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Effects of Predation Environment and Food Availability on Somatic Growth in the Livebearing

Fish *Brachyrhaphis rhabdophora*

(Pisces: Poeciliidae)

Brittany Herrod Gale

A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Master of Science

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ABSTRACT

Effects of Predation Environment and Food Availability on Somatic Growth in the Livebearing Fish *Brachyrhaphis rhabdophora*
(Pisces: Poeciliidae)

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Master of Science

Variation in somatic growth rates has interested biologists for decades because of the relationship between growth and other fitness-determining traits (i.e. fecundity, survival, and body size), and the corresponding effect of somatic growth on production of organisms humans use for food. The interaction between genetic variation in growth rates and environmentally induced variation in growth rates shows the pattern of growth across multiple environments (i.e. the reaction norm) that clarifies the history and potential future of evolutionary change in growth rates among populations. Theoretical predictions suggest variation in predator-induced mortality rates can influence mean growth rates and the shape of the reaction norm for growth. The adaptive growth hypothesis predicts that mean growth rates would evolve in response to environmental pressures, such as mortality rates, at different body sizes. Few studies, however, have focused on variation in reaction norms for growth in response to resource availability between high-predation and low-predation environments. We used juvenile *Brachyrhaphis rhabdophora* from high-predation and low-predation environments to test for variation in mean growth rates and for variation in reaction norms for growth at two levels of food availability in a common-environment experiment, and we compared field somatic growth rates in juveniles from the same two environments (high-predation and low-predation).

In the common-environment experiment, mean growth rates did not differ between predation environments, but the interaction between predation environment and food level took the form of a crossing reaction norm for both growth in length and growth in mass. Fish from low-predation environments exhibited no significant variation in growth rate between high and low food amount treatments. In contrast, fish from high-predation environments exhibited wide variation in growth rates between low and high food treatments, with higher food availability resulting in higher growth rates. In the field, individuals in the high-predation environment grow at a faster rate than those in a low-predation environment at the smallest sizes (comparable to sizes in the common-environment experiment). These data provide no evidence for evolved differences in mean growth rates between predation environments. However, fish from high-predation environments exhibited greater plasticity in growth rates in response to resource availability suggesting that increased risk of predation could drive variation in food availability for prey and consequent selection for plasticity.

Keywords: crossing reaction norm, growth rate, food availability, predation, *Brachyrhaphis rhabdophora*, life history, Costa Rica

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TABLE OF CONTENTS

TITLE PAGE.....	i
ABSTRACT	ii
ACKNOWLEDGMENTS.....	iii
TABLE OF CONTENTS.....	iv
LIST OF TABLES.....	v
LIST OF FIGURES.....	vi
Introduction.....	1
Materials and Methods.....	4
Results.....	8
Discussion.....	9
Literature Cited.....	14
Table 1.....	18
Figure 1.....	19
Figure 2.....	20

LIST OF TABLES

Table 1. Results of mixed model analysis of covariance for growth in standard length and growth in wet mass of <i>Brachyrhaphis rhabdophora</i> in a common-environment experiment.....	18
-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------	----

LIST OF FIGURES

Figure 1.19

A. Least-squares means (± 1 standard error) of growth in standard length of juvenile *B.*

rhabdophora from high-predation (Javilla) and low-predation (Grande) environments at low and high levels of food availability in a common-environment experiment.

B. Least-squares means (± 1 standard error) of growth in wet mass of juvenile *B. rhabdophora*

from high-predation (Javilla) and low-predation (Grande) environments at low and high levels of food availability in a common-environment experiment.

Figure 2.20

Growth in standard length (mm/day) of juvenile *B. rhabdophora* from high-predation (Javilla) and low-predation (Grande) environments plotted against beginning standard length in the field mark-recapture experiment. Lines are smoothed splines (SAS PROC GLIMMIX) representing the nonlinear relationship between growth and beginning standard length. Splines for the two locations were significantly different ($\chi^2 = 10.12$, $df = 4$, $p < 0.05$).

