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SURVIVAL AND DEVELOPMENT OF LARVAL ODONATES (ANISOPTERA) AND FEMALE OVIPOSITION SITE CHOICE IN RESPONSE TO PREDATORY FISH

A Thesis
Presented in partial fulfillment of requirements
for the degree of Master of Science
in the Department of Biology
The University of Mississippi

By

Kevin M. Potts

May 2020

ABSTRACT

The reproductive success of many aquatic insects is highly dependent on where they deposit their eggs. Not all habitats are created equal. Some are more favorable than others for larval development. Therefore it would be evolutionarily advantageous for an ovipositing female to differentiate between them and choose the most suitable for her offspring's survival. Numerous studies have shown that many species with complex life-cycles representing a diverse array of taxonomic groups sort themselves non-randomly among habitat patches on the basis of perceived habitat quality. In the case of dragonflies, insufficient evidence exists to support the hypothesis that this group can assess relevant indicators of patch quality and use those cues to select habitat. I conducted a series of experiments to investigate what effects a predatory fish, the green sunfish (Lepomis cyanellus), had on larval dragonfly performance and development and adult female habitat selection behavior. Developmental studies were performed to determine the degree of consumptive and non-consumptive effects of L. cyanellus and how they affect survival and other fitness correlates of larval dragonflies. I found that larval survival is significantly affected by the presence of uncaged L. cyanellus, but not affected by caged L. cyanellus. Caged L. cyanellus did not have an effect on fitness correlates, suggesting larvae are not capable of detecting fish. I examined whether female dragonflies actively avoid ovipositing in sites containing predatory fish which potentially inflict significant fitness costs via offspring predation. Results indicated that female adults of three common species of dragonflies did not discern between habitat patches based on the presence or absence of fish predators. This suggests that members of this group either rely on a bet-hedging or risk-spreading strategy, utilize a form

of philopatry, or the presence of fish predators may not be an important factor for odonates in oviposition site selection. There is a mismatch between the results of the oviposition and development experiments, suggesting there is much more to learn about how dragonflies select habitat for their offspring, how their decisions affect aquatic community assembly, and how these can be used to inform conservation efforts designed to protect threatened odonate species.

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CHAPTER 1:

LARVAL ODONATE PERFORMANCE IN RESPONSE TO LEPOMIS CYANELLUS (CONSUMPTIVE AND NON-CONSUMPTIVE EFFECTS)

Introduction

Post-colonization species sorting is a critical determinant of community assembly and metacommunity dynamics models (Leibold et al. 2004, Binckley and Resetarits 2005, McCauley et al. 2008). Species sorting refers to the differential mortality of individuals in response to environmental and biological conditions in their habitat that affect the distributions and abundances of species within a community (Leibold et al. 2004, Binckley and Resetarits 2005). In aquatic ecosystems, these conditions can include temperature, water chemistry, pond desiccation, competition, resource availability, disease, and predation.

Predation is a critical determinant of post-colonization community structure in aquatic systems that can dictate species composition, richness, and overall population dynamics (Brooks and Dodson 1965, Morin 1981, 1984, Petranka and Fakhoury 1991, Binckley and Resetarits 2002, Abrams et al. 2007). If introduced into previously fishless habitats, predatory fish can have powerful effects on invertebrate prey populations by affecting abundances not only via direct consumption but also through non-consumptive effects, thereby potentially extirpating susceptible species from an aquatic habitat (Wellborn et al. 1996, Binckley and Resetarits 2002, Eby et al. 2006). In addition to the direct effect of mortality, the mere presence of predators can

reduce the fitness of prey by affecting fitness correlates such as growth, larval periods, and size at metamorphosis due to the prey's behavioral and morphological anti-predator responses (Sih 1980, Werner and Gilliam 1984, Johansson and Samuelsson 1994, Abrams and Rowe 1996, Lima 1998, Relyea 2001, 2007). Induced states of anti-predator responses can result in sub-optimal foraging and resource allocation compared to populations lacking predation risk (Sih 1982, Abrams and Rowe 1996, Relyea 2001, Werner 2016). The benefit of these anti-predator responses comes at the cost of decreased energy intake, a trade-off that results in increased survival but decreased growth, development, and fecundity (Lima 1998).

Predator induced phenotypic plasticity has been extensively studied in many aquatic organisms with complex life cycles (Grant and Bayly 1981, Harvell 1990, McCollum and Van Buskirk 1996, Van Buskirk 2000). These phenotypic changes ultimately affect an organism's size at metamorphosis or its time to metamorphosis (Abrams and Rowe 1996, Benard 2004). In a literature review of 40 development experiments on amphibians and aquatic insects, predator cues alone affected larval development in 22 cases either affecting size, age at metamorphosis, or both (Benard 2004). In most cases, predator cues only affect one of these fitness correlates; either the larval period is extended, or individuals emerge at a smaller size (Benard 2004).

Cues from predators can also elicit morphological changes to prey through predator-induced phenotypes, creating two or more morphs of a single species called polyphenisms. Polyphenisms induced by the threat of predation have been described in a variety of taxa including caudates (Wilbur and Collins 1973, Van Buskirk and Schmidt 2000, Michimae and Wakahara 2002), anurans (McCollum and Van Buskirk 1996, Van Buskirk 2000, Schoeppner and Relyea 2009), and cladocerans (Grant and Bayly 1981, Miyakawa et al. 2013).

Some predator-induced morphological phenotypes have been described in odonates. In the naiads of the fish sensitive dragonfly species *Leucorrhina dubia*, the lengths of the abdominal spines were significantly longer on individuals collected from bodies of water with fish as opposed to individuals that came from fishless ponds (Johansson and Samuelsson 1994, Johansson 2002). The same study also showed that it took fish longer to handle the long-spined naiads as opposed to the short-spined naiads, suggesting abdominal spine length is a defensive morphological adaptation in *L. dubia* that is induced by cues produced by its predators (Johansson and Samuelsson 1994, Johansson 2002). Another developmental study by Mccauley et al. (2011) found that nonlethal effects from a fish predator created enough stressors in larvae of the odonate species *Leucorrhinia intacta* to affect survival rate and the frequency at which larvae successfully complete eclosion from the final larval instar into the adult stage.

Surveys of ovipositing females alone can over-estimate pond quality, so counting emerging adults is a better metric for assessing habitat quality than simply determining adult oviposition preference or sampling larvae (Raebel et al. 2010). It is important to disentangle the effects of habitat selection from the effects of post-colonization processes, both of which play essential roles in determining community assembly and species sorting models (Wellborn et al. 1996, Leibold et al. 2004, Vonesh et al. 2009, Kraus and Vonesh 2010). The data gained from such studies should address whether there are consumptive and/or non-consumptive post-colonization effects of sharing habitat with predatory fish on dragonfly larvae. Therefore results may explain whether an evolutionary selection pressure exists for individual female odonates to select oviposition sites based on habitat quality.

My developmental experiments investigate deviations in survival rates and multiple metrics of fitness in two different species of dragonflies subjected to two treatments: fishless

control pools and pools containing *Lepomis cyanellus*. The fitness correlates being compared are body length at emergence and length of larval period. The consumptive effects study had no constraints on the fish and allowed consumption of larvae to occur. The non-consumptive effects study isolated the fish from the larvae, preventing consumption. These studies test the hypothesis that the consumptive and non-consumptive effects of predatory fish have a negative impact on larval dragonfly survival and development. I predict in both cases that patches containing *L. cyanellus* will produce fewer dragonflies surviving to the adult stage, and those that do will have reduced size at metamorphosis and a longer developmental larval period compared to naiads in a fishless patch.

