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REPORT

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# Remote sensing of temperature-dependent mosquito and viral traits predicts field surveillance-based disease risk

**Andrew J. MacDonald**[1] | **David Hyon**[1] | **Samantha Sambado**[2] | **Kacie Ring**[2] | **Anna Boser**[1]

[1]Bren School of Environmental Science & Management, University of California, Santa Barbara, California, USA

[2]Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California, USA

**Correspondence**
Andrew J. MacDonald
Email: macdonald@bren.ucsb.edu

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## Abstract

Mosquito-borne diseases contribute substantially to the global burden of disease, and are strongly influenced by environmental conditions. Ongoing and rapid environmental change necessitates improved understanding of the response of mosquito-borne diseases to environmental factors like temperature, and novel approaches to mapping and monitoring risk. Recent development of trait-based mechanistic models has improved understanding of the temperature dependence of transmission, but model predictions remain challenging to validate in the field. Using West Nile virus (WNV) as a case study, we illustrate the use of a novel remote sensing-based approach to mapping temperature-dependent mosquito and viral traits at high spatial resolution and across the diurnal cycle. We validate the approach using mosquito and WNV surveillance data controlling for other key factors in the ecology of WNV, finding strong agreement between temperature-dependent traits and field-based metrics of risk. Moreover, we find that WNV infection rate in mosquitos exhibits a unimodal relationship with temperature, peaking at ~24.6–25.2°C, in the middle of the 95% credible interval of optimal temperature for transmission of WNV predicted by trait-based mechanistic models. This study represents one of the highest resolution validations of trait-based model predictions, and illustrates the utility of a novel remote sensing approach to predicting mosquito-borne disease risk.

KEYWORDS
Central Valley, California; *Culex tarsalis*; ECOSTRESS; field-based model validation; temperature-dependent $R_0$; trait-based models; West Nile virus

## INTRODUCTION

Mosquito-borne diseases are some of the most persistent health challenges globally. This distinction is underpinned by their rapid response to changing environmental and sociopolitical conditions including suitable temperature (Paz, 2015), available breeding habitat (Bowden et al., 2011), political turmoil (Kilpatrick &

Randolph, 2012), and the increasing pace of introductions of vector species and pathogens to novel regions (e.g., global invasion of *Aedes* spp. and flaviviruses to the Americas; introduction of *Anopheles stephensi* to sub-Saharan Africa). These characteristics of mosquito vectors and pathogens complicate efforts to control them, despite substantial funding and public health interventions, as well as research efforts.

Mosquito-borne disease risk is further compounded by the pace of global change, leading to potentially rapid changes in environmental suitability for disease transmission (Bowden et al., 2011; Kilpatrick & Randolph, 2012). Will mosquitos and the pathogens they transmit expand or shift their distributions (Ryan et al., 2019)? Will they adapt in situ, through behavioral responses like shifting seasonality, or through evolutionary adaptation (Couper et al., 2021)? The potential for rapid response of mosquito-borne diseases to environmental change has underscored the importance of prediction and forecasting to understand consequences for health.

One important approach to forecasting impacts of changing climate on mosquito-borne disease risk is characterizing the temperature dependence of transmission through mosquito and pathogen trait-based mechanistic models (Mordecai et al., 2013; Shocket et al., 2020). Key mosquito and pathogen traits—from biting rates and mosquito lifespans, to transmission efficiency—are sensitive to temperature (Mordecai et al., 2019). Combining the influence of these traits on the relative $R_0$ of mosquito-borne diseases through mechanistic models has led to improved predictions of the optimal temperature for malaria transmission (Mordecai et al., 2013) and future forecasts of the shifting suitability for arboviruses (Ryan et al., 2019). However, these models rely on temperature–trait relationships measured in laboratory studies, and field-based model validation remains a challenge (Mordecai et al., 2019).

