5-1-2016

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Recommended Citation

Broyles, Whitnee, "PREDATOR DRIVEN EVOLUTION OF BRAIN SIZE ACROSS THREE PREDATION INTENSITIES IN NATURAL POPULATIONS" (2016). *2016 Spring Honors Capstone Projects*. 12.
https://mavmatrix.uta.edu/honors_spring2016/12

PREDATOR DRIVEN EVOLUTION OF BRAIN SIZE ACROSS THREE PREDATION INTENSITIES IN NATURAL POPULATIONS

by

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Presented to the Faculty of the Honors College of
The University of Texas at Arlington in Partial Fulfillment
of the Requirements
for the Degree of

HONORS BACHELOR OF SCIENCE IN BIOLOGY

THE UNIVERSITY OF TEXAS AT ARLINGTON
May 2016

ACKNOWLEDGMENTS

This entire endeavor would not have happened without the dedication of my mentor, Dr. Matthew Walsh. I owe my utmost gratitude to him for his unending guidance, communication, and teaching. He has allowed me to expand my education beyond what I had imagined, and I am truly honored to have worked in his lab.

I would especially like to thank my husband, Geordie Broyles, who encouraged me during times of frustration and praised me during times of accomplishment. His endless love and patience have provided me the support I needed to succeed in this journey.

Lastly, I am much indebted to my parents who have provided for my education. I could not have realized this goal without their love and support. I am grateful for the values they instilled in me as a child that have shaped me into the woman and student I am today.

April 15, 2016

ABSTRACT

PREDATOR DRIVEN EVOLUTION OF BRAIN SIZE ACROSS THREE PREDATION INTENITIES IN NATURAL POPULATIONS

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The University of Texas at Arlington, 2016

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Vertebrates exhibit extensive variation in brain size, but why such diversity exists has been an area of interest for decades. Recent selection experiments revealed that the evolution of larger brains enhances survival in the presence of predators; increased predation should thus favor larger brains. This project tested the influence of predator-induced mortality on the evolution of brain size by exploring Trinidadian killifish (*Rivulus hartii*) from communities that vary in predation intensity for differences in brain size. This work showed that male (but not female) *Rivulus* from sites that lack predators exhibited significantly larger brains than males from sites with large piscivorous fish capable of eating adult *Rivulus*. Brain size did not differ between sites that varied in the presence of a gape-limited predator of *Rivulus*. These results argue that increased male brain size is favored in less risky environments due to fitness benefits of higher cognitive function.

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CHAPTER 1

INTRODUCTION

There is no doubt that brain size varies greatly among animals, and that there are clear benefits and costs to increased brain size (Kotrschal et al., 2013). The benefits of a larger brain size include increased cognitive and learning capacities which, in turn, are correlated with higher survival in the wild (Sol et al., 2007). However, these abilities come at the expense of allocation towards other traits; increased brain is associated with smaller guts size and fewer offspring (Tsuboi et al., 2014; Kotrschal et al., 2013; Kotrschal et al., 2015). This cost-benefit competition is an important factor in creating a competent yet energetically sustainable brain size. However, the exact ecological factors that drive this variability are unclear (Kotrschal et al., 2013). Few studies have explored the environmental conditions that drive the evolution of brain size in nature. The vast majority of our understanding of brain size variation stems from artificial-selection experiments and broad comparisons across distant taxa (Kotrschal et al., 2013; Brydges et al., 2008; Isler and Schaik, 2006). Some research even suggests that encephalization and brain size can be driven by complex factors such as foraging strategy, social interaction, and group size (Aiello and Wheeler, 1995). This is further supported by research that correlates increased brain size with parental care type, advanced social behavior, and increased survival in risky environments (Gonzalez-Voyer et al., 2008; Kotrschal et al., 2015). Tests of these hypotheses and, more generally, tests of the factors that determine brain size are now needed.

Recent research identified predators as a key driving force in the evolution of brain size. Kotrschal et al. 2012 selected for larger brains in a species of fish and showed that the evolution of a larger brain is associated with enhanced spatial memory and survival in the presence of predators (Burns and Rodd, 2008; Kotrschal et al., 2015). This leads to the hypothesis that a species in an environment with predators would evolve a larger brain than the same species in an environment that lacks predators. However, these selection experiments occurred under benign conditions in the lab (Kotrschal et al., 2015; Kotrschal et al., 2013) and do not include additional ecological interactions within the natural community. This is important because comparisons among natural populations between sites with and without predators actually predict the opposite trajectory of adaptation; increased predation intensity is correlated with increased boldness but declines in cognitive function and spatial learning (Fraser et al., 2001; Brydges et al., 2008). Since cognitive function has been clearly linked to brain size, this suggests that predation leading to less cognitive ability selects for smaller brain size.

