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Oviposition responses of two mosquito species to pool size and predator presence: varying trade-offs between desiccation and predation risks

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Natural selection is predicted to favor females that can detect risks of desiccation and predation when choosing among temporary pools for oviposition. Pool size may serve both as a cue for desiccation risk and as a predictor for future colonization by predators or for the probability of present, undetected predators. Therefore, oviposition responses to pool size are expected to interact with the presence of predators that can be detected. We measured oviposition by two mosquito species, *Culiseta longiareolata* and *Culex laticinctus*, in a mesocosm experiment, crossing two pool surface sizes with presence or absence of the hemipteran predator, *Notonecta maculata*, which is chemically detectable by mosquitoes. Both mosquito species strongly avoided *Notonecta* pools. Using a mechanistic statistical model, we accounted for the higher encounter rate of females with larger pools, and determined their true oviposition preferences for pool size. *C. laticinctus* showed a clear preference for larger pools, but *C. longiareolata*, a species with larvae more vulnerable to predation, showed no significant preference for pool size. This study confirms the importance of risk of predation in explaining oviposition patterns, and suggests a possible inter-specific variation in the trade-off between predation and desiccation risks.

Keywords: oviposition habitat selection; desiccation risk; predation; predation risk; temporary pools; hydroperiod

Introduction

Two major influences on larval survival of insects and amphibians that deposit progeny in temporary pools are predation and desiccation. In general, these two risk factors are inversely related; with increasing pool size, the risk of desiccation decreases (Brooks and Hayashi 2002; Waterkeyn et al. 2008; Ripley & Simovich 2009; Vanschoenwinkel et al. 2009), but predator abundance (Woodward 1983; Skelly 1996; Wellborn et al. 1996; Wilcox 2001) and predator diversity (Spencer et al. 1999; Eitam & Blaustein 2004; Eitam et al. 2004; Jocque & Field 2014) tend to increase, although there is considerable variation in predation risk among similar-sized pools.

Natural selection is predicted to favor the ability of gravid females to select pools with hydroperiods of sufficient length for progeny to successfully develop and metamorphose (Mokany & Mokany 2006; Segev et al. 2011), and pools in which the risk of predation is not high. A growing body of literature indicates that the females of many species avoid ovipositing in pools containing predators that are dangerous to their progeny. Examples include mosquitoes (reviewed in Vonesh & Blaustein 2010), other insects (Brodin et al. 2006; Resetarits & Binckley 2009), anurans (Binckley & Resetarits 2008; Indermaur et al. 2010), and urodeles (Sadeh et al. 2009). Habitat preference, therefore, requires the perception and interpretation of informative environmental cues which convey risk of desiccation and predation.

The assessment of predation risk may involve various direct cues for the presence of predators, such as detection of predator-released kairomones (Petranka et al. 1987; Silberbush et al. 2010), cues from injured or ingested conspecifics (Wisenden & Millard 2001; Bourdeau 2010), or to a lesser extent, visual (Martin et al. 2010; Schulte et al. 2013) or vibrational (Warkentin et al. 2007) detection of predators. However, the absence of such direct cues does not ascertain future absence of predators. Similarly, desiccation risk corresponds to a future event for which direct cues do not exist. As such, pool size may serve as a predictor for both risk of predation and risk of desiccation (Wellborn et al. 1996).

To gauge pool size as an indicator of the risks of predation and desiccation, females may cue in on pool depth or on its surface dimensions (e.g. surface area, perimeter), which are often related to habitat permanence (Brooks & Hayashi 2002; Waterkeyn et al. 2008; Ripley & Simovich 2009; Vanschoenwinkel et al. 2009). Some amphibian species appear to be able to gauge depth or volume and oviposit accordingly (Segev et al. 2011) but studies on dipterans which deposit their eggs from above or on the water surface differ in their conclusion as to whether these insects are capable of such an assessment. Reiskind and Zarrabi (2012) found that ovipositing *Aedes albopictus* females preferred to oviposit in artificial pools with a medium surface area over greater or larger surface areas, and also preferred pools with greater depth. Arav and

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Blaustein (2006) found that *Culiseta longiareolata* showed no preference for artificial pools of equal surface area but different depths. Conversely, Fischer and Schweigmann (2004) found that oviposition in three *Culex* species was positively correlated to both surface area and depth.

There is limited previous work which has addressed how and if a temporary pool species searching for an oviposition site can gauge both risk of predation and pool hydroperiod. In this study, we ask how oviposition pool selection by mosquitoes is influenced by a combination of predation risk and pool size (serving as a proxy for hydroperiod), allowing ovipositing females to select a pool which balances the lower desiccation risk found in longer lasting pools with additional cues indicating a lower risk of predation.

