THE PENNSYLVANIA STATE UNIVERSITY
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SIZE-DEPENDENT PREDATION RISK IN TADPOLES

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ABSTRACT

Prey often respond to predation risk by changing their behavior, a phenomenon that can have strong impacts on ecosystems. Tadpoles are important components of aquatic ecosystems, and typically respond to predator cues by reducing their activity level. Different predators likely present different levels of risk to tadpoles, and these risks may change as tadpoles grow larger and become faster. As a result, tadpoles should change their activity levels to match the level of risk represented by chemical cues of specific predators. In this study, I measured the feeding rates (or risk) of different predators on small and large wood frog (*Rana sylvatica*) tadpoles, and tested how tadpoles of each size class responded behaviorally to the cues of these different predators. Eight tadpoles from each size class were placed into controlled environments with different predators (newts, dragonfly larvae, backswimmers, and predaceous diving beetles). These predators were allowed to feed on the tadpoles for 2 hours, and the number of remaining tadpoles was counted. I found that dragonfly larvae were the most effective predators on tadpoles and that, across all predators, predation rate decreased as tadpole size increased. Next, I examined the behavior of tadpoles when introduced to cues of these various predators. This was conducted by placing eight tadpoles from each size class into a controlled environment with a predator cue, and observing their activity level over 30 minutes. I found that tadpoles decreased their activity level to the same extent regardless of predator cue and the size of the tadpole. This research contributes to our understanding of the predator-prey relationships in these organisms. My results suggest that these tadpoles do not alter their responses depending on predator risk, or they assess the risk of different predators using information not measured in this study (e.g., the number of tadpoles consumed). This research provides useful insight into the workings of aquatic ecosystems and the various effects that predators can have on tadpoles during their various pre-metamorphic stages.

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Chapter 1

Introduction

Predators can influence all aspects of an animal's life. They can affect behavior (Kerfoot and Sih 1987; Lima and Dill 1990), morphology (Dodson 1989; Alder and Harvell 1990), and life history features (e.g. Crowl and Covich 1990; Skelly and Werner 1990; Peckarsky et al. 1993; Scrimgeour and Culp 1994). These changes, especially in behavior, can dramatically impact an ecosystem (Schmitz et al. 2004; Werner and Peacor 2003). Not only will population density decrease due to predation, but changes in prey behavior in response to predators often decrease food intake (Skelly and Werner 1990; Skelly 1992; Peckarsky et al. 1993), leading to increased abundance of their prey/diet.

Tadpoles are important components of aquatic ecosystems. They feed on detritus and primary producers including phytoplankton (Johnson 1991) and periphyton (Kupferberg et al. 1994), playing an important role in energy availability and nutrient cycling in aquatic ecosystems. The ability of tadpoles to consume nuisance algae and recycle nutrients is important for an aquatic ecosystem (Pryor 2003; Seale 1980). Tadpoles' role in an ecosystem can be drastically affected by the presence of specific predators. Tadpoles are known to reduce their activity in the presence of predators to avoid detection (e.g., Relyea 2004 and references therein; Miner et al. 2005), which decreases tadpole foraging and can yield enhanced growth of periphyton (Peacor and Werner 1997; Peacor and Werner 2001; Nyström and Åbjörnsson 2000; Werner and Anholt 1993).

Tadpoles are prey for a number of aquatic predators, such as fish, salamanders, and insects (Brodie and Formanowicz 1983; Caldwell et al 1980; Crump 1984; DeBenedictis 1974;

Heyer et al 1975; Heyer and Muedeking 1976; Formanowicz 1986). Each predator presents a different level of risk to tadpoles based on factors such as their size, speed, and effectiveness at capturing prey (Brodie and Formanowicz 1983; Formanowicz 1986; Caldwell et al. 1980). For example, smaller predators that consume their food whole may be limited in the size of the prey they can eat, while larger predators or predators that dismember their prey before eating it may not have that limitation (Urban 2010). Predators also feed at different rates (Relyea 2001) and may eat varying numbers of tadpoles at a given time. Importantly, the risk posed by each predator may change as tadpoles grow. As tadpoles become larger, they ought to be less vulnerable to size-limited predators and will also swim faster allowing them to escape or avoid some predators (Werner and Anholt 1993; Sih and Kats 1994). I expect, therefore, that there should be a positive relationship between the risk posed by the predator and how strongly the tadpoles respond to cues of that predator. A more dangerous predator should elicit a greater response from smaller, more susceptible tadpoles. Conversely, tadpoles of a less susceptible size will not respond to a less dangerous predator.

