Both consumptive and non-consumptive effects of predators impact mosquito populations and have implications for disease transmission

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Abstract

Predator-prey interactions influence prey traits through both consumptive and non-consumptive effects, and variation in these traits can shape vector-borne disease dynamics. Meta-analysis methods were employed to generate predation effect sizes by different categories of predators and mosquito prey. This analysis showed that multiple families of aquatic predators are effective in consumptively reducing mosquito survival, and that the survival of *Aedes*, *Anopheles*, and *Culex* mosquitoes is negatively impacted by consumptive effects of predators. Mosquito larval size was found to play a more important role in explaining the heterogeneity of consumptive effects from predators than mosquito genus. Mosquito survival and body size were reduced by non-consumptive effects of predators, but development time was not significantly impacted. In addition, *Culex* vectors demonstrated predator avoidance behavior during oviposition. The results of this meta-analysis suggest that predators limit disease transmission by reducing both vector survival and vector size, and that associations between drought and human West Nile virus cases could be driven by the vector behavior of predator avoidance during oviposition. These findings are likely to be useful to infectious disease modelers who rely on vector traits as predictors of transmission.

Introduction

While it is well-known that predation reduces vector populations through consumptive effects, non-consumptive effects of predators can also greatly impact prey demographics (Preisser et al., 2005). Mosquitoes are vectors of a variety of debilitating and deadly diseases, including malaria, lymphatic filariasis, and arboviruses, such as chikungunya, Zika, and dengue (Weaver and Reisen, 2010, World Health Organization (WHO), 2020). Consequently, there is motivation from a public health perspective to better understand the different drivers of variation in mosquito traits that can ultimately impact vector population growth and disease transmission. In addition, recent work has suggested that incorporation of vector trait variation into disease models can improve the reliability of their predictions (Cator et al., 2020). In this study, systematic review and meta-analysis methods are used to synthesize a clearer understanding of the consumptive and non-consumptive effects of predators on mosquito traits, including survival, oviposition, development, and size.

Mosquito insecticide resistance is recognized as a growing problem (Hancock et al., 2018, Hemingway and Ranson, 2000, Liu, 2015) leading some to suggest that control efforts should rely more heavily on “non-insecticide based strategies” (Benelli et al., 2016). The consumptive effects of predators on mosquitoes have previously been harnessed for biocontrol purposes. Past biocontrol efforts have used predators such as cyclopoid copepods (Kay et al., 2002, Marten, 1990, Russell et al., 1996, Veronesi et al., 2015) and mosquitofish (Pyke, 2008, Seale, 1917) to target the mosquito’s aquatic larval stage. The strength of the consumptive effects of these predators on mosquitoes can be influenced by multiple factors, including predator-prey size ratio and temperature. Predator-prey body size ratios tend to be higher in freshwater habitats than other types of habitats (Brose et al., 2006), and attack rate tends to increase with temperature (Kalinoski and DeLong, 2016, Dam and Peterson, 1988), though other studies suggest a unimodal response to temperature (Uiterwaal and Delong, 2020, Englund et al., 2011).

Predators can also have non-consumptive effects on prey (Peacor and Werner, 2001), and these effects are thought to be more pronounced in aquatic ecosystems than in terrestrial ecosystems (Preisser et al., 2005). Non-consumptive effects of predators are the result of the prey initiating anti-predator behavioral and/or physiological trait changes that can aid in predator avoidance (Hermann and Landis, 2017, Lima and Dill, 1990). Such plasticity in certain prey traits may also result in energetic costs (Lima, 1998). Predator detection is key for these trait changes to occur and can be mediated by chemical, tactile, and visual cues (Hermann and Thaler, 2014). In mosquitoes, exposure to predators is known to affect a variety of traits including behavior, size, development, and survival (Arav and Blaustein, 2006, Bond et al., 2005, Roberts, 2012, Roux et al., 2015, Zuharah et al., 2013). Experimental observations of predator effects on mosquito size and development are inconsistent and results sometimes vary by mosquito sex. For example, exposure to predation was found to increase the size of *Culex pipiens* mosquitoes (Alcalay et al., 2018) but decrease the size of *Culiseta longiareolata* (Stav et al., 2005). In addition, female *Aedes triseriatus* exhibited shorter development times when exposed to predation at high nutrient availability (Ower and Juliano, 2019), but male *C. longiareolata* had longer development times in the presence of predators (Stav et al., 2005). In some cases, a shared evolutionary history between predator and prey organisms can strengthen the non-consumptive effects of predators on mosquitoes (Buchanan et al., 2017, Sih, 1986).

This investigation assesses the consumptive and non-consumptive effects of predators on mosquito traits and describes how these effects could impact disease transmission. The roles of vector genus, predator family, mosquito larval instar (an indicator of prey size), and temperature are also examined as potential moderators of predator effects. Non-consumptive effects of predators are expected to cause a smaller reduction in mosquito survival than consumptive effects because, in practice, measures of consumptive effects always include both consumptive and non-consumptive effects. Based on previous findings, larger predators are more likely to consumptively reduce mosquito survival (Kumar et al., 2008). In addition, *Aedes* mosquito larvae may be more vulnerable to consumptive predation than other genera because of the high degree of motility observed in this genus (Dieng et al., 2003, Marten and Reid, 2007, Soumare and Cilek, 2011). The oviposition response to predation is expected to be weakest among *Aedes* species that oviposit above the water line, due in part to their delayed-hatching eggs (Vonesh and Blaustein, 2010). Predation is predicted to reduce mosquito size and lengthen development time, consistent with the reduced growth response observed in other insect systems (Hermann and Landis, 2017). Certain non-consumptive effects of predation, particularly oviposition site selection and decreased vector size, are likely to play important roles in the dynamics of mosquito-borne disease.

Materials and Methods

Literature Screening:

A systematic search was conducted for studies on predation of mosquitoes that were published between 1970 and July 1, 2019 using both PubMed® and Web of Science™ search engines, according to the PRISMA protocol (Moher et al., 2009). Mosquito vectors of the *Anopheles* and *Aedes* genera were specifically highlighted in our search terms because these genera contain the vector species that transmit malaria, yellow fever, and dengue – the three most deadly mosquito-borne diseases worldwide (Hill et al., 2005). Searches included 18 combinations of three vector predation terms (mosquito predat*, *Anopheles* predat*, *Aedes* predat*) and six trait terms (survival, mortality, development, fecundity, dispers*, host preference). Abstracts from the 1,136 studies were each screened by two different co-authors, using the “metagear” package in R (Lajeunesse, 2016, R Core Team, 2020). If either screener thought the study had information relevant to predation of mosquitoes, or both screeners thought the abstract was ambiguous, the study was read in full. This resulted in 306 studies that were fully reviewed to determine if any predation data could be extracted (Fig 1).

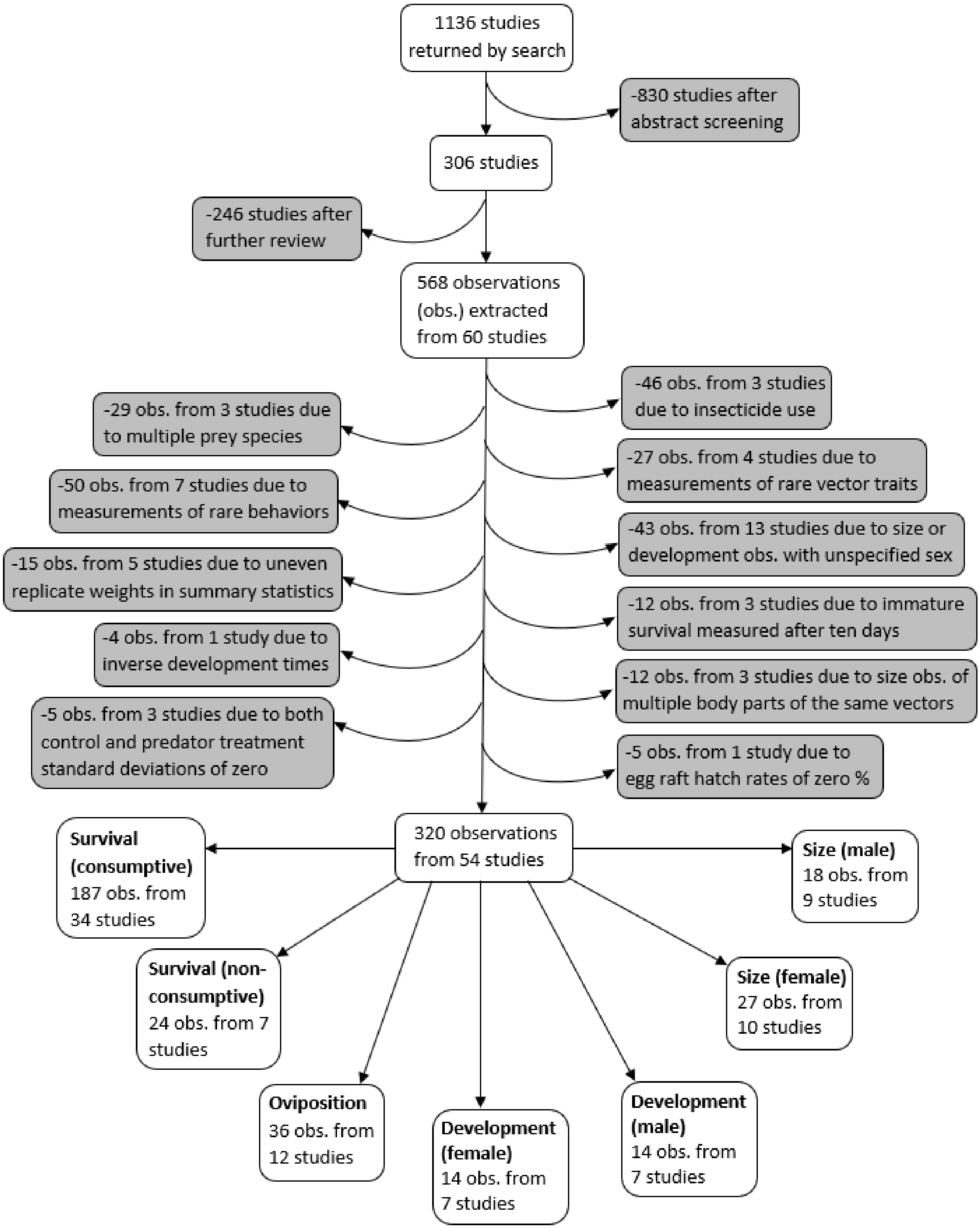

Fig 1. Flowchart demonstrating the literature search, screening process, data exclusions, and the resulting seven different vector trait data subsets

Study Exclusion Criteria:

Data were extracted from studies that collected data on non-consumptive and/or consumptive effects of predators on mosquitoes. Studies were required to have a mean, error measurement, and at least two replicates for both control and predator treatments. The control treatment was required to have all the same conditions as the predator treatment, such as prey density and type of water, without the predators. Studies that were not published in English and studies that did not differentiate between predators of multiple families were excluded. Studies were also excluded if oviposition by free-flying female mosquitoes could have interfered with observing the consumptive effects of predators on vector survival. The final database comprised data extracted from 60 studies (Table S1). The data included observations from laboratory experiments, as well as semi-field experiments, in which mesocosms of different treatments were observed in outdoor settings.

Data Extraction:

Variables related to the publication, the vector, the predator, and the effect size (Table 1) were extracted from each study. Data from tables and text were recorded as they were published, and data from figures were extracted using WebPlotDigitizer (Rohatgi, 2020). Error measurements that were not originally presented as standard deviations were converted to standard deviations prior to the effect size calculation.

Table 1: Variables extracted from included studies

Variable	**Description**
Publication data:	
Title	Full study title
Journal	Name of journal that published the study
Year	Year of publication
Study environment	Environment where the experiment took place: lab or semi-field
Vector data:	
Order, Family, Genus, Species	Taxonomic identification
Trait	Outcome that was measured (e.g., survival, development, etc.)
Stage	Life stage: egg, larva, pupa, or adult
Larval instar	Early (1st and 2nd instars), late (3rd and 4th instars), both, or NA (eggs, pupae, or adults)
Sex	Male or female
Predator data:	
Phylum, Class, Order, Family, Genus, Species	Taxonomic identification
Starved	Whether the predator was starved: yes or no
Time starved	Amount of time that the predator was starved (in minutes)
Predation effect	Consumptive or non-consumptive
Effect size data:	
Units	Units of extracted data
Control mean	Average of the outcome measured among the controls
Control standard deviation	Standard deviation of the outcome measured in the controls
Control number of replicates	Number of control replicates
Predation mean	Average of the outcome measured in the predator treatment
Predation standard deviation	Standard deviation of the outcome measured in the predator treatment
Predation number of replicates	Number of predation replicates
Experiment ID	Alphabetic assignment to mark observations sharing a control group or representing the same prey individuals as originating from the same experiment
Additional data:	
Experiment time (days)	Duration of the experiment in days
Data source	Graph or text
Number of predators	Number of predators with access to prey, or “cue” if there are no predators with direct access to prey
Number of prey (vectors)	Number of mosquito prey that are exposed to predation
Arena volume (mL)	Volume of the arena where prey encounter predators
Time exposed to predator(s)	Amount of time (in days) when the predator has direct access to the mosquito prey
Temperature (°C)	Temperature during the predation interaction
Type of predator cue	Predator cues, or cues from both predator(s) and dying conspecifics; NA for observations with a consumptive predation effect

Data Exclusions:

A PRISMA plot of literature inclusion and exclusion is provided in Figure 1. Observations where insecticide was used were excluded because insecticides are known to interfere with consumptive and non-consumptive effects of predators (Delnat et al., 2019, Janssens and Stoks, 2012). In addition, observations from experiments with mosquito prey of two or more species were excluded because it was not possible to account for effects from apparent competition or prey-switching. Observations of vector fecundity, vector competence, behavioral traits other than oviposition, as well as observations where the vector trait was marked as “other” were not analyzed because each of these traits were only recorded from three or fewer studies.

