

## PREDATOR-INDUCED SHIFTS IN MOSQUITO OVIPOSITION SITE SELECTION: A META-ANALYSIS AND IMPLICATIONS FOR VECTOR CONTROL

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### ABSTRACT

The global resurgence and emergence of new mosquito-borne diseases and increasing resistance of mosquitoes to chemical pesticides have prompted renewed interest in biocontrol methods that use aquatic predators of mosquito larvae. For disease vectors with complex life cycles, like mosquitoes, in which adults are terrestrial and choose aquatic habitats in which to deposit their offspring, shifts in oviposition site selection may have important consequences for vector population dynamics and epidemiology. While there have been numerous studies of mosquito oviposition site selection, methodology and results vary, making it difficult to evaluate the general importance of predator-induced shifts in oviposition site selection for biocontrol scenarios. Here we use meta-analysis to provide a quantitative framework for examining variation in mosquito oviposition responses to predators. Overall, we find a broad pattern of predator avoidance among mosquito and predator taxa. The primary factor explaining variation in oviposition response appears to be taxonomic and/or life-history related—avoidance is weakest or non-existent in *Aedes* species that oviposit eggs above water in container habitats. Responses also varied among predators. Generally, oviposition avoidance was strongest in response to fish and insects, weak or nonexistent in response to notostracans, urodeles, or dipterans, and there is limited evidence that some mosquitoes are attracted to cyclopoid crustaceans. Our results highlight that predator avoidance during oviposition is common, but not ubiquitous, in mosquitoes and needs to be considered when evaluating the likely efficacy of aquatic predators for biocontrol.

*Keywords:* biocontrol, colonization, complex life cycle, culicid, disease, habitat selection, vector

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## INTRODUCTION

The global resurgence and emergence of new mosquito-borne diseases (Gubler, 1998; Gratz, 1999), coupled with concerns about the redistribution of mosquito-vectored diseases due to global climate change (Epstein et al., 1998; Gould and Higgs, 2009) and increasing resistance of arthropods to chemical pesticides (Corbel et al., 2007; Whalon et al., 2008) have prompted renewed interest in biocontrol using mosquito predators as an important component of integrated mosquito control strategies (Lacey and Orr, 1994; Kumar and Hwang, 2006). Since predation on adult mosquitoes is thought to be unlikely to provide reliable control (Collins and Washino, 1985) and is difficult to assess, applications of biological control of mosquitoes have focused on a wide variety of predators of mosquito larvae and pupae, including fish (Gerberich and Laird, 1985; Walton, 2007), larval anurans (Spielman and Sullivan, 1974), aquatic insects (Bay, 1974; Chesson, 1984; Chandra et al., 2008), microturbellarian flatworms (Case and Washino, 1979; Blaustein and Dumont, 1990), and crustaceans (Marten, 1990; Kay et al., 2002; Nam et al., 2005). The effectiveness of these predators in controlling mosquitoes can vary among taxa due, for example, to species-level differences in predator-prey interactions, and within taxa due to variation in ecological context (Bay, 1974; Collins and Washino, 1985; Kumar and Hwang, 2006). Thus, while there is increasing need for effective biocontrol methods, the successful application of biocontrol remains challenging.

Historically, basic predator-prey ecology has focused on predator consumption of prey and the density-mediated indirect effects in food webs that arise from consumption (Peckarsky et al., 2008). Similarly, the application of predators for biocontrol has also focused on their consumptive effects on target (i.e., mosquito larvae and pupae) and non-target aquatic organisms (see reviews: Bay, 1974; Collins and Washino, 1985; Gerberich and Laird, 1985; Kumar and Hwang, 2006). However, a growing body of research has highlighted that predators also have non-consumptive effects on prey (Preisser et al., 2005; Preisser and Bolnick, 2008). Taxa may alter their morphology, development, or life history, and behavior in response to predator cues in order to reduce predation risk (i.e., inducible defenses, Tollrian and Harvell, 1999). However, these responses to predators often involve fitness trade-offs that have consequences for prey populations and communities (Black and Dodson, 1990; DeWitt, 1998; Bernard and Fordyce, 2003). Thus, the net or total predator effect includes both consumptive and non-consumptive components, and recent reviews show that the non-consumptive effects are often as large as, or larger than, the lethal effects of predators (Preisser et al., 2005; Pangle et al., 2007). To understand how predators shape prey populations, either from a basic or applied perspective, it is important to understand both types of predator effects.

