Morphological and Behavioral Effects of Multiple Predators and Prey Cues on Wood Frog Tadpoles (*Rana sylvatica*)

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Submitted in fulfillment of the senior thesis requirements of the Department of Biology at Allegheny College and approved by the thesis committee.

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Spring 2012

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Abstract:

Phenotypic plasticity is the ability of a single genome to produce alternative forms of morphology, physiology and behavior in an organism. Previous studies indicate that different predators elicit different types of morphological plasticity in tadpoles. The purpose of this study was to determine how tadpole morphology changes in the presence of two different predators, specifically the green darner dragonfly nymph (*Anax junius*) and bluegill (*Lepomis macrochirus*). Also tested was whether or not the cue of an attacked wood frog tadpole (*Rana sylvatica*) would overcome the predator cues and cause the tadpoles to assume a different morphology and behavior. Based on the results of previous research, I hypothesized that the attacked wood frog tadpole cues would cause greater morphological and behavioral responses than predator only cues. Thus, I also hypothesized that when tadpoles are placed in the presence of multiple predators; the morphological and behavioral response that the tadpoles will exhibit will correspond to the predator that is the greatest natural threat. I found that wood frog tadpoles in cattle tanks did not exhibit any significant shifts in body metrics with both predators present, versus no predators and single predators. There was a date effect indicating that the tadpoles grew during the experiment. One explanation for the absence of responses is that the experiment was initiated too late in the tadpole development; i.e., phenotypic plasticity in tail lengths, tail heights, tail widths, and body lengths may be difficult to detect unless predator cues are initiated before the tadpoles emerge from eggs.

Introduction:

Phenotypic plasticity is the ability of one genome to elicit multiple phenotypes in the forms of morphology, physiology, and behavior in response to environmental conditions (West-Eberhard, 1989). All plasticity is physiological, however it can manifest itself in changes in biochemistry, morphology, behavior and life history. Phenotypic plasticity can be passive, anticipatory, instantaneous, delayed, permanent, reversible, adaptive and non-adaptive (Whitman and Agrawal, 2010). Resulting changes from plasticity can be harmful or can even become a highly integrated adaptive change in the organism to help them escape from predators naturally present in their environment. The timing, speed and specificity are all crucial parts to the adaptive nature of phenotypic plasticity. There are numerous physiological mechanisms in play to produce the phenotypic plasticity often times observed; some of the physiological mechanisms include transcription, translation and producing systemic or local responses (Whitman and Agrawal, 2010).

Life history, morphological, behavioral and plasticity

One way for organisms to live across a gradient of environments is speciation. Speciation involves having the one organism become two completely different organisms in the different environments. Speciation occurs by gradual changes in genetic composition of the two organisms from generation to generation, this happens by having the two organisms in the two different environmental locations be reproductively separate from one another (Rosenzweig, 1995). Another way for organisms to live across a gradient of environments is phenotypic plasticity, the ability for the organism to assume variable morphologies, behaviors and physiological states. When predators are absent, the organism simply goes about living in the most efficient way. However, when predators are present the organism must develop defense

mechanisms to avoid predators. When predators are present there are many ways that organisms can change their morphology, behavior and physiology such that it is still efficient for the organism to grow from larval form to adult form and still spend energy on avoiding the predators most efficiently (Rosenzweig, 1995).

Morphological plasticity is a very common form of phenotypic plasticity and it can be expressed in many different ways for different organisms. An example of morphological plasticity is that when grasshoppers are exposed to low quality high fiber food sources, the grasshoppers have the ability to respond by developing larger mandible muscles (Yang and Joern, 1994). The ability of the grasshoppers to respond to changes in food source allows for the grasshoppers to continue surviving in changing environmental conditions. Morphological plasticity is also common in response to predators being present. For example, snails, when exposed as eggs to chemical cues of crayfish predators attacking snails, the snails developed twice as large shells as those not exposed to predator cues (Crowl and Covich, 1990). By growing larger earlier, the snails could escape predation by becoming too large to be handled by the crayfish.

Behavior of organisms can also be altered by plasticity. A good example of behavioral plasticity is a study that was done by Doving and Lestein (2009), who studied minnows in a tank with natural predators. When a minnow had been chased or even bitten by a predator the minnow excreted a substance known as schreck, which serves as an alarm substance for the other minnows. The reaction of the other minnows in the tank from the schreck was that they began sudden fright, rapid swimming into hiding places, and emergence and then rapid swimming to another hiding place to avoid the feeding fish (Doving and Lestein, 2009). Normally minnows

would not swim around frantically but since the schreck substance was emitted, the minnows had the ability to recognize the substance and react to it, causing them to elicit a different behavior.

Tadpole Plasticity

Tadpoles are a well-known study organism for morphological plasticity. Tadpoles live in a range of environments from temporary ponds to permanent ponds and from living in such a range of environments they have many different predators which elicit many different morphologies and behaviors (Bowerman et al. 2010). One example of behavioral plasticity in tadpoles is that when they sense the presence of predators and become less active and forage less (Lima and Dill, 2010). Tadpoles, specifically wood frog tadpoles (*Rana sylvatica*), have many predators, including diving beetles, whirligig beetles, dragonfly nymphs, giant water bugs, fish and salamanders (Lannoo, 2005). In addition to behavioral responses, tadpoles have the ability to elicit morphological differences in their tail and bodies in response to each predator (Bernard, 2006). For the details of this morphological plasticity with the species of tadpole and the type of predator refer to table 1. Each of these phenotypic responses are finely tuned to the specific predator present because the responses can be very costly (Hettyey et al. 2010).