Due to protandry, the earlier emergence of males to maximize their reproductive success, mosquitoes respond to sex-specific selective forces that influence their development time and body size (Kleckner et al., 1995). Under low resource conditions, female mosquitoes are likely to maximize body mass by extending their development time, whereas males tend to minimize their development time at the expense of lower body mass (Kleckner et al., 1995). Observations of mosquito development time and body size in our database that were not sex-specific were excluded so that these vector traits could be analyzed while controlling for sex. In addition, some size and development time predator means did not necessarily represent an evenly weighted average of the replicates. For example, if a total of twenty mosquitoes from three different predator replicates survived to adulthood, the mean size and development time of those twenty individuals may have been reported. To represent an evenly weighted average of the replicates, it is necessary to first calculate summary statistics among multiple individuals that emerge from the same replicate, and then report the average of the replicatespecific means. Observations that might have been influenced by uneven representation of replicates were excluded to prevent pseudo-replication from altering later meta-analyses.

For consumptive observations where life stage-specific survival was reported after more than 10 days of predator exposure, only data on survival marked by adult emergence were included for analysis. Effects observed among immature vector stages after such a long period of predator exposure were not analyzed because they could have resulted from a combination of non-consumptive effects on development, and consumptive effects on survival. Development time observations that were reported as the inverse of development time (units of days^{-1}) were excluded because although their means could be converted to units of days, their standard deviations could not be converted to match units of days. In cases where multiple body sections of the same mosquitoes were measured to produce multiple size observations, only the wing measurement was included in the analysis to prevent pseudo-replication. Observations in which both the control and the predator treatments had standard deviations of zero were excluded because the meta-analysis methods did not support non-positive sampling variances.

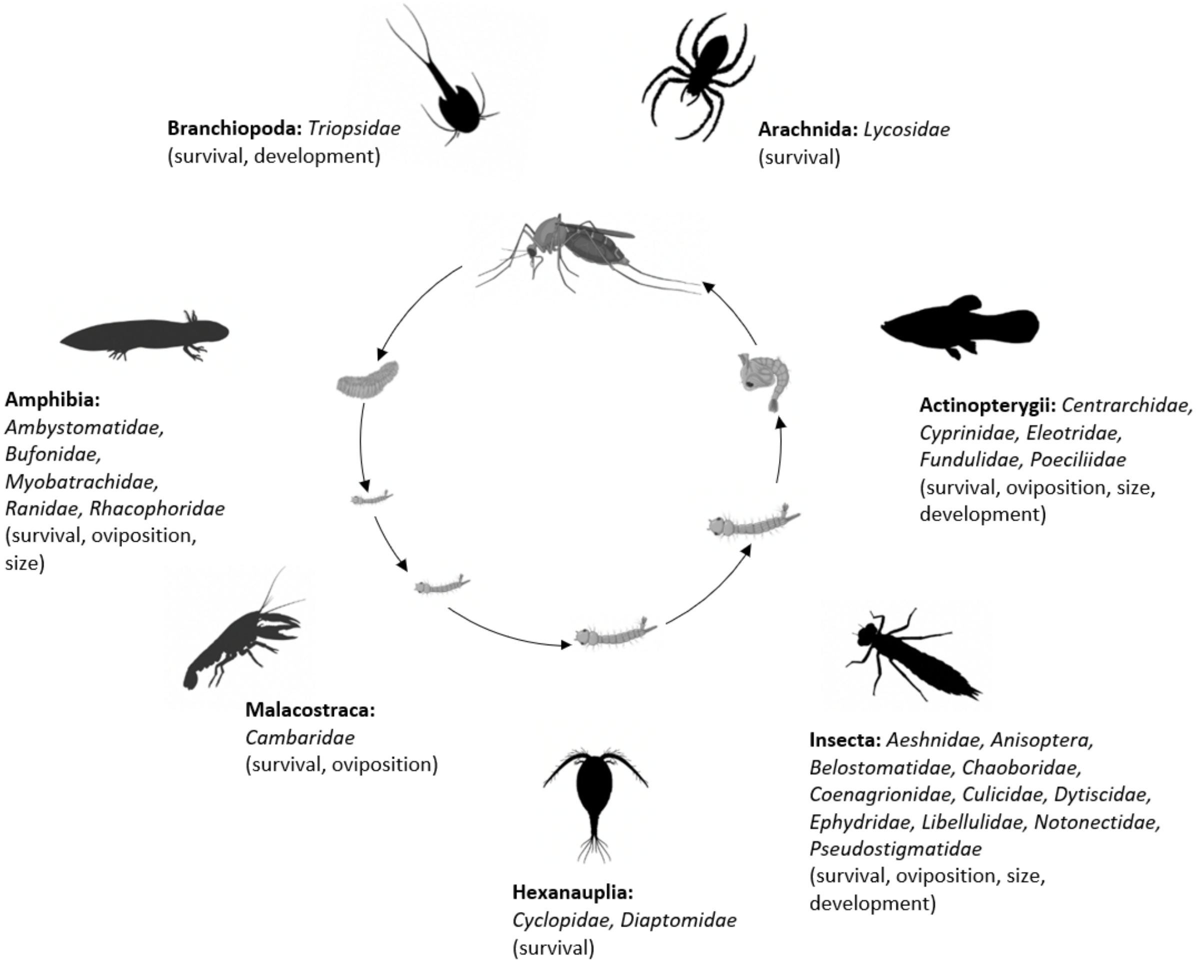

Fig 2. Mosquito predator classes (bold font) and families (italicized font) included in the database and the vector traits that they may influence (in parentheses); predator images not to scale, and placed randomly with respect to the different mosquito life stages

Image sources:

phylopic.org (CC BY 3.0 or public domain): Actinopterygii (creator: Milton Tan), Arachnida (creators: Sidney Frederic Harmer & Arthur Everett Shipley, vectorized by Maxime Dahirel), Branchiopoda (creator: Africa Gomez), and Insecta (creator: Marie Russell)

BioRender.com: Amphibia, Hexanauplia, and Malacostraca class silhouettes; mosquito larval instars, pupa, and blood-feeding adult

Trishna Desai: mosquito egg raft

Exclusions and Data Substitutions for Predator Treatment Means of Zero:

One study that was included in our database reported egg survival data as the hatch rate of field collected *Culex pervigilans* rafts (Zuharah et al., 2013). However, mosquitoes have been shown to lay eggs independent of mating (O'Meara, 1979), and hatch rates of zero have previously been observed in rafts laid by *Culex* females that were held separately from males (Su and Mulla, 1997). Thus, hatch rates of zero were excluded from further analysis because these values may represent unfertilized egg rafts, rather than a strong impact of predators on survival. Twenty of the 187 consumptive survival observations had a predation mean of zero, and each of these zeros resulted from experiments that began with a specified number of live larvae. Consumptive survival zeros were each replaced with 0.5% of the starting number of mosquito prey to avoid undefined effect sizes. In addition, there was one zero out of the 36 oviposition predation means; this value had units of “number of egg rafts laid” and was replaced with 0.5 rafts. Similar methods for replacing zero values in the treatment mean with small non-zero values have previously been employed (Thapa et al., 2018).

The final analysis dataset included seven subsets: consumptive effects on survival, non-consumptive effects on survival, oviposition, development (female and male), and size (female and male). The data included 187 observations from 34 studies of consumptive survival, 24 observations from seven studies of non-consumptive survival, 36 observations from 12 studies of oviposition, 14 observations from seven studies of female development, 14 observations from seven studies of male development, 27 observations from 10 studies of female size, and 18 observations from nine studies of male size (Fig 1). These observations covered seven different classes of predator families (Fig 2).

Data Analysis:

Measuring Effect Sizes and Heterogeneity

All analyses were conducted in R version 4.0.2 (R Core Team, 2020). For each subset of trait data (Fig 1), the ratio of means (ROM) measure of effect size was calculated using the "escalc" function from the "metafor" package; this effect measure is equal to a log-transformed fraction, where predation mean is the numerator and control mean is the denominator (Viechtbauer, 2010). Random effects models, using the "rma.uni" function, were run with the ROM effect sizes as response variables; each model had a normal error distribution and a restricted maximum likelihood (REML) estimator for τ^2, the variance of the distribution of true effect sizes (Viechtbauer, 2010). Although these random effects models could not account for multiple random effects or moderators, they provided overall estimates of the ROM effect sizes and estimates of the I^2 statistics. Each I^2 statistic represented the percentage of total variation across studies due to heterogeneity (Higgins et al., 2003). If the I^2 statistic was equal to or greater than 75%, the heterogeneity was considered to be high (Higgins et al., 2003), and high heterogeneity has previously motivated further testing of moderators (Vincze et al., 2017).

Assessing Publication Bias

Publication bias was assessed by visually inspecting funnel plots and conducting Egger's regression test ("regtest" function) with standard error as the predictor (Sterne and Egger, 2001, Viechtbauer, 2010). If the Egger's regression test showed significant evidence of publication bias based on funnel plot asymmetry, the "trim and fill" method ("trimfill" function) was used to estimate how the predation effect size might change after imputing values from missing studies (Duval and Tweedie, 2000b, Duval and Tweedie, 2000a, Viechtbauer, 2010). The trim and fill method has previously been recommended for testing the robustness of conclusions related to topics in ecology and evolution (Jennions and Moller, 2002). Of the two trim and fill estimators, R_0 and L_0, that were originally recommended (Duval and Tweedie, 2000b, Duval and Tweedie, 2000a), the L_0 estimator was used in this study because it is more appropriate for smaller datasets (Shi and Lin, 2019).

Testing Moderators

Data subsets that had high heterogeneity, observations from at least 10 studies, and no evidence of publication bias according to Egger’s regression results were analyzed further using multilevel mixed effects models with the “rma.mv” function (Viechtbauer, 2010, Higgins et al., 2020). All multilevel mixed effects models had normal error distributions, REML estimators for τ^2, and accounted for two random factors: effect size ID, and experiment ID nested within study ID. Moderators, such as predator family, vector genus, larval instar (directly correlated to prey size), and temperature, were tested within each data subset to determine if they affected the observed heterogeneity in ROM effect sizes. For categorical moderators, the intercept of the multilevel mixed effects model was removed, allowing an analysis of variance (ANOVA) referred to as the “test of moderators” to indicate if any of the categories had an effect size different than zero. For data subsets with observations from 10 to 29 studies, only one moderator was tested at a time to account for sample size constraints. For subsets with observations from a higher number of studies (30 or more), up to two moderators were tested at once, and interaction between moderators was also tested. The small sample corrected Akaike Information Criterion (AICc) was used to compare multilevel mixed effects models and to select the model of best fit within each data subset; differences in AICc greater than two were considered meaningful (Burnham and Anderson, 2004).

Both the database and the R code file showing all analyses will be made publicly accessible from the Dryad Digital Repository.

Results

Random Effects Models:

Each data subset (Fig 1) had an I^2 statistic of greater than 75%, indicating high heterogeneity (Higgins et al., 2003). Random effects model results showed that predators consumptively decreased mosquito survival with an effect size of -1.23 (95% CI -1.43, -1.03), p-value <0.0001, and non-consumptively reduced survival with a smaller effect size of -0.11 (95% CI -0.17, -0.04), p-value = 0.0016. In addition, predators non-consumptively reduced oviposition behavior with an effect size of -0.87 (95% CI -1.31, -0.42), p-value = 0.0001, and mosquito body size was non-consumptively reduced by predators in both males and females; the female effect size was -0.13 (95% CI -0.19, -0.06), p-value = 0.0002, and the male effect size was -0.03 (95% CI -0.06, -0.01), p-value = 0.0184. There was not a significant non-consumptive effect of predators on either male or female development time; the female effect size was -0.01 (95% CI -0.09, 0.07), p-value = 0.7901, and the male effect size was -0.04 (95% CI -0.12, 0.04), p-value = 0.3273.

