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HABITAT CHARACTERISTICS THAT DRIVE HABITAT SELECTION IN *HYLA*
CHRYSOSCELIS (SOUTHERN GRAY TREEFROG) AND AQUATIC INSECTS

A Thesis:
Presented in partial fulfillment of requirements
for the degree of Master of Science
in the Department of Biology
The University of Mississippi
May 2023

by

Ruric O. Bowman

May 2023

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ABSTRACT

Organisms must navigate complex landscapes selecting suitable habitats that will minimize costs to themselves or their offspring and maximize fitness. Habitat characteristics influence a patch's quality and organisms may prioritize certain characteristics when selecting among patches. Canopy cover and patch size are two important habitat characteristics that organisms use to evaluate a patch's quality. To understand whether canopy cover or patch size are a better determinant of patch quality for southern gray treefrogs, *Hyla chrysoscelis* and aquatic insects I implemented a compromise design that provided two suboptimal patch types (large, closed canopy and small, open canopy patches) for colonization. A total of 158,980 *H. chrysoscelis* eggs were collected during the experiment with the majority laid in large, closed canopy patches. The preference of *H. chrysoscelis* for large, closed canopy patches suggests that patch size is prioritized over canopy cover when selecting higher quality patches. Aquatic insects showed mixed responses, but most species preferred large, closed canopy patches with only one species *Bidessonotus inconspicuus* preferring small, open canopy patches. These results demonstrate that individual species preferences for one patch type over another drive differences in aquatic community assemblages. These studies show the complexity of habitat selection in colonizing aquatic organisms and how individual species prioritize certain habitat characteristics over others to select patches with the highest quality. Results from studies like this can help create more nuanced and balanced approaches for restoring and conserving vital aquatic habitats. The simplistic approach of "build it and they will come" may not be entirely true or it may lead

to the creation of low-quality patches that cannot support the large diversity of aquatic organisms.

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BACKGROUND

Habitat selection is an important decision-making process that can impact individuals (Losier et. al., 2015, Paterson and Blouin-Demers, 2018), populations (Pulliam and Danielson, 1991, Matthiopoulos et. al., 2015), and entire communities (Resetarits et. al., 2021). Organisms must assess the surrounding environment and make decisions that will provide the greatest benefit and minimize potential costs, thereby maximizing fitness. When organisms select a patch for short-term use, such as grazing sites for ungulates (Allred et. al., 2011, Díaz Falú et. al., 2014) and basking sites for turtles (Dubois et. al., 2009), they are practicing transient habitat selection (Resetarits, 2021). Identifying optimal patches that provide resources needed at that moment is important for an individual's fitness (Losier et. al., 2015, Matthiopoulos et. al., 2015, Paterson and Blouin-Demers, 2018). Mobile organisms that aren't confined to one habitat and have the ability to move freely between different patches may have an advantage over sessile or less-mobile organisms since they can easily escape potential threats and leave when resources become scarce (Hugie and Grand, 1998).

Many organisms require habitats that can support either themselves or their offspring for extended periods of time (Resetarits and Wilbur, 1989, Price, 2010, Dumas et. al., 2014, Lagos et. al., 2015, Resetarits and Pintar, 2016, Tavares et. al., 2018, Han et. al., 2019, Cuartas-Villa and Webb, 2021, Gould et. al., 2021, Ensaldo-Cárdenas et. al., 2021, Eversole and Henke, 2022). It is critical for organisms that select habitats for long-term use, referred to as demographic habitat selection (Resetarits, 2021), to colonize patches that optimize their fitness prospects. Examples include attachment sites for sessile marine invertebrates (Price, 2010, Dumas et. al.,

2014, Lagos et. al., 2015), nesting sites for birds and reptiles (Han et. al., 2019, Cuartas-Villa and Webb, 2021, Eversole and Henke, 2022), oviposition sites for amphibians (Resetarits and Wilbur, 1989, Gould et. al., 2021) and colonization/oviposition sites for aquatic invertebrates (Resetarits and Pintar, 2016, Tavares et. al., 2018, Ensaldo-Cárdenas et. al., 2021). Failing to select optimal habitats for offspring survival and growth can have dramatic impacts on individual fitness, population dynamics, and population persistence (Matthiopoulos et. al., 2015).

Aquatic habitats vary naturally along environmental gradients and across landscapes. This environmental variation forces organisms to make complex decisions by weighing a variety of environmental factors simultaneously (Resetarits, 2021, Resetarits et. al., 2021). For example, nutrient availability (Pintar et. al., 2018), temperature (McNamara et. al., 2021), and ultraviolet light (Ensaldo-Cárdenas et. al., 2021) can all influence patch selection by aquatic organisms. Patch quality is also influenced by what other organisms are present within a patch (Resetarits and Binckley, 2009, Resetarits et. al., 2018). Whether a patch contains predators, competitors, or even conspecifics may impact patch quality and deter colonization (Resetarits and Wilbur, 1989, Resetarits and Binckley, 2009, Resetarits et. al., 2018). The endless combination of environmental variables and organismal pressures simultaneously make each patch unique and limits the number of ideal patches.

Selection of suitable habitats may be increasingly difficult in human-altered ecosystems because cues used to assess patch quality may be less reliable (i.e., ecological traps, Battin, 2004, Robertson and Hutto, 2006). Anthropogenic activities such as introducing fish into previously fishless habitats, draining temporary aquatic habitats, destroying surrounding forests, and increasing nutrients through runoff have all dramatically altered aquatic habitats that aquatic organisms require to complete their life cycle (Stuart et. al., 2004, Sievers et. al., 2018, Irfan and

Alatawi, 2019 a review). With anthropogenic activities degrading and reducing the number of available patches, organisms may struggle to find a patch suitable for colonization.

The high variability of natural habitats coupled with anthropogenic degradation makes it highly unlikely that “perfect” habitats exist. Therefore, many organisms must compromise when deciding what patches to colonize (Resetarits, 2021). For example, one patch might have an abundance of resources, but also contain many competitors, while another might have no competitors but limited resources. Adults may therefore weigh these factors and prioritize characteristics that are the most important for offspring growth and survival.

Each species has its own unique criteria for identifying ideal patches which promotes species sorting and creates different community structures (Resetarits et. al., 2021).

Understanding why organisms prioritize one patch over another provides insight into what drives patch selection and how organisms determine which characteristics are the most important. This can aid conservation programs in creating and preserving habitats these organisms will use for reproduction and colonization. With the ever-increasing pressures humans are imposing on the natural world it is important to decipher what factors drive habitat selection and how anthropogenic activities may impact the distribution, abundance, and persistence of organisms. The goal of this research is to examine how habitat size and canopy cover, two habitat characteristics previously identified as important to many colonizing taxa (Binckley and Resetarits, 2007, Resetarits and Binckley, 2009, Resetarits et. al., 2018, Resetarits et. al., 2019, Resetarits et. al., 2022), are prioritized and selected by ovipositing treefrogs and colonizing aquatic insects. Many amphibians and aquatic insects have complex life cycles that contain a terrestrial adult stage and an aquatic larval stage. These organisms are thus important links between terrestrial and aquatic ecosystems, and between patches in aquatic systems (Baxter et.

al., 2005, Resetarits et. al., 2005). Understanding the prioritization of certain patches by aquatic organisms for colonization can help elucidate how environmental characteristics influence perceived patch quality and provide insight into the complexity of habitat selection.

CHAPTER 1: CANOPY COVER OR PATCH SIZE AS POTENTIAL DRIVERS OF HABITAT SELECTION FOR *HYLA CHRYSOSCELIS* (SOUTHERN GRAY TREEFROG)

Introduction

Temporary aquatic habitats often act as refugia for larval amphibians because they typically lack various predators, such as fish and larger aquatic insects, that are commonly found in more permanent aquatic habitats (Rothenberger and Baranovic, 2021). Temporary aquatic habitats therefore often equate to increased survival for larval amphibians. However temporary aquatic habitats also come with challenges. For example, these habitats are more susceptible to drying, which can impose severe risks for larval survival particularly in species with prolonged developmental periods (e.g., most ranid species including, American Bullfrogs, *Lithobates catesbeianus*) (Cook et. al., 2013, Edge et. al., 2016). Amphibians with short developmental periods are better able to exploit and colonize vernal pools and other temporary aquatic habitats.

Selection of oviposition sites by amphibians is influenced by predators (Resetarits and Wilbur, 1989, Resetarits et. al., 2018), competitors (Resetarits and Wilbur, 1989), resource availability (Dey, 2010), habitat location (Binckley and Resetarits, 2007, Resetarits et. al., 2022), and temperature (Kern et. al., 2013). By examining how these variables relate to the distribution of eggs, one can begin to understand the factors that govern decision rules underlying selection of oviposition sites and how they may be hierarchically assessed.

The factors that contribute to selection of oviposition sites have been extensively studied in the southern gray treefrog, *Hyla chrysoscelis* (Resetarits and Wilbur, 1989, Binckley and

Resetarits, 2007, Resetarits et. al., 2018). *H. chrysozelis* is a relatively common species throughout much of its range in the eastern, central, and southern United States (Powell et. al., 2016) and is a facultative breeder (Lanthrop et. al., 2005) that may use either temporary or more permanent aquatic habitats for oviposition (Resetarits and Wilbur, 1989). Like most anurans, males of this species call from potential oviposition sites and females approach calling males and initiate amplexus (Godwin and Roble, 1983). Females will then carry the mounted male to oviposition sites which may or may not be in the same pond in which the male was calling, since male calling site preferences and female oviposition site preferences may be somewhat mismatched (Resetarits and Wilbur, 1989, Resetarits and Wilbur, 1991).