Table 1: Review of previous studied effects of different predators on different frog and toad tadpoles (modified from Bernard 2006).

Prey	**Predator**	**Size at meta-morphosis**	**Time to meta-morphosis**	**Growth rate**	**Morph change**	**Behavior**	**Study**
Western Toad	Back-swimmer	None	Earlier	Not tested	Not tested	Not tested	Chives et al. 1999
Common toad	Dragonfly	None	Earlier	No effect half way into larval period	Not tested	Reduced activity	Laurila et al. 1998
Common toad	Beetle	Smaller	Earlier	None	Narrower tail fin	Not tested	Lardner 2000
Common tree frog	Beetle	None	None	None	Significantly deeper tail	Not tested	Lardner 2000

Red legged frog	Dragonfly	Larger	Later	Not tested	Not tested	Reduced activity	Barnett & Richardson 2002
Pool Frog	Dragonfly	Larger	Later	Not tested	Not tested	Reduced activity	Altwegg 2002
Water frog	Dragonfly	None	Later	Not tested	Deeper tail fin	Not tested	Van Buskirk & dragonfly Saxer 2001
Wood Frog	Dragonflies	None	Later	Not tested	Induced morphology	Not tested	Relyea 2001
Common frog	Salmon	Larger	Later	None	Not tested	Reduced activity	Nicieza 2000

Variation of responses to predators among the different species of tadpoles differs, however they all do elicit predator-induced changes in morphology and behavior. Wood frog tadpoles become less active when in the presence of dragonfly nymphs than do green frog tadpoles. Wood frogs develop deeper tails when they are in the presence of dragonfly nymphs compared to green frog tadpoles and bullfrog tadpoles (Relyea, 2001). Green frogs tend to develop longer bodies compared to wood frogs and bullfrogs, which tend to develop shorter bodies by when in the presence of dragonfly nymphs.

There is also a variation of responses to different predators within the same species. Wood frog tadpoles (*Rana sylvatica*) in the presence of fish only reduce their activity by 5% more than the reduced activity when they were in the presence of dragonfly nymphs only (Relyea, 2001). Muscle depth stayed relatively the same when wood frog tadpoles were in the presence of dragonfly nymphs compared to when the wood from tadpoles were not in the presence of any predators. However when wood frog tadpoles were in the presence of fish, the muscle depth increased by about 20% (Relyea, 2001). This increase of muscle depth helps the wood frog tadpole to have better ability to swim away from the fish faster and thus avoid becoming the prey.

Goals and Hypotheses

In my study I focused on how two different predators would affect the morphological and behavioral plasticity's of wood frog tadpoles (*Rana sylvatica*). I decided to choose wood frog tadpoles because there are a lot of studies on how they respond to a variety of predators, but there are no studies that focus on how wood frog tadpole respond to different predators at the same time. It is also not clear whether wood frog tadpoles respond in different ways to predators fed hetero-specific prey versus those fed wood frog tadpoles. The two predators that were chosen for this study were the green darner dragonfly nymph (*Anax junius*) and bluegill (*Lepomis macrochrius*). These two predators cause the morphology of tadpole's tails in different directions; specifically the *Anax junius* causes the *Rana sylvatica* to develop shorter tails and wider bodies (Relyea, 2001). Bluegills (*Lepomis macrochirus*) cause tadpoles to develop longer bodies and tails. For the different food sources, the conspecific food source was *Rana sylvatica* and the hetero-specific food source was damselflies.

The purpose of this study was to compare the effects of multiple predators on *Rana sylvatica*, and to study the effects of conspecific and hetero-specific food sources for the different predators. I hypothesized that (1) *Rana sylvatica* will develop the morphology to avoid predation of *Anax junius*, which the wood frog tadpoles have naturally coevolved with in temporary ponds, (2) conspecific food source will overcome hetero-specific food source and cause the morphological and behavioral changes to become even more exaggerated, and (3) when predators consume conspecific food source the behavioral changes of the *Rana sylvatica* will overcome the morphological changes caused by the predators being present.

Methods:

Site:

The study was conducted at Bousson Experimental Research Forest and at Allegheny College Meadville, Pennsylvania. The eggs were collected from temporary ponds at Bousson and transferred back to Allegheny College for a few weeks. Once the cattle tanks were set up, then the tadpoles were transferred back out to Bousson for the remainder of the experiment.

Experimental Set up:

To create mesocosms, leaves that were found on the ground around the edges of the ponds at Bousson were gathered and randomly dispersed into the cattle tanks. Approximately 200-300 grams were put on the bottom of each cattle tank (Relyea, 2003). Cattle tanks, with diameter of 1.5m, were filled with water 1m deep, with some pond water mixed in to establish the mesocosm.

Wood frog egg clutches were collected from four different ponds located around Bousson. The eggs were transferred back to Allegheny College cold room for approximately 3 weeks at a temperature of 10 degrees Celsius to slow down the hatching of the eggs. Tadpoles were randomly assigned to each of the treatments, for a total of 40 tadpoles per treatment. There were a total of seven different treatments (Table 2). The control, not shown in the table, was simply wood frog tadpoles with no predators present. The predators were held in guppy breeder cages, (17.5 cm x 7.5 cm x 10 cm) for every treatment with green darner dragonfly nymphs (*Anax junius*) there were two cages with one green darner dragonfly nymph per cage. For every treatment with bluegill (*Lepomis macrochirus)* there was one cage with one bluegill (Relyea, 2001). For treatments with both predators present, there were a total of three cages in the cattle tank, one bluegill and two green darner dragonfly nymphs.