Trinidadian killifish, *Rivulus hartii*, are well suited to study factors that may influence brain size. *Rivulus* are located across communities that differ in predation intensity but not physical habitat or environment, as they are close in proximity and separated physically by waterfalls (Walsh et al, 2010; Walsh and Reznick, 2009). These localities include: (1) *Rivulus* only sites (RO) where *Rivulus* is the only species, (2) *Rivulus/*guppy sites (RG) where *Rivulus* and the guppy, *Poecilia reticulate,* are the only fish species present, and (3) high predation sites (HP) where *Rivulus* co-occur with several species of piscivorous fish such as *Crenicichla alta* and *Hoplias malabaricus* (Reznick and Ender, 1982; Walsh and Reznick, 2010). These community differences are key to studying predator-induced mortality evolutionary shifts. *Rivulus* in HP sites suffer increased mortality rates compared to those in RO sites, as predators in HP sites are capable of consuming all class-sizes of *Rivulus* (Walsh and Reznick, 2009). On the other hand, predators in RG sites are gape-limited and only prey upon juvenile *Rivulus,* causing a decline in abundance of *Rivulus* while adult *Rivulus* survival rates differ little between RO and RG populations (Walsh and Reznick, 2009). Predator-induced mortality has been associated with genetic divergence of life history traits among these populations and thus provide the opportunity to study conditions that drive evolutionary shifts (Walsh and Reznick, 2008).

This project tested the influence of increased predation on the evolution of brain size and associated trade-offs with gut size among *Rivulus* from high predation, *Rivulus*/guppy, and *Rivulus*-only sites. All populations were first reared in a common environment for two generations and second generation lab reared fish were compared for variation in brain size and gut size (an indicator of metabolic function). The main prediction is that an increase in predation will select for larger brain size (see Kotrschal et al., 2015; Kotrschal et al., 2013). Failing to support this hypothesis would suggest that more complex factors drive brain size evolution and that additional ecological interactions within the community may play a role.

CHAPTER 2

MATERIALS AND METHODS

2.1 Common Garden Experiments

The common garden experiments were performed previously and are all published (see Walsh and Reznick, 2008, 2010, 2011). The protocols for fish collection, rearing, and the experimental details will thus be described briefly. Wild caught *Rivulus* were collected from the Aripo, Guanapo, and Quare Rivers. The first lab reared generation was obtained by randomly pairing wild-caught males and females from each locality. Their eggs were subsequently incubated in petri dishes, and newly hatched larvae were reared on a diet of liver paste and Brine shrimp *nauplii*. All fish were reared to maturity in aquaria at a density of 8-10 fish per tank. The second generation was obtained by mating one female from each lineage in the first generation with a male from the same locality but with different lineage as to maintain the diversity of the wild-caught stocks. They were reared under the same conditions as the first generation for 20 days. The fish were placed into individual aquaria and distributed among two food treatments: 1) high food level that mimics rates of growth in high predation or RG sites or 2) low food levels that approximate rates of growth observed in RO sites. Quantified portions of liver paste and Brine shrimp *nauplii* were given in the morning and the afternoon respectively, and the fish were reared to maturity. Males were immediately euthanized while all females were euthanized approximately two-weeks after attaining sexual maturation. Each specimen was preserved individually in formalin.

2.2 Quantification of Brain and Gut Size

Each fish was first weighed and recorded for total body weight. To dissect each fish, a ventral cut was made slightly left of the mid-sagittal line from approximately 2mm above the pectoral girdle to approximately 2mm past the anus. Two more transverse cuts were made, one from the posterior end of the existing cut up through the gill slit and the other from the anterior end of the existing cut to the spine, as to create a flap to reveal the internal organs. The gut was cut at the tip of the anus to remove the posterior end and then cut across where the anterior part of the gut constricted. The total wet weight of each gut was then recorded. To measure brain size, the brain stem was severed from the rest of the spinal cord by cutting transversely across from the top of each gill slit. Then the lower jaw and all tissue between the roof of the mouth and the braincase were removed from the rest of the skull. The perimeter of the skull was cut and the lower braincase was peeled back to reveal the brain. The brain was removed, including the optic nerves, then weighed and photographed. The brain photographs were analyzed for optic tectum length, a good indicator of brain size (REF).

