

**UNIVERSIDADE FEDERAL DE SÃO CARLOS
CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E RECURSOS NATURAIS**

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**A INFLUÊNCIA DA COMPLEXIDADE E COR DO AMBIENTE SOBRE O
COMPORTAMENTO DE EMERGÊNCIA E SELEÇÃO DE HABITAT EM
ODONATA**

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Dissertação apresentada ao Programa de Pós-graduação em Ecologia e Recursos Naturais - PPGERN, para a obtenção do título de mestre em ecologia.

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Centro de Ciências Biológicas e da Saúde
Programa de Pós-Graduação em Ecologia e Recursos
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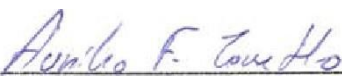
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DEDICATÓRIA

À minha amada esposa, que me deu filhos maravilhosos.

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RESUMO GERAL

Compreender quais traços comportamentais influenciam a ocupação dos animais nos diferentes habitats é indispensável para entender os processos ecológicos. As diferentes características do habitat, como a complexidade visual do ambiente, a presença de estruturas tridimensionais, o risco de predação e os padrões de coloração de fundo, podem atuar como pressões seletivas sobre o comportamento animal e influenciar a seleção do habitat e os ciclos de vida. A presente dissertação buscou evidenciar como as larvas de Odonata se comportam em diferentes tipos de microhabitat em experimentações controladas. No primeiro capítulo, testou-se a hipótese de que as larvas selecionam microhabitats, analisando a preferência por ambientes com baixa ou alta complexidade, e por habitats claros ou escuros em cinco experimentos laboratoriais. Os resultados sugerem que larvas de Odonata exibem preferência por microhabitats mais escuros, independentemente do risco de predação ou disponibilidade de abrigo. Além disso, o nível de complexidade visual do microhabitat pode também ter influência sobre a seleção de habitat. No segundo capítulo, testou-se a hipótese de que a complexidade do habitat prediz as taxas de emergência e mortalidade em larvas de Coenagrionidae (Zygoptera) em um sistema de aquários complementados com estruturas tridimensionais para simular habitats com maior e menor complexidade ambiental. Os resultados mostram que habitats com maior complexidade podem elevar as taxas de emergência e reduzir as taxas de mortalidade, destacando a importância da complexidade do habitat como uma das condições favoráveis à dinâmica populacional. Esta dissertação acrescenta à literatura evidências de como a estrutura do habitat pode favorecer táxons com determinados comportamentos e estratégias da seleção de habitat, possibilitando desvendar questões ecológicas sobre a dinâmica populacional, a dispersão, ocorrência e distribuição ao longo de escalas temporais e espaciais de comunidades de insetos aquáticos.

Palavras-chave: Ecologia comportamental. Biodiversidade. Libélulas. Donzelinhas. Comportamento animal. Ecologia aquática.

ABSTRACT

Understanding which behavioral traits influence animal occupation in different habitats is indispensable for understanding ecological processes. Different habitat characteristics, such as the visual complexity of the environment, the presence of three-dimensional structures, the risk of predation and the background color patterns, can act as selective pressures on animal behavior and influence habitat selection and life-cycles. The present dissertation sought to unravel how Odonata larvae behave in different types of microhabitat in controlled trials. In the first chapter, we tested the hypothesis that the larvae select microhabitats, analyzing the preference for environments with low or high complexity, and for light or dark habitats in five laboratory experiments. The results suggest that Odonata larvae show preference for darker microhabitats, regardless of the risk of predation or shelter availability. In addition, the level of visual complexity of the microhabitat may also have influence on habitat selection. In the second chapter, we tested the hypothesis that habitat complexity predicts emergence and mortality rates in Coenagrionidae (Zygoptera) larvae in a system of aquaria complemented with three-dimensional structures to simulate habitats with greater and lesser environmental complexity. The results show that habitats with higher complexity may increase larval emergence rates and reduce mortality rates, highlighting the importance of habitat complexity as one of the favorable conditions for population dynamics. This dissertation adds evidence to the literature on how habitat structure can favor taxa with certain behaviors and strategies of habitat selection, making it possible to unravel ecological questions on population dynamics, dispersion, occurrence and distribution over spatial and temporal scales of aquatic insects communities.

Keywords: Behavioral ecology. Biodiversity. Dragonflies. Damselflies. Animal behavior. Aquatic ecology.

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1. INTRODUÇÃO GERAL

A compreensão dos processos e mecanismos que regem a distribuição e ocorrência dos organismos no ambiente é um dos grandes desafios da Ecologia. A distribuição espacial dos organismos no ambiente pode ser determinada tanto pelo comportamento animal como por características do habitat (RICHARDSON et al., 2014). Em animais com ciclos de vida complexos, como insetos aquáticos, a exploração e seleção do habitat são cruciais para a compreensão dos padrões de biodiversidade, uma vez que os mecanismos de dispersão de formas imaturas e adultas diferem de forma drástica. A visão tradicional da Ecologia de Comunidades de insetos aquáticos é a de que os animais possuem uma fidelidade ao microhabitat e pouca mobilidade, caracterizando uma estrutura de metacomunidades. Entretanto, processos migratórios e síndromes comportamentais destes insetos, embora sejam particularmente pouco estudados, são conhecidos pela presença de eventos de *drift* e mobilidade das formas imaturas que podem influenciar os padrões da biodiversidade (HEINO et al., 2014; BROOKS et al., 2017).

Se pouco se sabe sobre estes comportamentos, menos ainda é conhecido sobre os processos que determinam estes padrões comportamentais (HEINO et al., 2014). Por exemplo, a personalidade ou síndrome comportamental de um indivíduo pode determinar a sua distribuição no ambiente (MIKOLAJEWSKI et al., 2015; MODLMEIER et al., 2015); predadores podem determinar a distribuição de insetos em uma metacomunidade por alterar seu comportamento (GRAINGER et al., 2017); a estrutura da vegetação pode determinar a ocupação do habitat (GUILLERMO-FERREIRA; DEL-CLARO, 2011) e a disponibilidade de presas também é outro fator que pode contribuir para a distribuição dos organismos (PINTAR; RESETARITS, 2017). Muitos estudos buscam compreender esses padrões comportamentais, no entanto, muitas vezes não são abordados de maneira interativa com as condições ambientais em que os animais geralmente estão inseridos (WHITE et al., 2014).

O estudo dos comportamentos de seleção e ocupação de habitat procuram elucidar através da ecologia comportamental alguns dos fatores que influenciam a distribuição dos organismos no ambiente. A seleção de habitat pode ser definida como “o processo pelo qual os indivíduos preferencialmente usam, ou ocupam, habitats com um conjunto não aleatório de variáveis” (MORRIS, 2003). Este processo, por fim, inclui dinâmicas populacionais e mecanismos intra- e interespecíficos que influenciam a abundância local e a distribuição dos indivíduos (MORRIS, 2003). A seleção, portanto, reflete mecanismos do comportamento animal ligados à movimentação dos indivíduos (MOORCROFT; BARNETT, 2008). Deste

modo, a análise do comportamento de seleção de habitat fornece uma abordagem importante para a identificação de características ambientais que definem os principais habitats de cada espécie.