Wood frog tadpoles (*Rana sylvatica*) are a model system for this type of study because their predators are well-documented and the tadpoles exhibit distinct reductions in activity when exposed to chemical cues of predators (Collins and Wilber 1979; Skelly et al. 1999). For this study, I tested whether the susceptibility of tadpoles to predation varied with predator species and tadpole size, and whether these factors influenced the behavioral response of these tadpoles to predator cues. I predicted that a more dangerous predator would cause a greater reduction in tadpole activity, especially for smaller, more vulnerable tadpoles, and that these tadpoles would respond most strongly to the cues of these predators.

Chapter 2

Materials and Methods

Study Animals

All of the predators and prey used in this study were collected from ponds in State Game Lands 176, Centre County, PA. Wood frog eggs from approximately 20 clutches were collected between April 15 and 22, 2013, from a single pond. Eggs were kept in plastic tubs or wading pools outdoors until all eggs had hatched, and the hatchling tadpoles were initially provided with alfalfa rabbit chow for food. Approximately 2000 tadpoles were then introduced to each of three cattle tank mesocosms covered with 60% shade cloth (to prevent colonization by unwanted animals and limit direct sunlight). Mesocosms were filled with 800 L of well-water, and provisioned 200 g of deciduous leaf litter (primarily *Quercus velutina* and *Q. prinus*) and 12.5 g of rabbit chow (for food), and inoculated with 1 L of water from a natural pond to introduce typical microorganisms (Skelly et al. 2002). The high density of tadpoles (though not unnatural; Biesterfeldt et al. 1993) resulted in depletion of food, so I periodically added additional rabbit chow, leaf litter, and grass clippings as needed. A subset of the tadpoles (approximately 4000) was removed from the tanks several weeks prior to the initiation of this study for use in another experiment, leaving approximately 500-1500 tadpoles per mesocosm for this study.

Four species of predators were used in this study: eastern red-spotted newts (Amphibia: Caudata, *Notophthalmus viridescens*; n = 10), dragonfly larvae (Insecta: Anisoptera, *Anax junius*; n = 6), adult backswimmers (Insecta: Hemiptera, *Notonecta irrorata*; n = 6), and adult predaceous diving beetles (Insecta: Coleoptera, *Dytiscus* sp.; n = 3). These predator species were used, as they are known to commonly co-occur with wood frog tadpole and have been either previously documented as tadpole predators (Van Buskirk and Arioli 2005; Michel 2011) or are expected to be likely to feed upon tadpoles. These predators were collected by dipnet from several different ponds. When not in use, the predators were housed in plastic tubs. The newts were housed in tubs that were 36 x 18 x 27 cm (L x W x D) in groups of 3 to 4 per tub with plastic mesh placed inside for perching and shelter. The dragonfly larvae, backswimmers, and diving beetles were housed individually in smaller tubs that were 18 x 12 x 8 cm (L x W x D) furnished with leaves and twigs. The tubs were kept inside a shed to maintain consistent environmental conditions for all the predators throughout the study. Each predator was provided one tadpole as food every other day.

Tadpoles were selected for experiments in order to correspond to two different size classes (80-120 mg, or 'small', and 320-480 mg, or 'large'). To do this, tadpoles were removed, at random, from the mesocosms using a net and transferred to a tub that was 36 x 18 x 27 cm (L x W x D) for easier capture for weighing. Each tadpole was transferred to a small, fine steel-mesh cup and a clean paper towel was used to remove excess water from the tadpole through the mesh. The tadpole was then placed on a scale and weighed to the nearest milligram. Tadpoles that were not within the mass range for either size class were returned to their home mesocosms.