The focal mosquito species of this study are *C. longiareolata* and *Culex laticinctus* and the predator is *Notonecta maculata*. Both *C. longiareolata* and *C. laticinctus* oviposit their full egg clutch as a single egg raft in temporary pools and generally in pools with open water (Blaustein & Margalit 1995). Like all mosquitoes, the surviving offspring of these species metamorphose and emerge from the pool in which they were oviposited. Although pools containing these species are generally small, they must hold water long enough for the larvae to complete metamorphosis, or else the larvae will desiccate. The predatory backswimmer, *N. maculata*, is a common and effective predator of the larvae of these two species (Blaustein 1998). Females of both of these mosquito species can detect *N. maculata* and other species of predatory backswimmers and avoid ovipositing in their presence (Kiflawi et al. 2003; Eitam & Blaustein 2004; Silberbush et al. 2014).

In a previous study, we investigated experimentally the combined influences of pool depth (with surface area held constant) and presence of backswimmers on oviposition habitat selection in the mosquito *C. longiareolata*, and found that although ovipositing females avoided pools containing predators, they displayed no preference for deep or shallow predator-free pools (Arav & Blaustein 2006). In the current study, we hypothesized that dipterans are more likely to be able to assess surface dimensions than depth, and we investigated experimentally the combined influences of pool surface area (with depth held constant) and the presence of backswimmers on oviposition habitat selection. As previously observed, we expected that mosquitoes would strongly avoid ovipositing in pools containing backswimmers irrespective of pool size. In the absence of backswimmers, the selection of one pool size over another by an ovipositing female is hypothesized to reflect the trade-off between risk of future predation and risk of desiccation.

Materials and methods

This experiment used 20 rectangular plastic containers as artificial pools in an outdoor experiment in the Hai Bar Nature Reserve on Mount Carmel, Israel (32° 43' N; 35° 03' E; 300 m asl). A previous study demonstrated that the

same oviposition avoidance results are obtained by experimental manipulation of predators in both natural rock pools and artificial pools (Blaustein et al. 2004). All pools in the current study were of the same height (14 cm) and were identical in all regards except in surface dimensions: half of the pools were 71 cm × 54 cm (surface area 3834 cm², perimeter 250 cm, volume 53.7 l), and the other half were 55 cm × 40 cm (surface area 2200 cm², perimeter 190 cm, volume 30.0 l). These different sized pools are hereafter referred to as “large” and “small” pools. In nature, *C. longiareolata* and *C. laticinctus* can be found along a larger range of surface areas, but the range used in this experiment is typical (Blaustein and Margalit 1995; Blaustein et al. 1995; Blaustein, unpublished data). The pools were arranged into five square blocks, with four pools in each block. The pools within each block were 0.5 m apart and the blocks were at least 1 m from each other. Each block contained two large and two small pools arranged randomly within the block, resting on the surface of the ground. The pools were filled to the top with tap water and maintained throughout the experiment at maximum volume by the addition of aged tap water as well as by rainfall. To reduce solar radiation and water temperature, we erected a 90% shade cloth over the pools at a height of approximately 2 m (most existing pools are naturally shaded in the spring, when this experiment was conducted). Nutrients were added to the pools on the first day in the form of TetraPond Floating Koi Sticks (Melle, Germany) at a concentration of approximately 0.7 g/l.

Twenty-four hours after the initial inundation, uncaged *N. maculata* predators were added. Some free-roaming predators may influence among-pool mosquito egg raft distributions by direct predation on egg rafts (Blaustein et al. 2014). However, previous work with the mosquitoes used here demonstrated that egg raft abundance in free versus caged predator pools for *N. maculata* (Blaustein & Mangel, unpublished data) and other notonectids (Eitam et al. 2002) were not different. The predators used in this experiment were fourth and fifth instars, i.e. penultimate and final nymphal instars, collected from natural pools. They were deprived of any dipteran prey for at least 24 hours prior to adding them to the experimental pools. Three *N. maculata* nymphs were added to the small pools and five to the large pools. This ratio reflected the ~1:1.74 ratio of surface areas and volumes of the small and large pools. This density of approximately one per 10 liters is also a common density for natural rock pools (Ward & Blaustein 1994) and is greater than the density of the one *N. maculata* per 30 liters that has been previously shown to be sufficient to cause *C. longiareolata* and *C. laticinctus* to avoid the same predator when ovipositing (Eitam & Blaustein 2004; Silberbush & Blaustein 2011). The predators were checked every second day. Predator mortality was rare, and any dead individuals were removed and replaced. We observed no predators naturally colonizing the pools.