Materials and Methods

Study Site

All experiments were performed at the University of Mississippi Field Station (UMFS) located in Lafayette County, MS. The UMFS encompasses 318 hectares and contains 223 ponds along with multiple streams, forests, and wetlands. This location is especially ideal for this study because it supports large populations of fish and aquatic insects, and hosts a wide variety and abundance of odonate species.

Study Species

To test the post-colonization effects of fish on larval dragonfly survival and growth, two separate studies were conducted to isolate the consumptive and non-consumptive effects on larval performance. The dragonfly species *Erythemis simplicicollis* (eastern pondhawk) and *Pachydiplax longipennis* (blue dasher) were used as models in these studies because they are

among the most abundant odonate species found at UMFS. Gravid females can be found from Spring-Fall as they employ a bivoltine life history strategy, producing two generations (cohorts) per year. *Lepomis cyanellus* (green sunfish) was employed as the predator in this experiment. *L. cyanellus* 's large body size and gape ensure that naiads of all sizes and species are susceptible to predation. *L. cyanellus* is one of the most widespread fishes in North America and is widely introduced to previously fishless waters both inside and outside of its native range (Lee et al. 1983). Its wide distribution and proficiency as an invader into new aquatic ecosystems make *L. cyanellus* a logical choice as the experimental predator in this study.

Eggs were collected from the first cohort that emerged in the spring. Those eggs spawned the second cohort that emerged in late summer from inside the experimental tanks (Corbet et al. 2006). The process of egg collection mirrors the methods described and employed by Schenk et al (2004) and was performed by first capturing a female dragonfly using an aerial insect net. While carefully grasping the wings pinched above the thorax, the terminal segments of the abdomen containing the ovipositor were repeatedly dipped into a small container of pond water kept at ambient temperature. If the female had recently mated and is gravid, the water triggers egg release. Eggs were collected in a small container until the female was depleted. These eggs were transferred into larger 1 L containers of dechlorinated water where they were mixed with egg clutches from multiple females. All eggs were incubated inside a greenhouse with moderately fluctuating day/night temperatures. Eggs were checked daily until they begin to hatch after 10-15 days and first instar larva emerged. The early instars were collected and counted via transfer pipette and separated into groups of 100 individuals. Each group of hatchlings likely contained individuals from multiple clutches, ensuring genetic heterogeneity within each tank. When randomly assigning groups of hatchlings to tanks, each sequential group alternated

between tanks containing the control and predator treatments to further ensure that genetics were not a confounding variable between the two treatments.

Experimental Design

The design of the two developmental experiments consisted of two 16 mesocosm (~1200L cattle tanks) arrays (one for each species) totaling 32 mesocosms. This setup created eight replicates per combination of species and treatment. Each mesocosm was filled with well water and inoculated with 1kg of dried leaf litter and a 1 L aliquot of zooplankton and phytoplankton from a nearby fishless pond to facilitate natural water quality conditions (Morin 1981). Mesocosms were left to age for 7 days, and during that time a fiberglass screen (1.3 × 1.13 mm openings) covered the tanks to prevent colonization. Eight of the mesocosms in each array received one *L. cyanellus* and the other eight remained fishless controls. Finally, all 32 mesocosms received 100 first instar dragonfly larvae for a total of 1600 initial larvae per species. The screens were tightly fitted over the tank and out of the water in order to close the system and prevent any oviposition or colonization, ensuring that treatments do not receive unequal food resources or external predators or competitors. Throughout the course of the experiments, all emerging *E. simplicicollis* and *P. longipennis* adults were captured, measured for total length, and total days to emergence were recorded.

Two separate sets of experiments were conducted to test the consumptive and non-consumptive effects of predatory fish on the development of the two model odonate species. During the summer of 2018, consumptive effects were tested by adding one individual *L. cyanellus* to eight of the 16 tanks in each array without restricting the ability of the fish to traverse its environment or consume dragonfly larvae. During the summer of 2019, the non-

consumptive effects were tested by adding a single caged *L. cyanellus* to eight of the 16 tanks in each array. The cage prevented the fish from causing direct mortality to larvae while still allowing the larvae to receive chemical cues from the fish. Empty cages were placed into control tanks to maintain the standardization of all tanks. Cages were mesh cylinders (height = 0.61m, diameter = 0.58m, volume = 0.16 m³, mesh = 1.3×1.13 mm openings).

Statistical Analysis

The survival rate for each tank was calculated by dividing the total number of emerged adults by the total number of larvae initially added to each tank at the start of the experiment. The survival rate to the adult stage in each treatment (Control vs. Fish) was analyzed using a general linear model ANOVA with treatment as a fixed factor and tank as a random factor using the *lmerTest* package in R (Bates et al. 2015). The length of larval period and body length metrics were also analyzed using general linear models. Larval period and body length models initially included treatment (Control vs. Fish) as a fixed factor, tank survival rate as a covariate to control for changes in larval density, and tank as a random factor. Survival rate had no significant impact on either variable and was dropped from the models. All analyses were set with $\alpha = 0.05$.

Results

Consumptive Effects

One *E. simplicicollis* development tank was excluded from analyses due to fish mortality. Additionally, two *E. simplicicollis* and one *P. longipennis* development tanks were excluded from analyses due to the invasion of *Pantala flavescens*, whose naiads consumed experimental naiads. *E. simplicicollis* began emerging in late-July and continued until early-September. *P. longipennis* began emerging in mid-August and continued until late-September. The sex of all individuals of both species was determined by inspecting the anal appendage for the presence of claspers (Male) or an ovipositor (Female).

At the termination of the experiment, 253 (19.5%) *E. simplicicollis* and 186 (12.4%) *P. longipennis* individuals survived to metamorphosis. The proportion of surviving individuals was significantly affected by the presence of a fish predator (Figure 1.1). In the case of *E. simplicicollis*, the mean survival rate from control tanks was 42.2%, while no individuals from predator tanks survived to the adult stage. In *P. longipennis*, the mean survival rate was 26.0% in the control tanks, and 0.5% in predator tanks, the latter representing only 4 individuals. Due to the lack of survivors from tanks containing the predator treatment, analysis of effects on body size and length of larval period could not be performed.

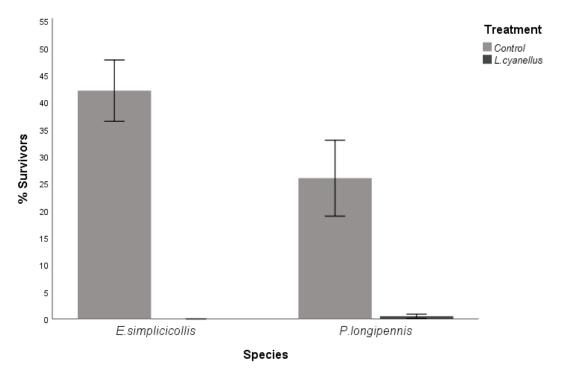


Figure 1.1. Survival rate of control versus uncaged predator treatments for *E. simplicicollis and P longipennis*. Survival rate is affected by cohabitation with *L. cyanellus* in *E. simplicicollis* and *P. longipennis*.

| Table 1.1. Analys | sis of varianc | e for consu | ımptive su | ırvival | | | | |
|-------------------|----------------|-------------|------------|---------|----|----------|--------|------------------------|
| | | E. simpli | cicollis | | | P. longi | pennis | |
| Source | df | SS | F | p (>F) | df | SS | F | <i>p</i> (> <i>F</i>) |
| Fish | 1 | 5744.4 | 65.627 | <0.001 | 1 | 2427.6 | 15.216 | 0.0018 |
| Residuals | 11 | 962.8 | | | 13 | 2074.0 | | |
| Total | 12 | 6707.2 | | | 14 | 4501.6 | | |

Non-Consumptive Effects

One *E. simplicicollis* tank was excluded from analyses due to the invasion of large numbers of dragonflies. *E. simplicicollis* began emerging in mid-July and continued until early-September. *P. longipennis* began emerging in mid-July and continued until late-September.