In aquatic systems, where terrestrial or dispersing adults are often able to select where to deposit their aquatic young or to colonize themselves, the presence of predators (or predator cues) may alter habitat selection behavior in prey. Many insects (see, e.g., Abjornsson et al., 2002; Binckley and Resetarits, 2005; Garcia and Mittelbach, 2008) and amphibians (see, e.g., Resetarits and Wilbur, 1989; Rieger et al., 2004) are able to detect the presence of potential aquatic predators of their offspring and avoid habitat patches

where predators are present. This has important implications for predator–prey dynamics in a patchy environment (Resetarits et al., 2005) and thus consequences for using predators for biocontrol. If we focus only on the consumptive effects of predators, the absence of prey taxa in a predator-occupied patch may be interpreted as evidence that the predator has killed them, and this patch represents a local “sink” (e.g., high mortality, low recruitment patch) and likely acts to reduce the regional (i.e., among patch) abundance of prey. Alternatively, if prey alter habitat selection in response to predators, their absence from a predator patch may simply indicate that they have chosen to colonize other patches. The consequence of habitat selection for regional abundance of prey will depend on factors such as the availability and quality of predator-free patches (Resetarits et al., 2005; Vonesh and Buck, 2007) and may be quite different from regional effects driven by predator consumption.

Recent studies have highlighted the importance of understanding predator effects on oviposition site selection in mosquitoes for biocontrol. A growing number of studies have demonstrated risk-sensitive oviposition site selection in mosquitoes (e.g., Chesson, 1984; Ritchie and Laidlaw-Bell, 1984; Angelon and Petranka, 2002; Blaustein et al., 2004; Eitam and Blaustein, 2004). Recent studies suggest links between mosquito oviposition behavior in response to predators and the epidemiology of mosquito-borne diseases (Ritchie and Montague, 1995; Spencer et al., 2002; Le Menach et al., 2005). Spencer et al. (2002) show through population modeling that adaptive habitat selection in which the mosquito *Culiseta longiareolata* avoids ovipositing in pools with the predator *Notonecta maculata* results in higher equilibrium population sizes of adult mosquitoes. Further, Le Menach et al. (2005) developed a spatially explicit model for malaria epidemiology that incorporates mosquito oviposition behavior. Their results highlight that even aquatic habitats that are net sinks for mosquitoes (e.g., sprayed with larvicide, or occupied by an effective predator) can still lead to increased malaria infection rates due to increased feeding activities of adult mosquitoes that are drawn to an area that harbors potential oviposition sites. They argue that strategies that deter oviposition and thus adult activity, rather than attract oviposition and then kill the larvae, may be more effective management strategies.

While the studies above highlight the potential importance of predator avoidance during oviposition site selection for mosquito biocontrol, results from existing empirical studies are mixed. Some studies reveal strong avoidance of specific predators (Angelon and Petranka, 2002; Eitam et al., 2002; Eitam and Blaustein, 2004), while other studies show no predator effects on oviposition (Juliano et al., 2009) or even attraction to predator habitats (Torres-Estrada et al., 2001). This variation may reflect biological differences among mosquito or predator taxa or may arise from differences in methodology. The goal of this paper is to provide a quantitative review of experimental studies assessing predation-risk-sensitive oviposition site selection in mosquitoes to better understand the factors driving variation among studies. Specifically, we employ a meta-analytic framework to test whether differences in oviposition responses can be explained by mosquito or predator taxonomy, life history, or experimental methodology.

## METHODS

### LITERATURE SEARCH

We reviewed literature for studies of predator-induced oviposition habitat selection that experimentally manipulate aquatic predators or their cues and measure mosquito oviposition response. We searched the online citation databases BIOSIS, ISI Science Citation Index, JSTOR, PubMed, and Web of Science for the following key words: oviposition, habitat selection, site selection, mosquito, predator avoidance, chemical detection, and biological control. We read all papers that appeared relevant and followed up on citations within those papers. We also examined the journals *American Naturalist*, *Ecology*, *Ecology Letters*, *Environmental Entomology*, *Freshwater Ecology*, *Journal of Animal Ecology*, *Journal of the American Mosquito Control Association*, *Journal of Medical Entomology*, *Medical and Veterinary Entomology*, *Journal of Vector Ecology*, *Oecologia*, and *Oikos* from 1985 through March 2009. In addition, we solicited authors for any unpublished data sets they were willing to share to increase our sample and enable us to better assess “file drawer” issues (Rosenthal, 1979) associated with publication bias.