We counted and removed dipteran egg clutches from the pools every other day. Over a 14-day period, we measured oviposition by four dipterans: three mosquito species (*C. longiareolata*, *C. laticinctus*, and *Culex pipiens*)

and a midge species, *Chironomus riparius*. The mosquito egg rafts were brought back to the laboratory for hatching and subsequent identification of fourth instar larvae. Only *C. longiareolata* and *C. laticinctus* oviposited in sufficient numbers for a meaningful analysis.

Analyses

Total numbers of egg rafts of each species per pool served as a dependent variable in a two-way analysis of variance, with pool size and presence or absence of predator as fixed factors. The effect of the spatial blocks was not significant and was absorbed into the error term. The data for both mosquito species were $\log(x + 1)$ transformed to achieve homogeneity of variance, which we tested using Levene's test.

The demonstration of a positive linear relationship between pool surface area and oviposition (Arredondo-Bernal & Reyes-Villanueva 1989; Blaustein et al. 2004) may indicate either a behavioral adjustment of oviposition based on habitat quality (i.e. an increasing preference for larger pools), or reflect the positive relationship between pool size and its probability of being encountered randomly. This confounding effect is further complicated by the various ways that pool sizes can be measured, depending on the way they are encountered or perceived by the organisms. We modeled pool encounter and selection as a binomial process, with a probability, p , for each observed oviposition event to occur in a large pool. In accounting for random encounter rates with pools of different surface sizes, we have to consider the different ways in which animals may perceive pool size, namely pool surface area and pool perimeter. For example, increased encounter rate may be related to surface area if the mosquito flies at a considerable height relative to pool area and detects the pool visually or by humidity plume. Alternatively, if the mosquito flies low relative to pool area, then the probability of encounter may be related to the perimeter of the pool. Therefore, we modeled the probability of each oviposition event to occur in a large pool as

$$p = m \frac{C_{\text{large}}}{C_{\text{large}} + w^{-1} \cdot C_{\text{small}}} + (1 - m) \frac{S_{\text{large}}}{S_{\text{large}} + w^{-1} \cdot S_{\text{small}}},$$

where m is the probability of perimeter-based pool encounters, C_{size} and S_{size} are pool perimeter and surface area, respectively, and w is an oviposition preference coefficient for large pools. A value of $w = 1$ indicates that the probability of oviposition into a large pool equals the relative size of large pools in the set of available pools. Values of $w > 1$ indicate the strength of active preference for large pools, while values of $w < 1$ indicate the strength of active preference for small pools. To quantify the preference of the mosquitoes for large or small pools, we looked for the combination of values of w and m that maximize the log-likelihood of our observed data. We set the confidence regions for w and m by including all parameter combinations within 2 log-likelihood units of the maximum log-likelihood (Bolker 2006). Since response to

predator presence was strong and independent of response to pool size, data for pools that contained predators were very sparse. Therefore, we excluded them from the analysis of pool size preference.

Results

C. longiareolata females strongly avoided *N. maculata* pools when ovipositing; of the total of 61 *C. longiareolata* egg rafts, 55 (90%) were oviposited in predator-free pools and 6 (10%) were oviposited in predator pools (Figure 1(a) and Table 1). Twenty-seven egg rafts (44%) were laid in small pools compared to 34 (56%) in larger pools. However, there was neither a statistically significant effect of pool size nor of a *Notonecta* \times pool size interaction (Figure 1(a) and Table 1).

Oviposition by *C. laticinctus* was significantly affected by both predator size and pool size (Table 1 and Figure 1(b)). Of a total of 80 *C. laticinctus* egg rafts, 67 (84%) egg rafts were found in predator-free pools and 13 (16%) in predator pools (Figure 1(b) and Table 1). In response to pool size, 67 (84%) and 13 (16%) were deposited in large and small pools, respectively (Figure 1(b) and Table 1). No significant interactive effect of predator and pool size was found (Figure 1(b) and Table 1).