2.3 Statistical Analyses

The focal populations were analyzed for differences in brain and gut size using general linear models. The comparisons between *Rivulus* from HP versus RO sites and RG versus RO sites were analyzed separately because the experiments were performed at different points in time. Fish community (high predation, Rivulus/guppy, Rivulus-only), food level (low, high), and the fish x food interaction were entered as fixed effects. River of origin was entered as a random blocking factor. Fish body size was entered as a covariate. Data for males and females were analyzed separately. Normality and homogeneity of variances was confirmed prior to each analysis.

CHAPTER 3

RESULTS

3.1 Brain Size

Male brain size was significantly larger ($p<0.05$) in Rivulus-only compared with high predation sites ($F_{1,79} = 7.53$; Fig. 3.1). The brain size of males were ~18% larger in Rivulus-only versus high predation sites. The brain of females did not differ significantly between RO and HP populations (~3%) ($F_{1,75} = 0.93$; Fig. 3.2). The brain size of males and females did not differ significantly between RO and RG populations ($F_{1,108}= 0.06$ and $F_{1,136}=0.23$ respectively; Fig. 3.3 and Fig. 3.4).

3.2 Gut Size

Male and female gut sizes were significantly larger ($p<0.05$) in high predation sites than *Rivulus* only sites (14% larger for males $F_{1,75}= 4.27$ and ~5% for females $F_{1,74}= 5.31$; Fig. 3.5 and Fig. 3.6). Variation in male gut size depended upon controlled food in the lab as the 'population x food' interaction was significant ($F_{1,81}= 9.62$, $p<0.05$); male gut size in fish from high predation sites was 31% larger than *Rivulus* from *Rivulus*-only sites under high food levels, but such differences disappeared under low food conditions (Fig. 3.7). Male and female gut sizes did not differ significantly between RG and RO populations ($F_{1,110}= 0.05$, $F_{1,136}= 0$; Fig 3.8 and Fig 3.9).

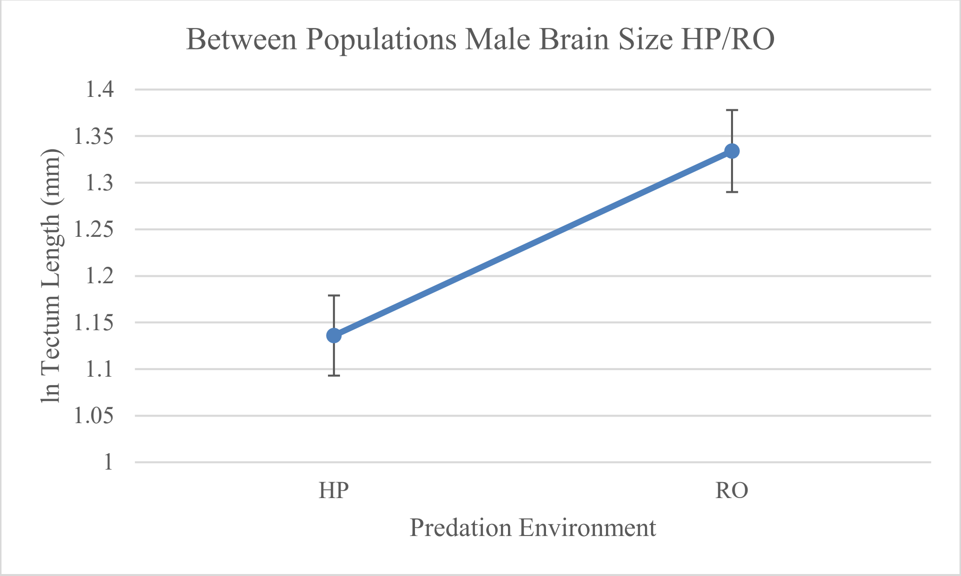

Figure 3.1: HP/RO Male Brain Size Comparison
Male *Rivulus* had sigificantly ($p<0.05$) larger brain size in *Rivulus*-only (RO) environments than high-predation (HP) environments