Introduction

Variation in somatic growth rates has interested biologists for decades because of the relationship between growth and other fitness-determining traits (i.e. fecundity, survival, and body size) and the corresponding effect of somatic growth on production of organisms humans use for food (Conover and Munch, 2002, Olsen et al., 2004, Birkeland and Dayton, 2005, Arendt and Wilson, 1999). Observed variation in growth rates among populations is in part due to underlying additive genetic variation for growth among individuals or populations as evidenced by the success of artificial selection on growth rates in domesticated plants and animals (Price, 1984, Careau et al., 2010, Biro and Post, 2008, Yamasaki et al., 2007). However, in many organisms growth rates are also responsive to variation in the environment and as such show a strong plastic effect in the phenotype (Conover et al., 2009, Belk et al., 2005, Liao et al., 2010, Gotthard et al., 1994, Forero-Montana et al., 2010, Conover and Schultz, 1995). Realized growth rates result from the interaction between variation from additive genetic sources and variation in response to environmental variation.

Because of this interaction between genetic variation in growth rates and environmentally induced variation in growth rates, it is the pattern of growth across multiple environments (i.e. the reaction norm) that clarifies the history and potential future of evolutionary change in growth rates among populations. Selection can act not only on variation in mean differences in growth rates, but also on variation in the shape or orientation of the reaction norm for growth across contrasting environments. Thus, the shape of the reaction norm can be molded by natural selection to improve performance under variable environmental conditions experienced by the population (Ricklefs, 2008). For example, the reaction norm for growth across a range of temperatures in northern leatherside chub, *Lepidomeda copei*, peaks at lower temperatures

compared to the reaction norm for growth across temperatures in the southern leatherside chub, *Lepidomeda aliciae*. Northern leatherside chub occur at more northerly latitudes and experience lower mean temperatures and shorter growing seasons compared to southern leatherside chub. The difference in reaction norms for growth across temperatures results in higher relative growth rates for northern leatherside chub in cooler environments and higher relative growth rates in southern leatherside chub in warmer environments (Belk et al., 2005, Johnson et al., 2004).

In many systems, presence or absence of predators corresponds to contrasting environments that select for differences in a wide variety of fitness-related traits in prey species (Reznick et al., 2001, Reznick and Endler, 1982, Johnson and Basolo, 2003, Johnson and Belk, 2001, Johnson and Zuniga-Vega, 2009, Langerhans et al., 2004). Theoretical predictions suggest variation in predator-induced mortality rates can influence mean growth rates and the shape of the reaction norm for growth (Arendt, 1997). The adaptive growth hypothesis predicts that mean growth rates would evolve in response to variation in mortality rates at different body sizes (Arendt, 1997). If mortality rates decrease at larger body sizes, then accelerated growth rates should evolve in smaller size classes. Conversely, if mortality rates increase as body size increases, there should be no selection for rapid growth rates (Arendt, 1997, Arendt and Wilson, 1999). Thus, mean growth rates might be expected to differ between high-predation environments and low-predation environments depending on the pattern of size-selective predation. Predation environment may also affect the shape of the reaction norm for growth across levels of resource availability (Zandona et al., 2011, Grether et al., 2001). High variance in resource availability over short time scales can select for high levels of plasticity in growth (i.e. a resource-sensitive reaction norm; Nylin and Gotthard, 1998). Less variability in resource availability may result in a relatively flat (i.e. insensitive), and non-plastic reaction norm for

growth (Stearns and Kawecki, 1994, Nylin, 1992). If predators increase the variability in available resources either by altering prey behavior or habitat use (Fraser and Gilliam, 1987, Fraser et al., 2004), then selection could act to increase the sensitivity of the reaction norm to resource availability (i.e. a strong plastic effect in growth rates depending on resource availability; Billman et al., 2011, Bolnick and Preisser, 2005, Grether et al., 2001).