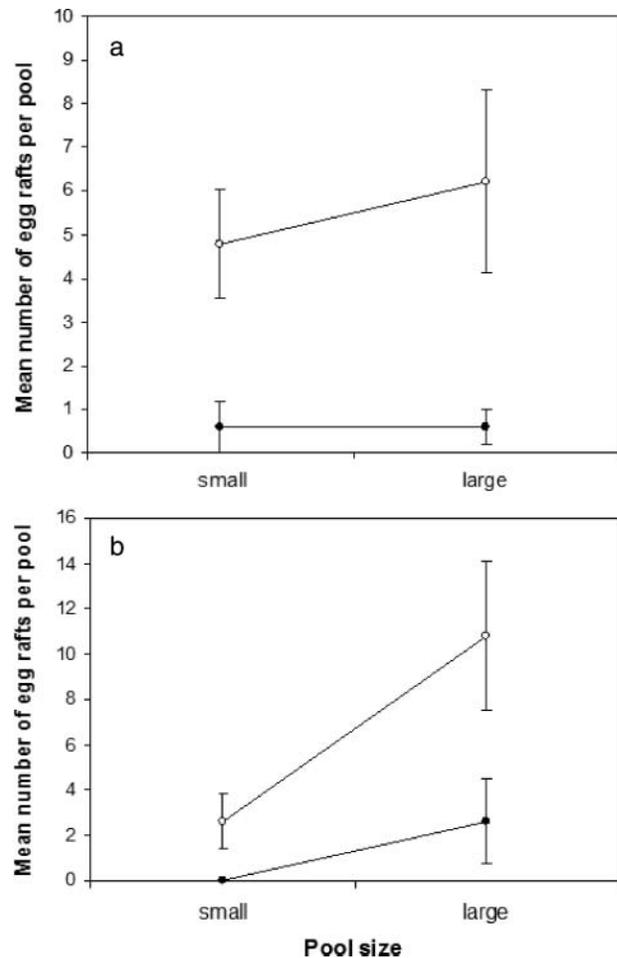


Figure 1. Number of egg rafts oviposited by *Culiseta longiareolata* (a) and *Culex laticinctus* (b) in large versus small, and predator (●) versus non-predator (○), pools. Error bars are ± 1 standard error.

Table 1. Two-way ANOVA of mean *Culiseta longiareolata* and *Culex laticinctus* oviposition in small and large pools, with and without predatory *Notonecta maculata*. Data were $\log(x + 1)$ transformed to achieve homogeneity of variance (Levene test).

Source of variance	SS	df	F	p-Value
<i>Culiseta longiareolata</i>				
Pool size	0.003	1	0.033	0.859
<i>Notonecta</i>	1.721	1	18.809	0.001
<i>Notonecta</i> × size	0.001	1	0.006	0.937
Error	1.464	16		
<i>Culex laticinctus</i>				
Pool size	0.848	1	5.903	0.027
<i>Notonecta</i>	1.273	1	8.862	0.009
<i>Notonecta</i> × size	0.011	1	0.080	0.781
Error	2.297	16		

The maximum likelihood estimate of the preference coefficient (w) for *C. laticinctus* was significantly larger than one ($w = 3.06$; confidence interval: 1.33–6.12; Figure 2 (b)), indicating a significant preference for large pools. For *C. longiareolata*, however, the maximum likelihood estimate did not deviate significantly from one ($w = 0.78$; 95% confidence interval: 0.44–1.70; Figure 2(a)), indicating no statistically significant preference for pool size.

The maximum likelihood estimates of the probabilities of perimeter-based pool encounters (m) were 0.18 and 0.88 for *C. longiareolata* and *C. laticinctus*, respectively. However, for both species, the confidence interval covered the entire possible value range ($0 \leq m \leq 1$; Figure 2 (a) and 2(b)), indicating that our experiment could not resolve which dominant dimension of pool surface is detected by ovipositing mosquitoes.

Discussion

While both mosquito species strongly avoided ovipositing in pools that contain predatory *N. maculata*, we observed different oviposition patterns in response to pool size for each species, potentially reflecting variation in the trade-off between desiccation and predation risks. *C. laticinctus* displayed a strong preference for the larger pools, while *C. longiareolata* showed no significant preference for pool surface area.

Previous studies assessing avoidance of the predator *N. maculata* by ovipositing *C. longiareolata* have shown consistent distributions of oviposition in predator-free and predator-inhabited pools following an approximately 9:1 ratio (Blaustein et al. 1995; Blaustein 1998; Spencer et al. 2002; Kiflawi et al. 2003; Blaustein et al. 2004; Silberbush et al. 2010). In this study, we found the same 9:1 oviposition ratio for this species. Predator avoidance by *C. laticinctus* is also consistent with the results of Kiflawi et al. (2003) and Eitam and Blaustein (2004). However, contrary to our prediction, avoidance of backswimmer predators did not eclipse the response to pool size in *C. laticinctus*. The preference of large pools both in the

