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**Differences In Consumption Rates Between Juvenile and Adult
Laccophilus fasciatus rufus (Coleoptera: Dytiscidae) On Larval
Culex quinquefasciatus (Diptera: Culicidae)**

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The University of Southern Mississippi

Differences in consumption rates between juvenile and adult *Laccophilus fasciatus rufus* (Coleoptera: Dytiscidae) on larval *Culex quinquefasciatus* (Diptera: Culicidae)

by

Carmen Bofill

A Thesis
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Abstract

With the increase of global temperature and human populations, prevalence of vector-borne diseases is becoming an issue for public health. Over the years these vectors have been notorious for developing resistance to human regulated insecticides. Thus, other forms of control, including the use of natural predators, have become an important topic in research. Research on member of the family of predaceous diving beetles (Dytiscidae) and their predatory ability to decrease aquatic mosquito larvae populations has been of recent interest. The purpose of this study is to 1) quantify consumption rates of the dytiscid *Laccophilus fasciatus rufus* juvenile and adults on *Culex quinquefasciatus* and 2) to test adult dytiscid prey preference between living and dead prey. For study 1, based on morphological differences between life stages and the energy requirements of growth for juvenile stages, I predicted that the juvenile stage of *L. f. rufus* would consume prey at a faster rates than adults, and for study 2, I predicted that when given the choice to scavenge dead prey or to attack living prey adult dytiscids will prefer to scavenge as a primary means of consumption.

For the consumption trials, nine aquaria were used each crossed with different densities of early or late stage mosquitoes and different densities of plants. To test prey preference, different prey treatments were used including 10 dead, 10 living, a combination of 10 dead and 10 living prey. In experiment 1, there was a significant effect of predator stage by prey stage where the adults consumed later instars at a faster rate than the juvenile dytiscids. In experiment 2, adult dytiscids ate three times as many dead versus living mosquito larvae. Studying these interactions will improve

our understanding of the effect of predation of predaceous diving beetles on mosquito populations under natural circumstances.

Key Words: *Culex quinquefasciatus*, *Laccophilus fasciatus rufus*, consumption rates, prey preference

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Chapter I: Introduction

The United States harbors approximately 169 species of mosquitoes, with the state of Mississippi home to 53 species (Jarratt 2004). Mosquitoes exploit two types of habitats for breeding: natural and artificial. Natural habitats include ponds, streams, lakes, roadside puddles, swamps, and marshes. Mosquitoes also often utilize artificial breeding sites (e.g., tires) because they can accumulate and hold water (Laird 1988) and are often in proximity to human hosts (Yee 2008). Even though mosquitoes have been found in all continents except Antarctica, the southeastern portion of the U.S. provides mosquitoes with ample opportunity to breed given annual high temperatures and humidity. Controlling mosquito populations is an important area of research given that they vector many different transmittable diseases such as West Nile, dengue, and malaria (Brogdon et al. 1998).

Although the application of insecticides has become a large part of mosquito population control, resistance to these chemicals has become increasingly apparent since the 1990s (Brogdon et al. 1998). Thus, other forms of control, including the use of natural predators have become an important topic in research. Research on larval mosquito population control via aquatic invertebrate and vertebrate predators has been of recent interest (Chandra et al. 2008). Such predators include aquatic insects (e.g., dragonflies, damselflies, diving beetles), snails, amphibians, and fish (Polis and Holt 1989). Although common in mosquito habitats, research on aquatic beetles (Order Coleoptera), and specifically predaceous diving beetles (Family Dytiscidae), has received little attention (Culler and Lamp 2009). This highly diverse family of predators (~ 4,000 species worldwide) play a structurally important role in aquatic

food webs (Thakare and Zade 2011) and are potentially important predators of mosquito larvae in natural habitats (Larson et al. 2000).