Predators and competitors are particularly important predictors of larval performance and thus of oviposition sites for this species (Resetarits and Wilbur, 1989). For example, the presence of fish (i.e., *Enneacanthus chaetodon*) and predatory salamanders (i.e., *Ambystoma maculatum*) can elicit a strong avoidance response (Resetarits and Wilbur, 1989). Intraspecific competition is also a strong determinant of patch quality with females avoiding pools that have already been colonized by conspecifics (Resetarits and Wilbur, 1989, Scott, 2020). Females also primarily lay egg masses in relatively larger patches (within the smaller end of the size range of temporary pools – often $> 9\text{m}^2$) versus medium and small patches, emphasizing that patch size is also an important characteristic in determining patch quality (Resetarits et. al., 2018, Resetarits et. al., 2022). However, selection of oviposition sites is also strongly influenced by canopy cover. For example, Binckley and Resetarits (2007) placed mesocosms in a field and forest and found that females preferred to oviposit in open canopy patches over closed canopy patches. Together these studies indicate that female *H. chrysozelis* choose oviposition sites with the fewest potential

predators (Resetarits and Wilbur, 1989, Resetarits et. al., 2018), that are large in size (Resetarits et. al., 2018), and located in habitats with open canopy (Binckley and Resetarits, 2007).

The goal of this study was to determine the relative importance of patch size and canopy cover in oviposition site choice in female *H. chrysoscelis*. These habitat characteristics often co-occur because larger ponds typically have less canopy cover. However, which characteristic is a more important determinant of patch quality remains unclear. To untangle preferences for these patch characteristics, I implemented a compromise design, wherein *H. chrysoscelis* females were presented with potential oviposition patches that varied in size (large or small) and canopy cover (open or closed). Resetarits (2021), successfully implemented a compromise design by presenting *H. chrysoscelis* with two patch sizes (large and small) and placed fish only in large patches. This experiment provided *H. chrysoscelis* with their preferred patch size (large patches) but reduced the patch quality by placing predators within those patches, forcing *H. chrysoscelis* females to either oviposit in large patches with predators or small patches without predators (Resetarits, 2021). Female *H. chrysoscelis*, overwhelmingly selected patches without predators, indicating that the presence of predators was a more important determinant of patch quality than patch size (Resetarits, 2021). For the current experiment, a similar design was implemented wherein *H. chrysoscelis* females were forced to choose between large, closed canopy patches or small, open canopy patches. This design was aimed at determining the relative importance of patch size and canopy cover in oviposition decisions by female *H. chrysoscelis* when no ideal oviposition site exists. Under a compromise scenario, female *H. chrysoscelis* may prioritize one habitat feature over another, presumably because this feature plays a more central role in offspring survival, or they may be unable to reconcile the conflict and no clear overall choice

emerges. Lack of a clear outcome may also result from variation among females in habitat preference or bet-hedging by individual females.

Methods

Study Site

The experiment was conducted at the University of Mississippi Field Station (UMFS) in Lafayette County, Mississippi. UMFS is 318 hectares primarily comprised of forested habitats, dominated by mixed hardwoods and conifer trees, and wetlands. This experiment was carried out in a large, treeless, overgrown field to represent natural open canopy habitat as well as in the surrounding forest, to represent natural closed canopy habitat.

Experimental Design and Set-up

Previous research found that *H. chrysosealis* females tend to oviposit in large, open canopy patches when given a choice (Binckley and Resetarits, 2007; Resetarits et. al., 2018). In the current experiment, I tested female *H. chrysosealis* prioritization of patch size versus canopy cover. To achieve this, a compromise design was implemented where the ideal habitat was removed (large open canopy patches) and *H. chrysosealis* were presented with two non-ideal patch types. I presented two suboptimal patch types consisting of large, closed canopy patches and small, open canopy patches to test how female *H. chrysosealis* prioritize patch size and canopy cover when selecting oviposition sites.

I used large (5.73m², 2650 L) and small mesocosms (1.13 m², 525L) that were split into three blocks with four mesocosms (two large and two small) placed in each (12 mesocosms in total). Large mesocosms were placed within a forest, representing closed-canopy habitat, and small mesocosms were placed within an overgrown field, representing open-canopy habitat.

Large and small mesocosms were placed 9 meters from the field edge and same sized mesocosms within a block were placed 5 meters away from each other (Fig. 1.1). A large and small mesocosm within a block were paired (i.e., L1 is paired with S1) and were a total of 18 meters apart.

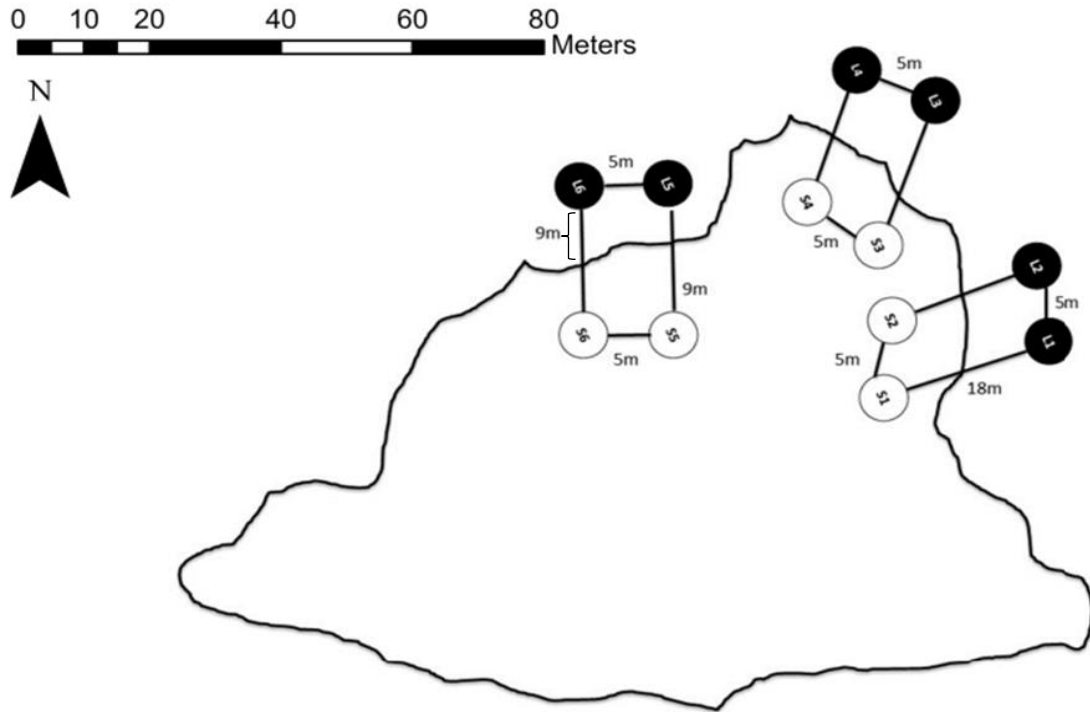


Figure 1.1: Experimental design testing *H. chrysoscelis* and aquatic insects' preference for either large, closed-canopy patches or small, open-canopy patches. Black dots represent large pools placed in a forest and white dots represent small pools placed in an overgrown field. Same sized pools were placed 5m apart and paired large and small pools were placed 18m apart. All pools were placed 9m from the field/forest edge.

Mesocosm tanks were the same color (green) and shape (cylindrical), however large mesocosms are 13 cm taller, so to make up for this difference each one was filled to the same

depth (= 50 cm). Thus, large mesocosms held approximately 2650 L and small mesocosms held approximately 525 L. Mesocosms within a block were filled on the same day with block 1 filled on May 29th, 2022, and blocks 2 and 3 filled on May 30th, 2022. Filling mesocosm at the end of May ensured that the canopy had fully grown in for closed canopy sites. Once all mesocosms within a block were filled, leaf litter was randomly assigned and placed in each, to act as a nutrient base. The amount of leaf litter added (large = 4.4 kg, small = 0.9kg) was scaled to the volume of mesocosms to achieve similar proportions between different sizes (large = 0.005kg/L, small = 0.009kg/liter). After the addition of the leaf litter, a screen lid was placed over the mesocosm to prevent colonization prior to the start of the experiment. On May 30th, 2022, all mesocosms were filled, allowing for screen lids to be submerged below the water line, marking the start of the experiment. Pendant Hobo Data loggers were added to each pool on May 30th, 2022 to take daily temperature and light intensity measurements every 15 minutes. Each data logger was attached to a square, ceramic tile placed atop the screens, so they remained in the center of each pool. Each day data loggers were examined and adjusted as needed to ensure accurate, consistent measurements.

Mesocosms act as a surrogate for temporary aquatic habitats and previous work has shown that *H. chrysoscelis* readily lay eggs in mesocosms (Resetarits et. al., 2018, Resetarits et. al., 2022). Eggs of *H. chrysoscelis* are easy to identify and collect from pools without harming them. *Hyla chrysoscelis* is a common species at the University of Mississippi Field Station and one of the only local species that routinely colonize mesocosms (Resetarits et. al., 2018, Resetarits et. al., 2022). They also have a relatively long breeding season (late March – August) allowing for experiments to be conducted over longer periods of time than species that might only oviposit on one or a few nights of the year (Resetarits et. al., 2018, Resetarits et. al., 2022).

Data Collection

All pools were checked for *H. chrysoscelis* eggs each morning starting on May 31st, 2022, and ending on August 23rd, 2022, (total of 84 days). Eggs were removed and photographed in the lab with a Nikon digital camera (D3300) mounted vertically on a studio copy stand. All photos were analyzed in ImageJ using a previously established protocol (Bohenek and Resetarits, 2017). Once images were analyzed, all eggs were taken to a nearby fishless pond, away from the study location.

Once per week, organic matter, including leaf litter, sticks, seeds, algae, and aquatic insects, were collected off the top of screen lids and taken back to the lab. Organic matter remained in sample containers until dried to obtain the dry weight. Once the dry weight was obtained the average amount of dried organic matter was calculated for each mesocosm by dividing the dried mass by mesocosm volume (large by 31.81m³ and small by 3.53m³). Hobo pendant data loggers were collected once a month (6/30/2022, 7/31/2022, and 8/23/2022) to export temperature and light intensity data and check battery life. Data loggers were reattached to the same ceramic tile and returned to the same pool. During the experiment several data loggers experienced malfunctions, to correct this a new data logger was selected and used for the remainder of the experiment.

