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Evaluating the Effects of Temperature and Precipitation on the Abundances of Disease Vectors

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Declaration

I declare that this dissertation is my own work. The data utilised in this project originates from the VecDyn database, collated by the Vectorbite Research Collaboration Network. I was responsible for data cleaning, obtaining climate data and analysis as described.

Word count: 5445

Abstract

Vector-borne diseases pose a severe threat to public health, with mosquito-borne diseases being a significant contributor to the global burden of infectious disease. Mosquitoes are heavily reliant on environmental conditions. Understanding the relationships between meteorological variables and mosquito abundance is important in developing effective early warning indicators of disease transmission. The temporal scale used to explore these relationships can have profound implications on the signatures observed. This study aimed to evaluate the influence of meteorological variables on the abundance of adult mosquitoes at different temporal aggregating scales. Utilising a newly built global database, I employ Generalised Linear Models and Akaike Information Criterion model selection to determine the relative importance of temperature and precipitation across three medically important mosquito genera. In addition, I estimate the thermal optima of abundance at different temporal aggregating scales to determine whether they match estimations of the thermal optima of disease R_0. My results indicate that temperature has a higher relative importance in describing mosquito abundance at lower temporal scales. The importance of precipitation, however, is captured at higher temporal scales. I attribute this to the stage at which meteorological variables will have the greatest impact on the mosquito life cycle. Precipitation principally has effects on early life stages, and therefore requires higher temporal scales for effects to be captured. Temperature, meanwhile, affects all stages of the mosquito life cycle, so is consistently reflected in abundance. I also find that the thermal optima between *Aedes* abundance and the R_0 of diseases they transmit are not significantly different, which reinforces that abundance is a key driver of R_0 predictions. This study highlights the need for associations between environmental variables and mosquitoes to be explored at lower temporal scales, and the importance of using temporal lags in environmental variables when modelling the abundance of mosquito disease vectors. Further, these results suggest that the similarity between the thermal optima of disease transmission and abundance could be utilised in assessing transmission risk in naive environments.

Keywords

Climate change; Long-term Data; Disease Transmission; Mosquito Abundance; Temperature; Precipitation; Statistical Models

1   Introduction

Vector-borne diseases constitute almost 17% of the global burden of infectious diseases, posing a severe threat to public health (World Health Organization, 2014). Of all vector-borne diseases, mosquito-borne diseases are of major importance, with one third of the worlds population directly affected (World Health Organization, 2014). Mosquitoes from the genera *Anopheles*, *Aedes* and *Culex* are of significant medical importance, transmitting notable human pathogens including malaria, dengue and multiple encephalitis viruses respectively. An estimated 3.4 billion people are at risk of contracting malaria globally (World Health Organization, 2018), and 4 billion people are believed to be at risk of dengue infection (Brady *et al.*, 2012). Given the large scale global infection rates of mosquito-borne disease and the limited efficacy of current medical practices, vector surveillance is essential in disease management (Khormi & Kumar, 2014).

Global climate change presents a significant challenge to mosquito-borne disease management (Githeko *et al.*, 2000). Changes in worldwide temperature (Hoegh-Guldberg *et al.*, 2018) and precipitation patterns (Meehl *et al.*, 2007; Collins *et al.*, 2013) will undoubtedly affect ecological systems, including mosquito-borne diseases, immensely. Mosquitoes have complex life cycles with an ontogenetic niche shift between aquatic larval and terrestrial adult life stages (Chaves *et al.*, 2012). Hence, their development and survival is heavily mediated by environmental conditions at all stages. Uncertainty surrounding climate projections and mosquito responses to meteorological variables remains problematic in predicting the global transmission risk of mosquito-borne diseases.

Changing environmental conditions can result in the expansion of mosquito geographic ranges, as previously unfavourable environments become more suitable (Jung *et al.*, 2016). Disease emergence and re-emergence is greatly facilitated by alterations in vector range, as pathogens can be transmitted to a naive environment lacking the systems to cope with outbreaks (Khormi & Kumar, 2014). Recent predictions have suggested that mosquitoes could expand their range extensively in the next century, allowing mosquito-borne diseases to spread into new regions (Jansen & Beebe, 2010; Kamal *et al.*, 2018). Understanding the environmental relationships of disease vectors is essential to accurately forecast potential range shifts in mosquito-borne diseases.

In addition, disease transmission rates are directly related to the abundance of vectors. Vector density is considered proportional to the rate of pathogen transmission between infected and susceptible hosts (Gage *et al.*, 2008). Similarly, abundance is a key determinant of the basic reproductive rate of disease (R_0), a commonly used disease transmission metric (Mordecai *et al.*, 2013). As mosquitoes are heavily reliant upon the environment, their population dynamics can be shaped by meteorological variables such as temperature and precipitation. Accordingly, surveillance is critical in early warning systems of mosquito-borne disease outbreaks.

As ectotherms, mosquitoes are unable to physiologically control their internal temperature. Therefore, they are dependent upon external heat sources at all life stages for survival and development (Githeko
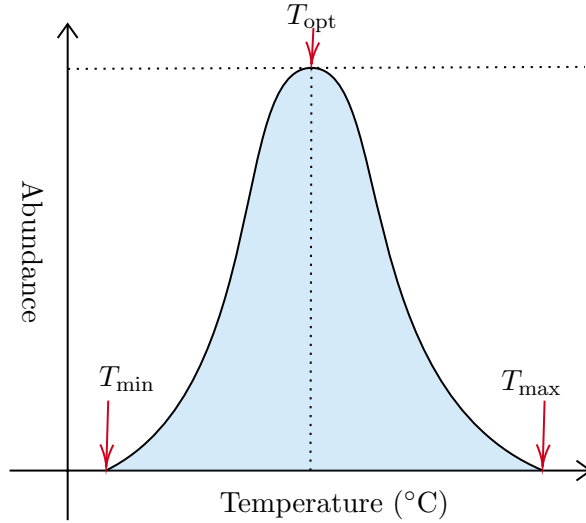
Figure 1: Depiction of a unimodal thermal performance curve for the abundance of mosquitoes. Abundance increases with temperature from a minimum temperature ($T_{\min}$), to a thermal optimum (T_{opt}). Thereafter, trait performance declines as temperature increases until a maximum temperature ($T_{\max}$) is reached. Abundance is zero below $T_{\min}$ and above $T_{\max}$. Actual curves are likely to deviate from this, for example with a left or right skew. Precipitation is expected to alter the height of the curve but not the shape. The unimodal curve is, however, an accurate reflection of the properties the Metabolic Theory of Ecology predicts.

et al., 2000), and are extremely sensitive to variations in ambient temperature (Dell *et al.*, 2011; Beck-Johnson *et al.*, 2013; Mordecai *et al.*, 2019). Existence of a relationship with temperature is well established, with mosquito developmental rate considered a function of temperature (Chaves *et al.*, 2012). Aquatic immature stages are sensitive to water temperature which can slow or accelerate their development (Githeko *et al.*, 2000). Likewise, at warmer temperatures female mosquitoes feed more frequently, thus facilitating transmission potential of diseases (Mirski *et al.*, 2012).

