Implications of habitat-mediated density dependence in Crawfish Frogs (*Lithobates areolatus*)

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Background

Density dependence is important in understanding the population dynamics of species. While there are exceptions (the Allee effect) where a minimum viable population is important, lower density populations often have higher individual survival. Rarely is density dependence the only factor impacting survival of a population, or a certain demographic of a population, environmental variables can also play a role. Ultraviolet radiation been shown to impact density dependence in frogs, by reducing the survival of individuals during their larval stage which reduces density dependence in later life stages (Blaustein et al. 2003). Environmental constraints can impact population dynamics by releasing a segment of the population from the limiting factors creating density dependence, or by making the limiting factors more limiting, or adding additional limitations. The introduction of new chemicals can limit growth at certain life phases, but some organisms are able to overcome these limitations in one phase by growing more in a later one (Boone 2005).

Density dependent relationships have been examined in many invertebrates. Species with longer life spans can have similar mechanisms but they are more difficult to tease apart. Amphibians provide a good vertebrate model organism because they have a fairly quick life cycle and the parts of their life cycle where they are thought to experience density dependence are fairly short (several weeks/months) instead of years as in larger longer lived organisms or organisms with different reproductive strategies. These ideas have been examined in several life stages (eggs Vonesh and De la Cruz 2002, aquatic larval and terrestrial juvenile stages Altwegg 2003, juvenile terrestrial stages Harper and Semlitsch 2007) but not often in differentiating habitat conditions. Patrick et al (2008) explained habitat and density dependence in wood frogs (*Rana sylvatica*) in relation to environmental covariates which could play a role by limiting growth or resources and including density dependence at densities where it would not occur under 'ideal' or 'typical' conditions. We have choosen the Crawfish Frog as our study organism (*Lithobates areolatus*). They are are a wetland dependent species during the breeding season and retreat to more terrestrial habitats the rest of the year. We are looking at a range of densities and two different habitattreatments to examine the role of restored versus unrestored wetland habitats. Non-restored habitats or those with non-native vegetation might not provide sufficient resources for the individuals or may create a more stressful environment by having different chemical or other triggers of stress (Didham et al. 2007).

Experimental Design

We created four rafts of mesocosms to be deployed at Woolsey Wet Prarie, a local restored wetland in Fayetteville, AR. Part of Woolsey Wet Prairie has been restored as part of a wetland mitigation project, and the rest in *Fescue* spp (a non-native grass that grows around the ponds)), a result of the grazing that used to occur on the property. Ponds are scattered throughout the property. Two rafts were deployed in the restored wetland portion of Woolsey, and two in the unrestored portion in a farm pond. Each raft in the farm pond habitat was given fescue grass and the restored wetland areas were given native grass (collected from the restored area). The following densities were repeated four times in each habitat type (1, 3, 6, 21, 24, 48 tadpoles). We selected these two habitats to see if the non-native fescue grass has a different impact on tadpole density then the restored wetland vegetation. We choose densities across a wide range to ensure that we picked densities extreme enough to be able to determine if there are density dependence effects.

Our responses is survival per unit area. We choose per unit area instead of per unit volume because we felt that the surface area for algae to grow (the water/air surface) was a limiting factor. To measure survival the mesocosms were checked at regular intervals and individuals in each mesocosm were counted. We predict that there will be density dependence, and that fescue grass will have more negative density dependence then prairie grass because it exudes chemicals which impact tadpoles. We predict that tadpoles will be less susceptible to density dependence in the restored wetland then the farm pond.

Model Description

I was given possible data to use in my model and used the script provided by Dr. Willson to obtain the gamma and density dependent scaling factor for each habitat type. We did this by varying the d and gamma values across a wide range, comparing the line to the possible values and finding the combination of values which had the lowest residuals (straight line distance along the y axis).

I used the density dependent scaling factor and gamma values in the time series model for each habitat type to look at the impacts of these variables on population growth as a whole. Our model is a time series model and allows the population to grow over time. It can also be used to examine variation in of a certain variable and the impact on resulting population size. I choose to vary adult survival and egg survival from 0 - 100% and examine the impact of our dd and gamma values. We are allowing the Fecundity of adults parameter to vary, which is a function of the number of tadpoles, their survival and the number of adults.

Results

Based on the analysis we completed in lab we determined our density dependent scaling factors and gamma values for both habitats (Table 1). Gamma less then 1 is under compensating and gamma greater then 1

Table 1: Results from Possible Data Model

Variable	Farm Pond	Restored Prairie
density dependent scaling factor	0.0059059	0.007007007
gamma	1.2	0.94

is over compensating for density dependence. Our pond tadpoles are slightly over compensating and the prairie slightly under compensating for density dependence. The density dependent factors vary between the two habitat types, with large values having a strong impact on the end population size. The results of these possible data show a stronger impact on density dependence in the farm pond than the prairie habitat. Though density dependence is playing a role in both systems.

