences in behavior in the presence and absence of predator cue, and the presence of predator cue as a whole. Overall, the behavioral results supported the idea that ancestral environment played a large role in the behavior of individuals.

I was testing the prediction that individuals that originated from populations where information about current predation risk is less reliable would use higher anti-predator behavior when predator cues were absent and lower anti-predator behavior when predator cues were present compared to individuals from environments where information was more reliable. However, I found no evidence that individuals whose

parents came from flow versus no flow environments differed in their anti-predator behavior. One explanation for this result is that the flow of water used in the behavioral trials is not disruptive enough for how snails estimate predation risk and therefore its presence has no effect on their behavior. This explanation seems rather unlikely. Many studies have shown that aquatic snails use chemical cues to detect the presence of predator and predation events (Beaty et al. 2016; Gustafson et al. 2014; Stevison et al. 2016). Another possibility is that my categorizing of sites as flow or no flow had errors or failed to consider variation in current and past flow rates. When collecting snails, I did not measure flow rate at the collection time and did not have a historical measurement of flow rates at collection sites. Thus, my site classification as flow versus no flow may have been inadequate and missed more subtle differences between sites. And finally, some of the collection sites are closely linked within watersheds, so there is a strong possibility of some gene flow between collection sites.

For these reasons, I chose to analyze the data in terms of how the average shape of individuals from a site affected their responses to the presence and absence of predator cues. The thought being that average shell shape and the effects of gene flow between sites might be a better estimation of past flow rates at a site than my classification. When I reanalyzed the data using average shape from a site, I found varying responses to the presence and absence of predator cues by shell shape (dv_site). When given predator cues, those with a shell shape commonly found with no flow environments tended to move higher and faster in cup location at each time step whereas those with shell shape commonly found with flow environments tended to stay in the same height in the cup at each time step (Figure 12). This suggests that when given the same environment and

cues, those that have a similar ancestral environment tended to react to predator cue strongly after detection. These results supported my initial predictions in that when in the absence of predator cues individuals from flow environments tended to show more anti-predator behavior than those from no flow environments. However, I did not expect that behavior would overlap between no flow shell shape individuals and flow shell shape individuals at the final time step.

The change in average location between a control cue and predator cue in a no flow treatment did not appear to be affected by whether snails came from flow or no flow environments. However, when viewing the overall change of location in the cup, it showed that snails went higher in the cup (an anti-predator behavior) during predator cue treatment than during control cue treatment. Lab reared individuals still respond to predator cues despite being naïve to encountering predator. This shows that the outcomes of the study can be related to the natural environment and that the predator cue used within the treatments was relevant to the types of predators present within the ancestral environment.

I found that the site from which the F_0 snails were collected affected how F_1 snails responded to the absence and presence of predator cues. For the most part, sites classified as no flow tended to be similar to each other. Similarly, sites classified as flow environments tended to be similar to each other. This suggests that flow and no flow sites produce different prey behavior. However, there were pairs of no flow and flow sites (Table 1) that showed similar prey behavior. These similarities might explain why it did not appear that prey behavior was different between flow and no flow ancestral environments. This may suggest that sites have some connectivity and were not

independent of one another. However, the only similar sites that are shown are Dugout Creek and Experimental Ponds, or Dugout Creek and Hinrich Lake. In addition, it appears that these sites are not close enough together to have gene flow as Dugout Creek is found in Perkins, Oklahoma and Hinrich Lake/Experimental Ponds is found in Stillwater, Oklahoma with no apparent watershed connection. The issue of site connectivity may be linked to collection periods experiencing high amounts of rain fall and could have allowed sites to be connected across streams and lakes. Distances between sites were not standardized and scale was not taken in to account to establish independent collection locations. Lastly, site persistence was not considered when collecting individuals; meaning that sites were only used if they were present during the collection period and were not monitored for persistence over time. This could explain the variation in results because snails could be coming from locations of unknown environment type.

I did find that individuals differed in the shape of their shells and that the shape was affected by the site from which an individual's parents were collected and by whether the site was a flow or no flow environment. Previous studies have found that the shape of *Physa acuta* shells vary between flow and no flow environments and that these are caused by both genetics and the environment (Gustafson et al. 2014). I found that snails from flow environments tended to have shorter spires and larger apertures whereas snails from no flow environments tended to have longer spires and smaller apertures. The shape differences shown between flow and no flow sites coincides the morphological differences of snails known within the field (Gustafson et al. 2014). This can explain the lack of behavioral results when looking at environment type as the differences in

morphology can give individuals a better survivability for their ancestral environment. These findings suggest that offspring retained the ancestral morphology and behavior from the previous generation despite not being exposed to the same type of environment.

I found that how individuals responded to the presence of predator cue was affected by the shape of their shell, but that it had no apparent effect on how they responded to the absence of predator cues or the presence of flowing water. When looking at divergence vectors calculated by the individual snail relative warp, shell shape only mattered for predator cue in no flow treatments. It showed that individuals who had a shell shape that was more common in flow environments (high dv_indiv) tended to be higher up in the cup than those who had a shell shape more common in no flow environments (Figure 10). The flow shape was shown to start higher in location across treatments and continue to rise in location over time compared to the shell shape more common in no flow environments. This does not support my initial predictions, as the individual shell shape did not seem to affect the behavior in control cue or flowing environments and during the presence of predator cue individuals derived from high flow environments were showing a stronger anti-predator response than individuals derived from no flow environments. However, it does show that individual morphology plays a role in the anti-predator behavior shown. This suggests that snail behavior is correlated with the shape of their shells and is similar to findings in the field (Stevison et al. 2016). The individual shape affected behavior only in presence of predator cue, while average population shape by site affected behavior in both the presence and absence of predator cue suggests that the population-level result cannot be explained by the individual's shell shape alone. I believe it might be an indication of not only how past history has

influenced the genetics of shell shape at a site, but has also influenced how individuals respond to the absence and presence of cues.

This is the first study to ever test how a cue and the informational environment shapes how much prey rely on predator cues to guide their behaviors. When prey live in an environment where they have cues that give very timely and accurate information about the current level of predation risk, then should foraging boldly when that information indicates they are safe and drastically reduce foraging when the information indicates they are at heightened risk (Luttbeg and Trussell 2013). However, when prey have evolved in an environment where those cues are less accurate, then their foraging should be less bold in the absence of predator cues and less reduced in the presence of predator cues. They should essentially evolve to put less weight on the information in the cues and rely more on other sources of information, such as a genetic predisposition that causes them to forage with more timidity. The results of this were not definitive. Based upon my categorization of the environments there was no evidence that environment affected how the prey behaved in the absence and presence of predator cues. However, I did find that the average shape of shells at a location did affect prey behavior and were indicative that the prey relied on ancestral environment to behave in a novel environment.

More studies are needed to investigate how informational environments shape how much prey depend on assessing current levels of predation risk and the resulting effects on prey behavior. Limitations identified in this research was the inability to test individuals with predator cue flow treatments, measuring of total mass, crush resistance, and measuring of flow rate at collection sites. Future studies might benefit from this data. For example, crush resistance and mass of offspring could explain some of the observed

behavioral differences across treatments, environment type, and add more information for morphology. I believe that a question that should be investigated in tandem with this research is measuring the predator abundance and diversity within collection sites. I believe that differences in the predators between sites may impact the behavior individuals exhibit from their ancestral environments. This may explain why specific sites do not show a response to the lab predator cue. A difference in predator composition at collection sites can account for the lack of response depending on the type and abundance of predators and can help create a predator cue geared towards the ancestral predator environment. Though there is much to explore from these outcomes, the main result from this study is that ancestral environments do affect the morphologies of snails and how individuals respond to the absence and presence of predator cues. This partially supports my hypothesis and I believe with further testing will be able to explain more about how informational environments affect behavior.

REFERENCES

Beaty LE, Wormington JD, Kensinger BJ, Bayley KN, Goeppner SR, Gustafson KD, Luttbeg B. 2016. Shaped by the past, acting in the present: transgenerational plasticity of anti-predatory traits. Oikos. 125:1570-1576.

Beckerman AP, Uriarte M, Schmitz OJ. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. Proceedings of the National Academy of Science. 94:10735-10738.