Table 2: Treatments of predators and what they will be fed. Not shown is the control.

Treatment 1: Bluegill Food Source= damsel flies	Treatment 2: Green Darner Dragonfly nymph Food Source= damsel flies	Treatment 3: Bluegill + Dragonfly Food Source= damsel flies
Treatment 4: Bluegill Food Source= wood frog tadpole	Treatment 5: Green Darner Dragonfly nymph Food Source: wood frog tadpole	Treatment 6: Bluegill + Dragonfly Food Source= wood frog tadpole

Observations and Calculations:

Observations were made once a week from June 3, 2011 until July 8, 2011 after which there were no more tadpoles in the cattle tanks to make observations upon. On each date, I measured 5 size metrics on each of 5 randomly selected tadpoles in each of the tanks. The metrics were mass (g), tail length, body length, tail height, and tail width (all in mm). Each of the size metrics were taken 3 times each the mean was recorded. Once I had the basic measurements I was able to calculate the following ratios; tail/body length, total length, mass/total length (condition), tail height/length, tail length/width, and tail height/width.

Statistics:

Results were analyzed by 2x2 ANOVA and 3x2 ANOVA, subsequent one way ANOVA and post-hoc multiple comparison tests using Statview 5.0.

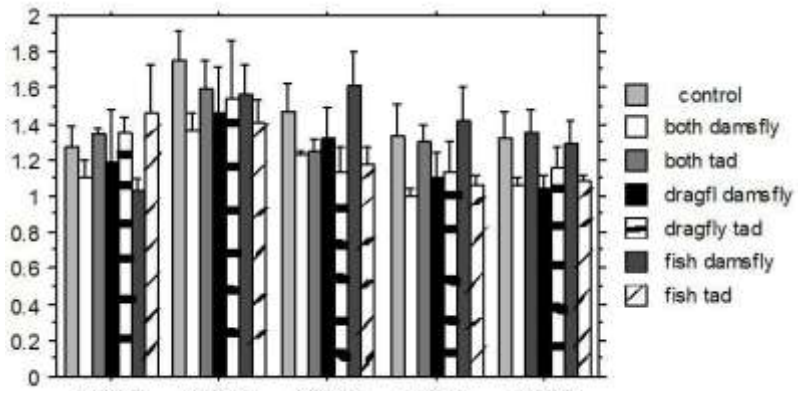
Results:

Overall Results:

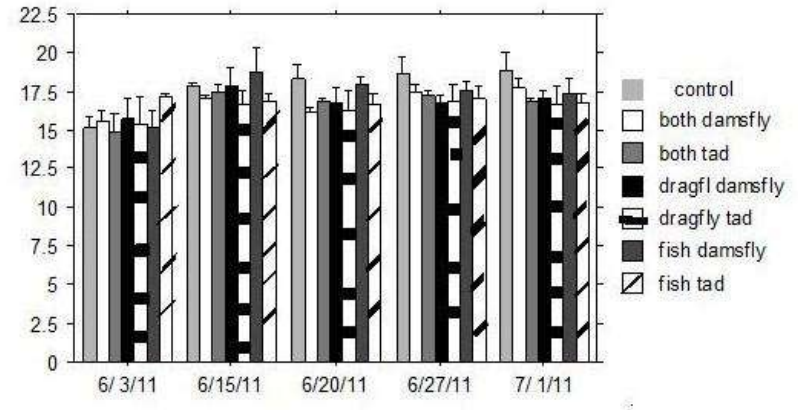
For all two-way ANOVAs (date x treatment) there was an overall date effect for all measurements ($p<0.05$). For mass (g), tail length (mm), tail height (mm), and tail width (mm)

there was an increase, meaning they grew. In the case of mass, it peaked on, June 15 and then it decreased slightly (Figure 1). The general tail trends are what you would expect; as the tadpoles got closer to emergence, the tails began to get smaller and were being reabsorbed into the body. I also ran a 1-way ANOVA after the initial analysis and it indicated that on any one date there was no significant date effect (Figure 2).

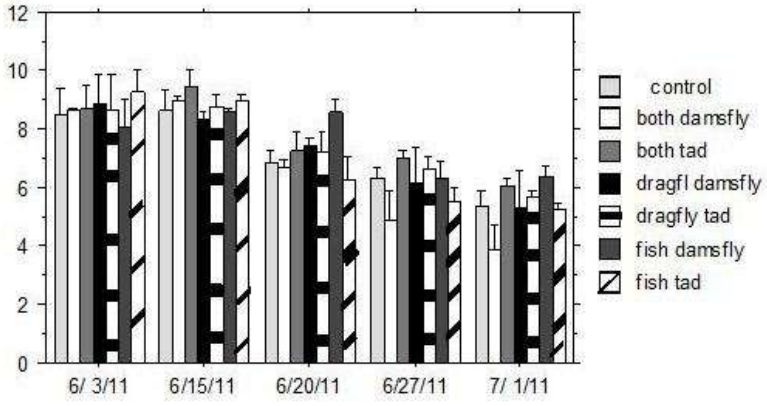
A. Mass (g)