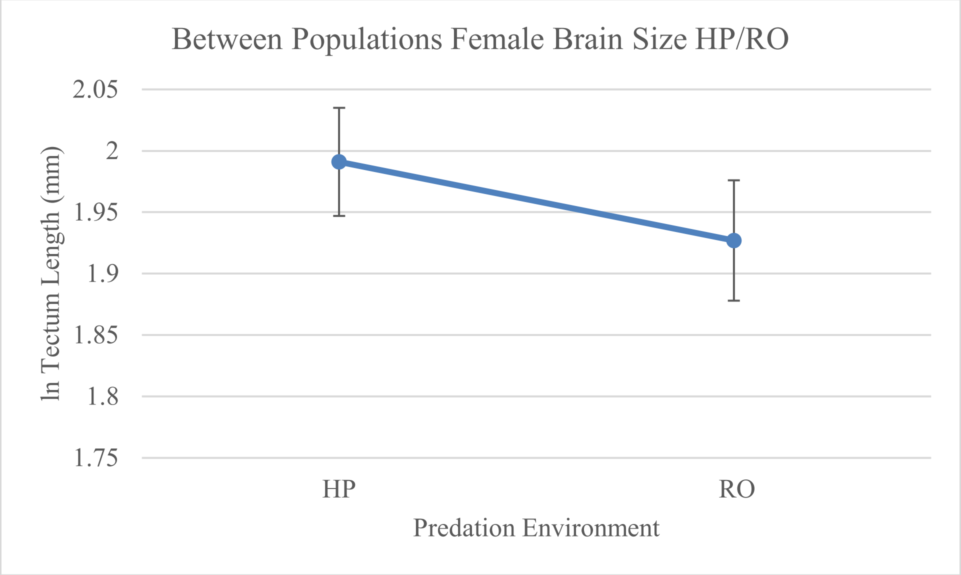

Figure 3.2: HP/RO Female Brain Size Comparison
Female *Rivulus* showed no significant difference between high-predation (HP) and *Rivulus*-only (RO) environments

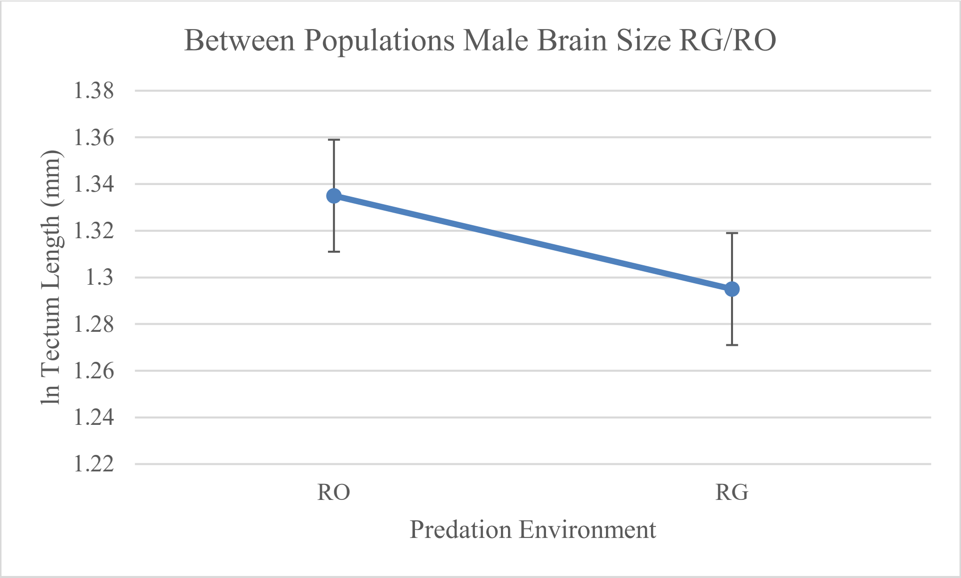

Figure 3.3: RG/RO Male Brain Size Comparison
Male *Rivulus* showed no significant difference between *Rivulus*/guppy (RG) and *Rivulus*-only (RO) environments

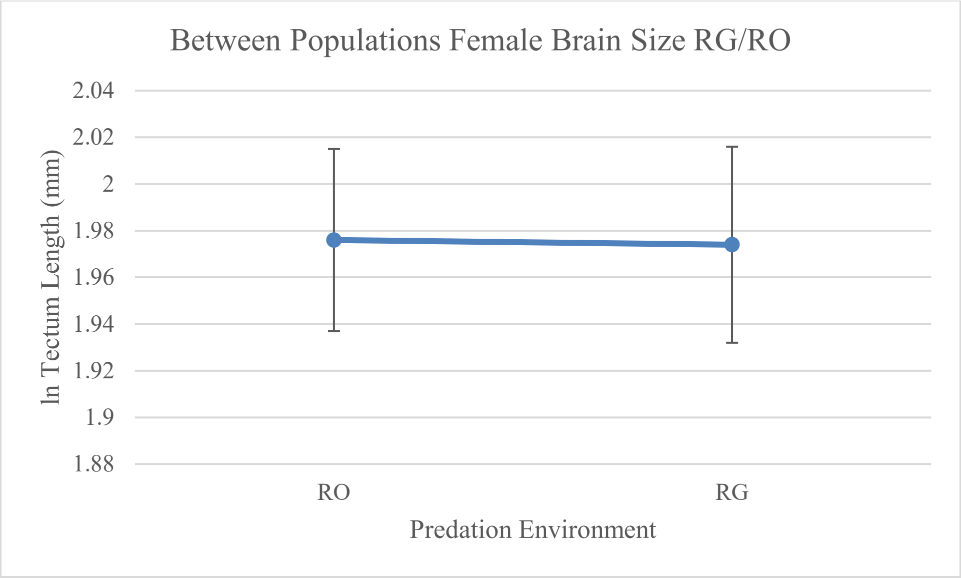

Figure 3.4: RG/RO Female Brain Size Comparison
Female *Rivulus* showed no significant difference between *Rivulus*/guppy (RG) and *Rivulus*-only (RO) environments