Predator Cue Collection and Behavioral Trials

The behavior of both 'small' and 'large' tadpoles was observed in response to cues of all four predator species. The activity levels of groups of same-sized tadpoles were observed before and after adding 'predator cue' – water in which the appropriate predator species had fed upon a tadpole. Predator cues were prepared by housing a predator with tadpoles for 2 hours, allowing the predator to consume the tadpole, and then harvesting the water. The cues from the three insect predators were collected by housing predators individually (to avoid cannibalism) in 500mL of water with a single tadpole. Newt cue was collected from three newts housed together in 1500mL of water and provided three tadpoles; these predators are much larger and needed more space. This maintained similar concentrations of predator cues (one predator and one prey item per 500 mL water). The water was then drained and frozen until it was needed for trials, to ensure that the cues were fresh (Carlson and Langkilde 2013).

Tadpoles of each size class (small and large) were separated into 24 groups each and eight were placed into 1800 mL of fresh water in opaque tubs that were 46 x 14 x 12 cm (L x W x D). The tadpoles were allowed to acclimate to the water for 10 minutes after which 10 mL of water was added by pipette to each tub. This acted as a control treatment, simulating the disturbance of introducing the predator cues. The tadpoles were given a further 30-minute acclimation period and then the activity of the tadpoles was observed unobtrusively every three minutes for 30 minutes. The number of tadpoles (out of 8) moving during each observation was recorded and averaged as a measure of activity level prior to predator cue addition (Jara and Perotti 2010).

The predator cues were then thawed and 10 mL of a single species' cue added to each tub of tadpoles. After a 30 minute acclimation period, the tadpole activity was again observed unobtrusively for 30 minutes, as before. These trials were replicated six times for each predator species and tadpole size class combination, resulting in a total of 48 trials. After each trial the tadpoles were returned to their home environment and were not used again in another behavioral trial.

I created a response variable representing the proportional change in activity between the control and predator cue additions. I analyzed the main effects of tadpole size and predator identity and the interaction term on activity change using an analysis of variance (ANOVA) model, followed by an additive ANOVA model with the (non-significant) interaction excluded.

Predator Risk Assay

The risk posed by each predator species was measured for 'small' and 'large' tadpoles by exposing groups of same-sized tadpoles to individual predators of the three of the species used in the Behavioral assays. Groups of eight tadpoles from one size class were placed into opaque tubs that were 46 x 14 x 12 cm (L x W x D), with 1800 mL of fresh water and one predator. The predator was allowed to prey on the tadpoles for 2 hours, and the number of surviving tadpoles was counted. Each predator species-tadpole size class combination was replicated between 3 and 5 times. The newt treatment was replicated 5 times for each tadpole size class and the dragonfly larvae and backswimmer insects were each replicated 3 times for each size class. Diving beetles were not used for the predator risk assay due to mortality of the beetles in the lab and the difficulty of collecting new ones.

For analysis of these data, I began with a basic ANOVA, but the residuals were not normal based on quantile-quantile plot. I therefore analyzed feeding rates of predators using Poisson regression, which is better for use with response variables based on counts. I used a likelihood ratio test (LRT) to test individual effects, comparing models with and without the effect terms. I first tested (and subsequently excluded) the interaction between predator species and tadpole size, and then tested the main effects in an additive model. After testing the overall predator effect using LRT, I assessed specific effects of different predator species by evaluating the slopes in the regression model.

Analysis of Behavior and Predator Risk

To test for a relationship between activity change and level of risk posed by the predator, I used a Pearson's Product-Moment Correlation. I tested for a correlation between average reduction in tadpole activity and average number of tadpoles eaten for each predator/size-class combination.

All analyses were conducted in R (version 3.0.2), with $p < 0.05$ considered statistically significant. For all analyses, diagnostic plots were examined to ensure that models were appropriately fit.

Chapter 3

Results

Behavioral Trials

There was no significant interaction effect between tadpole size and predator species on tadpole activity ($F_{3,40}$=1.23, p=0.31), indicating that any differences between size classes were similar for each predator type. In all treatments, tadpole activity in the presence of predator cue was uniformly reduced below the activity under control conditions (Figure 1). Using the additive ANOVA model, I found no variation in tadpole activity in response to the different predators ($F_{3,43}$=0.71, p=0.55) or between the two tadpole size classes ($F_{1,43}$=0.14, p=0.71).

