Meteorological and Hydrological Influences on the Spatial and Temporal Prevalence of West Nile Virus in *Culex* Mosquitoes, Suffolk County, New York

Meteorological and Hydrological Influences on the Spatial and Temporal Prevalence of West Nile Virus in *Culex* Mosquitoes, Suffolk County, New York

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ABSTRACT The factors determining the spatial and temporal distribution of West Nile virus (family *Flaviviridae*, genus *Flavivirus*, WNV) activity are not well understood. Here, we explore the effects of hydrological and meteorological conditions on WNV infection among *Culex* genus mosquitoes collected during 2001–2009 in Suffolk County, Long Island, NY. We show that WNV infection rates in assayed pools of *Culex* mosquitoes are associated in both space and time with hydrological and meteorological variability. Specifically, wet winter, warm and wet spring conditions, and dry summer conditions are associated with the increased local prevalence of WNV among *Culex* mosquitoes during summer and fall. These findings indicate that within Suffolk County, and for a given year, areas at risk for heightened WNV activity may be identified in advance by using hydrology model estimates of land surface wetness and observed meteorological conditions.

KEY WORDS West Nile virus, hydrology, meteorology, transmission, amplification

West Nile virus (family *Flaviviridae*, genus *Flavivirus*, WNV) first appeared in North America in New York City during 1999 (Marfin and Gubler 2001). Since its introduction, this mosquito-borne pathogen has spread throughout the continent. The arrival of WNV in many North American locales was marked by large numbers of WNV infections among avian, equine, and human hosts (USGS 2010). After these initial epidemics, the virus did not disappear but instead settled into a pattern of endemicity in which outbreaks of variable size develop in some years but not others.

There is ongoing need to improve our understanding of how and why these hot spots of increased WNV activity develop in space and time. Some of this spatial–temporal variability is no doubt linked to environmental variability, including changes in meteorological and hydrological conditions. With more than a decade of recorded WNV activity and the development of gridded, high-resolution meteorological and hydrological observations, there is now considerable opportunity to examine and understand how environmental conditions affect WNV amplification and transmission dynamics in both space and time. In particular, we can use meteorological and hydrological data to identify how weather and land surface wetness influence 1) the distribution, abundance, and age structure of vector mosquitoes; 2) the zoonotic transmission, amplification, and prevalence of WNV in both vector mosquito and vertebrate host populations; and 3) the transmission of WNV to dead-end hosts, including humans.

Robust associations between environmental conditions and indicators of WNV activity can lead to predictive frameworks for identifying areas at risk for WNV in real time (Shaman and Day 2005; Day and Shaman 2008). This ability to monitor WNV activity will facilitate more efficient appropriation of vector control resources and public health interventions aimed at reducing human West Nile (WN) cases.

Our focus for this study is Suffolk County, Long Island, NY. We examine the statistical association between local meteorological and hydrological conditions and the presence of WNV in pools of gravid and light trap collected *Culex* mosquitoes during 2001–2009.

Materials and Methods

Study Area. In 1999, West Nile virus was discovered within Suffolk County and was found in mosquitoes, birds, and horses. Since then, WNV has been found each year infecting a combination of humans, mosquitoes, birds, and horses. East of New York City, Suffolk County has a land area of $\approx 2.4 \times 10^9$ m^2 (912 square miles) and occupies the eastern portion of Long Island, NY. Generally, the western portion the county consists of densely populated residential areas and commercial properties. The eastern portion of the county is rural with a less dense human population and more open space and agriculture. Natural areas are

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found throughout the county but are more prevalent in the eastern portion. Natural woodlands (pineland or hardwood forests) and freshwater wetlands are found throughout the county with coastal salt marshes primarily on the south shore and east end.

Mosquito Pool Data. Our study focuses on WNV-assayed pools of *Culex* spp. mosquitoes. *Culex* mosquitoes have been identified as vectors of WNV throughout the world (Hayes et al. 2005). Three species of *Culex* predominate in Suffolk County, NY: *Culex pipiens* L., *Culex restuans* Theobald, and *Culex salinarius* Coquillett, and all three species have tested WNV positive within Suffolk County (Rochlin et al. 2009). In the northern United States, enzootic WNV transmission is thought to occur primarily via *Cx. pipiens* and *Cx. restuans* (Kulasekera et al. 2001; Andreadis et al. 2004). Epizootic WNV transmission may be primarily due to *Cx. pipiens* (Kilpatrick et al. 2005, Hamer et al. 2008) and *Cx. salinarius* (Kulasekera et al. 2001; Andreadis et al. 2004).