Previous model validation efforts have relied on pairing relatively coarse weather data with either similarly coarse (e.g., county-level case reporting for West Nile virus [WNV]; Shocket et al., 2020) or sparse (e.g., aggregation of the results of limited field studies; Mordecai et al., 2013) transmission data. However, such scales may not represent ecologically relevant associations of temperature with metrics of disease risk, like entomological inoculation rates or human case reporting. Here, we use a novel remote sensing approach (Boser et al., 2021) in combination with highly spatially resolved vector surveillance data to both provide novel field-based validation of trait-based mechanistic models (Mordecai et al., 2019; Shocket et al., 2020) and assess the performance of the remote sensing approach of Boser et al. (2021) in predicting mosquito-borne disease risk. Specifically, using WNV in California's Central Valley as a case study, we quantify temperature—and temperature-dependent mosquito and viral traits—across the diurnal cycle at high spatial resolution (70 m), and use this information to predict adult female *Culex tarsalis* mosquito abundance and infection with WNV.

We find key temperature-dependent traits, transmission efficiency and mosquito abundance, reliably predict metrics of WNV risk—minimum infection rate (MIR) and adult female mosquito abundance, respectively—in the field, controlling for key biotic and abiotic conditions relevant to WNV dynamics. Moreover, WNV infection rates in vector mosquitos peak almost precisely at the optimal temperature for WNV transmission predicted by Shocket et al. (2020). These results provide robust, high spatial resolution validation of temperature-dependent, trait-based mechanistic models, as well as validate a novel remote sensing-based approach to high spatial resolution mosquito-borne disease risk mapping and prediction (Boser et al., 2021) that could prove valuable to vector-borne disease ecology across regions and ecological contexts.

# METHODS

## Study region

This study was conducted in the northern Central Valley of California, which encompasses the Sacramento metropolitan area, smaller cities and towns, part of the Sacramento River delta, and diverse agricultural landscapes that include rice production, row crops, and orchards. Rainy winters and crop irrigation provide breeding habitat for mosquitos, while hot, dry summers are ideal for mosquito development and population growth.

## WNV surveillance data

Mosquito and WNV surveillance is conducted throughout the year by California's mosquito and vector control districts, and includes number of mosquitos by life stage, sex, and species collected by trap type and per trap night. Mosquito pools are also screened for WNV infection, primarily during peak transmission season from late spring to early fall. All trap stations include latitude and longitude, and date of collection. Mosquito and WNV surveillance data were acquired from VectorSurv, through a CalSurv data request (#000058), for the northern Central Valley—Sacramento, Solano, Napa, Yolo, Colusa, Sutter, Placer, Yuba, Nevada, Contra Costa, San Joaquin, El Dorado, and Amador counties—from 2010 to 2020 (Figure 1a). To group nearby trap stations that were unlikely to represent independent samples based on daily