The Egger's regression test results showed that the non-consumptive survival subset, both development time subsets (male and female), and the female size subset exhibited funnel plot asymmetry indicative of publication bias. The "trim and fill" procedure identified missing studies in the non-consumptive survival subset and the female size subset, but the procedure did not identify any missing studies in either of the development time subsets. Three studies were estimated to be missing from the non-consumptive survival data, and accounting for imputed values from missing studies resulted in a shift in the predation effect size from -0.11 (95% CI -0.17, -0.04), p-value = 0.0016, to -0.13 (95% CI -0.20, -0.07), p-value <0.0001. Two studies were estimated to be missing from the female size data, and accounting for imputed values from these missing studies shifted the predation effect size from -0.13 (95% CI -0.19, -0.06), p-value = 0.0002, to -0.10 (95% CI -0.17, -0.03), p-value = 0.0083. Shifts in effect size estimates due to the trim and fill procedure were minor and did not cause any of the observed effects of predators to change direction or become insignificant.

Table 2: Candidate multilevel mixed effects models of consumptive effects from predators on mosquito survival, fitted to dataset of effect sizes (n = 187 from 34 studies), and ranked by corrected Akaike's information criterion (AICc).

Moderator(s)	**Test of Moderators (degrees of freedom, p-value)**	**AICc**	**ΔAICc**
predator family x vector genus	28, <0.0001	500.5	0
predator family	19, <0.0001	507.0	6.5
predator family + vector genus	23, <0.0001	508.1	7.6
vector genus	5, <0.0001	573.0	72.5
none	----	576.5	76.0

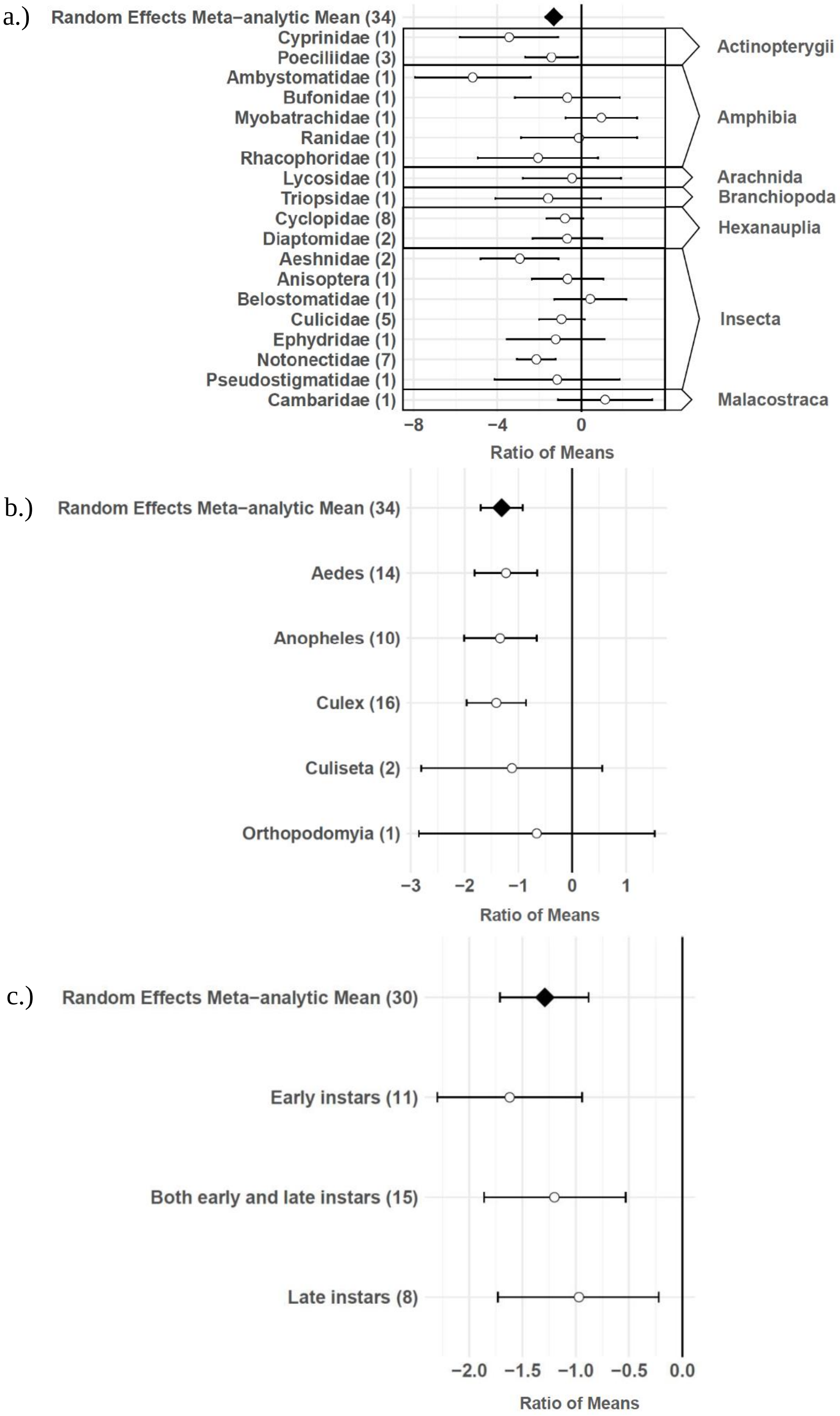

Fig 3. Effect sizes and 95% confidence intervals for consumptive effects of predators, for different categories of moderators (with number of studies in parentheses): a.) predator family with predator class in the right-hand column, b.) vector genus, and c.) larval instar

Table 3: Candidate multilevel mixed effects models of consumptive effects from predators, fitted to dataset of effect sizes where larval instar is not missing (n = 163 from 30 studies), and ranked by corrected Akaike's information criterion (AICc).

Moderator(s)	**Test of Moderators (degrees of freedom, p-value)**	**AICc**	**ΔAICc**
predator family x larval instar	25, <0.0001	429.2	0
predator family + larval instar	19, <0.0001	443.5	14.3
predator family x vector genus	25, <0.0001	455.0	25.8
predator family	17, <0.0001	456.8	27.6
predator family + vector genus	21, <0.0001	458.4	29.2
larval instar	3, <0.0001	503.1	73.9
vector genus	5, <0.0001	504.7	75.5
none	----	508.5	79.3

Multilevel Mixed Effects Models:

The consumptive survival and oviposition data subsets met the criteria of high heterogeneity, observations from at least 10 studies, and no evidence of publication bias. Therefore, these data subsets were tested for moderators using multilevel mixed effects models. Predator families that decreased mosquito survival included Cyprinidae: -3.44 (95% CI -5.79, -1.09), p-value = 0.0042; Poeciliidae: -1.42 (95% CI -2.67, -0.16), p-value = 0.0270; Ambystomatidae: -5.18 (95% CI -7.94, -2.42), p-value = 0.0002; Aeshnidae: -2.93 (95% CI -4.80, -1.07), p-value = 0.0020; and Notonectidae: -2.14 (95% CI -3.07, -1.21), p-value <0.0001 (Fig 3a). Vector genera that experienced significant decreases in survival due to consumptive effects of predators included *Aedes*: -1.23 (95% CI -1.81, -0.65), p-value <0.0001; *Anopheles*: -1.34 (95% CI -2.01, -0.66), p-value = 0.0001; and *Culex*: -1.41 (95% CI -1.96, -0.86), p-value <0.0001 (Fig 3b). Among all 187 consumptive survival observations from 34 studies, the best model fit, according to AICc value, was achieved when an interaction between predator family and vector genus was included in the model (Table 2). However, among the 163 larval stage consumptive survival observations from 30 studies, adding an interactive term between larval instar (an indicator of prey size) and predator family had a greater improvement on model fit than adding an interactive term between vector genus and predator family (Fig 3c, Table 3). Temperature did not affect the heterogeneity of consumptive survival data, either as a linear moderator: -0.01 (95% CI -0.10, 0.07), p-value = 0.7559, or a quadratic moderator: 0.00 (95% CI 0.00, 0.00), p-value = 0.8184. The best oviposition model fit, according to AICc value, was achieved when vector genus was added as a moderator (Table 4). The mean oviposition effect size was not significantly different than zero for *Aedes*: 0.32 (95% CI -2.14, 2.79), p-value = 0.7970, or *Culiseta*: -0.61 (95% CI -1.83, 0.62), p-value = 0.3329, but for *Culex* mosquitoes, oviposition was significantly decreased by predator presence: -1.69 (95% CI -2.82, -0.56), p-value = 0.0033 (Fig 4).

Table 4: Candidate multilevel mixed effects models of non-consumptive effects of predators on mosquito oviposition behavior, fitted to dataset of effect sizes (n = 36 from 12 studies), and ranked by corrected Akaike's information criterion (AICc).

Moderator(s)	Test of Moderators (degrees of freedom, p-value)	AICc	ΔAICc
vector genus	3, 0.0149	122.1	0
none	----	125.2	3.1
predator family	12, 0.8855	167.9	45.8

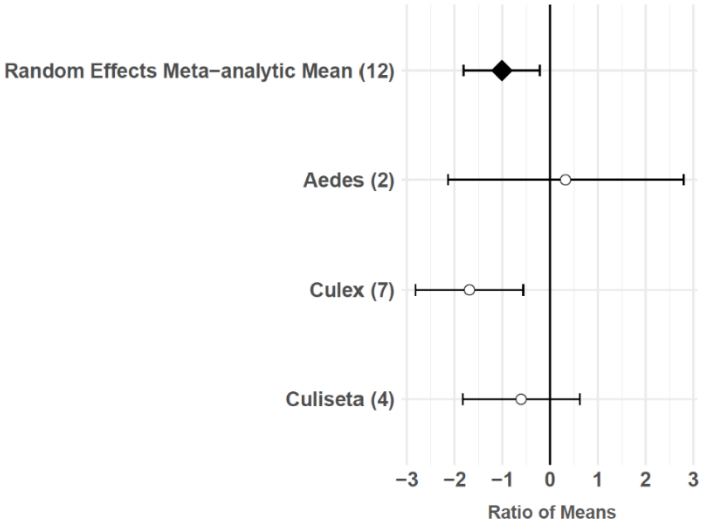

Fig 4. Oviposition effect sizes and 95% confidence intervals for different categories of vector genus (with number of studies in parentheses)

Discussion

In this study, laboratory and semi-field empirical data were obtained through a systematic literature review and used to conduct a meta-analysis that assessed consumptive and non-consumptive effects of predators on mosquito prey. Some results agree with previously observed trends, such as greater consumptive effects from larger predators (Kumar et al., 2008, Peters, 1983) and no oviposition response to predator cues among container-breeding *Aedes* mosquitoes (Vonesh and Blaustein, 2010). However, this meta-analysis revealed additional trends. Mosquito larval instar had an important role in moderating consumptive effects of predators, likely because of its direct correlation to prey size. Furthermore, a small, but significant, decrease in mosquito survival due to non-consumptive effects of predators was observed, suggesting that mosquitoes can be “scared to death” by predators (Preisser et al., 2005). Both male and female body sizes were also reduced among mosquitoes that had been exposed to predators, and predator avoidance during oviposition was observed among female *Culex* mosquitoes. Effects of predators on different vector traits, particularly survival, body size, and oviposition behavior, have the potential to influence infectious disease dynamics.

Consumptive effects of predators on survival:

Several larger predators reduced mosquito survival, including freshwater fish (Cyprinidae and Poeciliidae), salamander larvae (Ambystomatidae), dragonfly larvae (Aeshnidae), and backswimmers (Notonectidae) (Fig 3a). This finding is consistent with a previous analysis which showed a positive linear relationship between predator body mass and ingestion rate across taxa (Peters, 1983). In addition, more effect size heterogeneity in the consumptive survival data was explained by an interaction between predator family and larval instar than was explained by an interaction between predator family and vector genus (Table 3). This result suggests that the relative sizes of predator and prey groups could play a more important role in determining consumptive mosquito survival than variations in predator responses to different behaviors of prey genera, which are likely to be shaped by the degree of shared evolutionary history between trophic levels (Buchanan et al., 2017). Larval instar is an indicator of mosquito size, and previous modelling work has provided evidence of prey size selection by predators to maximize energetic gain (Mittelbach, 1981). While smaller cyclopoid copepods are more effective against early instar mosquito larvae (Dieng et al., 2002), larger predators including tadpoles, giant water bugs, dragonfly larvae, fish, and backswimmers are more effective against late instar larvae (Kweka et al., 2011).

Non-consumptive effects of predators on survival:

Exposure to predation cues significantly lowered mosquito survival, and this non-consumptive effect has also been observed in dragonfly larvae prey (*Leucorrhinia intacta*) that were exposed to caged predators (McCauley et al., 2011). The reduction in mosquito survival from non-consumptive effects of predators was significantly smaller than the reduction that was observed from consumptive effects. This is partially due to the practical constraints of most experimental designs, which cause consumptive and non-consumptive effects of predators on survival to be grouped together and reported as consumptive effects. The greater impact of combined consumptive and non-consumptive effects, in comparison to only non-consumptive effects, has previously been observed in pea aphids (*Acyrthosiphon pisum*) (Nelson et al., 2004).