Although mosquitoes may be susceptible to dytiscid predation in natural systems, this study is also interested in understanding the feeding behavior among these dytiscids when given the choice between dead mosquito larvae and ones that are living. Even though this family of diving beetle is notorious for being freshwater predators, scavenging on dead animal material has been noted in the field and in the laboratory (Larson and Roughley 1991). Little research has been done regarding the extent to which these dytiscids scavenge. The reason for this is because general assumptions have been made on the entire family's predatory ability. More species specific work needs to be further investigated in order to determine scavenging rates and their effect on community structure. Adult *Laccophilus fasciatus rufus*, along with other dytiscids, have structures that allow flying between one aquatic ecosystem and another (Zimmerman 1970). This feature, along with its scavenging behavior, allows the transfer of nutrients between different aquatic habitats (Payne and Moore 2006). This transfer of energy between tangential ecosystems includes the dytiscid itself. Specifically, dytiscids may consume prey, fly to an adjacent aquatic ecosystem, and then be eaten by a predator, thus transferring energy from one system to another. The amount of energy transferred is unknown but may be important.

Intentional prey selection is another aspect that plays a role in scavenging among dytiscids. Members of the family Dytiscidae have many ways to detect which type of prey surrounds them. Utilization of vision, chemoreception, and vibration gives these predators the ability to recognize and choose prey (Hagen, Bombosch, and McMurtry

1976). Prey selection for this particular species of adult dytiscids may be due to energy expenditure. These beetles are ambush predators, which entails that they must recognize, capture, and drag their prey to the bottom while chewing on the prey (Young 1967, Formanowicz 1982). Adult dytiscids are not adept as hunters when compared to their larval counterparts, who are obligate predators and need movement of living prey to elicit a response (Johnson et al. 2003). Thus, when given a choice, one might predict that adult beetles would choose to scavenge in order to conserve energy for future dispersal and/or reproduction. The purpose of this study was to 1) quantify consumption rates of *L. f. rufus* adults (Fig. 1.1) and juveniles (Fig 1.2) on the mosquito *Culex quinquefasciatus*, and 2) test adult dytiscid prey preference between living and dead prey.

For Experiment 1, based on morphological differences between life stages of *L. f. rufus* and the energy requirements of growth for larval stages, it is predicted that the juvenile beetles will consume prey at a faster rate than adults. For Experiment 2, I predicted that when given the choice to scavenge dead prey or to attack live prey, adult dytiscids will prefer to scavenge as their primary means of consumption. This reasoning comes from prior work by Klecka and Boukal (2012) who showed that juvenile *Dytiscus* did not have a major prey preference and nearly depleted the resources given to them, whereas adult *Dytiscus* exhibited a preference for some prey. Additionally, Kehl and Dettner (2003) concluded that adult dytiscids chose to scavenge on dead Copepoda and Cladocera when given the option between dead and living prey. Studying these interactions will improve our understanding of the effect

of dytiscids on mosquito populations and may help to a better understanding of their bio-control abilities in nature.



(Figure 1.1 adult *Laccophilus fasciatus rufus*)
Photo by D.A. Yee



(Figure 1.2 juvenile *Laccophilus fasciatus rufus*)
Photo by D.A. Yee

Chapter 2: Literature Review

Complex Life Cycle

A complex life cycle (Fig. 2.1) is a maturation cycle in which different morphological changes occur during the growth of an organism (Wilbur 1980). Examples of animals that have a complex life cycle include most insects, amphibians (e.g., frogs), and many marine invertebrates. Some insects exhibit indirect metamorphosis (stages include larvae, pupa, and adult), as opposed to direct

metamorphosis where the emerging young are just smaller versions of the adults so no morphological changes occur. Even though appearance may change, behavior also may vary across the life cycle. In complex life cycles, larval and adult stages often occur in different habitats, have different diets, and are exposed to different predators. For insects like those being studied in this project, eggs are laid in a freshwater habitat with adults eventually emerging onto a terrestrial environment (Schmidt et al., 2013).