Cripps IL, Munday PL, McCormick MI. 2011. Ocean acidification affects prey detection by a predatory reef fish. PLoS ONE. 6:7.

Dall SXR, McNamara JM, Leimar O. 2015. Genes as cues: phenotypic integration of genetic and epigenetic information from a Darwinian perspective. Trends in Ecology & Evolution. 1935:1-7.

Fogarty DT, Elmore DR, Fuhlendorf, SD, Loss SR. 2018. Variation and drivers of airflow patterns associated with olfactory concealment and habitat selection. Ecology. 99(2):289-299.

Gustafson KD, Kensinger BJ, Bolek MG, Luttbeg B. 2014. Distinct snail (*Physa)* morphotypes from different habitats converge in shell shape and size under common garden conditions. Evolutionary Ecology Research. 16:77-89.

Ives AR, Dobson AP. 1987. Antipredator behavior and the population dynamics of simple predator-prey systems. The American Naturalist. 130(3):431-447.

Kats LB, Dill LM. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. Écoscience. 5(3):361-394.

Large SI, Smee DL, Trussell GC. 2011. Environmental conditions influence the frequency of prey responses to predation risk. Marine Ecology Progress Series. 422:41-49.

Lima SL. 1998. Stress and decision making under the risk of predation: recent developments from behavioral reproductive, and ecological perspectives. Advances in the Study of Behavior. 27:215-290.

Lürling M, Scheffer M. 2007. Info-disruption: pollution and the transfer of chemical information between organisms. Trends in Ecology and Evolution. 22(7):374-379.

Luttbeg B, Trussell GC. 2013. How the informational environment shapes how prey estimate predation risk and the resulting indirect effects of predators. The American Naturalist. 181(2).

Luttbeg B. 2017. Re-examining the causes and meaning of the risk allocation hypothesis. The American Naturalist. 189(6):644-656.

Peckarsky BL, Abrams PA, Bolnick DI, Dill LM, Grabowski JH, Luttbeg B, Orrock JL, Peacor SD, Preisser EL, Schmitz OJ, Trussell GC. 2008. Revisiting the classics: considering nonconsumptive effects in textbook examples of predator-prey interactions. Ecology. 89(9):2416-2425.

Preisser EL, Bolnick DL, Benard MF. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology. 86(2):501-509.

Schmidt KA, Dall SXR, Van Gils JA. 2010. The ecology of information: an overview on the ecological significance of making informed decisions. Oikos. 119:304-316.

Schmitz OJ. Direct and indirect effects of predation and predation risk in old-field interaction webs. The American Naturalist. 151(4):327-342.

Sih A, Ferrari MOC, Harris DJ. 2010. Evolution and behavioural responses to human-induced rapid environmental change. Evolutionary Applications. 4:367-387.

Smee DL, Weissburg MJ. 2006. Clamming up: environmental forces diminish the perceptive ability of bivalve prey. Ecology. 87(6):1587-1598.

Stevison B, Kensinger B, Luttbeg B. 2016. Different morphological traits influence predator defense and space use in *Physa acuta*. American Malacological Bulletin. 34(2):79-84.

Weissburg MJ, Ferner MC, Pisut DP, and Smee DL. 2002. Ecological consequences of chemically mediated prey perception. Journal of Chemical Ecology. 28(10):1953-1970.

Wilder SM, DeVito J, Persons MH, Rypstra AL. 2005. The effects of moisture and heat on the efficacy of chemical cues used in predator detection by the wolf spider *Pardosa milvina* (Araneae, Lycosidae). The Journal of Arachnology. 33(3):857-861.

Group	Site	Site Abbrev.	GPS Loc
1	Meridian Pond	MP	36.114577, -97.106796
	Stillwater Creek	SC	36.110928, -97.104863
2	Sanborne Lake	SB	36.155519,-97.078144
	Cow Creek	CC	36.123213,-97.099770
3	Experimental Ponds	EP	36.134649, -97.189510
	Dugout Creek	DC	35.952617,-97.030267
4	Hinrich Lake	HL	36.105858,-97.085673
	Boomer Creek	CBC	36.130173, -97.056278
5	Whittenberg Lake	WL	36.178907, -97.073356
	Brush Creek	BRC	36.101635, -97.00937

Table 1: Sites organized by the grouping they were collected in and their corresponding GPS locations.

Model	ΔAIC	df	Weight
Time	0.0	5	0.52
LOC*Time	1.5	7	0.25
LOC+Time	1.8	6	0.21
Null	8.0	4	0.01
LOC	9.9	5	0.00

Table 2: Akaike model comparison results of how snail locations in cups during exposure to control cue in no flow treatments was affected by whether snails were collected from flow or no flow environments (LOC) and the time step in the trial (Time). For all of the models individual ID nested within site was the random effect.

Model	ΔAIC	df	Weight
Time	0.0	5	0.56
LOC+Time	1.2	6	0.32
LOC*Time	3.1	7	0.12
Null	49.7	4	0.00
LOC	50.8	5	0.00

Table 3: Akaike model comparison results of how snail locations in cups during exposure to predator cue in no flow treatments was affected by whether snails were collected from flow or no flow environments (LOC) and the time step in the trial (Time). For all of the models individual ID nested within site was the random effect.

Model	ΔAIC	df	Weight
Time	0.0	5	0.43
LOC+Time	0.5	6	0.33
LOC*Time	1.3	7	0.23
Null	20.1	4	0.00
LOC	20.7	5	0.00

Table 4: Akaike model comparison results of how snail locations in cups during exposure to control cue in flow treatments was affected by whether the snails were collected from flow or no flow environments (LOC) and the time step in the trial (Time). For all of the models individual ID nested within site was the random effect.

Model	ΔAIC	df	Weight
Null	0.0	3	0.69
LOC	1.6	4	0.31

Table 5: Akaike model comparison results of the change in average location in a cup from control cue to predator cue from no flow treatment. For all of the models site was the random effect.

Model	ΔAIC	df	Weight
SITE*Time	0.0	22	0.9927
SITE+Time	9.8	13	0.0072
SITE	17.9	12	0.00
Time	46	4	0.00
Null	54.1	3	0.00

Table 6: Akaike model comparison results of how snail locations in cups during exposure to control cue in no flow treatments was affected by the site where the snails were collected (SITE) and the times step in the trial (Time). For all of the models individual ID was the random effect.

Model	ΔAIC	df	Weight
SITE*Time	0.0	22	1
SITE+Time	36.2	13	0.00
SITE	85.9	12	0.00
Time	8.3	4	0.00
Null	136	3	0.00

Table 7: Akaike model comparison results of how snail locations in cups during exposure to predator cue in no flow treatments was affected by the site where snails were collected (SITE) and the time step in the trial (Time). For all of the models individual ID was the random effect.

Model	ΔAIC	df	Weight
SITE*Time	0.0	22	1
SITE+Time	14.8	13	0.00
Time	17.9	12	0.00
SITE	35.0	4	0.00
Null	38.0	3	0.00

Table 8: Akaike model comparison results of how snail locations in cups during exposure to control cue in flow treatments was affected by the site where snails were collected (SITE) and the time step in the trial (Time). For all of the models individual ID was the random effect.

For Environment Type (Flow/No Flow)				
Type 3 Tests of Fixed Effects				
Effect	Num DF	Den DF	F - Value	Pr>F
LOC	1	68.2	0.45	0.5037
VAR	12	769	3.93	<0.0001
CENT	1	511	0.52	0.4713
LOC*VAR	12	769	2.31	0.0068
VAR*CENT	12	769	4.03	<0.0001

Table 9: Analysis of shape (VAR) and size (CENT) differences between snails from flow vs. no flow locations.

For Site				
Type 3 Tests of Fixed Effects				
Effect	Num DF	Den DF	F - Value	Pr>F
SITE	9	548	3.28	0.0007
VAR	12	775	3.27	0.0001
CENT	1	548	0.09	0.7677
SITE*VAR	108	1602	2.56	<0.001
CENT*VAR	12	775	3.31	0.0001

Table 10: Analysis of shape (VAR) and size (CENT) differences between snails from different sites.