Given that *H. chrysoscelis* are nocturnal amphibians, light intensity data was separated into nighttime and daytime light intensity based off the sunrise and sunset in Oxford, MS, USA. Only the nighttime light intensity data (8PM to 6AM) was incorporated into statistical analyses for oviposition site choice from each pool on each day. Average temperature was used for each pool over each day.

Statistical Analyses

The response variable for this experiment is the total number of eggs laid per patch. To test for statistical differences in habitat preference, a two factor ANOVA was performed to determine if there was a preferred habitat for oviposition (Oksanen et. al., 2022). Block was a random effect and patch size/canopy cover was a fixed effect. Statistical tests were all performed using R version 4.1.1 (R Core Team, 2021) along with RStudio version 1.4.1103.

An Akaike information criterion (AIC) model was used to determine which environmental variables (organic matter, nighttime light intensity, and temperature) should be incorporated in a full model. To examine the AIC scores for each model the dredge() function was used in the MuMIn package in RStudio (Barton, 2020). The zeroinfl() function in the pscl package was used due to the high number of zeros within the dataset to account for zero inflation (Zeileis et. al., 2008). The best model included nighttime light intensity and temperature with an AIC score of 93,975.9.

glm(Number_of_Eggs ~ Size + Temp + Light, data = data, family = poisson)

A generalized linear model was then conducted using the glm() function with number of eggs as the response variable, patch type as a fixed effect (represented by size here), and temperature and nighttime light intensity as covariates (Rizopoulos, 2023). Block was removed from this model since AIC indicated that it was not important to include.

Results

Environmental Results

Temperatures in large, closed canopy patches ranged from 19.4°C to 30.1°C with an average temperature of 25.0°C (Table 1.1). In small, open canopy patches, temperatures ranged from 20.5°C to 41.3°C with an average temperature of 28.9°C (Table 1.1). The average light intensity during nighttime hours for large, closed canopy patches was 0.137 lum/ft² and 0.993 lum/ft² for small, open canopy patches (Table 1.2). The average amount of organic matter in large, closed canopy patches was 0.93g/m³ and the average amount of organic matter in small, open canopy patches was 0.22g/m³ (Table 1.3).

Table 1.1: Table showing the average temperature (°C) ± standard deviation for each patch along with the overall average temperature across all patches of the same size.

<u>Large-Closed</u> <u>Patch ID</u>	<u>Average Temperature (C)</u>	<u>Small-Open</u> <u>Patch ID</u>	<u>Average Temperature (C)</u>
L1	25.2 ± 1.79	S1	29.0 ± 3.71
L2	25.2 ± 1.76	S2	29.2 ± 3.97
L3	24.5 ± 1.70	S3	28.5 ± 4.21
L4	25.8 ± 1.56	S4	28.4 ± 3.57
L5	25.1 ± 1.72	S5	29.2 ± 3.95
L6	24.3 ± 1.64	S6	29.0 ± 3.56
Average	25.0 ± 1.77	Average	28.9 ± 3.80

Table 1.2: Table showing the average night-time light intensity (lum/ft²) ± standard deviation for each patch between the hours of 8PM and 6AM.

<u>Large-Closed</u> <u>Patch ID</u>	<u>Average Night-time</u> <u>Light Intensity (lum/ft²)</u>	<u>Small-Open</u> <u>Patch ID</u>	<u>Average Night-time</u> <u>Light Intensity (lum/ft²)</u>
L1	0.215 ± 1.29	S1	0.665 ± 4.33
L2	0.350 ± 1.83	S2	1.19 ± 6.22
L3	0.091 ± 0.587	S3	1.57 ± 6.27
L4	0.073 ± 0.662	S4	0.558 ± 3.39
L5	0.087 ± 0.614	S5	1.20 ± 5.99
L6	0.023 ± 0.238	S6	1.03 ± 5.21
Average	0.137 ± 1.01	Average	0.993 ± 5.29

Table 1.3: Table showing the average amount of organic matter (g/m³) ± standard deviation found within each pool.

<u>Large-Closed</u> <u>Patch ID</u>	<u>Average Organic</u> <u>Matter (g/m³)</u>	<u>Small-Open</u> <u>Patch ID</u>	<u>Average Organic</u> <u>Matter (g/m³)</u>
L1	0.26 ± 0.12	S1	0.051 ± 0.071
L2	0.38 ± 0.34	S2	0.27 ± 0.48
L3	1.62 ± 0.64	S3	0.21 ± 0.18
L4	0.74 ± 0.36	S4	0.31 ± 0.47
L5	1.60 ± 1.06	S5	0.15 ± 0.065
L6	1.13 ± 0.46	S6	0.31 ± 0.53
Average	0.93 ± 0.77	Average	0.22 ± 0.36

Oviposition Results

Female *H. chrysoscelis* laid 158,980 eggs, spread over 60 nights, with every mesocosm having eggs laid within it at least once. A total of 147,760 eggs were laid in large, closed canopy mesocosms and 11,220 eggs were laid in small, open canopy mesocosms. Significantly more eggs were laid in large, closed canopy mesocosms than small, open canopy mesocosms (F=40.97, P<0.001, Fig. 1.2). A higher proportion of eggs were laid during all but one laying

event in large, closed canopy pools (Fig. 1.4). A greater number of eggs were laid at the beginning of the experiment than at the end (Fig. 1.4). Results from the generalized linear model indicated that patch type, temperature, and nighttime light intensity all significantly predicted the number of eggs laid in each patch type, supporting the results from the two-way ANOVA.

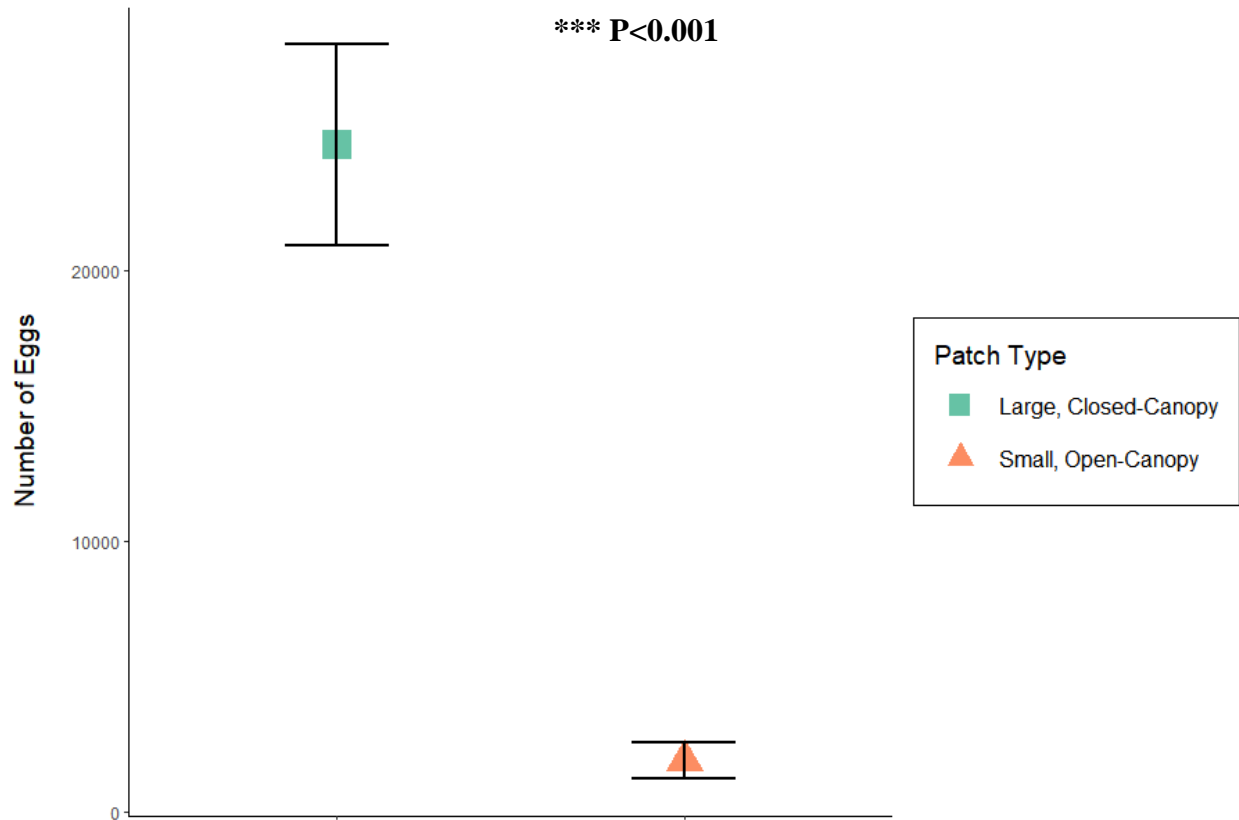


Figure 1.2: The mean abundance \pm S.E. of *H. chrysoscelis* eggs laid in large, closed canopy and small, open-canopy patches.