### DATA COLLECTION

We categorized studies by: published or unpublished, field or laboratory, scale of experimental venue [area ( $m^2$ ); volume ( $m^3$ )], study duration (days), interval at which habitat selection was assessed (days), whether eggs and/or larvae were regularly removed, presence of cover or refugia, mosquito taxa (genus, species), mosquito life stage assessed (eggs or larvae), mosquito oviposition strategy (eggs deposited alone or in rafts, in water or out), predator taxa (order, genus, species), predator abundance and density, and the manner in which predators were manipulated (e.g., chemical cue only, caged, free-roaming). For each comparison, we recorded the mean and standard deviation for eggs or egg rafts deposited in the predator absent and predator (or cue) present treatments and the per-treatment sample size. The data were extracted from the text, tables, or calculated by measuring values from figures using ImageJ software (<http://rsbweb.nih.gov/ij/>). Individual papers often contributed more than one comparison (e.g., a single paper might include data for multiple mosquito species, etc.) and we calculated the effect sizes and variance for each comparison separately. For the studies that report a time series of responses, we averaged the effect sizes to obtain a single estimate. For papers that included multiple studies that varied levels of heterogeneity, i.e., experimental location, predator or prey species, temperature, life stages, or repeated studies across multiple seasons—all effect sizes were retained. For experiments with different densities of the same predator, these results were pooled except when testing for effects of predator number or density.

### EFFECT SIZES

The effect size for each comparison was calculated as the natural log of the response ratio. The response ratio is the ratio of oviposition in the predator treatments (P) to that

of the predator-free (C) treatments. This effect size metric provides an estimate of the proportionate change in oviposition in response to the presence of predators (Rosenberg et al., 2000). The natural log of the response ratio has preferred statistical properties (Hedges et al., 1999) and is calculated as:

$$\ln RR = \ln\left(\frac{\bar{X}^P}{\bar{X}^C}\right) = \ln(\bar{X}^P) - \ln(\bar{X}^C)$$

with variance

$$V_{\ln RR} = \frac{(s^P)^2}{N^P(\bar{X}^P)^2} + \frac{(s^C)^2}{N^C(\bar{X}^C)^2}.$$

where  $\ln RR$  is the natural log of the response ratio,  $\bar{x}$  indicates treatment means,  $s$  indicates treatment variances,  $N$  indicates sample sizes, and superscripts  $P$  and  $C$  refer to treatments with predators and those without. However,  $\ln RR$  is undefined when the response ratio is negative or zero. We therefore calculated the natural log of the response ratio +1. The  $\ln RR$  ranges between  $-\infty$  and  $+\infty$ , a value of 0 indicates no difference between treatments, negative values indicate predator avoidance, and positive values indicate predator attraction.

#### STATISTICAL ANALYSES

Statistical analyses were implemented using MetaWin V.2 (Rosenberg et al., 2000). We estimated the cumulative log response ratio ( $\bar{\bar{E}}$ ) which weights the contribution of the effect size from each comparison by the reciprocal of the sampling variance (Hedges and Olkin, 1985; Rosenberg et al., 2000). Comparisons among groups were made using a mixed model, which partitions variance explained by the categorical variable, variance among studies (within categories), and the within-study variance. The significance of the variance explained by the categorical variable was evaluated by resampling the data 5,000 times and examining whether the resulting bias-corrected bootstrapped 95% confidence intervals overlapped zero and whether the confidence intervals for each category overlapped. We used simple regression to test whether the effect size is a function of continuous predictor variables venue size, experimental duration, the interval at which habitat selection was accessed, and predator number and density. We focus on univariate analyses due to our small sample sizes and collinearity among predictor variables. Implications for potential lack of independence among predictor variables is discussed below. To evaluate the potential for publication bias we (1) compared effect sizes between published and unpublished studies, and conducted (2) a Spearman rank-order correlation to check for correlation between variance and sample size and effect size, and (3) Rosenthal's fail-safe test (Rosenthal, 1979).