A possible explanation comes from the Metabolic Theory of Ecology, which links the metabolic rate of an organism to its body mass and temperature, connecting the complex patterns observed in biological systems to basic principles within chemistry, physics and biology (Brown *et al.*, 2004; Savage *et al.*, 2004). Ectotherm trait performance can usually be defined by a unimodal curve (Figure 1), peaking at an intermediate temperature (T_{opt}) and declining to zero at higher and lower threshold temperatures (Dell *et al.*, 2011). Although the relationships between temperature and trait performances follow similar patterns, the thermal optima of traits can be markedly different as a result of acclimitisation and adaptation (Beck-Johnson *et al.*, 2013). The thermal optima of vector abundance, therefore, can shift as underlying traits acclimitise. This could have profound implications on a disease's transmission potential. Projected increase in global temperatures and the utility of studying thermal optima in modelling disease transmission has resulted in T_{opt} of vector traits becoming of substantial interest in mosquito-borne disease research (Mordecai *et al.*, 2019).

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The effect of precipitation on mosquito abundance is, by contrast, less clear. Water sources are utilised as sites for the development of aquatic larval life stages, and are required as a site for oviposition (Koenraadt & Harrington, 2008). Many mosquito species have been shown to utilise human-made artificial containers for oviposition (Miyagi *et al.*, 1992; Koenraadt & Harrington, 2008). Rainfall can increase the number of breeding sites through temporary pool formation in these containers, whilst also supplementing existing water bodies. These temporary pools can be enriched in microbial communities, which have been postulated to produce metabolites that attract more gravid female mosquitoes (Bentley & Day, 1989; Ponnusamy *et al.*, 2008) and also support larval development (Travanty *et al.*, 2019). On the contrary, there is evidence that rainfall flushes breeding sites, reducing the larval population and the bacterial concentration larvae predate upon (Koenraadt & Harrington, 2008). Seidahmed & Eltahir (2016) have hypothesised that flushing-drying events caused by monsoon rainfalls results in reduced outdoor breeding in *Aedes aegypti*. Seeking clarity on the associations between precipitation and mosquito abundance is of the utmost importance in consideration of a predicted increase in the incidence of extreme events such as drought and flooding (Hoegh-Guldberg *et al.*, 2018).

A substantial number of studies have predicted disease transmission risk, however, comparatively few studies have investigated the influence of meteorological variables on mosquito abundance directly (Galardo *et al.*, 2009; Chen *et al.*, 2010; Mordecai *et al.*, 2017; Dawson *et al.*, 2019). There have been conflicting reports on the relative importance of temperature and precipitation on the abundances of mosquitoes (DeGaetano, 2005; Wang *et al.*, 2011; Poh *et al.*, 2019). Current studies have formulated complex models, primarily focusing on narrow spatial ranges and a limited range of species, thus lacking the power to offer the generalisations required for early warning systems in naive regions (Chaves *et al.*, 2012). In the light of global climate change, development of early warning systems of vector-borne disease is vital.

Furthermore, as the mosquito life cycle is composed of several developmental processes it is imperative that we consider delayed effects of meteorological variables. With respect to abundance, current statistical models have focused on monthly lags in time (DeGaetano, 2005; Galardo *et al.*, 2009; Jian *et al.*, 2016; Li *et al.*, 2019). Mosquito development occurs at finer temporal resolutions, therefore monthly scales will not capture key interactions. Identification of patterns at a higher resolution is fundamental to effective early warning system development.

In this study, I aim to answer the following questions:

1. What is the relative importance of temperature and precipitation for predicting mosquito abundances at different temporal aggregations?

2. Which temporal lags in temperature and precipitation are the best predictors of mosquito abundance?

3. Does T_{opt} of abundance differ between mosquito genera, or from the T_{opt} of R_0 for diseases they spread?

Here, to answer these questions, I utilise a newly built global database of vector abundances and statis-

tical models to elucidate the interaction between mosquito abundance and the environmental variables temperature and precipitation. I utilise model selection methods to determine whether temporal lags of meteorological variables are effective predictors of mosquito abundance, thus accounting for development of pre-adult life stages in predictions of adult emergence.

2 Methods

2.1 Mosquito Abundance Data

I obtained 5,173,511 million mosquito trap count data points from the VecDyn global database (Vector-Byte RCN, 2019), composed of 95 species from 3 genera (*Aedes*, *Anopheles* and *Culex*), in 16 locations of North America and Africa (Figure S1). This database has been built from independent sources including mosquito surveillance programs and published studies. These independent sources operate in vastly different ways, utilising different combinations of trap types and protocols. Trap types are known to have different efficacies, and new trap types are regularly under development (DiMenna *et al.*, 2006; Farajollahi *et al.*, 2009; Karki *et al.*, 2016). To control for any trap variability, I only used datasets from sources that employed one trap type. Following this, I had 2,969,756 mosquito trap counts from 6 sampling methods. The total number of species reduced to 66 from the 3 genera, but the number of locations was unchanged. Available data spanned from the year 1998 to 2018. The New Jersey Trap accounted for the vast majority of data points ($\sim$80%), followed by CDC light traps ($\sim$17.5%). The remaining trap types were variants of light traps, baited light traps, live specimen catches and gravid traps, and constituted less than 2.5% of data points. Thereafter, each dataset was given a unique identifier.

To investigate the effects of temporal aggregations in mosquito abundance modelling, I aggregated data from the same locations to the weekly and monthly temporal scales, creating two new data frames. On a weekly scale, I aggregated trap counts to the week of the year. I aggregated trap counts of the same species in the same location by calculating the mean for that period of time. By doing so, I was able to account for the numbers of traps that had been employed during a time period, which often differed.