B. Body Length (mm)



C. Tail Height (mm)



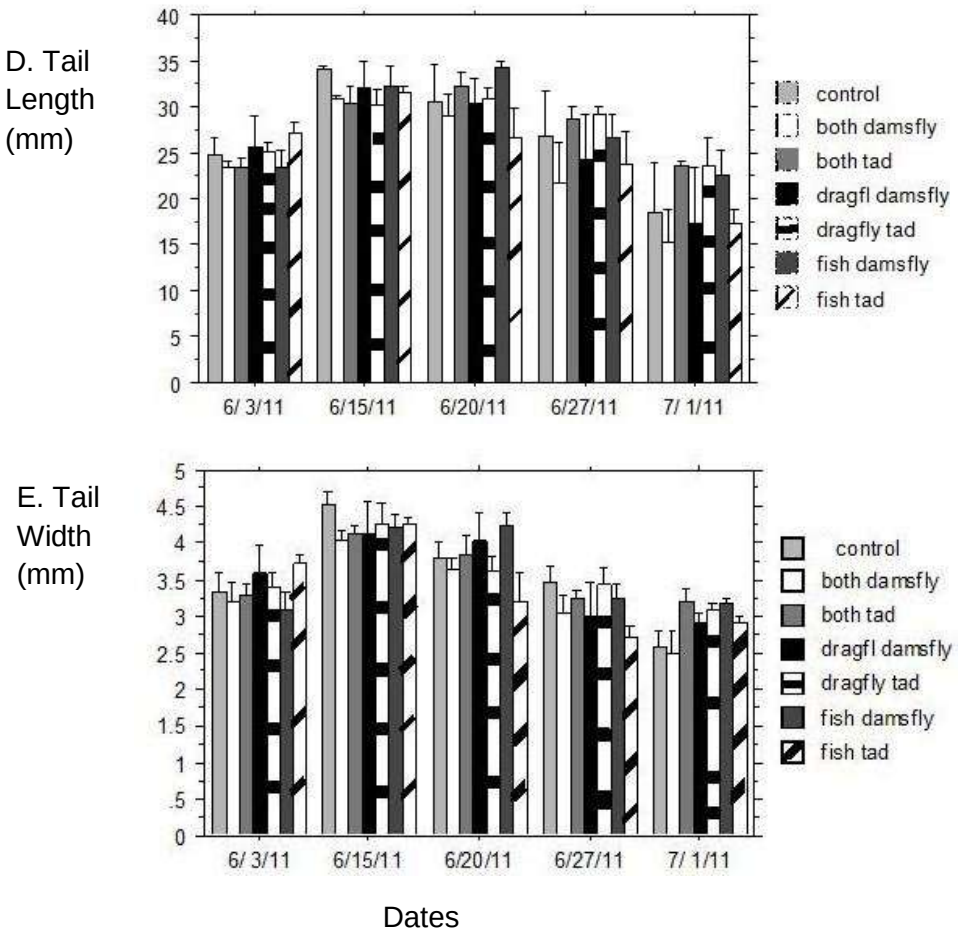


Figure 1: Mean data for all dates (+/- 1 S.E.) A. Mass ($p<0.003$) B. Body Length ($p<0.003$) C. Tail Height ($p<0.001$) D. Tail Length ($p<0.001$) E. Tail Width ($p<0.001$)

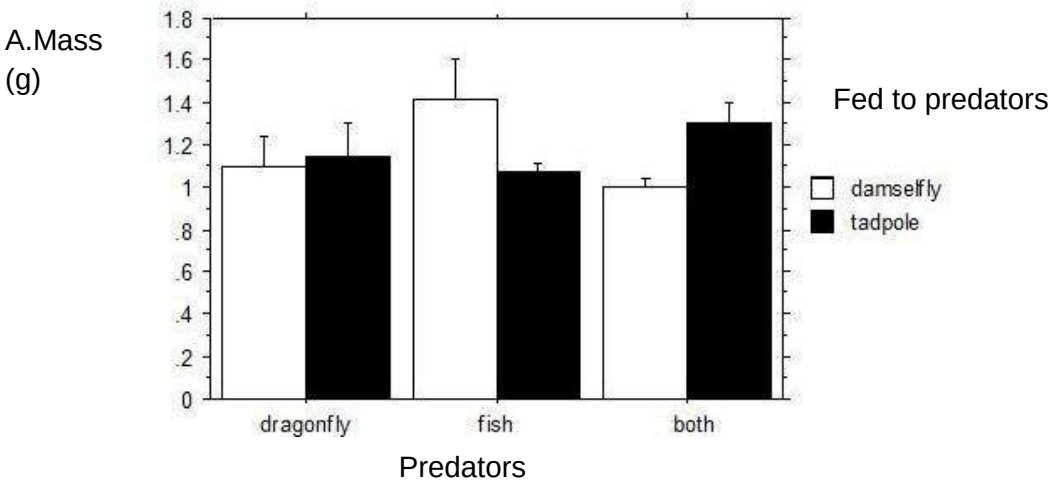
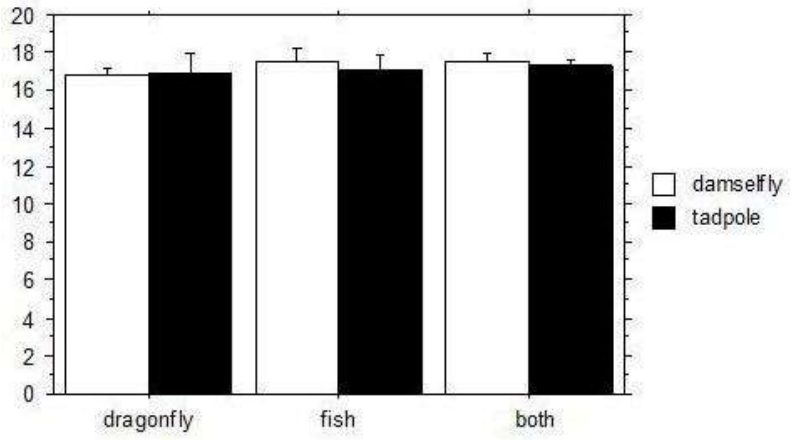
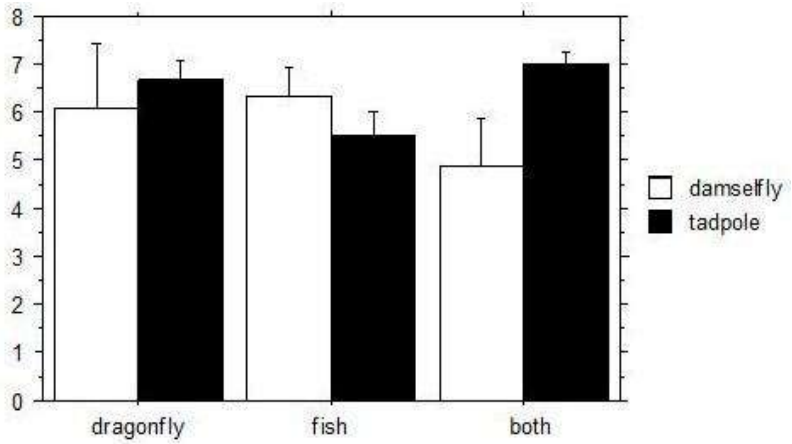