#### RESULTS

The database used for these analyses included 32 studies making 75 individual com-

parisons. Most data (75%) originated from publications (published or in press between 1984 and October 2009) but 18 previously unpublished comparisons (25%) were also included. These data include experimental studies of predator-induced oviposition for 14 species of mosquito (6 genera) in response to 22 species of putative predators (Data available at <http://www.has.vcu.edu/bio/pages/jrvonesh/>). Collectively, the data reveal a pattern of predator avoidance among studies. Predator treatments received 53% of the eggs received by controls ( $\bar{E}$   $-0.64$  bias-corrected CI:  $-0.87$  to  $-0.40$ ). While overall studies show a pattern of avoidance, species varied in their response ( $Q_{11.61} = 23.13$ ,  $p = 0.033$ , Fig. 1). We were able to estimate the cumulative effect size for the 11 mosquito

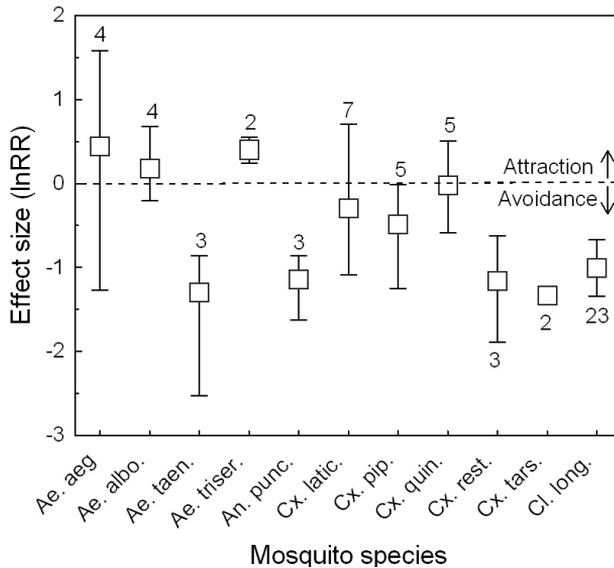


Fig. 1. Cumulative log response ratio (lnRR) effect size estimates ( $\bar{E}$ ) and bias-corrected 95% confidence intervals for oviposition response to predators for 11 species of mosquito, Ae.aeg = *Aedes aegypti*, Ae. albo = *Ae. albopictus*, Ae. taen = *Ae. taeniorhynchus*, Ae. triser = *Ae. triseriatus*, An. punc = *Anopheles punctipennis*, Cx. latic = *Culex laticinctus*, Cx. pip = *Cx. pipiens*, Cx. quin = *Cx. quinquefasciatus*, Cx. rest = *Cx. restuans*, Cx. tars = *Cx. tarsalis*, Cs. long = *Culiseta longiareolata*. A value of zero indicates that there was no difference in oviposition in predator and predator-free treatments. Positive values indicate attraction to predator pools, negative values indicate avoidance. Numbers over confidence intervals indicate sample size (i.e., number of comparisons in database). Data from: Abjornsson et al., 2002; Angelon and Petranka, 2002; Arav and Blaustein, 2006; Blaustein unpubl. data; Blaustein, 1998; Blaustein et al., 2004, 2005; Chesson, 1984; Eitam and Blaustein, 2004; Eitam et al., 2002; Garcia, 2006, unpubl. data; Juliano et al., 2009; Kiflawi et al., 2003a,b; Kraus and Vonesh, unpubl. data; Lowenberger and Rau, 1994; Munga et al., 2006; Petranka and Fakhoury, 1991; Reminger and Juliano, unpubl. data; Ritchie and Laidlaw-Bell, 1994; Sherrat and Church, 1994; Silberbush and Blaustein, 2008; Stav et al., 1999, 2000; Tietze and Mulla, 1991; Torres-Estrada et. al., 2001; Van Dam and Walton, 2008; Vonesh et al., 2009; Vonesh and Gallitano, unpubl. data; Walton et al., unpubl. data.

