Journal of Medical Entomology Advance Access published April 25, 2016

Journal of Medical Entomology, 2016, 1–10
doi: 10.1093/jme/tjw042
Research article

Vector-Borne Diseases, Surveillance, Prevention

Predicting West Nile Virus Infection Risk From the Synergistic Effects of Rainfall and Temperature

L. Shand,[1] W. M. Brown,[2] L. F. Chaves,[3] T. L. Goldberg,[4] G. L. Hamer,[5] L. Haramis,[6] U. Kitron,[7] E. D. Walker,[8] and M.O. Ruiz[2,9]

[1]Department of Statistics, University of Illinois, Urbana, IL 61801 (lshand2@illinois.edu), [2]Department of Pathobiology, University of Illinois, Urbana, IL 61801 (wmbrown@illinois.edu; moruiz@illinois.edu), [3]Institute of Tropical Medicine (NEKKEN), Nagasaki University, Japan (lchaves@nagasaki-u.ac.jp), [4]Department of Pathobiological Sciences, University of Wisconsin, Madison, WI 53706 (tgoldberg@vetmed.wisc.edu), [5]Department of Entomology, Texas A&M University, College Station, TX 77843 (ghamer@ta-mu.edu), [6]Division of Environmental Health, Illinois Department of Public Health, Springfield, IL 62761 (LINN.HARAMIS@ILLINOIS.GOV), [7]Department of Environmental Sciences, Emory University, Atlanta, GA 30322 (ukitron@emor-y.edu), [8]Department of Microbiology and Molecular Genetics, Michigan State University, East Lansing, MI 48824 (walker@m-su.edu), and [9]Corresponding author, e-mail: moruiz@illinois.edu

Received 7 August 2015; Accepted 17 March 2016

Abstract

Mosquito-based surveillance is a practical way to estimate the risk of transmission of West Nile virus (WNV) to people. Variations in temperature and precipitation play a role in driving mosquito infection rates and transmission of WNV, motivating efforts to predict infection rates based on prior weather conditions. Weather conditions and sequential patterns of meteorological events can have particularly important, but regionally distinctive, consequences for WNV transmission, with high temperatures and low precipitation often increasing WNV mosquito infection. Predictive models that incorporate weather can thus be used to provide early indications of the risk of WNV infection. The purpose of this study was first, to assess the ability of a previously published model of WNV mosquito infection to predict infection for an area within the region for which it was developed, and second, to improve the predictive ability of this model by incorporating new weather factors that may affect mosquito development. The legacy model captured the primary trends in mosquito infection, but it was improved considerably when calibrated with local mosquito infection rates. The use of interaction terms between precipitation and temperature improved model performance. Specifically, temperature had a stronger influence than rainfall, so that lower than average temperature greatly reduced the effect of low rainfall on increased infection rates. When rainfall was lower, high temperature had an even stronger positive impact on infection rates. The final model is practical, stable, and operationally valid for predicting West Nile virus infection rates in future weeks when calibrated with local data.

Key words: West Nile virus, climate and weather, risk model, Illinois

Since the introduction of West Nile virus (WNV) into the Western Hemisphere via New York City in 1999, WNV has spread throughout the Americas and poses an ongoing and serious threat to human and animal health. Over 40,000 cases of illness from WNV were reported through public health surveillance systems in the United States between 1999 and 2014 (CDC 2014). The number and location of cases has varied each year, and the ability to predict outbreaks has proven to be challenging. After a period of relatively low activity between the years 2008 to 2011, a large outbreak in 2012, with 5,674 human cases reported in the United States, renewed concern about the need for public health preparedness, and spurred efforts to determine better ways to anticipate and reduce the risk of exposure to WNV (Nasci 2013).

Mosquito-based surveillance is a recommended, standard, and practical way to estimate the risk of transmission of WNV and other mosquito-borne pathogens to people (Macdonald 1956, Moore et al. 1993, Hokit et al. 2013). Select species of mosquitoes in the genus *Culex* comprise over 95 percent of the positive tests for WNV in the United States and are the primary focus of mosquito surveillance efforts (Andreadis 2012). After trapping of blood-fed vector mosquitoes and virus diagnostic testing, the minimum infection rate and the maximum likelihood estimator for mosquito infection rates based on pooled samples are common measures used to estimate the true infection rate (Walter et al. 1980, Hepworth 2005, Gu et al. 2003, Biggerstaff 2009, Ebert et al. 2010).

Variations in temperature and precipitation play a role in driving the WNV infection rate and transmission, motivating efforts to predict WNV mosquito infection rates from prior weather conditions. Warmer weather increases potential for transmission because it reduces the number of days between virus ingestion to effective transmission (extrinsic incubation period), shortens the length of time between bloodmeals (gonotrophic cycle), and leads to an earlier start to seasonal mosquito activity (Turell et al. 2001, 2005; Dohm et al. 2002; Reisen et al. 2010; Hartley et al. 2012). Mosquito abundance also generally increases with warmer temperatures, but very hot conditions can have the opposite effect, and shorter life spans in *Culex* mosquitoes may reduce transmission, as fewer individuals live long enough to become infectious (Chaves et al. 2013, Ciota and Kramer 2013).

Hydrologic conditions also affect WNV transmission. *Culex* mosquitoes reproduce in standing water, but heavy rainfall can reduce *Culex* survival both at the adult stage and during larval development (Gardner et al. 2012, Jones et al. 2012). Rainfall influences near-surface humidity, and studies have found that higher humidity induced oviposition in gravid *Culex nigripalpus* (Day and Curtis 1999) and *Culex quinquefasciatus* (Chaves and Kitron 2011). Thus, rainfall may increase the potential for pathogen transmission as females seek bloodmeals prior to oviposition. The frequency, strength, and timing of rainfall events can also affect water chemistry and the degree to which standing water is suitable for mosquito preadult development (Shaman and Day 2007, Chaves and Kitron 2011, Gardner et al. 2013).

The net result of these effects is that high temperatures combined with low precipitation have often led to higher than average mosquito infection, but these effects vary by region, and the effect of rainfall is especially variable. Weekly patterns of lower than average rainfall and higher temperature, for example, explained about 70 percent of the variability in WNV mosquito infection rates in a study focused on the Chicago, Illinois area (Ruiz et al. 2010). Similarly, drought followed by wet conditions preceded the reporting of WNV human illness in Florida (Shaman et al. 2005). Drought, during which mosquitoes and birds are in closer proximity due to reduced water availability, could cause local sylvatic amplification of WNV, and subsequent rainfall could then allow dispersal of infected vectors and hosts (Shaman et al. 2005). Especially during very hot and dry periods, human-introduced water can create mosquito habitats that might not be otherwise available (Reisen et al. 2008, Barker et al. 2009, Becker et al 2014). The relationship between prior rainfall and WNV outbreaks has varied in prior analyses. Outbreaks of WNV in Europe in 2010, for example, were preceded two to four weeks earlier by warmer than average conditions, but the outbreaks were less clearly associated with relative humidity and rainfall (Paz et al. 2013). Similarly, warmer than average winter temperatures and higher than average rainfall preceded the 2012 outbreak in Dallas, TX, but variables that measured rainfall were not significant in a multivariate analysis (Chung et al. 2013).