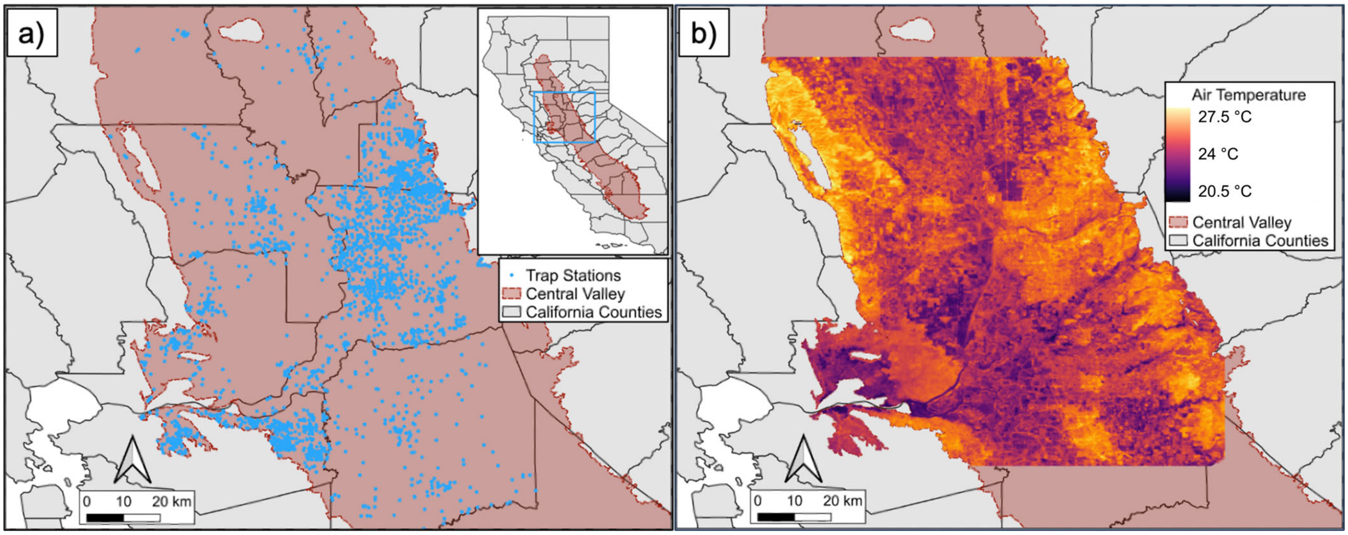

**FIGURE 1** Maps illustrating (a) location of mosquito trap stations within the northern Central Valley study region (inset map of California) and (b) ECOSTRESS-based air temperature estimates averaged across the diurnal cycle for the summer season when mosquito abundance and West Nile virus transmission peak.

dispersal distances of *Culex* mosquitos (Reisen & Lothrop, 1995), trap stations were spatially aggregated using hierarchical clustering. In brief, clusters were created using a complete-linkage hierarchical clustering method with tree height cutoff of ~3000 m using the hclust function in the stats package (R Core Team, 2022), resulting in ~1500 m (1.5 km) radius buffers around trap station cluster centroids. Each cluster contains distinct trap stations, so clusters of trap stations do not contain duplicate surveillance data.

Following trap station clustering, we calculated weekly averages of (1) number of mosquitos per trap night and (2) minimum WNV infection rates (MIR) for each trap station cluster by week observation using the following equation: $\text{MIR} = ([\text{number positive pools} \div \text{number specimens tested}] \times 1000)$. The surveillance data were then subset to the beginning of June through end of September 2018–2020, to match available imagery from the ECOSTRESS sensor (see below). This data subset was then collapsed by trap station cluster to obtain a single observation per cluster of average MIR and average number of mosquitos per trap night over the peak transmission season. Data processing was restricted to only adult *Cx. tarsalis* females, the primary rural WNV vector in the agriculturally dominated Central Valley.

## Temperature-dependent traits

We employ a novel method developed and outlined in Boser et al. (2021) for measuring air temperature across the diurnal cycle at high spatial resolution using remote sensing. These high spatial resolution temperature measurements (Figure 1b) are then used to calculate and map temperature-dependent mosquito and viral traits (Boser et al., 2021). In brief, ECOSTRESS is a NASA sensor onboard the International Space Station, capable of collecting highly accurate land surface temperature (LST) at high spatial resolution (70 m). Temperature measurements occur at variable times of day due to the non-sun synchronous orbit of the sensor, with sensor revisit times averaging approximately once every two days in this region resulting in high spatial resolution temperature measurements across the diurnal cycle. From LST, we model air temperature using meteorological station temperature measurements across the Central Valley (Boser et al., 2021), since LST tends to be higher during the peak of the day and cooler at night than air temperature.

We then apply the mechanistic relationships for key mosquito and viral traits for *Cx. tarsalis* and WNV across the diurnal temperature cycle produced from ECOSTRESS, following Boser et al. (2021). Specifically, we focus on: (1) transmission efficiency, $b(T)$, the proportion of infected mosquitos that become infectious, with virus present in saliva; and (2) mosquito abundance, $M(T)$, which is influenced by egg-to-adult development rate (MDR), survival probability ($p_{\text{EA}}$), and lifetime fecundity (eggs per female per day, EFD, times lifespan, $1/\mu$) Equation (1; Mordecai et al., 2019)

$$M(T) = \frac{\text{EFD}(T)\, p_{\text{EA}}(T)\, \text{MDR}(T)}{\mu(T)^2}. \tag{1}$$

We focus on transmission efficiency, $b(T)$, as a modeled proxy for WNV MIRs, and mosquito abundance, $M(T)$, as a modeled proxy for mosquitos per trap night from

WNV surveillance (Appendix S1: Figures S1 and S2). Finally, we summarize temperature-dependent traits within ~1500 m radius buffers, to approximate average weekly *Culex* mosquito dispersal distances reported in the literature (Reisen & Lothrop, 1995), centered on each trap station cluster to assess the relationship between modeled traits and field surveillance.