species for which there were multiple comparisons. *Aedes taeniorhynchus*, *Anopheles punctipennis*, *Culex pipiens*, *Cx. restuans*, *Cx. tarsalis*, and *Cs. longiareolata* avoided predator habitats, while *Ae. aegypti*, *Ae. albopictus*, and *Cx. quinquefasciatus*, *Cx. laticinctus* showed no overall preference, although *Cx. laticinctus* also show a trend toward avoidance (Fig. 1). *Aedes triseriatus* appears to be attracted to *Toxorhynchites rutilus* larvae (Fig. 1); however, this result is based on only two comparisons and likely reflects *A. triseriatus* attraction to conspecific larvae, which were also present in the comparison with the most positive effect size, rather than attraction to the predator itself (Juliano, unpubl. data). Species level patterns are largely consistent with differences among genera ( $Q_{4,68} = 8.86, p = 0.042$ ) where *Anopheles* (2 species,  $n = 5, \bar{E} = -1.13, CI: -1.51$  to  $-0.84$ ), *Culex* (5 species,  $n = 31, \bar{E} = -0.56, CI: -0.89$  to  $-0.22$ ), *Culiseta* (1 species,  $n = 23, \bar{E} = -1.03, CI: -1.36$  to  $-0.67$ ), and *Uranotaenia* (1 species,  $n = 2, \bar{E} = -1.83, CI: -2.1$  to  $-1.57$ ) all tended to avoid predators, while *Aedes* (4 species,  $n = 13, \bar{E} = -0.073, CI: -0.75$  to  $0.49$ ) showed no response. This taxonomic pattern is largely conflated with differences in oviposition strategies among taxa ( $Q_{2,70} = 5.37, p = 0.026$ ), in which species that oviposit on the water (either egg rafts or single eggs) tended to have a stronger avoidance than taxa that place their eggs above water (Fig. 2). However, it should be noted that sample sizes for all taxa except *Cs. longiareolata* were very small (generally  $n < 5$ ) and thus the estimates are quite sensitive to the specific characteristics of each study (e.g., predator type used).

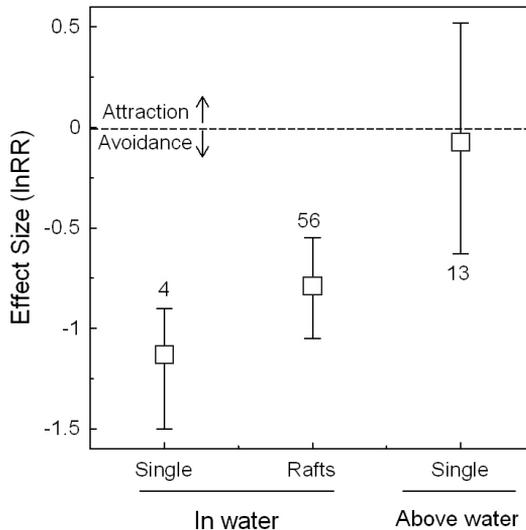


Fig. 2. Cumulative log response ratio (lnRR) effect size estimates ( $\bar{E}$ ) and bias-corrected 95% confidence intervals for oviposition response for mosquitoes that with different oviposition strategies, including eggs laid singly or as rafts in water and eggs laid singly above the water line. Numbers over confidence intervals indicate sample size.

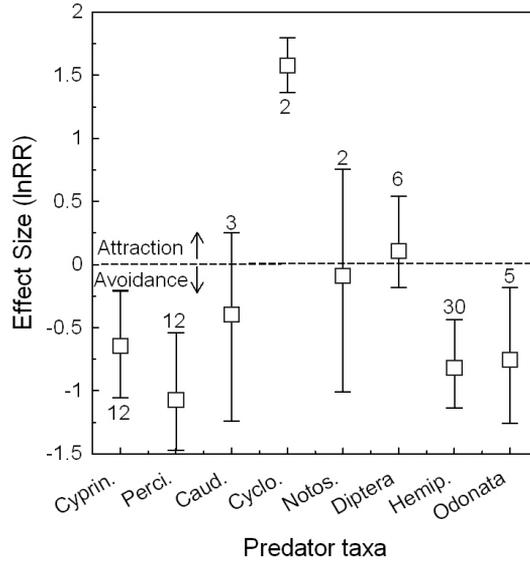


Fig. 3. Cumulative log response ratio (lnRR) effect size estimates ( $\bar{E}$ ) and bias-corrected 95% confidence intervals for oviposition response to different predator orders, including Cyprinodontiformes (Cyprin.) and Perciformes (Perci.) fishes, urodele larvae (Caud.), cyclopoid copepods (Cyclo.) and notostracan (Notos.) crustaceans, Dipteran (Diptera), and hemipteran (Hemip) and larval odonate (Odonata) insects. Numbers over confidence intervals indicate sample size.