Prior studies have focused on variation in somatic growth rates in fishes in contrasting environments. Male *B. rhabdophora* from high and low-predation environments exhibit no difference in mean growth rates on an *ad libitum* diet (Johnson, 2001). Female Trinidadian guppies (*Poecilia reticulata*) exhibited higher growth rates in high-predation environments compared to low-predation environments, but no difference in reaction norms for growth across levels of food availability when tested in a common environment (Arendt and Reznick, 2005). Utah chub (*Gila atraria*) and bluegill sunfish (*Lepomis macrochirus*) grow faster and to a larger asymptotic body size in high-predation environments compared to populations found in low-predation environments in natural systems (field-based back-calculated growth rates derived from annuli on otoliths; Johnson and Belk, 1999, Belk and Hales, 1993). However, in a common environment, mean growth rates of bluegill sunfish did not differ between populations from high and low-predation environments (Belk, 1995). Although several studies have quantified differences in mean growth rates between high-predation and low-predation environments, few studies have focused on variation in reaction norms for growth in response to resource availability between high-predation and low-predation environments. It is clear that results from these studies are mixed in support of the predictions of growth differences outlined above.

Populations of the tropical, livebearing fish *Brachyrhaphis rhabdophora* provide an opportunity to determine if mean growth rates or reaction norms for growth in response to

resource availability vary between high-predation and low-predation environments. This species occurs in both high-predation and low-predation environments and mortality rates differ dramatically between these two types of environments (Johnson and Zuniga-Vega, 2009). In addition to the effects of mortality rate, food availability may vary seasonally in coordination with wet and dry seasons (Winemiller, 1993, Jennions et al., 2006). Variation in mortality rates and resource availability among populations provides conditions that may select for variation in mean growth rates or reaction norms for growth (i.e. plasticity). To test the generality of effects of predation environment on the evolution of growth rates, studies in comparable systems that test for both variation in the mean and in the reaction norm for growth are required. We used juvenile *Brachyrhaphis rhabdophora* from high-predation and low-predation environments to test for variation in mean growth rates and for variation in reaction norms for growth at two levels of food availability in a common-environment, and we compared field somatic growth rates in juveniles from the same two environments (high-predation and low-predation).

Materials and Methods

Effects of predation environment and food availability: common-environment experiment

To determine the effect of predation environment, food availability, and their interaction on growth rates, we conducted a common-environment experiment (Rader et al., 2005) using juvenile, second-generation, lab-raised (F2) *Brachyrhaphis rhabdophora*, from multiple families. The common-environment experiment followed a split-brood design, where whole units were families, and subunits were fish. In this common-environment experiment, F2 juveniles from both high-predation and low-predation environments (6 families from Rio Javilla and 5 families from Quebrada Grande respectively; for specific map locations of these rivers systems, view

Johnson and Belk, 2001) were randomly assigned and raised at two different levels of food availability (treatments were within families). Using this design we were able to quantify the effect of predation environment, food availability, and their interaction on growth rate.

To avoid mortality of newly born individuals from handling stress, we estimated beginning length and mass from measurements of newborn individuals from the same locations (Rio Javilla and Quebrada Grande) that were not used in the experiment (Grande average sizes at 0 days for standard length= $8.50 \text{ mm} \pm 0.47 \text{ SD}$, for wet mass= $0.012 \pm 0.002 \text{ SD}$, $n= 52$; Javilla average size at 0 days for standard length= $7.74 \text{ mm} \pm 0.30 \text{ SD}$, for wet mass= $0.008 \pm 0.001 \text{ SD}$, $n= 21$). Fish from the low-predation environment (Quebrada Grande) were significantly longer at birth (i.e. standard length) than fish from the high-predation environment (Rio Javilla) ($t= 6.85$, $df= 71$, $p < 0.001$). Fish from the low-predation environment were significantly heavier at birth (i.e. wet mass) than fish from the high-predation environment ($t= 871$, $df= 71$, $p < 0.001$). Thus, these average beginning length and mass values are good surrogates for individual measurements (standard length distributions overlap by 15.6% and the wet mass distributions overlap by 8.5%). Fish were placed in individual housing cups on day of birth and randomly assigned to either a high or low food treatment. The high food treatment was 15% of somatic mass per day (5% fed at three times per day) and the low food treatment was 3% of somatic mass fed once daily in accordance with methods in Reznick, 1983. To compensate for growth, food amounts were increased weekly based on the average estimated growth rate from a pilot study. Fish fed on the low food treatment consumed all food given. Fish fed on the high food treatment generally did not consume all food, so a food amount of 15% of somatic mass per day was comparable to an *ad libitum* feeding regime.