Model	ΔAIC	df	Weight
Time	0.0	5	0.57
dv_indiv+Time	1.7	6	0.25
dv_indiv*Time	3.6	7	0.10
Null	4.5	4	0.06
dv_indiv	6.2	5	0.03

Table 11: Akaike model comparison results of how snail locations in cups during exposure to control cue in no flow treatments was affected by calculated divergence vector per individual (dv_indiv) and the time step in the trial (Time). For all of the models individual ID nested within site was the random effect.

Model	ΔAIC	df	Weight
dv_indiv+Time	0.0	6	0.57
dv_indiv*Time	1.9	7	0.22
Time	2.0	5	0.21
dv_indiv	54.6	5	0.00
Null	56.7	4	0.00

Table 12: Akaike model comparison results of how snail locations in cups during exposure to predator cue in no flow treatments was affected by the calculated divergence vector per individual (dv_indiv) and the time step in the trial (Time). For all of the models individual ID nested within site was the random effect.

Model	ΔAIC	df	Weight
Time	0.0	5	0.61
dv_indiv+Time	1.6	6	0.27
dv_indiv*Time	3.4	7	0.11
Null	13.7	4	0.00
dv_indiv	15.3	5	0.00

Table 13: Akaike model comparison results of how snail locations in cups during exposure to control cues during flow treatments was affected by the time step in the trial (Time). For all of the models individual ID nested within site was the random effect.

Model	ΔAIC	df	Weight
dv_site*Time	0.0	7	0.47
dv_site+Time	0.9	6	0.31
Time	2.1	5	0.17
dv_site	5.4	5	0.03
Null	6.6	4	0.02

Table 14: Akaike model comparison results of how snail locations in cups during exposure to control cue in no flow treatments was affected by average divergence vector per site and the time step in the trial (Time). For all of the models individual ID nested within site was the random effect.

Model	ΔAIC	df	Weight
dv_site*Time	0.0	7	1.00
Time	13.7	5	0.00
dv_site+Time	14.9	6	0.00
Null	68.4	4	0.00
dv_site	69.6	5	0.00

Table 15: Akaike model comparison results of how snail locations in cups during exposure to predator cue in no flow treatments was affected by average divergence vector per site and the time step in the trial (Time). For all of the models individual ID nested within site was the random effect.

Model	ΔAIC	df	Weight
Time	0.0	5	0.56
dv_site+Time	1.2	6	0.32
dv_site*Time	3.1	7	0.12
Null	13.7	4	0.00
dv_site	14.8	5	0.00

Table 16: Akaike model comparison results of how snail locations in cups during exposure to control cue in flow treatments was affected by the time step in the trial (Time). For all of the models individual ID nested within site was the random effect.

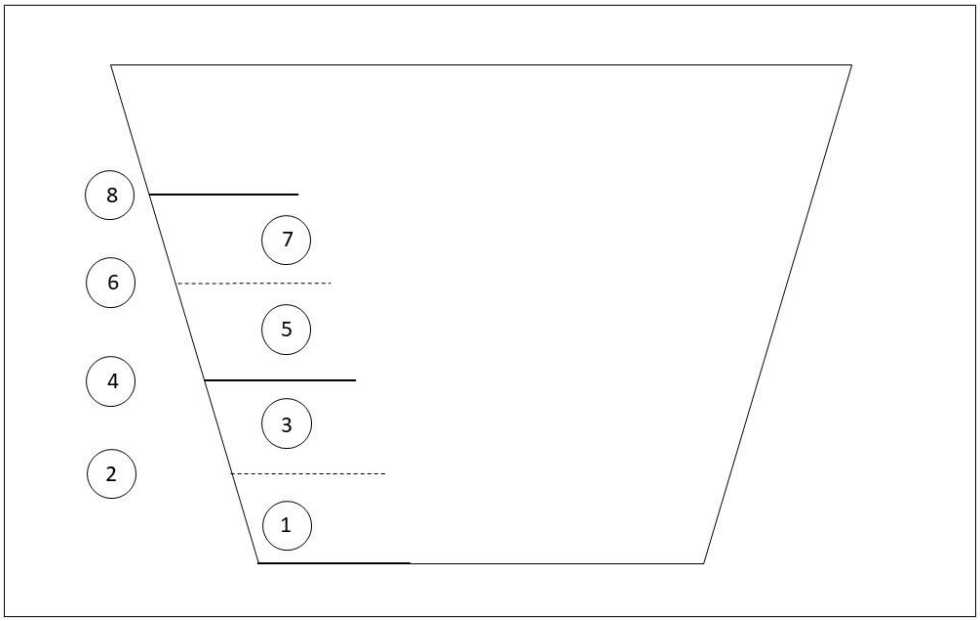

Figure 1: Scoring grade along the side of the cup. One means on the bottom or in the bottom region. Two means on the dotted line. Three means between the dotted line and the middle of the cup. Four means on the line in the middle of the cup. Five means between four and the dotted line. Six means on the dotted line. Seven means between six and the water surface. Eight means on the water surface or out of the water completely.

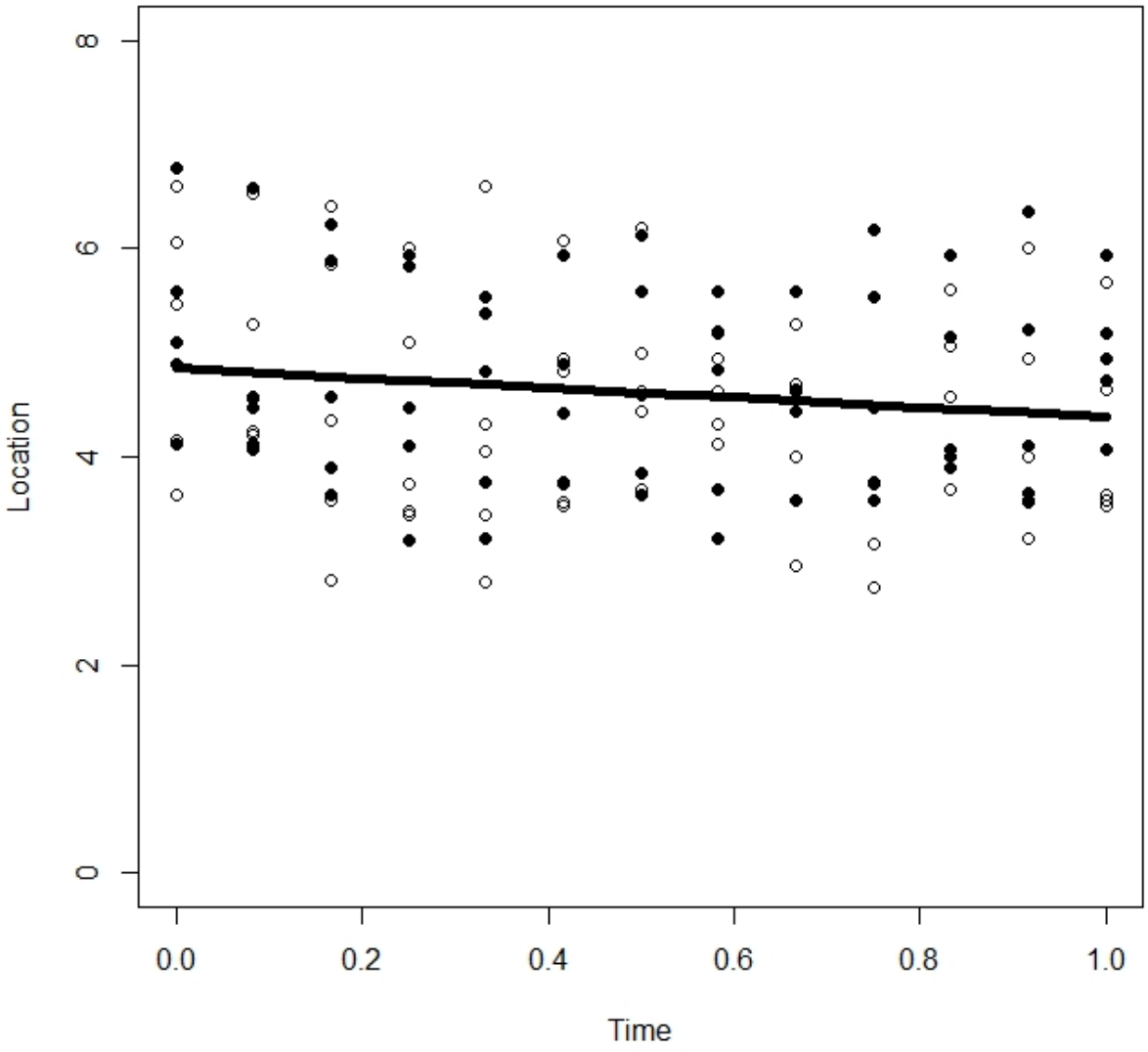

Figure 2: Predictions from the best supported model for predicting snail locations when exposed to control cues during no flow treatments. This is represented through prediction lines using the top model, Time + (1|Site/Snail) as well as showing the average location of individuals grouped by site as time increased during behavioral trials. Filled in points are no flow sites and unfilled are flow sites.