O conjunto de condições ambientais direcionam a seleção dos indivíduos que possuam os atributos (e.g. comportamentos, preferência de habitat) necessários para a sobrevivência sob pressões seletivas em determinados habitats, atuando como filtro ecológico na composição estrutural da comunidade (POFF, 1997). Compreender o contexto natural dos habitats e a ecologia comportamental pode fornecer, portanto, ferramentas preditivas sobre muitos aspectos, seja sobre os impactos antrópicos, alterações climáticas ou a fragmentação da paisagem (WHITE et al., 2014). Entretanto, raramente os mecanismos do comportamento que conduzem os padrões de fenômenos físicos e biológicos em ecossistemas aquáticos são identificados (WHITE et al., 2014). Portanto, compreender esses mecanismos comportamentais pode permitir conhecer melhor os processos que regulam o movimento e dispersão dos indivíduos em seus habitats e extrapolar estas relações para escalas espaciais e temporais maiores (HEINO et al., 2014), o que favorece o gerenciamento de comunidades naturais no contexto da conservação (KOKKO; LÓPEZ-SEPULCRE, 2006).

Diante do exposto, a presente dissertação buscou evidenciar se a coloração e a complexidade do ambiente se relacionam com mecanismos comportamentais de seleção de habitat em Odonata. A dissertação se divide em dois capítulos. O primeiro capítulo buscou testar a hipótese de que as larvas de Odonata possuem uma preferência por microhabitats de acordo com a cor de fundo e a complexidade visual. O segundo capítulo destaca a importância da complexidade estrutural do habitat para a integridade e manutenção das comunidades de insetos aquáticos, bem como a distribuição e ocorrência de odonatos em relação ao estado e estrutura de conservação da vegetação aquática (e.g. GUILLERMO-FERREIRA; DEL-CLARO, 2011; RAEBEL et al., 2012). Neste capítulo, objetivou-se testar a hipótese de que a complexidade estrutural tem impacto positivo sobre as taxas de mortalidade e de emergência de larvas de Odonata. A partir destes capítulos, a presente dissertação buscou contribuir para o corpo de literatura que sugere que características do habitat podem influenciar o comportamento dos indivíduos e determinar a ocorrência e distribuição de odonatos em diferentes ambientes naturais. Entretanto, futuras pesquisas são necessárias para responder se a cor do substrato e a complexidade visual/estrutural determinam a preferência e distribuição *in situ* e em maiores escalas espaciais e temporais, conseqüentemente, se o comportamento de seleção de habitat afeta a distribuição de comunidades de insetos aquáticos.

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2. CAPÍTULO I

Habitat selection of larval odonates depends on background visual patterns

Abstract

Determining which environmental traits enable animals to inhabit and choose preferred habitats is key to understand ecological processes. Habitat complexity and background color patterns can act as selective pressures on animal behavior, and ultimately affect habitat choice. To investigate the role of environmental features on habitat selection, we addressed whether dragonfly and damselfly naiads show preference between dark/light or complex environments. We collected last instar naiads of *Micrathyria didyma* (Odonata: Libellulidae) and *Acanthagrion lancea* (Odonata: Coenagrionidae) in the Neotropical Savanna, and conducted five experiments in laboratory conditions. In one experiment, we tested if naiads exhibit preference for leaves in contrast with a white background. The second experiment compared preference for white and black backgrounds. Since both experiments showed significant preference for darker backgrounds, we included a predator in the black background in a third experiment, and a macrophyte in the white background in a fourth experiment. This way, we were able to include favorable and unfavorable conditions to the habitat of choice. The results of these experiments showed that naiads choose darker backgrounds independently of predation risk, and that macrophytes are as attractive as a dark background. In the fifth experiment, we tested whether habitat choice is influenced by environmental complexity. The results suggest that coenagrionids, but not libellulids, prefer more complex environments. Overall, our results suggest that naiads exhibit behavioural preferences for background color and complexity, which may ultimately drive habitat occupation.

Keywords: larvae, behavioral ecology, shelter, hiding, movement.

Introduction

Studying the several underlying mechanisms that produce patterns of animal distribution is one of the main goals in ecology. Despite its obvious relevance to community ecology, dispersal is a neglected trait and probably one of the main drivers of the distribution of individuals, populations and communities (Curry & Baird, 2015; Heino, *et al.*, 2017). Since dispersal events are strikingly hard to monitor under natural conditions, another approach is to examine one of the by products of dispersal, that is habitat preference and selection.

Habitat selection theory plays a key role in explaining habitat occupation. The theory predicts that the ability to move and disperse to different patches with the highest expected fitness may determine spatial redistribution of individuals among habitat patches (Morris, 2003). In heterogeneous environments, the ability to choose a suitable habitat may be one of the most important adaptations for animal survival. It may be even more important for predators, given that habitat selection may be crucial for both predation risk avoidance and prey capture (Heck & Crowder, 1991).

The study of how animals choose specific backgrounds may then unravel how behavioral and morphological traits interact to avoid predator/prey detection (Uy *et al.*, 2017) and ultimately affect abundance, richness and species composition (Binckley & Reseraris, 2005). The traditional view of aquatic insects ecology is that animals exhibit site fidelity and low mobility, characterizing a metacommunity structure. However, dispersal and movement behavioral patterns, although underexplored, may shape the observable patterns of occurrence and distribution of aquatic insects. If little is known about their behavior, less is known about the processes that rule freshwater animals' movements across habitats (Heino *et al.*, 2015). For instance, predator behavior may determine the distribution of a whole metacommunity by altering prey behavior (Grainger *et al.*, 2017). Habitat occupancy and movement in the environment may vary according to several environmental factors, such as the distribution of resources and predation risk (Winandy *et al.*, 2017). Therefore, understanding the habitat requirements of aquatic predators can reveal whether its occurrence is dependent on environmental characteristics, such as background traits, and allows us to extrapolate its effects to prey assemblage.

Habitat characteristics may provide different features along space/time, forming patches that may be differentially occupied by individuals (Matthiopoulos *et al.*, 2015) and ultimately affect their distribution in the surrounding environment. For instance, the visual and structural characteristics of the habitat can affect the biological and physiological aspects of an organism,

especially when it refers to behavior, affecting the efficiency of prey consumption by predators (Xiao *et al.*, 2016) and dispersal ability (Andersen *et al.*, 2016; Suhling *et al.*, 2017). Background color and environmental complexity may decrease detection by predators and prey, once animals tend to choose sites that provide shelter and a place to hide (Merilaita & Stevens, 2011; Xiao *et al.*, 2016). Several animal species choose habitats with complex structures, such as vegetation, as shelter and for camouflage (Merilaita, 2003; Xiao & Cuthill, 2016). Odonates have been recently suggested as key tools for environmental assessments (Valente-Neto *et al.*, 2016; Miguel *et al.*, 2017), due to the high dependency of naiads on microhabitat and environmental composition (Corbet, 1999), and of adults on factors such as light (Henry *et al.*, 2017), volatile cues (Fрати *et al.*, 2016) and vegetation structure (Guillermo-Ferreira & Del-Claro, 2012). Animals with complex life-cycles, such as odonates, go through ontogenetic changes that allow them to occupy different niches during the aquatic larval life stage and the aerial adult stage (Stoks & Córdoba-Aguilar, 2012). Therefore, a better understanding of habitat preference of naiads may provide useful information for further studies that consider animal occurrence and distribution of Odonata in aquatic and even terrestrial environments. in aquatic environments.