The purpose of our study was twofold. First, we assessed the ability of a previously published model of WNV mosquito infection developed for the Chicago region (Ruiz et al. 2010) to predict infection for a subset of that region—specifically for DuPage County, IL. For this objective, we compared the measured WNV mosquito infection rate (MIR) for the period from 2004 to 2013 with the MIR estimated by a linear model that resulted from the prior work (see Supplementary Materials [online only]), referred to henceforth as the "legacy model." Then, we worked with public health and mosquito abatement personnel in DuPage County in 2014 to learn about the local characteristics of mosquito testing and delivery of public health warnings, so that a predictive model for WNV could be developed and implemented effectively in this setting. Second, we refined the legacy model both to develop a model that takes into account the local conditions and to exploit weather data more fully by considering interaction effects between rainfall and temperature. The broader context of this work is to provide a practical, generalizable, and operationally valid approach to predicting WNV mosquito infection that can be incorporated into public health assessments using data from prior weather conditions.

Fig. 1. Map of the study region with the two weather station locations and the average number of trap locations at which mosquitoes were tested. The legacy model was developed from data combined from Cook and DuPage counties. The current objectives focus on DuPage County, only. The average number of traps is for the years from 2005 to 2014 summarized for hexagons of 200 hectares. (Online figure in color.)

Materials and Methods

Study Region

DuPage County, IL, is located west of the city of Chicago (Fig. 1). It comprises an area of 848 km^2 and is the second most populous county in the state of Illinois, with a population of 932,126 in 2013 (US Census Bureau). Mosquito control in the county is organized through a combination of mosquito abatement districts, townships, municipalities, and several large landholders. The study period of interest was from 2005 to 2014, and model development included data on weather conditions and mosquito infection rates during this period. All data were organized by week, with weeks starting on Saturday.

Weather Data

Daily temperature and precipitation measures were based on two local weather stations: Midway (MDW) and O'Hare (ORD) (Fig. 1). Weekly precipitation (rainfall in cm) was calculated from the daily average for each week from the two stations. Weekly

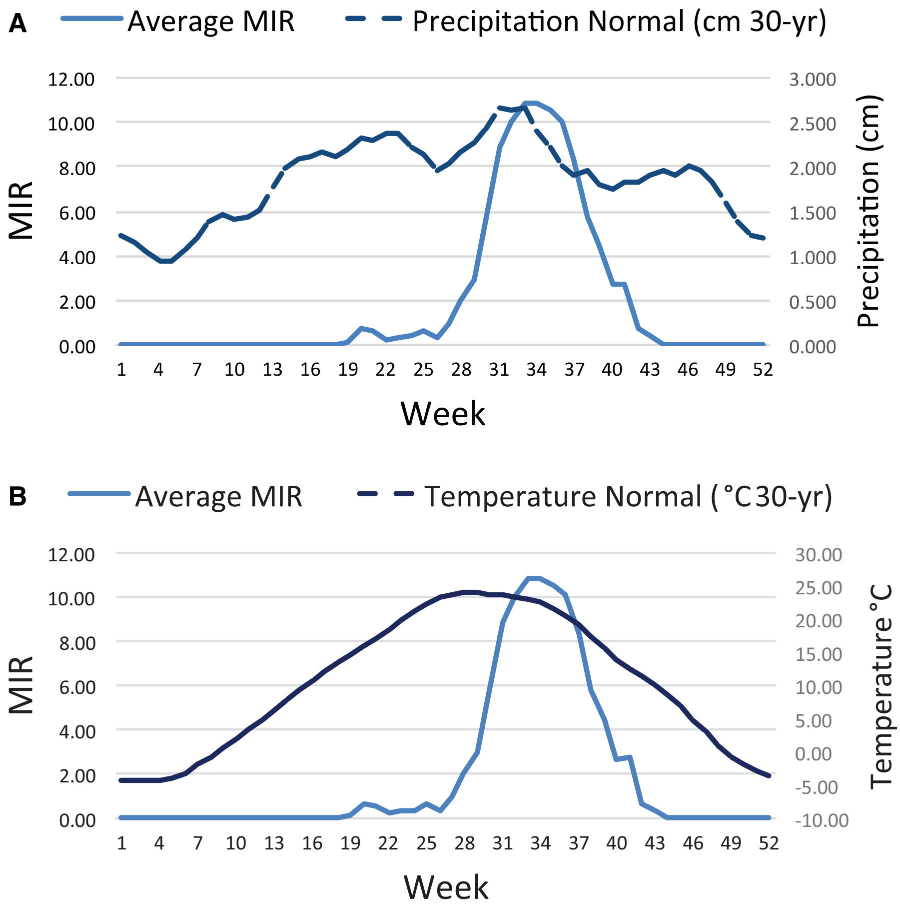

Fig. 2 (**A**) Average weekly Mosquito Infection Rate (*MIR*) with normal precipitation and (**B**) average MIR with normal temperature. The average MIR is a weekly average from the DuPage County study area from 2005 to 2014. (Online figure in color.)

temperature was measured as the mean of the temperature (°C) from the daily temperature readings from the two stations. Temperature data were further used to calculate a variable called a "Degree Week" (*DW*) constructed similarly to the more common Degree Day, but with differences accumulated over weeks, rather than days (Ruiz et al. 2010). The *DW* is the cumulative sum of the difference of all prior weekly temperatures from a threshold value of 22°C. The temperature threshold of 22°C was used because compared to other values, it led to the highest correlation between *DW* and the weekly local MIR based on cross-correlations across a range of threshold values from 10° to 24°C and time lags from 1 to 10 wk (Baker et al. 1984, Curriero et al. 2005, Kunkle et al. 2006). For a given week: $\Delta DW = T_{mean} - T_{base}$ if the weekly Temperature (T_{mean}) is greater than the threshold ($T_{base} = 22°C$) and 0 otherwise. To remove the seasonal trend from the model, weather variables were measured as the weekly differences from the 30-year Climate Normals for 1981–2010, provided by the U.S. National Weather Service (Fig. 2). These differences captured the patterns outside the seasonal trends and focused the analysis on characterizing how weeks differed from the expected values. We also considered variables that measured the prior year's average precipitation as was done in Ruiz et al. (2010). To improve our understanding of this relationship with *MIR*, we considered the effect of the average precipitation for four equal parts of the prior year starting with week 1, rather than the year as a whole.