Mosquito oviposition site selection has been examined in response to the presence of 22 species of predators from 9 order. However the majority of studies (73%) have focused on notonectid (2 genera, 6 species, 30 comparisons) and fish predators (3 families, 4 genera, 5 species). Indeed, nearly 40% of comparisons used the backswimmer *Notonecta maculata* ( $n = 17$ ) or the mosquitofish *Gambusia affinis* ( $n = 12$ ). Some variation in mosquito oviposition response can be explained by differences among these predator types ( $Q_{7,63} = 33.89, p = 0.002$ , Fig. 3), although this effect was largely driven by a single study ( $Q_{6,62} = 9.64, p = 0.16$  without study) that showed very strong attraction, rather than avoidance, of *Ae. aegypti* to the cyclopoid *Mesocyclops longisetus* ( $n = 2, \bar{E} = 1.58, CI: 1.36$  to  $1.80$ ). Poeciliid (*Gambusia affinis*,  $n = 12, \bar{E} = -0.65, CI: -1.06$  to  $-0.21$ ) and centrarchid fishes (*Enneacanthus gloriosus*, 2 species of *Lepomis*,  $n = 10, \bar{E} = -1.25, CI: -1.67$  to  $-0.92$ ), backswimmers (*Anisops sardea*, 5 species of *Notonecta*,  $n = 30, \bar{E} = -0.85, CI: -1.21$  to  $-0.48$ ), and dragonfly larvae (2 species,  $n = 5, \bar{E} = -0.76, -1.32$  to  $-0.28$ ) all induced shifts in oviposition. Urodeles (2 species), the notostracan crustacean, *Triops longicaudatus*, and dipteran predators (3 species from 3 families) did not elicit oviposition avoidance (Fig. 3). The number of predators used in an experiment was not related to oviposition response ( $Q_{1,64} = 0.015, p = 0.90$ ). Experiments run at high predator densities showed a weaker avoidance response ( $Q_{1,68} = 30.65, p < 0.001$ ). However, this pattern appears to arise because studies using crustaceans and larval cor-

ethrellid fly predators generally showed no predator avoidance or attraction and these studies, coincidentally, were run at the highest predator densities (i.e.,  $>5L^{-1}$ ). When we examined within specific predator groups for which we had sufficient sample size, there were no effects of density (hemipterans:  $Q_{1,28} = 0.078, p = 0.78$ ; poeciliid fishes:  $Q_{1,10} = 0.01, p = 0.92$ ; centrarchid fishes:  $Q_{1,10} = 0.42, p = 0.52$ ).

While there was considerable variation in methodology among studies, this variation was generally not predictably related to variation in mosquito responses. Lab studies ( $n = 11, Q_{1,71} = 6.19, p = 0.005$ ) and studies without any aquatic cover (e.g., leaf litter;  $n = 28, Q_{1,71} = 8.04, p = 0.005$ ) appeared to elicit weaker predator avoidance compared to field studies or studies with cover present. These groups were largely conflated, so it is unclear what is actually driving this pattern. Further, this pattern seems to be largely driven by a few lab studies with crustacean predators. Other methodological differences were not significant predictors of oviposition response, including whether studies assessed oviposition responses by counting eggs or larvae ( $Q_{1,69} = 0.62, p = 0.36$ ), whether eggs or larvae were removed regularly or allowed to accumulate ( $Q_{1,69} = 1.38, p = 0.38$ ), study duration (range: 0.4–84d,  $Q_{1,69} = 2.07, p = 0.15$ ), interval between assessment of oviposition response (range: 0.4–84d,  $Q_{1,69} = 0.69, p = 0.4$ ), and experimental venue area (range: 0.01–26m<sup>2</sup>,  $Q_{1,69} = 1.63, p = 0.20$ ) and volume (range: 0.02–8000L,  $Q_{1,69} = 0.33, p = 0.56$ ). Interestingly, the manner in which predators were presented to mosquitoes also had no effect upon oviposition habitat selection. Studies in which the predator was free-roaming were not significantly different from effect sizes to studies in which the predator was caged or in which predator cues were presented (effect sizes: cue only =  $-0.34$ ; caged predator =  $-1.00$ ; free roaming predator =  $-0.62$ ;  $Q_{2,71} = 2.71, p = 0.17$ ;  $Q_{2,67} = 1.69, p = 0.49$  with crustacean study removed).

Diagnostic tests do not reveal strong evidence of publication bias among these studies. Visual analysis of funnel and normal quantile plots suggest the effect sizes are normally distributed, that cumulative effect size is independent of sample size, and variation in effect sizes tend to decrease with increasing samples (Rosenberg et al., 2000). Cumulative effect sizes from published ( $n = 53, \bar{E} = -0.14, C.I. = -0.76$  to  $0.44$ ), in review ( $n = 2, \bar{E} = -0.70, CI: -0.89$  to  $-0.55$ ), and unpublished “file drawer” data sets provided by authors ( $n = 18, \bar{E} = -0.38, CI: -0.80$  to  $-0.002$ ) were not different ( $Q_{2,73} = 6.89, p = 0.94$ ). Further, Rosenthal’s fail-safe test estimated that 3078 unpublished zero-effect studies were necessary to lower our estimate to the point where we cannot reject a null hypothesis of no oviposition response. We found no correlation between the standardized effect size and study variance ( $\rho = 0.013, p = 0.91$ ). A positive correlation might have indicated a publication bias in which larger effect sizes in one direction (e.g., negative affects indicating predator avoidance) are more likely to be published than smaller effect sizes.