Here, we addressed whether Coenagrionidae and Libellulidae (Odonata) naiads exhibit microhabitat preference, examining the role of background choice in an aquatic predator. We hypothesized that naiads show a clear preference for specific backgrounds. We expected that:

(i) naiads would prefer darker backgrounds that most resembles its natural habitat - adult dragonflies may select dark sites for oviposition (Bernáth *et al.*, 2002), where the larvae are supposed to develop;

(ii) habitat selection would occur to minimize predation risk (e.g. Carrascal & Alonso, 2006), in other words, naiads would not prefer dark backgrounds when there is a predator there - previous studies have shown that coenagrionid larvae can detect the presence of a predator and adjust their behavior according to the risk of predation (Johansson, 1993);

(iii) naiads would prefer a complex structure (i.e. macrophyte) than dark backgrounds considering that complex habitats provide shelter and perches (Rantala *et al.*, 2004);

(iv) naiads would prefer habitats with higher environmental visual complexity/heterogeneity, since more complex environments provide more protection against predators (Rantala *et al.*, 2004; Grof-Tisza *et al.*, 2017).

These assumptions may explain the distribution and occurrence of odonate immatures in freshwater environments, hence, providing insight whether habitat selection may consist of a mechanism of aquatic insects distribution.

Materials and methods

Fieldwork

Naiads were collected at an Experimental Station of Aquaculture at the Federal University of São Carlos (UFSCar) (21°59'17.38"S, 47°53'03.54"W) and at a pond in the Ecological Park of São Carlos (21°59'10.15"S, 47°52'32.93"W). We collected *Micrathyrina didyma* (Anisoptera: Libellulidae) and *Acanthagrion lancea* (Zygoptera: Coenagrionidae) naiads with "D" nets between January and May 2017. Since naiads may exhibit ontogenetic behavioral shifts (Dixon & Baker, 1988), naiad body size was controlled by collecting only last instar individuals (15.5cm±1.75). We used the term "naiad", since recent discussion suggests this is the most appropriate term for odonates immatures (Büsse & Bybee, 2017). To verify if there was a correlation between naiads size and background preference, a General Linear Model (GLM) was made a priori, and the results show that body size had no influence on habitat selection (Supplementary file S1).

Laboratory experiments

To address whether naiads choose between different backgrounds, we conducted five experiments in the laboratory (Fig. 1). For each experiment, we used a sample of 20 individuals of each species. The naiads were introduced into test arenas (140 mm diameter Petri dish) divided into different habitat types. These habitat types were set under the Petri dish in order to not influence water conditions, hence, naiads had no direct contact with the substrates. The experiments consisted in introducing an individual naiad in the central part of the dish in an isolated area for acclimation. The experimental naiad was inserted in the arena inside an opaque ring during the acclimation period, which constrained the visual field to the center of the arena only. Additionally, each naiad was inserted in the middle of the background options, in order to avoid preference derived from its initial position in the arena. After a period of acclimatization (that is, until the naiad moved), we observed the habitat preference of each naiad by recording the time spent in each habitat during the focal observations, noting a positive response when the naiad walked towards a background type and had at least the head in the

selected habitat. To avoid bias in background preference, the experimental arena was rotated 180 degrees every trial. Focal observations lasted 300 seconds for experiment 1 and 60 seconds for the other experiment, which was sufficient time for naiads to show a behavioral response. A longer time of observation was needed in experiment 1 because the naiad had more habitats to choose.

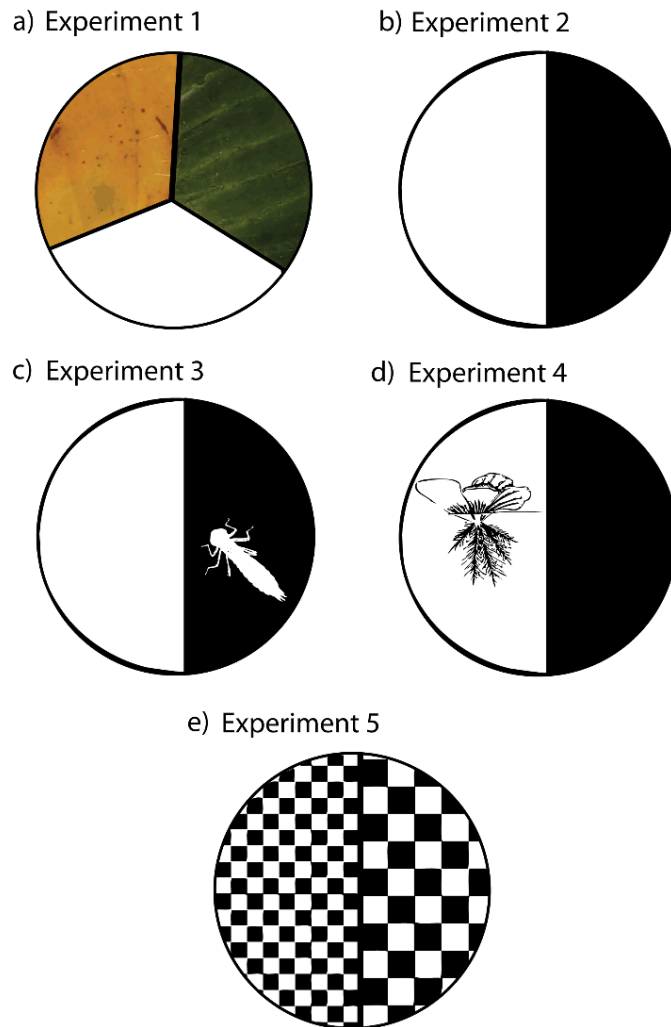


Figure 1. Experimental arenas where dragonflies and damselflies were tested for background choice: (a) Experiment 1, with white background against yellow and green leaves; (b) Experiment 2, white against black background; (c) Experiment 3, same as before, but with a predator on the black background; (d) Experiment 4, same as before, but with a macrophyte on the white background; Experiment 5, where two levels of background complexity were presented.

Experiment 1. In this experiment, we divided the testing arena in three habitat types: i) natural dark leaf, ii) natural non-dark leaf, and iii) white paper (Fig. 1a). Leaves were collected at the same site of the naiads. This experiment was conducted to answer whether naiads prefer darker natural habitats. A white background option was chosen as a control for possible bias for a true light habitat, since light colored leaves do not necessarily represent a brighter background.

Experiment 2. After naiad choice in experiment 1, to confirm habitat choice between dark and light environments, we divided the arena in two areas: i) light, with white paper underneath; and ii) dark, with black paper under the dish (Fig. 1b). This experiment was made to confirm naiad preference for darker backgrounds (see results).

Experiment 3. To investigate the role of predation risk on habitat choice, we conducted a similar experiment to Experiment 2, but added a predator (*Anax amazili* naiad, Odonata: Aeshnidae) to the dark area (Fig. 1c). The predator is much larger than our experimental species and is known as an intra-guild predator. The predator was collected at the same local as the experimental naiads. This experiment was conducted to answer whether naiads will change their preference from darker backgrounds (see results) to lighter backgrounds under predation risk.