2.2 Meteorological Data

I obtained meteorological data from the National Oceanic and Atmospheric Administration Climate Prediction Center (NOAA CPC) database for Daily Maximum Temperature (°C) and Daily Total Precipitation (mm) (NOAA CPC, 2019). The NOAA CPC database is available on a global longitudinal and latitudinal grid range of 0.5° x 0.5°, and a temporal scale ranging from 01-01-1979 to the present day. Compared to other available options, the NOAA CPC database provides high spatial resolution on a global scale with an extensive temporal scale. The drawback of using this database, however, is that

mean daily temperature is not available. Consequently, I utilised the daily maximum temperature, which still reflects the temporal dynamics of ambient temperature.

Weather data was downloaded as Network Common Data Form (NetCDF) files. NOAA CPC NetCDF files orientate their longitudinal co-ordinates on a range from $0°$ to $360°$, whereas VecDyn data is orientated as $-180°$ to $180°$. Therefore, I used the Climate Data Operator (CDO) command line tool for Linux operating systems to realign the NetCDF files to the VecDyn database regime (Schulzweida, 2019).

I extracted meteorological data from NetCDF files using the ncdf4 package in R (Pierce, 2019). For each required trap data point, I matched the closest available meteorological data to the latitude and longitude co-ordinates. If no meteorological data was available, I input missing values for the meteorological variable.

For data aggregated at weekly and monthly scales, I collated daily meteorological data for the full period of the aggregation. Precipitation is episodic, so is recorded on a cumulative level over time. By comparison, ambient temperature is a continuous measure. Therefore, I summed daily total precipitation to total precipitation (mm) per time aggregation. For temperature aggregations, I calculated the mean of daily maximum temperature, forming the average daily maximum temperature (mean $°C$) over the time period.

Herein, for simplicity I refer only to temperature and precipitation to prevent confusion when considering different aggregating scales. At the daily scale, temperature refers to the maximum temperature ($°C$) on the day of the trap collection and precipitation refers to the total precipitation (mm) on the day of trap collection. At the weekly and monthly scales, temperature refers to the average daily maximum temperature ($°C$) and precipitation refers to the total precipitation (mm) over the time period.

2.3 Relative Importance of Meteorological Variables

2.3.1 Data Pre-processing

The models I utilised had a maximum of four parameters, therefore I filtered datasets to remove any with less than 5 total data points, 5 unique total precipitation values and 5 unique maximum temperature values to facilitate successful model fitting and prevent overfitting models. I also removed any datasets that were composed of less than 5 non-zero trap catches to maximise model fitting.

2.3.2 Model fitting

Upon inspection of data, I found that datasets were not normally distributed. Therefore, to assess the effect of the meteorological factors on mosquito abundance and account for non-normality, I used generalised linear models (GLMs). As abundance cannot fall below zero and was aggregated from multiple traps, it could be considered a continuous, non-negative variable measure. Therefore, I used a gamma family distribution with a log-link function. Trap catches could take the value of zero. As logarithm of zero is mathematically undefined, I transformed all trap catches by adding 1 before modelling.

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The relationship of abundance with temperature and precipitation can be represented by quadratic functions (Wang *et al.*, 2011). Therefore, I incorporated quadratic functions of variables into 3 GLMs of the form:

$$log(E(A+1)) = aT^2 + bT, \quad \epsilon \sim Gamma(\alpha, \beta) \tag{1}$$

$$log(E(A+1)) = aP^2 + bP, \quad \epsilon \sim Gamma(\alpha, \beta) \tag{2}$$

$$log(E(A+1)) = aT^2 + bT + cP^2 + dP, \quad \epsilon \sim Gamma(\alpha, \beta) \tag{3}$$

where A is abundance, T is the average daily maximum temperature (°C), P is the total precipitation (mm), and a, b, c and d are coefficients of model terms. In addition, ϵ is the error term of the model, α is the shape parameter and β is the rate parameter of the gamma distribution.

2.3.3 Model Evaluation

For each model, I calculated the Akaike Information Criterion corrected for small sample sizes (AICc), also referred to as a second-order AIC (Burnham & Anderson, 2002). AICc is a statistical test which quantifies the goodness-of-fit of a model using maximum likelihood methods. AICc penalises more complex models with a larger parameter space, and also datasets with small sample sizes. As sample size increases, AICc tends toward AIC. I preferred AICc to conventional AIC due to the varied nature of the datasets being utilised. AICc is calculated as follows:

$$AICc = -2(ln(likelihood)) + 2k(\tfrac{n}{n-k-1}) \tag{4}$$

where n is the sample size, k is the number of parameters in the model. As I was identifying the single best model for each dataset, I identified the best model as the one with the lowest AICc value. Datasets where the best fitted model did not include temperature were removed from thermal optima analyses.

In multivariate analyses, high correlations between predictor variables in a model can lead to unreliable estimates of regression coefficients. I checked each independent variable for multicollinearity using a Variance Inflation Factor (VIF), which is calculated as follows:

$$VIF = \frac{1}{1 - R^2_{x_1}} \tag{5}$$

Variables with values greater than 3 indicate high multicollinearity and were removed from analyses (Zuur

179 *et al.*, 2010).

2.4 Temporal Lag Term Analysis

2.4.1 Data Pre-processing

To identify the best temporal lags in meteorological variables I aggregated datasets to the week of the year. I removed datasets with less than 5 data points, and with less than 5 non-zero weekly trap catches. This was to ensure that datasets with limited quality for modelling abundance would not influence results, and to facilitate model fitting.

After consideration of mosquito biology, I matched temperature and precipitation data of up to 4 weeks preceding trap catches to each weekly aggregation (Dawson *et al.*, 2019).

2.4.2 Lag Term Identification

To determine the best lag for meteorological variables, I used GLMs with a gamma family distribution and a log-link function as in section 2.3.2. The models employed can be expressed in the form:

$$log(E(A_t + 1)) = aT_{t-j}^2 + bT_{t-j}, \quad \epsilon \sim Gamma(\alpha, \beta) \tag{6}$$

$$log(E(A_t + 1)) = cP_{t-j}^2 + dP_{t-j}, \quad \epsilon \sim Gamma(\alpha, \beta) \tag{7}$$

where A is average weekly mosquito abundance, T is temperature, P is precipitation, t is the week of the year and j is the number of weeks preceding. a, b, c, and d are term coefficients.