## Abiotic and biotic controls

Many other factors may influence WNV risk, including humidity (Paz, 2015), standing water for breeding (Kovach & Kilpatrick, 2018), land cover (Bowden et al., 2011) and host abundance, including reservoir bird hosts (Kilpatrick et al., 2007). To capture these factors in our analysis, we include additional key biotic and abiotic characteristics, summarized by trap station cluster across the summer months of 2018–2020 (Appendix S1: Table S1). We include abundance of key passerine bird hosts—house sparrows, house finches, western scrub jays, American robins, and American crows—both individually and summed to quantify overall "competent" bird abundance, as well as overall bird diversity using modeled bird abundance data from the Cornell Lab of Ornithology, ebird Status and Trends (Fink et al., 2020). We also include human and livestock (cattle and chickens) density as a measure of overall blood meal host availability from WorldPop (www.worldpop.org) and the UN FAO, respectively (Gilbert et al., 2018). We also include cumulative precipitation (mm) and average vapor pressure deficit (in kilopascal) from gridMET (Abatzoglou, 2013), enhanced vegetation index (EVI) from MODIS, drought severity (Palmer Drought Severity Index) from gridMET (Abatzoglou, 2013), standing water from the European Commission's Joint Research Centre Global Surface Water database (Pekel et al., 2016), area of irrigated agriculture from irrMapper (Ketchum et al., 2020), and a categorical variable for the dominant land cover type from the 2019 National Land Cover Dataset—agriculture (reference category in models), developed, natural and wetland (Dewitz & USGS, 2021). Finally, we include other temperature-dependent mosquito traits (i.e., biting rate, $a(T)$, and abundance, $M(T)$, in the WNV MIR models) that might influence the relationship between the focal trait and vector surveillance (Mordecai et al., 2019). Data availability is described in Appendix S1: Table S1 (MacDonald, 2024).

## Statistical analysis

All analyses were conducted in R version 4.2.2 (R Core Team, 2022). To remove the effects of spatial autocorrelation, we spatially thinned the trap station clusters so that the distance between trap station cluster centroids was at least 3 km, resulting in a random subset of trap station clusters that maximizes the number of retained data points, and that avoids overlap of the 1500-m-radius buffers around each trap station cluster centroid (Appendix S1: Figure S3). Spatial thinning was achieved using the ensemble.spatialThin function in the BiodiversityR package (Kindt & Coe, 2005). If residual spatial autocorrelation was still present in full or best fit models (see below), according to Moran's $I$ tests on model residuals, the $x$ and $y$ coordinates of trap station clusters were added as additional controls in the final models.

To model the relationship between temperature-dependent traits, derived from ECOSTRESS, and field-based WNV surveillance, we use generalized linear models (GLMs) with a Tweedie response distribution and log link function using the package glmmTMB (Brooks et al., 2017). The Tweedie distribution is in the exponential family and is useful for modeling outcome data that have a point mass at zero and a skewed positive distribution when greater than zero (Gilchrist & Drinkwater, 2000), as is the case for MIR and mosquitos per trap night in our surveillance dataset. We standardized ($z$-score transformed) all variables, with the exception of categorical land cover, to allow for interpretation of relative effect sizes.

We first specified models with just the focal trait (i.e., MIR as a function of modeled transmission efficiency and mosquitos per trap night as a function of modeled mosquito abundance). We then specified full models with all relevant control variables, and used backward stepwise variable selection by Akaike information criterion (AIC) using the stepAIC function in the MASS package (Venables & Ripley, 2002) to select the best fit models, ensuring limited collinearity in the final set of predictors using the performance package (Lüdecke et al., 2021). To ensure that model results were robust to model selection approach, we undertook an all possible model comparison with model selection by $\text{AIC}_c$ using the dredge function in the MuMIn package (Barton, 2023). Finally, we specified full and best fit models, as above, using a quadratic function of air temperature in place of the temperature-dependent traits. We do so to assess the shape of the relationship between temperature alone, derived from ECOSTRESS, and field surveillance-based estimates of WNV risk (i.e., MIR). The full suite of model results and diagnostics is presented in Appendix S1: Figures S4–S6, Tables S2–S9.