Experiment 4. To answer if naiads prefer habitats with macrophytes, another experiment similar to Experiment 2 was carried out, but adding a small macrophyte (*Pistia* sp.) to the light area (Fig. 1d). Macrophytes were also collected at the same site of the naiads. The collected macrophytes had enough water column in the petri dish to float. We conducted this experiment to address whether the structural complexity of a suitable habitat is able to change the naiad preference for darker backgrounds.

Experiment 5. To address whether naiads prefer more complex habitats, we divided the testing arena in two visual complexity types, with checkered patterns of black and white, with squares measuring 16mm² or 4mm² (Fig. 1e). Backgrounds with larger squared patterns represent a smaller fractal complexity and a more conspicuous dark background, while smaller checkered patterns may represent a more visually complex habitat and a lighter environment (Tonetto *et al.*, 2015). Therefore, we conducted this experiment to answer whether habitat visual complexity may influence habitat selection in dragonflies and damselflies.

Different sets of individuals were used in each experiment. All background options had the same area in each experiment. In all experiments, we recorded the time each naiad spent in each alternative background option. Experiments were conducted in an experimental room with controlled temperature (28±1°C), water pH (6.5±0.1) and photoperiod (12:12).

Statistical analysis

We analyzed background selection for each experiment using Generalized Linear Mixed Models (GLMM). For each experiment, the residence time of each naiads in each area was defined as a continuous dependent variable, naiads preference and size were considered as

fixed effects, while individuals were inserted as random effects. Bonferroni correction was applied for the GLMM tests, hence, significance at $\alpha = 0.005$. All the tests were performed in the IBM SPSS 20.0 software.

Results

The results demonstrate that larvae may show patterns of background preference (Table 1).

Experiment 1. Libellulid and the coenagrionid naiads exhibited preference for darker leaves (Figure 2a, GLMM, $F = 7.020$, $p = 0.002$; $F = 31.098$, $p < 0.001$, respectively).

Experiment 2. Both libellulids and coenagrionids showed preference for the black background (Fig. 2b, GLMM, $F = 58.945$, $p < 0.001$; $F = 12.837$, $p = 0.001$, respectively).

Experiment 3. Libellulids had a longer residence time on the black background even when the predator was in this area (Fig. 2c, GLMM, $F = 28.239$, $p < 0.001$). Coenagrionids also preferred the black background, even with a predator in this area (Fig. 2c, GLMM, $F = 21.539$, $p < 0.001$).

Experiment 4. From the individuals tested in experiment 4, six libellulid naiads remained on macrophytes located on the white area, while 14 individuals remained longer on the black area (without macrophytes). Libellulids showed no preference for the dark background, nor for the macrophytes in the white background (Fig. 2d, GLMM, $F = 7.983$, $p = 0.007$). Coenagrionids also exhibited no preference, since seven naiads remained longer on the dark background, while 13 naiads occupied the macrophyte present on the light background, demonstrating that the presence of macrophytes may alter the preference for darker backgrounds (Fig. 2d, GLMM, $F = 3.721$, $p = 0.061$).

Experiment 5. *M. didyma* naiads did not present significant preference for any visual complexity patterns (Fig. 2e, GLMM, $F = 2.488$, $p = 0.123$), of the 20 individuals tested, 8 remained longer in the background of high complexity and 12 in the background of low complexity. However, *A. lancea* naiads showed significant preference for the background with higher complexity (Fig. 2e, GLMM, $F = 13.519$, $p = 0.001$).

Table 1. Results of the Generalized Linear Mixed Models showing the latency of dragonfly and damselfly naiads in each experimental set up, and the resulting background preference. Significant results are marked in bold after Bonferroni correction.

	<i>Acanthagrion lancea</i> (Zygoptera: Coenagrionidae)			<i>Micrathyria didyma</i> (Anisoptera: Libellulidae)		
	Time (s)	F	<i>p</i>	Time (s)	F	<i>p</i>
Experiment 1						
<i>green</i>	178.1±16.01			145.9±28.66		
<i>yellow</i>	87.95±14.06	31.098	<0.001	130.85±29.31	7.020	0.002
<i>white</i>	35.25±6.6			23.25±15.26		
Experiment 2						
<i>black</i>	44.4±5.68	12.837	0.001	52.65±4.17	58.945	0.001
<i>white</i>	15.6±5.68			7.35±4.17		
Experiment 3						
<i>black/predator</i>	46.9±5.14	21.539	<0.001	48.75±4.98	28.239	<0.001
<i>white</i>	13.1±5.14			11.25±4.98		
Experiment 4						
<i>black</i>	21.6±6.1	3.721	0.061	40.75±5.38	7.983	0.007
<i>white/macrophyte</i>	38.4±6.1			19.25±5.38		
Experiment 5						
<i>high complexity</i>	45.25±5.8	13.519	0.001	23.1±6.18	2.488	0.123
<i>low complexity</i>	14.75±5.8			36.9±6.18		