At the termination of the experiment, 541 (36.1%) *E. simplicicollis* and 696 (43.5%) *P. longipennis* individuals survived to metamorphosis. Caged predators did not affect the probability of survival to metamorphosis for either dragonfly species (Figure 1.2). The mean

survival rate of *E. simplicicollis* in the control treatment was 38.9%, and in the caged predator treatment 35.4%. In *P. longipennis*, the mean survival rate was 44.8% in the controls, and 42.3% in the predator treatment. Length of larval period did not differ in response to predator presence for either *E. simplicicollis* or *P. longipennis* (Figure 1.3a). When accounting for sex, there was still no difference in larval period. (Figure 1.3b, c). Similarly, there was no significant main effect of a caged predator on body length at emergence for either species (Figure 1.4a), even when accounting for sex (Figure 1.4b, c).

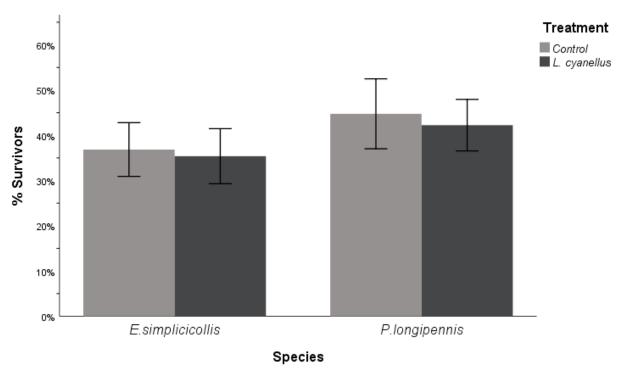
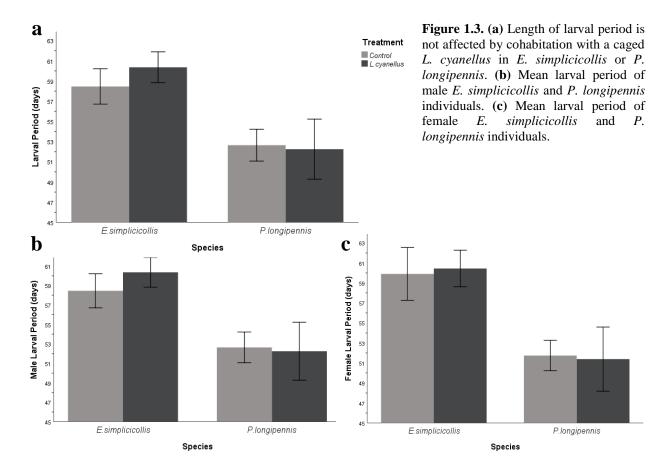


Figure 1.2. Survival rate of control versus caged predator treatments for *E. simplicicollis and P longipennis*. Survival rate is not affected by cohabitation with a caged *L. cyanellus* in *E. simplicicollis* or *P. longipennis*.

| Table 1.2. Analys | sis of varianc | e for non-c | onsumptiv | e survival rate | | | | |
|-------------------|----------------|-------------|-----------|-----------------|----|----------|--------|------------------------|
| | | E. simpli | cicollis | | | P. longi | pennis | |
| Source | df | SS | F | p (>F) | df | SS | F | <i>p</i> (> <i>F</i>) |
| Fish | 1 | 8.2 | 0.030 | 0.865 | 1 | 25 | 0.0677 | 0.798 |
| Residuals | 13 | 3556.7 | | | 14 | 5171 | | |
| Total | 14 | 3564.9 | | | 15 | 5196 | | |



| Table 1.3. Analysis | of varianc | e for lengt | h of larval | period | | | | | |
|----------------------------|------------|-------------|-------------|--------|-----------|----|-----------|--------|------------------------|
| | | | | | All Sexes | | | | |
| | | E. simpli | cicollis | | | | P. longij | oennis | |
| Source | df | SS | F | p (>F) | | df | SS | F | p (>F) |
| Fish | 1 | 3.5 | 0.150 | 0.705 | | 1 | 105.2 | 2.573 | 0.134 |
| Survivors | 1 | 1.4 | 0.060 | 0.810 | | 1 | 15.0 | 0.366 | 0.556 |
| Fish × Survivors | 1 | 0.3 | 0.012 | 0.914 | | 1 | 131.4 | 3.212 | 0.098 |
| Residuals | 11 | 252.7 | | | | 12 | 490.7 | | |
| Total | 14 | 257.9 | | | | 15 | 742.3 | | |
| | | | | | Males | | | | |
| | | E. simpli | cicollis | | | | P. longij | oennis | |
| Source | df | SS | F | p (>F) | | df | SS | F | p (>F) |
| Fish | 1 | 6.7 | 0.389 | 0.545 | | 1 | 84.9 | 1.982 | 0.185 |
| Survivors | 1 | 4.7 | 0.270 | 0.8143 | | 1 | 2.5 | 0.058 | 0.814 |
| Fish × Survivors | 1 | 0.3 | 0.020 | 0.1927 | | 1 | 81.6 | 1.905 | 0.193 |
| Residuals | 11 | 190.4 | | | | 11 | 514.3 | | |
| Total | 14 | 202.1 | | | | 14 | 683.3 | | |
| | | | | | Females | | | | |
| | | E. simpli | cicollis | | | | P. longij | oennis | |
| Source | df | SS | F | p (>F) | | df | SS | F | <i>p</i> (> <i>F</i>) |
| Fish | 1 | 0.8 | 0.019 | 0.891 | | 1 | 90.9 | 1.938 | 0.189 |
| Survivors | 1 | 0.0 | 0.0001 | 0.994 | | 1 | 4.6 | 0.098 | 0.759 |
| Fish × Survivors | 1 | 0.3 | 0.007 | 0.933 | | 1 | 114.3 | 2.438 | 0.144 |
| Residuals | 11 | 479.8 | | | | 11 | 562.5 | | |
| Total | 14 | 480.9 | | | | 14 | 772.3 | | |

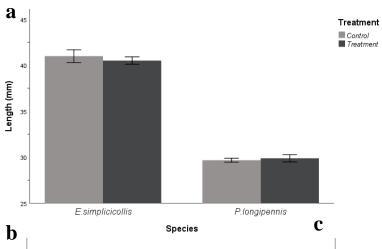


Figure 1.4. (a) Adult body length is not affected by cohabitation with a caged *L. cyanellus* in *E. simplicicollis* or *P. longipennis*. (b) Mean body length of male *E.* and *P. longipennis* individuals. (c) Mean body length of female *E. simplicicollis* and *P. longipennis* individuals.