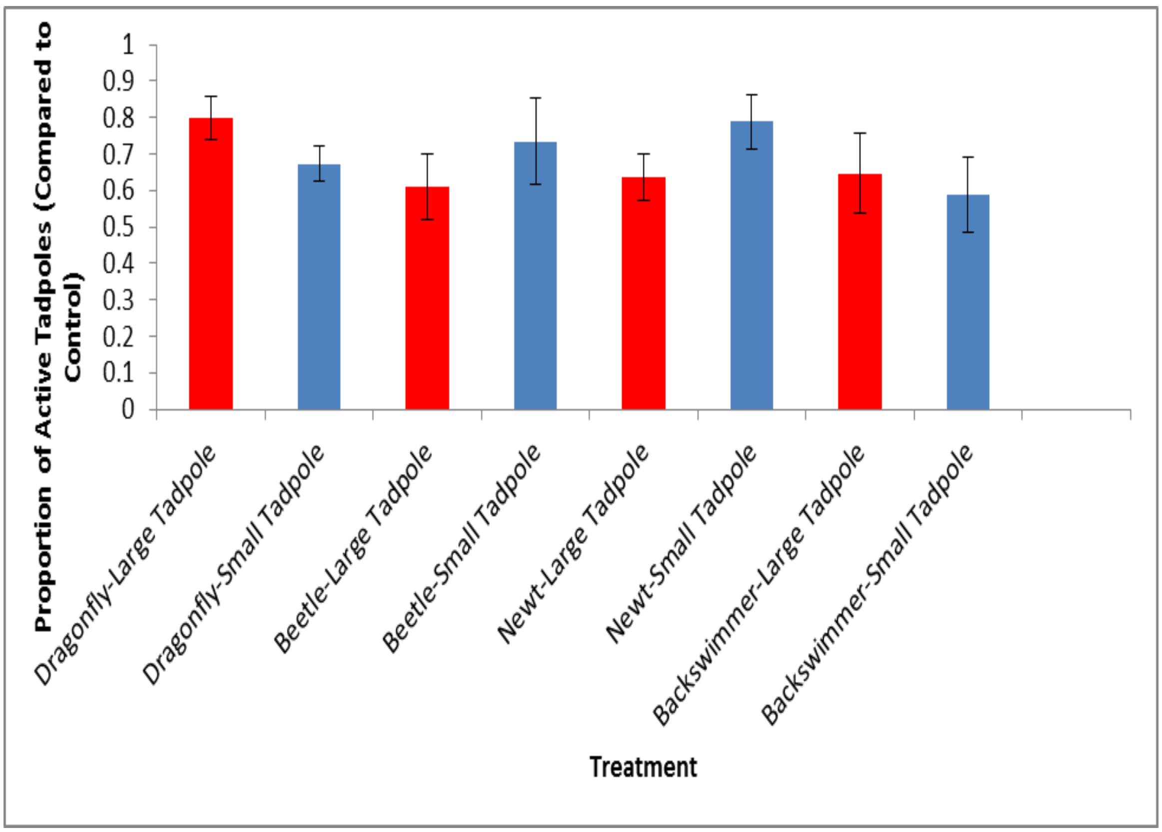

Figure 1. Behavior Trials-The change in the proportion of active tadpoles in the presence of a predator compared to during the control trials (with no predator) for large (red bars) and small (blue bars) tadpoles exposed to 4 different predator species. Bars show means +/- 1 standard error.

Predator Risk Assay

The interaction between predator species and tadpole size was not significant for the number of tadpoles consumed (χ^2_2=1.77, p =0.41), suggesting that the size-sensitivity of predation risk was similar for each predator; smaller tadpoles were eaten at a higher rate overall (p=0.00027, z=3.64) (Figure 2). However, there was significant variation in predation risk among predators (χ^2_2=9.61, p=0.008). Dragonfly larvae ate significantly more tadpoles than backswimmers (z=2.41, p=0.016) and newts (z=2.61, p=0.009), which did not differ from each other (p=0.74, z=0.33).