Mosquito Data

The results of mosquito pools tested for WNV during the years from 2005 to 2013 from specimens collected from gravid traps located in DuPage County were provided by the Illinois Department of Public Health (IDPH). These data were submitted to the IDPH Web Portal, where Illinois agencies upload WNV mosquito test results. For 2014 data, mosquito test results were received directly from the DuPage County Department of Public Health. Test results were selected to include only the most common female vector species mosquitoes, which in this region are *Culex pipiens* and *Culex restuans* (Hamer et al. 2008, Andreadis 2012). PCR and VecTests were reported from 2005 to 2007 and PCR and RAMP tests, from 2009 to 2014. PCR tests comprised from 49 percent to 65 percent of all samples, depending on the year. The IDPH protocol stipulates pool sizes no larger than 50 individuals, and 19,115 (99 percent) of the 19,345 pools tested were within this guideline. The number of gravid trap locations in the study region during the years of interest varied from 136 trap locations in 2007 to 72 in 2014 (Fig. 1). Test result data were grouped by week and the *MIR* was calculated for a given week where: minimum infection rate = 1000 × (number of positive pools)/ (total number of mosquitoes in pools tested), using the CDC Excel Add-in for pooled infection rates (Biggerstaff 2009). As with the weather data, the *MIR* variable was calculated as the difference from the countywide average *MIR* from 2005–2013 (Fig. 2).

Table 1. DuPage County West Nile virus-related annual conditions data summary

Year	MIR mean (SD)	Week of max MIR (peak)	Avg Prec. (cm) of 3 wk before peak week[a]	*DW* at peak week[a]	WNV human cases
2005	5.57 (6.14)	32	−0.74	11.95	47
2006	6.88 (8.50)	34	−0.68	6.67	43
2007	2.76 (3.18)	33	1.23	−1.52	10
2008	1.13 (1.77)	37	0.59	−2.31	1
2009	0.78 (0.77)	37	0.36	−5.22	0
2010	5.66 (6.90)	35	−1.61	16.98	17
2011	2.63 (3.73)	36	−0.77	12.46	2
2012	8.74 (7.91)	32	−0.08	29.02	56
2013	4.52 (5.56)	36	−1.40	5.42	6
2014	3.27 (5.07)	35	3.42	−0.57	6

[a] Differences from weekly averages using the 30-yr Normal of both temperature and precipitation.

Model Development

To determine how well the legacy model published in Ruiz et al. (2010) performed for DuPage County alone, we first used the coefficients from the weather-only (*MIR* independent) version of this model and local weather station data and compared visually the actual *MIR* for DuPage County with the predicted weekly *MIR* values. For the new model, initially, we considered all weather variables—including 1–8 wk lags of temperature and rainfall and the prior year's precipitation measured in quarters, halves, and the full year. We used Pearson's correlation *r* values to assess the strength of associations between weather variables and *MIR* at different time lags to determine how far back in time to include weekly lagged weather variables and to determine the relative strength of the associations with prior seasons' precipitation.

Using the same general approach as the legacy model, we developed new linear regression models to predict the weekly DuPage County *MIR*. All models were fitted using the least squares method with the R package *stats* (R Development Core Team 2013). We selected the model variables using adjusted R^2 (R^2adj) and Akaike Information Criteria (AIC) with both backward and forward stepwise regression with a significance level threshold of $\alpha = 0.1$. Calendar weeks 18–38 (from the end of April to mid-September) from each year were used to develop the model. Data were treated as a weekly time series, with weekly weather data starting four weeks prior to the *MIR* data, to account for the temporal lags prior to the first *MIR* measurement in week 18.

We investigated the effect of the temporal autocorrelation of *MIR* by developing *MIR* lag dependent models that included prior levels of *MIR* to predict future levels. We then added all interaction terms between the temperature and precipitation weekly lagged weather variables in interactions models. One important practical goal was to determine if it was possible to use the *MIR* measured from mosquitoes collected and tested during the current season for real-time predictions. Thus, we compared four model types in the model development phase: *MIR* dependent models without and with interaction terms, and *MIR* independent models without and with interaction terms.

The new models for DuPage County were fitted initially using data from the years 2005 through 2012, while data from 2013 and 2014 were used to test the models' predictive ability. Since the difference from the weekly average MIR was used to fit the model, the *MIR* weekly averages were added to the model estimates to produce the predicted *MIR* values. The predicted residual sum of squares (PRESS), calculated as the sum of squared errors of out-of-sample prediction values for 2005 to 2013, was used as a measure to compare the model predictions (Chaves and Pascual 2007). Out-of-sample predictions were made by randomly dropping one weekly observation at a time to predict, while using the remainder of the data to fit the model. Once we selected the best model for DuPage County and were reaching the end of the 2014 mosquito season, we refit the model including the year 2013 data to recalculate and improve the models' coefficients. Finally, we compared the best new local model with the legacy model predictions, using the mean square prediction error (MSPE) and standard error (SE) of MSPE for model prediction for the year 2014, a year that was not used to fit the coefficients of either of the two models.

Results

Data Exploration

During the study period, the three years with the highest rates of human illness in DuPage County were 2005, 2006, and 2012, with at least 40 or more cases of WNV illness (Table 1). These years also had high average mosquito infection rates of 5.57, 6.88, and 8.74, respectively. In the two years 2010 and 2013, average *MIR* was similar to the years with more human illness, but the peak *MIR* week was later. Weekly precipitation was often lower in the three weeks prior to the peak *MIR* and the DW temperature higher at the peak *MIR* week during higher MIR years.

The initial comparison between the actual *MIR* and predicted *MIR* using the legacy model for DuPage County indicated that the model captured the main trend of infection rates but did not always correctly estimate the amplitude or timing of mosquito infection, especially in years with low infection rates (Fig. 3A).

Weekly average precipitation showed moderate correlation with *MIR*. The assessment of correlations between weather variables and *MIR* at different weekly time lags determined that the average weekly precipitation and *DW* were most strongly correlated with *MIR* at lags 1–4, with correlation dropping after a 4-wk lag (Fig. 4). The correlation between *MIR* and *DW* was particularly strong at short lags and showed a clear pattern of decreasing correlation with increased time lag. The Pearson's correlations between MIR and lagged MIR were 0.88 ($n = 209$, $P < 0.0001$) at 1 wk and 0.73 ($n = 208$, $P < 0.0001$) at 2 wk. We found that the average precipitation of weeks 27–39 of the previous year showed the highest negative correlation with *MIR* (Table 2). Therefore, we considered this variable in the new DuPage County MIR model.