| b | · | Species | c | | |
|------------------|------------------|---------------|--------------------|------------------|----------------|
| Male Length (mm) | | | Female Length (mm) | | - - |
| 25 | E.simplicicollis | P.longipennis | 25 | E.simplicicollis | P.longipennis |
| | Sp | ecies | | Spe | cies |

| T 11 1 4 4 4 1 : | c · | C 1 1 | 1 .1 | | | | | | |
|----------------------------|--------------|------------|----------|------------------------|-----------|----|-----------|--------|------------------------|
| Table 1.4. Analysis | s of varianc | e for body | length | | | | | | |
| | | | | | All Sexes | | | | |
| _ | | E. simpli | cicollis | | | | P. longij | oennis | |
| Source | df | SS | F | p(>F) | | df | SS | F | p(>F) |
| Fish | 1 | 0.75 | 0.312 | 0.587 | | 1 | 0.22 | 0.318 | 0.583 |
| Survivors | 1 | 2.67 | 1.111 | 0.314 | | 1 | 0.73 | 1.077 | 0.319 |
| Fish × Survivors | 1 | 1.71 | 0.711 | 0.417 | | 1 | 0.50 | 0.735 | 0.408 |
| Residuals | 11 | 26.42 | | | | 12 | 8.14 | | |
| Total | 14 | 31.55 | | | | 15 | 9.59 | | |
| | | | | | Males | | | | |
| | | E. simpli | cicollis | | | | P. longij | oennis | |
| Source | df | SS | F | <i>p</i> (> <i>F</i>) | | df | SS | F | <i>p</i> (> <i>F</i>) |
| Fish | 1 | 1.18 | 0.616 | 0.449 | | 1 | 0.74 | 0.760 | 0.401 |
| Survivors | 1 | 3.44 | 1.792 | 0.207 | | 1 | 0.32 | 0.331 | 0.576 |
| Fish × Survivors | 1 | 1.67 | 0.872 | 0.370 | | 1 | 1.09 | 1.119 | 0.311 |
| Residuals | 11 | 21.11 | | | | 11 | 11.68 | | |
| Total | 14 | 27.4 | | | | 14 | 13.83 | | |
| | | | | | Females | | | | |
| | | E. simpli | cicollis | | | | P. longij | oennis | |
| Source | df | SS | F | p (>F) | | df | SS | F | p (>F) |
| Fish | 1 | 0.24 | 0.069 | 0.798 | | 1 | 0.29 | 0.432 | 0.523 |
| Survivors | 1 | 1.20 | 0.346 | 0.568 | | 1 | 1.12 | 1.695 | 0.217 |
| Fish × Survivors | 1 | 1.38 | 0.398 | 0.451 | | 1 | 0.29 | 0.443 | 0.518 |
| Residuals | 11 | 38.18 | | | | 11 | 7.94 | | |
| Total | 14 | 41.0 | | | | 14 | 9.64 | | |

Discussion

Consumptive Effects

The outcome of the consumptive development study provided irrefutable evidence that dragonfly naiad survival was affected by *L. cyanellus*, but could not determine the predator's effect on other fitness correlates due inadequate survival in the predator treatment. Naiads that share their habitat with a predatory fish are exceptionally unlikely to survive the larval stage, so that non-consumptive effects may be irrelevant. The degree to which predation depressed the survival rate of naiads in this experiment certainly suggests that any clutch of eggs laid with predatory fish is likely to result in a complete loss of reproductive output for the parent.

If *E. simplicicollis* or *P. longipennis* larvae have any behavioral or morphological defenses against fish predators (Johansson and Samuelsson 1994, Johansson 2002, Brodin et al. 2006), they were not evident or effective in this experiment. If they restricted activity to avoid fish, the tradeoff of reduced foraging was too strong as even if they avoided predation, they could not consume enough food to develop and metamorphose in time before environmental conditions became too cold for adult dragonflies to withstand.

Non-Consumptive Effects

The results of the non-consumptive development study revealed that when direct consumption is removed from the system, larval performance of *E. simplicicollis* and *P. longipennis* is still not affected by cohabitation with *L. cyanellus*. The survival rate for both species of dragonflies did not significantly differ between treatments, so there was no predator induced mortality, which has been observed with other odonates (McCauley et al. 2011). The caged fish treatment did not affect either of the evaluated fitness correlates as compared to the

control treatment. Total body length and length of larval period of the experimental group did not differ from the control group, which contradicts *a priori* hypotheses developed based on a review of similarly structured developmental studies in which a majority of invertebrate larvae experience some form of predator-induced plasticity (Benard 2004). However, the results of this experiment are largely in line with those of a study investigating non-lethal effects of predators on the larvae of *Leucorrhinia intacta* by McCauley et al (2011). In that similarly designed experiment, their study species (*Leucorrhinia intacta*) showed no difference in body size between control groups and those subjected to a caged pumpkinseed sunfish (*Lepomis gibbosus*). Conversely, McCauley et al. (2011) found a reduction in survival in the caged fish treatment that was not seen in our experiment.

I provide clear evidence that the larvae of two common species of dragonflies are highly susceptible to mortality by a generalist predatory fish. The reproductive output of an adult female *E. simplicicollis* or *P. longipennis* that oviposits into an environment analogous to that of the experimental mesocosms would likely be reduced to zero due to direct consumption by *L. cyanellus*. The results of the effects of caged predator presence conclusively show that larval dragonflies of these species do not respond morphologically or behaviorally when exposed to cues from a fish predator. The absence of deviation of the measured fitness correlates between control and treatment larvae indicate that the larvae did not exhibit anti-predator responses to chemical cues from caged fish and their foraging and energy intake were not affected.

Non-consumptive effects of predators on the growth rate, life cycle, and survival of prey has ramifications for understanding community dynamics and predator-prey interactions. The works of other researchers on odonate behavior in response to predators are indicative that anti-predator behavior, predator-induced plasticity, and the overall ability to avoid predation by fish

vary on a species to species basis. Whereas the larva of the species used in this experiment did not display any tolerance to fish, odonate species such as Leucorrhinia intacta (McCauley et al. 2011), Leucorrhinia dubia (Johansson and Samuelsson 1994), and some members of genus Enallagma (McPeek 1989) do show behavioral and/or morphological responses to fish that make them at least somewhat tolerant to fish predation. The ability or inability of odonate larvae to detect chemical cues from fish predators and use those signals to adjust their behavior and resource allocation has implications for community assembly as it may explain why odonate species that are sympatric as aerial adults may not be found together as larvae in the same aquatic habitat patches (Morin 1984, Semlitsch 1988, McPeek 1990). The consumptive and nonconsumptive effects of fish on prey fitness have broader implications due to the continued expansion of human society into natural spaces, especially as wetland habitat is lost and novel fish species are introduced into new and previously fishless habitats via anthropogenic mediation. In these conditions, fish intolerant species are more likely to be threatened with population decline, notably rare endemic species which tend to be specialists when it comes to their habitat requirements (Sahlen 2005, Suhonen et al. 2014, Khelifa and Mellal 2017). For the advancement of our understanding of community dynamics, predator-prey interactions, and biodiversity conservation, the repercussions of consumptive and non-consumptive effects of predators on their prey warrants further scientific investigation.

CHAPTER 2:

OVIPOSITION SITE SELECTION OF *PACHYDIPLAX LONGIPENNIS*, *PANTALA FLAVESCENS*, AND *LIBELLULA INCESTA* IN RESPONSE TO *LEPOMIS CYANELLUS*

Introduction

The reproductive success of many insects is highly dependent on the oviposition site choice of adult females (Rausher 1983, Singer 1984, Petranka and Fakhoury 1991, Resetarits 1996, McGuffin et al. 2006). Heavy selection pressure due to variation in habitat quality (e.g., predators, competitors, resources) and the strong effect it has on offspring performance has driven the evolution of non-random habitat site selection. This process more accurately explains the uneven distribution of species and individuals across a metacommunity landscape than other community assembly processes such as random distribution and post-colonization species sorting (Resetarits 1996, Leibold et al. 2004, Rieger et al. 2004). Oviposition habitat selection is a form of parental care where females assess patch quality in order to select a habitat that will maximize offspring growth and survival, thus maximizing their genetic contribution to the next generation (Rausher 1983, Singer 1984, Resetarits and Wilbur 1989, Rieger et al. 2004). Aquatic insects have relatively short life-spans at sexual maturity and experience relatively few reproductive events; in addition, many aquatic insects also deposit their entire reproductive output into a single habitat patch. These combined traits emphasize the importance of oviposition habitat selection because a single mistake can greatly diminish or obliterate fitness in a breeding adult (Blaustein 1999). Individuals selecting habitats that maximize resource availability, minimize

competition for space and resources, and avoid/limit the effects of predators will maximize their potential reproductive success by improving the performance of their offspring (Rausher 1983, Singer 1984, Werner and Gilliam 1984, Resetarits 1996, Relyea 2001, 2007).