Fish were fed Wardley Small Fry Liquid Food for the first two weeks (14 days) and were fed finely ground TetraMin Flakes for the remainder of the time (26 days). The experiment ran for 40 days. *Brachyrhaphis rhabdophora* can mature in as little as 87 days (Johnson, 2001), so the 40 day experimental period avoided confounding of growth and reproduction. At the end of 40 days, wet masses and standard lengths of each fish were recorded. We assumed pre-maturation growth of both males and females would be the similar since it is impossible to differentiate between putative males or females before about 35 days (Johnson, 2001).

To create a common environment for the experiment, two large tubs were set up that held fifty housing cups each. Housing cups (0.95 liters) were randomly assigned to a tub and a location in the support device (maintaining all cups at approximately 0.5 m from the bottom of the tub). The housing cups were opaque to avoid visual cues among experimental individuals. Each tub was equipped with a submersible water heater and a water pump to help maintain uniformity in water temperature throughout the tubs. The temperature in the tubs was maintained at 29 degrees C \pm 0.3. This temperature was selected because it is in the middle of the range of temperatures in which *B. rhabdophora* are found in their natural environment (Bussing, 1998), and was the temperature at which they reproduced successfully and consistently in the lab (B. Gale, unpublished data).

To analyze the data from the common-environment experiment we first determined growth rates by subtracting the ending size measurements from the average beginning size measurements (depending on population of origin) for each individual fish. The natural log transformation of growth of standard length and wet somatic mass (hereafter standard length and wet mass) were used as response variables. We used a mixed model analysis (Proc MIXED, Littell et al., 1996) with food availability and location of origin (high-predation or low-predation

environments) as predictor variables. The interaction between location of origin and food level was also included in the model. Families (i.e. sibling groups) were treated as a random blocking effect. We examined the residuals and removed 4 fish with extremely large residuals from the analysis (2 from high-predation environments and 2 from low-predation environments).

Effects of predation environment: field study

To determine the effects of predation environment on growth rates of juvenile *B. rhabdophora* in the field, we used a serial mark-recapture design over a 4 week period during the late dry season (January-February). For a complete description of the mark-recapture procedure, refer to Appendix A of Johnson and Zuniga-Vega, (2009). All fish used had at least one recapture size measurement within the 4 week time frame. We calculated growth rates for the juvenile size classes from a high-predation (Rio Javilla) and a low-predation (Quebrada Grande) location. Average individual growth rate was calculated by taking the difference between the first measured standard length and the last standard length recorded from each individual fish divided by the number of days that had transpired between those initial capture and recapture dates.

To analyze the data from the serial mark-recapture field work we used a general linear model design. The response variable was growth in mm/day, predation environment was the predictor variable, and the covariate was beginning standard length. We modeled the effect of the covariate with a smoothing spline (SAS PROC GLIMMIX). We examined the residuals and found no outliers or deviations from assumptions of normality or equal variances, so data were not transformed. To test for a difference between locations in the effect of the covariate (beginning standard length), we compared a model with one spline (i.e. no effect of predation

environment on relationship between growth and beginning standard length) to a model with two splines (i.e. different relationship between growth and beginning standard length for each predation environment).