Figure 2: Mean data for 6-27 (+/- 1 S.E.) A. Mass ($p= 0.9829$) B. Body Length ($p= 0.8801$) C. Tail Height ($p= 0.3455$) D. Tail Length ($p= 0.2875$) E. Tail Width ($p= 0.8546$).

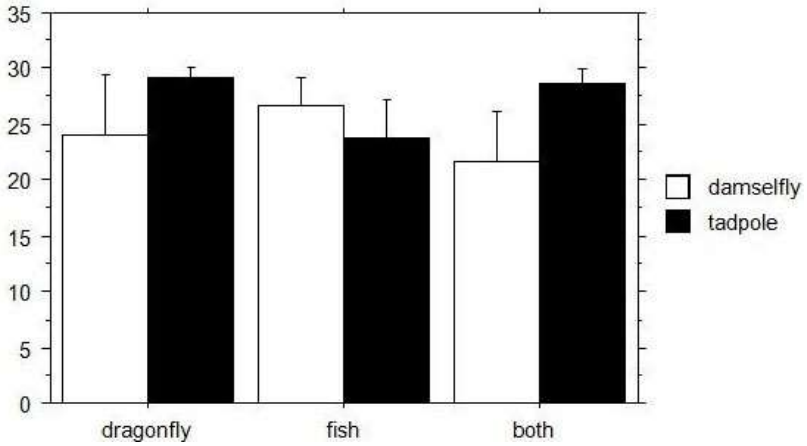
B. Body Length (mm)



C. Tail Height (mm)



D. Tail Length (mm)



Predators Present

Fed to predators

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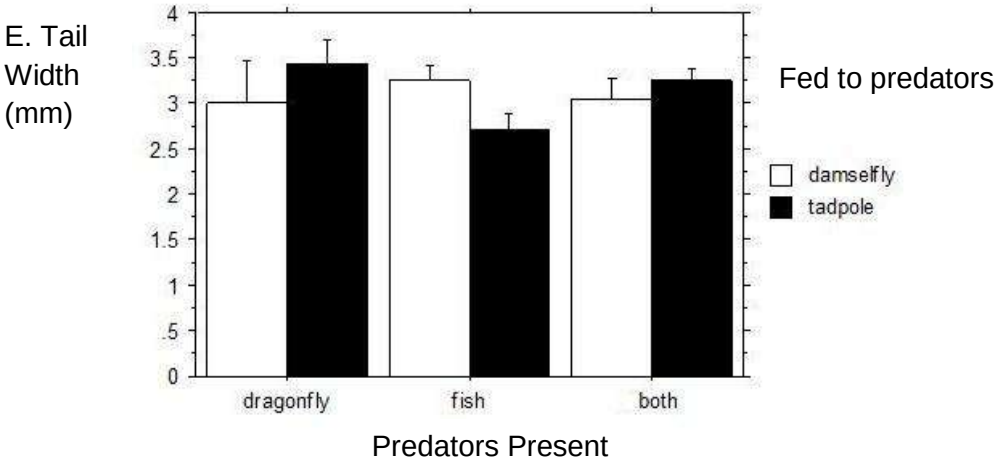


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Ratio Results:

I calculated a variety of ratios to explore shifts in allometry among body parts including; total length, tail/body length, condition (mass/total length), tail height/length, tail length/width, and tail height/width. A protected 1-way ANOVA was ran, it indicated that on any given day there was no significant ratio data (Figure 3).