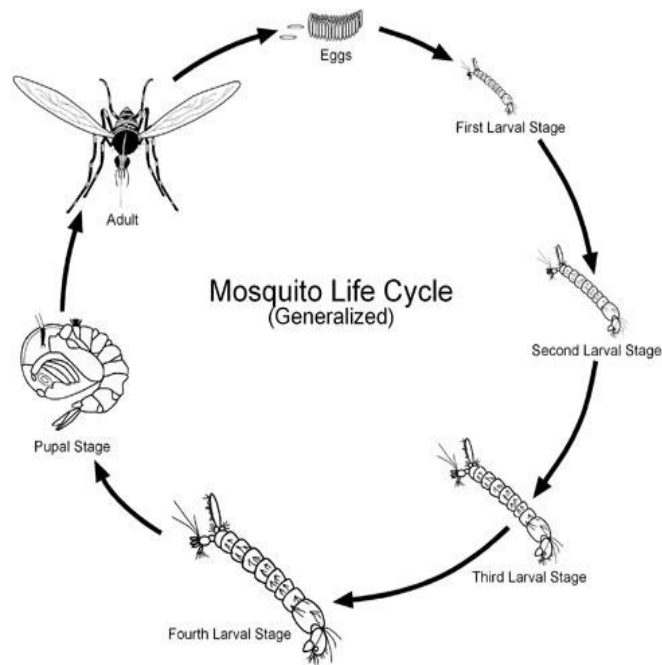


Fig. 2.1 Morphological Changes of Different Life Stages (Scott Charlesworth, Purdue University)

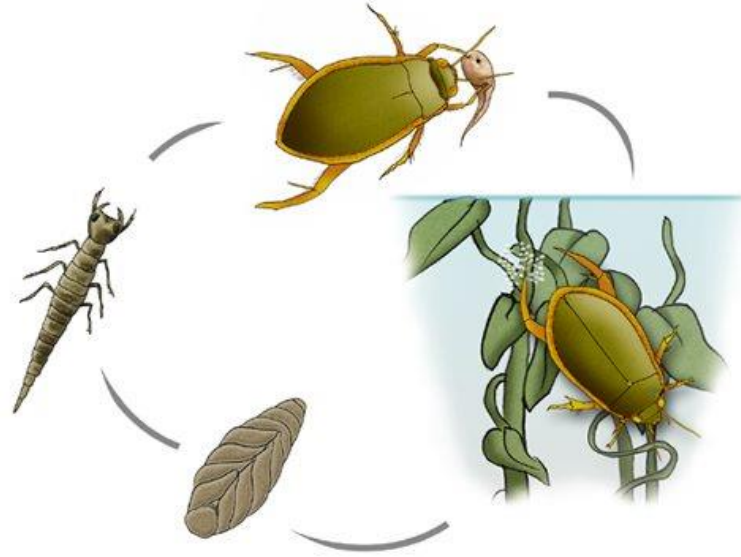


Figure 2.2 Diving Beetle Life Cycle (Andrew Howells, Australian Museum)

Predator-Prey Interactions

The bio-control of enzootic vectors is of great value to public health research and natural predator-prey interactions such as the ones studied here are important for gaining knowledge of how they may affect populations of vectors and their community structure. Alto et al. (2012) observed the lethal and non-lethal effects of a predatory midge on different species of larval mosquitoes. In his research, he explained that consumption of prey was not the only way that a predator helped shape community structures, but non-lethal interactions were just as important. The presence of a predator in a system can alter prey's survivorship, behavior, and density due to "intimidation". The result from this study indicated that in the presence of the predator there was a lower survivorship and thinning of density of the native mosquito larvae, *Aedes triseriatus*, a common vector for LaCrosse encephalitis.

The research that has focused on predator-prey interactions in aquatic ecosystems is relatively sparse for the number of species that occur in these habitats, especially

members in Dytiscidae, which are typically the top predator in these fishless habitats. These observations on predator-mediated effects give us an idea of how these seemingly small interactions assist in shaping community structure, behavior, and density of different species in an aquatic environment.

Distribution of *Culex quinquefasciatus* and *Laccophilus fasciatus rufus*

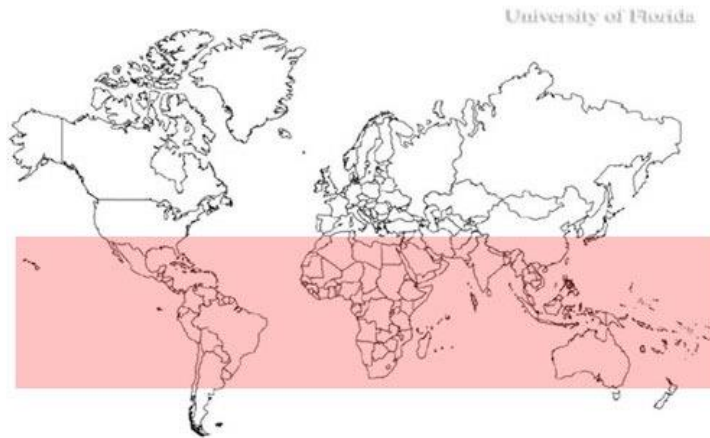


Fig. 2.3 Distribution of *Culex quinquefasciatus*. (Stephanie Hill, University of Florida)