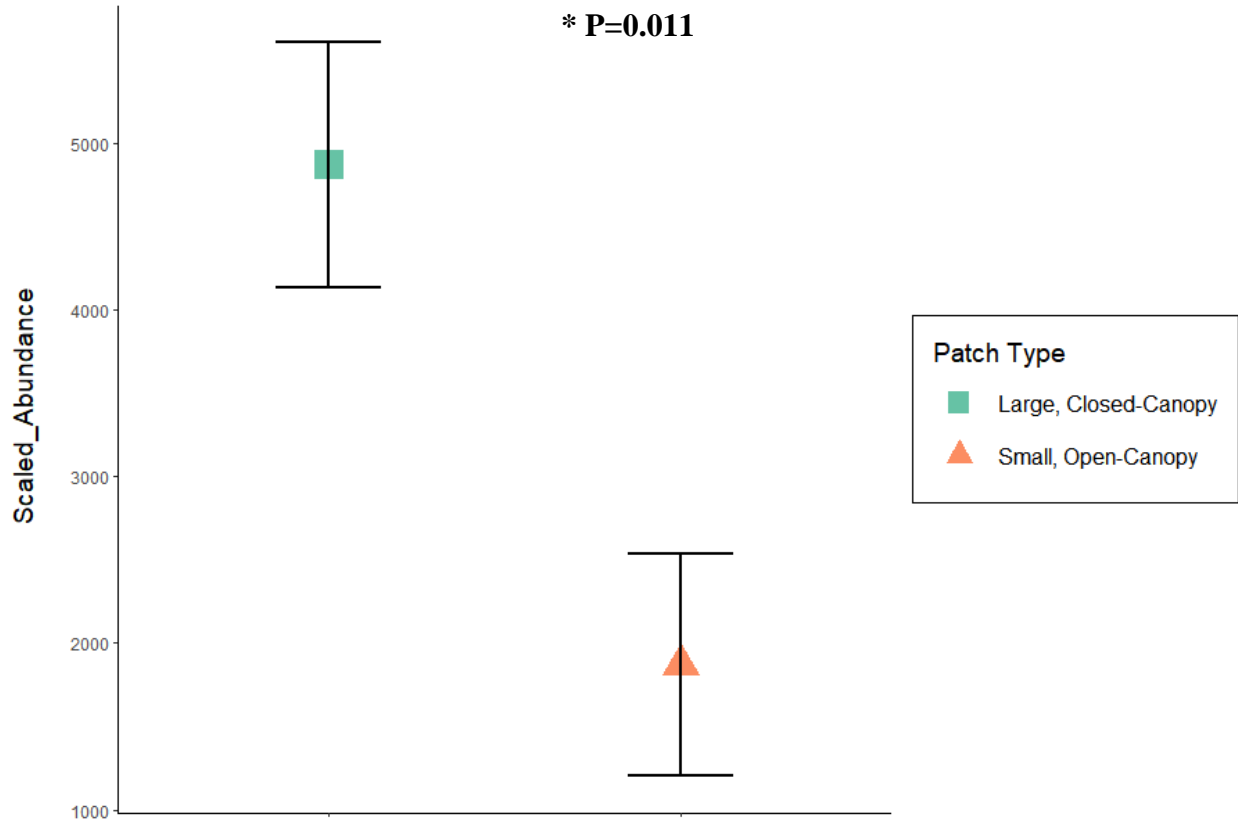


Figure 1.3: Scaled abundance \pm S.E. of *H. chrysoscelis* eggs laid in large, closed canopy and small, open-canopy patches. Large, closed canopy patches were scaled by dividing the total number of eggs laid by 5.73m^2 and small, open canopy patches were divided by 1.13m^2 .

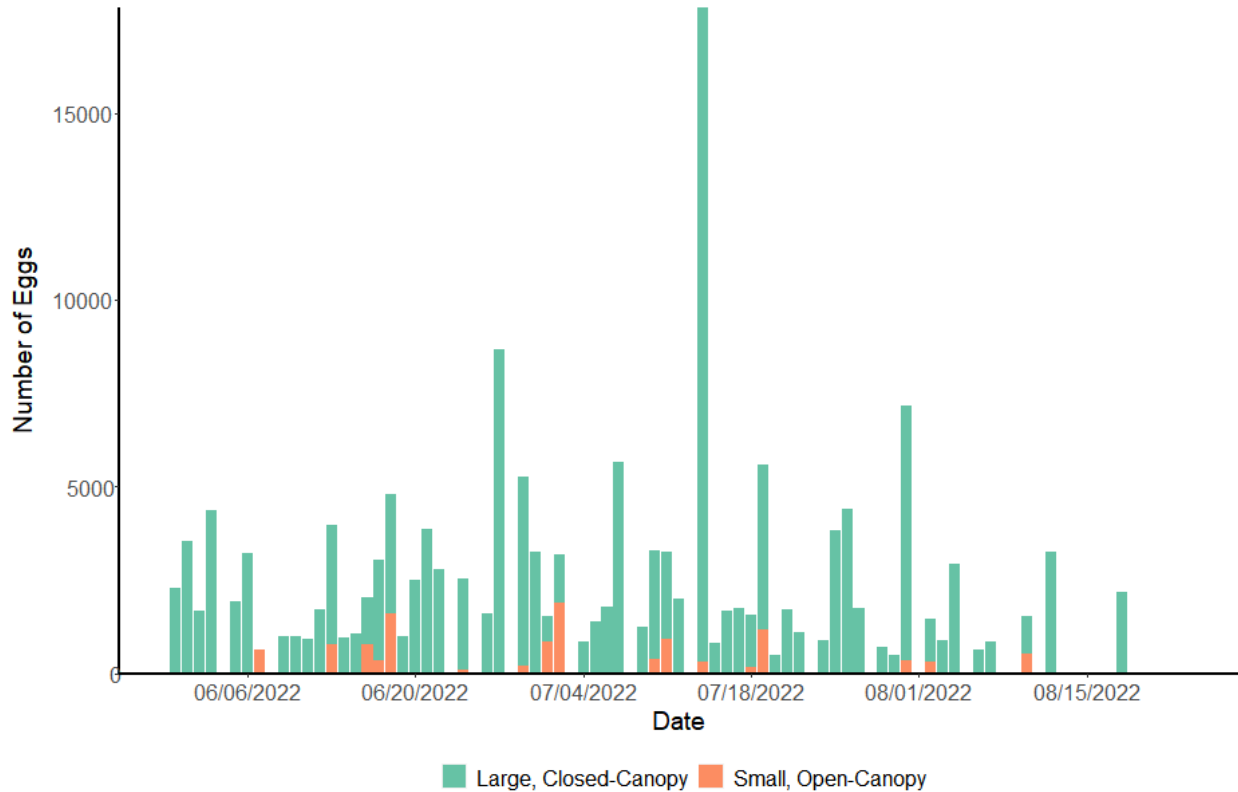


Figure 1.4: The proportion of *H. chrysoscelis* laid in large, closed canopy patches and small, open canopy patches through the duration of the experiment.

Discussion

Canopy cover and patch size are two common habitat characteristics that naturally vary and lead to the creation of unique patches. Research has established that changes in patch size of just a few square meters (Resetarits et. al., 2019, Resetarits, 2021, Resetarits et. al. 2022) and the growth of canopy cover (Binckley and Resetarits, 2009), can impact a patch’s perceived quality to colonizing organisms. Colonizing aquatic organisms including treefrogs, mosquitoes, aquatic beetles and true bugs have all shown strong preferences for habitat size, on a small scale of only 1 – 6m² (Bohenek et. al., 2017, Resetarits et. al., 2018, Resetarits, et. al., 2019, Resetarits, 2021,

Resetarits et. al., 2022). Each taxon has unique criteria to evaluate patches and the perceived quality of patches which creates unique community assemblages through species sorting (Resetarits et. al., 2018). Female southern gray treefrogs (*Hya chrysoseclis*), have a strong preference for larger patches (Resetarits et. al., 2018) and for open canopy patches (Binckley and Resetarits, 2007).

This experiment examined whether patch size (small or large) along with canopy cover (open or closed canopy) affect oviposition site choice in female *H. chrysoseclis* by forcing individuals to select oviposition sites between two patch types. I found that large, closed canopy patches received overwhelmingly more eggs (147,760) compared to the small, open canopy patches (11,220), indicating a clear preference for large, closed canopy patches over small, open canopy patches. These results suggest that patch size may be a more important determinant of patch quality and that prioritization of patch size is quite strong. These results are also supported by prior experiments that have shown female *H. chrysoseclis* prefer larger patches when patch size was tested against a variety of other habitat characteristics (Resetarits et. al., 2018, Resetarits et. al., 2022). However, there is a caveat to this trend, where if a patch contains certain predators that patch's quality is perceived as low and female *H. chrysoseclis* will select predator-free patches even if those are smaller (Resetarits et. al., 2021).

Studies have been conducted that individually tested the effects of patch size (Resetarits et. al., 2018) and canopy cover (Binckley and Resetarits, 2007) but this is the first experiment where these characteristics were combined to try and decipher which may be a more important determinant of patch quality for female *H. chrysoseclis*. These prior experiments have established the importance of large, open-canopy patches for *H. chrysoseclis* oviposition but in an ever-changing landscape these habitats may become limiting which is why females were

provided the opportunity to prioritize canopy cover against patch size when selecting oviposition sites in the current experiment.

Why female *H. chrysoscelis* might prefer larger patches even if those patches reside in landscapes that are suboptimal is not well understood. Larger patches may take longer to dry providing more time for offspring to reach maturity and reducing the risk of desiccation before metamorphosing (Brooks, 2004, Green et. al., 2013). This is important to help ensure population persistence (Green et. al., 2013). Also, larger patches provide greater space for offspring which can decrease intraspecific competition and increase foraging opportunity. However, the overwhelming selection of larger patches may also lead to higher densities that could alter oviposition selection (Resetarits and Wilbur, 1989). Such density-dependent effects were not examined in the current experiment because eggs were removed daily to prevent the accumulation of *H. chrysoscelis* tadpoles.

Although open-canopy habitats are the preferred choice, possibly because their higher primary productivity leads to greater food availability for *H. chrysoscelis* tadpoles (Skelly et. al., 2002), being in closed-canopy environments may also have some benefits. For example, closed-canopy patches are primarily located within forests where *H. chrysoscelis* reside during the day until they descend for mating. The proximity of closed canopy patches to daytime retreats may thus reduce the distance that adults would have to travel when locating oviposition sites, which, may also reduce the risk of predation (Wells, 2010). However, closed canopy environments reduce the amount of light received which impacts primary production and decreases food availability for *H. chrysoscelis* tadpoles (Skelly et. al., 2002). The lack of primary production may be partly outweighed by nutrient input from fallen leaf litter since allochthonous detritus does impact food availability (Webster and Benfield, 1986 a review).

One possibility is that female *H. chrysoseelis* are simply ovipositing in the first patches that they encounter as they emerge from daytime retreats located in forested areas. However, Resetarits et. al. (2022) established that female *H. chrysoseelis* will pass up suboptimal patches to locate optimal patches. Resetarits et. al., (2022), crossed patch size with distance from forest edge with smaller patches closer to the forest and larger patches farther away. They found that medium patches received significantly more eggs than smaller patches even though they were located farther away from the forest edge (Resetarits et. al., 2022). Moreover, eggs were found in small, open canopy patches indicating that at least some female *H. chrysoseelis* selected those patches for colonization.