For each dataset, GLMs were applied for each meteorological variable at weekly lags (j) in the range 0 to 4, meaning that a total of 10 GLMs were applied per dataset. The best lag for each meteorological variable was evaluated using AICc model selection (see section 2.3.3 Model Evaluation).

To determine whether the lag terms identified as best were better predictors of abundance, I built a model incorporating the best identified lag terms in the form of equation 3, and compared this to a model with no lags. I evaluated the models using AICc to identify the proportion of datasets that each model was considered best for.

I also utilised ΔAICc methods to ascertain the proportion of datasets the lagged and non-lagged models were considered best or comparable to the best model in. Here, the ΔAICc of a model is the absolute difference between the model's AICc score and the lowest scoring models AICc. Models with a ΔAICc score less than 2 are considered comparable to the best model (Johnson & Omland, 2004).

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2.5 Thermal Optima of Abundance

2.5.1 Estimating Thermal Optima

For each dataset, and at each of the 3 temporal aggregating levels, I determined the thermal optimum of mosquito abundance. I estimated the thermal optima using the coefficients of the best fitting model from section 2.3.3 with respect to temperature, finding where the derivative of the quadratic function equals zero. Thus, I estimated T_{opt} using the following equation:

$$T_{\mathrm{opt}} = -\frac{b}{2a} \tag{8}$$

where a is the coefficient of the quadratic term in the fitted function with respect to temperature, and b is the coefficient of the linear term.

In all cases, I checked whether the estimated T_{opt} was derived from coefficients forming a quadratic curve with a maxima or a minima (Figure 3). Quadratic functions with a maxima can be identified when the coefficient a of T is less than 0. I filtered estimated T_{opt} to remove cases where a was not less than 0, and therefore derived from a minima. Finally, I determined whether the derived T_{opt} were within the range of sampled temperatures. Those that were not within the sampling range were unlikely to be reliable estimations of T_{opt}, so were removed from analysis.

2.5.2 Comparison to Thermal Optima of Disease Transmission Rates

I obtained literature predictions for the T_{opt} of basic reproductive number (R_0), a commonly used disease transmission metric, for diseases transmitted by *Aedes*, *Culex* and *Anopheles*. These were predicted using the model developed by Mordecai *et al.* (2013) (Equation S1). I compared the mean of each genera's T_{opt} of abundance to the predicted T_{opt} of disease R_0 using a one sampled t-test. Data for the T_{opt} of abundance were checked for normality using a Shapiro-Wilk test (Table S1).

2.6 Statistical Analyses

All statistical analyses were performed in R version 3.4.4 using the packages "data.table", "car" and "ggplot2" (R Core Team, 2018).

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3 Results

3.1 Meteorological Model Evaluation

Meteorological models were applied to all 212 datasets for all temporal aggregations, however due to data quality limitations a small number of datasets did not converge on all models, and therefore were removed from analyses. Consequently, 205 datasets were compared for daily scale analyses, 209 at the weekly aggregation and 209 at the monthly aggregation. I found that no datasets exceeded the threshold value of 3 for multicollinearity when checked with VIF.
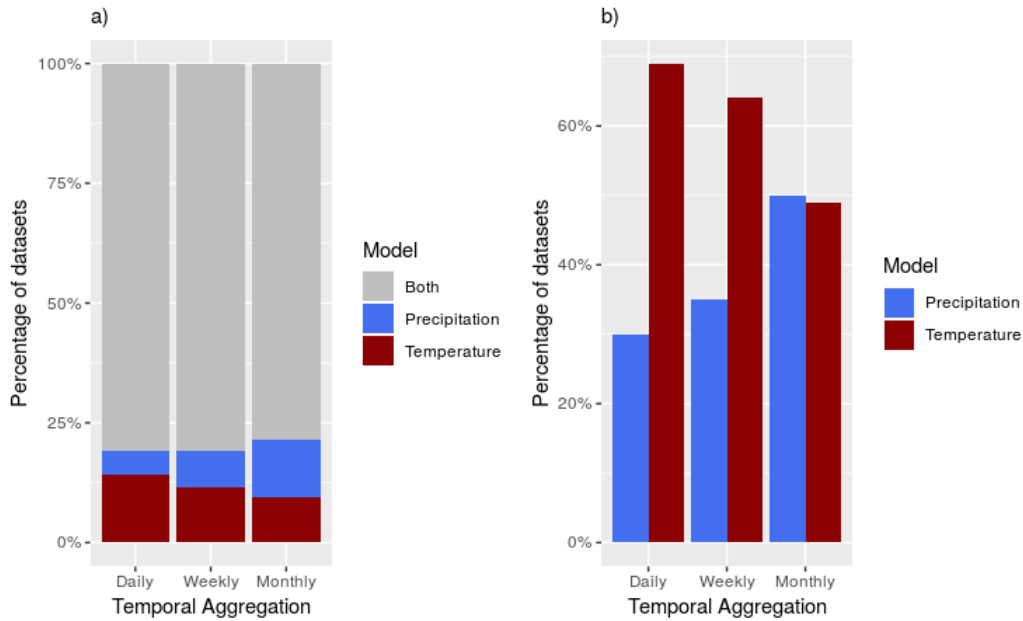

Figure 2: The percentage of mosquito trap count datasets that Generalized Linear Models featuring quadratic functions of average daily maximum temperature (red), total precipitation (blue) or both (grey) meteorological variables fitted best when compared using AICc across temporal aggregations. (a) shows the percentage of models considered best by AICc when all three models are compared, whilst (b) shows the percentage of models considered best by AICc when only univariate models with temperature and precipitation are compared (Daily $n = 205$, Weekly $n = 209$, Monthly $n = 209$)

I applied AICc model selection to identify whether GLMs incorporating precipitation, temperature or both variables were a better predictor of mosquito trap catches. The model incorporating both meteorological variables was unequivocally most frequently considered best across all temporal aggregations (Figure 2a). Interestingly, as temporal aggregating scales increase from daily to monthly, the percentage of temperature models favoured by AICc selection decreases from 14.1% of datasets at daily aggregations to 11.4% at weekly, and to 9.6% at monthly aggregations. By contrast, models featuring exclusively total precipitation were favoured by only 5.4% of datasets on the daily aggregating scale. This increased upon aggregating

at higher temporal scales. At the weekly scale this increased to 7.6% and to 12% of datasets at monthly level.