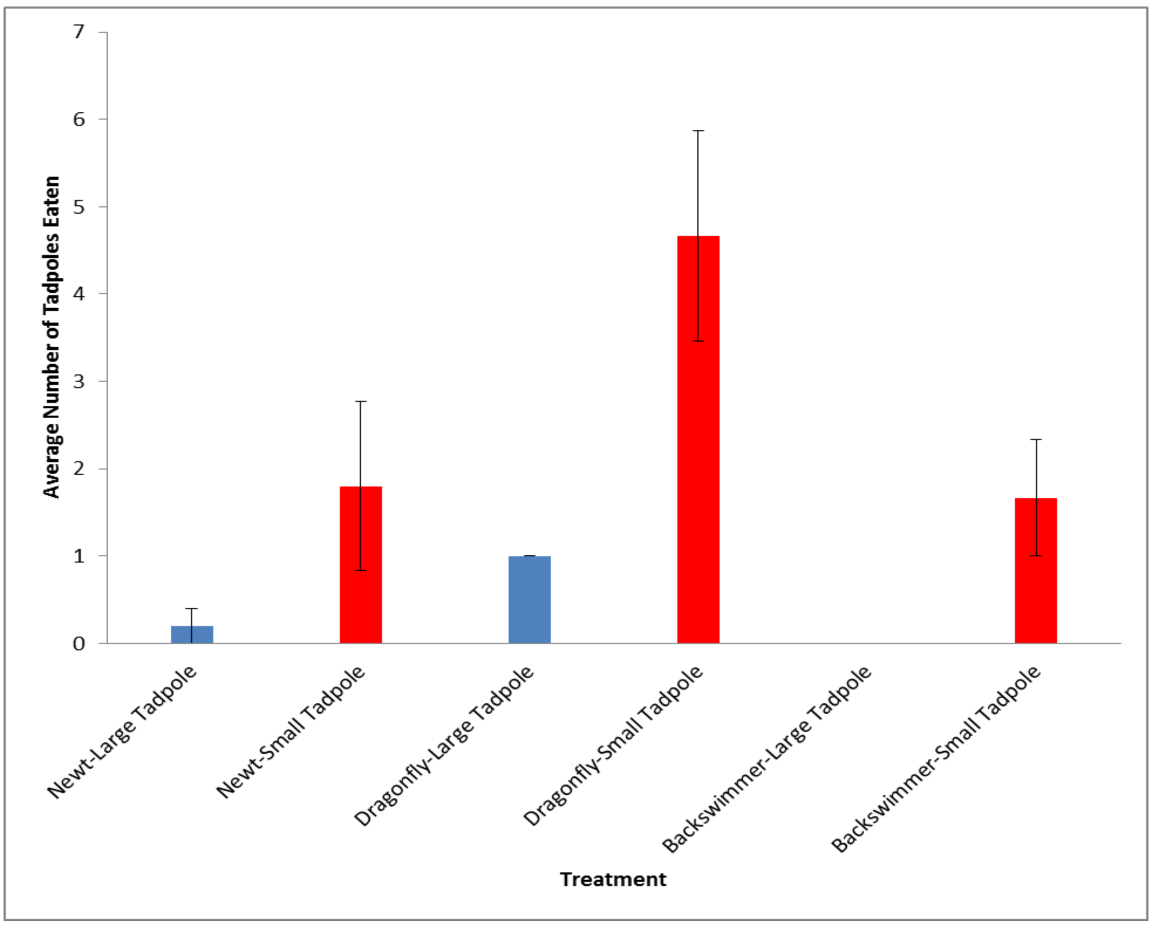

Figure 2. Predator Risk Assay-The average number of large (blue bars) and small (red bars) tadpoles consumed by four predator species within 2 hours. Bars show means +/- 1 standard error.

Analysis of Behavior and Predator Risk

The Pearson's Product-Moment Correlation showed that there was no relationship between the level of risk presented by a predator and the change in tadpole activity in response to predator cues ($r=0.03$, $t_4=0.05$, $p=0.96$) (Figure 3).

