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Do container size and predator presence affect *Culex* (Diptera: Culicidae) oviposition preferences?

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ABSTRACT

Organisms with complex life cycles typically do not exhibit parental care. Hence, the ability of adult females to choose quality oviposition sites is critical for offspring success. Gravid females of many insect taxa have the capability to detect environmental conditions in water-holding containers (e.g., resource level, presence of competitors or predators) and to choose the sites that are most suitable for offspring growth and development. Mosquitoes may also detect physical container characteristics related to water permanence such as surface area, volume, or container size, and some species such as those in the genus *Culex* have been shown to prefer larger containers. However, predators may also preferentially colonize larger containers; thus, ovipositing females may face decisions based on cues of site quality that balance the costs and benefits for offspring. We used a field experiment to evaluate the oviposition preferences of two *Culex* species in response to experimental container size and predator abundances within the containers. We found that both species avoided ovipositing in the largest containers, which have high abundances of *Chaoborus* sp. and dragonfly larvae (predators). However, the container size most commonly chosen for oviposition (15-L buckets) also had high mean abundance per liter of dragonfly larvae. These results suggest either prey naiveté or reduced vulnerability of these species to dragonflies compared to *Chaoborus* sp. Other potential mechanisms for the observed patterns are discussed.

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Introduction

Organisms with complex life cycles rarely provision young; thus, the ability of adult females to choose high-quality oviposition sites is crucial for offspring success. Females of many taxa can detect cues of site quality such as resource availability (Singer, 1986), the degree of intra- or interspecific competition (Almohamad et al., 2010), and the presence of predators (Andrade et al., 2016), and may choose the sites that maximize offspring success (Sih, 1986; Blaustein et al., 2004; Andrade et al., 2016). Predation pressure can strongly influence oviposition site choice by gravid females (Sih, 1986; Kerfoot and Sih, 1987), particularly for aquatic insects that occupy 'container' habitats. These containers can be natural (e.g., tree holes, bromeliad tanks) or artificial (e.g., tires, cemetery vases) and are commonly occupied by a variety of micro- and macroinvertebrates, including insects with aquatic juvenile stages. Mosquitoes commonly colonize these habitats, and some species show strong preferences regarding oviposition site choice (Blaustein et al., 1995).

Mosquito oviposition in response to a predation risk is thought to be a result of co-evolution between mosquito prey and predators (Kerfoot and Sih, 1987). Differences in evolutionary exposure to specific predators among mosquito species may cause differential responses to cues (i.e., chemical or physical) of predator presence (Blaustein et al., 1995). Further, for many mosquito species, there is a tradeoff between competitive ability and vulnerability to predation that can produce diverse oviposition responses to the presence of predators ranging from strong avoidance (Vonesh and Blaustein, 2010) to neutral (i.e., lack of response) (Andrade et al., 2016); in some cases, mosquitoes may even prefer sites holding predators (Albeny-Simões et al., 2014).

In addition to predation, the physical container characteristics may also influence mosquito oviposition site choice. Container size, surface area and depth may indicate water permanence, whereby larger containers have lower risk of drying during the larval development period (Reiskind and Zarrabi, 2012; Segev et al., 2011; Burroni et al., 2007). Larger containers may also have higher resource capacity (Harrington et al., 2008), and several

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species have been shown to prefer containers with characteristics indicative of greater water holding capacity (Wong et al., 2011; Torrisi and Hoback, 2013). However, larger containers can also support higher abundances of all organisms (Connor and McCoy, 2001), including competitors and predators (Sunahara et al., 2002), and predators typically have longer development times and may preferentially occupy larger containers (Sunahara et al., 2002). Mosquitoes may avoid ovipositing in larger containers to reduce the risk of predation for offspring (Reiskind and Zarrabi, 2012). It is also expected that for species with rapid larval development, container size likely does not influence oviposition preferences to the same extent as in species with longer development periods.

We used a field experiment to evaluate the oviposition preferences based on container size in two, locally common *Culex* species (*Culex eduardoi* and *Culex* sp. 1). We then assessed the relationships between container size and the abundances of common predators. We hypothesized that predator abundances would be highest in larger containers, and that *Culex* females would avoid ovipositing in larger containers due to high predator abundances.