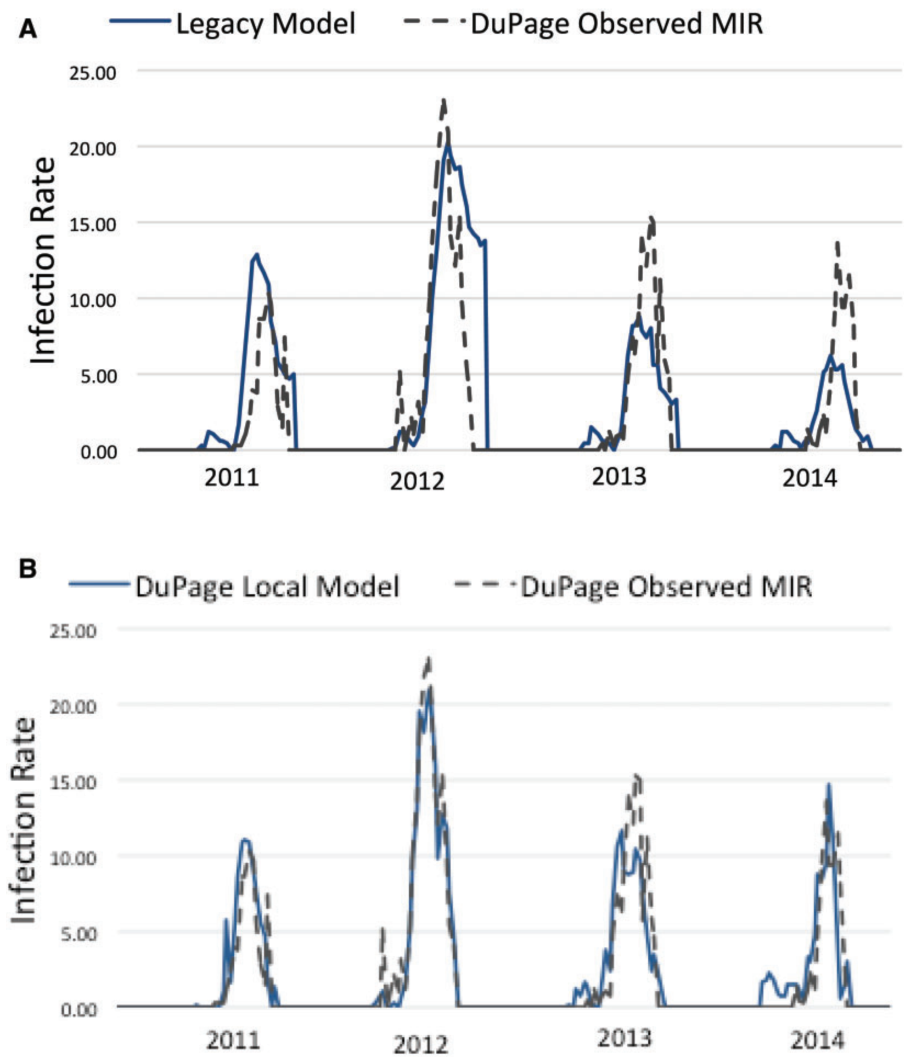

Fig. 3. (**A**) Measured *MIR* and legacy model estimates (Predicted *MIR* = a + 0.35 (3wk *Prec.* moving average at 3-wk lag) + 0.42 (*DW* at 1-wk lag) − 1.57 (*previous year prec.*)) (MSPE* 2.640). (**B**) Measured *MIR* and new model estimates with interactions (MSPE 1.826). *Mean squared prediction error. Supplementary Material (online only) includes a graph of the full range of years shown as a subset of four years in Figure 3A. (Online figure in color.)

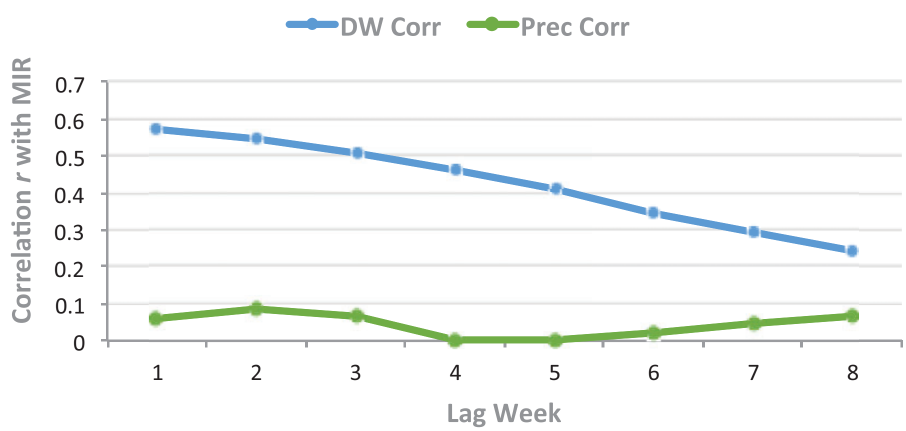

Fig. 4. Correlations between weather variables and DuPage MIR at lags of from 1 to 8 wk. (Online figure in color.)

Table 2. Pearson's correlation (r) between *MIR* and the previous year's average precipitation over blocks of 52, 26, and 13 wk

Values	Wk 1–52	Wk 1–26	Wk 27–52	Wk 1–13	Wk 14–26	Wk 27–39	Wk 40–52
r	−0.262	0.014	−0.439	−0.063	0.048	−0.460	−0.091
P-value	< 0.001	0.853	< 0.001	0.391	0.514	< 0.001	0.213

Table 3. Variable effects (standard errors) and fit of four model types: 1) Main effect model dependent on MIR, 2) Main effect model independent of MIR, 3) Interaction model dependent on MIR, 4) Interaction model independent of MIR

Terms	Model 1	Model 2	Model 3	Model 4
R^2 adjusted	0.661	0.511	0.721	0.658
PRESS	0.635	0.481	0.635	0.537
AIC	340.6	409.0	315.2	353.5
Main Effects (at week lag)				
MIR (2nd order)	0.14(0.02)***		0.11(0.02)***	
Week	−0.08(0.05)	−0.25(0.06)***	−0.10(0.05)*	−0.23 (0.05)***
Prec. (1)			0.06(0.04)	0.09(0.05)*
Prec. (2)	−0.06(0.04)	−0.09(0.05)	−0.05(0.04)	−0.03(0.05)
Prec. (3)			−0.07(0.04)	−0.09(0.05)
DW (1)	0.72(0.12)***	0.99(0.14)***	1.12(0.23)***	1.21(0.25)***
DW (2)			0.01(0.32)	0.13(0.36)
DW (3)			−0.59(0.32)	−0.83(0.37)*
DW (4)	−0.53(0.11)***	−0.41(0.13)**	0.01(0.21)	0.42(0.26)
Previous Year Prec. (wks 27–39)	−0.14 (0.05)***	−0.30(0.05)***	−0.08(0.04)	−0.18(0.05)***
Interaction Terms				
Prec. (1) × DW (2)			−0.83(0.20)***	−1.15(0.22)***
Prec. (1) × DW (3)			0.86(0.20)***	1.13(0.22)***
Prec. (2) × DW (2)			0.89(0.37)*	1.29(0.41)**
Prec. (2) × DW (3)			−1.71(0.51)**	−2.53(0.57)***
Prec. (2) × DW (4)			0.78(0.22)***	1.18(0.24)***
Prec. (3) × DW(1)			0.72(0.26)**	0.83(0.29)**
Prec. (3) × DW(2)			−0.68(0.25)**	−0.85(0.28)**
DW(2) × DW(4)			−0.12(0.03)***	−0.71(0.17)***
DW(2) × DW(3)				0.55(0.18)**

R^2 adjusted and predicted residual sum of squared errors (PRESS) are reported for each model. * indicated the variable is significant at 5% level, ** significant at 1% level, and *** significant at 0.1% level.

