The effects of resource competition and predation on *Aedes triseriatus* and *Culex pipiens*

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Abstract

This experiment investigates the effects that both competition for resources and predation have on two species of mosquitoes: *Aedes triseriatus* and *Culex pipiens* with a predator *Mesocyclops longisetus,* a copepod and whether these results are consistent with Leibold’s keystone predation model. To investigate these effects, there is a varying resource level with or without predation. *Aedes triseriatus* lived up to its competitive name and successively produced more adults than *Culex pipiens* at every resource level with and without predation. This did not align with Leibold’s keystone predation model, but there are some telling reasons why that may be.

Introduction

Leibold (1996) introduced a model with two competitors, a single resource, and a predator. This predator was noted as a keystone predator because it preys on both species and has the ability to create coexistence between the two competitors where it otherwise would not have been. This ability to allow for coexistence happens when there is a competitive tradeoff. One species must be the better competitor and one must be better at avoiding the predator. When this tradeoff occurs, coexistence can be found, more interestingly though is when coexistence is found. With varying resource levels and a constant rate of predation, there will be different outcomes in the competing species survival. At low resource levels, the better competitor will outcompete the more predator-resistant species, at intermediate levels of resources, this is where we expect to see coexistence and at high resource levels, it is expected that the more predator resistant species will outcompete the better competitor (Leibold 1996). The intermediate level of resource variation is where there is a possibility of coexistence, but to obtain the actual levels, it would be necessary to evaluate impact that each species has on the resource and predator and also to evaluate each species minimum resource level that allows for zero growth (r\*-value).

This experiment will test Leibold’s keystone predation model using two species of mosquito larvae: *Aedes triseriatus* (Aedes) and *Culex pipiens* (Culex). Aedes is a tree hole mosquito native to North America and Culex is a nonnative species that was introduced quite some time ago into North America but has since become quite adjusted to life in the Americas (Juliano 2017). Both of these species can be found in man-made containers that collect rain water, such as rain barrels, discarded tires, cemetery vases, flower pots and many more (Juliano 2017). Aedes is the better competitor for resources, and Culex is better at evading the predator (Murrell & Juliano 2012), Mesocyclops *longisetus,* a copepod. They will both be competing for liver powder, the resource. This experiment meets all of the requirements for Leibold’s keystone predation model, so we would expect that the results of this experiment would in fact align with Leibold’s model in that both resource level and predation will be significant for the competing species. This also implies that resource level and competition should have a greater effect on Culex than on Aedes, and predation should have a greater effect on Aedes than on Culex.

Methods

*Experimental*

This was a four week long experiment that took place in an environmental chamber. The chamber was set at 24° C on a photophase cycle for which there was fourteen hours of daytime and ten hours of nighttime. Two species of mosquitos: Aedes and Culex were kept in plastic containers with holes punched into the tops and 400mL of water from the lab that is equivalent to rain water. Each container either had 50 larvae of Culex, fifty larvae of Aedes, or 50 larvae of both Culex and Aedes and either had a predator, one copepod, or didn’t. These larvae were hatched less than 24 hours before we placed them in the containers. Each of the containers with different species combinations was given either a high (10mg), medium (5mg), or low (2.5mg) amount of liver powder for the resource. Each of these combinations was replicated three times (Table 1), resulting in 54 total containers. For the first couple of days when pupae were not expected, the larvae were not checked. After the first couple of days, the containers were checked for pupae every day and were fed the given their assigned level of resource every Thursday for the duration of the experiment. When the pupae were found in the containers, they were pipetted out of the containers and into vials marked with the treatment and replica number. The treatment being: predator (P) or no predator (NP), resource level, and what species were in the container Aedes (A), Aedes and Culex (AC), or Culex (C). From there, the vials were checked each day as well, for eclosion to adulthood. When they reached adulthood, they were added to the datasheet with the date, what sex they were, what species, and what container they came from. We analyzed this data using SAS to interpret the impacts of the treatments on the different species containers.