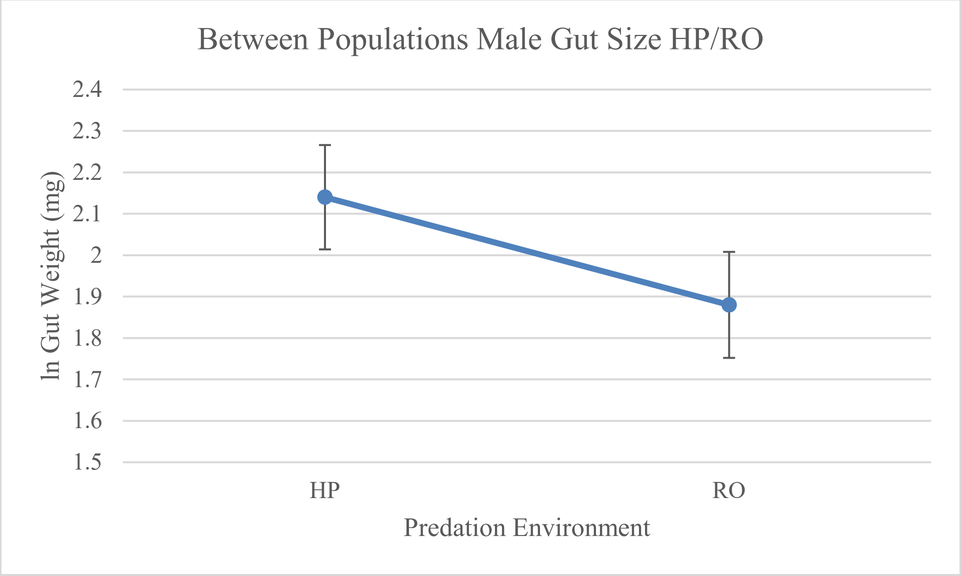

Figure 3.5: HP/RO Male Gut Size Comparison
Male *Rivulus* had significantly ($p<0.05$) larger gut size in high predation (HP) environments than in *Rivulus*-only environments

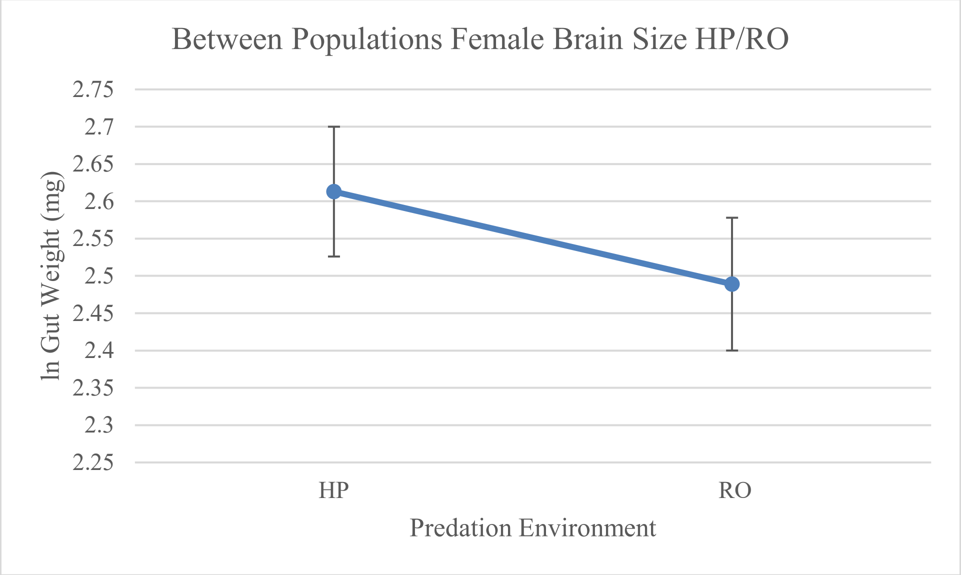

Figure 3.6: HP/RO Female Gut Size Comparison
Female *Rivulus* had significantly ($p<0.05$) larger gut size high predation (HP) environments than in *Rivulus*-only environments