## RESULTS

The best-fit models predicting adult female *Cx. tarsalis* per trap night included temperature-dependent mosquito abundance modeled from ECOSTRESS ($M(T)$), competent bird abundance, bird diversity (Shannon index), precipitation, area of irrigated agriculture, EVI, vapor pressure deficit, area of standing water, cattle density, dominant land cover, and $x$ and $y$ coordinates of trap station clusters. The model estimates a strong positive association between temperature-dependent mosquito abundance and mosquitos per trap night from field-based surveillance ($\exp(\hat{\beta}) = 1.42$ [1.02–1.97], Figure 2a; Appendix S1: Figure S4, Tables S2–S4). Specifically, for a one SD increase in temperature-dependent mosquito abundance, the model predicts a 42% increase in the number of mosquitos per trap night. In addition, mosquitos per trap night were positively associated with competent bird host abundance, precipitation, area of irrigated agriculture and wetland land cover, and negatively associated with overall bird diversity, EVI, vapor pressure deficit, area of standing water, and developed land cover (Figure 2a; Appendix S1: Figure S4, Tables S2–S4).

Best fit models predicting WNV MIRs in adult female *Cx. tarsalis* included temperature-dependent transmission efficiency modeled from ECOSTRESS ($b(T)$), bird diversity, EVI, vapor pressure deficit, mosquito biting rate, area of standing water, human population and chicken density, dominant land cover, and $x$ and $y$ coordinates of trap station clusters. The model estimates a strong positive association between temperature-dependent transmission efficiency and MIR ($\exp(\hat{\beta}) = 1.84$ [1.14–2.95], Figure 2b; Appendix S1: Figure S5, Tables S5–S7). Specifically, for a one SD increase in temperature-dependent transmission efficiency, the model predicts an 84% increase in MIR. In addition, MIR was positively associated with bird diversity and EVI, and negatively associated with mosquito biting rates ($a(T)$) and human population density (Figure 2b; Appendix S1: Figure S5, Tables S5–S7).

In models predicting MIRs from field surveillance with ECOSTRESS-based air temperature in place of