Mosquito collections were made throughout Suffolk County during 2001–2009 by using both Centers for Disease Control and Prevention (CDC) gravid and CDC miniature light traps (John W. Hock Co., Gainesville, FL). Gravid traps were baited with rabbit-chow infusion and light traps were baited with dry ice. Mosquito surveillance was conducted weekly from approximately early June to early October, depending on mosquito population levels and the presence of WNV. At the beginning of each season, trapping sites were guided by the historical presence of WNV. As the seasons progressed, mosquito surveillance was expanded to locations with newly identified WNV in humans, birds, and horses. Approximately half of the traps were operated in and around various town, county, and state parks.

Collected mosquitoes were anesthetized with dry ice and identified to species. *Cx. pipiens*, *Cx. restuans*, and *Cx. salinarius* have similar morphological characteristics that can be compromised by physical damage during collection (Crabtree et al. 1995; Debrunner-Vossbrinck et al. 1996). Thus, historically in New York, *Cx. pipiens* and *Cx. restuans* are combined (i.e., *Cx. pipiens/restuans*) for arboviral testing (Bernard et al. 2001). *Cx. salinarius* specimens are separated from the other *Culex* species whenever possible, but again, due to damage to identifying characters during collection, *Cx. salinarius* may be unintentionally included in *Cx. pipiens/restuans* pools (Bernard and Kramer 2001).

For arboviral analysis, specimens were submitted to the New York State Department of Health (Arbovirus Laboratory, Wadsworth Center). West Nile virus analysis was performed by real-time reverse transcription-polymerase chain reaction (PCR) and all non-*Culex* specimens were placed in Vero cell culture to attempt isolation of other arboviruses (Lukacik et al. 2006). Specimens were submitted in pool sizes of 10-100 specimens (mean = 28.7; median = 25) according to New York State Department of Health protocol (Bernard et al. 2001; Lukacik et al. 2006). To meet this requirement when mosquito numbers are low, specimens of identical species from the same location may

Table 1. Number of trap locations used each year in Suffolk County, Long Island, NY

Yr	No. of trap locations	No. of *Culex* pools tested	No. of WNV-positive *Culex* pools
2001	75	721	48
2002	101	786	30
2003	89	1,088	33
2004	58	613	7
2005	104	1,051	69
2006	63	858	54
2007	47	432	12
2008	95	643	40
2009	50	775	15

The table also lists the annual numbers of *Culex* pools tested for WNV and the number positive.

be combined from the gravid and light traps or combined over 2 wk, which allows for increased arboviral testing while coarsening the temporal resolution of the record.

Table 1 presents the yearly number of trap locations, as well as the number of *Culex* pools assayed for WNV and the number positive for WNV. Non-*Culex* mosquitoes also were collected, pooled, and assayed for WNV during 2001-2009 (in total, 5,000 additional pool assays, or 28% of all mosquito pools); however, *Culex* pools accounted for 96.6% of positive pools. Only *Culex* pools are included in this analysis.

Hydrological and Meteorological Data. For this study, we used Mosaic hydrology model estimates of soil moisture conditions (Koster and Suarez 1996). The Mosaic hydrology model divides the land surface into square grid cells, each with a multilayer soil column structure. Local surface meteorological conditions are used to integrate the model through time and compute column-averaged water and energy fluxes at the land surface and within the soil column. Each grid cell is further divided into a "mosaic" of tiles, each representing different vegetative surfaces, which account for variability of surface characteristics within the cell area. Observed vegetation distributions are used to determine the partitioning of tiles, and the water and energy balances in each tile are simulated independently.

Mosaic model simulations are produced through the North American Land Data Assimilation Systems (NLDAS) project-2 and are available in hourly time steps at 0.125° resolution from 1979 through the present (Mitchell et al. 2004; Schaake et al. 2004, NLDAS 2010). At this resolution (≈13 by 13 km), each grid cell resolves hydrologic conditions at a geographic scale matching the upper limit of the flight range reported for *Cx. tarsalis* in California (Reisen et al. 1992) and represents an area in which the vector mosquito population and WNV transmission dynamics are probably localized. The Mosaic model uses three soil layers with thicknesses from top to bottom of 10, 30, and 160 cm, respectively, and a uniform rooting depth of 40 cm. Water storage in each model column layer is the weighted average of the water storage from the column tiles.
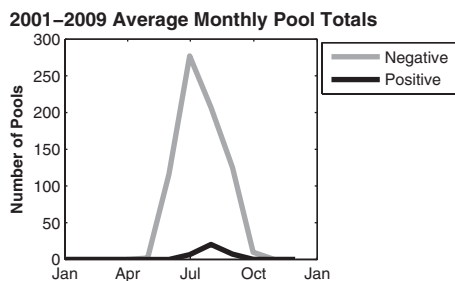
2001–2009 Average Monthly Pool Totals

Fig. 1. Average monthly numbers of WNV negative and positive *Culex* pools in Suffolk County during 2001–2009.