## DISCUSSION

In order to develop effective biocontrol strategies that use predators of arthropod disease

vectors, it is important to understand the total effects of predators on the target species. Recent reviews (Peacor and Werner, 2004) highlight that non-lethal effects of predators may be large relative to their lethal effects, and thus need to be considered to estimate total predator effects. Here we review experimental evidence for a non-lethal effect of predators on oviposition site selection by mosquitoes. Overall, we find a broad pattern of avoidance of ovipositing in habitats with predator cues; mosquitoes as a group oviposited 47% fewer eggs in predator-present versus predator-free pools. Predator avoidance behavior was observed in several species or genera that are known vectors of important human and/or animal diseases. For example, *Anopheles* mosquitoes, which transmit malaria, on average oviposited 70% more eggs in predator-free habitats.

At the local scale of a single breeding site, our results suggest that habitats with fish, backswimmers, and dragonfly larvae could receive fewer eggs and thus have lower initial larval densities. If initial differences in larval abundance persist (e.g., Vonesh et al., 2009), these predators could reduce local recruitment of adults from these patches both by reducing larval survival (i.e., the consumptive effect) but also by reducing colonization (Spencer et al., 2002). This suggests that even relatively ineffective predators (in terms of low rates of consumption) could have important effects on local recruitment by modifying habitat selection. How the local effects of predator avoidance scale up to the regional (i.e., among patch) level depends on the availability of predator-free patches and whether eggs not laid in predator patches can be redirected to remaining predator-free sites or are lost (Ritchie and Montague, 1995; Osenberg et al., 2006). Redirection can be costly as time spent moving among patches may increase adult mortality (Service, 1993; Reiskind and Wund, 2009); however, field evidence suggests redirection can occur (i.e., "habitat compression" sensu Resetarits et al., 2005). For example, Howard and Omlin (2008) document a field study in which Nile tilapia (*Oreochromis niloticus*) were introduced to 2 of 3 adjacent (<150 m) abandoned fish ponds. Upon fish introduction, they observed an immediate decrease in *Anopheles* and culicine larvae in the fish pools, but also a simultaneous three-fold increase in larval mosquito densities in the predator-free pools. There was no change in the regional (i.e., sum of all three pools) abundance of larval mosquitoes because of the increase in mosquito abundance in the control pool. However, increases in larval abundance do not necessarily translate into increased adult recruitment. The contribution of eggs redirected from predator habitats to predator-free sites to regional recruitment may depend upon the degree to which resources are limiting in predator-free habitats (i.e., whether larval recruitment is strongly density dependent (Juliano, 2010, this volume)).

While predator avoidance was the most common oviposition response to aquatic predators, not all mosquito taxa avoided aquatic predators. Understanding this variation in mosquito responses may have important implications for choosing effective biocontrol agents. Of the 11 species for which we were able to estimate an among-study cumulative effect size estimate, five species had estimates that overlapped zero. While our limited sample size and the lack of independence among some of our predictor variables limits our ability to interpret the factors driving variation in oviposition responses to predators, in general, we found that *Aedes* species that lay single eggs above the water

line exhibited weaker responses to predators during oviposition. Mosquitoes that can detect predator cues, detect the immediate predation risk which might be quite different when the above-water eggs of *Aedes* hatch weeks or even years later.

There is also evidence that some predators might actually attract oviposition. Torres-Estrada et al. (2001) found that the copepod, *Mesocyclops longisetus*, may secrete chemicals that attract oviposition by *A. aegypti*. This experiment used sterile distilled water in controls, and it is possible that mosquitoes were actually attracted to the increased microbes and nutrients in copepod predator treatments, rather than attracted to the predators themselves. However, if larval mosquito predators attract oviposition to habitats that are ultimately lethal, these predators should cause greater local and metapopulation declines than predators that have no effect on oviposition site selection (Delibes et al., 2001; Kristan, 2003). Predation trials also indicate that cyclopoid copepods are effective at consuming mosquito larvae (Marten, 1990), and recent field trials show *Mesocyclops* spp. to be effective biocontrol agents (Kay et al., 2002; Nam et al., 2005). This combination of traits appears very attractive from the biocontrol perspective; high consumption rates should reduce recruitment from local habitat patches, while oviposition attraction may create regional sinks which draw mosquitoes away from predator-free sites to low recruitment predator habitats. Further, because of oviposition attraction, it may be possible to obtain effective biocontrol at regional scales even if it is not possible to establish predator populations in all suitable habitats (i.e., in contrast to the oviposition deterrence example above). However, while desirable, evidence of oviposition attraction by aquatic predators is limited and further studies are needed to explore this issue.