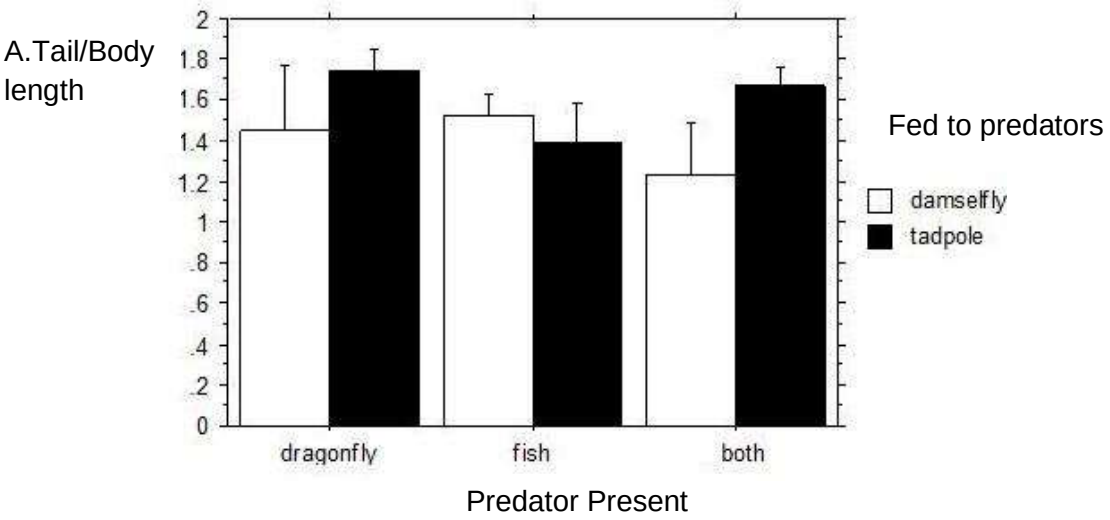
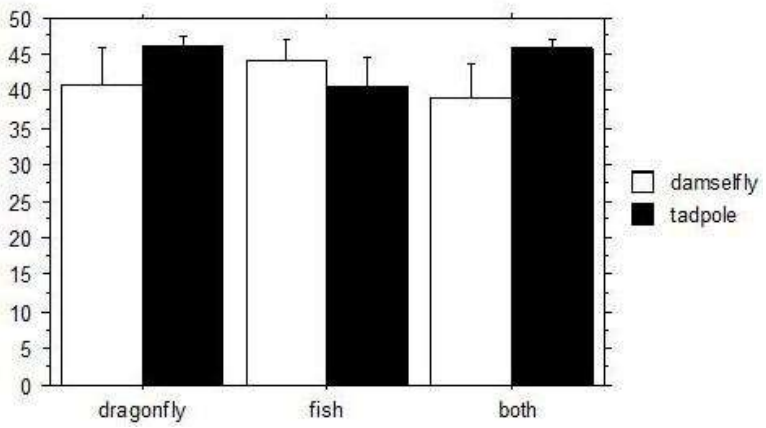
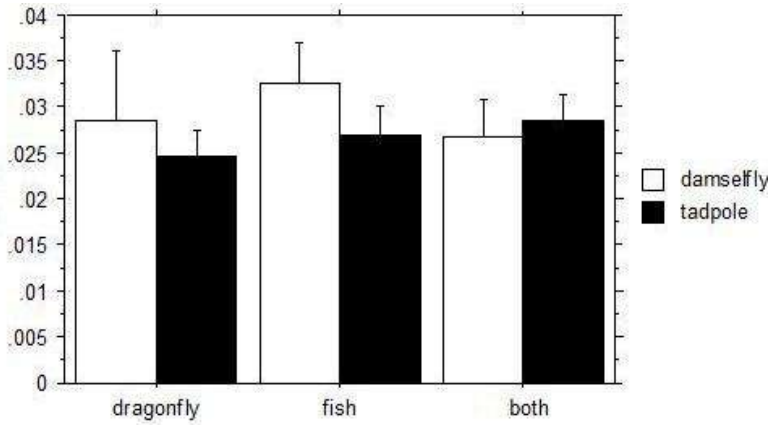


Figure 3: Mean ratio data (+/- 1 S.E.) A. Tail/Body length (p= 0.24) B. Total length (p= 0.33) C. Condition (p=0.49) D. Tail Height/Length (p=0.83) E. Tail Length/Width (p=0.18) F. Tail Height/Width (p=0.16).

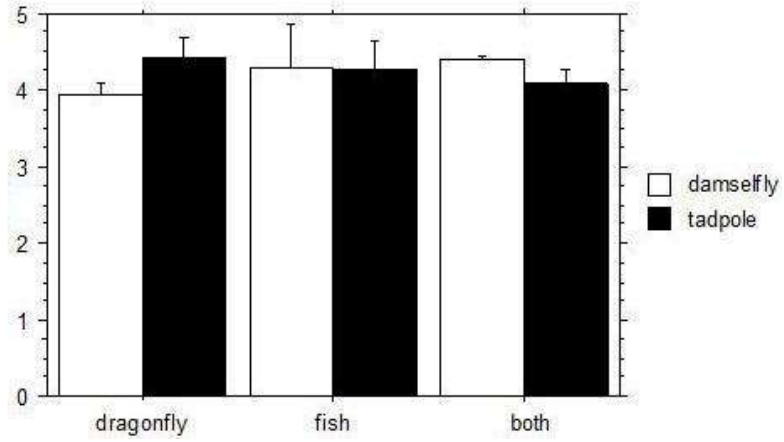
B. Total Length (mm)