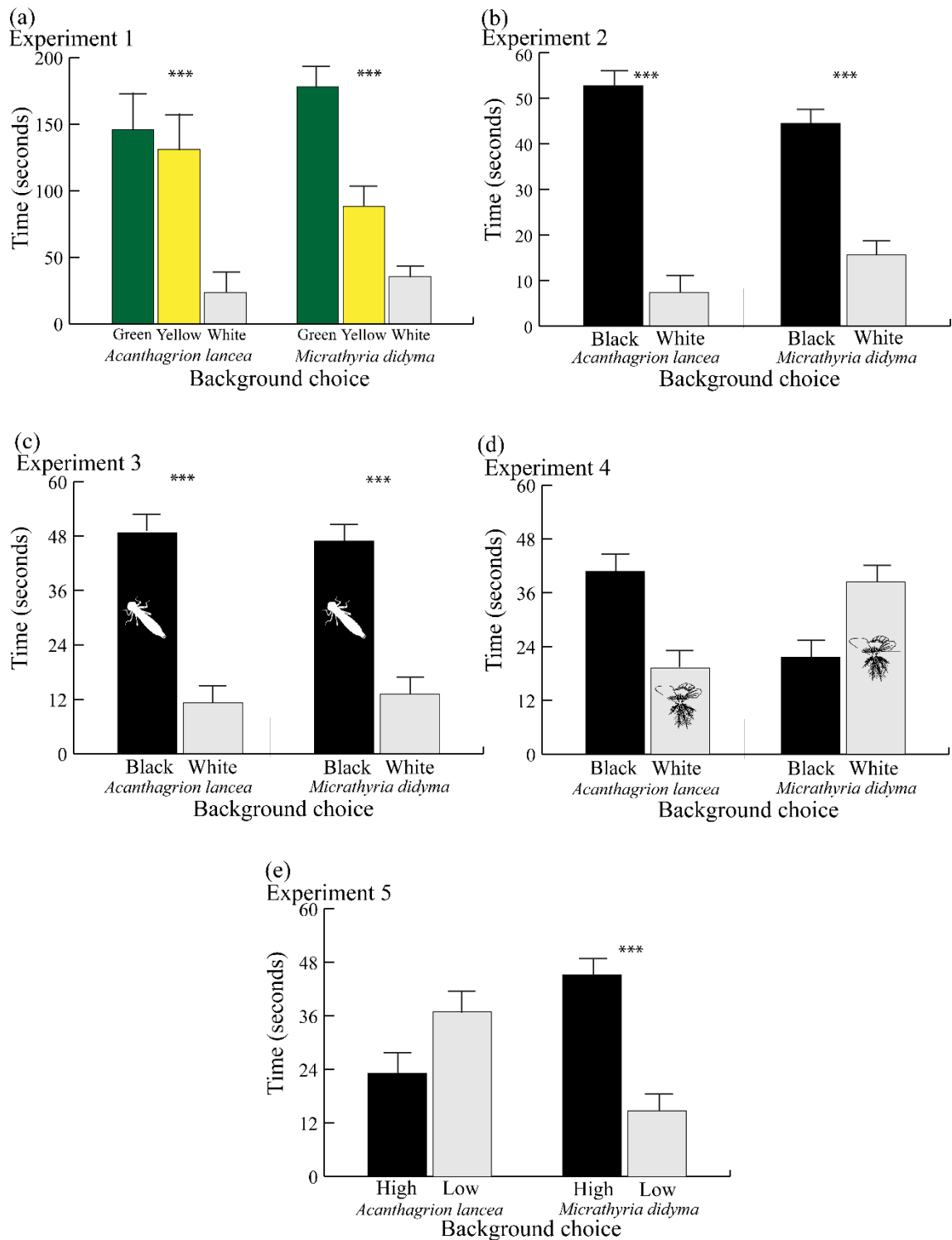


Figure 2. Background preference of odonate naiads in each experiment: (a) Experiment 1, where naiads preferred green leaves over yellow ones and a white background; (b) Experiment 2, where the black background was preferred by all naiads over the white background; (c) Experiment 3, where the presence of a predator did not inhibit black background preference among naiads; (d) Experiment 4, where preference for black backgrounds decreased when macrophytes were present on the white background; and (e) Experiment 5, where damselfly naiads actively chose between backgrounds with high or low complexity, but dragonflies showed no preference. *** = $p \leq 0.001$.

Discussion

Our results show that odonate naiads may exhibit preference for certain background and complexity. *M. didyma* and *A. lancea* naiads showed preference for darker background and leaves, regardless of the presence of a predator. In general, many aquatic insects have complex habitat affinities, providing protection against abiotic stress factors and reducing the risk of predation (Warfe & Barmuta, 2004). It is known that some odonate naiads are usually found under habitat structures, such as debris or vegetation (Wellborn & Robinson, 1987; Rantala *et al.*, 2004), providing habitats with low light intensity and consequently avoiding predation risk (Henrikson, 1988). Therefore, seeking and hiding on dark backgrounds may be a primary strategy in naiads, which may be more expressed than predator detection and avoidance. The same absence of anti-predation behavior was observed in *Leucorrhinia dubia* (Van der Lind.) (Odonata: Libellulidae), when studied in lakes and in laboratory experiments with the presence of predatory fish (Henrikson, 1988).

The results also show that coenagrionid naiads may select for habitats with higher visual complexity, however, libellulids did not present any significant preference for complexity levels. For example, preference for dark backgrounds was equivalent to the choice for macrophytes, indicating that complex structures may be attractive for odonate naiads. Libellulid naiads may exhibit a fossorial habit, when individuals occupy the space between debris and macrophyte roots and stems (Corbet, 1999). This behavioral trait may be the reason why visual complexity was not determinant for libellulid habitat choice. Coenagrionids actively chose the more visually complex habitats, which corroborate our initial hypothesis that naiads choose environments that provide complex backgrounds that may indicate the presence of shelter (e.g. Verdonschot & Peeters, 2012). Likewise, coenagrionids showed a higher behavioral response towards macrophytes, indicating that damselfly naiads clasping behavior towards complex structures may be an adaptation for habitat selection. For example, naiads of the damselfly *Enallagma cyathigerum* (Coenagrionidae), independently of predation risk and food availability, actively select habitats with more structured and complex vegetation (Verdonschot & Peeters, 2012).

Complex habitat structures, such as macrophyte roots, offer refuge that decrease predation risk (Burks *et al.*, 2001; Rantala *et al.*, 2004; Klecka & Boukal, 2014; Grof-Tisza *et al.*, 2017) and mortality (Tavares *et al.*, 2017) in odonates. However, some studies suggest that complexity may also reduce predation success in dragonflies (Fulan & Anjos, 2015). A study with *Aeshna viridis* (Aeshnidae) showed that naiads exhibit affinity for *Stratiotes aloides*

macrophytes, which have thorns that inhibit fish predation (Rantala *et al.*, 2004). The diversity of structural elements promotes a higher habitat complexity, which in turn decrease detection by predators and increase odonate naiads survival (Grof-Tisza *et al.*, 2017). However, high habitat complexity is not an isolated factor that favors anti-predator strategies, but it is only one among multiples factors that can affect mortality, which depends on behavioral interactions between prey and predators (Klecka & Boukal, 2014).

Here, we show how animals may choose specific microhabitat characteristics, unraveling how behavioral traits may drive the evolution of habitat selection strategies (e.g. Uy *et al.*, 2017) and determine the distribution of taxa in the environment. Moreover, our results add evidence to the role microhabitat visual complexity has on animal ecology and evolution (Tomkins *et al.*, 2011; Kovalenko *et al.*, 2012). It is known that animals may choose habitats according to its complexity (Merilaita, 2003; Xiao & Cuthill, 2016), hence, habitat complexity may also have an intrinsic relationship with odonate behavior (Moum & Baker, 1990; Corbet, 1999; Johansson & Nilsson-Örtman, 2013). In conclusion, we suggest that odonate naiads choose suitable microhabitats according to background color and visual complexity, which may ultimately influence the distribution and occurrence in natural environments. Future studies should address whether substrate color and environmental complexity determines overall Odonata habitat preference and distribution *in situ* and in larger spatial scales (e.g. Matthiopoulos *et al.*, 2015) Another possibility is to study how habitat selection behaviors affect the distribution of aquatic insects communities in freshwater environments.

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3. CAPÍTULO II

The relationship between habitat complexity and emergence rate in damselflies

Abstract

Environments with higher complexity harbor a greater biodiversity and can directly influence on certain behaviors of aquatic animals. Here, we tested whether habitat complexity predicts odonate larvae emergence and mortality rates by rearing larvae in aquaria with or without artificial complexity. The results show a shorter emergence time rate in more complex environments, and a higher mortality rate on less complex habitats.

Keywords: Odonata; dragonfly; structural complexity; aquarium systems.

Introduction

Habitat complexity has been recently considered one of the major factors that may impact species diversity (Kovalenko et al., 2012). Several studies support this prediction, suggesting that both species abundance and richness are higher in more complex environments (Gotceitas and Colgan, 1989; Warfe and Barmuta, 2004; Ferreira et al., 2014; Klecka and Boukal., 2014). Furthermore, complex habitats have a great potential to modify trophic interactions and niche availability (Warfe and Barmuta, 2004; Flynn and Moon, 2011).

A great deal of research has sought to unravel the effects of habitat complexity and heterogeneity on the biology of a wide range of taxa. Recent evidence suggests that complex environments may drive the selection of specific behaviors and impact the ecology of animals and plants, such as oviposition in insects (Bonebreake et al., 2010), community structuring of mammals (August, 1983; Hohnen et al., 2016), fishes (Ding et al., 2015), birds (Castaño-Villa et al., 2014) and aquatic macroinvertebrates (Kovalenko et al., 2014; Mazão and Bispo, 2016; Milesi et al., 2016), establishment of freshwater macroalgae (Tonetto et al., 2014), animal mating behavior (Myhre et al., 2013) and ultimately affect population dynamics (Peterman and Semlitsch, 2013).