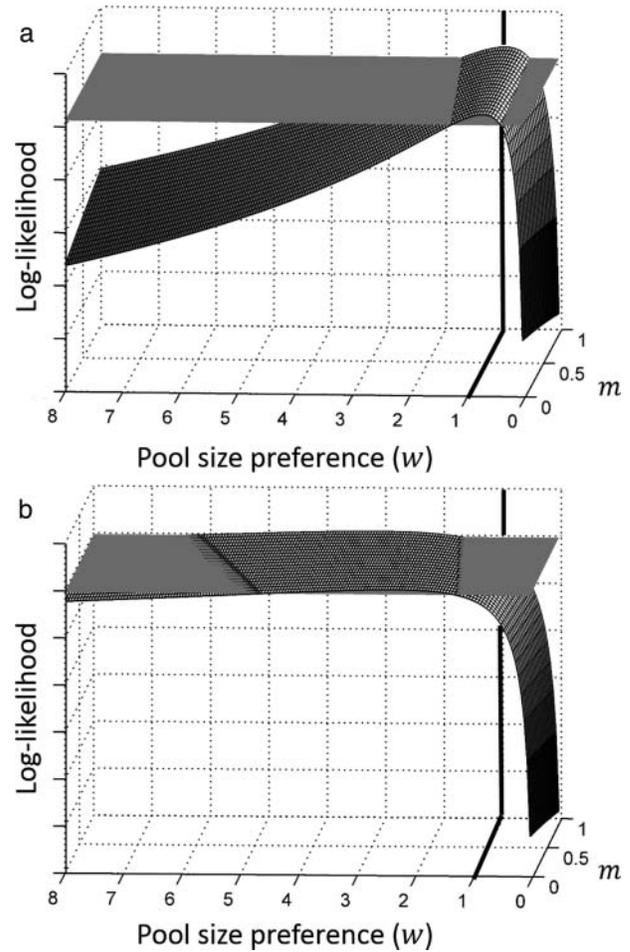


Figure 2. Likelihood surfaces (webbed) of preference for large pools (w) and mode of pool encounter (m) combinations for (a) *Culiseta longiareolata* and (b) *Culex laticinctus*. The region of the likelihood surface that is above the horizontal cut-off plane (smooth gray) represents the confidence region for the parameter estimates. The confidence region for *C. longiareolata* is narrow around the w value of 1, indicating that this species does not display preference for pool size. In contrast, the confidence region for *C. laticinctus* excludes the w value of 1, and its higher values indicate a strong preference for large pools.

presence and in the absence of backswimmers suggests that the risk of desiccation is substantial in this species.

We cannot definitively rule out that ovipositing mosquitoes may respond to pool size only because of risks of desiccation and predation and encounter probability. Larger pools, for example, may have more food resources for mosquito larvae. However, we think this an unlikely alternative to responding to desiccation risk; a large body of literature has demonstrated that ovipositing mosquitoes can detect food resources for their progeny (Afify & Galizia 2015), including for *C. longiareolata* (Blaustein & Kotler 1993), rather than have to rely on indirect cues such as habitat size.

Preference for larger pools by *C. laticinctus* but not by *C. longiareolata* apparently cannot be explained by developmental times. *C. longiareolata* and *C. laticinctus* larvae, when developing together, were found to have similar development times (Blaustein, unpublished data). The differential preference for larger pools may be

explained by the relative vulnerabilities of the larvae to predators: *C. longiareolata* larvae are more vulnerable to predation than *C. laticinctus* larvae (Blaustein 1998). Larger and longer lasting pools tend to contain greater abundance and diversity of predators (Woodward 1983; Spencer et al. 1999; Wilcox 2001; Sunahara et al. 2002; Resetarits & Binckley 2009), and *Notonecta* species, in particular, have been shown to be more likely to colonize larger pools (Wilcox 2001). Thus, reduced risk of desiccation in larger pools may be counterbalanced by a greater increase in risk of predation, resulting in low selective pressure on *C. longiareolata* females to be able to distinguish between pools of different sizes when selecting an oviposition site.

The demonstration of a positive linear relationship between pool surface area and oviposition (Arredondo-Bernal & Reyes-Villanueva 1989; Blaustein & Margalit 1994) may indicate a behavioral adjustment of oviposition based on habitat quality. However, it may also simply reflect the positive relationship between pool size and its probability of being encountered randomly. We used a mechanistic statistical model intended to differentiate between these confounding factors. We could detect true preference for larger pools by *C. longiareolata* females; however, this resulted in more conservative confidence intervals for the assessment of pool size preference. Since pool surface areas and perimeters co-varied, the model could not assess by which of these surface dimensions the mosquitoes encounter pools and assess habitat size. Further refinement of the experimental design to include a wider range of pool sizes in terms of both perimeter and area would allow these confidence intervals to be narrowed and allow our statistical approach to ascertain which habitat dimensions ovipositing organisms detect in assessing habitat size.

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Disclosure statement

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