Figure 3.7: HP/RO Male Gut Size Population x Food Interaction
Male gut size in high-predation (HP) and *Rivulus*-only (RO) depended upon food levels; the population x food interaction was significant

Figure 3.8: RG/RO Male Gut Size Comparison
Male *Rivulus* showed no significant difference in gut size between *Rivulus*-only (RO) and *Rivulus*-guppy (RG) environments

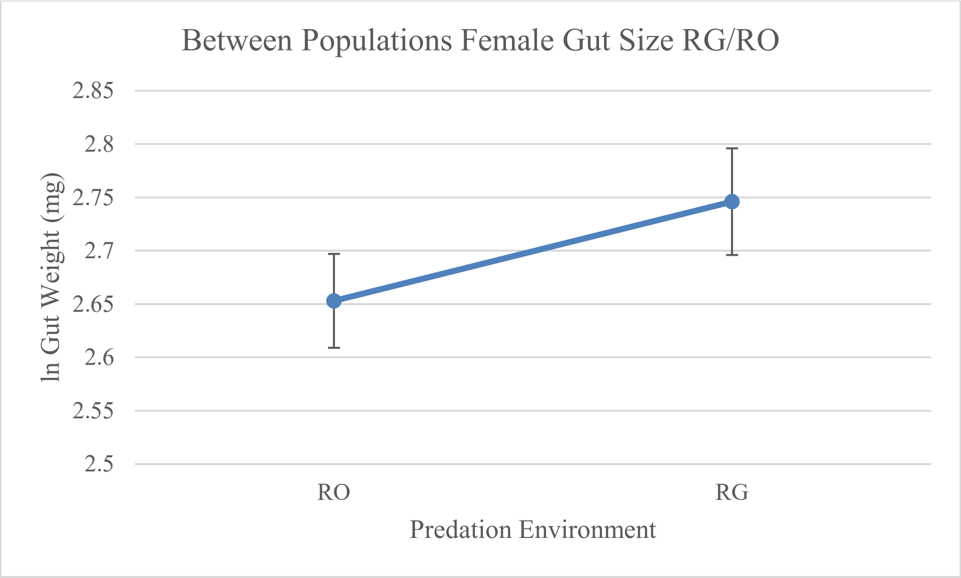

Figure 3.9: RG/RO Female Gut Size Comparison
Female *Rivulus* showed no significant difference in gut size between *Rivulus*-only (RO) and *Rivulus*-guppy (RG) environments

CHAPTER 4

DISCUSSION

This study showed that increased predation by large piscivorous fish exerts selection on the brain size of males (but not females). Male Rivulus from Rivulus-only sites exhibited larger brains than fish from high predation sites (Fig. 3.1). Females showed no significant difference in brain size between high predation and Rivulus-only sites (Fig. 3.2). The significantly smaller brain sizes observed in male *Rivulus* that co-occur with piscivores compared to localities where *Rivulus* are the only species present oppose the prediction that predator-induced mortality selects for larger brain size. The results also did not support the prediction that increased brain size would cause a decrease in gut size. With these results opposing previous artificial selection experiments and the expensive tissue hypothesis (Kotrschal et al., 2013; Kotrschal et al. 2015; Aiello and Wheeler, 1995), it seems more complex interactions are responsible for explaining the relationship between predation level and brain size, particularly among males. The potential causes of these trends are discussed below.

In *Rivulus* communities, males defend territories and actively court females. However, habitat use varies across the predator communities. In communities with predators, they are more confined to stream margins so males must exhibit increased boldness to be able to interact with potential mates. However, in communities where *Rivulus* are the only fish species present, they are commonly observed in open water, but these sites are also characterized by a higher density of *Rivulus* and fewer resources (Gilliam et al., 1993; Walsh et al., 2010). Therefore, these males have increased opportunities (and need) for foraging and interactions with other males and females. Based on previous studies showing that fish from high predation communities are slower at spatial learning tasks than those from low predation communities (Brydges et al., 2008), and knowing that problem solving positively correlates with brain size, it seems that selection likely favors a larger brain size in *Rivulus* in low predation environments. That is, a larger brain in low predation regimes translates into improved fitness because the higher cognitive function allows improved foraging and mating opportunities. However, this begs the question of why *Rivulus* that live alone did not exhibit differences in brain size when compared with *Rivulus* from sites with guppies (*Poecilia reticulata*) (Fig. 3.3 and Fig. 3.4). It is important to recognize the nature of the predatory interactions between *Rivulus* and guppies is highly size- and/or stage-specific. Guppies are gape-limited and prey upon small (immature) size-classes of Rivulus (Walsh and Reznick, 2010). Since adult *Rivulus* in RG communities do not experience mortality by guppies, adult mortality rates are similar between RG and RO communities (Walsh et al. 2011). If selection on brain size depends upon the ecological conditions experienced by adults, the lack of divergence in brain size between RG and RO sites is not entirely surprising.