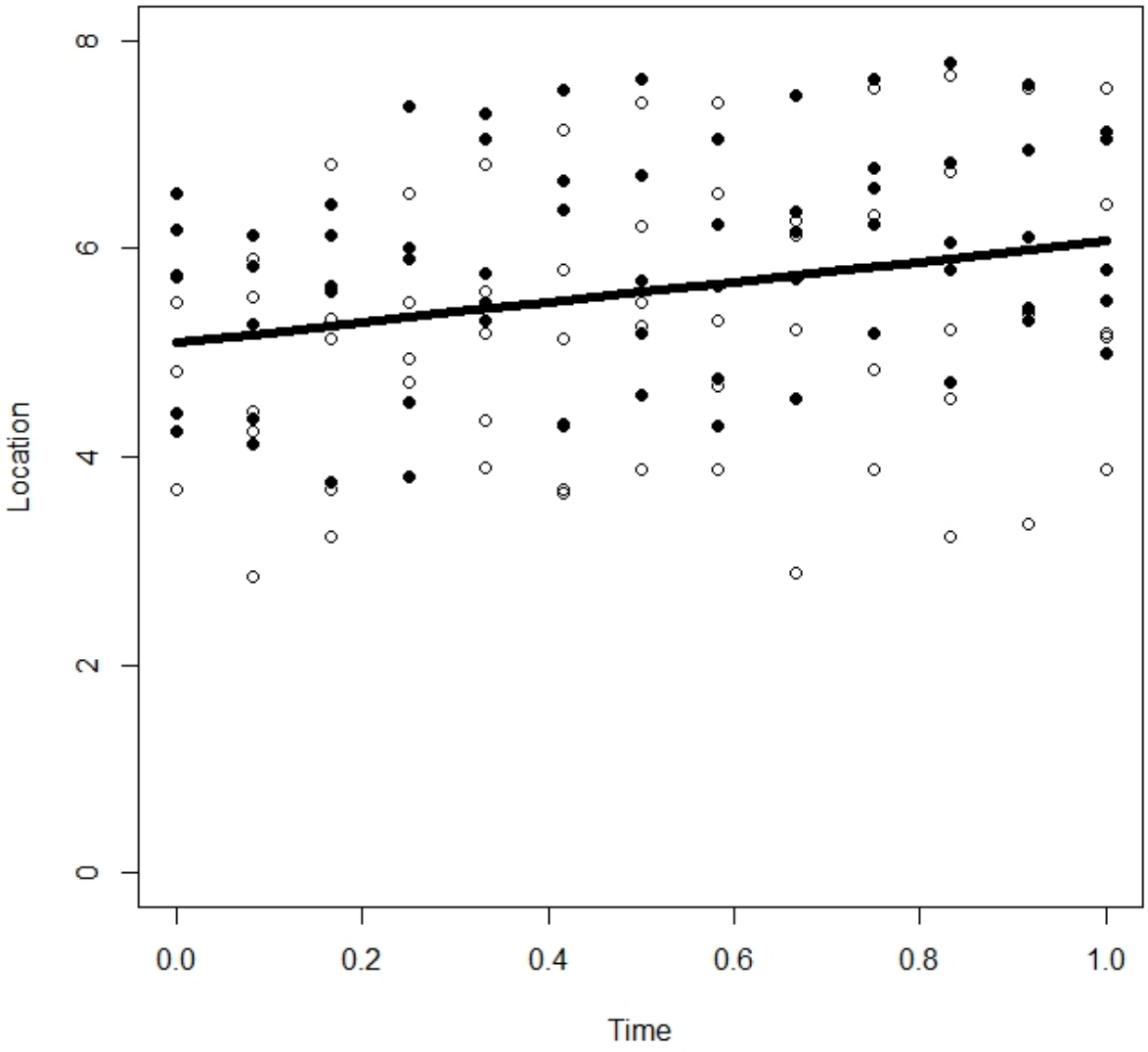

Figure 3: Predictions from the best supported model for predicting snail locations when exposed to predator cues during no flow treatments. This is represented through prediction lines using the top model, Time + (1|Site/Snail) as well as showing the average location of individuals grouped by site as time increased during behavioral trials. Filled in points are no flow sites and unfilled are flow sites.

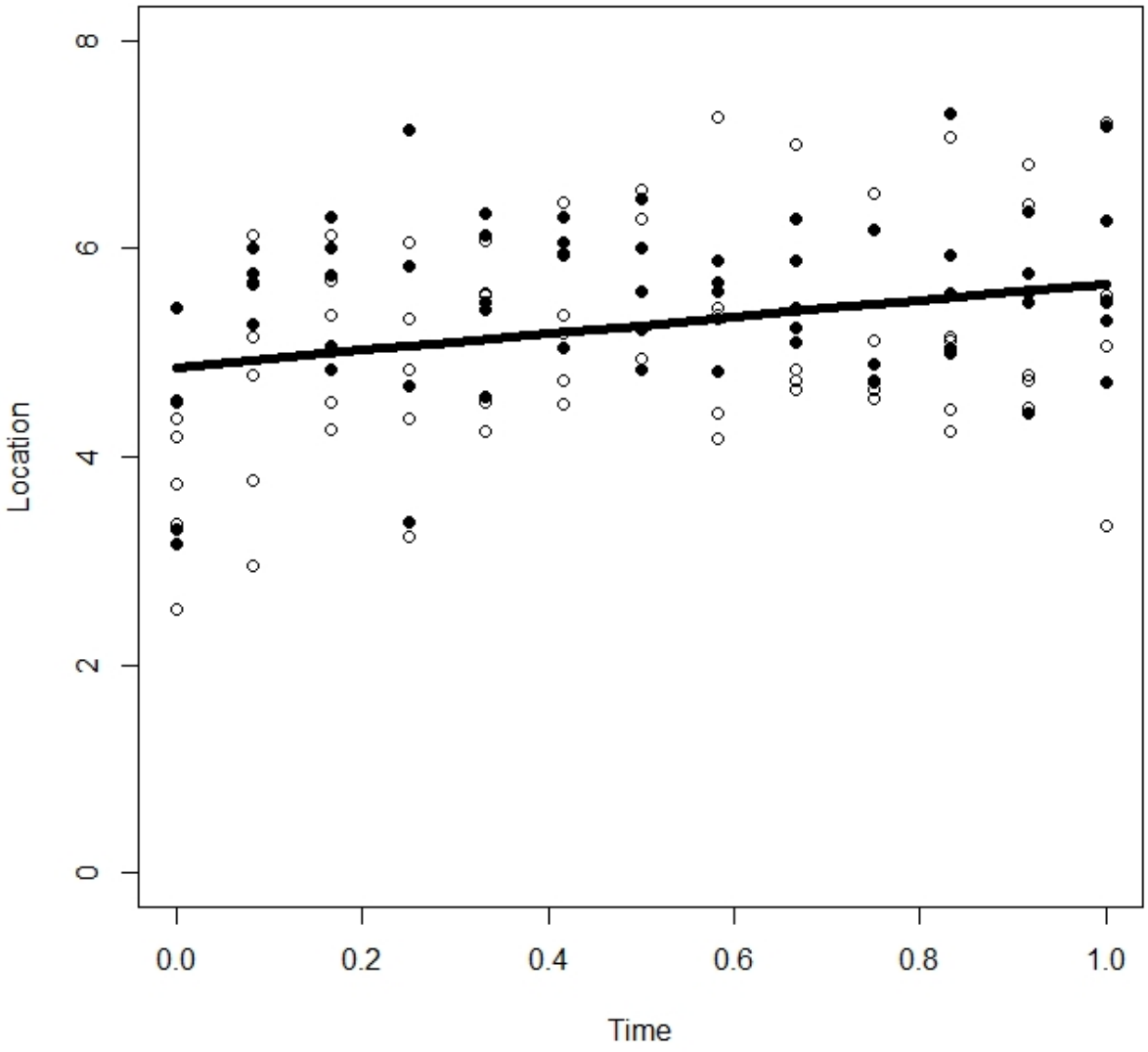

Figure 4: Predictions from the best supported model for predicting snail locations when exposed to flow treatment. This is represented through prediction lines using the top model, Time + (1|Site/Snail) as well as showing the average location of individuals grouped by site as time increased during behavioral trials. Filled in points are no flow sites and unfilled are flow sites.