Many aquatic insects utilize fishless or temporary habitats due to their susceptibility to predation by residents of many permanent aquatic habitats, particularly fish (Petranka and Fakhoury 1991, Resetarits 1996, Wellborn et al. 1996). Consumption, as well as nonconsumptive effects (i.e., the threat of predation), by fish induce a heavy fitness cost for aquatic insecs, and in response, some species of insects have evolved sensory and behavioral adaptations to detect predatory fish via chemical cues and subsequently avoid patches containing them (Petranka and Fakhoury 1991, Resetarits 1996, Silberbush and Blaustein 2008, Eveland et al. 2016). Patterns of colonization in response to predators have been well documented in multiple aquatic taxonomic groups including Order Coleoptera, Order Hemiptera, Family Culicidae, Order Anura, and Order Caudata (Petranka and Fakhoury 1991, Kats and Sih 1992, McGuffin et al. 2006, Binckley and Resetarits 2008, Shaalan and Canyon 2009). Colonization rates and population and community dynamics of aquatic beetles are significantly impacted by the presence of fish predators through decreased abundance, species richness, and altered species composition (Binckley and Resetarits 2005, Resetarits and Pintar 2016). Tree frog species Hyla chrysoscelis, Hyla squirella, and Hyla femoralis are all known to avoid laying eggs in habitat patches containing fish that are predators of their offspring (Resetarits and Wilbur 1989, Binckley and Resetarits 2002, Rieger et al. 2004). Similarly, mosquitoes of the genus *Culex* strongly avoid ovipositing in habitats containing the Western Mosquitofish (Gambusia affinis) (Angelon and Petranka 2002, Eveland et al. 2016).

Habitat selection by odonates on the other hand, is not well understood, especially for dragonflies (Anisoptera). Odonate larvae are susceptible to fish predation and there are significant differences between the odonate community structures in aquatic habitats that contain fish and those without fish (McPeek 1990, Johansson and Brodin 2003, Johansson et al. 2006). Larval dragonflies (naiads) play an important role as mesopredators in fishless ponds because they have the ability to influence a significant portion of the aquatic invertebrate and amphibian communities through both consumptive and non-consumptive effects (Fauth 1999, Meadows et al. 2017). As both aquatic larvae and terrestrial adults, anisopterans are voracious predators that play a role in providing a top-down effect that limits populations of abundant invertebrate primary consumers and lower level heterotrophs (Shaalan and Canyon 2009, Meadows et al. 2017). In addition to consumptive effects, evidence suggests that the presence of dragonfly naiads can significantly deter mosquito oviposition (Stav et al. 2000). These qualities have the potential to make odonates an effective biocontrol agent of mosquitoes and other insect vectors of disease that develop in aquatic habitats (Mandal et al. 2008, Shaalan and Canyon 2009). These top-down consumptive and non-consumptive effects on grazing organisms by dragonfly naiads can contribute to a trophic cascade in the food web, influencing the abundance of zooplankton, phytoplankton, and periphyton in aquatic habitats (Stav et al. 2000, Knight et al. 2005).

According to a global assessment of the conservation status of odonates, approximately 10–15% of odonate species are threatened with extinction, and a high proportion of those are endemic species with specialized niches (Clausnitzer et al. 2009). The primary causes of extinction in odonates are habitat destruction, pollution, and the establishment of exotic fish facilitated by humans (Eby et al. 2006, Clausnitzer et al. 2009). A better understanding of oviposition habitat selection by odonates can facilitate the conservation of threatened species.

Predatory fish may create an ecological trap, wherein sensory cues emitted from the habitat are dishonest indicators of the true quality of a site (Delibes et al. 2001). These ecological traps may deceive adult females to leave their progeny in an environment in which they are very unlikely to survive to adulthood (Horváth et al. 1998, Schlaepfer et al. 2002, Raebel et al. 2010, Šigutová et al. 2015).

Current and historical oviposition choice literature primarily focuses on insect species in Order Coleoptera, Order Hemiptera, Family Culicidae, and the class Amphibia, specifically Order Anura due to their prevalence and convenience as model systems. These studies have tested a multitude of factors, including predator presence, resource availability, water quality, canopy cover, and competitor density (Binckley & Resetarits, 2009; Pintar & Resetarits, 2017; Fairchild, Faulds, & Matta, 2000). For many species, the factor bearing the largest effect on the oviposition decision of females is the presence/absence of predators (Petranka et al. 1987, Binckley and Resetarits 2002, Silberbush and Blaustein 2008, Resetarits and Pintar 2016, Resetarits and Silberbush 2016). The presence of predatory fish results in strong oviposition and colonization avoidance in anurans and aquatic insects, and the addition of fish into previously fishless habitats results in sharp declines in existing populations of these groups (Resetarits, 2001; Resetarits & Binckley, 2009; Resetarits, Rieger, & Binckley, 2004; Silberbush & Blaustein, 2008). There are few studies on the effects of predators on odonate oviposition site choice, and most survey behavior at natural ponds, making it difficult to isolate factors contributing to habitat selection decisions. Controlled studies have the advantage of reducing confounding factors as well as limiting observational errors that are likely to occur in visual encounter surveys of natural ponds.

The primary mechanism utilized by odonates to detect predators is also debated. As opposed to other orders of aquatic insects that rely primarily on chemical cues from predator released kairomones (Petranka and Fakhoury 1991, Relyea 2001, Silberbush and Blaustein 2008), a study by McGuffin et al. (2006) did not support the hypothesis that Enallagma damselflies (Zygoptera) could detect the chemical cues of predatory fish. This study, as well as others (Horváth et al. 1998, Wildermuth 1998, Šigutová et al. 2015), suggest that visual cues, particularly polarotaxis (detection of reflected polarized light), are the dominant sensory modalities utilized by odonates for selecting oviposition habitat based on characteristics such as depth, vegetation structure, and trophic state of habitat. It has yet to be tested whether fish can be detected via effects of reflectance of polarized light, but using vision alone to spot fish would be unreliable. Another study by McPeek (1989) determined that habitat selection in these Enallagma damselflies was not due to active selection in response to habitat quality, but was instead due to philopatry to natal ponds. Additionally, these *Enallagma* damselflies were unable to discriminate between fishless and fish-containing habitats when given the choice (McPeek 1989). These uncertainties demonstrate the need for further research into the oviposition selection ecology of odonates, especially in Anisoptera which may use very different tactics for oviposition site selection than Zygoptera. This may stem from their larger size, higher trophic level, and propensity to disperse long distances as adults (Utzeri et al. 1984, McPeek 1989, Michiels and Dhondt 1991, Conrad et al. 1999).