Model Selection

After observing the timing of data availability following mosquito collection and testing in the county, we determined that the data for a 2-wk lagged autoregressive *MIR* term may be available for use in a real-time prediction model, but the data would not be available in time for including the 1-wk lagged *MIR*. Initial model diagnostics revealed additional temporal correlation among the residuals, even after the seasonal de-trending of *MIR*. Thus, we also included the temporal variable *week* as a predictor. *Week* was a more significant and influential variable in the *MIR*-independent models. The four best models, after AIC variable selection, based on the R^2_{adj} and the smallest AIC included variables significant with $P < 0.1$. As a last step, the least important interaction terms were also excluded in cases where the model fits were not significantly changed as a result. From 6 to 19 variables were selected for the four models (Table 3).

Comparing model structures, two things became clear. First, in the models that included prior *MIR* (models 1 and 3), *MIR* had an exceptionally strong effect on the model prediction in all cases; and second, the interaction terms significantly improved the model fit. The *MIR*-dependent model with interaction effects (model 3) explained the most variation ($R^2_{adj} = 0.721$; AIC = 315.2), but the strong contribution of the interaction terms was seen especially when *MIR* from previous weeks was not included in the model (comparison of model 2 and model 4). Though the autoregressive *MIR* term was an important factor statistically, we determined that its inclusion in the model could overwhelm the effect of weather on *MIR* prediction. In other words, the *MIR* autoregressive terms tended to mimic the prior weeks' *MIR* pattern, making predictions less sensitive to actual changes in weather.

Based on these observations, we decided that the *MIR*-independent models were preferred. They modeled more clearly the relationship of next week's *MIR* with the weather variables and obviated the need to wait for field-based collections and testing. We then considered whether implementation of the more complex interaction term model was warranted over a simpler model. For DuPage County, the best independent main effects model (model 2) explained only about half of the variation in *MIR* ($R^2_{adj} = 0.451$; AIC = 409.0), whereas the best *MIR*-independent 2nd order interaction model (model 4) explained 66 percent (AIC = 353.5). For these reasons, we selected the latter model for implementation. The larger PRESS statistic of 0.537 of model 4 also showed the strength of this model over model 2 (PRESS = 0.481). Quadratic terms were also tested in model construction due to a possible quadratic relationship between *MIR* and *DW* lags seen in the exploratory analysis, but these did not improve the model. Finally, comparing the best local model with the legacy model, the 2014 MSPE and SE of the new local DuPage model was 4.54 and 1.70, respectively, which was lower (less error) when compared to the legacy model MSPE of 5.52 and SE 2.08.

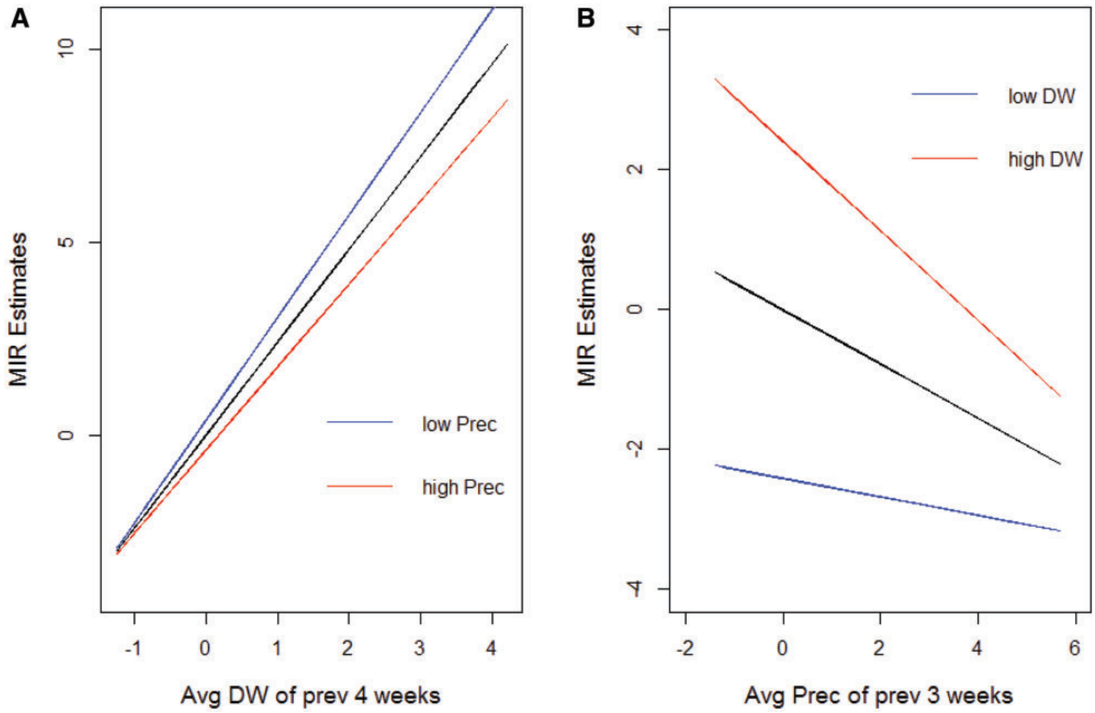

Fig. 5. Interaction plots between the variables *DW* and *precipitation* of preceding weeks and the variable *MIR*. All variables are measured as the difference from the weekly average. Covariates were scaled before plotting. (**A**) Effect of *DW* when precipitation is low/high. Equation of solid line: $MIR = -0.003 + 2.41 * DW$. (**B**) Effect of precipitation when *DW* is low/high. Equation of solid line: $MIR = -0.003 - 0.39 * prec$. (Online figure in color.)

Model Inference

The best model's final variable selection included weekly precipitation (*prec*) at 1 to 3 wk lags, weekly *DW* at 1 to 4 wk lags, the average precipitation in the third quarter of the previous year (*previous year prec. weeks 27–39*), and 9 interaction terms, for a total of 17 factors (Table 3). All of the included terms had significant effects at $\alpha = 0.1$ on *MIR* predictions. As with the legacy model, *DW* had a larger overall effect on infection rate than precipitation.