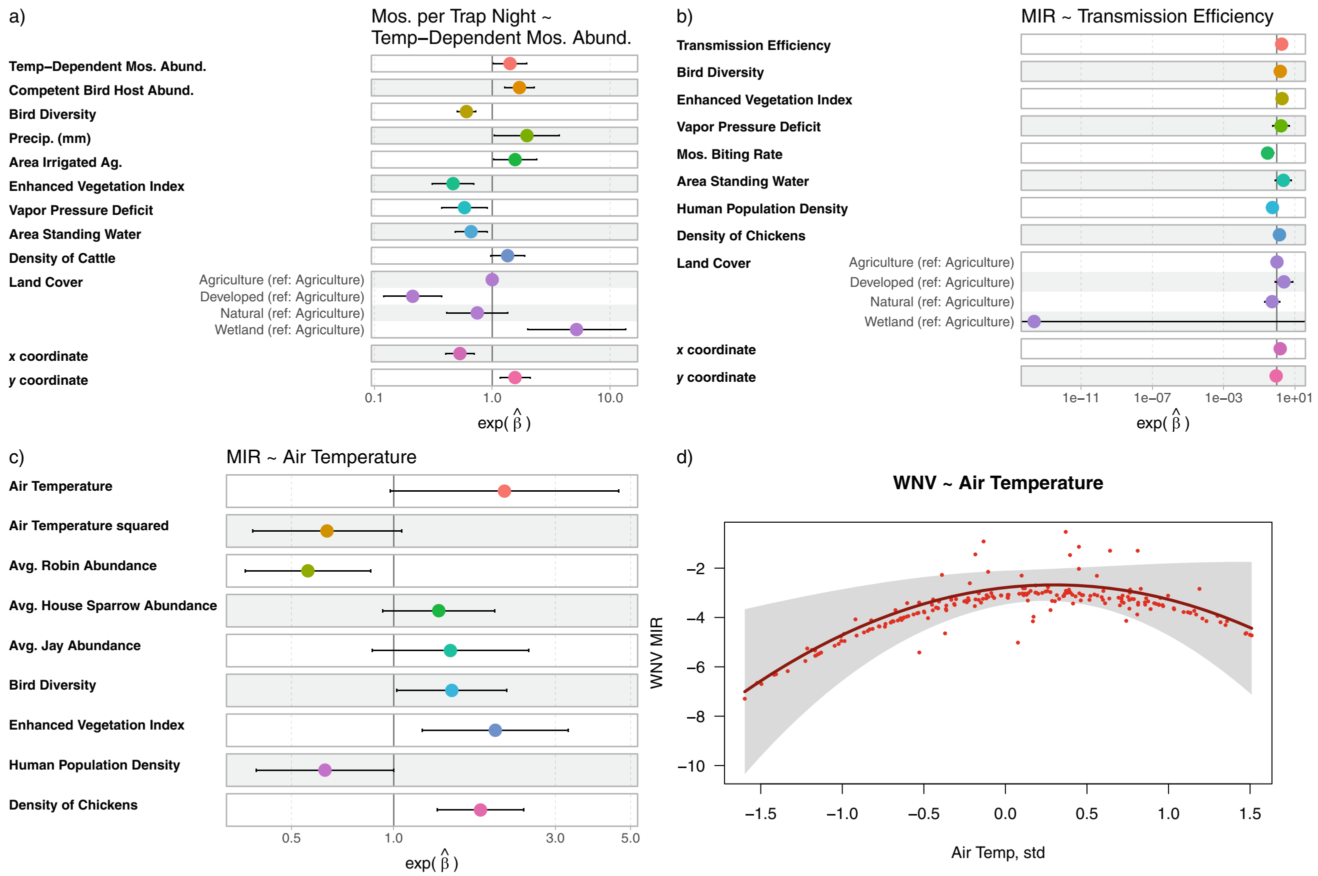

**FIGURE 2** Coefficient plots for (a) adult female *Culex tarsalis* mosquitos per trap night predicted by temperature-dependent mosquito abundance ($M(T)$); (b) West Nile virus minimum infection rates (MIR) in *Cx. tarsalis* predicted by temperature-dependent West Nile virus transmission efficiency ($b(T)$); and (c) West Nile virus MIRs in *Cx. tarsalis* predicted by air temperature. Panel (d) is a partial residual plot illustrating the nonlinear relationship between ECOSTRESS-based air temperature estimates and West Nile virus MIRs in *Cx. tarsalis*. Partial residual plot is based on models predicting standardized MIR for the purposes of visualization (Appendix S1: Table S9).

temperature-dependent traits (Figure 2c; Appendix S1: Figure S6, Tables S8 and S9), we identify a clear unimodal relationship between temperature and MIR that peaks at ~24.6–25.2°C (Figure 2d), almost precisely in the center of the range of predicted optimal temperature for transmission of WNV by *Cx. tarsalis* (22.9–25.9°C) (Shocket et al., 2020).

## DISCUSSION

Mosquito-borne diseases threaten human health globally and remain a significant public health challenge due to the sensitivity of mosquito vectors and pathogen transmission to rapidly changing environmental conditions (Bowden et al., 2011; Kilpatrick & Randolph, 2012; Paz, 2015). There has therefore been significant interest in modeling the response of mosquito-borne diseases to key environmental parameters like temperature (Hartley et al., 2012), as well as in mapping transmission risk to better understand current and future threats to human health (Ryan et al., 2019). Recent advances in trait-based mechanistic modeling of the temperature dependence of pathogen transmission (Mordecai et al., 2019) have improved understanding of the potential responses of mosquito-borne diseases to changing climate. However, field-based validation of model predictions has been a significant challenge, due in part to a dearth of high spatial resolution temperature estimates that can be combined with similarly high resolution surveillance data (Mordecai et al., 2019).

Here, we overcome these challenges using a novel remote sensing approach to estimating air temperature at high spatial resolution, and across the diurnal cycle (Boser et al., 2021). We find good agreement between temperature-dependent mosquito and viral traits, and entomological metrics of risk from high resolution field surveillance data, as well as validate predictions of optimal temperature for transmission of WNV by *Cx. tarsalis* from trait-based mechanistic models (Shocket et al., 2020).