The connection between brain size and learning is an important component of fitness for Rivulus in RO and RG sites (Brydges et al., 2008; Ingley et al., 2014). In high predation, risk taking behavior is key for male fitness. Boldness, or tendency to take risks, is much higher in individuals who reside with predators than those who live in communities without predators and such differences in boldness are much larger in males than females

(Ingley et al., 2014). For instance, studies have shown that female guppies favor ‘bolder’ males (Godin and Dugatkin, 1996). Increased male boldness thus leads to increased mating success. Boldness has also been shown to correlate positively with foraging success and predator escape response (Godin and Dugatkin, 1996; Ioannou et al., 2008). It thus seems that a successful strategy for males in high predation sites is to be bolder at the expense of learning and cognitive ability. This leads to the hypothesis that the observed differences in male brain size between HP and RO sites underlie divergent patterns of behavior and learning.

4.1 Gut Size Variation

Research has shown that organisms typically respond to declines in food availability by producing longer guts as this can increase levels of nutrient absorption (Relyea et al., 2004; Sullam, et al., 2014). In natural populations of *Rivulus*, *Rivulus* are less abundant and experience increased resources in HP sites (Gilliam et al., 1993; Walsh, et al., 2010; Walsh, et al., 2011). However, this current study found that *Rivulus* from HP sites maintained larger gut size than RO sites and that *Rivulus* from RO and RG sites did not differ in gut size between populations (Fig. 3.5-3.6 and Fig. 3.8-3.9). Interestingly, male gut size differed between HP and RO populations under high food levels, but this difference disappeared under low food levels (Fig. 7). Specifically, the HP male gut sizes remained the same between food levels, but the RO male gut sizes increased under low food availability. The cause of population differences in gut size and gut size plasticity is currently unclear. It is possible that increased predation in HP sites selects for a larger gut as a means of increasing fitness by optimally converting resources into energy for growth and/or reproduction (see Walsh & Reznick, 2008). In RO sites, increased opportunity to forage may lead to higher gut plasticity.

CHAPTER 5

CONCLUSION

This study used Trinidadian killifish Rivulus hartii from populations spanning a gradient in predator-induced mortality to explore the influence of predation on the evolution of brain size (Walsh, et al., 2011; Walsh and Reznick, 2010). Increased predation by large piscivorous fish was associated with the evolution of a smaller brain size in males but not females (Fig. 3.1 and Fig. 3.2). However, this difference was not observed between sites that differ in the presence and absence of a smaller gape-limited predator (Fig. 3.3 and Fig. 3.4). The sex-specific differences illustrate the complex interactions that drive shifts in brain size, as the male's role and investment in mating and foraging were important ecological factors effected by predation level (Urban, 2007; Gilliam, Fraser & Alkins-Koo, 1993; Walsh, et al., 2010). Increased predation favors bolder behavior in males which, in turn, enhances their fitness. This increased boldness comes at the cost of decreased learning capability and a smaller brain (Ingley, Rehm and Johnson, 2014; Godin and Dugatkin, 1996; Brydges, Heathcote & Braithwaite, 2007). Future experimental tests are needed to directly evaluate the link between these ecological factors (mating, foraging, and predation) and brain size.

REFERENCES

Aiello, L. C., & Wheeler, P. (1995). The Expensive-Tissue Hypothesis: The Brain and the Digestive System in Human and Primate Evolution. Current Anthropology, 36(2), 199-221.

Brydges, N. M., Heathcote, R. J., & Braithwaite, V. A. (2008). Habitat stability and predation pressure influence learning and memory in populations of three-spined sticklebacks. Animal Behaviour, 75(3), 935-942.

Burns, J. G., & Rodd, F. H. (2008). Hastiness, brain size and predation regime affect the performance of wild guppies in a spatial memory task. Animal Behaviour, 76(3), 911-922.

Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N., & Skalski, G. T. (2001). Explaining Leptokurtic Movement Distributions: Intrapopulation Variation in Boldness and Exploration. The American Naturalist, 158(2), 124-135.

Gilliam, J. F., Fraser, D. F., & Alkins-Koo, M. (1993). Structure of a Tropical Stream Fish Community: A Role for Biotic Interactions. Ecology, 74(6), 1856.