Considering the overall effect of the weather variables, an increase in average *DW* in the four prior weeks led to higher than average infection rate estimates. Precipitation effects varied, however, with a positive effect of rainfall in the week immediately prior, but a negative effect in the second and third prior weeks. Unlike *DW*, rainfall four weeks prior did not have an effect on the model estimates. The strongest main effects variable was *DW* with a 1-wk lag with an effect of 1.10. For precipitation, the strongest variable was lower than average precipitation during weeks 27–39 of the previous year, which led to higher MIR estimates with an effect of −0.21.

Discussion

Since temperature and precipitation are largely interdependent events, interaction terms more realistically represented the relationship between temperature and precipitation and their combined effect on infection rate. This was an important improvement over the legacy model and provided insight into how weather affected the mosquito infection rate. In particular, the interaction terms revealed that though higher *DW* generally increased *MIR*, higher *DW* two weeks prior in combination with higher than average precipitation in weeks 1, 2, and 3 prior each resulted in lower *MIR*. In other words, higher precipitation slightly reduced the magnitude of temperature's effect on *MIR*, as seen by the effect of *DW* on *MIR* decreasing from 2.41 to a magnitude of 2.16 when the average precipitation in preceding weeks is below average by 1.85 cm (Fig. 5A). In addition, with lower than average precipitation, temperature became an even stronger predictor of *MIR* (Fig. 5A) and with lower than average temperatures, precipitation had minimal to no effect on *MIR* (Fig. 5B). Refer to the Supplementary Materials (online only) for figures with all interaction plots.

The legacy model (Ruiz et al 2010) captured the overall shape of the mosquito infection curve when applied to a subregion of the area for which it was developed, but these significant improvements were possible by developing a new model to account for local weather conditions, by using the local *MIR*, by introducing additional terms, and by using more years of data in the model. We found that the general linear regression approach used by the legacy model, with *MIR* based on prior weather conditions, provided a reproducible methodology to estimate *MIR* in a location and time period that was not part of the original model. The assessment of the use of prior *MIR* in the new DuPage County model led us to conclude that a model that is not dependent on *MIR* measured in previous weeks is both statistically sound and operationally preferred. In situations where the MIR can be reliably measured across the entire study region, the MIR-dependent model may give good predictions most weeks, but with the caution that a prediction immediately after a rapid change in weather may not capture the true effect of weather and thus overemphasize the effect of past *MIR*. The inclusion of significant interaction terms between rainfall and temperature greatly improved the model's fit and provided more detailed insight into the relationship between weather and mosquito infection rate.

Both higher temperature and below average precipitation led to an increase in MIR, which conforms to prior expectations (Shaman et al. 2005, Paz and Albersheim 2008, Paz et al. 2013).

Additionally, temperature had a greater influence than precipitation on mosquito infection as demonstrated in the results of all four models, where the effect of *DW* had a much stronger effect than the precipitation variables (see Table 3). Significant interactions revealed that when temperature was much lower than average, low precipitation had little to no effect on the prediction and when precipitation was much lower than average, temperature had an even greater influence. It is this second situation that is most likely to lead to illness from WNV, and we recommend that public health personnel should develop the information they provide to the public on the risk of WNV in the following week by incorporating both the predicted MIR and the prior weather patterns.

Because lower than average precipitation during weeks 27–39 of the previous year resulted in higher *MIR* during the current mosquito season, the next summer's *MIR* can be approximated prior to the onset of the WNV season, a point also made by Hahn et al. (2015). Reasons behind the significance of the previous fall and winter's precipitation remain unclear. It is possible, for example, that less rainfall during the fall and winter are correlated with the amount of rainfall during later periods, and the effect is indirect rather than direct. It is also possible that this variable improves the model mostly during the early part of the season, and it may not be as important for the critical period of virus amplification. Less moisture in the soil at the start of the season might lead to a more patchy distribution of mosquito larval sites, thus influencing spatial patterns of interactions between birds and mosquitoes. Vegetation characteristics, related to the avian hosts and their interactions with WNV vectors, may also be affected by weather (Gibbs et al. 2006, LaDeau et al. 2008). Mosquito abundance may be higher following a dry fall due to a reduction of predator species (Walsh et al. 2008). Abundance may also be affected by a mild winter, with higher survival rates of overwintering *Culex pipiens* and *restuans*, while cooler weather earlier in the fall may lead to earlier, more successful hibernation, and earlier warmer conditions in the spring could provide conditions for early emergence (Walsh et al. 2008). The simple linear models used in the current study would not be suitable to determine these complex biological interactions. However, both precipitation and temperature during the prior year and the winter and spring weeks leading up to mosquito season of the same year should be evaluated in future work.

Several factors may influence the calculation of MIR estimates used to build the models. For WNV surveillance, the best policy management decisions are often tempered by funding and public perceptions related to pesticide use and to the risk of human illness (Shaw et al. 2010, Tedesco et al. 2010, Dickenson and Paskewitz 2012). Thus, temporal and spatial variability in testing effort and in mosquito abatement is likely, but it is difficult to measure. Pooled samples for testing mosquitoes are another issue. The testing of mosquitoes is usually done with pools of variable size, rather than testing individuals. This characteristic, in combination with the relative inability to discriminate between latent and active infection levels, and the differences in results from different testing methods can lead to errors in the measurement of mosquito infection rates (Bustamante and Lord 2010, Speybroeck et al. 2012). Although of interest from a research perspective, these measures are not easily managed across administrative areas, and different approaches in other places may need to be considered if this *MIR* model is applied in other locations.

An important area of research is to explore more fully the effects of weather on avian hosts, mosquito abundance, and human behavior relative to the risk of WNV illness. The relationship between mosquito infection and the abundance of *Culex* vectors could not be assessed in our analysis, so the model does not use a vector index measure, which is often used to determine the risk of human exposure (e.g., Chung et al. 2013). Abundance measures were not available in this study because the number of tested mosquitoes, not the full count from each collection was recorded in the IDPH database. DuPage County did have some light trap and larval sampling to monitor vector mosquito abundance, but these were not collected systematically across all entities and could not be incorporated into the model.

One future analysis would be to determine how weather influences the abundance of vector mosquito populations both temporally and spatially (see Yoo 2014 for example), and develop an approach to incorporate this into predictions of MIR. For example, Lebl et al. (2013) analyzed light trap counts of *Culex* mosquitoes relative to weather in northeast Illinois and found abundance was positively correlated with temperature during the prior two weeks and negatively associated with increased wind speed. Chaves et al. (2013) found that *Culex pipiens* abundance in the island of Jeju-do Korea was positively associated with temperature, but with heterogeneities at local scales, as mosquito abundance decreased with rainfall in the north, while it increased with minimum temperature in the south. Morin and Comrie (2013) developed a climate-based approach to link temperature and rainfall conditions in the southern United States to the population dynamics of the WNV vector *Culex quinquefasciatus* and extended their approach to consider future conditions under climate change, finding that dry and hot conditions may reduce populations. Kunkel et al. (2006) used a long-term database on vector mosquito abundance in Central Illinois to link weather to the so-called "crossover" of the early-season dominance of *Culex restuans* that gives way to the later-season *Culex pipiens*. The timing of their crossover was related to weather and often coincided with WNV amplification (Westcott et al. 2011). Studies that incorporate both biotic and abiotic factors to model mosquito abundance are relatively rare, and future work should be directed in this area to create a more nuanced WNV risk estimate.