Non-consumptive effects of predators on body size:

While predators did not significantly impact mosquito development time through non-consumptive effects in either sex, mosquito body size was decreased by the non-consumptive effects of predators in both sexes. Smaller body size is associated with lower reproductive success in mosquitoes because smaller females lay fewer eggs (Blackmore and Lord, 2000, Lyimo and Takken, 1993, Oliver and Howard, 2011, Styer et al., 2007, Tsunoda et al., 2010), and smaller males produce less sperm (Hatala et al., 2018, Ponlawat and Harrington, 2007). These effects suggest that predation could non-consumptively reduce mosquito population growth. The smaller size of mosquitoes exposed to predators could also limit disease transmission. Vector lifespan contributes disproportionately to disease transmission because older vectors are more likely to have been exposed to pathogens, more likely to already be infectious after having survived the extrinsic incubation period, and more likely to survive long enough to bite subsequent hosts (Cator et al., 2020). It is well-established that smaller mosquito body size is associated with shorter mosquito lifespan (Araújo et al., 2012, Hawley, 1985, Reisen et al., 1984, Reiskind and Lounibos, 2009, Xue et al., 2010). Therefore, non-consumptive effects of predators may limit the transmission of mosquito-borne diseases.

Non-consumptive effects of predators on oviposition behavior:

Predator presence also non-consumptively reduced oviposition behavior in adult female mosquitoes. Meta-regression results showed that *Culex* females significantly avoid oviposition sites that contain predators or predator cues, but *Aedes* and *Culiseta* females do not avoid these sites, despite a slight non-significant trend towards predator avoidance in *Culiseta* (Fig 4). Both *Culex* and *Culiseta* mosquitoes have an “all-or-none” oviposition strategy (Johnson and Fonseca, 2014), in which they lay hundreds of rapidly-hatching eggs in rafts on the water’s surface (Day, 2016). Such an oviposition strategy is conducive to evolving predator avoidance behaviors, and a previous meta-analysis showed significant predator avoidance in both *Culex* and *Culiseta* during oviposition (Vonesh and Blaustein, 2010). Conversely, it is likely that an oviposition response to predation is not particularly advantageous for *Aedes* because the delayed hatching of their eggs (Day, 2016) can prevent the level of predation risk at the time of oviposition from matching the level of predation risk present in the eventual larval environment (Vonesh and Blaustein, 2010). The predator avoidance response in *Aedes* species that lay their eggs above the water's edge in containers has previously been described as "non-existent" (Vonesh and Blaustein, 2010). Both *Aedes* species included in this study's oviposition data subset, *Ae. albopictus* and *Ae. aegypti*, meet the criterion of ovipositing above water in containers (Juliano, 2009). Predator avoidance during oviposition has previously been found to increase the mosquito population size at equilibrium (Spencer et al., 2002). However, this study's results and those of a previous meta-analysis (Vonesh and Blaustein, 2010) suggest that models of oviposition site selection, such as those using parameters from Notonectidae predators and *Culiseta* prey (Kershenbaum et al., 2012), are not generalizable to *Aedes* vectors.

Implications for West Nile virus disease dynamics:

Predator avoidance during oviposition by *Culex* mosquitoes (Fig 4) may be of particular importance to West Nile virus (WNV) disease dynamics. Previous work has shown that *Cx. pipiens*, *Cx. restuans*, and *Cx. tarsalis* all avoid predator habitats (Vonesh and Blaustein, 2010), and that *Cx. pipiens* is the primary bridge vector of WNV responsible for spill-over transmission from avian reservoir hosts to humans (Fonseca et al., 2004, Hamer et al., 2008, Kramer et al., 2008, Andreadis, 2012). *Cx. pipiens* mosquitoes can live in permanent aquatic environments, such as ground pools (Amini et al., 2020, Barr, 1967, Dida et al., 2018, Sulesco et al., 2015), ponds (Lühken et al., 2015), stream edges (Amini et al., 2020), and lake edges (Vinogradova, 2000) that are more common in rural areas, but *Cx. pipiens* are also found in urban and suburban residential areas, where they typically breed in artificial containers (Sulesco et al., 2015), including tires (Lühken et al., 2015, Nikookar et al., 2017, Verna, 2015), rainwater tanks (Townroe and Callaghan, 2014), and catch basins (Gardner et al., 2012). Artificial containers are less likely to harbor larger predators, such as freshwater fish (Cyprinidae and Poeciliidae), salamander larvae (Ambystomatidae), dragonfly larvae (Aeshnidae), and backswimmers (Notonectidae) because temporary aquatic environments cannot support the relatively long development times of these organisms. The mean dispersal distance of adult *Culex* mosquitoes is greater than one kilometer (Ciota et al., 2012, Hamer et al., 2014), and female *Cx. pipiens* have exhibited longer dispersal distances after developing in the presence of a fish predator (Alcalay et al., 2018). Therefore, predator avoidance during oviposition may cause *Cx. pipiens* populations to disperse from permanent aquatic environments in more rural areas to artificial container environments in urbanized areas, where humans are known to be at a higher risk for WNV infection (Brown et al., 2008).

Predation cue levels may be altered by climate conditions, and these changes in cue levels can impact WNV transmission to humans. Drought has previously been associated with human WNV cases (Johnson and Sukhdeo, 2013, Marcantonio et al., 2015, Roehr, 2012, Shaman et al., 2005, Epstein and Defilippo, 2001, Paull et al., 2017), but the association has been described as “paradoxical” (Johnson and Fonseca, 2014) or “counterintuitive” (Johnson and Sukhdeo, 2013) and has thus far lacked a clear biological or ecological mechanism. Under drought conditions, the density of aquatic organisms increases and predation pressures can intensify due to compressed space and high encounter rates (Amundrud et al., 2019). A previous study of a stream ecosystem found that impacts of fish predation are more severe during the dry season (Dudgeon, 1993). In addition, reductions in water volume can facilitate consumption of mosquito larvae prey by crane fly larvae (Tipulidae), whereas consumptive predation by tipulids was not observed at a higher water level (Amundrud et al., 2019). Although experimental oviposition studies tend to provide only predator-present and predator-absent options to gravid female mosquitoes (Arav and Blaustein, 2006, Ohba et al., 2012), some studies have found that mosquitoes also respond to a gradient of predation cues (Roux et al., 2014, Silberbush and Blaustein, 2011). Ovipositing females exhibit a preference for sites with a lower predator density (Silberbush and Blaustein, 2011), and the frequency of anti-predator behavior has been shown to increase with concentration of predation cues (Roux et al., 2014). Therefore, as predation cue levels increase due to drought, permanent aquatic habitats are likely to transition from suitable oviposition sites for one generation of female mosquitoes, to unsuitable oviposition sites for the next generation.

When suitable oviposition sites are absent, females retain their eggs until sites become available (Bentley and Day, 1989). The reproductive potential of *Cx. pipiens* females is not diminished by egg retention periods that are up to five weeks long; this allows gravid females enough time to find the best available oviposition sites, which are often container habitats with low predation risk located in residential areas (Johnson and Fonseca, 2014). The migration of gravid female *Cx. pipiens* to residential areas increases the risk of WNV spill-over to humans because these egg-bearing vectors are likely to have already blood-fed once or multiple times (Clements, 1992), and therefore have a relatively high risk of WNV infection. This is consistent with studies that have reported associations between drought and WNV-infected mosquitoes in urban and residential areas (Johnson and Sukhdeo, 2013, Paull et al., 2017). In addition, vertical transmission of WNV from gravid females to their eggs may occur during oviposition (Rosen, 1988), when the virus is transmitted to the next generation by an accessory gland fluid that attaches the eggs together to form a raft (Nelms et al., 2013). Because the rate of vertical transmission in *Cx. pipiens* increases with the number of days since WNV infection (Anderson et al., 2008), extended searches for oviposition sites due to drought conditions could increase the frequency of vertical transmission. However, the impact of vertical transmission on WNV epidemics is thought to be minimal because when transmission to an egg raft did occur, only 4.7% of the progeny were found to be infected as adults (Anderson et al., 2008), and only about half of those infected adults are estimated to be female. In summary, the movement of *Cx. pipiens* females toward more residential areas, combined with potential limited WNV amplification due to increased vertical transmission, suggests that the vector trait of predator avoidance during oviposition by *Cx. pipiens* females is the behavioral mechanism underlying previously observed associations between drought and human WNV cases.

Implications for mosquito-borne disease modelling:

Although the aquatic phase of the mosquito life cycle is often overlooked in mathematical models of mosquito-borne pathogen transmission (Reiner et al., 2013), vector survival at immature stages plays an important role in determining mosquito population abundance, which is an essential factor for predicting disease transmission (Beck-Johnson et al., 2013). The results of this study show that mosquito survival decreases among the *Aedes, Anopheles,* and *Culex* genera due to consumptive effects of predators (Fig 3b), and that there is also a reduction in mosquito survival due to non-consumptive effects. Other studies have demonstrated that aquatic predators dramatically impact mosquito survival and abundance. For example, a biocontrol intervention relying on the application of copepod predators eliminated *Aedes albopictus* from three communes in Nam Dinh, Vietnam, where dengue transmission was previously detected, and reduced vector abundance by 86-98% in three other communes (Kay et al., 2002). Conversely, the annual abundance of *Culex* and

Anopheles mosquitoes was observed to increase 15-fold in semi-permanent wetlands in the year following a drought, likely because the drought eliminated aquatic predators from wetlands that dried completely, and mosquitoes were able to re-colonize newly-formed aquatic habitats more quickly than their most effective predators (Chase and Knight, 2003).

While relationships between temperature and different vector traits, such as fecundity and lifespan, have been incorporated into models of temperature effects on mosquito population density (El Moustaid and Johnson, 2019), models of predator effects on vector borne disease transmission have focused primarily on the impacts of predation on vector survival. Previous models have shown that predators of vector species can decrease or eliminate pathogen infection in host populations as vector fecundity increases (Moore et al., 2010). The findings of this meta-analysis suggest that predators also decrease vector fecundity through non-consumptive effects on vector body size. In addition, the entomological inoculation rate (EIR) is likely to be reduced by effects of predators on mosquito fecundity and lifespan, as well as effects of predators on mosquito survival. The EIR has been defined as the product of three variables: (m) the number of mosquitoes per host, (a) the daily rate of mosquito biting, and (s) the proportion of mosquitoes that are infectious (Beck-Johnson et al., 2013). Based on this study’s findings, predators are likely to decrease the number of mosquitoes per host by reducing mosquito survival through both consumptive and non-consumptive effects, and by reducing mosquito fecundity through non-consumptive effects on body size. In addition, predators are likely to decrease the proportion of mosquitoes that are infectious by shortening the vector lifespan through non-consumptive effects on body size. The relationship between mosquito body size and biting rate is unclear, with some studies showing higher biting rates among larger mosquitoes (Araújo et al., 2012, Gunathilaka et al., 2019), and others reporting higher biting rates among smaller mosquitoes (Farjana and Tuno, 2013, Leisnham et al., 2008). The links between factors that influence the EIR and observed effects of predators on mosquito prey demonstrate the necessity of including both consumptive and non-consumptive effects of predators in models of mosquito-borne disease.

Conclusion

This meta-analysis on mosquito predation demonstrates that predators not only play an important role in directly reducing mosquito populations, but also have non-consumptive effects on surviving mosquitoes that may ultimately reduce further population growth and decrease disease transmission. While families of larger sized predators were effective in reducing mosquito survival, other factors, such as impacts on native species, as well as the economic cost of mass-rearing and field applications (Kumar and Hwang, 2006, Pyke, 2008), should be carefully considered before selecting a predator as a suitable biocontrol agent. Predictive disease models are likely to be more reliable when the non-consumptive effects of predation are incorporated. Although exposure of mosquito larvae to predators is commonplace in outdoor field settings, it remains rare in most laboratory-based assessments of vector traits. Therefore, mosquitoes observed in nature are likely to have smaller body sizes than those observed under optimal laboratory conditions. It is important for disease modelers to recognize these impacts of predation on vector traits as they can reduce mosquito population growth and limit disease transmission due to shorter vector lifespans. Within the WNV disease system, consideration of the oviposition behavioral response to predation cues by *Culex* vectors can greatly improve current understanding of the association between drought and human cases. This study provides general estimates of the effects of predators on selected mosquito traits for use in predictive disease models.

Future directions:

Modelling efforts that aim to optimize the application of biocontrol predators should also consider incorporating predator effects on vector survival, fecundity, and lifespan. These additions to predictive models of various biocontrol interventions are likely to help public health officials choose the most cost-effective strategies for limiting disease transmission. In the sixty-study database that was compiled, only one study was designed to directly measure the effect of larval-stage predation on vector competence (Roux et al., 2015). Therefore, future efforts to assess the impact of predators on mosquito-borne disease transmission should prioritize experimental studies in which infected mosquito larvae are observed throughout an initial period of aquatic exposure to predators, followed by a period of blood-feeding in the adult stage.