*Statistical Methods*

All figures and tables can be found in the appendix. Using the data analysis platform, SAS, the data was analyzed using both ANOVA and MANOVA. The ANOVA analysis had three classes: competition, predator, and resource. ANOVA was used to investigate the significance of these classes on Culex and Aedes (Tables 2a,b). To look at the effects that predation, resource level, and competition had on a single species, ANOVA was used with a generalized linear model (GLM). The results of the Bonferroni were also used for analysis and interpretation of data (Table 3a,b). For the effects of predation and resource level on the competing species containers, it was necessary to invoke the powers of MANOVA. Within MANOVA, a canonical correlation analysis was completed to better understand and interpret the effects of the classes (predation and resource level) on the competing species. To get the significance of the different classes, predator and resource level, the GLM MANOVA was run with the data that was solely comprised of the containers with both species. The MANOVA analysis gives the significance of predation and resource level on the both species containers. Where the dependent variables are Aedes and Culex and the independent variables are the classes. This analysis gives the impact of the predation and resource levels on the species when they are competing. Significance levels can be found in Tables 4a and 4b. Using the classes that were found significant, MANOVA contrasts were ran within the model to better understand the classes that had a significant impact on the species. The contrast function was used to investigate the effects of the three resource levels with and without predation on the competing species adult eclosion outcomes. Contrast was also used to investigate the impact that varying resource levels from low to high, with and without predation had on each species. The impact should be positive and significant for both species because it is raising the resource level by a large amount. This will give a better depiction of what effect predation is having from one resource level to another rather than what is happening at each resource level individually.

Results

Within ANOVA, several factors were found to have a significant impact on Aedes eclosion to adulthood. Predation and resource level had the largest effect on the species and predation combined with resource level was significant as well. The class that was not significant across the board for Aedes though was competition (Table 2a). The ANOVA for Culex showed significant impacts on the species from competition, resource, the combined effects of competition and predation, the combined effects of competition and resource, and the combined effects of competition, resource, and predation (Table 2b). Figure 1. compares the difference in means for the adult species and the effects that the classes had on the species’ enclosion. From Table 2b. and Figure 1., it is obvious that Culex is much more effected by competition and resource level than Aedes is, and Aedes is much more effected by predation, especially at high resource levels, as we predicted.

The MANOVA showed that predation and resource abundance had a significant effect on Aedes, but the combined effect of predation and resource abundance was not significant (Table 4). For Culex, predation, resource level, and the combined effect of predation and resource level had a significant impact on the species. The standardized canonical coefficients and Pillai’s trace were also significant for this analysis, see Table 4, therefore concluding that all three classes had significant impacts on the competing species containers as a whole. The largest Pillai’s trace was from the resource abundance class, signifying that resource abundance had the largest effect on the system.

The first contrast compared the different resource levels with and without predation. Both high and medium resource levels with predation compared to without predation had a significant impact on the population for Aedes. As for Culex, only the high resource level with predation compared to without predation had a significant impact on the populations eclosion to adulthood (Table 5). The high resource no predator/high resource with predator treatment, was considered significant on both of the species, but in different directions. This contrast had a significant, but negative impact on Culex and a minor, insignificant impact on Aedes. At this high resource level with a predator, we expect Culex to outcompete Aedes, but when the predator is no longer in the equation, Aedes will outcompete Culex every time. Therefore, this contrast had a significant impact on Culex because it is the one being most effected by the change in predation to no predation (Figure 2). The treatment medium resource level with predation/ medium resource level without predation, had a positive, significant impact on Aedes, and although this treatment wasn’t considered significant for Culex, the canonical coefficient was larger than one, showing that there was positive effect on Culex from this treatment, just not a significant one. Aedes, unsurprisingly, benefited more from the lack of a predator, but at this intermediate resource level, so did the Culex (Figure 3). The contrast involving low resources with and without predation were insignificant in both species, although insignificant, the relief from the predator did have a large positive impact on the Aedes population, unsurprisingly. The relief from the predator for Culex at this low resource level had no effect on the species because at low levels of resource for the predator and without the predator in the competing containers, there was no Culex pupae (Figure 4). This low resource negatively affected both species and was most likely below each species’ r\*-value and that is why the predator had little to no effect at this level because the species were reproducing so infrequently already because there was not enough resources to sustain the population. Aedes even at high resource levels with predation did better than Culex in terms of having larger numbers reach adulthood and they outcompeted Culex at every other level as well (Figure 5). This contradicts the hypothesis that our model would align well with Leibold’s keystone predation model.

