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>
<thead>
<tr>
<th>Variable Description</th>
<th>Publication data:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Title</td>
<td>Full study title</td>
</tr>
<tr>
<td>Journal</td>
<td>Name of journal that published the study</td>
</tr>
<tr>
<td>Year</td>
<td>Year of publication</td>
</tr>
<tr>
<td>Study environment</td>
<td>Environment where the experiment took place: lab or semi-field</td>
</tr>
</tbody>
</table>

| 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 (1\(^{st}\) and 2\(^{nd}\) instars), late (3\(^{rd}\) and 4\(^{th}\) 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 replicate-
specific 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 $\tau^2$, 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 \( \tau^2 \), 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).

<table>
<thead>
<tr>
<th>Moderator(s)</th>
<th>Test of Moderators (degrees of freedom, p-value)</th>
<th>AICc</th>
<th>ΔAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>predator family x vector genus</td>
<td>28, &lt;0.0001</td>
<td>500.5</td>
<td>0</td>
</tr>
<tr>
<td>predator family</td>
<td>19, &lt;0.0001</td>
<td>507.0</td>
<td>6.5</td>
</tr>
<tr>
<td>predator family + vector genus</td>
<td>23, &lt;0.0001</td>
<td>508.1</td>
<td>7.6</td>
</tr>
<tr>
<td>vector genus</td>
<td>5, &lt;0.0001</td>
<td>573.0</td>
<td>72.5</td>
</tr>
<tr>
<td>none</td>
<td>----</td>
<td>576.5</td>
<td>76.0</td>
</tr>
</tbody>
</table>
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).

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

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).

<table>
<thead>
<tr>
<th>Moderator(s)</th>
<th>Test of Moderators (degrees of freedom, p-value)</th>
<th>AICc</th>
<th>ΔAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>vector genus</td>
<td>3, 0.0149</td>
<td>122.1</td>
<td>0</td>
</tr>
<tr>
<td>none</td>
<td>----</td>
<td>125.2</td>
<td>3.1</td>
</tr>
<tr>
<td>predator family</td>
<td>12, 0.8855</td>
<td>167.9</td>
<td>45.8</td>
</tr>
</tbody>
</table>

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

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<th>Behavior</th>
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References


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.


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

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.

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

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.

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.

(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

ORR, B. K. & RESH, V. H. 1989. Experimental test of the influence of aquatic macrophyte

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.

to the net effects of a predator. Proceedings of the National Academy of Sciences, 98,
3904.

The ecological implications of body size. Cambridge: Cambridge University Press.

Colonization across gradients of risk and reward: Nutrients and predators generate