Similarly, when AICc model selection was applied only to univariate models of precipitation and tempera-ture, at higher aggregating scales datasets favour precipitation more frequently (Figure 2b). Precipitation increases from 30.2% at the daily scale, to 36% at the weekly aggregation and 50.2% at monthly aggre-gations. Consequently the percentage of datasets favoured by temperature models decreases.

3.2   Meteorological Lag Term Identification

I also identified the single best temporal lag in each meteorological variable on a weekly aggregating scale using AICc model selection. Table 1 shows the proportion of models that had the lowest AICc values for temperature and precipitation. A lag of t-4 weeks in temperature models was most frequently favoured via AICc (26.9%), although models with no lag (t) in temperature were favoured in a similar percentage of datasets (26%). Intermediate time lags in temperature showed very similar frequencies at which they were favoured (Table 1). These proportions were consistent for datasets from *Aedes* and *Culex*, however *Anopheles* deviated, favouring no lag and a lag of t-2.

Table 1: The weekly lags in Average Daily Maximum Temperature and Total Precipitation that were considered best when incorporated in Univariate Generalized Linear Models. Models were evaluated using AICc model selection. Lags of 0-4 weeks were considered and comparisons made within each meteorological variable.

Average Daily Maximum Temperature					
Genus	t	$t-1$	$t-2$	$t-3$	$t-4$
Aedes	23 (23.5%)	17 (17.3%)	15 (15.3%)	15 (15.3%)	28 (28.6%)
Anopheles	13 (28.9%)	6 (13.3%)	12 (26.7%)	9 (20%)	5 (11.1%)
Culex	18 (27.7%)	9 (13.8%)	5 (7.7%)	10 (15.4%)	23 (35.4%)
Total	54 (26%)	32 (15.4%)	32 (15.4%)	34 (16.3%)	56 (26.9%)
Total Precipitation (mm)					
Genus	t	$t-1$	$t-2$	$t-3$	$t-4$
Aedes	15 (15.3%)	23 (23.5%)	24 (24.5%)	25 (25.5%)	11 (11.2%)
Anopheles	10 (22.2%)	10 (22.2%)	6 (13.3%)	9 (20%)	10 (22.2%)
Culex	10 (15.4%)	11 (16.9%)	14 (21.5%)	16 (24.6%)	14 (21.5%)
Total	35 (16.8%)	44 (21.2%)	44 (21.2%)	50 (24%)	35 (16.8%)

Total precipitation models with a lag of t-3 weeks were favoured most frequently (24%). Models incorpo-rating lags t-1 and t-2 weeks were favoured by 21.2% of datasets each whilst those with no lag (t) and t-4 were favoured by only 16.8% of datasets each (Table 1).

The lag terms of each meteorological variable that were favoured most frequently were then incorporated into a lagged model which I compared against a non-lagged model. I applied these models to all 209

datasets at a weekly aggregation. Through AICc methods, I found that the lagged model was favoured more frequently ($n = 118$, 56.5%) than a model considering no lags in meteorological variables ($n = 91$, 43.5%). Similarly, using ΔAICc model selection, the lagged model was considered best or comparable to best in 131 (63.6%) datasets, which is considerably more than the non-lagged model ($n = 100$, 47.8%). The lagged model was more frequently considered at least comparable to the best model across all genera (Table 2).

Table 2: The number and percentage of mosquito abundance datasets favouring gamma-GLMs incorporated lags or not ($n = 209$) when compared through ΔAICc methods. The lagged model includes Average Daily Maximum temperature with a weekly lag of t-4 and Total Precipitation of t-3.

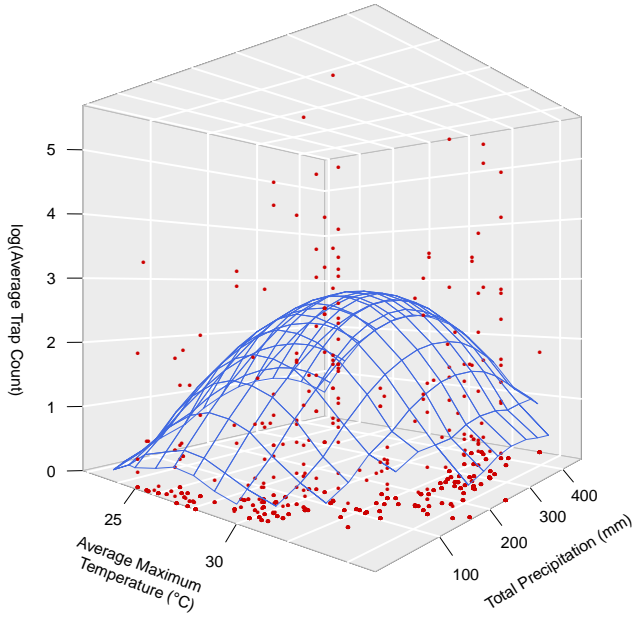|	Lagged Model	Non-lagged Model
Aedes	65 (65.7%)	46 (46.4%)
Anopheles	28 (62.2%)	24 (53.3%)
Culex	38 (55.3%)	30 (46.2%)
Total	131 (62.7%)	100 (47.8%)

3.3 Thermal Optima

Following data pre-processing, a total of 212 datasets were available to estimate T_{opt}. From these, I obtained 91 estimates of T_{opt} of which 40 were from *Aedes*, 17 were from the genera *Anopheles* and 34 were from *Culex* (Table 3).
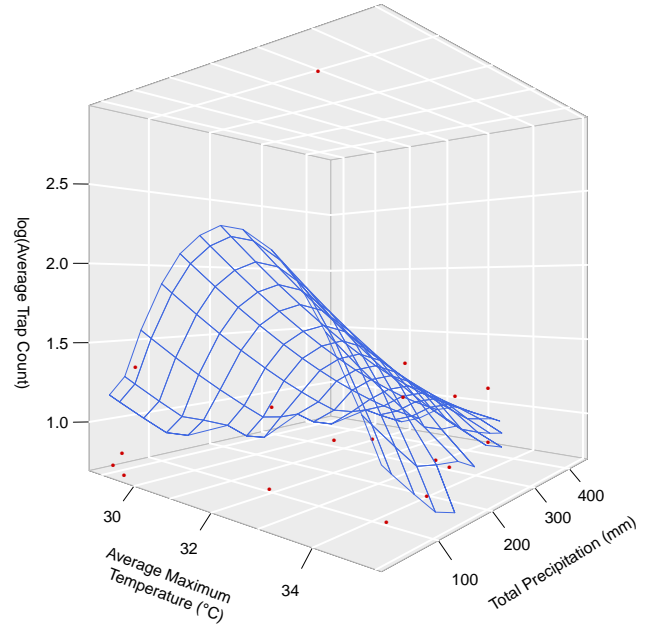
From 40 *Aedes* datasets, the mean estimated T_{opt} of abundance was 29.31°C (± 0.767) for data on the daily scale. This was not significantly different to the estimated T_{opt} of dengue transmission which is 29.1°C (df = 39, t = 0.268, p = 0.790). Similarly, there was not a statistically significant difference between the estimated T_{opt} of Zika transmission and that of *Aedes* abundance (df = 39, t = 0.529, p-value = 0.6).