Therefore, habitat selection is important to avoid predation risk (Bishop and Byers, 2015) and to increase larval survival of aquatic insects (Knorp and Dorn, 2016). For instance, macrophytes exhibit a high structural complexity enabling a lower risk of intra and inter guild predation and provide substrates for odonate larval emergence (Flynn and Moon, 2011). Furthermore, roots and stems of macrophytes may show the ideal complexity levels for the

emergence of odonate larvae, exhibiting the necessary surface area not only to dilute population density, but also for larvae to perch on (Hadjoudj et al., 2014).

Thus, here we addressed whether habitat complexity may predict larval emergence of Coenagrionidae damselflies (Odonata: Zygoptera). Hence, we quantified emergence and mortality rates of last instar larvae reared in two different levels of habitat complexity and under predation risk. We expected that the least complex environment would elicit larvae to emerge earlier, given that animals would be more exposed to predation risk stress.

Materials and methods

Fieldwork was carried out on September 02, 2016, in a pond at the São Carlos Ecological Park, São Carlos, São Paulo State, Brazil (21°59'10.15"S, 47°52'32.93"W) where we collected damselfly larvae using a D-net. We transported larvae to the lab in plastic vials, where we sorted individuals using white plastic trays with a light source underneath. We selected 240 last instar larvae of *Acanthagrion lancea* Selys, 1876, *Telebasis willinki* Fraser, 1948 and *Oxyagrion terminale* Selys, 1876 and randomly assigned them into four 100 L (25 × 40 cm) aquaria, all containing sterilized sand as substrate and PVC pipes to pump water through the system (Fig. 1a, b). Two aquaria were randomly defined as treatment, where we added six squared PVC plates measuring 15 × 15 cm with 18 attached green straws to mimic macrophyte stems (Fig. 1c, d) in each aquarium, simulating a habitat with high environmental complexity. The other two aquaria were defined as control and had no straws. All aquaria were connected through a series of connecting pipes.

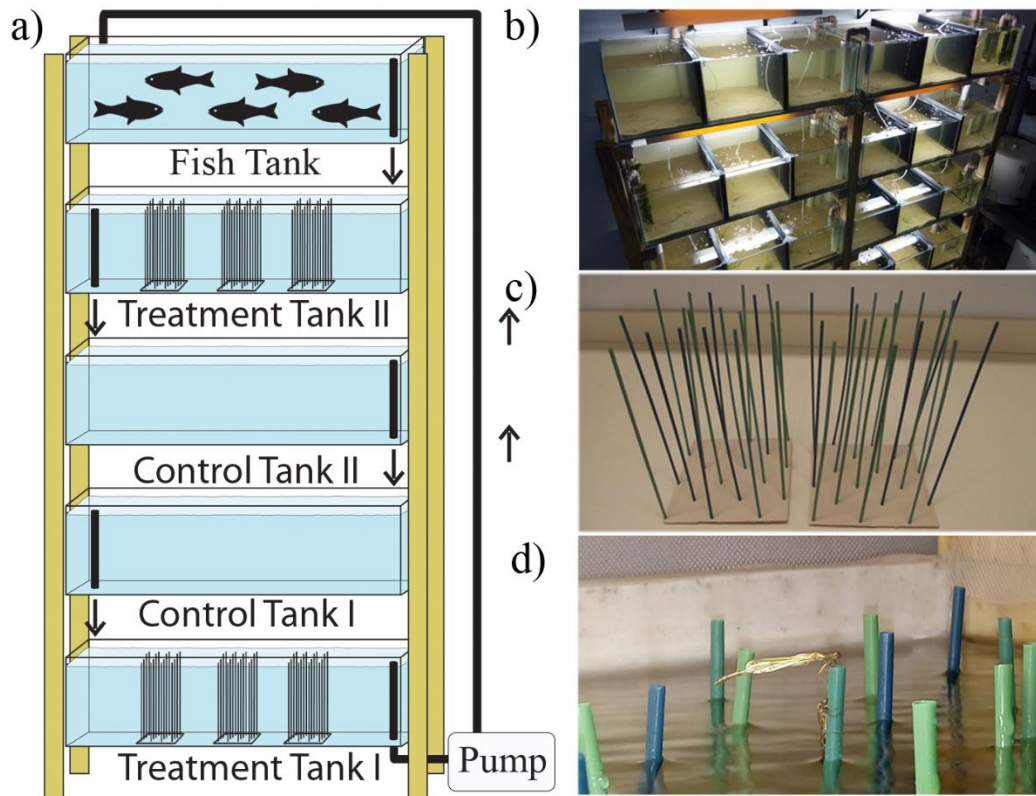


Fig.1 Experimental setup: (a) scheme showing the layout of aquaria, including the experimental (control and treatment groups) aquaria and the fish tank connected through a series of pipes to a water pump; (b) the real experimental setup showing the individual aquaria; (c) PVC plates with attached straws to simulate structural complexity; and (d) a damselfly that recently emerged by using a straw as substrate. Setae represent the water flow direction.

To include the effects of predators on larvae behaviour, we connected the experimental aquaria to two other aquaria containing fishes, serpa tetra *Hyphessobrycon eques* (Steindachner, 1882) (Teleostei, Characidae). Fishes and damselfly larvae were collected in the same pond. This experimental set guaranteed the presence of fish kairomones in the water, which behave as negative stimulus to odonate larvae that can recognize predators based on chemosensory cues (McPeck, 1990; Wisenden et al., 1997). We kept the aquaria in a closed room with constant temperature 25 ± 1 °C, pH levels at 6.8-7.0, and 12:12 h photoperiod. We checked the aquaria daily for larval emergence rates (i.e. the number of larvae that emerged on each day) by collecting the exuviae and adults, which were stored into glass tubes and properly tagged according to emergence site and date. The teneral adults were kept alive in the tube for 24 h to wait for exoskeleton sclerotization and color maturation. Hence, individuals were subsequently preserved in 100% ethanol for species identification. Exuviae were also preserved in 100% ethanol. We continued this process until the last live larva (16 consecutive days), the time required for the appearance of most larvae. During the study period, we also collected dead individuals to estimate mortality rates (i.e. the number of dead larvae per day).

After normality tests (Shapiro-Wilk, $p = 0.001$), we log transformed data for analyses. To analyze whether habitat complexity predicts larvae emergence rates, we compared control and treatments groups with pairwise t-tests, considering each date as a sample state. We used chi-square tests with Yates correction to analyze the difference in mortality rates between control and treatment groups. All analyses and graphs were made using the Statistica® 10 software.

Results

During the experiment, we observed 29 emerging larvae in the control group, while 81 were observed in the treatment group, totalling 110 larvae. In the control group 22 larvae used the PVC pipes as substrate and 7 larvae used the aquarium glass to perch on. In the treatment group, larvae also perched on PVC pipes and aquarium glasses (11 and six respectively). However, most larvae used the straws as perch ($N = 64$ larvae). The results show there is a clear difference on the emergence time between control and treatment groups (Fig. 2) (Paired t-test, $t = -2.514$, $p = 0.023$). The results also show that the control group had a greater mortality rate when compared to the treatment group (Chi-square, $\chi^2 = 16.178$, $p = 0.0001$).