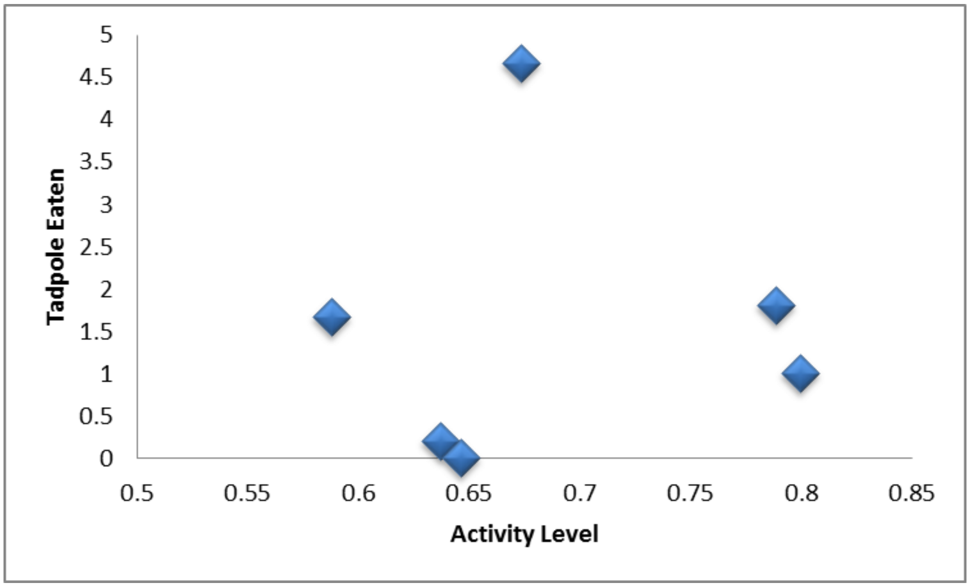

Figure 3. Analysis of Behavior and Predator Risk-The number of tadpoles eaten by a predator versus the changes in tadpole activity level in the presence of that predator (each point represents a different predator).

Chapter 4

Discussion

This study of various predators' effect on wood frog tadpoles sought to determine if predators that posed a greater risk to tadpoles had a greater effect on tadpoles overall behavior at the size at which they were most susceptible. I hypothesized that a predator that ate more tadpoles of a certain size class would have a greater influence on the behavior of tadpoles of that size. Similarly, I anticipated that a predator that posed very little risk to a size class would have less effect on their behavior. The results of my research reveal that dragonfly larvae were the greatest threat to tadpoles of both size classes, followed by backswimmers and then newts, and that smaller tadpoles were more vulnerable to predation by all predator species. Unexpectedly, the presence of predator cues caused a decrease in activity of the tadpoles regardless of size class and predator type, and there was no relationship between the strength of the tadpoles' anti-predator response and the risk posed by the predator.

The smaller tadpoles were likely more vulnerable to predation because they were easier to catch. This is likely because swimming ability of tadpoles increases with size, until metamorphic changes begin which slows them down again, making them more difficult for predators to catch (Formanowicz 1986). My results are in concurrence with the current literature, which demonstrates that dragonfly larvae are a very dangerous predator to both large and small tadpoles (Jara and Perotti 2010). This is likely due to the fact that dragonfly larvae are a large predator and so can feed on both larger and smaller tadpoles (Jara and Perotti 2010). The difference in predation effectively of backswimmers and newts should be addressed in future research; for example, by quantifying the behavior of these predators during foraging/hunting and how these influence prey capture.

I expected that there would be a relationship between risk associated with specific predators and the tadpoles' response to their presence. One potential explanation for why this was not the case in this study may be that the predator cues were of equal concentration. In a natural environment, a more dangerous predator would capture and consume more tadpoles and therefore omit stronger cues of tadpole predation. . Accordingly, other work has indicated that behavior in another species was most responsive to the number of tadpoles killed by the predator (Van Buskirk and Arioli 2002). I controlled for this by feeding each predator a single tadpole to standardize the strength of the cues. In addition, I did not vary prey size when preparing the predator cue and this might be an important signal or threat. To create the predator cues, I chose one tadpole from the small size class to feed to each predator. In a natural environment, a predator that is more dangerous to large tadpoles would eat a large tadpole. The biomass of prey consumed can be responsible for phenotypic change in that same prey species (McCoy et al. 2012) and may similarly cause changes in prey behavior. My findings suggest that tadpoles may primarily evaluate the risk of a predator based on the number or size of conspecifics it consumes rather than its specific identity or the size of the tadpole.

Future studies might test the importance of the characters of tadpole prey on the response of conspecific tadpoles to cues of the threat in a similar manner to this current study but taking these new considerations into account. Making adjustments during cue collection such as by feeding different numbers or sizes of tadpoles to predators, could provide important insight into the relationship between predator risk and behavioral response, and facilitate prediction of subsequent effects on the ecosystem.

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Areas of Research Interest

- My research interest is primarily to understand predator/prey relationships and the consequences of interactions between the species for the broader community.