The prey species used in this study is the southern house mosquito, *Culex quinquefasciatus*. The species is considered by some a subspecies of *Culex pipens*, which is generally found in areas above 39° latitude, whereas *Culex quinquefasciatus* is found below 36° latitude (Fig. 1.3) (Barr 1957). Between these two areas, hybrids of these subspecies are found. This species often inhabits open water with high nutrient content (sewage ponds), as well as isolated container habitats (e.g., tires) (Yee et al. 2012).

The predaceous diving beetle *Laccophilus fasciatus* has three subspecies: *L. f. rufus*, *L. f. fasciatus*, and *L. f. terminalis*. The two main differences between these three subspecies are geographic location and size. *Laccophilus f. terminalis* is generally only found on the west coast of North America and into Mexico, *L. f.*

fasciatus is only found in the country of Mexico, and *L. f. rufus* resides in all the United States on the eastern seaboard and even some states in the central U.S. It has been noted that the subspecies *L. f. rufus* appears to be smaller in the Southeastern states.

Not only are *C. quinquefasciatus* and *L. f. rufus* found in the same area in the U.S., they also display habitat overlap. Individuals of *L. f. rufus* are generally found in muddy sediments and often found in roadside ditches and ponds (Zimmerman 1970). *Culex quinquefasciatus* are also found in ponds, lagoons, and other locations such as septic tanks (Burke et al. 2010). These species also co-occur in the same habitats in and around Hattiesburg, MS (personal observation).

This research project is centered on these two species because of their availability, lack of knowledge about their interactions, and medical importance of the mosquito prey. Species of *Culex* are the primary vector for West Nile encephalitis in humans (Jarratt 2004).

Prey Selection

In a study by Klecka and Boukal (2012), the juveniles of different species of *Dytiscus* proved to be obligate predators and did not show a preference for any particular prey. Adult *Dytiscus* however were choosier when it came to what they ate, proving that they can identify and select specific prey. Adult dytiscids are considered poor predators compared to their larval counterparts because they are often observed to be clumsier (Jakinovich 1970). Adult dytiscids are mainly visual predators but also detect prey via vibrations and chemoreception through the aqueous environment

(Culler et. al 2014). Prey that are damaged or are recently deceased may provide cues that the dytiscid can use to locate the prey (Larson et. al, 2000).

Juvenile dytiscids utilize different techniques to recognize and hunt prey. They have been observed to display sit-and-pursue, sit-and-wait, and active hunting modes (Yee 2010). Due to the fact that the adults are clumsy, they may select prey that are less difficult to capture, including dead or dying individuals; scavenging on dead animals seems more energetically favorable for adults (Bosi 2001). Many studies have been done to test the preference of dytiscids on different prey, but those that have examined dead versus living prey are scarce. In an experiment by Velasco and Milian (2008) it was described that members of *Thermonectus marmoratus*, the sunburst diving beetle, acted as scavengers rather than predators when given the choice between living and dead prey. A similar result was seen in Kehl and Dettner (2003) when it was observed that species of *Scarodytes halensis*, when given a choice, hunted dead planktonic crustacean (Copepod and Cladocera) rather than living ones.

Chapter 3: Methodology

Adult *L. f. rufus* were collected from aquatic habitats in and around Hattiesburg, MS using an aquatic D-net and small hand nets. After capture, adults were taken back to the laboratory and placed into separate plastic cups (100 mL) with lids to prevent escape. A small stick was added to each cup to serve as a perch along with filtered pond water. Adults were fed once daily (i.e., frozen chironomid larvae, live mosquitoes) until experimental trials began.