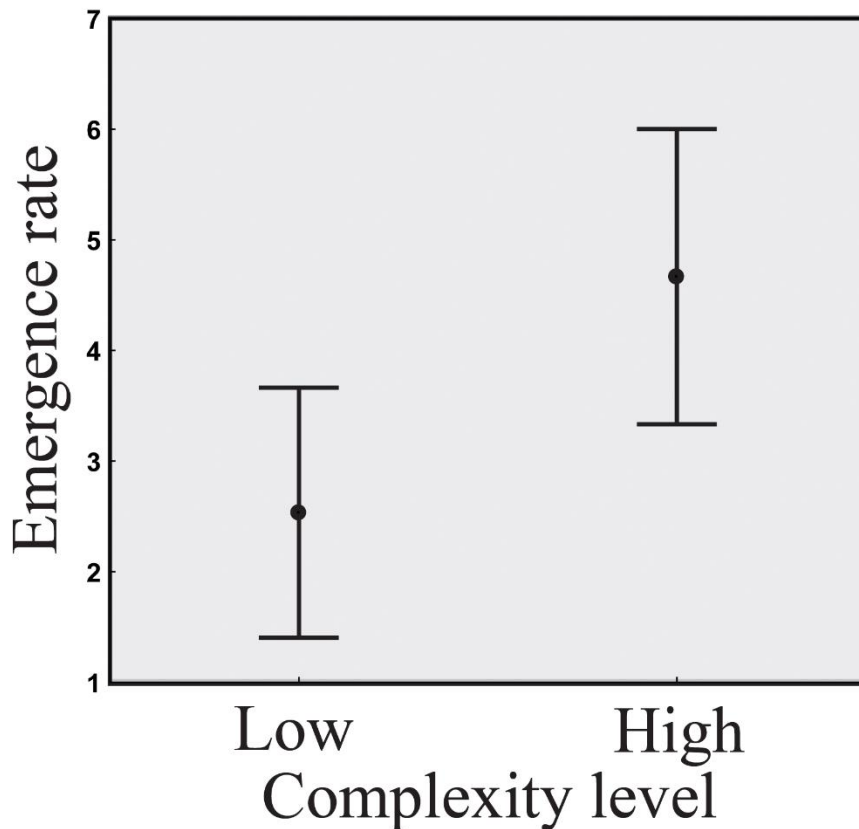


Fig. 2 Difference of larval emergence rates (emerged larvae per day) between control (low complexity) and treatment (high complexity) groups over 16 days of experiment. Results are shown as mean \pm SD.

Discussion

Our results show that habitats with greater complexity may lead to higher larval emergence rates. In general, aquatic insects prefer complex habitats with greater microhabitat availability, protection from predation and from abiotic stress factors (Warfe and Barmuta, 2004). Moreover, there is also the benefit of having a larger living area (Kovalenko et al., 2012). Environments with a variety of macrophytes exhibit the necessary habitat complexity to create protection and to diminish population density, being ideal for emergence of odonate larvae (Zebsa et al., 2014; Boda et al., 2015; Knorp and Dorn, 2016). For instance, larvae of *Enallagma cyathigerum* (Zygoptera, Coenagrionidae) prefer more complex habitats (Verdonschot and Peeters, 2012). This could suggest that environments with less complexity would cause greater stress to larvae due to higher exposure to predators (Flynn and Moon, 2011). Accordingly, larvae inhabiting environments with greater complexity may have a larger substrate area for climbing to emerge. Given this scenario of less stress and higher perch availability in complex environments, larvae would emerge faster than the individuals in a less complex habitat, hence, contradicting our initial hypothesis that low habitat complexity would elicit faster emergence.

Stress may also cause mortality and increase larval premature emergence attempts. For instance, temperature stress is known to decrease survival rates and cause an earlier emergence (McCauley et al., 2015). The development rate and emergence time are also greatly affected by photoperiod (Śniegula et al., 2014) and population density (Cardoso-Leite et al., 2014). Substrate availability may decrease the amount of competition between larvae, thus, greater larval densities with less substrate may also increase stress. All these factors can accelerate the development process, thus causing the larvae to attempt to emerge earlier and lead to greater mortality rates due to failed molting. Indeed, our results show that mortality rates were higher in habitats with lower complexity.

Notwithstanding, higher habitat complexity can also result into complications for the larvae. The more complex the environment, the harder can it be for larvae to obtain food (Warfe and Barmuta, 2004; Saha et al., 2009). In addition to that, some predators also prefer habitats with greater complexity, which may increase the encounter rate between other odonate larvae and predators (Warfe and Barmuta, 2004; Ferreira et al., 2014). For instance, a myriad of aquatic insect species preferentially inhabits macrophytes with complex root system, what may increase competition and predation (Ferreiro et al., 2014). Given this set of evidence, complexity could be a determining factor for emergence of odonate larvae due to the high costs involved in living in such complex environments.

Conclusion

In conclusion, we suggest that environmental complexity may be an underlying factor in the population dynamics of tropical damselflies by influencing time of emergence and mortality rates. Our study highlights the importance of habitat complexity and macrophyte populations for the integrity and maintenance of aquatic insect communities, as well as the distribution and occurrence of odonates in relation to aquatic vegetation conservation status and structure (Guillermo-Ferreira and Del-Claro, 2011; Raebel et al., 2012; Oliveira-Júnior et al., 2015). Future studies on habitat complexity are fundamental for better understanding the ecological processes that mediate recruitment and emergence syndromes in Odonata, providing useful information for species conservation and population studies.

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4. DISCUSSÃO GERAL

Os resultados apresentados nesta dissertação sugerem que existe preferência por padrões de coloração de fundo escuros, mesmo com o risco potencial de predação. Esse comportamento pode ser uma estratégia primária, mais expressiva do que detectar os predadores. Entretanto, a complexidade visual e a presença de macrófitas não foram determinantes para larvas de libelúlídeos, pois muitos dos indivíduos dessa família ocupam espaços fossoriais entre detritos, raízes e hastes de macrófitas (CORBET, 1999), conferindo baixa intensidade luminosa e consequentemente evitando o risco de predação (HENRIKSON, 1988). Por outro lado, os coenagrionídeos são “*claspers*” que escolhem ativamente os habitats mais visivelmente complexos e se agarram a eles (CORBET, 1999), o que fornece uma vantagem em busca de abrigos (VERDONSCHOT; PEETERS, 2012).

Em ambientes heterogêneos, a capacidade de *cripsis* pode ser uma adaptação importante para animais (ENDLER, 1990). A dissimulação pode ser ainda mais importante para os predadores, uma vez que a *cripsis* pode ser crucial tanto para a prevenção do risco de predação como para o sucesso da captura de presas (e.g. ANDERSON; DODSON, 2014). Entre os vários aspectos funcionais do comportamento animal, evitar a predação por animais orientados visualmente é uma das forças seletivas mais fortes (ENDLER, 1978), excepcionalmente nos trópicos (ROSLIN et al., 2017). Portanto, o estudo de como os animais selecionam fundos específicos para se esconder pode desvendar como os traços comportamentais são selecionados para evitar a detecção de predadores/presas (UY et al., 2017).