While there was considerable variation in methodology among studies, these differences explained little of the variation in mosquito oviposition responses. In some instances, this was surprising. For example, the importance of using chemical cue or caged predator treatments (where consumption is prevented) to isolate the non-lethal effects of predators from the total effects of free-roaming predators has been considered a key element of the design of these types of experiments. In the absence of a non-lethal predator treatment, it is difficult to disentangle predator effects on oviposition from direct consumption of eggs. Indeed, we might expect that free-roaming predators would produce more negative effect sizes, if predators both scare adults away and eat eggs. However, for the studies examined here, we found no difference between free-roaming, caged, and chemical cue predator manipulations. This suggests that many of these predators may not actually consume eggs, but are likely predators of mosquito larvae after they hatch. This assumption is untested for some studies, but others specifically address whether predators eat eggs (Chesson, 1984; Eitam et al., 2002). For example, Eitam et al. (2002) and Stav et al. (1999) specifically tested for consumption of eggs by *Anisops* backswimmers and *Anax* dragonfly larvae, respectively. *Anisops* did not consume eggs. Thus, the reduced numbers of eggs rafts in pools containing free-swimming backswimmers can be attributed to their effects on oviposition, not egg predation. The larval dragonflies did consume some egg rafts; however, even when egg predation rates were taken into consideration, there was still evidence of predator avoidance during oviposition.

We also anticipated that study duration and whether colonizing mosquitoes (i.e., eggs

or early instar larvae) were allowed to remain or removed from the experiment would explain some of the variation among studies. Studies of oviposition site selection in mosquitoes and other taxa show that adults may be sensitive to a variety of cues about larval habitat quality when making oviposition decisions, shifting oviposition in response to not only predators but indicators of resource quality and the presence of conspecifics or competitors (Resetarits and Wilbur, 1989; Blaustein and Kotler, 1993; Mokany and Shine, 2003; Munga et al., 2006; Binckley and Resetarits, 2008). Thus, we might predict that the initial strength of habitat selection response to an experimental predator might change as the aquatic community is allowed to assemble (Kraus and Vonesh, 2010). While this pattern did not emerge from the overall meta-analysis, time series data on the strength of oviposition habitat selection within a study system is uncommon and we encourage researchers to be cognizant that methodological decisions regarding these aspects of study design are expected to affect the strength of oviposition behavior.

The global resurgence and emergence of new mosquito-borne diseases (Gubler, 1998; Gratz, 1999) and increasing resistance of arthropods to chemical pesticides (Campos and Andrade, 2003; Whalon et al., 2008) have prompted renewed need for effective biocontrol strategies, and understanding mosquito behavior is likely to be an important component toward effective management (Bentley and Day, 1989; Pates and Curtis, 2005). Recent studies specifically highlight that oviposition site selection by mosquitoes can have important consequences for adult populations (Ritchie and Montague, 1995; Spencer et al., 2002) and disease epidemiology (Le Menach et al., 2005). Our review shows that in addition to their effects on mosquito abundance mediated via consumption of larvae, a variety of aquatic predators also induce shifts in oviposition site selection. Thus, management using aquatic predators from mosquito biocontrol should take this into consideration in order to understand the total effect of the predator on the target species. This should be taken into account also when designing experiments to assess the efficacy of biological control agents of mosquitoes. The typical experimental design of no predator versus predator-stocked water plots and then counting immatures or emergence implicitly assumes random oviposition. Thus, such a design is likely to over-estimate the efficacy of a tested predator to reduce mosquitoes (Spencer et al., 2002). Developing chemical methods for manipulating oviposition is already an area of research for vector management (Xue et al., 2005, 2006; Silberbush et al., 2010). An integrated understanding of both the effects of aquatic predators on larval survival and adult oviposition may yield more effective biocontrol strategies for mosquito-borne diseases.

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