The main intent of our work was to build a stable local model that would provide a reliable way to predict MIR quickly and effectively. With our model, we were able to provide regionally calibrated model-based estimates of MIR two to three weeks sooner than MIR estimation that needed test results from mosquitoes collected by a variety of agencies to be completed by all groups and compiled into a common MIR value. Of immediate interest would be to apply our methods to other locations to develop a similar weather-only model for further comparison where vegetation and landscape factors are different from those in northern Illinois. We do not expect that our model will apply to all other locations, but we expect that its general structure can form a template for similar MIR prediction models elsewhere and ultimately may be a way to estimate MIR, even in the absence of lab testing for WNV.

Supplementary Data

Supplementary data are available at *Journal of Medical Entomology* online.

Acknowledgments

This research was made possible through funding from the Wheaton Mosquito Abatement District, the Forest Preserve District of DuPage County, and the DuPage County Health Department. A. Bolds encouraged the initiation of the operational model and facilitated communication with the mosquito abatement and public health agencies in DuPage County. This material is also based upon work supported by the National Science Foundation

Ecology of Infectious Diseases program under Awards 0429124 and 0840403.

References Cited

Andreadis, T. G. 2012. The contribution of *Culex pipiens* complex mosquitoes to transmission and persistence of West Nile virus in North America. J. Am. Mosq. Control 28: 137–151.

Baker, D., B. Sharratt, H. Chiang, J. Zandlo, and D. Ruschy. 1984. Base temperature selection for the prediction of European corn borer instars by the growing degree day method. Agric. For. Meteorol. 32: 55–60.

Barker, C. M., B. G. Bolling, W. C. Black, C. G. Moore, and L. Eisen. 2009. Mosquitoes and West Nile virus along a river corridor from prairie to montane habitats in eastern Colorado. J. Vector Ecol. 34: 276–293.

Becker, B., P. T. Leisnham, and S. L. LaDeau. 2014. A tale of two city blocks: Differences in immature and adult mosquito abundances between socioeconomically different urban blocks in Baltimore (Maryland, USA). Intl. J. Environ. Res. Public Health 11: 3256–3270.

Biggerstaff, B. J. 2009. PooledInfRate, Version 4.0: A Microsoft Office Excel Addin to Compute Prevalence Estimates from Pooled Samples computer program, version By Biggerstaff, B. J., Fort Collins, CO.

Bustamante, D. M., and C. C. Lord. 2010. Sources of error in the estimation of mosquito infection rates used to assess risk of arbovirus transmission. Am. J. Trop. Med. Hyg. 82: 1172–1184.

CDC. 2014. West Nile Virus Statistics and Maps, Division of Vector-Borne Diseases, (http://www.cdc.gov/westnile/statsMaps/) (accessed 15 December 2014).

Chaves, L. F., and M. Pascual. 2007. Comparing models for early warning systems of neglected tropical diseases. PLoS Neglect Trop. D 1: e33.

Chaves, L. F., and U. D. Kitron. 2011. Weather variability impacts on oviposition dynamics of the southern house mosquito at intermediate time scales. B Entomol. Res. 101: 633–641.

Chaves, L. F., Y. Higa, S. H. Lee, J. Y. Jeong, S. T. Heo, M. Kim, N. Minakawa, and K. H. Lee. 2013. Environmental forcing shapes regional house mosquito synchrony in a warming temperate island. Environ. Entomol. 42: 605–613.

Chung, W. M., C. M. Buseman, S. N. Joyner, S. M. Hughes, T. B. Fomby, J. P. Luby, and R. W. Haley. 2013. The 2012 West Nile encephalitis epidemic in Dallas, Texas. JAMA – J. Am. Med. Assoc. 310: 297–307.

Ciota, A. T., and L. D. Kramer. 2013. Vector-virus interactions and transmission dynamics of West Nile virus. Viruses 5: 3021–3047.

Curriero, F. C., S. M. Shone, and G. E. Glass. 2005. Cross correlation maps: A tool for visualizing and modeling time lagged associations. Vector-Borne Zoonotic Dis. 5: 267–275.

Day, J. F., and G. A. Curtis. 1999. Blood feeding and oviposition by *Culex nigripalpus* (Diptera: Culicidae) before, during, and after a widespread St. Louis encephalitis virus epidemic in Florida. J. Med. Entomol. 36: 176–181.

Dickenson, K., and S. Paskewitz. 2012. Willingness to pay for mosquito control: How important is West Nile virus risk compared to the nuisance of mosquitoes? Vector-Borne Zoonotic Dis. 12: 886–892.

Dohm, D. J., M. L. O'Guinn, and M. J. Turell. 2002. Effect of environmental temperature on the ability of *Culex pipiens* (Diptera: Culicidae) to transmit West Nile virus. J. Med. Entomol. 39: 221–225.

Ebert, T. A., R. Brlansky, and M. Rogers. 2010. Reexamining the pooled sampling approach for estimating prevalence of Infected insect vectors. Ann. Entomol. Soc. Am. 103: 827–837.

Gardner, A. M., G. L. Hamer, A. M. Hines, C. M. Newman, E. D. Walker, and M. O. Ruiz. 2012. Weather variability affects abundance of larval *Culex* (Diptera: Culicidae) in storm water catch basins in suburban Chicago. J. Med. Entomol. 49: 270–276.

Gardner, A. M., T. K. Anderson, G. L. Hamer, D. E. Johnson, K. E. Varela, E. D. Walker, and M. O. Ruiz. 2013. Terrestrial vegetation and aquatic chemistry influence larval mosquito abundance in catch basins, Chicago, USA. Parasite Vector 6: 9.

Gibbs, S. E., M. C. Wimberly, M. Madden, J. Masour, M. J. Yabsley, and D. E. Stallknecht. 2006. Factors affecting the geographic distribution of West Nile virus in Georgia, USA: 2002–2004. Vector-Borne Zoonotic Dis. 6: 73–82.

Gu, W., R. Lampman, and R. J. Novak. 2003. Problems in estimating mosquito infection rates using minimum infection rate. J. Med. Entomol. 40: 595–596.

Hahn, M. B., A. J. Monaghan, M. H. Hayden, R. J. Eisen, M. J. Delorey, N. P. Lindsey, R. S. Nasci, and M. Fischer. 2015. Meteorological conditions associated with increased incidence of West Nile virus disease in the United States, 2004–2012. Am. J. Trop. Med. Hyg. 92: 1013–1022.