C. Condition (g/mm)



D. Tail Height/ Length



Predators Present

Fed to predators

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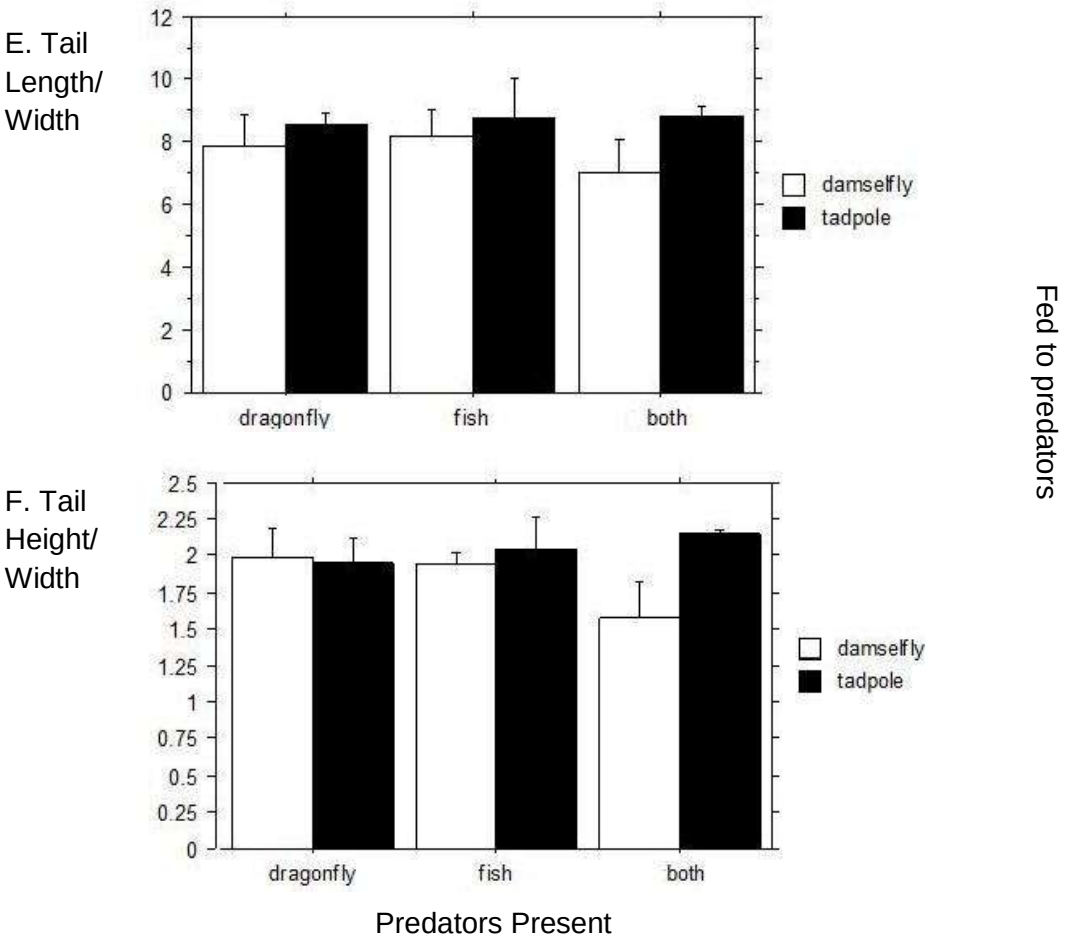


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Discussion:

The purpose of this experiment was to test the effects of cues from multiple predators and prey on wood frog tadpoles (*Rana sylvatica*). I expected to observe that (1) *Rana sylvatica* will develop the morphology to avoid predation of *Anax junius*, with which the wood frog tadpoles have naturally coevolved, (2) conspecific food source would overcome hetero-specific food source and cause the morphological and behavioral changes to become even more exaggerated;

and (3) when predators consume conspecific food source the behavioral changes of the *Rana sylvatica* would overcome the morphological changes caused by the predators being present.

This study was novel in the fact that it looked at multiple predators on tadpoles, in this case the green darner dragonfly nymph (*Anax junius*) and bluegill (*Lepomis macrochirus*) at the same time, as it often happens in nature. Also, this study was unique in the fact that it looked at how the conspecific and hetero-specific food source of the predators present affects the morphology and behavioral changes observed in the tadpoles. Morphological and behavioral effects of one predator on many different species of frog and toad tadpoles has been extensively studied (Relyea, 2003). There also have been several other studies on the predation of tadpoles and the anti-predatory phenotypic plasticity response. A review article was done by Bernard (2006), in the review article Bernard put together a large table, which I modified to include only the frogs and toads (table 1), that shows a summary of all the studies that have looked into morphological and behavioral effects on tadpoles when in the presence of predators.

The main significant results found were that there was an overall date effect when treatments were compared over the duration of the study. This shows that in fact the tadpoles did change in morphology overtime. However, when only one date is looked at, the results showed that there were no significant results. This suggests that measurements on a given date were not different enough to say that the differences occurred because of the treatments and not by chance.

One measurement that showed a significant difference between treatments over all dates was mass ($p = 0.0470$). When looking at figure 1.a it shows that between June 20th and July 1st, the treatments control and fish fed damselflies always seemed to be the highest mass. This could

be because bluegill (*Lepomis macrochirus*), the fish used, does not naturally co-evolve with the wood frog tadpoles (*Rana sylvatica*). The control did not contain any predators so therefore the tadpoles did not assume any predatory risk and were able to go about foraging the most efficient way. The treatments that seemed to consistently have the lowest mass were when the green darner dragonfly nymph (*Anax junius*), which was present regardless of whether or not the food source was conspecific or hetero-specific. With this observation it seems to contradict my second hypothesis that when predators consume conspecific instead of hetero-specific food sources that the morphological and behavioral changes would be exaggerated.

There also seemed to be a general trend in the basic measurement graphs. When both predators were present it resembled more so the trends of when there was just a green darner dragonfly nymph present. When the green darner dragonfly nymph was present, it did in fact cause differing results from when bluegill were present, however not significantly different (Figure 2 b, c, d, e). There is a trend in which body length, tail length, tail height, and tail width are all greater when the green darner dragonfly nymph and both predators were fed conspecific food source over hetero-specific food source. If I had found that the results were significant it would have supported my first hypothesis that green darner dragonfly nymph predatory cues would overcome bluegill predator cues, however the results were not significant ($p >> 0.05$) and thus I must falsify my first hypothesis.