Two studies from the compiled database examined the compatibility of predators with *Bacillus thuringiensis* var. *israelensis* (*Bti*), a commonly used bacterial biocontrol agent (Chansang et al., 2004, Op de Beeck et al., 2016). Previous studies have supported the simultaneous application of cyclopoid copepod predators and *Bti* (Marten et al., 1993, Tietze et al., 1994), but additional analyses are needed on the use of *Bti* with other families of mosquito predators. Populations of other insect pests, such as the southern green stink bug (*Nezara viridula*), are known to be regulated by both predators and parasites (Ehler, 2002). The literature search conducted for this meta-analysis returned studies on water mite parasites (Rajendran and Prasad, 1994) and nematode parasitoids (de Valdez, 2006) of mosquitoes, and ascogregarine parasites have previously been evaluated as biocontrol agents against *Aedes* mosquitoes (Tseng, 2007). A more thorough review of the impacts of parasites and parasitoids on vector traits, such as survival, fecundity, and lifespan, is needed before incorporating these potential biocontrol agents into integrated vector control plans.

Author Contributions

Conceptualization, all authors; data curation, MCR, CMH, ZG, CR, FEM, MVE, TD, NLG, SLH, ACM; formal analysis, investigation, methodology, and validation MCR, CMH, ZG, CR, MVE, ACM; project administration, MCR, CMH, ACM; software, MCR, CMH, MVE, ZG, ACM; supervision CMH, NLG, SLH, AGP, ACM; visualization, MCR, CMH, TD, ACM; writing— original draft, MCR; writing—review and editing, all authors. None of the authors have any competing interests to declare.

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Supplementary Information

Table S1: Publications included in the database and their types of vector trait data

Publication	**Vector Trait**			
	Survival	Behavior	Size	Development
(Alcalay et al., 2018)	☒	☐	☒	☒
(Alcalay et al., 2019)	☐	☒	☐	☐
(Arav and Blaustein, 2006)	☐	☒	☐	☐
(Beketov and Liess, 2007)	☒	☐	☒	☒
(Blaustein et al., 2005)	☐	☒	☐	☐
(Blaustein and Margalit, 1996)	☒	☐	☐	☐
(Bond et al., 2005)	☐	☐	☒	☒
(Bowatte et al., 2013)	☒	☒	☐	☐
(Bucciarelli et al., 2019)	☒	☐	☐	☐
(Calliari et al., 2003)	☒	☐	☐	☐
(Chandrasegaran et al., 2018)	☐	☒	☐	☐
(Chansang et al., 2004)	☒	☐	☐	☐
(Cuthbert et al., 2018)	☒	☐	☐	☐
(Cuthbert et al., 2019a)	☒	☐	☐	☐
(Cuthbert et al., 2019b)	☐	☒	☐	☐
(de Valdez, 2007)	☐	☒	☐	☐
(Dieng et al., 2002)	☒	☐	☐	☐
(Dieng et al., 2003)	☒	☐	☐	☐
(Farajollahi et al., 2009)	☒	☐	☐	☐
(Fischer et al., 2012)	☐	☐	☒	☒
(Fontana-Bria et al., 2017)	☐	☐	☒	☒
(Futami et al., 2008)	☒	☐	☐	☐
(Grill and Juliano, 1996)	☒	☒	☒	☒
(Griswold and Lounibos, 2005)	☒	☐	☐	☐
(Irwin and Paskewitz, 2009)	☒	☐	☐	☐
(Kalimuthu et al., 2017)	☒	☐	☐	☐
(Knight et al., 2004)	☒	☐	☐	☒
(Kraus and Vonesh, 2010)	☐	☒	☐	☐
(Krol et al., 2019)	☒	☐	☐	☒
(Kweka et al., 2011)	☒	☐	☐	☐
(Marten et al., 2000a)	☒	☐	☐	☐
(Marten et al., 2000b)	☒	☐	☐	☐
(Mercer et al., 2005)	☒	☐	☒	☐
(Micieli et al., 2002)	☒	☐	☐	☐
(Minakawa et al., 2007)	☒	☐	☐	☐
(Nannini and Juliano, 1998)	☒	☐	☐	☐
(Ohba et al., 2012)	☒	☒	☒	☐
(Op de Beeck et al., 2016)	☐	☐	☒	☒
(Orr and Resh, 1989)	☒	☐	☐	☐
(Pintar et al., 2018)	☐	☒	☐	☐
(Roberts, 2012)	☐	☒	☒	☒
(Roberts, 2018)	☐	☐	☒	☒
(Roux et al., 2015)	☒	☐	☒	☒

Publication (continued)	**Vector Trait (continued)**			
	Survival	Behavior	Size	Development
(Rubbo et al., 2011)	☒	☒	☒	☐
(Schrama et al., 2018)	☒	☐	☐	☐
(Silberbush et al., 2015)	☒	☐	☐	☒
(Silberbush and Blaustein, 2008)	☐	☒	☐	☐
(Silberbush and Blaustein, 2011)	☐	☒	☐	☐
(Soghigian et al., 2017)	☒	☒	☐	☐
(Staats et al., 2016)	☐	☒	☐	☐
(Stav et al., 2005)	☒	☐	☒	☒
(Subramaniam et al., 2015)	☒	☐	☐	☐
(Tietze and Mulla, 1990)	☒	☐	☐	☒
(van Uitregt et al., 2012)	☒	☒	☒	☒
(van Uitregt et al., 2013)	☐	☒	☒	☐
(Veronesi et al., 2015)	☒	☐	☐	☐
(Wallace and Merritt, 1999)	☒	☐	☒	☒
(Yanoviak, 1999)	☒	☐	☒	☐
(Zuharah et al., 2013)	☒	☐	☐	☐
(Zuharah and Lester, 2010)	☒	☐	☐	☐

References

ALCALAY, Y., TSURIM, I. & OVADIA, O. 2018. Female mosquitoes disperse further when they develop under predation risk. *Behavioral Ecology*, 29**,** 1402-1408.

ALCALAY, Y., TSURIM, I. & OVADIA, O. 2019. Multi-scale oviposition site selection in two mosquito species. *Ecological Entomology*, 44**,** 347-356.

AMINI, M., HANAFI-BOJD, A. A., AGHAPOUR, A. A. & CHAVSHIN, A. R. 2020. Larval habitats and species diversity of mosquitoes (Diptera: Culicidae) in West Azerbaijan Province, Northwestern Iran. *Bmc Ecology*, 20.

AMUNDRUD, S. L., CLAY-SMITH, S. A., FLYNN, B. L., HIGGINS, K. E., REICH, M. S., WIENS, D. R. H. & SRIVASTAVA, D. S. 2019. Drought alters the trophic role of an opportunistic generalist in an aquatic ecosystem. *Oecologia*, 189**,** 733-744.

ANDERSON, J. F., MAIN, A. J., DELROUX, K. & FIKRIG, E. 2008. Extrinsic incubation periods for horizontal and vertical transmission of West Nile virus by Culex pipiens pipiens (Diptera: Culicidae). *J Med Entomol*, 45**,** 445-51.

ANDREADIS, T. G. 2012. THE CONTRIBUTION OF CULEX PIPIENS COMPLEX MOSQUITOES TO TRANSMISSION AND PERSISTENCE OF WEST NILE VIRUS IN NORTH AMERICA. *Journal of the American Mosquito Control Association*, 28**,** 137-151.

ARAÚJO, M. D., GIL, L. H. S. & E-SILVA, A. D. 2012. Larval food quantity affects development time, survival and adult biological traits that influence the vectorial capacity of Anopheles darlingi under laboratory conditions. *Malaria Journal*, 11.

ARAV, D. & BLAUSTEIN, L. 2006. Effects of pool depth and risk of predation on oviposition habitat selection by temporary pool dipterans. *Journal of Medical Entomology*, 43**,** 493-497.

BARR, A. R. 1967. Occurrence and distribution of the Culex pipiens complex. *Bulletin of the World Health Organization,* 37**,** 293-296.

BECK-JOHNSON, L. M., NELSON, W. A., PAAIJMANS, K. P., READ, A. F., THOMAS, M. B. & BJØRNSTAD, O. N. 2013. The effect of temperature on Anopheles mosquito population dynamics and the potential for malaria transmission. *PLoS One,* 8**,** e79276.

BEKETOV, M. A. & LIESS, M. 2007. Predation risk perception and food scarcity induce alterations of life-cycle traits of the mosquito Culex pipens. *Ecological Entomology,* 32**,** 405-410.

BENELLI, G., JEFFRIES, C. L. & WALKER, T. 2016. Biological Control of Mosquito Vectors: Past, Present, and Future. *Insects,* 7.

BENTLEY, M. D. & DAY, J. F. 1989. Chemical ecology and behavioral aspects of mosquito oviposition. *Annu Rev Entomol,* 34**,** 401-21.

BLACKMORE, M. S. & LORD, C. C. 2000. The relationship between size and fecundity in Aedes albopictus. *Journal of Vector Ecology,* 25**,** 212-217.

BLAUSTEIN, L., BLAUSTEIN, J. & CHASE, J. 2005. Chemical detection of the predator Notonecta irrorata by ovipositing Culex mosquitoes. *Journal of Vector Ecology,* 30**,** 299-301.

BLAUSTEIN, L. & MARGALIT, J. 1996. Priority Effects in Temporary Pools: Nature and Outcome of Mosquito Larva-Toad Tadpole Interactions Depend on Order of Entrance. *Journal of Animal Ecology,* 65**,** 77-84.

BOND, J. G., ARREDONDO-JIMENEZ, J. I., RODRIGUEZ, M. H., QUIROZ-MARTINEZ, H. & WILLIAMS, T. 2005. Oviposition habitat selection for a predator refuge and food source in a mosquito. *Ecological Entomology,* 30**,** 255-263.

BOWATTE, G., PERERA, P., SENEVIRATHNE, G., MEEGASKUMBURA, S. & MEEGASKUMBURA, M. 2013. Tadpoles as dengue mosquito (Aedes aegypti) egg predators. *Biological Control,* 67**,** 469-474.

BROSE, U., JONSSON, T., BERLOW, E. L., WARREN, P., BANASEK-RICHTER, C., BERSIER, L. F., BLANCHARD, J. L., BREY, T., CARPENTER, S. R., BLANDENIER, M. F. C., CUSHING, L., DAWAH, H. A., DELL, T., EDWARDS, F., HARPER-SMITH, S., JACOB, U., LEDGER, M. E., MARTINEZ, N. D., MEMMOTT, J., MINTENBECK, K., PINNEGAR, J. K., RALL, B. C., RAYNER, T. S., REUMAN, D. C., RUESS, L., ULRICH, W., WILLIAMS, R. J., WOODWARD, G. & COHEN, J. E. 2006. Consumer-resource body-size relationships in natural food webs. *Ecology,* 87**,** 2411-2417.

BROWN, H. E., CHILDS, J. E., DIUK-WASSER, M. A. & FISH, D. 2008. Ecological factors associated with West Nile virus transmission, northeastern United States. *Emerg Infect Dis,* 14**,** 1539-45.

BUCCIARELLI, G. M., SUH, D., LAMB, A. D., ROBERTS, D., SHARPTON, D., SHAFFER, H. B., FISHER, R. N. & KATS, L. B. 2019. Assessing effects of non-native crayfish on mosquito survival. *Conservation Biology,* 33**,** 122-131.

BUCHANAN, A. L., HERMANN, S. L., LUND, M. & SZENDREI, Z. 2017. A meta-analysis of non-consumptive predator effects in arthropods: the influence of organismal and environmental characteristics. *Oikos,* 126**,** 1233-1240.

BURNHAM, K. P. & ANDERSON, D. R. 2004. Multimodel Inference: Understanding AIC and BIC in Model Selection. *Sociological Methods & Research,* 33**,** 261-304.

CALLIARI, D., SANZ, K., MARTINEZ, M., CERVETTO, G., GOMEZ, M. & BASSO, C. 2003. Comparison of the predation rate of freshwater cyclopoid copepod species on larvae of the mosquito Culex pipiens. *Medical and veterinary entomology,* 17**,** 339-342.

CATOR, L. J., JOHNSON, L. R., MORDECAI, E. A., EL MOUSTAID, F., SMALLWOOD, T. R. C., LADEAU, S. L., JOHANSSON, M. A., HUDSON, P. J., BOOTS, M., THOMAS, M. B., POWER, A. G. & PAWAR, S. 2020. The Role of Vector Trait Variation in Vector-Borne Disease Dynamics. *Frontiers in Ecology and Evolution,* 8.

CHANDRASEGARAN, K., SINGH, A., LAHA, M. & QUADER, S. 2018. Playing it safe? Behavioural responses of mosquito larvae encountering a fish predator. *Ethology Ecology & Evolution,* 30**,** 70-87.