Species of the *Anopheles* genus were estimated to have a thermal optimum of 29.35 (± 0.914) for abundance on the daily scale, and this was significantly different to the estimated T_{opt} of transmission for malaria (mu = 25.4, df = 16, t = 4.325, p-value < 0.001). The predicted optimum temperature for *Culex* abundance was 27.2°C (± 0.802), and was also considered to be significantly different from the mean of the estimated T_{opt} for West-nile Virus (df = 34.575, t = 3.301, p-value = 0.002). Genera level comparisons yielded no statistically significant difference using a linear model (p = 0.112). Results for data aggregated on the weekly and monthly scales are found in Table 3.
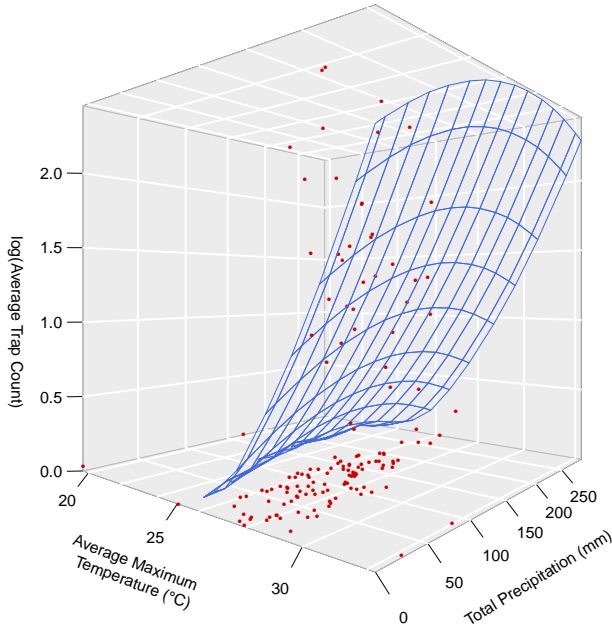
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a) *Culex salinarius* in Manatee County, USA

b) *Culex* in Hernando County, USA

c) *Anopheles funestus* in Uganda

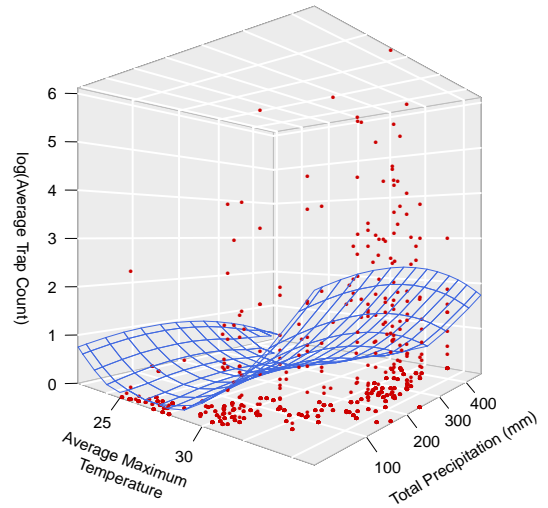**d)** *Aedes atlanticus* in Manatee County, USA

Figure 3: Exemplar 3D scatter-surface plots showing the data points (red) and the fitted surface plane of a model incorporating quadratic functions of both Average Daily Maximum Temperature (°C) and Total Precipitation (mm). Thermal optima of abundance could be derived from (a) and (b), but not from (c) due to the maxima of the quadratic with respect to temperature being out of range, or (d) because the quadratic function does not produce a maxima, rather the estimated coefficients produce a minima. All plots use data on the daily temporal scale.

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Table 3: The predicted T_{opt} for basic reproductive rate (R_0) of selected mosquito borne diseases from Mordecai *et al.* (2019) compared against the estimated T_{opt} of mosquito abundance for the genus of transmission vectors. Comparison is made using one sample t-tests, using the predicted T_{opt} of disease R_0 as a threshold (μ). The standard error of mean T_{opt} of abundance (SE) and the number of estimated T_{opt} (n) are displayed. Significantly different T_{opt} are denoted by *.

Vector-borne Disease	Predicted T_{opt} of R_0 (°C)	Vector Genera	Temporal Scale	Mean T_{opt} of Abundance (°C)	($\pm$) SE	n	p Value
Malaria	25.4	*Anopheles*	Daily	29.35	0.914	17	p <0.01 *
			Weekly	28.56	0.782	15	p <0.01 *
			Monthly	27.22	0.598	18	p <0.01 *
Dengue	29.1	*Aedes*	Daily	29.31	0.767	40	0.7902
			Weekly	28.89	0.649	38	0.752
			Monthly	27.54	0.516	34	p <0.01 *
Zika	28.9	*Aedes*	Daily	29.31	0.767	40	0.6
			Weekly	28.89	0.649	38	0.9919
			Monthly	27.54	0.516	34	0.0127 *
West-Nile virus	24.3	*Culex*	Daily	27.2	0.802	34	0.002 *
			Weekly	27.99	0.670	27	p <0.01 *
			Monthly	27.25	0.551	30	p <0.01 *

4 Discussion

4.1 Relative importance of Temperature and Precipitation

Although previous studies have demonstrated the relative importance of temperature and precipitation on the abundance of individual mosquito species at narrow spatial ranges (DeGaetano, 2005; Galardo *et al.*, 2009; Wong *et al.*, 2011; Li *et al.*, 2019; Poh *et al.*, 2019), investigating the effect of temporal aggregating scales is critical in developing effective measures for mosquito-borne disease management. Here, I utilise a newly built global database to elucidate the relative importance of meteorological variables in predicting mosquito abundances across three medically important mosquito genera. My results demonstrate that at lower temporal scales, univariate models incorporating temperature are better predictors of mosquito abundance than those with only precipitation. At higher temporal scales, however, the relative importance of precipitation increases. This result has implications for mosquito abundance models, highlighting the need to develop models using lower temporal scales.