Experimental Design

Experiment 1: Juvenile and adult consumption trials

To quantify predation rates on mosquitoes, both juvenile and adult beetles were used separately in feeding trials. Feeding trials were conducted in small plastic aquaria (203 x 152 x 127 mm) filled with 3.93 L filtered pond water collected from ponds in the study area. During each trial, adults and larvae were housed in nine aquaria (n =18 for this experiment) that varied in plant and prey density. In each aquarium, 3 different levels of plants were utilized based on stem density: 0, 3, and 6 stems, hereafter no, low, and high plant densities. The plant species that was used is *Ludwigia palustris*, a plant that is commonly found in dytiscid habitats in the study area (Pitcher 2010). Testing predation on mosquitoes under different plant densities has been shown to affect predator-prey interactions (Savino and Stein 2011, Yee 2010) and I hypothesized that when plant density increases, consumption of mosquito larvae will decrease as plants may provide a refuge for prey. In addition, in other systems different levels of prey can also affect predation rates (Alto et al. 2012). Prey density trials consisted of three prey levels: 5, 10, or 15 of either early or late instar *Culex quinquefasciatus*, hereafter low, medium, and high prey. Performing this experiment on different sized prey lets us see which predator life stage has a greater effect on prey populations of different sizes. Plant density (3), prey density (3), and prey stage (2) were crossed to yield 18 combinations that were replicated 5 times for each beetle stage. Uneaten mosquitoes were counted after 4 hrs in each aquarium. Aquariums with both mosquito larvae and adult/juvenile dytiscids were placed in an

incubator with a temperature of 27° C on a 14:10 (dark:light) photoperiod (approximate summer conditions for the study area).

Experiment 2: Prey Selection

Experiment 2 was set up in a similar fashion as Experiment 1. As results from Experiment 1 did not produce differences in predation rates among prey densities or plant densities these treatments were excluded from Experiment 2. It was also seen that adult dytiscids consumed more late instar mosquito larvae, therefore early instars were not used. Specifically, I used different prey treatment levels to examine prey preference for adult beetles only: 10 dead mosquito larvae, 10 living larvae, and 10 dead and 10 living. Each treatment level was replicated six times.

Procedures

No species-level taxonomic keys exist to distinguish between different dytiscid larvae. Thus, to assure that the correct species of *Laccophilus* was being used, breeding of adults in a controlled setting was necessary. Specifically, *L. f. rufus* males and females will be identified and placed in large plastic tubs containing aquatic plants, water, food, and substrate. Tubs will be covered and left for the duration of the experiment at the USM Science Park, located approximately 5 miles east of the Hattiesburg campus, during which time adults will likely mate and females will lay eggs. Tubs will be checked daily for the presence of larvae.

Analyses

For Experiment 1, a four-way analysis of variance (ANOVA) was used to determine if differences existed in predation rates among the different plant densities

(3), prey densities (3), and prey stages (2) between larvae and adult beetle predators. A Tukey's test was then conducted to assess differences among specific treatment levels while controlling for experimental-wise error rates. A $\log(x + 1)$ transformation was applied to the raw data to meet assumptions of normality.

For Experiment 2, a one-way ANOVA was used to test for differences between prey treatments. Specifically, I compared the percent of prey eaten by adult dytiscids in the living, dead, of the combination of living and dead treatment levels.

Chapter 4: Results

In Experiment 1, ANOVA resulted in a significant effect of predator stage and prey stage by predator stage interaction, whereas other effects were not significant (Table 1). Specifically, adult beetles consumed late instar mosquitoes at a higher rate when compared to the rate at which the juvenile dytiscids ate them, whereas both life stages of predator consumed early instar prey at the same rate (Fig. 4.1). There were no differences in consumption of the different mosquito stages for either beetle stage (Fig. 4.1).

Table 1. Results of 4-way ANOVA showing effects of predator stage (juvenile, adult), prey stage (early or late instar mosquito larvae), plant density (low, medium, high), and prey density (5, 10, or 15 mosquito larvae) and all their interactions on consumption rates of mosquito prey. Significant effects are presented in bold.