The big take away message here is that it appears patch size is an extremely important characteristic for determining patch quality for female *H. chrysoseelis* even at a relatively small size scale (1 – 6m²). The only factor that has been tested thus far that has an even stronger impact on patch quality than patch size is the presence/absence of predators or conspecifics (Resetarits and Wilbur, 1989, Resetarits et. al., 2018, Scott, 2020, Resetarits, 2021). These results, however, do not conclude that canopy cover is not important for patch quality but instead show how complicated the process of habitat selection is for colonizing aquatic organisms. Colonizing organisms must navigate the complex array of habitat characteristics to determine a patch's quality and how a patch impacts an organism's fitness. My results show that these organisms are using characteristics even at this small scale and these characteristics play a major role in habitat selection. Numerous environmental characteristics impact the perceived quality of a patch and this experiment, along with many others, indicate that some may be more impactful than others (Resetarits and Wilbur, 1989, Resetarits et. al., 2018, Resetarits, 2021, Resetarits et. al., 2022).

Using a compromise design allowed for teasing apart patch size and canopy and show that even at a small scale these characteristics play a major role in habitat selection.

In an ever-changing world, the quantity and quality of aquatic habitats is likely to become limiting, forcing many organisms into these complex decisions when selecting suitable patches. To try and curb human caused disturbances, habitat restoration programs aim to create, restore, and preserve habitats to maintain and hopefully increase biodiversity. However, taking approaches like “build it and they will come” or “one size fits all” may not be the best solution when it comes to creating habitats for colonizing organisms. These stances may assist some species but, given the large diversity of aquatic organisms it is likely that a more nuanced and balanced approach needs to be applied. Understanding how species prioritize different habitat characteristics can lead to the creation of more tailored restoration programs that in the long-term are more successful because it leads to the creation of higher quality habitats that are best suited for species of concern. Information from studies like the present one can also be used to implement species specific approaches. Either way, applying how organisms prioritize certain habitat characteristics in restoration programs can create suitable patches for many organisms.

CHAPTER 2: CANOPY COVER OR PATCH SIZE AS POTENTIAL DRIVERS OF HABITAT SELECTION FOR AQUATIC INSECTS

Introduction

Flight capable aquatic insects can emigrate from patches that no longer have adequate resources to support themselves or their offspring, or they may have life cycles that involve obligate dispersal (Petersen et. al., 2004, Bowman and Smith, 2021). Emigrating may allow individuals to find new patches with abundant resources, but leaving a patch comes with both the uncertainty of potential immigration sites and the potential risk of predation from terrestrial predators (Ulyshen, 2011). Aquatic habitats reflect polarized light which aquatic insects can detect and use as a means of locating patches for colonization (Ensaldo-Cárdenas et. al., 2021). Under the concept of random colonization, larger patches tend to have greater immigration rates possibly because they have a larger area that increases detection (Lomolino, 1990, Smith, 2008). However, simply locating a patch does not mean that patch is suitable for colonization because organisms may actively search for patches that have certain environmental characteristics (Morris, 2003, Resetarits et. al., 2005, Resetarits et. al., 2019, Scott et. al., 2021). For example, temperature (McNamara et. al., 2021), presence of predators and/or competitors (Resetarits and Binckley, 2009, Resetarits et. al., 2019, Scott et. al., 2021), patch size (Scott et. al., 2021, Resetarits et. al., 2019), and habitat location (Binckley and Resetarits, 2007, Binckley and Resetarits, 2009, French and McCauley, 2018) have all been shown to influence colonization of aquatic insects.

With numerous environmental variables and the vast diversity of aquatic insects it is not surprising that each species might have its own criteria for identifying a suitable patch. For example, adult predatory insects may select patches with the largest variety/abundance of prey items (Pintar and Resetarits, 2017). Insects with an adult terrestrial stage and larval aquatic stage, such as dragonflies and stoneflies, might select patches in a similar way to amphibians, where they identify suitable patches for their offspring (Smith and Storey, 2018). Adult aquatic insects that both colonize and reproduce in aquatic habitats may use a combination of cues to locate patches that have food for adults and ideal conditions for offspring (Pintar and Resetarits, 2017, Resetarits et. al., 2019). Preferences for certain habitats shape the community structure of aquatic ecosystems with each insect selecting its own preferred conditions leading to aggregation or segregation of species (species sorting).

In nature, aquatic patches vary along environmental gradients and across landscapes creating a mosaic of unique habitats. This variation may contribute to differences in aquatic insect patch preferences, allowing for segregation across different patches and reducing competition (Resetarits and Binckley, 2009, Resetarits and Binckley, 2013, Resetarits et. al., 2019, Scott et. al., 2021). For example, aquatic beetles prefer fishless patches, but when incorporating patch size, species segregate among different patches with some preferring small patches (*Copelatus glyphicus*, *Paracymus*, *Enochrus ochraceus*, *Cymbiodyta chamberlaini*) and other species preferring larger patches (*Tropisternus collaris*, *Thermonectus blatchelyi*, *Laccophilus proximus*) (Resetarits et. al., 2019). Mosquitoes can colonize more temporary habitats because of their short life cycle (Westby et. al., 2021) while other aquatic insects require more permanent aquatic habitats for reproduction (Wissinger, 1988). The combination of different patch preferences and patch requirements creates unique community structures through

the dispersal of aquatic insects among available patches (Resetarits and Binckley, 2013, French and McCauley, 2018, Resetarits et. al., 2019).

Two common habitat characteristics that may influence colonization rates of aquatic insects are patch size and canopy cover. These characteristics have been shown to individually impact aquatic insect patch preferences with the majority of species preferring open canopy patches and segregating across patch sizes (Binckley and Resetarits, 2007, Binckley and Resetarits, 2009, Resetarits et. al., 2019). However, these patches may become limiting due to human degradation that reduces the quantity and quality of these habitats (Heino et. al., 2009 a review) and/or the presence of competitors/predators (Binckley and Resetarits, 2005, Resetarits and Binckley, 2009, Resetarits et. al., 2019). This may force certain species to compromise between sets of non-ideal patches which can increase competition among species and reshape community structures and dynamics (Resetarits et. al., 2019). With few ideal habitats, aquatic insects may congregate within the limited number of preferred patches, resulting in high competition among colonists (Resetarits et. al., 2019). This can also create patches with high diversity as many insects may colonize the few ideal patches and some patches may have relatively low diversity if few to no insects colonize (Resetarits et. al., 2019, Scott et. al., 2021). Factors that contribute to habitat selection by aquatic insects have been extensively studied (Resetarits et. al., 2019, Scott et. al., 2021). Threat of predation can have a strong influence on colonization, deterring aquatic insects from colonizing patches with predatory fish (*Enneacanthus obesus*, *Fundulus chrysotus*, *Notemigonus crysoleucas*) (Resetarits and Binckley, 2009, Resetarits et. al., 2021). Colonizing aquatic insects will segregate among patch sizes, exhibiting species specific preferences for different sized patches (Resetarits et. al., 2019, Scott et. al., 2021). Also, canopy cover influences patch selection in aquatic insects with most aquatic

beetles and hemipterans preferring open canopy patches over closed canopy patches (Binckley and Resetarits, 2007, Binckley and Resetarits, 2009). These studies indicate that the majority of aquatic insects choose patches with the smallest chance of predation (Resetarits and Binckley, 2009, Resetarits et. al., 2021), ideal patch size (Resetarits et. al., 2019, Scott et. al., 2021), and have open canopies (Binckley and Resetarits, 2007, Binckley and Resetarits, 2009).

The goal of my study is to determine how aquatic insects prioritize colonization sites of different patch size and canopy cover. To address this question, I placed large patches in closed canopy habitats and small patches in open canopy habitats, presenting potential colonizing insects with two patch types. This specific design allows for me to tease apart whether patch size (large or small) or canopy cover (open or closed) drives colonization preference. Aquatic insects may weigh the relative benefits of colonizing a patch based on size (large or small) or canopy cover (open or closed canopy). Colonization might be influenced by priority effects since some species (predatory hemipterans and beetles) might feed upon future colonizers, but by removing aquatic insects weekly it largely precludes these effects (Fukami, 2015). Analyzing the presence or absence of certain species allows for 1) testing the effects of patch quality on habitat selection in individual species of aquatic insects and 2) generating a sense of how patch quality impacts community structure of aquatic systems.

Methods

Study Site

The experiment was conducted at the University of Mississippi Field Station (UMFS) in Lafayette County, Mississippi, USA. UMFS is 318 hectares primarily comprised of forested habitats, dominated by mixed hardwoods and conifer trees, and wetlands. This experiment was

carried out in a large, treeless, overgrown field to represent natural open canopy habitat as well as in the surrounding forest, to represent natural closed canopy habitat. The experiment was conducted at the end of May, to ensure that the full canopy had grown in for the forested sites.

Experimental Design and Set-up

Previous research has found that aquatic insects prefer to colonize open canopy patches (Binckley and Resetarits, 2007, French and McCauley, 2018) but when presented with different patch sizes (large and small) aquatic insects segregate among the different patches (Resetarits et al., 2019). To test the hypothesis that canopy cover and patch size influence patch selection in aquatic insects, I implemented a design with large (5.73m², 2650 L) and small mesocosms (1.13 m², 525L) split into three blocks of four mesocosms (two large and two small with 12 total mesocosms). Large mesocosms were placed within a forest, representing closed-canopy habitat, and small mesocosms were placed within an overgrown field, representing open-canopy habitat. Large and small mesocosms were placed 9 meters from the field edge and same sized mesocosms within a block were placed 5 meters away from each other (Fig. 2.1). A large and small mesocosm within a block were paired (i.e., L1 is paired with S1) and placed 18 meters apart.