In mosquitoes precipitation predominantly has an impact on early life stages. Precipitation is episodic in nature, so lower temporal aggregations will not necessarily capture significant precipitation events. As mosquitoes can take several weeks to develop and emerge (Couret *et al.*, 2014; Dawson *et al.*, 2019), using higher temporal aggregations can capture the effects of meteorological variables on early life stages, including larval development and the oviposition of previous generations (Jian *et al.*, 2016). Hence, the role of precipitation in mosquito abundance can be observed at higher aggregating scales, where its relative importance in models aligns with that of temperature at the monthly scale (Figure 2b).

Comparatively, precipitation is not essential to mosquito life history. The existence of permanent water bodies means that oviposition can still occur even in the absence of precipitation. Although precipitation may provide higher quality or greater availability of breeding sites, it is not integral to mosquito abundance. (Roiz *et al.*, 2010) have postulated that for container-breeding mosquitoes such as *Aedes albopictus*, the importance of precipitation is reduced by human activity and water usage. Given the possibility of alternative sites for oviposition and the supplementary nature of precipitation, its lower relative importance on the daily level is unsurprising.

The present study demonstrates that aggregating scales can have profound impacts on the signatures we observe in mosquito abundance data, and therefore has implications on the operational strategies of mosquito surveillance systems and abundance modelling.

4.2   Temporal Lags in Weather Variables

Employing model selection methods, I identified biologically relevant lags of temperature and precipitation that were the best predictors of mosquito abundance at weekly aggregations. I found that the best lag of precipitation for predicting abundance was a lag of t-3 weeks. Given that mosquitoes take between 1 and 3 weeks to develop from egg to emergence (Couret *et al.*, 2014), this result appears to be consistent with the mosquito life cycle. Similarly, temperature at a lag of t-4 weeks was most frequently the best predictor of abundance suggesting that temperature during oviposition of previous generations and early life stages has a high relative importance to abundance.

The delayed effects of meteorological variables on mosquito abundance has previously been investigated. (Poh *et al.*, 2019) recently considered the effect of lagged environmental variables as predictors of *Culex quinquefasciatus* abundance, finding that a lag in temperature of 9 months could be utilised in models to predict abundance. Though this lag may provide predictive power, the biological relevance of such temporal lags is dubious. Therefore, application to alternative ecological systems could prove to be difficult.

Overall, I found that a lagged model was more frequently the best model for predicting mosquito abundance across all datasets. This result indicates that future models of mosquito population dynamics should incorporate lags at the weekly level to ensure that developmental effects of temperature and precipitation are fully reflected in predictions.

4.3   Thermal Optima

Models of disease R_0 are regularly under development, however validation of such models has proven difficult due to a lack of relevant disease case or abundance data. The present study is one of the first to utilise vector abundance data to verify the predicted T_{opt} of R_0. The model developed by Mordecai *et al.* (2019) predicts the thermal optima of disease R_0 from the thermal performance of underlying traits.

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These traits include determinants of vector abundance such as egg-to-adult development rate, survival probability and lifetime fecundity. I show that for *Anopheles* and *Culex*, the T_{opt} of abundance and that of diseases they transmit are significantly different. This suggests that there are other life-history traits in the model that meaningfully influence the T_{opt} for R_0, resulting in dissimilarity. In contrast, *Aedes* were not significantly different to the R_0 T_{opt} of Zika or dengue. This infers that *Aedes* abundance is a principal driver of transmission in these diseases. The implications of this could be vital to the management of *Aedes*-borne diseases, emphasising the importance of mosquito surveillance.

This analysis has assumed that the estimated R_0 for diseases by Mordecai *et al.* (2019) are accurate, however the model has two important limitations to consider. Firstly, the model predicts T_{opt} of disease R_0 from estimates of thermal performance for underlying traits. Each of these estimates is likely to have a degree of uncertainty, which can be amplified when combined in the model. There is, therefore, the potential for the magnitude of error in predictions of R_0 T_{opt} to be significant. Additionally, the model assumes that temperature is a constant throughout lifetime, however in reality this is not the case. Trait performance under variable temperature has been shown to outperform those under constant conditions near thermal limits, whilst performance under variability decreases when compared to constant conditions towards T_{opt} (Bernhardt *et al.*, 2018). Future extensions of this model should look to incorporate variability to better reflect true conditions.

The lack of a statistically significant difference between the T_{opt} of the 3 genera suggests that generalisations of thermal optima for mosquito abundance may be possible. However, our analyses was limited to genera level comparisons because data quality and breadth was not sufficient for a species level comparison. Mordecai *et al.* (2017) have previously predicted that the vectors *Aedes aegypti* and *Ae. albopictus* have significantly different optimum temperatures for the R_0 of malaria transmission, attributing this to underlying adult survival rates. Consequently, future studies should aim to extend analysis to the species level to inform mosquito-borne disease management systems.

4.4 Limitations and Caveats

In addition to those mentioned above, there were a number of limitations to the study. Using a global database collated from multiple sources, it is inevitable that operational activity can be vastly different, for which supplied details may be incomplete. A number of VecDyn's datasets originate from mosquito control organisations who aim to use surveillance data to inform insecticide applications. Effective insecticide application will result in a depletion of recorded abundance. The database, at present, does not record when insecticides have been applied, resulting in the potential loss of key signatures for mosquito-environment associations. Previous studies have demonstrated that incorporating larvicide into models can improve predictions (Ripoche *et al.*, 2019; Dawson *et al.*, 2019). Recently, the need for standardised operational strategies in mosquito surveillance has been recognised, and new approaches have been implemented (Hoekman *et al.*, 2016).

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Furthermore, VecDyn data is currently zero inflated and the interpretation of these data points is not clear, limiting their utility. In some cases, the database inferred zeros for species that had been trapped previously at a given location, but no data explicitly recorded. This does not necessarily mean that the species were being actively recorded at all times. This is likely to be a contributor to zero inflation of records. Clarification of this practice is essential for future model building. Here, I have made the assumption that zeros provide information because they represent points in time and space where local abundance was insufficient to be detected in current trapping methods.