A cor predominante e a heterogeneidade do ambiente podem interferir nos aspectos biológicos e fisiológicos de um organismo, especialmente quando se refere ao comportamento, por exemplo, afetando a eficiência da captura de presas por predadores (XIAO et al., 2016). Como estratégia, os predadores podem selecionar habitats adequados e usar o ambiente circundante para se esconderem (EDMUNDS, 1974; POLO-CAVIA; GOMEZ-MESTRE, 2017). A cor de fundo e os padrões visuais complexos podem então diminuir a detecção por predadores e presas, uma vez que os animais tendem a escolher locais crípticos (STEVENS; MERILAITA, 2011; XIAO et al., 2016). Por exemplo, besouros Chrysomelinae apresentam uma grande diversidade de padrões de coloração que refletem diferentes estratégias sobre o comportamento anti-predação. Esses insetos se beneficiam de seus habitats (plantas hospedeiras), com um forte efeito de seleção, refletindo esses padrões de coloração com respostas de camuflagem (TAN et al., 2017). Os peixes *Gobius paganellus* vivem em ambientes

de costões rochosos marinhos com grande complexidade de fundo, composto por uma ampla diversidade de organismos sésseis, e promovendo uma grande diferenciação nos padrões de luminosidade de cores e luminância (luminosidade percebida), o que confere a esses animais um ambiente próprio para camuflagem. Além disso, esses peixes têm a plasticidade de alterar seus padrões de coloração e luminância em fundos mais claros ou mais escuros em minutos (STEVENS et al., 2014). Para a espécie de gafanhotos *Sphingonotus azureus* o risco de predação é uma causa que direciona uma resposta comportamental adaptativa nos padrões de luminosidade corporal, se ajustando aos padrões de luminância com a correspondência de fundo do habitat, aumentando seu grau de *cripsis* (EDELLAR et al., 2017). Assim, a seleção de habitats adequados pode ser particularmente importante para os predadores, pois dependem de características ambientais para camuflagem e sucesso de captura de presas (ANDERSON; DODSON, 2014).

Os resultados também sugerem que habitats com maior complexidade podem influenciar a taxa de emergência e mortalidade em larvas de odonatos. Muitas espécies de insetos aquáticos têm afinidade à ambientes com maior disponibilidade de microhabitats complexos com a finalidade de conferir proteção contra predadores e outros fatores de stress ambiental (WARFE; BARMUTA, 2004). Além disso, esses habitats mais complexos proporcionam maiores áreas de substrato para as larvas e, conseqüentemente, maiores chances de sucesso de emergência em relação a habitats menos complexos. Larvas de *Aeshna viridis* são encontradas exclusivamente em habitats com alta complexidade compostos por macrófitas (*Stratiotes aloides*), promovendo refúgio e proteção para essa espécie sobre uma ampla distribuição (RANTALA et al., 2004). Nesse cenário de menor stress e disponibilidade de locais para emergência, as larvas podem emergir mais rapidamente. Entretanto, locais onde há presença de peixes insetívoros, mesmo com disponibilidade estrutural no habitat, a sobrevivência e emergência das larvas pode ser reduzida (WERNER; MCPPEEK, 1994).

A complexidade ambiental afeta em grande parte o comportamento dos indivíduos e das populações. Por exemplo, alterando-se a complexidade do habitat pode-se alterar o comportamento de salmões, tornando-os menos agressivos (CHURCH; GRANT, 2018). A complexidade estrutural do ambiente pode alterar dinâmicas de interações predador-presa, favorecendo presas capazes de se esconder (KEISER et al., 2018). A densidade de estruturas complexas no ambiente pode reduzir a atividade de peixes sob risco de predação, aumentando a frequência de comportamentos anti-predatórios (AJEMIAN et al., 2015); e afetar a eficiência na procura de hospedeiros por himenópteros parasitóides (KRUIDHOF et al., 2015).

Os trabalhos apresentados nessa dissertação adicionam evidências de como traços comportamentais podem impelir a evolução de estratégias de seleção de habitat em uma escala local, como exemplo dos achados de Uy et al. (2017), possibilitando desvendar questões ecológicas funcionais sobre as espécies em maior amplitude e conseqüentemente elucidar questões sobre a dinâmica populacional, suas ocorrências e distribuições ao longo do tempo e do espaço. Um exemplo desse processo é constatado em *Phyllomacromia contumax* (Selys, 1879) e *Phyllomacromia picta* (Hagen in Selys, 1871); indivíduos dessas espécies podem voar centenas de quilômetros sobre ambientes áridos e se estabelecerem em lagos artificiais muito distantes dos locais regulares de reprodução (SUHLING et al., 2016).

Compreender os mecanismos e processos ecológicos em relação às características da biodiversidade, a distribuição e ocorrência das espécies, pode fornecer ferramentas preditivas que auxiliem o gerenciamento ambiental de comunidades naturais, estabelecendo critérios legais para subsidiar políticas de conservação ambiental e para ações de proteção sobre o uso adequado dos recursos geridos pelo Homem (KOKKO; LÓPEZ-SEPULCRE, 2006; MACE et al., 2008). No entanto, novos estudos são necessários para compreender como as características do ambiente determinam a preferência geral do habitat por animais, conseqüentemente aguçar novas questões que possam esclarecer como se organiza a distribuição *in situ* e em maiores escalas espaciais e como as síndromes comportamentais de seleção de habitat afetam essas distribuições de comunidades de insetos aquáticos em ambientes de água doce.

5. CONSIDERAÇÕES FINAIS

Habitats de água doce representam um dos ecossistemas mais ameaçados do mundo (DUDGEON et al., 2005). Apesar de ocuparem menos de 1% da superfície do planeta, esses ecossistemas continentais contêm 10% de todas as espécies registradas (STRAYER; DUDGEON, 2010) e sua grande maioria, cerca de 126.000 espécies é representada por insetos (60,4%) (BALIAN et al., 2007). Entretanto, estudos sobre essa biodiversidade carecem de dados mais básicos (CARDOSO et al., 2011). Estes ecossistemas são os que mais têm sofrido com ações antrópicas, e em muitos casos de extinção de alguns desses grupos de invertebrados se deve a respostas sobre distúrbios ocorridos em seus habitats (REVENGA et al., 2005). Portanto, proteger os recursos de água doce é uma questão urgente, sendo um consenso geral entre muitos pesquisadores e agentes públicos sobre a necessidade de diagnosticar ameaças sobre uma ampla gama de escalas e dimensões da biodiversidade (VÖRÖSMARTY et al., 2010).

Parte dessa ameaça aflige não somente a diversidade taxonômica, mas a diversidade comportamental (CORDERO, 2017). As atividades humanas estão impactando o comportamento das espécies e alterando dinâmicas populacionais, afetando processos ecológicos dos quais dependemos (WONG; CANDOLIN, 2015). Portanto, conhecer o comportamento das espécies, suas preferências por determinados habitats e o efeito do ambiente sobre esses comportamentos permitirá não somente uma maior compreensão dos processos ecológicos, dos padrões de ocorrência e distribuição dos organismos, mas também permitirá a conservação destes comportamentos e, conseqüentemente, estes processos.

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