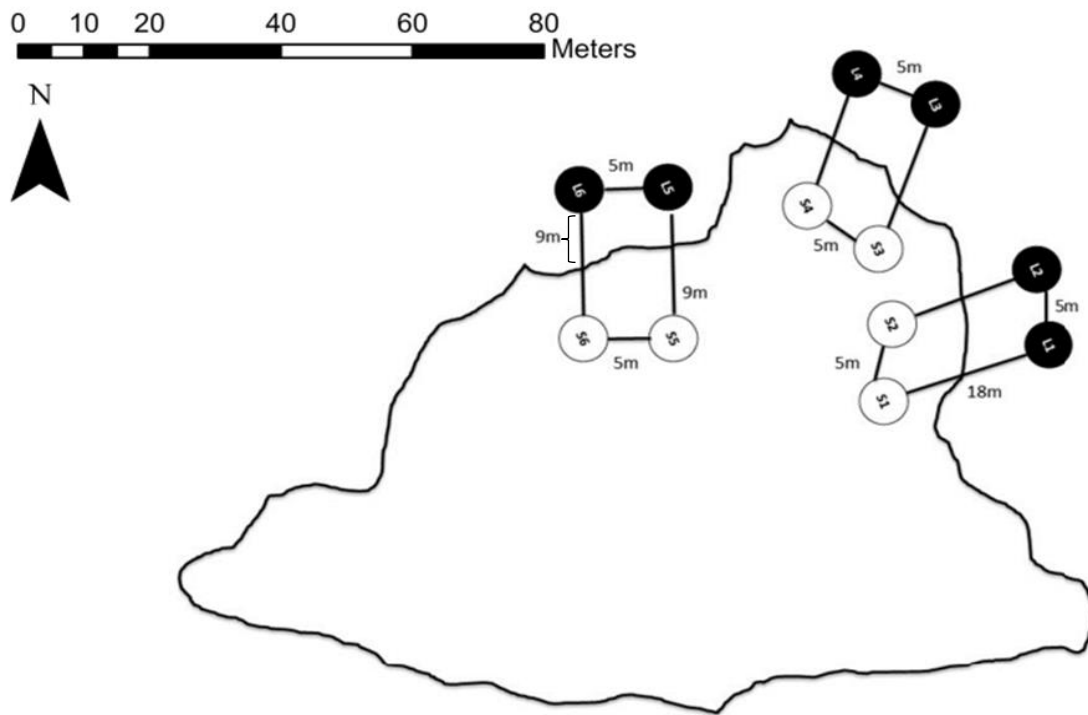


Figure 2.1: Experimental design testing *H. chrysoscelis* and aquatic insects' preference for either large, closed-canopy patches or small, open-canopy patches. Black dots represent large pools placed in a forest and white dots represent small pools placed in an overgrown field. Same sized pools will be placed 5m apart and paired large and small pools will be placed 18m apart. All pools will be placed 9m from the field/forest edge.

Mesocosms were the same color (green) and shape (cylindrical), however large mesocosms were 13 cm taller, so to make up for this difference each mesocosm was filled to the same depth (=50 cm). Thus, large mesocosms held approximately 2650 L and small mesocosms held approximately 525 L. Pools within a block were filled on the same day with well-water. Block 1 was filled on May 29th, 2022, and blocks 2 and 3 were filled on May 30th, 2022. On May 30th, 2022, all mesocosms had been filled and leaf litter was randomly assigned and placed in

each mesocosm to act as a nutrient base. The amount of leaf litter added (large = 4.4 kg, small = 0.9kg) was scaled to the volume of mesocosms to achieve similar proportions between different sizes (large = 0.005kg/L, small = 0.009kg/liter). Screen lids were placed over mesocosms to prevent colonization prior to the start of the experiment. On May 30th, 2022, all mesocosms were filled and the screen lids were pushed down below the water line, marking the start of the experiment. Pendant Hobo Data loggers were added to each mesocosm to take temperature and light intensity measurements every 15 minutes. Each data logger was attached to a square, ceramic tile allowing it to remain in the center of each pool. Data loggers were examined each day and adjusted as needed to ensure accurate measurements are being taken.

Study Organisms

The University of Mississippi Field Station contains a diverse assemblage of aquatic insects including over 40 species of aquatic/semiaquatic hemipterans (Pintar and Resetarits, 2020a) and over 130 species of aquatic beetles (Pintar and Resetarits, 2020b). This study focused on aquatic beetle (Coleoptera) and aquatic true bugs (Hemiptera) colonization. These organisms were the focus of prior experiments that investigated aquatic insect colonization preferences and there is good documentation of species that are present at the study location (Pintar and Resetarits, 2020a, Pintar and Resetarits, 2020b).

Data Collection

Once per week, organic matter (including leaf litter, sticks, seeds, and algae) and aquatic insects, were collected off the top of screen lids and taken back to the lab. All Hemiptera and Coleoptera were separated from the organic matter and stored in 70% ethanol for future

identification. Organic matter remained in sample containers until dried to obtain the dry weight. Pendant data loggers were collected once a month to export data and check battery life. Data loggers were then reattached to the same ceramic tile and returned to the same pool. During the experiment several of the Hobo Pendant Data Loggers experienced malfunctions and had to be replaced.

Insect Identification

Insects were identified to the lowest possible taxonomic level (species for most, genus for some). To identify aquatic insects a combination of resources were used including Epler's keys to aquatic hemipterans (Epler, 2006) and coleopterans of Florida (Epler 2010), previous comprehensive lists of aquatic insects at the UMFS, (Pintar and Resetarits, 2020a, Pintar and Resetarits, 2020b) and An Introduction to the Aquatic Insects of North America (Merritt and Cummins, 2019).

Statistical Analysis

Since this study used different sized mesocosms (large and small) to examine community assemblage and species preferences I adjusted for area by dividing the number of insects found in a pool by the surface area of that pool. Hence, insect abundances in small mesocosms were divided by 1.13m² and in large mesocosm abundances were divided by 5.73m². Individual species/genera responses were only analyzed separately if their total abundances were greater than 35 individuals. Two-way ANOVAs were performed to assess individual species responses with patch type as the fixed effect and block as a random effect. All individual specie responses were conducted using the vegan package (Okasanen et. al., 2022) and all dot plots were made

using the ggplot2 package (Wickham, 2016) in R version 4.1.1 (R Core Team, 2021) along with RStudio version 1.4.1103.

There were a total of 5 metrics used for community level analysis: (1) abundance of total insects, (2) taxonomic richness, (3) alpha diversity, (4) assemblage structure, and (5) beta diversity. A linear mixed model was used to test for differences in total insect abundances between the two patch types using the lme4 package (Bates et. al., 2015) in R version 4.1.1 (R Core Team, 2021). A PERMANOVA was used to test for differences in assemblage structure between the two patch types. The PERMDISP function was then used to test for homogeneity of multivariate dispersions. To further analyze which species contributed the most to dissimilarity between patch types I performed a Similarity Percentages (SIMPER) test. PERMANOVA, PERMDISP, and NMDS plot used PRIMER 7 with the PERMANOVA+ add-on (Anderson et. al., 2015, Clarke and Gorley, 2015).

Results

Environmental Results

Temperatures ranged in large, closed canopy patches from 19.4°C to 30.1°C with an average temperature of 25.0°C (Table 2.1). In small, open canopy patches, temperatures ranged from 20.5°C to 41.3°C with an average temperature of 28.9°C (Table 2.1). The average amount of organic matter in large, closed canopy patches was 0.93g/m³ and the average amount of organic matter in small, open canopy patches was 0.22g/m³ (Table 2.2).

Table 2.1: Table showing the average temperature ($^{\circ}\text{C}$) \pm standard deviation for each patch along with the overall average temperature across all patches of the same size.

<u>Large-Closed</u> <u>Patch ID</u>	<u>Average Temperature (C)</u>	<u>Small-Open</u> <u>Patch ID</u>	<u>Average Temperature (C)</u>
L1	25.2 \pm 1.79	S1	29.0 \pm 3.71
L2	25.2 \pm 1.76	S2	29.2 \pm 3.97
L3	24.5 \pm 1.70	S3	28.5 \pm 4.21
L4	25.8 \pm 1.56	S4	28.4 \pm 3.57
L5	25.1 \pm 1.72	S5	29.2 \pm 3.95
L6	24.3 \pm 1.64	S6	29.0 \pm 3.56
Average	25.0 \pm 1.77	Average	28.9 \pm 3.80

Table 2.2: Table showing the average amount of organic matter (g/m^3) \pm standard deviation found within each pool.

<u>Large-Closed</u> <u>Patch ID</u>	<u>Average Organic</u> <u>Matter (g/m^3)</u>	<u>Small-Open</u> <u>Patch ID</u>	<u>Average Organic</u> <u>Matter (g/m^3)</u>
L1	0.26 \pm 0.12	S1	0.051 \pm 0.071
L2	0.38 \pm 0.34	S2	0.27 \pm 0.48
L3	1.62 \pm 0.64	S3	0.21 \pm 0.18
L4	0.74 \pm 0.36	S4	0.31 \pm 0.47
L5	1.60 \pm 1.06	S5	0.15 \pm 0.065
L6	1.13 \pm 0.46	S6	0.31 \pm 0.53
Average	0.93 \pm 0.77	Average	0.22 \pm 0.36

Insect Colonization Results

A total of 1,334 insects were collected from mesocosms during the experiment, 1,130 adult aquatic beetles (Coleoptera, five families) of 32 species (Table 2.3) and 204 aquatic true bugs (Hemipteran, four families) of eight species (Table 2.4). Dytiscidae (14 species) and Hydrophilidae (15 species) dominated the beetle composition (98% of total individuals and 91% of total aquatic beetle species). Only 24 individuals were found from the other 3 families.

Table 2.3: Abundances of all Coleoptera collected during the experiment.