Additionally, as a consequence of using a global database, environmental variables were collected at a lower spatial resolution than is capable when working with singular regional datasets. Consequently, it is plausible that associative signatures are distorted by spatial averaging. Remote sensing techniques would greatly improve this, however the vast temporal and spatial scales utilised in this study rendered remote sensing impractical.

It should also be noted that spatial biases exist in the database at present (Figure S1). Datasets utilised are most commonly from North America, with few on the African continent. Species from *Aedes*, *Anopheles* and *Culex* are known to have wide distributions across the globe, and disease risk is greatest in tropical regions (Ryan *et al.*, 2019). Extending the database's distribution would be beneficial to its utility in disease transmission studies.

4.5   Conclusion

In conclusion, I have demonstrated that temperature has a greater relative importance in predicting mosquito abundances than precipitation at lower temporal scales, however this balances at higher temporal scales. To improve predictive models of mosquito abundance using temperature and precipitation, lower temporal scales such as weekly aggregations should be implemented. I have also shown that short-term lags in weather variables are better predictors of mosquito abundance than immediate conditions. Future models of early warning systems would benefit from incorporating such short term lags to predict periods of high mosquito abundance.

Finally, the present study is the first of its kind to compare the T_{opt} of mosquito abundance with predicted T_{opt} for disease R_0. The dissimilarity between T_{opt} suggests that for Zika and dengue, transmission is heavily driven by vector abundance. In malaria and West-Nile virus, factors other than vector abundance are significant influencers in the model. These results have important implications on mosquito borne disease management and surveillance strategies.

Data and Code Availability

The data that support the findings of this study are openly available via the following Google Drive: https://drive.google.com/open?id=14-P9Kms1QHvowu7fBPFhFWA2pInOhZsc

These data were derived and extended from the following publicly available resource: http://vectorbyte.org/vecdyn

The code utilised throughout this study is available on Github at: https://github.com/dw4415/Project

Acknowledgements

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Supplementary Information

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September 2019

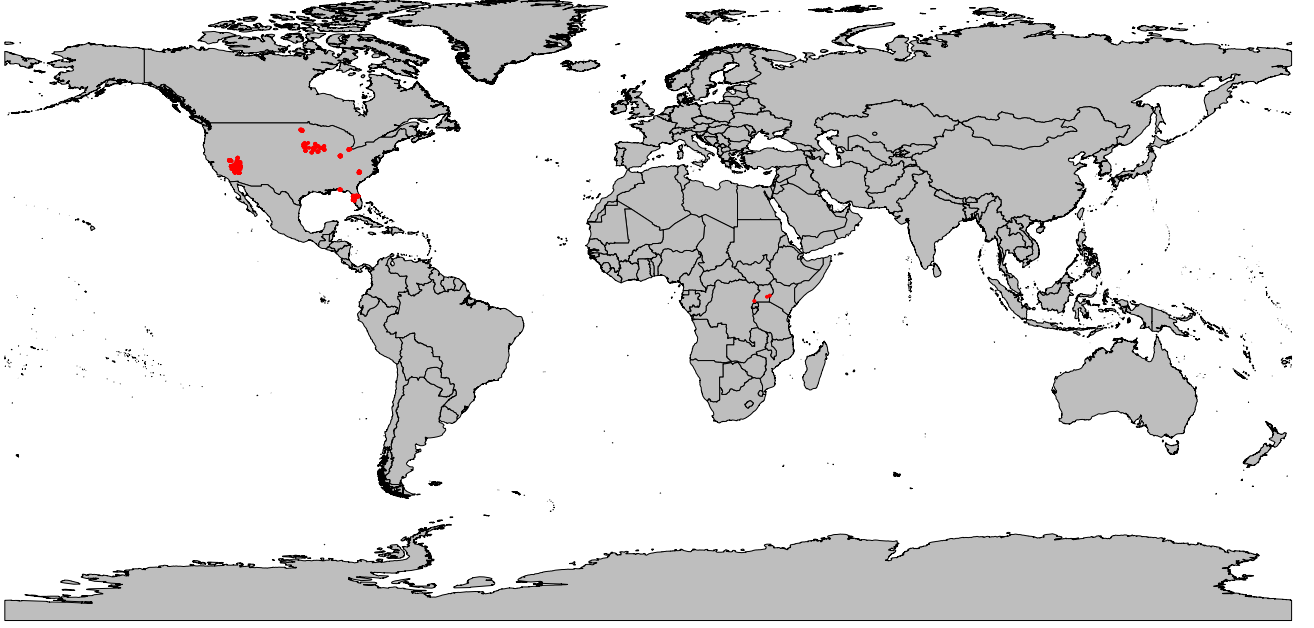Submitted for the MSc in Computational Methods in Ecology and Evolution

Figure S1: Distribution of the datasets from the VecDyn database for *Aedes, Anopheles* and *Culex* mosquitoes after data pre-processing ($n = 212$). Data is predominantly in North America, with a few datasets in Africa.

Equation S1

The model by Mordecai et al., (2019) used to predict the thermal optima (T_{opt}) of basic reproductive rate (R_0), which is used for comparisons against the T_{opt} of abundance is:

$$R_0(T) = \sqrt{\frac{a(T)^2 b(T) c(T) exp(-\mu(T)/PDR(T)) EFD(T) p_{EA}(T) MDR(T)}{Nr\mu(T)^3}} \tag{1}$$

where MDR is egg-to-adult development rate, p_{EA} is survival probability, EFD is eggs per female per day, PDR is the pathogen development rate, a is adult mosquito mortaility rate and μ is the inverse of lifespan. Parameters b and c correspond to vector competence, r is the host recovery rate, N is the density of hosts and T is temperature-dependence of the associated parameter traits.

Table S1: The results of a Shapiro-Wilk test of normality for the estimated T_{opt} each genus at each temporal aggregating scale. All were found to be normally distributed.

Genus	Temporal Aggregating Scale	W	p-Value
Aedes	Daily	0.949	0.069
	Weekly	0.959	0.172
	Monthly	0.970	0.470
Anopheles	Daily	0.919	0.142
	Weekly	0.918	0.182
	Monthly	0.972	0.836
Culex	Daily	0.953	0.150
	Weekly	0.962	0.428
	Monthly	0.919	0.257