One explanation for why there was an absence of developmental shifts in body-part morphology is that the tadpoles need to be exposed to predator cues earlier in development (as in Crowl and Covich 1990). The idea that the plasticity of body-parts is affected by the timing of exposure to predatory cues is supported by an article by Whitman and Agrawal (2010). One major factor that they said effects the phenotypic plasticity is timing. In my experiment the wood

frog tadpoles (*Rana sylvatica*) were exposed to the predator cues from June 1st through July 8th, when there were no more tadpoles to study because they all had morphed into frogs. I believe that if the tadpoles were exposed to the predatory cues before the tadpoles emerged from the eggs that the results may have been significant.

Some potential future studies would include having the wood frog tadpoles exposed to predatory cues from the time that the egg clutches are collected. By exposing the wood frog tadpoles to the predatory cues from the time they are collected as eggs until they morph into frogs it gives a longer period of time for which they are exposed to the predator cues and thus gives a better chance at detecting small changes in the tail and body lengths. Another potential future study would be to put more predators in the cattle tanks with the tadpoles. I put one blue gill, two green darner dragon fly nymphs in the cattle tanks with the tadpoles which came from an experiment done by Relyea (2001). I am not sure that the abundance of the predators was sufficient for the size of the cattle tanks and the abundance of tadpoles. For a future study I would recommend doubling the amount of predators present, hence having two bluegills per cattle tank and four green darner dragonfly nymphs and decreasing the amount of tadpoles per cattle tank from 40 to 20. By having more abundant predator cues and fewer tadpoles to be affected by the cues, I believe that it could be easier to detect small changes in the tadpole's tail and body measurements.

I have come to three major conclusions based on the results of my experiment. My first conclusion is that when there are multiple predators present the morphological plasticity of the tadpoles seem to assume the predator that coevolves with the tadpole rather than trying to assume either both plasticity's or the plasticity of the non-coevolved predator. Second, conspecific versus hetero-specific food source does not make a huge difference in the

morphological and behavioral effects elicited by the wood frog tadpoles. Lastly, the food source of the predator apparently does not overcome the presence of the predator, and that tadpoles respond more directly to the cues of the predator versus what the predator has consumed.

Acknowledgements:

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Appendix A: Table of all P values

Table 3: Table of all P values calculated. For all dates 3-way ANOVA was used and for single dates 2-way ANOVA was used. Bold values represent significant p-values. Date*= date effect found.

Ratio Measurements												
	Tail/ Body L		**Total Length**		**Condition**		**Tail H/L**		**Tail L/W**		**Tail H/W**	
	Date*	Treatment	Date*	Treatment	Date*	Treatment	Date*	Treatment	Date*	Treatment	Date*	Treatment
All Dates	**<0.0001**	0.1444	**<0.0001**	0.2292	**0.0414**	0.5744	**<0.0001**	0.8582	**0.0005**	0.5990	**<0.0001**	0.5362
	Predator	Food	Predator	Food	Predator	Food	Predator	Food	Predator	Food	Predator	Food
6/3/2011	0.5216	0.4710	0.5739	0.5768	0.8100	0.0406	0.3992	0.7621	0.6646	0.6801	0.4611	0.7088
6/15/2011	0.9243	0.4169	0.7811	0.3925	0.9221	0.3369	0.3675	0.1694	0.9480	0.1294	0.2825	0.7171
6/20/2011	0.6033	0.7605	0.9684	0.4701	0.2912	0.0767	0.7502	0.4031	0.9033	0.1210	0.6924	0.7959
6/27/2011	0.7055	0.2496	0.9533	0.3358	0.7908	0.4921	0.9456	0.8388	0.8058	0.1809	0.7582	0.1660
7/1/2011	0.8641	0.2101	0.9834	0.3861	0.7433	0.7027	0.4721	0.3685	0.9791	0.4071	0.5843	0.6345
7/8/2011	0.8970	**0.0391**	0.1902	0.1878	0.5322	0.2767	N/A	N/A	N/A	N/A	N/A	N/A

Basic Measurements											
		Mass		**Body Length**		**Tail Length**		**Tail Height**		**Tail Width**	
		Date*	Treatment	Date*	Treatment	Date*	Treatment	Date*	Treatment	Date*	Treatment
All Dates		**0.0003**	**0.0470**	**0.0003**	0.2032	**0.0001**	0.2225	**0.0001**	0.1788	**0.0001**	0.2970
		Predator	Food	Predator	Food	Predator	Food	Predator	Food	Predator	Food
Early Dates	6/3/2011	0.9678	0.0710	0.7491	0.7872	0.4755	0.5015	0.9902	0.6526	0.5504	0.4013
	6/15/2011	0.9950	0.7526	0.7558	0.2321	0.8038	0.5178	0.1807	0.1468	0.8229	0.6418
	6/20/2011	0.3540	0.0669	0.4580	0.5843	0.9924	0.4911	0.7060	0.1563	0.9365	0.1000
Late Dates	6/27/2011	0.6053	0.9829	0.6400	0.8801	0.2875	0.2875	0.8009	0.3455	0.6424	0.8546
	7/1/2011	0.4937	0.4322	0.8246	0.3310	0.9518	0.2893	0.4653	0.3930	0.4973	0.1726
	7/8/2011	0.3778	0.5056	0.2905	0.7138	0.1942	**0.0174**	0.4283	**0.0326**	0.5169	0.5590