<u>Family/Species</u>	<u>Patch Type</u>		<u>Total</u>
	<u>Large, Closed-Canopy</u>	<u>Small, Open-Canopy</u>	
Dryopidae (1 species)	1	0	1
<i>Helichus fastigiatus</i>	1	0	1
Dytiscidae (14 species)	565	191	756
<i>Acilius fraternus</i>	13	0	13
<i>Acilius mediates</i>	3	0	3
<i>Bidessonotus inconspicuus</i>	20	18	38
<i>Copelatus caelatipennis princeps</i>	1	0	1
<i>Copelatus chevrolati</i>	1	3	4
<i>Copelatus glyphicus</i>	353	139	492
<i>Desmopachria spp.</i>	1	4	5
<i>Hydaticus bimarginatus</i>	111	1	112
<i>Hydrocolus spp.</i>	2	0	2
<i>Ilybius gagates</i>	36	0	36
<i>Laccophilus fasciatus</i>	4	21	25
<i>Meridiorhantus calidus</i>	3	1	4
<i>Neoporus blanchardi</i>	4	1	5
<i>Thermonectus basillaris</i>	13	3	16
Haliplidae (1 species)	3	1	4
<i>Peltodytes muticus</i>	3	1	4
Hydraenidae (1 species)	16	3	19
<i>Hydraena marginicollis</i>	16	3	19
Hydrophilidae (15 species)	316	34	350
<i>Berosus infuscatus</i>	0	2	2
<i>Cymbiodyta chamberlaini</i>	177	0	177
<i>Cymbiodyta vindicate</i>	40	0	40
<i>Enochrus blatchleyi</i>	1	0	1
<i>Enochrus cinctus</i>	6	0	6
<i>Enochrus consortus</i>	2	0	2
<i>Enochrus fimbriatus</i>	1	0	1
<i>Enochrus hamiltoni</i>	2	1	3
<i>Enochrus ochraceus</i>	63	18	81
<i>Helochares maculicollis</i>	2	1	3
<i>Hydrochara soror</i>	12	0	12
<i>Hydrochara spangleri</i>	1	0	1
<i>Paracymus spp.</i>	2	11	13
<i>Tropisternus blatchleyi</i>	6	1	7
<i>Tropisternus lateralis</i>	1	0	1

Table 2.4: Abundances of all Hemipterans collected during the experiment.

<u>Family/Species</u>	<u>Patch Type</u>		<u>Total</u>
	<u>Large, Closed-Canopy</u>	<u>Small, Open-Canopy</u>	
Corixidae	6	1	7
<i>Hesperocorixa spp.</i>	1	0	1
<i>Tichocorixa calva</i>	5	1	6
Gerridae (1 species)	7	3	10
<i>Gerris comatus</i>	3	0	3
<i>Gerris marginatus</i>	1	0	1
<i>Limnoporus canaliculatus</i>	3	3	6
Mesoveliidae	10	0	10
<i>Mesovelia mulsanti</i>	10	0	10
Notonectidae (14 species)	170	7	177
<i>Notonecta irrorata</i>	170	7	177

The overall abundance of insects that colonized the pools was not significantly different between the patch types when adjusted for the size of the pool. There was a significantly higher species richness in large, closed canopy patches than small, open canopy patches ($F=89.40$, $P<0.001$). Alpha diversity was significantly greater in large, closed canopy patches ($F=69.05$, $P<0.001$) however, beta diversity was not significantly different between patches. There was a significant difference in assemblage structure (PERMANOVA) between the two patch types ($F=7.57$, $P<0.001$, Fig. 2.2).

Non-metric MDS

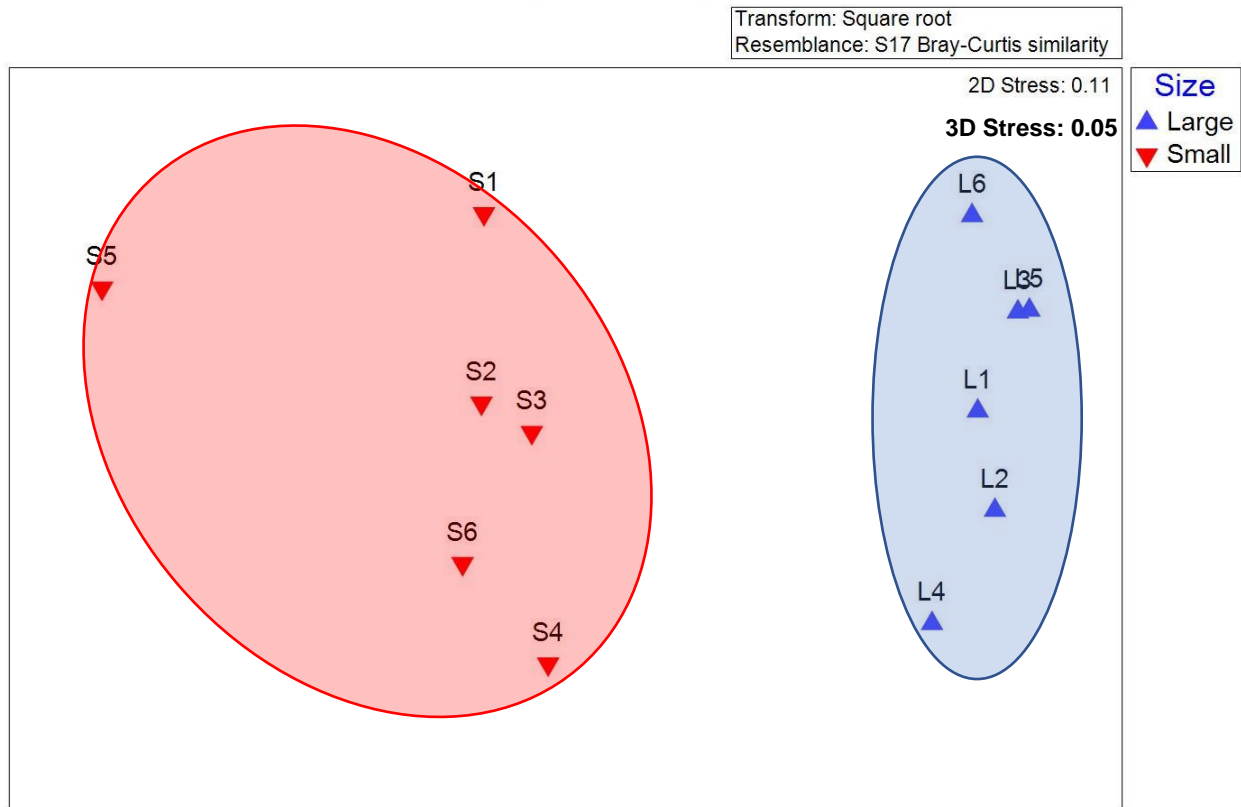


Figure 2.2: Nonmetric multidimensional scaling plot visualizing aquatic insect assemblages between the two patch types (Large, Closed-Canopy and Small, Open-Canopy).

The individual species preferences for seven species of aquatic beetles and one species of aquatic hemipterans were analyzed as these met the threshold for individual analysis.

Cymbiodyta chamberlaini (F=17.12, P=0.001, Fig. 2.3a), *Hydaticus bimarginatus* (F=25.35, P<0.001, Fig. 2.3b), *Cymbiodyta vindicata* (F=6.88, P=0.028, Fig. 2.3c), and *Ilybius gagates* (F=49.52, P<0.001, Fig. 2.3d) had significantly higher abundances in large, closed canopy pools. *Bidessonotus inconspicuus* was the only species of beetle that had a significantly higher abundance in small, open canopy patches (F=10.28, P=0.011, Fig. 2.3e). *Notonecta irrorata* had a significantly greater abundance in large, closed canopy mesocosms (F=6.44, P=0.032, Fig. 2.3f). The other two species of aquatic beetle, *Copelatus glyphicus* (Fig. 2.3g) and *Enochrus ochraeus* (Fig. 2.3h) did not have significantly different abundances between the two patch types.