Hamer, G. L., U. D. Kitron, J. D. Brawn, S. R. Loss, M. O. Ruiz, T. L. Goldberg, and E. D. Walker. 2008. *Culex pipiens* (Diptera: Culicidae): a bridge vector of West Nile virus to humans. J. Med. Entomol. 45: 125–128.

Hartley, D. M., C. M. Barker, A. Le Menach, T. Niu, H. D. Gaff, and W. K. Reisen. 2012. Effects of temperature on emergence and seasonality of West Nile virus in California. Am. J. Trop. Med. Hyg. 86: 884–894.

Hepworth, G. 2005. Confidence intervals for proportions estimated by group testing with groups of unequal size. J. Agric. Biol. Environ. St 10: 478–497.

Hokit, G., S. Alvey, J. M. Geiger, G. D. Johnson, M. G. Rolston, D. T. Kinsey, and N. Tall Bear. 2013. Using undergraduate researchers to build vector and West Nile virus surveillance capacity. Intl. J. Environ. Res. Public Health 10: 3192–3202.

Jones, C. E., L. P. Lounibos, P. P. Marra, and A. M. Kilpatrick. 2012. Rainfall influences survival of *Culex pipiens* (Diptera: Culicidae) in a residential neighborhood in the mid-Atlantic United States. J. Med. Entomol. 49: 467–473.

LaDeau, S. L., P. P. Marra, A. M. Kilpatrick, and C. A. Calder. 2008. West Nile virus revisited: Consequences for North American ecology. Bioscience 58: 937–946.

Lebl, K., K. Brugger, and F. Rubel. 2013. Predicting *Culex pipiens/restuans* population dynamics by interval lagged weather data. Parasite Vector 6: 129.

Macdonald, G. 1956. Theory of the eradication of malaria. B World Health Organ 15: 369–387.

Moore, C.G.M., R. G. McLean, C. J. Mitchell, R. S. Nasci, T. F. Tsai, C. H. Calisher, A. A. Marfin, P. S. Moore, and D. J. Gubler. 1993. Guidelines for Arbovirus Surveillance Programs in the United States. Division of Vector-Borne Infectious Diseases, Centers for Disease Control and Prevention, Fort Collins, CO.

Morin, C. W., and A. C. Comrie. 2013. Regional and seasonal response of a West Nile virus vector to climate change. B Natl. Acad. Sci. USA 110: 15620–15625.

Nasci, R. S. 2013. Monitoring and controlling West Nile Virus: Are your prevention practices in place? J. Environ. Health 75: 42–44.

Paz, S., and I. Albersheim. 2008. Influence of warming tendency on *Culex pipiens* population abundance and on the probability of West Nile fever outbreaks (Israeli Case Study: 2001–2005). Ecohealth 5: 40–48.

Paz, S., D. Malkinson, M. S. Green, G. Tsioni, A. Papa, K. Danis, A. Sirbu, C. Ceianu, K. Katalin, E. Ferenczi, H. Zeller, and J. C. Semenza. 2013. Permissive summer temperatures of the 2010 European West Nile fever upsurge. PLoS ONE 8: e56398.

R Development Core Team 2013. R: A language and environment for statistical computing. computer program, version By R Development Core Team, Vienna, Austria (http://www.R-project.org/)

Reisen, W. K., Y. Fang, and A. C. Brault. 2008. Limited interdecadal variation in mosquito (Diptera: Culicidae) and avian host competence for Western equine encephalomyelitis virus (Togaviridae: Alphavirus). Am. J. Trop. Med. Hyg. 78: 681–686.

Reisen, W. K., T. Thiemann, C. M. Barker, H. Lu, B. Carroll, Y. Fang, and H. D. Lothrop. 2010. Effects of warm winter temperature on the abundance and gonotrophic activity of *Culex* (Diptera: Culicidae) in California. J. Med. Entomol. 47: 230–237.

Ruiz, M. O., L. F. Chaves, G. L. Hamer, T. Sun, W. M. Brown, E. D. Walker, L. Haramis, T. L. Goldberg, and U. D. Kitron. 2010. Local impact of temperature and precipitation on West Nile virus infection in *Culex* species mosquitoes in northeast Illinois, USA. Parasite Vector 3: 19.

Shaman, J., and J. F. Day. 2007. Reproductive phase locking of mosquito populations in response to rainfall frequency. PLoS ONE 2: e331.

Shaman, J., J. F. Day, and M. Stieglitz. 2005. Drought-induced amplification and epidemic transmission of West Nile virus in southern Florida. J. Med. Entomol. 42: 134–141.

Shaw, I. G. R., P. F. Robbins, and J. P. Jones. 2010. A Bug's life and the spatial ontologies of mosquito management. Ann. Assoc. Am. Geogr. 100: 373–392.

Speybroeck, N., C. J. Williams, K. B. Lafia, B. Devleesschauwer, and D. Berkvens. 2012. Estimating the prevalence of infections in vector populations using pools of samples. Med. Vet. Entomol. 26: 361–371.

Tedesco, C., M. Ruiz, and S. McLafferty. 2010. Mosquito politics: Local vector control policies and the spread of West Nile virus in the Chicago region. Health Place 16: 1188–1195.

Turell, M. J., M. L. O'Guinn, D. J. Dohm, and J. W. Jones. 2001. Vector competence of North American mosquitoes (Diptera: Culicidae) for West Nile virus. J. Med. Entomol. 38: 130–134.

Turell, M. J., D. J. Dohm, M. R. Sardelis, M. L. Oguinn, T. G. Andreadis, and J. A. Blow. 2005. An update on the potential of north American mosquitoes (Diptera: Culicidae) to transmit West Nile Virus. J. Med. Entomol. 42: 57–62.

Walsh, A. S., G. E. Glass, C. R. Lesser, and F. C. Curriero. 2008. Predicting seasonal abundance of mosquitoes based on off-season meteorological conditions. Environ. Ecol. Stat. 15: 279–291.

Walter, S. D., S. W. Hildreth, and B. J. Beaty. 1980. Estimation of infection rates in population of organisms using pools of variable size. Am. J. Epidemiol. 112: 124–128.

Westcott, N. E., S. D. Hilberg, R. L. Lampman, B. W. Alto, A. Bedel, E. J. Muturi, H. Glahn, M. Baker, K. E. Kunkel, and R. J. Novak. 2011. Predicting the seasonal shift in mosquito populations preceding the onset of the West Nile virus in Central Illinois. B Am, Meteorol. Soc. 92: 1173–1180.

Yoo, E. H. 2014. Site-specific prediction of West Nile virus mosquito abundance in Greater Toronto area using generalized linear mixed models. Intl. J. Geogr. Inf. Sci. 28: 296–313.