Results

Effects of predation environment and food availability; from the common-environment experiment

Growth in length did not differ between predation environments, but was affected by food amount; there was also a significant interaction between predation environment and food amount (Table 1). Similarly, growth in mass did not differ between predation environments, but was affected by food amount and by the interaction between predation environment and food amount (Table 1). The interaction between predation environment and food level took the form of a crossing reaction norm for both growth in length and mass. Fish from low-predation environments exhibited no significant variation in growth rate between high and low food amount treatments. In contrast, fish from high-predation environments exhibited significant variation in growth rates between low and high food treatments (Fig. 1).

Effects of predation environment; from the field

The model with two splines fit significantly better than the model with one spline ($\chi^2=10.12$, $df=4$, $p < 0.05$), indicating that the relationship between growth rate and beginning standard length differed between high and low-predation environments. Smaller juveniles grow faster than larger juveniles in both locations. At smaller sizes (comparable to sizes tested in the

common-environment experiment), individuals from the high-predation environment grow at a faster rate than those from a low-predation environment (Fig. 2).

Discussion

Mean growth rates of juvenile *B. rhabdophora* do not differ in the common-environment experiment, but the reaction norms of response to food availability (i.e. the plastic response) do differ between high-predation and low-predation environments. Growth rates change in response to variation in food availability in high-predation environments, but not in low-predation environments. This result begs the question why phenotypic plasticity would occur in one population but not in the other. Plasticity can evolve in response to variation in the environment that occurs over a temporal scale that is shorter than the expected lifetime (Thompson, 1991, DeWitt, 2004, Orizaola et al., 2012, Relyea, 2002). We know that food availability varies seasonally with wet and dry seasons (Winemiller, 1993, Jennions et al., 2006, Grether et al., 2001), and in the laboratory, *B. rhabdophora* can live 2-3 years (fish in the field, however, are less likely to live that long; Johnson and Zuniga-Vega, 2009), so the evolution of plastic responses to food availability is not unexpected.

Why would plasticity in response to food availability evolve in high-predation environments and not in low-predation environments? One possibility is that the direct and indirect effects of predation may enhance variability in food resources between the two habitat types (Arendt, 1997, Luttbeg et al., 2003, Bolnick and Preisser, 2005). Prey often respond behaviorally to the presence of predators and balance feeding activities with the risk of predation (Lima and Dill, 1990, Tirok and Gaedke, 2010, Stamps, 2007). Variation in risk of predation

could drive variation in food availability for prey and consequent selection for plasticity (Sih, 1992, Relyea, 2002, Fraser and Gilliam, 1987, Dernekbası et al., 2010).

We found no evidence for genetically based differences in mean growth rate between fish from high-predation and low-predation environments, a pattern previously documented for male *B. rhabdophora* (Johnson, 2001). However, we did observe differences in mean growth rate between fish from high-predation and low-predation environments in the field at juvenile stages (Fig. 2). The only way to reconcile these two outcomes given the results of the common-environment experiment is to ascribe the difference in growth rate observed in the field to environmental effects or to a GXE (genetic by environment) interaction. Two possibilities exist for how this environmental effect could be caused. First, if resources are more available in high-predation environments compared to low-predation environments we would expect to see higher growth rates in high-predation environments consistent with our observation (Arendt and Reznick, 2005). High-predation environments could have higher resources because of lower densities of conspecifics or because of general characteristics of high-predation environments such as lower canopy cover and higher resultant primary production (Grether et al., 2001, Reznick et al., 2001, Bolnick and Preisser, 2005, Zandona et al., 2011, Johnson, 2002). Second, resources could be somewhat equally available between high-predation and low-predation environments, but they could be abundant relative to the food levels provided in the common-environment experiment. Under conditions of equal but high food availability, growth rates in high-predation environments would be higher than those in low-predation environments consistent with the pattern found in the high food level treatment of the common environment experiment (Fig. 1). We do not know how the levels of food availability compared between the experiment and the field, but resulting growth rates (in mm/day) were about 3-4 times higher in

the field than the lab for comparable sized individuals. This suggests that the difference observed in the field could be due to overall high levels of food availability and a consequent increased growth rate in fish from high-predation environments.