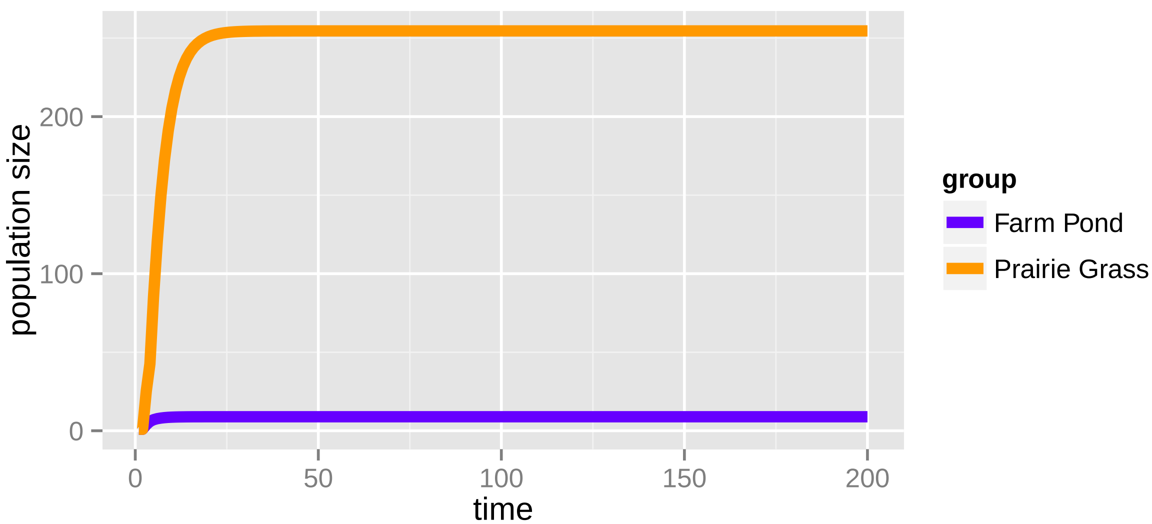

Figure 1 - Our initial population model using the parameters given to us in class

Figure 1 shows the higher ending population size in the Prairie Grass habitat with an ending population size of `254.57` and `8.91` in the Farm Pond. The 95% confidence intervals of our initial survival percentages increase as density increases, suggesting a lack of heterozygasticity in the data and they overlap between the two groups, suggesting that these differences are not significant. I did not compute the 95% confidence intervals for our model predictions, but they likely have the same issues as the underlying data. This is hypothesized data and the real data may not have the same issues.

The impacts of a d and gamma are not equally felt by each part of the population. In Figure 2 we examine the impact of these values on the survival off eggs and adults. Figure 2a (egg survival) shows similar patterns to Figure 1, with the farm pond having lower population `263.41` compared with restored prairie `12.61`. The impact on adult survival is difficult to assess in the full graph, but once the axis are clipped there is a difference. The prarie grass habitat has a greater population size then the farm pond, and it reaches very high - `8.472977\times 10^{4}` - population densities when adult survival is above 90%. The farm pond does not have such a dramatic response - `12.61`.