Importantly, these temperature-dependent traits are significant predictors of entomological metrics of WNV risk from field-based surveillance even in models controlling for other biotic and abiotic factors relevant to mosquito biology and WNV ecological dynamics (Bowden et al., 2011; Kilpatrick et al., 2007; Reisen & Lothrop, 1995). Bird host abundance and land cover characteristics relevant to mosquito breeding are also important predictors of the field-based metrics of WNV risk. For example, area of irrigated agriculture and wetland land cover are positively associated with mosquito abundance. Interestingly, area of standing water is negatively associated with mosquito abundance, which may be a function of the region of interest; large areas of standing water in this part of the Central Valley are primarily associated with the brackish Sacramento and San Joaquin Delta, which may be less ideal for *Cx. tarsalis* breeding than other water sources like irrigation ditches, storm drains, and seasonal wetlands (Reisen & Lothrop, 1995). EVI, a metric of vegetation greenness, is positively associated with WNV MIR, as is overall bird diversity, which may be the case if overall abundance of highly competent hosts is elevated in high diversity bird communities.

While our novel remote sensing-based approach to risk mapping of WNV yields good agreement between temperature-dependent traits and field-based WNV surveillance, validating mechanistic model predictions, the approach does have some limitations. First, the mechanistic models from which our temperature-dependent traits are derived are necessarily simplified representations of the mosquito development and viral transmission processes (Mordecai et al., 2019). For example, the egg-to-adult development rate (MDR), encompasses multiple developmental stages and processes from timing of eggs to hatch, to development from larvae to pupae and adults. Each of these stages may respond differently to temperature, as will timing from adult emergence to female maturity and oviposition. This simplification is often necessary to make mechanistic models more interpretable and to simplify their parameterization while still capturing relevant dynamics. However, simplification may also lead, in our context, to disconnects between trait-based predictions and observed abundance or infection rates in the field, if for example some process is not accurately captured that has an outsized impact on the system. Another important limitation is that the revisit time of the ECOSTRESS sensor limits our temperature estimates to a single high spatial resolution diurnal temperature profile during the peak summer season. This may be more useful in regions with relatively consistent temperatures during distinct transmission seasons, like the Central Valley, but perhaps less so where conditions are more variable and transmission occurs variably year-round. Thus, the results we present from our study region may not be generalizable to these different ecological contexts. Cloud cover is also an issue for many applications of remote sensing, so this approach may be more challenging to implement in regions with significant cloud cover, particularly in tropical regions where vector surveillance may be limited, and remote sensing approaches potentially more valuable. Finally, the approach relies on meteorological station data to model air temperature from LST, so regions with sparse meteorological stations may also present a challenge.

High spatial and temporal resolution, globally consistent satellite imagery is increasingly available, and presents novel opportunities for mosquito-borne disease ecology, risk mapping, and future forecasting. Here we assess the performance of a novel remote sensing approach to temperature-dependent risk mapping (Boser et al., 2021) in predicting entomological metrics of WNV risk in the Central Valley of California, and present one of the highest resolution validations of temperature-dependent mechanistic model predictions (Mordecai et al., 2019; Shocket et al., 2020) of mosquito-borne disease transmission to date. We show that our approach, integrating across the diurnal temperature cycle, is well suited to capturing the nonlinearity of temperature–trait relationships, and to predicting mosquito-borne disease risk in the field.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Final datasets used in the analyses and reproducible code for all results and figures, along with additional shapefiles and bird species list used in data processing, are available in Zenodo in MacDonald (2024) at https://doi.org/10.5281/zenodo.13344415. Sources of data used in this study, except for West Nile virus surveillance data, are publicly available and cited in the manuscript text, Appendix S1: Table S1, References. The raw West Nile virus surveillance data are available by request through CalSurv using the query details provided in Appendix S1: Table S1.

## ORCID

*Andrew J. MacDonald* https://orcid.org/0000-0003-0172-7749

*Samantha Sambado* https://orcid.org/0000-0002-2594-3641

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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