Growth rates in the wild decline as size increases, more so in the high-predation environment than in the low-predation environment. This is consistent with the adaptive growth hypothesis that predicts that if mortality rates increase at larger sizes then selection should act to decrease growth rate and prolong the time spent in the smaller size class. In high-predation environments mortality rates increase with size especially as individuals approach the largest size class (Johnson and Zuniga-Vega, 2009). From the perspective of the adaptive growth hypothesis, fish in high-predation environments should grow rapidly early to minimize the time to reproductive maturity, and then grow slowly thereafter to decrease the probability or increase the time to transitioning into the largest size class with the highest mortality rate (Conover and Present, 1990, Arendt, 1997, Arendt and Wilson, 1999). Fish in the low-predation environment face no such selective effects from the mortality schedule. In the low-predation environment mortality rates decrease with size especially in the transition to the largest size class (Johnson and Zuniga-Vega, 2009). Hence, in low-predation environments selection may be stronger on body size directly (for gains in fecundity, etc.) rather than on growth rate and how quickly body size may be attained (Creighton et al., 2009, Johnson and Zuniga-Vega, 2009). In high-predation environments elasticities related to growth in the juvenile life stages are important, whereas they are not important in the low-predation environments. Thus, selection for increased growth rates may occur in high-predation environments and not in low-predation environments. Because of the potential differences in the variability of resource availability, the ability to use resources

efficiently may be under selection in high-predation environments and not in low-predation environments (Johnson and Zuniga-Vega, 2009).

Why would our results differ from the pattern of reaction norms found in the Trinidadian guppy? Arendt and Reznick (2005) found differences in mean growth rate in guppies from high and low predation environments, but no difference in the shape of the reaction norm between predation environments. In contrast, we found no difference in mean growth rate in *B. rhabdophora* between high and low predation environments, but a significant crossing reaction norm for growth at different resource levels between predation environments. The first possibility is that the pattern of the evolution of growth rates is unique between the two species and is not consistent between predator environments. Such a result would be surprising given the uniformity and consistency of evolved differences in life history traits exhibited by Trinidadian guppies and *B. rhabdophora* between predation environments (Johnson and Belk, 2001). A more likely explanation might be small differences in methodology between the two studies. We examined growth of both sexes during the first 40 days after birth. Arendt and Reznick (2005) examined growth of females from about 4 weeks of age to after the first reproductive bout. Growth patterns of guppies in this study are averaged between periods of the life cycle when guppies are not reproducing and periods when much energy is being allocated to reproduction. In contrast, our study examines only pre-reproductive growth periods over the earliest ages after birth. Patterns of growth and reaction norms for growth may vary throughout ontogeny. The significant effect of beginning size on growth rate in the field experiment suggests that evolved differences in growth pattern and rate observed in the common-environment experiment may be specific to particular life stages or periods of growth. Additional studies using consistent

methods and life stages should be conducted to clearly differentiate effects of predation environment on the evolution of growth.

In summary, we found no differences in mean growth between high-predation and low predation populations reared under common environmental conditions. However, there was an important interaction between predation environment and food availability—fish from high-predation environments were responsive to variation in food availability while fish from low-predation environments were not. This change in phenotypic plasticity shown by the crossing reaction norm between population types (predation environment) suggests an evolved difference in growth pattern between predation environments in *B. rhabdophora*.