Methods

Study area

This experiment was conducted at the *Floresta National de Chapecó* (27°06′39 S; 52°45′11 W) in Guatambú, Santa Catarina, Brazil. The vegetation is composed mainly of mixed ombrophilous forest and lies within the Atlantic forest biome, with a total area of 1604.35 ha. The area has humid subtropical climate with an average annual rainfall around 1600 mm and average monthly temperatures of 22 °C in the summer (28.9 °C max) and 10.4 °C in the winter (4.4 °C min). Previous observations revealed a diverse micro- and macroinvertebrate community occupying artificial container inhabitants, with over thirteen taxa and at least 15 species. The majority of mosquitoes that colonize containers belong to the genus *Culex*, where the most dominant mosquito species is *C. eduardoi*, followed by *Culex* sp. 1 (Albeny-Simões, pers. obs.).

Experimental design

Experimental microcosms (black plastic containers) were established along four, 300-m individual transects. Each transect contained 1-L ($n = 8$), 15-L ($n = 4$), 100-L ($n = 2$) and 200-L ($n = 1$) containers placed 20 m apart. Because the smallest containers (1 L) are expected to be more variable over time, we included a higher number of container replicates for smaller containers ($n = 8$ per transect, 24 total). We then collected 8, 4 and 2 sub-samples from the 200-L ($n = 4$), 100-L ($n = 8$) and 15-L ($n = 16$) containers, respectively. The position of containers along the transects was designed to keep a minimal distance between same-sized containers and to ensure roughly equal probablilty of adult female mosquito encounter with the various container sizes. This resulted in a distance of 40, 80, 160, and 320 m between the 1-L cups, 15-L buckets, 100-L and 200-L barrels, respectively, along each pair of contiguous transects (Fig. 1). In order to assure colonization by microbiota, 0.3 g/L of field-collected, mixed-species, previously dried leaf litter was added to each container. We used tap water to fill the containers to 70% maximum volume. The water level was not manipulated thereafter, and the containers were permitted to undergo natural colonization by invertebrates. After a 15-day colonization period, the containers were sampled every two weeks for 105 days ($n = 7$ sampling periods).

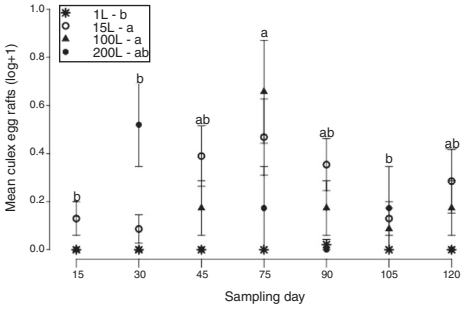

Fig. 1. Numbers of eggs rafts number as a function of sampling days and container size. The 100 and 200-L barrels are represented by closed triangles and closed circles, respectively. The open circles represent the 15-L buckets, and asterisks represent the 1-L cups. The bars represent standard error. Different letters indicate different means among the treatments.

Egg raft sampling

Egg rafts were searched for by direct observation of the water surface in containers. Using a white plastic spoon, all surface egg rafts were collected from the water surface and stored individually in Eppendorf tubes. Each container was inspected for 10 min. The egg rafts were then transported to the Entomology Laboratory at the Community University of the Chapecó Region in Chapecó, SC, Brazil. The egg rafts were inspected under a stereoscopic microscope, and those already hatched were not considered in the analysis. For species identification, the rafts were placed individually in 250-mL Nalgene® plastic containers holding 100 mL of tap water. After hatching, the larvae were reared to fourth instar by a single feeding with 0.02 g of TetraFin® gold fish flakes. For larval identification, the fourth-instar larvae were mounted on slides and identified following the methods described by Forattini (1965).

Predator sampling

The predators in the containers were sampled by sieving all water content from half of the 1-L cups every sampling period (i.e., destructive sampling) and by sub-sampling the other container sizes. The 15-L buckets were sampled using a coffee filter made with cloth, and the 100 and 200-L barrels were sampled using a conical, 52 cm height × 18 cm radius plankton net. The predators collected in the samples were placed in a 500-mL plastic container and fixed in 70% ethanol for later identification to the lowest possible taxonomic level.

Data analysis

We perform a repeated-measures ANOVA to evaluate the effects of container size, sampling day and the interaction on the number of *Culex* egg rafts (both species) and those of *C. eduardoi* and *Culex* sp. 1 individually. We also tested for effects of predator abundances of the two most common taxa (dragonfly and *Chaoborus* sp. larvae) combined, then for the effects of these taxa individually. We then used AIC-based model selection ((Table 3) to determine the importance of the main treatment effects (container size and sample period) and important predatory taxa (dargonfly larvae and *Chaoborus* sp.) both combined and separated on the numbers of egg rafts of both mosquito species (combined and separately). For each analysis, the response variable was tested for normality using a Shapiro–Wilk test. Non-normal data were log-transformed in order to adjust the data distribution. All statistical analyses were carried out using the free software R (R Development Core Team, 2014).

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