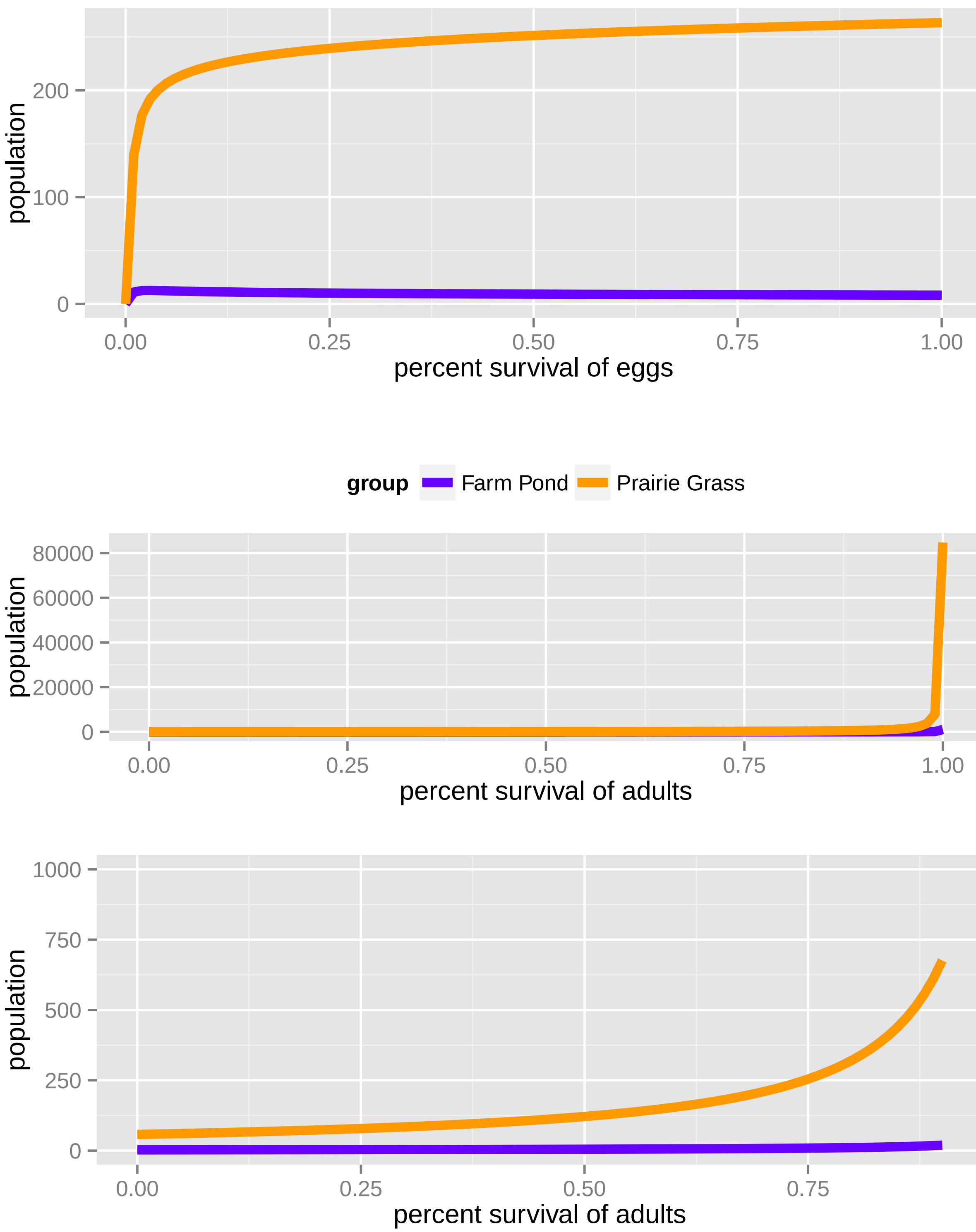

Figure 2 - Sensativity analysis of egg and adult survival in both habitat types. The second adult survival graph has the x and y axis clipped to provide a clearer view of differences at lower survival percentages

Discussion

Understanding why we see differences between the habitats requires further investigation into the differences in temperature, food availability and other factors which may impact crawfish frog tadpole survival. There are several things which may have been at play. The first and perhaps most obvious when standing on the site, is the difference in vegetation. Fescue is an invasive grass, and may not have provided the diversity of food of native prairie grass. Some invasive grasses also exude chemicals to reduce competition with other grasses, if the cut grass is able to exude these chemicals it could have an impact on the frog's survival, or their food's abundance or nutritional value. Farm ponds generally have less vegetation, at least above water, this could impact the temperature of the water (unshaded water might fluctuate more frequently and reach higher highs). The restored wetland area at Woolsey is a series of wetland impoundments with water control structures. The flooding and drawing down of these wetlands as part of mimicing natural wetland hydrology regimes could impact the temperature, oxygen and other factors of the water (Rundle and Fredrickson 1981, Fredrickson and Taylor 1982). Swings in temperature may have impacted the tadpoles development and survival, or had an impact on available food resources. Because of the presence of the mesocosm we can rule out differences in predators between the two sights since, to our knowledge, no predation (other then by their fellow tadpoles) occurred. In the wild though differences in type and density of predator could also play a role.

Crawfish frogs are more specialized then many frog species, living in crawfish burrows during part of the year and relying on wet prairie wetlands for breeding (Hoffman et al. 2010). Because of this specialization they might be limited by factors that would not limit a more general frog, like a southern leopard frog (*Lithobates sphenocephalus*), which overlaps in habitat with the crawfish frog, but not completely. This should be taken into consideration before extrapolating beyond crawfish frogs. Since the restored wetland areas are able to support higher populations of crawfish frogs then work should be done to restore the rest of Woolsey Wet Prairie if the objective is to increase the population of crawfish frogs. Because of their unique biology in needing coincident terrestrial habitats with crawfish burrows special consideration would need to be made to how the property should be restored and if efforts should be put forth to protect adjacent properties which may serve as non-breeding habitat (Hoffman et al. 2010). Work done using drift fences to try and capture crawfish frogs has shown that they will often wait at these barriers all night before returning to the wetland (Heemeyer et al. 2010). This would have large implications for connectivity between wetland and terrestrial areas in the face of development.

The biggest limitation of this study is co-variation of the vegetation type with the habitat type, which prevents us from being able to differentiate between the two variables. Sample size may also be limiting. The hypothesized data has fairly large amount of variation, which might be dampened by a larger sample size, or by the real data when it is collected in the coming months. The simplest next step would be to do a completely factorial design and include habitat type and vegetation type as two separate covariates. It would also be interesting to add in additional treatments, such as increased temperature or the introduction of fertilizer or other pollutant to see if they impact density. Both would be future risks at Woolsey, between climate change and the increasing urbanization of the surrounding landscape, and would not be unique challenges to crawfish frogs across their range, so would be additionally helpful for crawfish frog conservation.

This is an exciting first look at the impacts of density dependence on Crawfish Frog population dynamics. With further work it can produce useful metrics to inform Crawfish Frog conservation and wetland management and help set realistic goals for population objectives. Our data suggest that there is density dependence among these frogs, which must be taken into account when managing and studying the population in the future.

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