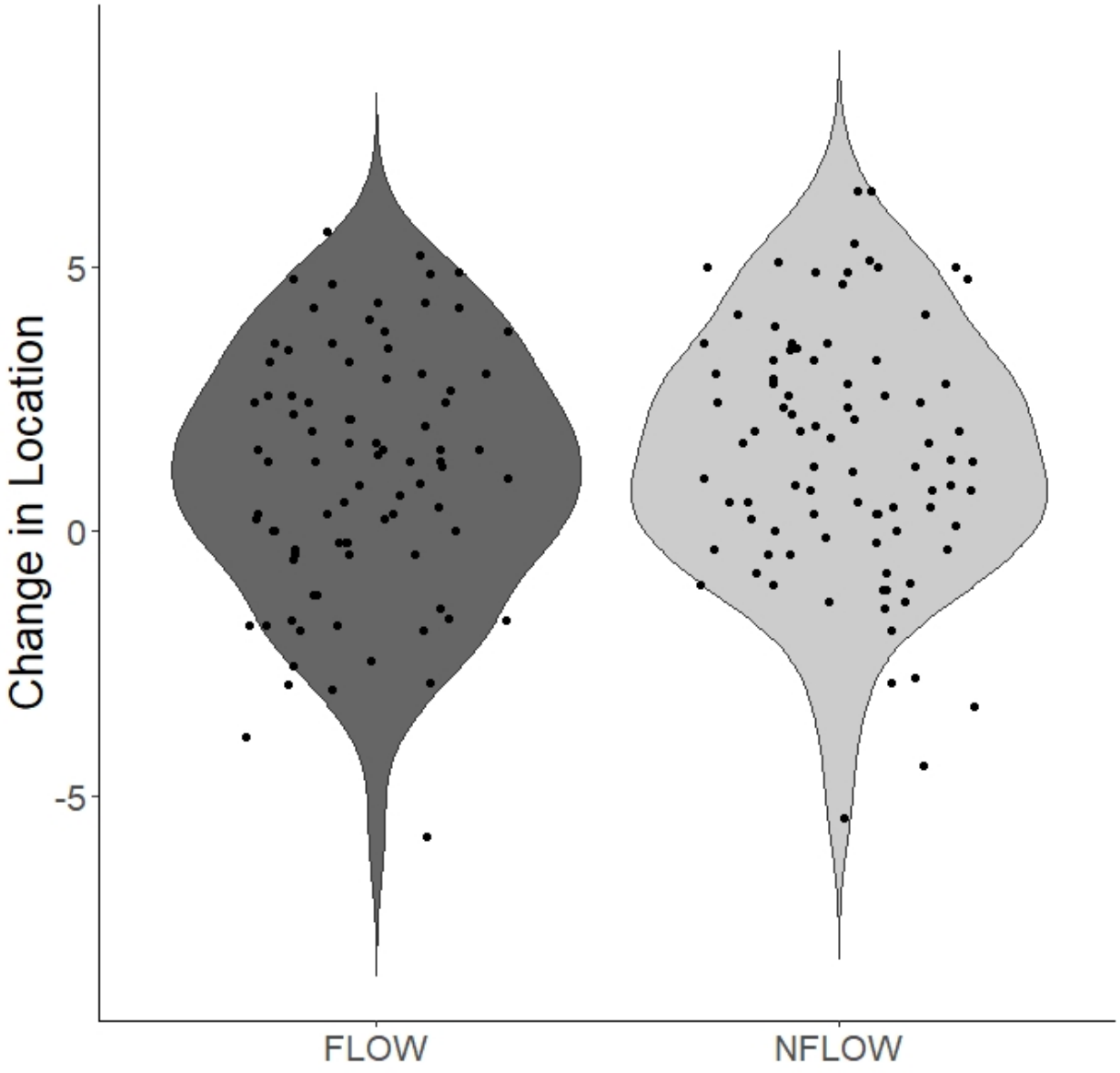

Figure 5: Change in average locations of snails between control and predator cue exposure in no flow treatments comparing snails from flow vs no flow environments.

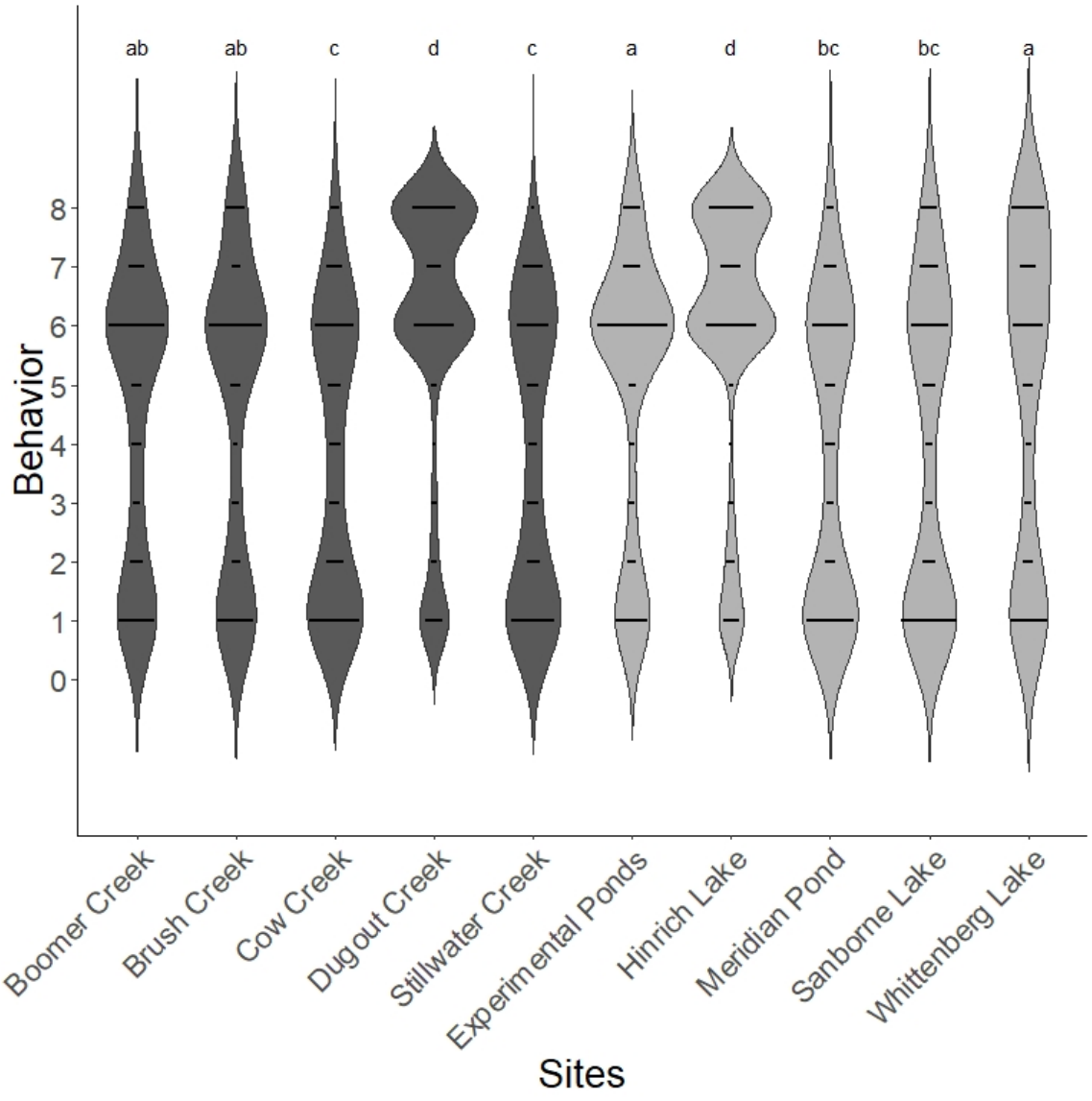

Figure 6: Distribution of observed locations of snails during control cue exposure in no flow treatment for different sites. Dark gray representing a flow environment site and light gray representing a no flow environment site.