Neural physiological studies of the most ancient lineage of insects, the bristletails (Archaeognatha), found that the brain of these ancient insects did not possess mushroom bodies, which are responsible for olfactory processing, and thus they areanosmic (no sense of smell) (Wheeler et al. 2001, Strausfeld et al. 2009, Regier et al. 2010). Likewise, Order Odonata is an

ancient taxa that represents one of the basal groups (Palaeoptera) from which modern flying insects (Neoptera) are evolutionarily derived, and likely lack well-developed chemosensory capabilities due to their close phylogenic proximity to other ancient insect lineages such as Archaeognatha (Strausfeld et al. 2009, Meusemann et al. 2010, Crespo 2011). The brain structure of odonates does contain mushroom bodies, but those bodies lack calyces and antennal lobes, both responsible for receiving olfactory input (Svidersky and Plotnikova 2004, Strausfeld et al. 2009, Crespo 2011). External antennae of odonates are highly reduced in size compared to insects that possess olfactory receiving brain structures (Strausfeld et al. 2009, Crespo 2011) (Figure 2.1). It is for these reasons, dragonflies are suggested to be anosmic, and cannot detect volatile chemicals from the air (Crespo 2011).

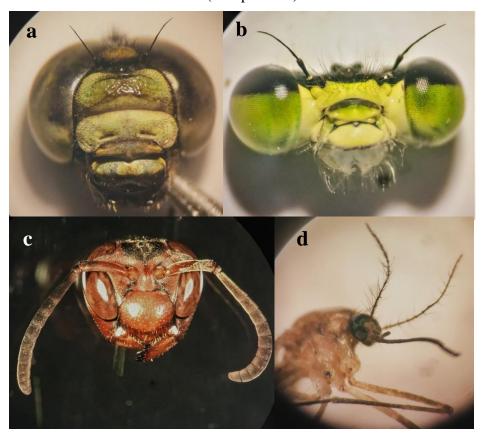


Figure 2.1. Comparison of external antennae size and complexity between (a) dragonfly (*Gomphaeschna furcillata*), (b) damselfly (*Ischnura posita*), (c) paper wasp (*Polistes carolina*), and (d) mosquito (*Culex restuans*). Members more modern insect lineages such as Orders Hymenoptera and Diptera are highly capable of olfactory reception, evident by their large complex antennal structures, while antennae are reduced in size and filiform in shape in odonates. Photo credit: Kevin M Potts.

Here, I investigated the effect of predatory fish on the habitat selection behavior of anisopterans using an outdoor mesocosm experiment in naturally colonized experimental landscapes. I created controlled environments where test variables could be easily and reliably manipulated and regulated to investigate the frequency of dragonfly oviposition between two treatments: fishless control pools and pools containing green sunfish (*Lepomis cyanellus*). I hypothesized that female dragonflies would avoid sites that incur fitness costs to their offspring by choosing to oviposit primarily in fishless habitat patches.

Materials and Methods

Study Species

The anisopteran models in my experiment were of the family Libellulidae, a highly abundant dragonfly family across North America and at my field site (UMFS). Libellulids are ideal for this study because they employ an exophytic oviposition strategy where females deposit their eggs in open water by repeatedly dipping the terminal segments of their abdomen into the water while in flight as opposed to ovipositing endophytically (inserting eggs into macrophytes) or epiphytically (laying eggs on the surface of macrophytes). Weekly dragonfly surveys were performed at the study site in order to identify all species present during the experiment (Table 2.1).

Table 2.1. List of Anisoptera species of family Libellulidae that have been personally identified at the UMFS and the relative abundance of each species.

| Genus | Species | Common Name | Relative Abundance |
|---------------|--|--|---|
| Libellula | luctuosa auripennis incesta cyanea flavida semifasciata | Widow Skimmer Golden-winger Skimmer Slaty Skimmer Spangled Skimmer Yellow-sided Skimmer Painted Skimmer Great Blue Skimmer | Common Uncommon Common Rare Uncommon Rare |
| Celithemis | elisa eponina fasciata | Calico Pennant Halloween Pennant Banded Pennant | Common Uncommon Common |
| Tramea | lacerata Carolina onusta | Black Saddlebags Carolina Saddlebags Red Saddlebags | Uncommon Uncommon Common |
| Ladona | deplanata | Blue Corporal | Common |
| Pachydiplax | longipennis | Blue Dasher | Common |
| Erythrodiplax | minuscule | Little Blue Dragonlet | Uncommon |
| Erythemis | simplicicollis | Eastern Pondhawk | Common |
| Pantala | flavescens | Wandering Glider | Common |
| Plathemis | lydia | Common Whitetail | Common |
| Perithemis | tenera | Eastern Amberwing | Uncommon |

Lepomis cyanellus (green sunfish) was used as the predator in this study. Lepomis cyanellus is an effective generalist predator with a relatively large body and gape size that allow for the consumption of sizable prey items, including dragonfly naiads. L. cyanellus is a common predator encountered by dragonfly larvae found in many permanent bodies of fresh water in North America (Lee et al. 1983). L. cyanellus is known to repel mosquito and beetle colonization and its chemical cues have strong effects on larval gray tree frog behavior (Petranka et al. 1987, Resetarits and Pintar 2016, Bohenek et al. 2017).

Experimental Design

To test the effect of fish on dragonfly habitat site selection, I constructed nine spatial blocks using mesocosms (~1200 L cattle tanks). Each block was composed of equal parts of two treatment types: 1) Fishless control tanks and 2) predator tanks containing two *L. cyanellus*. Blocks contained four mesocosms in 2018, and were reduced to two mesocosms in 2019. All tanks within each block were placed 7m apart. Each block was constructed at a different geographical location at the UMFS as anisoptera species are not distributed evenly across the landscape (Potts, personal observation) (Figure 2.2). All mesocosms were prepared in an identical fashion to the development studies in regards to water volume (1000 L), leaf litter (1 kg), and plankton (1 L) then covered with a fiberglass screening. Half of the mesocosms in each block received two equivalently sized *L. cyanellus* assigned randomly and the screens were pushed down into the water to allow colonization and create a physical barrier between the fish and any ovipositing adult dragonflies or other colonizing insects. All fish used in the experiment were captured from ponds located within the UMFS.

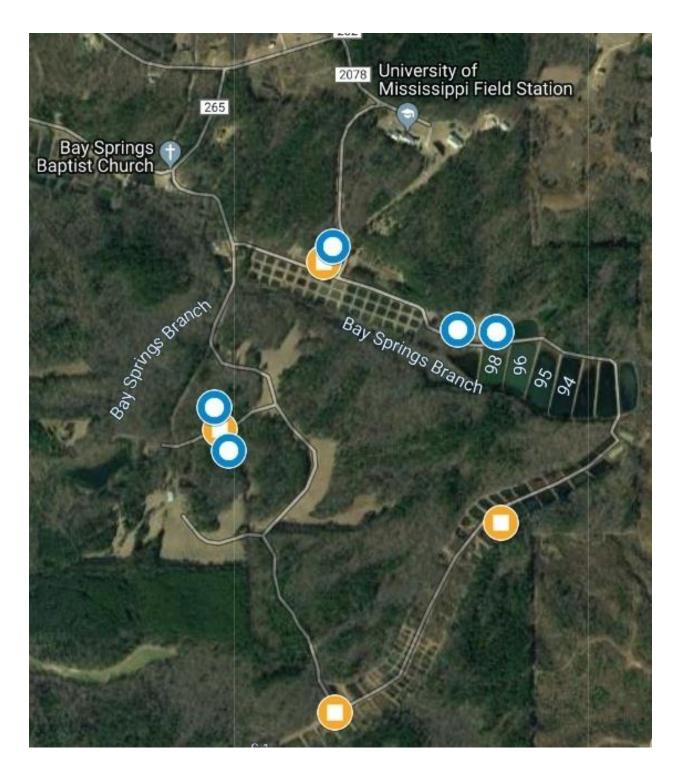


Figure 2.2. Locations of blocks in oviposition experiment at UMFS. Square symbols represent 2018 sites, and circle symbols represent 2019 sites.