Table 1. Results of 4-way ANOVA

Factor	df	F	P-value
Predator stage (D)	1,108	4.48	0.0367
Prey Stage (P)	1, 108	0.02	0.8835
Plant density (L)	2, 108	0.13	0.8823
Prey density (S)	2, 108	0.11	0.8919
D x P	1, 108	9.48	0.0026
D x L	2, 108	0.13	0.8782
D x S	2, 108	0.09	0.9163
P x L	2, 108	0.24	0.7892
P x S	2, 108	1.67	0.1926
L x S	4, 108	0.39	0.8122
D x P x L	2, 108	0.37	0.6898
D x P x S	2, 108	0.08	0.9222
D x L x S	4, 108	0.28	0.8895
P x L x S	4, 108	0.29	0.8839
D x P x L x S	6, 108	0.08	0.9901

For Experiment 2, there were significant differences in consumption by adult beetles on the different prey types ($F_{3, 16} = 5.944$, $P = 0.0064$). Specifically, adults generally consumed more dead mosquitoes than living mosquitoes, either alone or when in combination (Fig. 4.2). Specifically, adult dytiscids ate about three times more dead mosquitoes than living mosquitoes when dead and living preys were

offered simultaneously. Although dytiscids did exhibit a preference for dead prey, they still consumed living larvae when no others were available (Fig. 4.2).

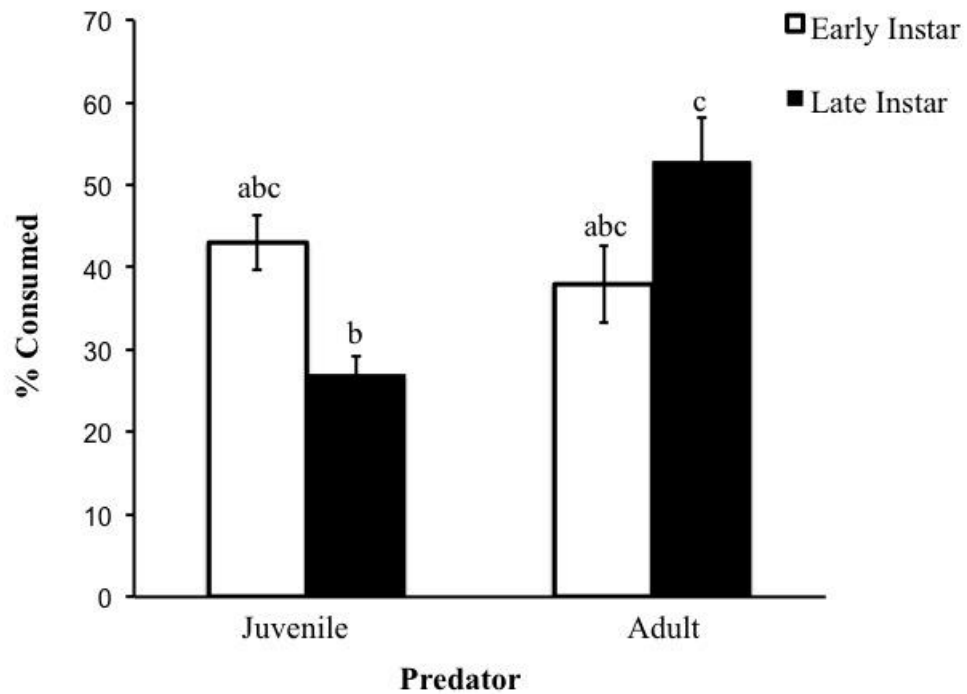


Fig. 4.1: Results of the significant interactions between predator stages (juvenile and adult) and prey stages (early and late instar *Culex quinquefasciatus*) on mean (\pm SE) consumption rates. Means that do not share a letter are significantly different.