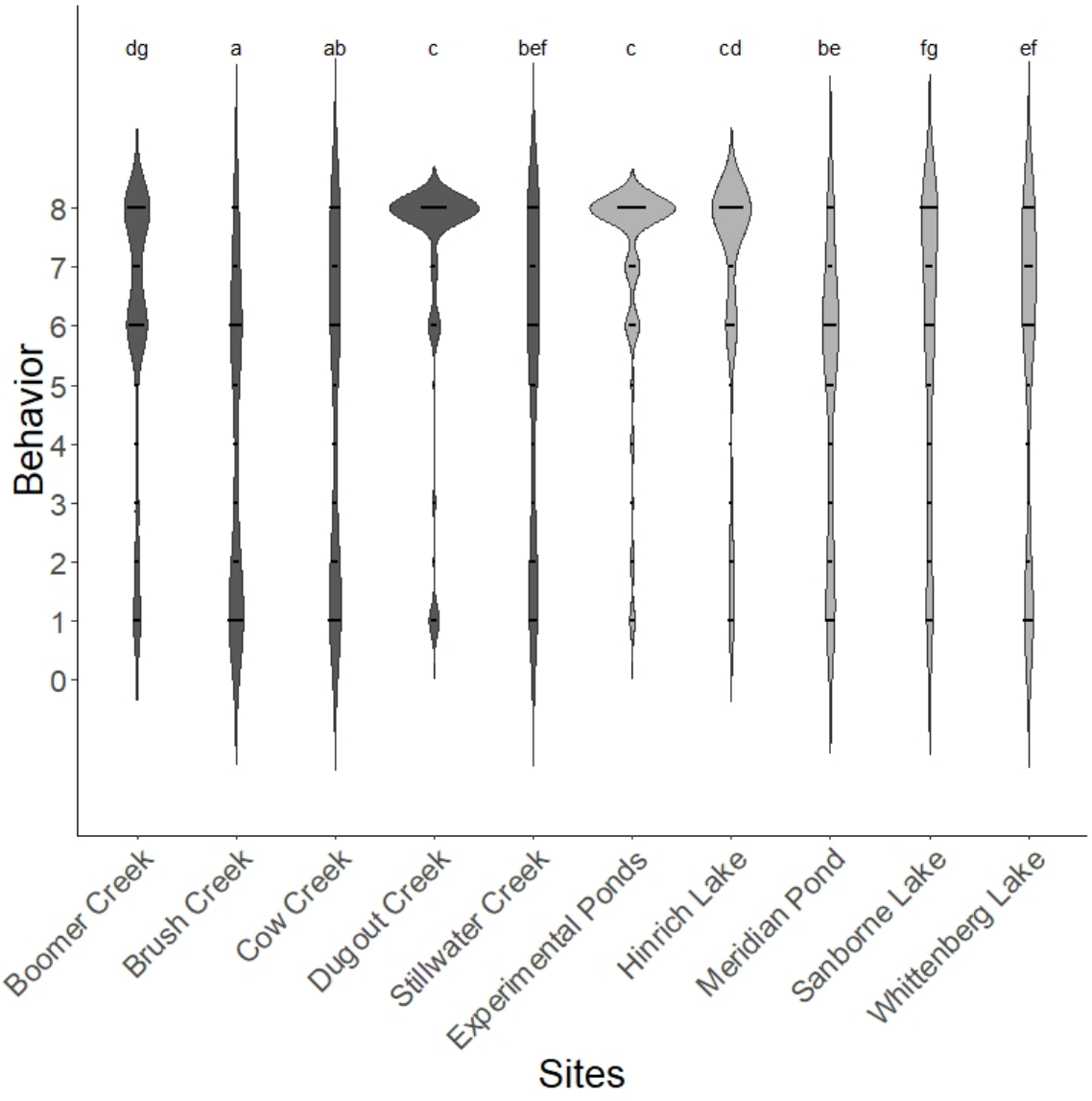

Figure 7: Distribution of observed locations of snails during predator cue exposure in no flow treatment for different sites. Dark gray representing a flow environment site and light gray representing a no flow environment site.

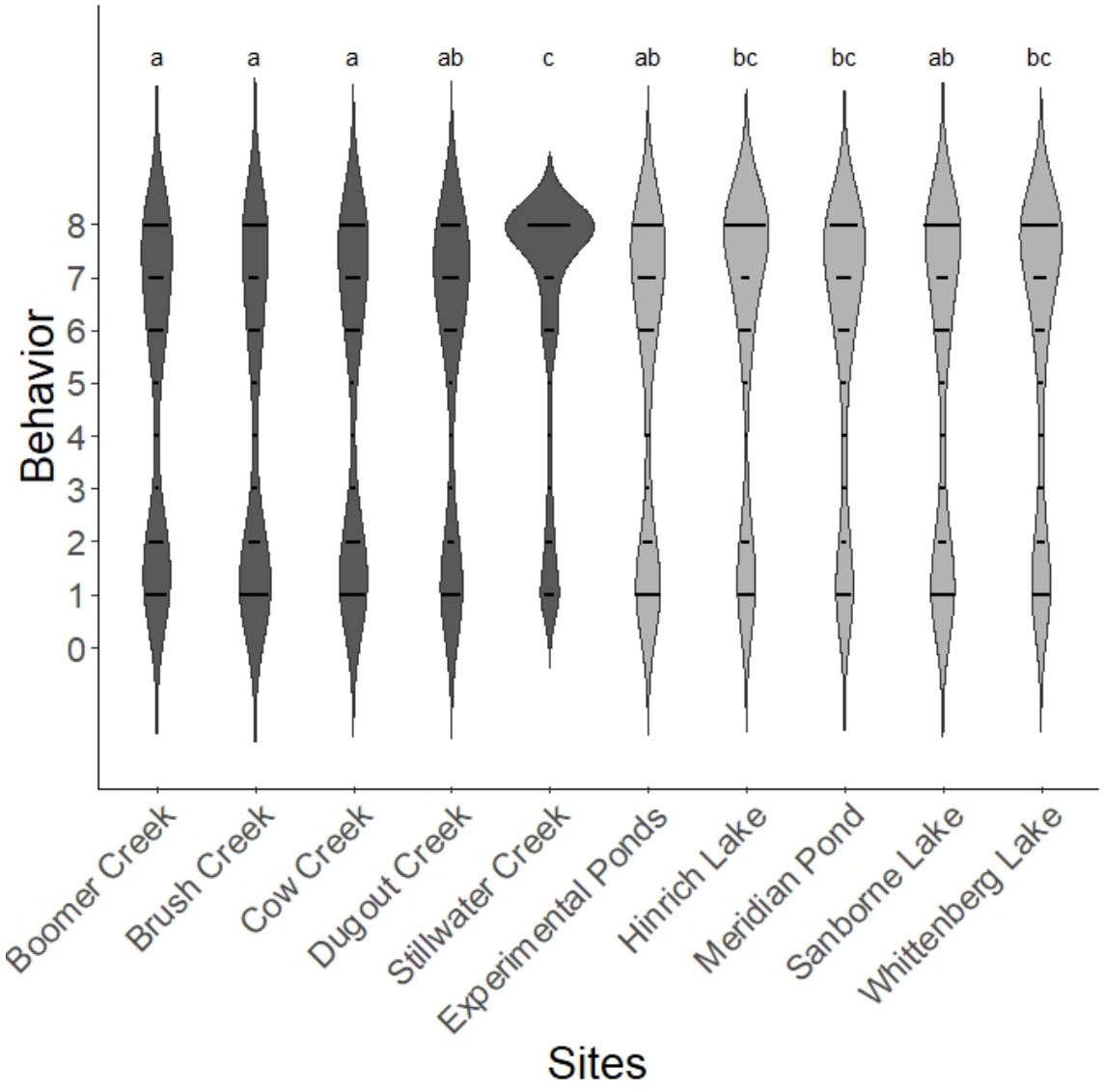

Figure 8: Distribution of observed locations of snails during control cue exposure in flow treatment for different sites. Dark gray representing a flow environment site and light gray representing a no flow environment site.