CHANSANG, U. R., BHUMIRATANA, A. & KITTAYAPONG, P. 2004. Combination of Mesocyclops thermocyclopoides and Bacillus thuringiensis var. israelensis: A better approach for the control of Aedes aegypti larvae in water containers. *Journal of Vector Ecology,* 29**,** 218-226.

CHASE, J. M. & KNIGHT, T. M. 2003. Drought-induced mosquito outbreaks in wetlands. *Ecology Letters,* 6**,** 1017-1024.

CIOTA, A. T., DRUMMOND, C. L., RUBY, M. A., DROBNACK, J., EBEL, G. D. & KRAMER, L. D. 2012. Dispersal of Culex mosquitoes (Diptera: Culicidae) from a wastewater treatment facility. *J Med Entomol,* 49**,** 35-42.

CLEMENTS, A. N. 1992. *The Biology of Mosquitoes: Development, Nutrition and Reproduction,* London, Chapman & Hall.

CUTHBERT, R. N., DALU, T., WASSERMAN, R. J., COUGHLAN, N. E., CALLAGHAN, A., WEYL, O. L. F. & DICK, J. T. A. 2018. Muddy waters: Efficacious predation of container-breeding mosquitoes by a newly-described calanoid copepod across differential water clarities. *Biological Control,* 127**,** 25-30.

CUTHBERT, R. N., DALU, T., WASSERMAN, R. J., WEYL, O. L. F., CALLAGHAN, A., FRONEMAN, W. & DICK, J. T. A. 2019a. Sex-skewed trophic impacts in ephemeral wetlands. *Freshwater Biology,* 64**,** 359-366.

CUTHBERT, R. N., ORTIZ-PEREA, N., DICK, J. T. A. & CALLAGHAN, A. 2019b. Elusive enemies: Consumptive and ovipositional effects on mosquitoes by predatory midge larvae are enhanced in dyed environments. *Biological Control,* 132**,** 116-121.

DAM, H. G. & PETERSON, W. T. 1988. THE EFFECT OF TEMPERATURE ON THE GUT CLEARANCE RATE-CONSTANT OF PLANKTONIC COPEPODS. *Journal of Experimental Marine Biology and Ecology,* 123**,** 1-14.

DAY, J. F. 2016. Mosquito Oviposition Behavior and Vector Control. *Insects,* 7.

DE VALDEZ, M. R. 2007. Predator avoidance behavior of Aedes aegypti mosquito larvae infected with mermithid nematodes (Nematoda: Mermithidae). *J Vector Ecol,* 32**,** 150-3.

DE VALDEZ, M. R. W. 2006. Parasitoid-induced behavioral alterations of Aedes aegypti mosquito larvae infected with mermithid nematodes (Nematoda : Mermithidae). *Journal of Vector Ecology,* 31**,** 344-354.

DELNAT, V., TRAN, T. T., JANSSENS, L. & STOKS, R. 2019. Resistance to a chemical pesticide increases vulnerability to a biopesticide: Effects on direct mortality and mortality by predation. *Aquat Toxicol,* 216**,** 105310.

DIDA, G. O., ANYONA, D. N., ABUOM, P. O., AKOKO, D., ADOKA, S. O., MATANO, A. S., OWUOR, P. O. & OUMA, C. 2018. Spatial distribution and habitat characterization of mosquito species during the dry season along the Mara River and its tributaries, in Kenya and Tanzania. *Infectious Diseases of Poverty,* 7.

DIENG, H., BOOTS, M., TUNO, N., TSUDA, Y. & TAKAGI, M. 2002. A laboratory and field evaluation of Macrocyclops distinctus, Megacyclops viridis and Mesocyclops pehpeiensis as control agents of the dengue vector Aedes albopictus in a peridomestic area in Nagasaki, Japan. *Medical and Veterinary Entomology,* 16**,** 285-291.

DIENG, H., BOOTS, M., TUNO, N., TSUDA, Y. & TAKAGI, M. 2003. Life history effects of prey choice by copepods: Implications for biocontrol of vector mosquitoes. *Journal of the American Mosquito Control Association*, 19**,** 67-73.

DUDGEON, D. 1993. THE EFFECTS OF SPATE-INDUCED DISTURBANCE, PREDATION AND ENVIRONMENTAL COMPLEXITY ON MACROINVERTEBRATES IN A TROPICAL STREAM. *Freshwater Biology*, 30**,** 189-197.

DUVAL, S. & TWEEDIE, R. 2000a. A nonparametric "trim and fill" method of accounting for publication bias in meta-analysis. *Journal of the American Statistical Association*, 95**,** 89-98.

DUVAL, S. & TWEEDIE, R. 2000b. Trim and fill: A simple funnel-plot-based method of testing and adjusting for publication bias in meta-analysis. *Biometrics*, 56**,** 455-463.

EHLER, L. E. 2002. An evaluation of some natural enemies of Nezara viridula in northern California. *BioControl*, 47**,** 309-325.

EL MOUSTAID, F. & JOHNSON, L. R. 2019. Modeling Temperature Effects on Population Density of the Dengue Mosquito Aedes aegypti. *Insects*, 10**,** 393.

ENGLUND, G., OHLUND, G., HEIN, C. L. & DIEHL, S. 2011. Temperature dependence of the functional response. *Ecology Letters*, 14**,** 914-921.

EPSTEIN, P. R. & DEFILIPPO, C. 2001. West Nile Virus and Drought. *Global Change and Human Health*, 2**,** 105-107.

FARAJOLLAHI, A., KESAVARAJU, B., NELDER, M. P., CRANS, S. C. & GAUGLER, R. 2009. An unusual larval collection and survival of Orthopodomyia signifera in the presence of the predator Toxorhynchites rutilus septentrionalis. *J Am Mosq Control Assoc*, 25**,** 370-3.

FARJANA, T. & TUNO, N. 2013. Multiple Blood Feeding and Host-Seeking Behavior in Aedes aegypti and Aedes albopictus (Diptera: Culicidae). *Journal of Medical Entomology*, 50**,** 838-846.

FISCHER, S., PEREYRA, D. & FERNÁNDEZ, L. 2012. Predation ability and non-consumptive effects of Notonecta sellata (Heteroptera: Notonectidae) on immature stages of Culex pipiens (Diptera: Culicidae). *Journal of Vector Ecology*, 37**,** 245-251.

FONSECA, D. M., KEYGHOBADI, N., MALCOLM, C. A., MEHMET, C., SCHAFFNER, F., MOGI, M., FLEISCHER, R. C. & WILKERSON, R. C. 2004. Emerging vectors in the Culex pipiens complex. *Science*, 303**,** 1535-1538.

FONTANA-BRIA, L., SELFA, J., TUR, C. & FRAGO, E. 2017. Early exposure to predation risk carries over metamorphosis in two distantly related freshwater insects. *Ecological Entomology*, 42**,** 255-262.

FUTAMI, K., SONYE, G., AKWEYWA, P., KANEKO, S. & MINAKAWA, N. 2008. Diving behavior in Anopheles gambiae (Diptera: Culicidae): avoidance of a predacious wolf spider (Araneae: Lycosidae) in relation to life stage and water depth. *J Med Entomol*, 45**,** 1050-6.

GARDNER, A. M., HAMER, G. L., HINES, A. M., NEWMAN, C. M., WALKER, E. D. & RUIZ, M. O. 2012. Weather variability affects abundance of larval Culex (Diptera: Culicidae) in storm water catch basins in suburban Chicago. *Journal of medical entomology*, 49**,** 270-276.

GRILL, C. P. & JULIANO, S. A. 1996. Predicting species interactions based on behaviour: Predation and competition in container-dwelling mosquitoes. *Journal of Animal Ecology*, 65**,** 63-76.

GRISWOLD, M. W. & LOUNIBOS, L. P. 2005. Competitive Outcomes of Aquatic Container Diptera Depend on Predation and Resource Levels. *Annals of the Entomological Society of America*, 98**,** 673-681.

GUNATHILAKA, H. N., UPILIKA, H., UDAYANGA, N. W. B. A. & AMARASINGHE, D. 2019. Effect of Larval Nutritional Regimes on Morphometry and Vectorial Capacity of Aedes aegypti for Dengue Transmission. *BioMed Research International,* 2019**,** 1-11.

HAMER, G. L., ANDERSON, T. K., DONOVAN, D. J., BRAWN, J. D., KREBS, B. L., GARDNER, A. M., RUIZ, M. O., BROWN, W. M., KITRON, U. D., NEWMAN, C. M., GOLDBERG, T. L. & WALKER, E. D. 2014. Dispersal of adult culex mosquitoes in an urban west nile virus hotspot: a mark-capture study incorporating stable isotope enrichment of natural larval habitats. *PLoS neglected tropical diseases,* 8**,** e2768-e2768.

HAMER, G. L., KITRON, U. D., BRAWN, J. D., LOSS, S. R., RUIZ, M. O., GOLDBERG, T. L. & WALKER, E. D. 2008. Culex pipiens (Diptera : Culicidae): A bridge vector of West Nile virus to humans. *Journal of Medical Entomology,* 45**,** 125-128.

HANCOCK, P. A., WIEBE, A., GLEAVE, K. A., BHATT, S., CAMERON, E., TRETT, A., WEETMAN, D., SMITH, D. L., HEMINGWAY, J., COLEMAN, M., GETHING, P. W. & MOYES, C. L. 2018. Associated patterns of insecticide resistance in field populations of malaria vectors across Africa. *Proceedings of the National Academy of Sciences of the United States of America,* 115**,** 5938-5943.

HATALA, A. J., HARRINGTON, L. C. & DEGNER, E. C. 2018. Age and Body Size Influence Sperm Quantity in Male Aedes albopictus (Diptera: Culicidae) Mosquitoes. *Journal of Medical Entomology,* 55**,** 1051-1054.

HAWLEY, W. A. 1985. THE EFFECT OF LARVAL DENSITY ON ADULT LONGEVITY OF A MOSQUITO, AEDES-SIERRENSIS - EPIDEMIOLOGICAL CONSEQUENCES. *Journal of Animal Ecology,* 54**,** 955-964.

HEMINGWAY, J. & RANSON, H. 2000. Insecticide resistance in insect vectors of human disease. *Annual Review of Entomology,* 45**,** 371-391.

HERMANN, S. L. & LANDIS, D. A. 2017. Scaling up our understanding of non-consumptive effects in insect systems. *Current Opinion in Insect Science,* 20**,** 54-60.

HERMANN, S. L. & THALER, J. S. 2014. Prey perception of predation risk: volatile chemical cues mediate non-consumptive effects of a predator on a herbivorous insect. *Oecologia,* 176**,** 669-676.

HIGGINS, J. P. T., THOMAS, J., CHANDLER, J., CUMPSTON, M., LI, T., PAGE, M. J. & WELCH, V. A. 2020. Cochrane Handbook for Systematic Reviews of Interventions. Cochrane.

HIGGINS, J. P. T., THOMPSON, S. G., DEEKS, J. J. & ALTMAN, D. G. 2003. Measuring inconsistency in meta-analyses. *BMJ (Clinical research ed.),* 327**,** 557-560.

HILL, C. A., KAFATOS, F. C., STANSFIELD, S. K. & COLLINS, F. H. 2005. Arthropod-borne diseases: vector control in the genomics era. *Nature Reviews Microbiology,* 3**,** 262-268.

IRWIN, P. & PASKEWITZ, S. 2009. Investigation of fathead minnows (Pimephales promelas) as a biological control agent of Culex mosquitoes under laboratory and field conditions. *J Am Mosq Control Assoc,* 25**,** 301-9.

JANSSENS, L. & STOKS, R. 2012. How does a pesticide pulse increase vulnerability to predation? Combined effects on behavioral antipredator traits and escape swimming. *Aquat Toxicol,* 110-111**,** 91-8.

JENNIONS, M. D. & MOLLER, A. P. 2002. Publication bias in ecology and evolution: an empirical assessment using the 'trim and fill' method. *Biological Reviews,* 77**,** 211-222.

JOHNSON, B. J. & FONSECA, D. M. 2014. The effects of forced-egg retention on the blood-feeding behavior and reproductive potential of Culex pipiens (Diptera: Culicidae). *Journal of Insect Physiology,* 66**,** 53-58.

JOHNSON, B. J. & SUKHDEO, M. V. K. 2013. Drought-Induced Amplification of Local and Regional West Nile Virus Infection Rates in New Jersey. *Journal of Medical Entomology,* 50**,** 195-204.

JULIANO, S. A. 2009. Species Interactions Among Larval Mosquitoes: Context Dependence Across Habitat Gradients. *Annual Review of Entomology,* 54**,** 37-56.