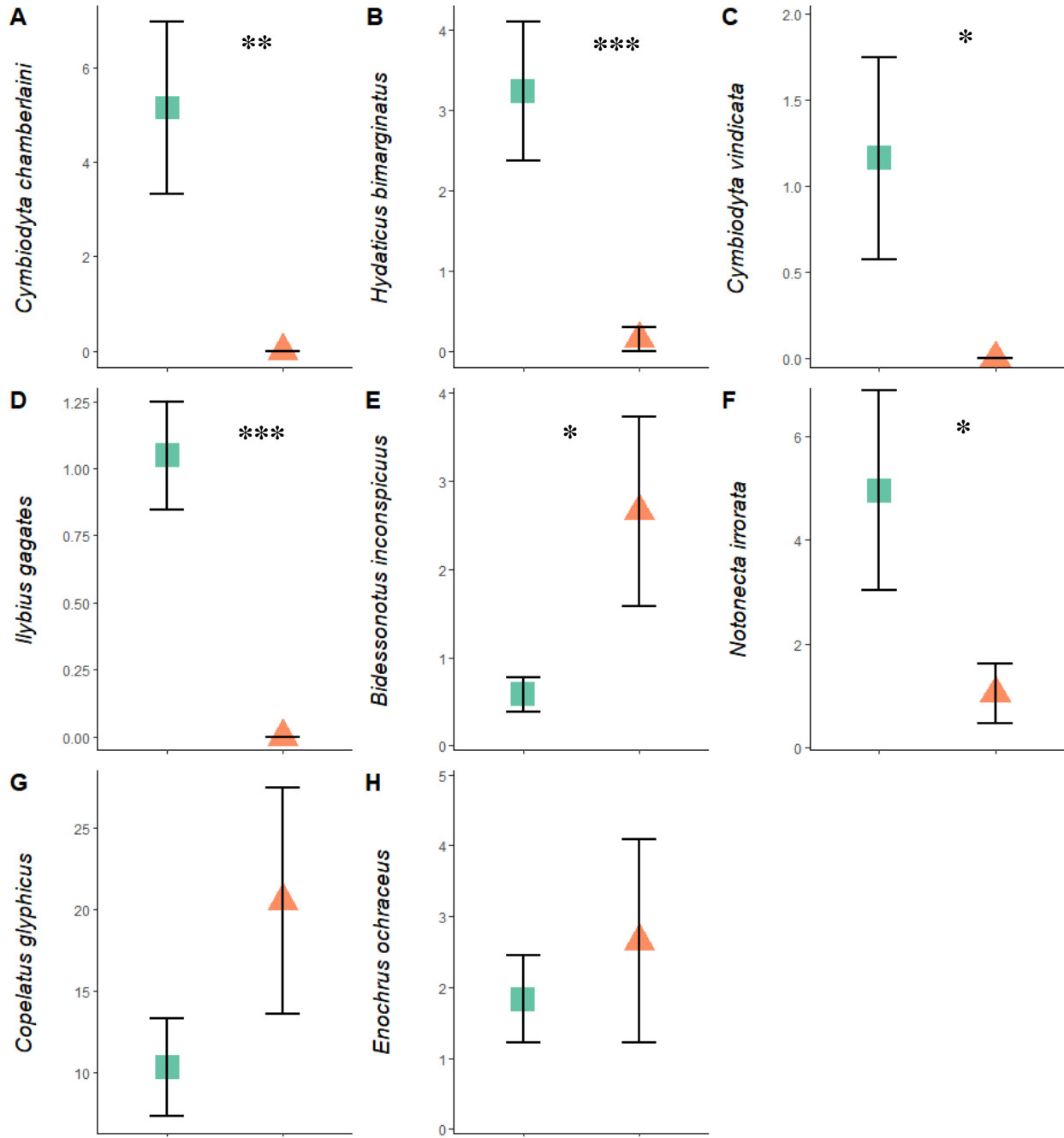


Figure 2.3a-h: Adjusted mean abundance \pm SE of each insect species that was individually analyzed (greater than 35 individuals) in the two patch types. Green squares represent large, closed canopy patches and orange triangles represent small, open canopy patches. The “*” represents $P < 0.05$, “**” represents a $P < 0.01$, “***” represents a $P < 0.001$.

Discussion

Aquatic biodiversity can be measured at local (community-level) and regional scales (metacommunity-level) with the movement of organisms among patches creating ecologically distinct communities (Resetarits et. al., 2005). Species will use a variety of patch characteristics to sort amongst available habitats, occupying individual niches (Binckley and Resetarits, 2007, Resetarits and Binckley, 2009, Resetarits et. al., 2018, Resetarits et. al., 2019, McNamara et. al., 2021, Enseldo-Cárdenas et. al., 2021). Coupling the concept of niche theory with that of habitat selection provides researchers with the opportunity to examine species specific perceptions of available patches while simultaneously considering how that patch plays a role in an organism's fitness. By combining these concepts, one can begin to develop a potential framework on what characteristics may make one patch more suitable than another.

There was no significant difference in the abundance of aquatic insects in large, closed canopy patches and small, closed canopy patches. However, individual responses of the most abundant taxa emphasized the concept of species sorting amongst available patches and resulted in the formation of distinct aquatic communities between the two patch types (large, closed canopy and small, open canopy). Aquatic beetles predominantly favored the large, closed canopy patches, apart from *Copelatus glyphicus* and *Enochrus ochraceus* that showed no patch preference and *Bidessonotus inconspicuus* that preferred small, closed canopy patches. The dominant species of hemipteran (*Notonecta irrorata*), preferred to colonize large, closed canopy patches over small, open canopy patches. Overall, aquatic beetles and hemipterans primarily preferred large, closed canopy patches but, not every species exhibited this patch preference, which likely resulted in the significant community differences among patches (Fig. 2.2, 2.3a-h). The segregation of species among patches is not surprising since aquatic insects exhibit species-

specific colonization preferences (Binckley and Resetarits, 2009, Resetarits et. al., 2019, Scott et. al., 2021).

Patch size and canopy cover are two common environmental characteristics that vary universally, creating a landscape of unique patches. Individually, these characteristics elicit strong responses from colonizing aquatic insects. Open canopy patches are preferred by numerous species of aquatic insects (Binckley and Resetarits, 2007). Binckley and Resetarits (2009) showed that aquatic insects will change patch preference as canopy growth occurs with aquatic insects colonizing those open canopy patches more frequently later in the year. However, for patch size, results seem to be species-specific suggesting that species tend to sort amongst available patch sizes (Resetarits, et. al., 2019, Scott et. al., 2021).

The preference for open canopy patches over closed canopy patches may be attributed to a few parameters that are associated with insect physiology and patch characteristics. Open canopy patches receive a greater amount of light which can lead to higher primary productivity and thus greater food availability for colonizers (Skelley et. al., 2002). Aquatic insects also use reflected polarized light to locate suitable habitats and open canopy patches reflect more light, potentially attracting more insects (Ensaldo-Cárdenas et. al., 2021). However, even with the potential benefits of open canopy patches, this study found the opposite response of colonizing insects with the majority preferring large, closed canopy patches.

These findings are likely the result of combining patch size and canopy cover into one experiment and indicate the complexity of habitat selection and how organisms must weigh a variety of patch characteristics. The small, open canopy patches had much higher and more variable temperatures than the large, closed canopy patches (Table 2.1) and aquatic insects prefer cooler temperature patches (McNamara et. al., 2021). The small, open canopy patches may have

been too warm for many species of colonizing insects forcing them to select the large, closed canopy patches.

A few species of aquatic insects did follow similar trends to prior research. *Notonecta irrorata*, a primary predator of aquatic beetles, had a strong preference for the larger patches similar to the results of another study (Resetarits et. al., 2019). Also, one species of beetle, *Bidessonotus inconspicuus*, preferred small, open canopy patches over the large, closed canopy patches (Binckley and Resetarits, 2007, Binckley and Resetarits, 2009). However, other species like *Copelatus glyphicus*, that in previous studies exhibited a strong preference for smaller patches over larger ones (Resetarits et. al., 2019) showed no preference for either patch in this experiment. Previous studies indicated that aquatic beetle preferences for the smaller patches may be a result of predatory species like *N. irrorata* colonizing patches first but, in this study we see the opposite with the majority of aquatic beetle species colonizing larger, closed canopy patches (Resetarits, et. al., 2019). By placing large patches in closed canopy ecosystems perhaps it makes it more difficult for aquatic beetles to recognize the threat of predation.

These results show the complex nature of habitat selection and how altering different patch characteristics may change an organism's preferences. Temperature (McNamara et. al., 2021), patch size (Resetarits et. al., 2019, Scott et. al., 2021), canopy cover (Binckley and Resetarits, 2007, Binckley and Resetarits, 2009), and the presence/ absence of conspecifics or predators (Binckley and Resetarits, 2005, Resetarits and Binckley, 2009, Resetarits et. al., 2019, Scott et. al., 2021) can all influence the quality of a patch, and these characteristics likely interact with one another to influence habitat selection. Organisms are constantly trying to make those decisions that maximize their fitness but, the quality and quantity of ideal habitats is fleeting forcing organisms to compromise between suboptimal patches. Our results reinforce this idea, by

showing that when patch characteristics are manipulated, patch colonization preferences may change to allow for the maximization of fitness. However, it must be noted that limitations exist since organisms often fall for ecological traps and do not have complete knowledge of the patch they are about to colonize (Battin, 2004). Nonetheless, understanding why colonizing aquatic organisms select one patch over another provides novel information about how patch characteristics play an important role in shaping communities and metacommunities.

RELEVANCE AND IMPORTANCE

Selecting suitable patches for colonization is important for aquatic organisms that rely on these habitats for food acquisition, reproduction, and shelter (Resetarits and Wilbur, 1989, Price, 2010, Dumas et. al., 2014, Lagos et. al., 2015, Resetarits and Pintar, 2016, Tavares et. al., 2018, Han et. al., 2019, Cuartas-Villa and Webb, 2021, Gould et. al., 2021, Ensaldo-Cárdenas et. al., 2021, Eversole and Henke, 2022). Natural variation among aquatic habitats through space and time creates a mosaic of unique habitats and aquatic organisms must navigate these landscapes assessing potential colonization sites to determine which ones will allow for the maximization of fitness (Resetarits, 2021, Resetarits et. al., 2021). Understanding why aquatic organisms select one patch over another provides insight into how organisms prioritize different patch characteristics.

For these experiments, I used a compromise design to examine how *Hyla chrysoscelis* and aquatic insects prioritize canopy cover and patch size. These are two common habitat characteristics that vary naturally and can be important determinants of a patch's quality (Binckley and Resetarits, 2007, Binckley and Resetarits, 2009, Resetarits et. al. 2018, Scott et. al., 2021, Resetarits et. al., 2022). For *H. chrysoscelis*, large, closed canopy patches were preferred over the small, open canopy patches, which indicates that patch size determines a better-quality patch. Numerous other studies have also shown the importance of patch size for colonizing *H. chrysoscelis* with the presence of predators/competitors being the only characteristic thus far to degrade the quality of large patches (Resetarits et. al., 2018, Resetarits et. al., 2022). For aquatic insects, responses varied among species with most preferring large,

closed canopy patches. These species-specific responses created unique community structures among the two patch types. Results from this work can be applied to conservation initiatives by providing a more nuanced and balanced approach to create habitats that benefit the largest number of aquatic organisms.

The quantity and quality of aquatic habitats is decreasing, especially in human-altered landscapes. Human manipulation of aquatic habitats degrades the quality of patches, resulting in the loss of ideal habitats and directly impacting aquatic organisms (Battin, 2004). With the ongoing decline of numerous aquatic organisms, particularly amphibians, and human alterations to the landscape as a primary factor contributing to this global issue (Blaustein et. al., 1994, Collins and Crump, 2009), it is imperative that we understand how to best manage our aquatic environments. This research demonstrates two different approaches that may help direct restoration programs. One approach being a species-specific program, relating to the work conducted on *H. chrysoscelis* to create habitats that provide an individual species with quality habitats. Understanding what drives species specific preferences for certain patches over others allows for conservationists to tailor restoration plans specifically designed for an individual species. The second approach is focused on creating a variety of habitats that support a large range of aquatic organisms. When examining aquatic insect responses we can see species disperse over a range of different aquatic patches, creating unique community structures. Designing restoration programs that create a range of aquatic habitats will support the largest diversity of aquatic organisms. It is still important for these programs to consider individual species preferences in order to design appropriate programs. The biggest take away here is that ideas like “build it and they will come” or “one size fits all” that have been implemented in the

past may not be the best practices for creating high quality aquatic habitats to support the large amount of aquatic biodiversity.

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