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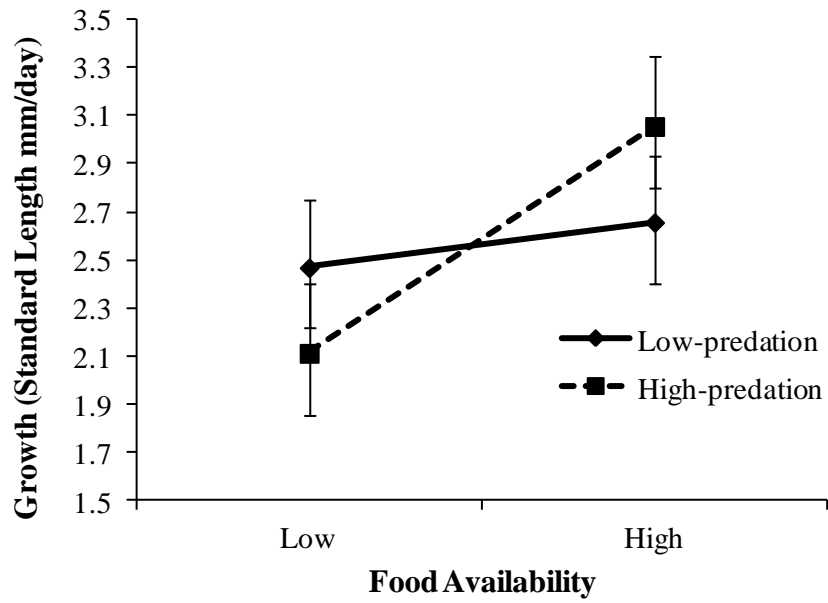
Table 1. Mixed model analysis of covariance results for growth in standard length and wet mass of *Brachyrhaphis rhabdophora* in a common-environment experiment.

Response Variable	Source of Variation	Degrees of freedom (num/den)	F-value	P-value
Standard Length	predation	1/10.4	0	0.9554
	food amount	1/118	25.99	<0.0001
	predation*food amount	1/118	11.58	0.0009
Wet Mass	predation	1/10.7	0.27	0.6151
	food amount	1/120	17.01	<0.0001
	predation*food amount	1/120	5.23	0.024

*Fractional degrees of freedom are due to the Kenward-Roger adjustment.

Figure 1.

A.



B.

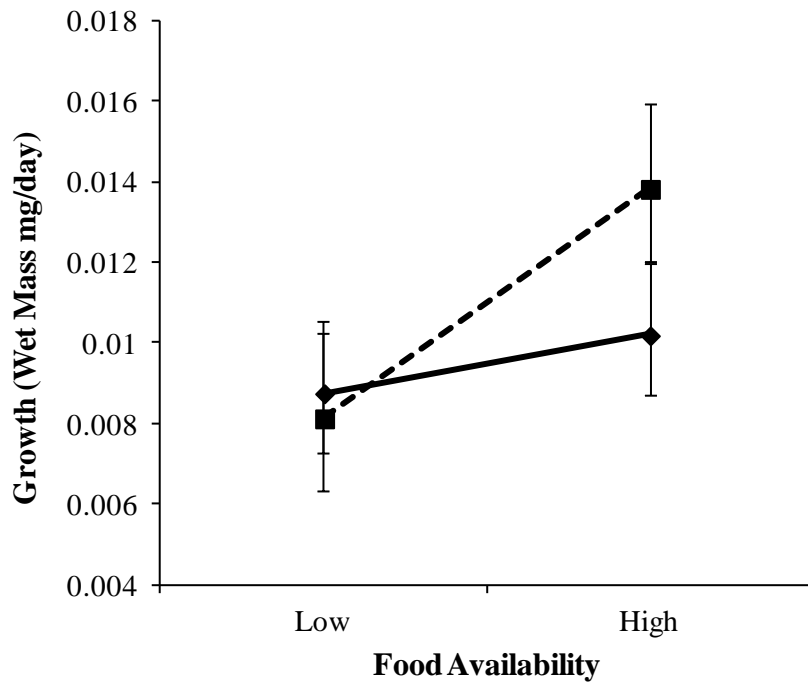


Figure 2.