Godin, J. G., & Dugatkin, L. A. (1996). Female mating preference for bold males in the guppy, Poecilia reticulata. Proceedings of the National Academy of Sciences, 93(19), 10262-10267.

Gonzalez-Voyer, A., Fitzpatrick, J. L., & Kolm, N. (2008). Sexual Selection Determines Parental Care Patterns In Cichlid Fishes. Evolution, 62(8), 2015-2026.

Ingley, S. J., Rehm, J., & Johnson, J. B. (2014). Size doesn't matter, sex does: A test for boldness in sister species of Brachyrhaphis fishes. Ecol Evol Ecology and Evolution.

Ioannou, C. C., Payne, M., & Krause, J. (2008). Ecological consequences of the bold–shy continuum: The effect of predator boldness on prey risk. Oecologia, 157(1), 177-182.

Isler, K., & Schaik, C. V. (2006). Costs of encephalization: The energy trade-off hypothesis tested on birds. Journal of Human Evolution, 51(3), 228-243.

Kotrschal, A., Buechel, S. D., Zala, S. M., Corral-Lopez, A., Penn, D. J., & Kolm, N. (2015). Brain size affects female but not male survival under predation threat. Ecology Letters Ecol Lett, 18(7), 646-652.

Kotrschal, A., Rogell, B., Bundsen, A., Svensson, B., Zajitschek, S., Brännström, I., . . . Kolm, N. (2013). Artificial Selection on Relative Brain Size in the Guppy Reveals Costs and Benefits of Evolving a Larger Brain. Current Biology, 23(2), 168-171.

Relyea, R. A., & Auld, J. R. (2004). Having the guts to compete: How intestinal plasticity explains costs of inducible defences. Ecology Letters, 7(9), 869-875.

Reznick, D., & Ender, J. (1982). Erratum: The Impact of Predation on Life History Evolution in Trinidadian Guppies (Poecilia reticulata). Evolution, 36(3), 634.

Sol, D., Szekely, T., Liker, A., & Lefebvre, L. (2007). Big-brained birds survive better in nature. Proceedings of the Royal Society B: Biological Sciences, 274(1611), 763-769.

Sullam, K. E., Dalton, C. M., Russell, J. A., Kilham, S. S., El-Sabaawi, R., German, D. P., & Flecker, A. S. (2014). Changes in digestive traits and body nutritional composition accommodate a trophic niche shift in Trinidadian guppies. Oecologia, 177(1), 245-257.

Tsuboi, M., Husby, A., Kotrschal, A., Hayward, A., Buechel, S. D., Zidar, J., . . . Kolm, N. (2014). Comparative support for the expensive tissue hypothesis: Big brains are correlated with smaller gut and greater parental investment in Lake Tanganyika cichlids. Evolution, 69(1), 190-200.

Urban, M. C. (2007). Risky prey behavior evolves in risky habitats. Proceedings of the National Academy of Sciences, 104(36), 14377-14382.

Walsh, M. R., & Reznick, D. N. (2008). Interactions between the direct and indirect effects of predators determine life history evolution in a killifish. Proceedings of the National Academy of Sciences, 105(2), 594-599.

Walsh, M. R., & Reznick, D. N. (2009). Influence Of The Indirect Effects Of Guppies On Life-History Evolution In Rivulus Hartii. Evolution, 64(6), 1583-1593.

Walsh, M. R., & Reznick, D. N. (2009). Phenotypic Diversification Across An Environmental Gradient: A Role For Predators And Resource Availability On The Evolution Of Life Histories. Evolution, 63(12), 3201-3213.

Walsh, M. R., & Reznick, D. N. (2011). Experimentally Induced Life-History Evolution In A Killifish In Response To The Introduction Of Guppies. Evolution, 65(4), 1021-1036.

Walsh, M. R., Fraser, D. F., Bassar, R. D., & Reznick, D. N. (2010). The direct and indirect effects of guppies: Implications for life-history evolution in Rivulus hartii. Functional Ecology, 25(1), 227-237.

BIOGRAPHICAL INFORMATION

Whitnee was born and raised in Abilene, Texas. She has known since the 10th grade that she wanted to practice medicine. After graduating from Cooper High School in 2012, she began attending the University of Texas at Arlington as a biology major and later declared both a chemistry and Spanish minor. Over the past four years, Whitnee joined the Honors College, has been involved in the Student National Medical Association, and worked on campus as a group exercise instructor for the Maverick Activities Center and as a Spanish tutor for TRiO Student Support Services. She began working in Dr. Walsh's lab in the summer of 2015 and has been under his mentorship for the completion of her Honors thesis. In the fall, Whitnee will be attending the University of Texas Medical Branch at Galveston for medical school. She aspires to be a bilingual physician.