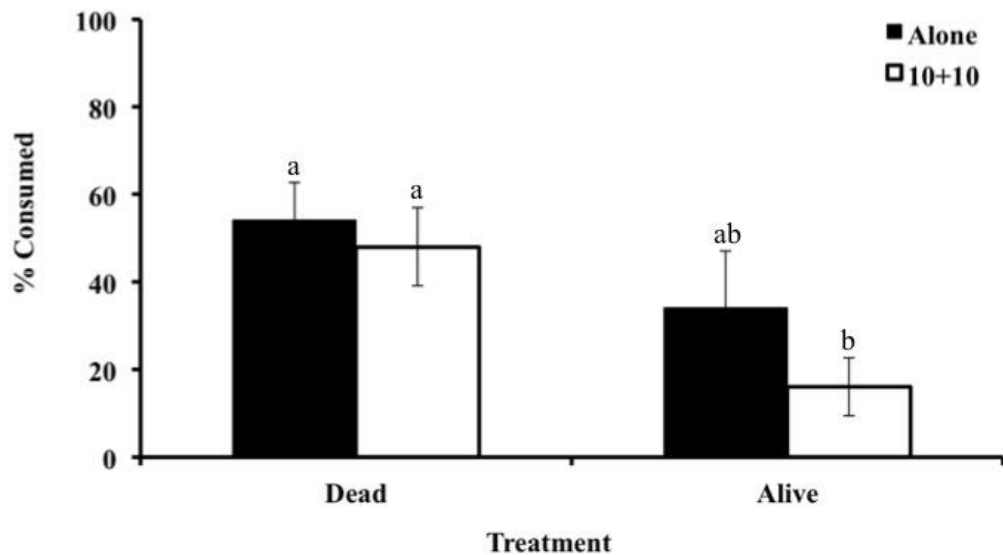


Figure 4.2: Results of a one-way ANOVA on mean (\pm SE) consumption of mosquitoes by adult dytiscids. Treatment levels included either 10 dead, 10 live, or a mixture of 10 living and 10 dead late instar mosquitoes (*Culex quinquefasciatus*). Means that do not share a letter are significantly different.

Chapter 5: Discussion

With the gradual prevalence of vector-borne diseases and insecticide resistance, research studies such as this one are of great importance to have a better understanding of biotic control of these mosquitoes in natural systems. Considering the capability of intense top-down predation by species in the family Dytiscidae and the lack of research that is available for these predators, this project increased our understanding of predatory abilities of *L. f. rufus*. The two main focuses of this

research project were to observe the consumption rates of different life stages of *L. f. rufus* and to test prey preference of adults for active predation or scavenging on a common mosquito in the southeast portion of the U.S. I predicted in the first experiment that juvenile dytiscids would consume earlier and later instar mosquito larvae at a faster rate when compared to the adult dytiscids. My experimental results did not support this prediction (Fig. 4.1). Consumption trials indicated that adult *L. f. rufus* consumed later instar mosquito larvae at a higher rate compared to the juvenile stage. This result is inconsistent with an experiment by Klecka and Boukal (2012) who saw that juvenile dytiscids (*Acilius* and *Hydaticus*) had no preference for prey stage and depleted all prey items given to them at a similar rate. My observations may be genus specific, although they will add to the overall knowledge of predation of the entire family of Dytiscidae. This life stage preference of prey by *L. f. rufus* also may be due to morphological differences. As juvenile dytiscids are much smaller than the adults it may be energetically favorable for them to attack smaller prey than to expend more energy trying to take down larger prey. One consequence of this work is to suggest that there may be a compounding effect upon prey populations in nature. Specifically, whereas juvenile predators may be selecting earlier instars, the adults consume later stages. Thus, the combined effect of both beetle life history stages on prey may be synergistic rather than additive. To determine if this is the case additional experiments, wherein adult and juvenile predators are presented with prey of both stages will need to be conducted.

In my trials plant density had no significant effect on consumption of mosquito prey. I utilized different plant densities because I hypothesized that higher plant

densities would provide refugia for prey and thus consumption rates would be lower. In Yee (2010), the presence of plants altered the behavior of larval dytiscids while attacking their prey. Specifically, feeding behavior and habitat domain differences were noted between three different genera of larval dytiscids, which then had an effect on predation rates among them. One possible explanation for the lack of an effect of plants could be that the plant stem densities used may not have been appropriate to allow prey to use as shelter or as a vantage point for predators. Another explanation could be that many different species of *Culex* are open water dwellers and would not be accustomed to utilizing the refugia (Clements 1999). Thus, even when offered plants as shelter, their natural tendencies would force them into the more open water areas of the aquaria.