To observe the oviposition behavior in real time at each mesocosm, I mounted 170° wide-angle action camera next to each mesocosm. Each camera was capable of recording video at a quality of 1080p at a frame rate of 60fps, providing sufficient quality to identify dragonflies to the species level and to clearly observe their oviposition behavior. Mesocosms were filmed simultaneously for approximately 80-90 minutes per day within the time window of 10:00-15:00 h, which is the period when most dragonfly oviposition occurs (Koenig and Albano 1985). Video recording occurred on days with optimal conditions for dragonfly activity: plentiful direct sunlight, moderate to high temperatures, and no precipitation. This experiment began in May 2018 and ended in September 2019.

Oviposition behavior was quantified using two metrics, the number of oviposition visits and the number of abdomen dips for each species observed. An oviposition visit is defined by a single female dragonfly depositing eggs in the same patch by dipping once or multiple times in succession without prolonged interruption. Oviposition dips are the number of times a female dragonfly dips its abdomen into the water during a single oviposition visit. Oviposition dips are used as a proxy for the actual number of eggs laid during a single event, which is virtually impossible to assess directly and accurately under natural or semi-natural conditions (Waage 1978, McVey 1984, Khelifa and Zebsa 2012).

Statistical Analysis

Statistical analysis of oviposition site choice was conducted using linear mixed model ANOVA in R using the lme4 package (Bates et al. 2015) with block as a random factor and treatment as a fixed factor. Each species was analyzed separately for number of oviposition visits and number of abdomen dips in each of the two treatment types. Oviposition visits and abdomen

dips data were transformed using a square root + 0.5 transformation (Sqrt(x + 0.5)). All analyses set $\alpha = 0.05$.

Results

During the summers of 2018 and 2019, roughly 1500 hours of video footage was recorded. Six species of dragonflies were observed ovipositing in the experiment. Of these six, only three species, in three different genera within Family Libellulidae, were observed with enough frequency to warrant analysis: *Pachydiplax longipennis* (blue dasher), *Pantala flavescens* (wandering glider), and *Libellula incesta* (slaty skimmer).

The control treatment received 31 oviposition visits from P. longipennis (4.3 \pm 3.6, tank mean \pm SE), 32 oviposition visits from P. flavescens (4.0 \pm 1.7), and 11 oviposition visits from P. longipennis (4.6 \pm 2.0), 35 oviposition visits from P. flavescens (4.8 \pm 2.3), and 9 oviposition visits from P. longipennis (4.6 \pm 2.0). There was no significant treatment effect of the presence of P. P0. P1. P1. P2. P3. There was no significant treatment effect of the presence of P3. P3. P4. P5. P6. P6. P8. P9. P9.

The number of dips per visit in the control treatment for *P. longipennis* was 41.2 ± 7.8 , *P. flavescens* 10.8 ± 1.8 , *L. incesta* 12.6 ± 3.9 . The number of dips per visit in the *L. cyanellus* treatment for *P. longipennis* was 28.0 ± 5.0 , *P. flavescens* 12.2 ± 1.9 , *L. incesta* 12.1 ± 5.4 . There was no significant treatment effect of the presence of *L. cyanellus* on the number of dips per oviposition visit for any of the three dragonfly species observed (Fig 2.4).

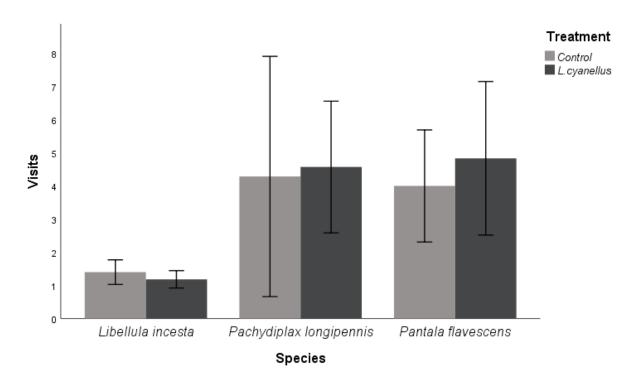


Figure 2.3. Mean oviposition visits for three focal dragonfly species across treatment types. There were no significant predator effects on any species.

| Table 2.2. Analysis of variance for oviposition visits | | | | | | | |
|---|----------|-------|-------|--------|---------|--|--|
| Species: L. incesta | | | | | | | |
| Source | Estimate | SE | df | t | p(> t) | | |
| Fixed Effects | | | | | | | |
| Fish | -0.079 | 0.149 | 13.51 | -0.529 | 0.605 | | |
| Random Effects | Variance | SD | | | | | |
| Block | 0.052 | 0.227 | | | | | |
| Residuals | 0.117 | 0.342 | | | | | |
| Species: P. longipennis | | | | | | | |
| Source | Estimate | SE | df | t | p(> t) | | |
| Fixed Effects | | | | | | | |
| Fish | 0.335 | 0.553 | 8.752 | 0.605 | 0.560 | | |
| Random Effects | Variance | SD | | | | | |
| Block | 0.765 | 0.874 | | | | | |
| Residuals | 1.068 | 1.033 | | | | | |
| Species: P. flavescens | | | | | | | |
| Source | Estimate | SE | df | t | p(> t) | | |
| Fixed Effects | | | | | | | |
| Fish | 0.011 | 0.149 | 8.116 | 0.075 | 0.942 | | |
| Random Effects | Variance | SD | | | | | |
| Block | 1.131 | 1.064 | | | | | |
| Residuals | 0.069 | 0.258 | | | | | |

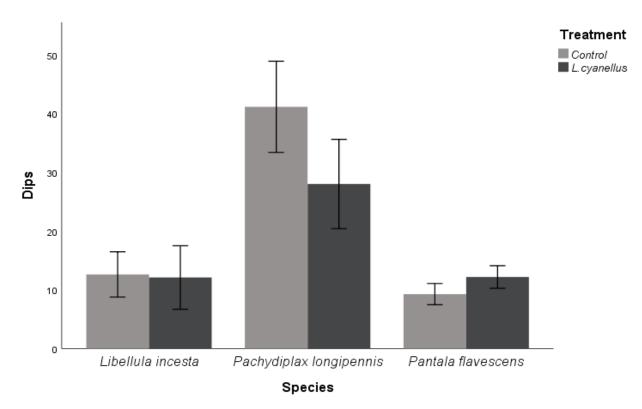


Figure 2.4. Mean dips per oviposition visit for three focal dragonfly species across treatment types. There were no significant predator effects on any species.

| Table 2.3. Analysis of variance for abdomen dips per oviposition visit | | | | | | |
|--|----------|-------|-------|--------|---------|--|
| Species: L. incesta | | | | | | |
| Source | Estimate | SE | df | t | p(> t) | |
| Fixed Effects | | | | | | |
| Fish | -0.145 | 0.548 | 16.03 | -0.199 | 0.845 | |
| Random Effects | Variance | SD | | | | |
| Block | 0.329 | 0.573 | | | | |
| Residuals | 2.518 | 1.587 | | | | |
| Species: P. longipennis | | | | | | |
| Source | Estimate | SE | df | t | p(> t) | |
| Fixed Effects | | | | | | |
| Fish | -1.317 | 0.821 | 61 | -1.604 | 0.114 | |
| Random Effects | Variance | SD | | | | |
| Block | 0.000 | 0.000 | | | | |
| Residuals | 10.62 | 3.259 | | | | |
| Species: P. flavescens | | | | | | |
| Source | Estimate | SE | df | t | p(> t) | |
| Fixed Effects | | | | | | |
| Fish | 0.424 | 0.328 | 65 | 1.288 | 0.202 | |
| Random Effects | Variance | SD | | | | |
| Block | 0.000 | 0.000 | | | | |
| Residuals | 1.807 | 1.344 | | | | |

Discussion

The results of the oviposition study reveal that none of the dragonfly species observed in this experiment showed a preference when given the choice between habitats with and without fish predators. For both number of visits and number of abdomen dips per visit, there was no significant effect of fish presence on oviposition habitat selection. There was some suggestion of deviation between treatments in the number of dips per visit in *P. longipennis*, albeit a weak difference. This keeps the door open to the possibility that *P. longipennis* females may lay more eggs during visits to fishless mesocosms than during visits to fish mesocosms, even though both types are visited with equal frequency, but whether that difference would be biologically meaningful for offspring survival and adult fitness is doubtful.