The next contrast I completed was to investigate the effects of low resources with predation to high resources with predation and low resources without predation to high resources without predation. It was obvious that resource level along with predation played an important role in the number of adult mosquitos, but I wanted to eliminate the levels and focus more on overlying effect. Varying the resource amount from low to high without a predator, shows that Aedes is significantly impacted, but Culex is not (Table 6). This is somewhat obvious, only because that without a predator, Aedes is expected to outcompete Culex and this shows that it does (Figure 7). From low to high resources with a predator, though, both species are significantly impacted in a positive way, but Culex is impacted twice the amount that Aedes is (Table 6). Although Culex did quite poor in this experiment, this contrast shows that predation at higher resource levels does benefit them more than it benefits Aedes which holds true to the preliminaries of Leibold’s keystone model, even though the results are not consistent. This means that something else might need to be adjusted in order for coexistence to play out.

Discussion

This experiment did not align with Leibold’s keystone predation model. When investigating the effects on a single species in all containers with classes, predation, resource, and competition, the results of this experiment align with the assumptions we made about each species. Assumptions being that Aedes is the better competitor and Culex better at evading the predator. When the investigation goes further into the competing species containers though, Aedes exclusively outcompetes Culex at all levels of resource variation, and although predation does have an impact on Aedes, the only time it benefits Culex is when resource levels are high, which is to be expected and is consistent with Leibold’s model. Even though there was a significant, positive impact of predation on Culex, Aedes still continued to produce more adults even at these high resource levels (Figure 5). According to Leibold’s model, the medium resource level is where we would expect coexistence to be fostered, that was not the case in this particular experiment though. At medium resource levels, with and without predation, Aedes still continued to outcompete Culex and drive them to very low numbers. At low resources, both species did poorly, and the addition of the predator had a negative effect on both species. Based on Leibold’s model, we could expect that the low resource level was far below both species r\*-values explaining why they both did so poorly. Aedes did notably better under these conditions than Culex did, which does follow Leibold’s model for the expectations of low resource with a predator.

The fact that this experiment did not align with the findings of Leibold (1996) could be due to a variety of things. In order to foster coexistence, Leibold (1996) mentions that coexistence will be seen at intermediate resource levels when each competitor is having the largest impact on the thing that impacts it most. In this case, we did not initially find the r\*-values for each species which would account for intermediate resource levels. To account for this error, we should have calculated both species r\*-values and then adjusted the amount of resource levels from there.

Another factor that could have played into this is that the copepod is only a predator at larval stages and even then is not an extremely effective predator. After one week, the containers were checked for surviving copepods and out of the initial 27, there were only six left. If we were to find another, possibly better, predator and take into effect the species minimum resource amount for zero growth, this experiment could have drastically different results. This experiment was not carried out to equilibrium, which can have an effect on the results as well. It should be noted though, that several of the containers had already been discarded due to no more larvae or pupae before the experiment ended, and the production of new pupae was slowing down drastically from when we started.

Although this experiment did not mirror Leibold’s keystone predation model, it did give an important insight on how these two species interact which can be important for future topics of species control. The success of adult mosquitos is directly related to the conditions of the aquatic habitat the juvenile stages grow in until eclosion (Hanly and Haase 2016). Mosquitos are also known vectors for popular diseases such as La Crosse virus and West Nile (Aliota et. al. 2016), understanding what impacts these species at the important juvenile stages could be extremely important in future disease prevention techniques.

Literature Cited

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