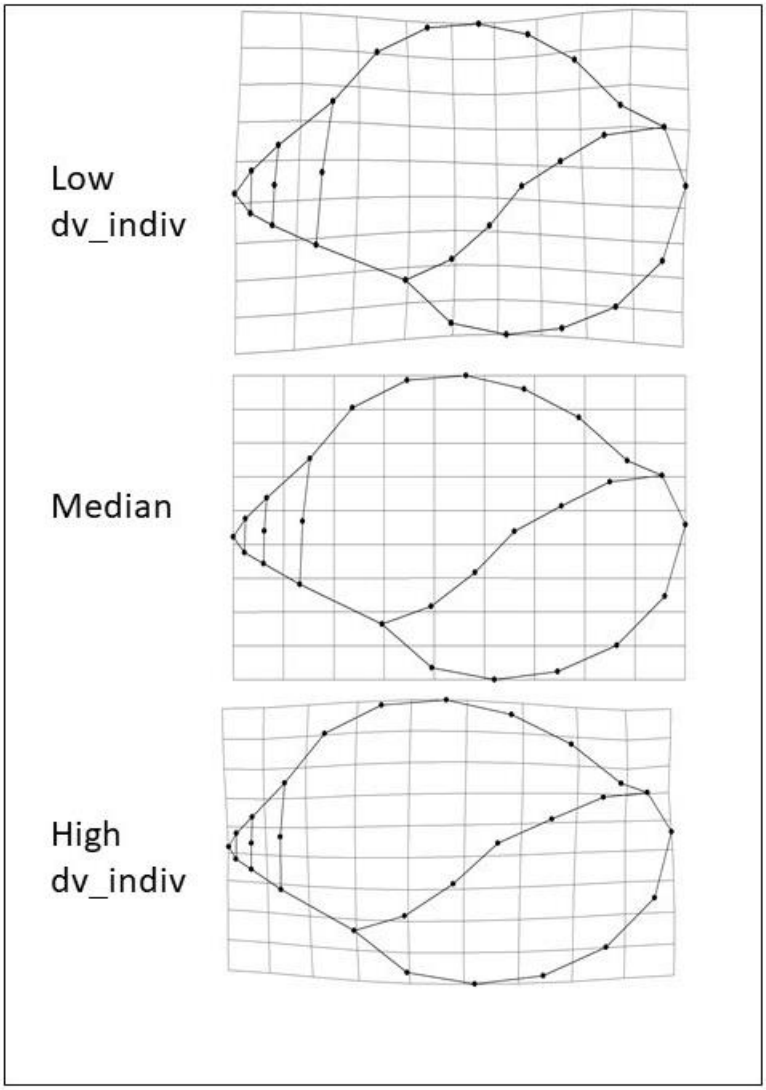

Figure 9: View of morphological differences between individuals that come from a no flow environment versus a flow environment. Low dv_indiv represents no flow morphology and high dv_indiv represents a flow morphology. Median represents a divergence vector of 0, the halfway point between flow and no flow morphology.

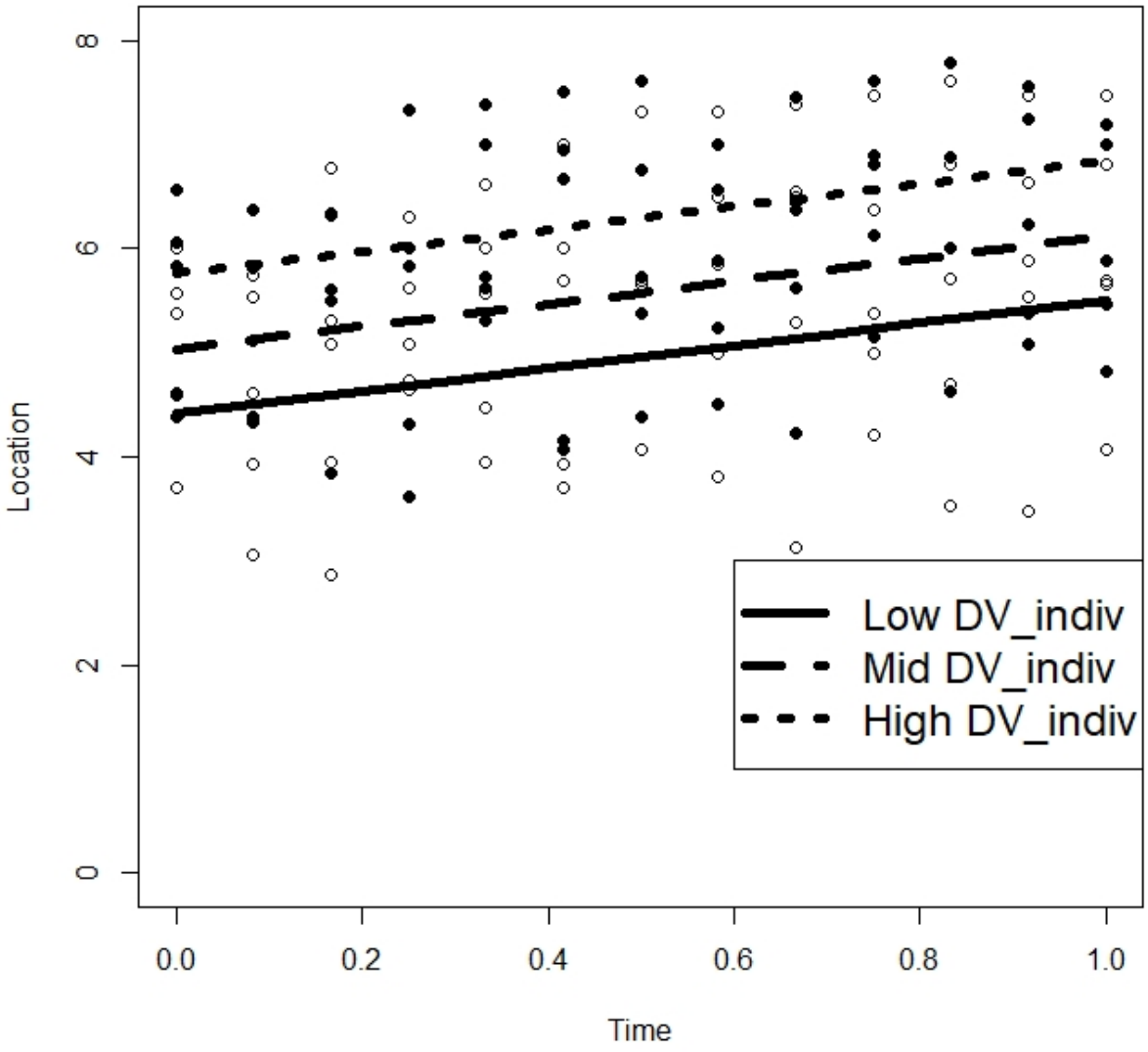

Figure 10: Predictions from the best supported model for predicting snail locations when exposed to predator cues during no flow treatments. This is represented through prediction lines using the top model, dv_indiv + Time + (1|Site/Snail) as well as showing the average location of individuals as time increased during the behavioral trials. Filled in points are no flow sites and unfilled are flow sites.