KALIMUTHU, K., PANNEERSELVAM, D. C., CHOU, C., LIN, S.-M., TSENG, L.-C., TSAI, K.-H., MURUGAN, K. & HWANG, J.-S. 2017. Predatory efficiency of the copepod Megacyclops formosanus and toxic effect of the red alga Gracilaria firma-synthesized silver nanoparticles against the dengue vector Aedes aegypti. *Hydrobiologia,* 785.

KALINOSKI, R. M. & DELONG, J. P. 2016. Beyond body mass: how prey traits improve predictions of functional response parameters. *Oecologia,* 180**,** 543-550.

KAY, B. H., NAM, V. S., VAN TIEN, T., YEN, N. T., PHONG, T. V., DIEP, V. T. B., NINH, T. U., BEKTAS, A. & AASKOV, J. G. 2002. Control of Aedes vectors of dengue in three provinces of Vietnam by use of Mesocyclops (Copepoda) and community-based methods validated by entomologic, clinical, and serological surveillance. *American Journal of Tropical Medicine and Hygiene,* 66**,** 40-48.

KERSHENBAUM, A., SPENCER, M., BLAUSTEIN, L. & COHEN, J. E. 2012. Modelling evolutionarily stable strategies in oviposition site selection, with varying risks of predation and intraspecific competition. *Evolutionary Ecology,* 26**,** 955-974.

KLECKNER, C. A., HAWLEY, W. A., BRADSHAW, W. E., HOLZAPFEL, C. M. & FISHER, I. J. 1995. PROTANDRY IN AEDES SIERRENSIS - THE SIGNIFICANCE OF TEMPORAL VARIATION IN FEMALE FECUNDITY. *Ecology,* 76**,** 1242-1250.

KNIGHT, T. M., CHASE, J. M., GOSS, C. W. & KNIGHT, J. J. 2004. Effects of interspecific competition, predation, and their interaction on survival and development time of immature Anopheles quadrimaculatus. *J Vector Ecol,* 29**,** 277-84.

KRAMER, L. D., STYER, L. M. & EBEL, G. D. 2008. A global perspective on the epidemiology of West Nile virus. *Annual Review of Entomology,* 53**,** 61-81.

KRAUS, J. M. & VONESH, J. R. 2010. Feedbacks between community assembly and habitat selection shape variation in local colonization. *Journal of Animal Ecology,* 79**,** 795-802.

KROL, L., GORSICH, E. E., HUNTING, E. R., GOVENDER, D., VAN BODEGOM, P. M. & SCHRAMA, M. 2019. Eutrophication governs predator-prey interactions and temperature effects in Aedes aegypti populations. *Parasites & Vectors,* 12.

KUMAR, R. & HWANG, J. S. 2006. Larvicidal efficiency of aquatic predators: A perspective for mosquito biocontrol. *Zoological Studies,* 45**,** 447-466.

KUMAR, R., MUHID, P., DAHMS, H. U., TSENG, L. C. & HWANG, J. S. 2008. Potential of three aquatic predators to control mosquitoes in the presence of alternative prey: a comparative experimental assessment. *Marine and Freshwater Research,* 59**,** 817-835.

KWEKA, E. J., ZHOU, G. F., GILBREATH, T. M., AFRANE, Y., NYINDO, M., GITHEKO, A. K. & YAN, G. Y. 2011. Predation efficiency of Anopheles gambiae larvae by aquatic predators in western Kenya highlands. *Parasites & Vectors,* 4.

LAJEUNESSE, M. J. 2016. Facilitating systematic reviews, data extraction and meta-analysis with the metagear package for r. *Methods in Ecology and Evolution,* 7**,** 323-330.

LEISNHAM, P. T., SALA, L. M. & JULIANO, S. A. 2008. Geographic variation in adult survival and reproductive tactics of the mosquito Aedes albopictus. *Journal of Medical Entomology,* 45**,** 210-221.

LIMA, S. & DILL, L. 1990. Behavioral Decisions Made under the Risk of Predation: A Review and Prospectus. *Canadian Journal of Zoology-revue Canadienne De Zoologie - CAN J ZOOL,* 68**,** 619-640.

LIMA, S. L. 1998. Nonlethal Effects in the Ecology of Predator-Prey Interactions: What are the ecological effects of anti-predator decision-making? *BioScience,* 48**,** 25-34.

LIU, N. N. 2015. Insecticide Resistance in Mosquitoes: Impact, Mechanisms, and Research Directions. *In:* BERENBAUM, M. R. (ed.) *Annual Review of Entomology, Vol 60.*

LÜHKEN, R., STEINKE, S., LEGGEWIE, M., TANNICH, E., KRÜGER, A., BECKER, S. & KIEL, E. 2015. Physico-Chemical Characteristics of Culex pipiens sensu lato and Culex torrentium (Diptera: Culicidae) Breeding Sites in Germany. *Journal of Medical Entomology,* 52**,** 932-936.

LYIMO, E. O. & TAKKEN, W. 1993. EFFECTS OF ADULT BODY-SIZE ON FECUNDITY AND THE PRE-GRAVID RATE OF ANOPHELES-GAMBIAE FEMALES IN TANZANIA. *Medical and Veterinary Entomology,* 7**,** 328-332.

MARCANTONIO, M., RIZZOLI, A., METZ, M., ROSA, R., MARINI, G., CHADWICK, E. & NETELER, M. 2015. Identifying the Environmental Conditions Favouring West Nile Virus Outbreaks in Europe. *Plos One,* 10.

MARTEN, G. G. 1990. Elimination of Aedes-Albopictus from Tire Piles by Introducing Macrocyclops-Albidus (Copepoda, Cyclopidae). *Journal of the American Mosquito Control Association,* 6**,** 689-693.

MARTEN, G. G., CHE, W. Y. & BORDES, E. S. 1993. Compatibility of Cyclopoid Copepods with Mosquito Insecticides. *Journal of the American Mosquito Control Association,* 9**,** 150-154.

MARTEN, G. G., NGUYEN, M., MASON, B. J. & NGO, G. 2000a. Natural control of Culex quinquefasciatus larvae in residential ditches by the copepod Macrocyclops albidus. *Journal of Vector Ecology,* 25**,** 7-15.

MARTEN, G. G., NGUYEN, M. & NGO, G. 2000b. Copepod predation on Anopheles quadrimaculatus larvae in rice fields. *Journal of Vector Ecology,* 25**,** 1-6.

MARTEN, G. G. & REID, J. W. 2007. Cyclopoid copepods. *Journal of the American Mosquito Control Association,* 23**,** 65-92.

MCCAULEY, S. J., ROWE, L. & FORTIN, M. J. 2011. The deadly effects of "nonlethal" predators. *Ecology,* 92**,** 2043-8.

MERCER, D. R., WETTACH, G. R. & SMITH, J. L. 2005. Effects of larval density and predation by Toxorhynchites amboinensis on Aedes polynesiensis (Diptera : culicidae) developing in coconuts. *Journal of the American Mosquito Control Association,* 21**,** 425-431.

MICIELI, M. V., MARTI, G. & GARCÍA, J. J. 2002. Laboratory evaluation of Mesocyclops annulatus (Wierzejski, 1892) (Copepoda: Cyclopidea) as a predator of container-breeding mosquitoes in Argentina. *Mem Inst Oswaldo Cruz,* 97**,** 835-8.

MINAKAWA, N., FUTAMI, K., SONYE, G., AKWEYWA, P. & KANEKO, S. 2007. Predatory capacity of a shorefly, Ochthera chalybescens, on malaria vectors. *Malaria Journal,* 6**,** 104.

MITTELBACH, G. G. 1981. FORAGING EFFICIENCY AND BODY SIZE - A STUDY OF OPTIMAL DIET AND HABITAT USE BY BLUEGILLS. *Ecology,* 62**,** 1370-1386.

MOHER, D., LIBERATI, A., TETZLAFF, J. & ALTMAN, D. G. 2009. Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *BMJ,* 339**,** b2535.

MOORE, S. M., BORER, E. T. & HOSSEINI, P. R. 2010. Predators indirectly control vector-borne disease: linking predator-prey and host-pathogen models. *J R Soc Interface,* 7**,** 161-76.

NANNINI, M. A. & JULIANO, S. A. 1998. Effects of the Facultative Predator Anopheles barberi on Population Performance of its Prey Aedes triseriatus (Diptera Culicidae). *Annals of the Entomological Society of America,* 91**,** 33-42.

NELMS, B. M., FECHTER-LEGGETT, E., CARROLL, B. D., MACEDO, P., KLUH, S. & REISEN, W. K. 2013. Experimental and natural vertical transmission of West Nile virus by California Culex (Diptera: Culicidae) mosquitoes. *J Med Entomol,* 50**,** 371-8.

NELSON, E. H., MATTHEWS, C. E. & ROSENHEIM, J. A. 2004. PREDATORS REDUCE PREY POPULATION GROWTH BY INDUCING CHANGES IN PREY BEHAVIOR. *Ecology,* 85**,** 1853-1858.

NIKOOKAR, S. H., FAZELI-DINAN, M., AZARI-HAMIDIAN, S., MOUSAVINASAB, S. N., ARABI, M., ZIAPOUR, S. P., SHOJAEE, J. & ENAYATI, A. 2017. Species composition and abundance of mosquito larvae in relation with their habitat characteristics in Mazandaran Province, northern Iran. *Bulletin of Entomological Research,* 107**,** 598-610.

O'MEARA, G. F. 1979. Variable expressions of autogeny in three mosquito species. *International Journal of Invertebrate Reproduction,* 1**,** 253-261.

OHBA, S.-Y., OHTSUKA, M., SUNAHARA, T., SONODA, Y., KAWASHIMA, E. & TAKAGI, M. 2012. Differential responses to predator cues between two mosquito species breeding in different habitats. *Ecological Entomology,* 37**,** 410-418.

OLIVER, J. & HOWARD, J. J. 2011. Fecundity of Wild-Caught Gravid Culiseta morsitans (Diptera: Culicidae). *Journal of Medical Entomology,* 48**,** 196-201.

OP DE BEECK, L., JANSSENS, L. & STOKS, R. 2016. Synthetic predator cues impair immune function and make the biological pesticide Bti more lethal for vector mosquitoes. *Ecological Applications,* 26**,** 355-366.

ORR, B. K. & RESH, V. H. 1989. Experimental test of the influence of aquatic macrophyte cover on the survival of Anopheles larvae. *J Am Mosq Control Assoc,* 5**,** 579-85.

OWER, G. D. & JULIANO, S. A. 2019. The demographic and life-history costs of fear: Trait-mediated effects of threat of predation on Aedes triseriatus. *Ecology and Evolution,* 9**,** 3794-3806.

PAULL, S. H., HORTON, D. E., ASHFAQ, M., RASTOGI, D., KRAMER, L. D., DIFFENBAUGH, N. S. & KILPATRICK, A. M. 2017. Drought and immunity determine the intensity of West Nile virus epidemics and climate change impacts. *Proceedings of the Royal Society B-Biological Sciences,* 284.

PEACOR, S. D. & WERNER, E. E. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. *Proceedings of the National Academy of Sciences,* 98**,** 3904.

PETERS, R. H. 1983. Ingestion. *In:* BECK, E., BIRKS, H. J. B. & CONNOR, E. F. (eds.) *The ecological implications of body size.* Cambridge: Cambridge University Press.

PINTAR, M. R., BOHENEK, J. R., EVELAND, L. L. & RESETARITS, W. J. 2018. Colonization across gradients of risk and reward: Nutrients and predators generate species-specific responses among aquatic insects. *Functional Ecology,* 32**,** 1589-1598.

PONLAWAT, A. & HARRINGTON, L. C. 2007. Age and body size influence male sperm capacity of the dengue vector Aedes aegypti (Diptera : Culicidae). *Journal of Medical Entomology,* 44**,** 422-426.

PREISSER, E. L., BOLNICK, D. I. & BENARD, M. F. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology,* 86**,** 501-509.

PYKE, G. H. 2008. Plague Minnow or Mosquito Fish? A Review of the Biology and Impacts of Introduced Gambusia Species. *Annual Review of Ecology Evolution and Systematics,* 39**,** 171-191.

R CORE TEAM 2020. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

RAJENDRAN, R. & PRASAD, R. S. 1994. A laboratory study on the life cycle and feeding behaviour of Arrenurus madaraszi (Acari: Arrenuridae) parasitizing Anopheles mosquitoes. *Ann Trop Med Parasitol,* 88**,** 169-74.

REINER, R. C., JR., PERKINS, T. A., BARKER, C. M., NIU, T., CHAVES, L. F., ELLIS, A. M., GEORGE, D. B., LE MENACH, A., PULLIAM, J. R., BISANZIO, D., BUCKEE, C., CHIYAKA, C., CUMMINGS, D. A., GARCIA, A. J., GATTON, M. L., GETHING, P. W., HARTLEY, D. M., JOHNSTON, G., KLEIN, E. Y., MICHAEL, E., LINDSAY, S. W., LLOYD, A. L., PIGOTT, D. M., REISEN, W. K., RUKTANONCHAI, N., SINGH, B. K., TATEM, A. J., KITRON, U., HAY, S. I., SCOTT, T. W. & SMITH, D. L. 2013. A systematic review of mathematical models of mosquito-borne pathogen transmission: 1970-2010. *J R Soc Interface,* 10**,** 20120921.