The results of this experiment suggest possible explanations, which are not mutually exclusive: 1) sensory mechanisms used by odonates to locate and select aquatic habitat cannot perceive sensory cues emitted by *L. cyanellus*. Avoidance of habitats containing *L. cyanellus* and other closely related sunfish via detection of predator-released kairomones has not been documented for odonates, but has been recorded in numerous species of treefrogs, mosquitoes, beetles, and other families of aquatic invertebrates with complex life cycles (Petranka et al. 1987, Eveland et al. 2016, Resetarits and Pintar 2016). The inability of any observed odonate species to avoid predator patches in this experiment demonstrates that odonates may rely on senses other than chemoreception for habitat selection such as polarotaxis, for which no current evidence exists to suggest it can be used for predator detection (Horváth et al. 1998, Wildermuth 1998). 2) Odonates primarily rely on cues from alternative environmental factors to determine offspring habitat quality. Though predators have a strong effect on non-random habitat selection in many species, it is not the only factor colonizing organisms consider. Published observations of

dragonfly oviposition preferences in natural ponds suggest that females are attracted to structural factors such as pond size, depth, canopy cover, and vegetation structure despite the presence of fish (Wildermuth 1994, Šigutová et al. 2015, French and McCauley 2018). This is reinforced by the fact that only 3 out of 20 total observed species frequently visited experimental mesocosms. 3) Odonates utilize a bet-hedging/risk-spreading strategy of habitat selection in which they deposit small numbers of eggs into a variety of different habitat patches in the hope that at least some of them are viable for offspring development. Dragonflies' capability to spread an egg clutch across multiple habitat patches in conjunction with their strong capacity to traverse vast distances may offset the cost of laying some of their eggs in fish habitats and is a possible explanation for why the ability to chemically detect potential aquatic predators is absent in adult odonates but exists in taxa that deposit entire clutches of eggs into a single habitat patch in a single event. The degree of risk spreading varies with dragonfly species. One species observed in this experiment, P. flavescens, is known for its transition through many habitat changes during the release of a single clutch of eggs (Schenk et al. 2004). A fourth scenario, that of philopatry as a means of avoiding fish – you lay eggs in the patch from which you emerged – is obviated here by the fact that none of these individuals emerged from our experimental patches or previous patches set up in the same locality. In addition, P. flavescens travel hundreds of miles following weather fronts seeking oviposition sites, so that philopatry is not a viable option (Anderson 2009, May 2013). To the contrary, this specific life history strategy of choosing newly formed pools may constitute an effective predator avoidance mechanism (Utzeri et al. 1984, McPeek 1989).

Other studies observing habitat selection in anisopterans record instances of all adults visiting a possible oviposition site regardless of sex or whether oviposition occurred (Steytler and Samways 1995, Samways and Steytler 1996, French and McCauley 2018). This experiment

focused explicitly on female oviposition activities due to the lack of evidence suggesting male presence alone is correlated to a habitat's suitability for offspring development. Presence alone can account for non-reproductive activities such as feeding, so only reproductive activities were recorded for data analysis. It should be noted that numerous male *P. longipennis* individuals were observed patrolling a large majority of the experimental mesocosms of both treatments, even at those that received very little or received zero oviposition visits from females.

Throughout this experiment, it was evident that male territorial behavior played a role in determining female oviposition. Male-male aggressive behavior was the most common territorial interaction displayed. *P. longipennis* females were often seen being chased away from mesocosms or having their oviposition interrupted before completion by males defending their territorial claims. Females that were not guarded by their mate were frequently antagonized and sometimes re-copulated by new males, preventing or cutting short oviposition visits. These observations are in line with normal territorial behavior for this species (Sherman 1983). In limited instances, male *P. longipennis* males were observed chasing off members of other dragonfly species as well.

Anecdotal evidence of predation risk to the adult female during oviposition was also observed during this experiment. *L. cyanellus* individuals were frequently caught on camera stalking and following *P. longipennis* females while they deposited eggs close to the water surface. On a few occasions, fish attempted to jump from the water and consume ovipositing dragonflies from beneath the fiberglass screening, deterring that individual from laying eggs and in most cases causing them to flee. In a subset of those instances, the female dragonfly promptly returned to continue ovipositing at the same location, seemingly undeterred by the direct danger posed by the predatory fish. Direct mortality of ovipositing female dragonflies by sunfish was

observed in natural ponds during field surveys, albeit these occurrences were quite rare (Potts, personal observation). While this study focused on habitat quality for larval performance, it is unclear if the predation threat of fish on ovipositing dragonflies plays a role in habitat site selection.

I conclude that the presence of a fish predator does not affect the oviposition site selection behavior in dragonflies. One advance of this study is the differentiation of two metrics used to quantify oviposition, oviposition visits and abdominal dips, each of which can provide different information used to draw conclusions on questions relating to habitat selection. The results of this study show that none of the observed species of dragonfly exhibited a preference towards fish or fishless habitats under the context of either metric of oviposition. These results suggest that adult dragonflies cannot detect fish due to the anosmic nature of their brain and/or that alternative biotic and abiotic factors may play a more essential role in how dragonflies select habitat for their offspring that maximizes larval fitness and performance. Further research testing a variety of environmental cues as well as those of other predators and competitors are necessary to better understand how complex life history decisions are made by odonates.

The mismatch observed between the results of the developmental experiments and the oviposition site selection experiment reinforce the findings of Raebel et al. (2010) in which they found a large discrepancy between ovipositing adult surveys and exuviae surveys at 29 ponds, and conclude that adult dragonflies overestimate pond quality when laying eggs. This general mismatch of results produces more questions about how dragonflies make habitat selection decisions in the face of a myriad of biotic and abiotic conditions that may affect their offspring's survival. However, there was a congruency in dragonflies' inability to chemically detect and respond to fish as adults and larvae in both studies. This work shows that the mechanism utilized

by anurans and more modern insects (Hemiptera, Coleoptera, Diptera, ect.) to chemically detect fish predators is not present in odonates and suggest that this sensory capability evolved later in the evolutionary tree of insects during the radiation of Infraclass Neoptera.

I have demonstrated that odonates exhibit an oviposition strategy that neglects the risk of potential predation to their offspring, a cost that can be negated by their ability to disperse their egg clutch amongst numerous habitat patches and localities. This strategy is in stark contrast to that of many other aquatic insect taxa whose habitat selection strategy revolves around the adaptation and use of chemical cues to avoid ovipositing in habitats bearing predators to their offspring. It remains unclear how the anosmic nature and less predictable oviposition behavior of odonates influences community structure and patterns of species distributions across multiple spatial scales. Given the important ecological role odonates serve as mesopredators and their increasingly threatened status, a better understanding of dragonfly oviposition site selection behavior is worthy of further scientific inquiry despite the methodological challenges of using these insects as models.

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VITA

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- 2019 **Potts, K. M.** and W. J. Resetarits, Jr. Oviposition Site Choice and Larval Development of Odonates (Anisoptera) in Response to a Predatory Fish. Ecological Society of America, Louisville, KY, August 2019.
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