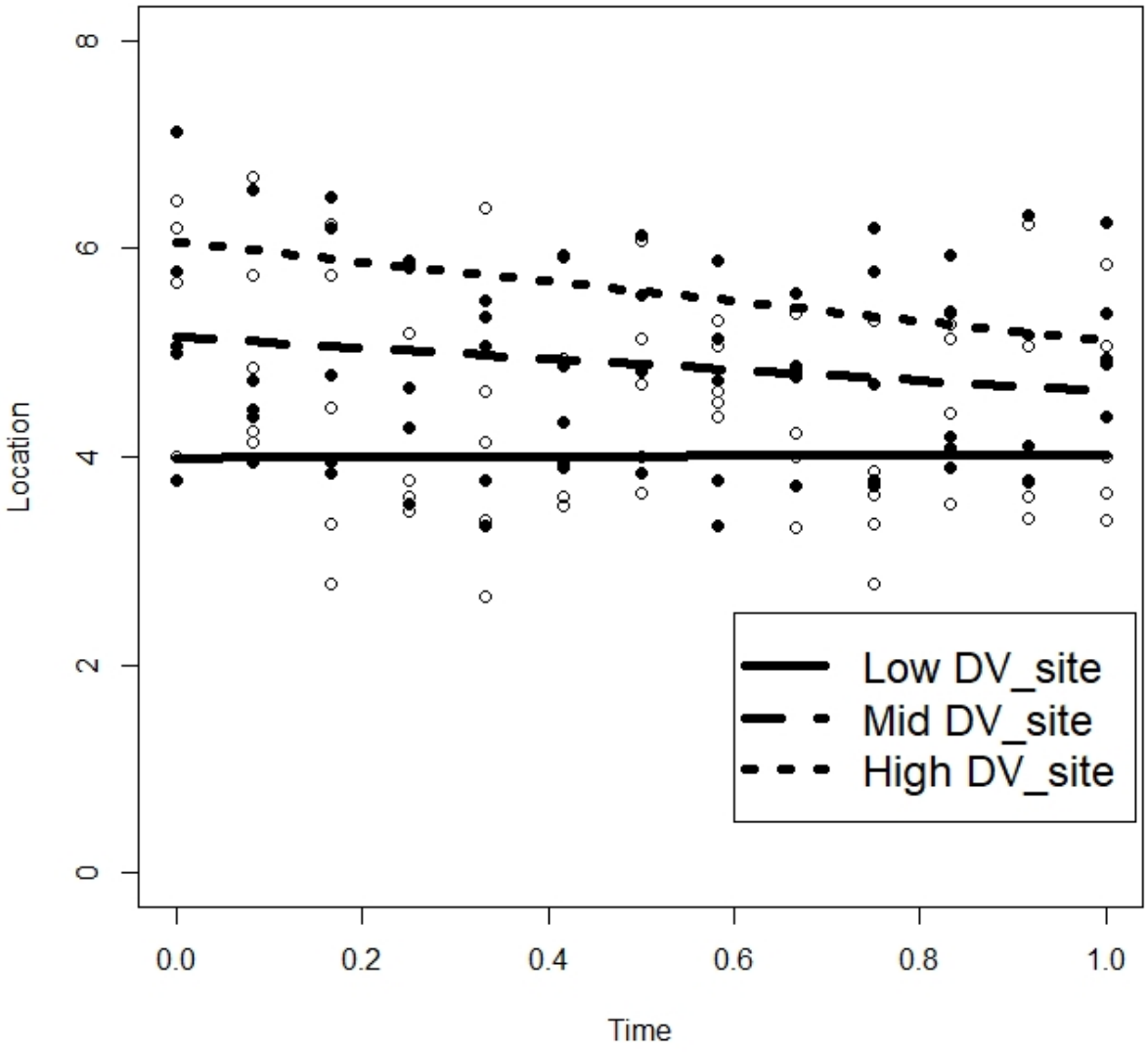

Figure 11: Predictions from the best supported model for predicting snail locations when exposed to control cues during no flow treatments. This is represented through prediction lines using the top model, dv_site * Time + (1|Site/Snail) as well as showing the average location of individuals as time increased during the behavioral trials. Filled in points are no flow sites and unfilled are flow sites.

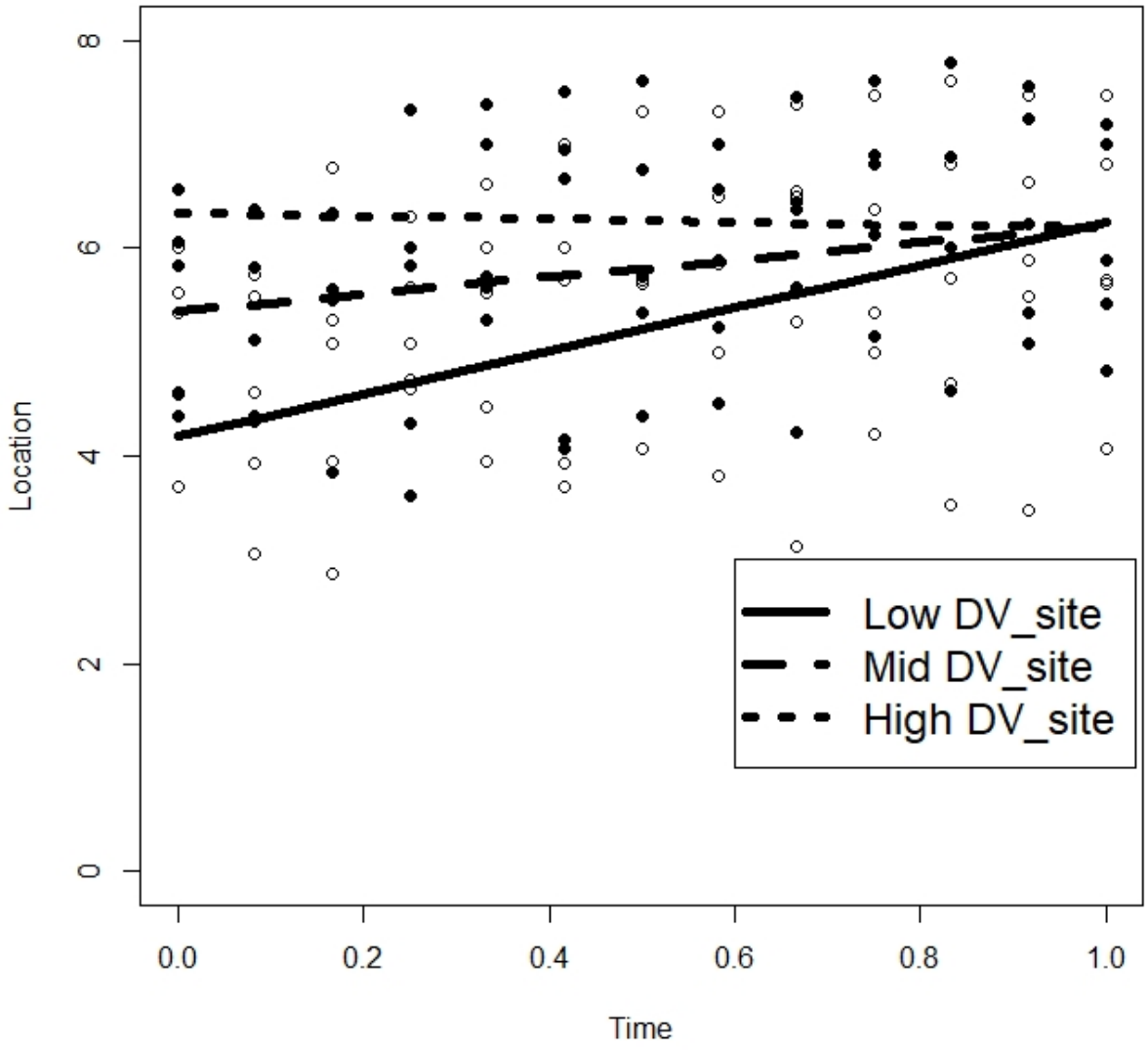

Figure 12: Predictions from the best supported model for predicting snail locations when exposed to predator cues during no flow treatments. This is represented through prediction lines using the top model, dv_site * Time + (1|Site/Snail) as well as showing the average location of individuals as time increased during the behavioral trials. Filled in points are no flow sites and unfilled are flow sites.

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VITA

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