REISEN, W. K., MILBY, M. M. & BOCK, M. E. 1984. THE EFFECTS OF IMMATURE STRESS ON SELECTED EVENTS IN THE LIFE-HISTORY OF CULEX-TARSALIS. *Mosquito News,* 44**,** 385-395.

REISKIND, M. H. & LOUNIBOS, L. P. 2009. Effects of intraspecific larval competition on adult longevity in the mosquitoes Aedes aegypti and Aedes albopictus. *Medical and Veterinary Entomology,* 23**,** 62-68.

ROBERTS, D. 2012. Responses of three species of mosquito larvae to the presence of predatory dragonfly and damselfly larvae. *Entomologia Experimentalis Et Applicata,* 145**,** 23-29.

ROBERTS, D. 2018. Predator feeding vibrations encourage mosquito larvae to shorten their development and so become smaller adults: Predator feeding vibrations. *Ecological Entomology*.

ROEHR, B. 2012. US hit by massive West Nile virus outbreak centred around Texas. *British Medical Journal,* 345.

ROHATGI, A. 2020. *WebPlotDigitizer* [Online]. Available: https://automeris.io/WebPlotDigitizer [Accessed 07/14/2020].

ROSEN, L. 1988. Further observations on the mechanism of vertical transmission of flaviviruses by Aedes mosquitoes. *Am J Trop Med Hyg,* 39**,** 123-6.

ROUX, O., DIABATE, A. & SIMARD, F. 2014. Divergence in threat sensitivity among aquatic larvae of cryptic mosquito species. *Journal of Animal Ecology,* 83**,** 702-711.

ROUX, O., VANTAUX, A., ROCHE, B., YAMEOGO, K. B., DABIRE, K. R., DIABATE, A., SIMARD, F. & LEFEVRE, T. 2015. Evidence for carry-over effects of predator exposure on pathogen transmission potential. *Proceedings of the Royal Society B-Biological Sciences,* 282**,** 20152430.

RUBBO, M. J., LANTERMAN, J. L., FALCO, R. C. & DANIELS, T. J. 2011. The Influence of Amphibians on Mosquitoes in Seasonal Pools: Can Wetlands Protection Help to Minimize Disease Risk? *Wetlands,* 31**,** 799-804.

RUSSELL, B. M., MUIR, L. E., WEINSTEIN, P. & KAY, B. H. 1996. Surveillance of the mosquito Aedes aegypti and its biocontrol with the copepod Mesocyclops aspericornis in Australian wells and gold mines. *Medical and Veterinary Entomology,* 10**,** 155-160.

SCHRAMA, M., GORSICH, E. E., HUNTING, E., BARMENTLO, S. H., BEECHLER, B. & VAN BODEGOM, P. M. 2018. Eutrophication and predator presence overrule the effects of temperature on mosquito survival and development. *PLoS Neglected Tropical Diseases,* 3.

SEALE, A. 1917. The Mosquito Fish, *Gambusia affinis* (Baird and Girard), in the Philippine Islands. *Philippine Journal of Science,* 12**,** 177-187.

SHAMAN, J., DAY, J. F. & STIEGLITZ, M. 2005. Drought-induced amplification and epidemic transmission of West Nile Virus in southern Florida. *Journal of Medical Entomology,* 42**,** 134-141.

SHI, L. Y. & LIN, L. F. 2019. The trim-and-fill method for publication bias: practical guidelines and recommendations based on a large database of meta-analyses. *Medicine,* 98.

SIH, A. 1986. ANTIPREDATOR RESPONSES AND THE PERCEPTION OF DANGER BY MOSQUITO LARVAE. *Ecology,* 67**,** 434-441.

SILBERBUSH, A., ABRAMSKY, Z. & TSURIM, I. 2015. Effects of fish cues on mosquito larvae development. *Acta Tropica,* 150**,** 196-199.

SILBERBUSH, A. & BLAUSTEIN, L. 2008. Oviposition habitat selection by a mosquito in response to a predator: are predator-released kairomones air-borne cues? *J Vector Ecol,* 33**,** 208-11.

SILBERBUSH, A. & BLAUSTEIN, L. 2011. Mosquito females quantify risk of predation to their progeny when selecting an oviposition site. *Functional Ecology,* 25**,** 1091-1095.

SOGHIGIAN, J., VALSDOTTIR, L. R. & LIVDAHL, T. P. 2017. A parasite's modification of host behavior reduces predation on its host. *Ecology and Evolution,* 7**,** 1453-1461.

SOUMARE, M. K. F. & CILEK, J. E. 2011. The Effectiveness of Mesocyclops Longisetus (Copepoda) for the Control of Container-Inhabiting Mosquitoes in Residential Environments. *Journal of the American Mosquito Control Association,* 27**,** 376-383.

SPENCER, M., BLAUSTEIN, L. & COHEN, J. E. 2002. OVIPOSITION HABITAT SELECTION BY MOSQUITOES (CULISETA LONGIAREOLATA) AND CONSEQUENCES FOR POPULATION SIZE. *Ecology,* 83**,** 669-679.

STAATS, E. G., AGOSTA, S. J. & VONESH, J. R. 2016. Predator diversity reduces habitat colonization by mosquitoes and midges. *Biology Letters,* 12**,** 20160580.

STAV, G., BLAUSTEIN, L. & MARGALIT, Y. 2005. INDIVIDUAL AND INTERACTIVE EFFECTS OF A PREDATOR AND CONTROPHIC SPECIES ON MOSQUITO POPULATIONS. *Ecological Applications,* 15**,** 587-598.

STERNE, J. A. C. & EGGER, M. 2001. Funnel plots for detecting bias in meta-analysis: Guidelines on choice of axis. *Journal of Clinical Epidemiology,* 54**,** 1046-1055.

STYER, L. M., MEOLA, M. A. & KRAMER, L. D. 2007. West Nile virus infection decreases fecundity of Culex tarsalis females. *Journal of Medical Entomology,* 44**,** 1074-1085.

SU, T. & MULLA, M. S. 1997. Physiological aspects of autogeny in Culex tarsalis (Diptera: Culicidae): influences of sugar-feeding, mating, body weight, and wing length. *J Vector Ecol,* 22**,** 115-21.

SUBRAMANIAM, J., MURUGAN, K., PANNEERSELVAM, C., KOVENDAN, K., MADHIYAZHAGAN, P., KUMAR, P. M., DINESH, D., CHANDRAMOHAN, B., SURESH, U., NICOLETTI, M., HIGUCHI, A., HWANG, J. S., KUMAR, S., ALARFAJ, A. A., MUNUSAMY, M. A., MESSING, R. H. & BENELLI, G. 2015.

Eco-friendly control of malaria and arbovirus vectors using the mosquitofish Gambusia affinis and ultra-low dosages of Mimusops elengi-synthesized silver nanoparticles: towards an integrative approach? *Environ Sci Pollut Res Int,* 22**,** 20067-83.

SULESCO, T. M., TODERAS, L. G., USPENSKAIA, I. G. & TODERAS, I. K. 2015. Larval Habitats Diversity and Distribution of the Mosquito (Diptera: Culicidae) Species in the Republic of Moldova. *Journal of Medical Entomology,* 52**,** 1299-1308.

THAPA, R., MIRSKY, S. B. & TULLY, K. L. 2018. Cover Crops Reduce Nitrate Leaching in Agroecosystems: A Global Meta-Analysis. *Journal of Environmental Quality,* 47**,** 1400-1411.

TIETZE, N. S., HESTER, P. G., SHAFFER, K. R., PRESCOTT, S. J. & SCHREIBER, E. T. 1994. INTEGRATED MANAGEMENT OF WASTE TIRE MOSQUITOS UTILIZING MESOCYCLOPS-LONGISETUS (COPEPODA, CYCLOPIDAE), BACILLUS-THURINGIENSIS VAR ISRAELENSIS, BACILLUS-SPHAERICUS, AND METHOPRENE. *Journal of the American Mosquito Control Association,* 10**,** 363-373.

TIETZE, N. S. & MULLA, M. S. 1990. Influence of tadpole shrimp, Triops longicaudatus (Notostraca:Triopsidae), stocking rate on Culex tarsalis development in experimental field microcosms. *J Am Mosq Control Assoc,* 6**,** 265-9.

TOWNROE, S. & CALLAGHAN, A. 2014. British Container Breeding Mosquitoes: The Impact of Urbanisation and Climate Change on Community Composition and Phenology. *PLOS ONE,* 9**,** e95325.

TSENG, M. 2007. Ascogregarine parasites as possible biocontrol agents of mosquitoes. *Journal of the American Mosquito Control Association,* 23**,** 30-4.

TSUNODA, T., FUKUCHI, A., NANBARA, S. & TAKAGI, M. 2010. Effect of body size and sugar meals on oviposition of the yellow fever mosquito, Aedes aegypti (Diptera: Culicidae). *J Vector Ecol,* 35**,** 56-60.

UITERWAAL, S. F. & DELONG, J. P. 2020. Functional responses are maximized at intermediate temperatures. *Ecology*.

VAN UITREGT, V. O., HURST, T. P. & WILSON, R. S. 2012. Reduced size and starvation resistance in adult mosquitoes, Aedes notoscriptus, exposed to predation cues as larvae. *Journal of Animal Ecology,* 81**,** 108-115.

VAN UITREGT, V. O., HURST, T. P. & WILSON, R. S. 2013. Greater costs of inducible behavioural defences at cooler temperatures in larvae of the mosquito, Aedes notoscriptus. *Evolutionary Ecology,* 27**,** 13-26.

VERNA, T. N. 2015. Species Composition and Seasonal Distribution of Mosquito Larvae (Diptera: Culicidae) in Southern New Jersey, Burlington County. *Journal of Medical Entomology,* 52**,** 1165-1169.

VERONESI, R., CARRIERI, M., MACCAGNANI, B., MAINI, S. & BELLINI, R. 2015. Macrocyclops Albidus (Copepoda: Cyclopidae) for the Biocontrol of Aedes Albopictus and Culex Pipiens in Italy. *Journal of the American Mosquito Control Association,* 31**,** 32-43.

VIECHTBAUER, W. 2010. Conducting Meta-Analyses in R with the metafor Package. *Journal of Statistical Software,* 36**,** 1-48.

VINCZE, E., SERESS, G., LAGISZ, M., DINGEMANSE, N. & SPRAU, P. 2017. Does Urbanization Affect Predation of Bird Nests? A Meta-Analysis. *Frontiers in Ecology and Evolution,* 5.

VINOGRADOVA, E. B. 2000. *Culex pipiens pipiens mosquitoes: taxonomy, distribution, ecology, physiology, genetics, applied importance and control,* Sofia, Bulgaria, Pensoft.

VONESH, J. R. & BLAUSTEIN, L. 2010. PREDATOR-INDUCED SHIFTS IN MOSQUITO OVIPOSITION SITE SELECTION: A META-ANALYSIS and IMPLICATIONS FOR VECTOR CONTROL. *Israel Journal of Ecology & Evolution,* 56**,** 263-279.

WALLACE, J. R. & MERRITT, R. W. 1999. Influence of microclimate, food, and predation on Anopheles quadrimaculatus (Diptera : Culicidae) growth and development rates, survivorship, and adult size in a Michigan pond. *Environmental Entomology,* 28**,** 233-239.

WEAVER, S. C. & REISEN, W. K. 2010. Present and future arboviral threats. *Antiviral Research,* 85**,** 328-345.

WORLD HEALTH ORGANIZATION (WHO). 2020. *Vector-borne diseases* [Online]. Available: https://www.who.int/news-room/fact-sheets/detail/vector-borne-diseases [Accessed 02/07/2021].

XUE, R. D., BARNARD, D. R. & MULLER, G. C. 2010. Effects of Body Size and Nutritional Regimen on Survival in Adult Aedes albopictus (Diptera: Culicidae). *Journal of Medical Entomology,* 47**,** 778-782.

YANOVIAK, S. P. 1999. Effects of Mecistogaster spp. (Odonata: Pseudostigmatidae) and Culex mollis (Diptera: Culicidae) on Litter Decomposition in Neotropical Treehole Microcosms. *The Florida Entomologist,* 82**,** 462-468.

ZUHARAH, W. F., FADZLY, N. & LESTER, P. J. 2013. Lethal and sublethal impacts of predaceous backswimmer Anisops wakefieldi (Hemiptera: Notonectidae) on the life-history traits of the New Zealand mosquito Culex pervigilans (Diptera: Culicidae). *J Med Entomol,* 50**,** 1014-24.

ZUHARAH, W. F. & LESTER, P. J. 2010. The influence of aquatic predators on mosquito abundance in animal drinking troughs in New Zealand. *Journal of Vector Ecology,* 35**,** 347-353.