I also found no relationship of prey density to consumption rates. In work by Formanowicz (1982), no difference was found in consumption rates in different prey densities (5) for three different species of juvenile dytiscids. He also noted no difference between predator searching times, handling time, and prey densities. Thus, the three species of larval dytiscids consumed and hunted at similar rates regardless of the number of prey. In this case, it did not seem to matter what density of prey I administered, suggesting that the dytiscids take the same amount of time to recognize, handle, and consume their prey. Additionally, Formanowicz (1982) attributed his results to the many different ways that juvenile dytiscids can hunt for prey. He observed that at low densities of prey the juvenile would actively search at all times, whereas in high densities of prey, they utilized a sit and ambush tactic. This switch in

hunting strategy, alongside similar recognition and capture times, allowed the predator to capture and consume the prey at similar rates no matter the density.

My results showed that beetles caused a significant decrease in mosquito densities at all life stages, and support the results of others who have found similar effect of dytiscids on mosquito larvae (e.g., Chandra et al. 2008, Culler and Lamp 2009, Formanowicz 1982). For example, Chandra et al. (2008) observed that in a 24-hour period, juvenile *Acilius sulcatus* (Coleoptera: Dytiscidae) ate on average 34 out of 200 late instar *C. quinquefasciatus* (~17%). The juvenile dytiscids used in our experiment consumed 28% of the late instar *C. quinquefasciatus* larvae offered (Fig 4.1), even though the amount of time for my trials were shorter than those by Chandra et al (2008). Many different control agents are utilized for population suppression of mosquito larvae including vertebrate predators such as non-game fish (Kern 2004). In an experiment that tested prey preference of dytiscids and mosquito fish it was observed that mosquito fish did not show a preference for mosquitoes, however dytiscids did prefer to prey upon mosquito larvae (Culler and Lamp 2009). Compilation of knowledge of different species of dytiscids may allow researchers to construct better bio control strategies that are more efficient than single species approaches.

Even though consumption rates were recorded, the true test to see if dytiscid are a good biocontrol agent was to observe prey preference when given the choice between dead mosquitoes and living ones. I observed that adult dytiscids generally consumed more dead prey over living prey, even when both types were offered (Fig. 4.2). The choice between living and dead prey appears to be a question of energy expenditure.

My results agreed with Velasco and Millian (2008) and Kehl and Dettner (2003) who found that when given a choice between living and dead prey adult dytiscids chose to scavenge on dead animal material rather than to hunt living prey. The prey items that Velasco and Millian (2008) administered to *Thermonectus marmoratus* were larval fish, mayflies, beetles, and dragonflies. They described that preference of dead vs. living was apparent. In addition *T. marmoratus* preferred the dead prey items that had softer cuticles. These prey items were easier to catch and chew; supporting my hypothesis that the adult beetles would choose prey items that appeared energetically favorable. A similar result was observed by Kehl and Dettner (2003) who also tested prey preference by giving the dytiscid *Scarodytes halensis* mixed treatments of dead and living plankton (Copepoda and Cladocera). It was observed that after 30 min more dead plankton were consumed. In my experiment adult *L. f. rufus* had the ability to attack living prey when given no choice, but attacked fewer living prey when dead prey were available. Scavenging on dead animal material seemed to be favorable if it requires lower energy expenditure and could possibly result in higher fitness for the species. Scavengers (especially ones that are capable of flight) can potentially transfer energy between tangential ecosystems (Payne and Moore 2006). Considering the prevalence of this species in local water bodies (Pitcher 2010), the rate at which it scavenges, and potential mobility, this could possibly impact nutrient cycles in areas that they inhabit, although such speculation requires more testing.

Beyond the work here, another research topic that needs further exploring is the compounding effect that both life stages of dytiscids would have on mosquito populations. Research on intraguild predation (wherein multiple predators compete

over the same prey and potentially consume one another) would be necessary, where the adult dytiscid would play the role top predator, the juvenile as the intermediate prey, and the mosquito larvae as the basal resource. Because I have found that adult dytiscids consume more late instar mosquito larvae and juvenile dytiscids consume more earlier stage larvae it could be possible that when in the same environment that they would have a synergistic effect on mosquito population control.

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