For this work, we used two Mosaic model-simulated estimates of land surface wetness: root zone soil moisture (RZSM), which represents water content in the top 40 cm of the soil column, and layer one soil moisture (L1SM), which represents water content in the top 10 cm of the soil column. Both RZSM and L1SM are in units of kilograms per square meter. For the analysis, the hourly RZSM and L1SM estimates were each temporally aggregated to monthly averages during the period 2001-2009 and compared with the spatiotemporal distribution of WNV-positive pools of trap-collected *Culex* mosquitoes.

In addition, meteorological conditions were included in the analysis. These data also were produced by NLDAS project-2 and are derived through spatial interpolation, temporal disaggregation, and vertical adjustment from station measurements and National Center for Environmental Prediction North American Regional Reanalysis (Mesinger et al. 2006). These meteorological data are also available in hourly time steps at 0.125° resolution from 1979 through the present (Cosgrove et al. 2003). Monthly averages of precipitation (surface rainfall and snowfall measured in millimeters per day), temperature (2-m above-ground air temperature in Kelvin), and specific humidity (2-m above ground measure of absolute humidity in kilograms per kilograms) were used in this analysis.

Statistical Analysis. To formally assess the effect of hydrological and meteorological variability on WNV prevalence we used a generalized linear model (GLM). The predictand was the annual percentage of *Culex* pools testing WNV positive within each NLDAS grid cell area. These percentage data are exponential, so we used a Poisson model with a dispersion parameter to account for inflated variance. In total, 116 grid cell-years exist in Suffolk County during 2001-2009, an average of ≈13 per year. All of these data were used in the analysis.

Regression was performed using combinations of the meteorological (precipitation, temperature, and specific humidity) and hydrological (RZSM or L1SM) monthly data as the predictor variables. WNV presence among *Culex* mosquito pools peaks in Suffolk County in August (Fig. 1); we therefore only tested meteorological and hydrological conditions during January–August in our GLM. Up to four predictor variables were tested at once: individual monthly con-

ditions of temperature, precipitation, specific humidity, and either RZSM or L1SM. RZSM and L1SM were not used in the same regression. An example regression would use March temperatures, June precipitation, and July RZSM to predict the annual percentage of WNV-positive *Culex* pools for each grid cell area in Suffolk County during 2001-2009.

In addition, we also tested GLMs with two monthly lags of the Mosaic hydrological condition estimates, e.g., March L1SM and July L1SM. This further discrimination allowed for variable hydrological effects through the year, in particular different effects during spring and summer when different *Culex* mosquito species are active and the effect of hydrology on WNV amplification may diverge. Such variable hydrological effects have been shown to affect arbovirus transmission rates in other regions of the United States (Shaman et al. 2002, 2005). Only single monthly meteorological data were included in these regressions, for up to a total of five explanatory variables. An example regression could use March temperatures, March specific humidity, June precipitation, February RZSM, and July RZSM.

Best-fit models were identified based on whole model goodness-of-fit among only the GLMs for which all parameter estimates were statistically significant ($P < 0.05$). Two goodness-of-fit metrics were used: model deviance and the Akaike Information Criterion (AIC). The two measures of goodness-of-fit were generally in accord with one another.

Temporal Cross-Validation. Leave-one-out temporal cross-validation (LOOTCV) also was performed. The GLM analysis was repeated using a subset of the full Suffolk County record in which 1 yr of data were omitted from the analysis. The parameter estimates and their significance for the LOOTCV model were examined and compared with the full model and the LOOTCV model was used to predict the percentage of WNV-positive *Culex* pools at each site for the omitted year. This process was repeated for each of the 9 yr (2001-2009) of data. The omitted year estimates were then compared with the observed percentage of WNV-positive *Culex* pools via calculation of root mean square error (RMSE). This RMSE was then compared with the RMSE for the full GLM model that included all 9 yr data.

Spatial Considerations and Anomaly Analysis. A greater percentage of *Culex* pools tested WNV positive in western Suffolk County than eastern Suffolk County (Fig. 2). This strong west–east gradient of WNV activity is mirrored by west–east gradients of meteorological and hydrological conditions. In particular, temperatures during spring and summer are warmer and L1SM and RZSM conditions throughout the year are drier in western Suffolk County than in eastern Suffolk County (Fig. 3). Precipitation does not show any consistent west–east gradient for the region; specific humidity mirrors temperature in the colder winter, but during summer more directly reflects proximity to warm open ocean waters. These observations indicate that land surface wetness conditions on Long Island are strongly influenced by tempera-
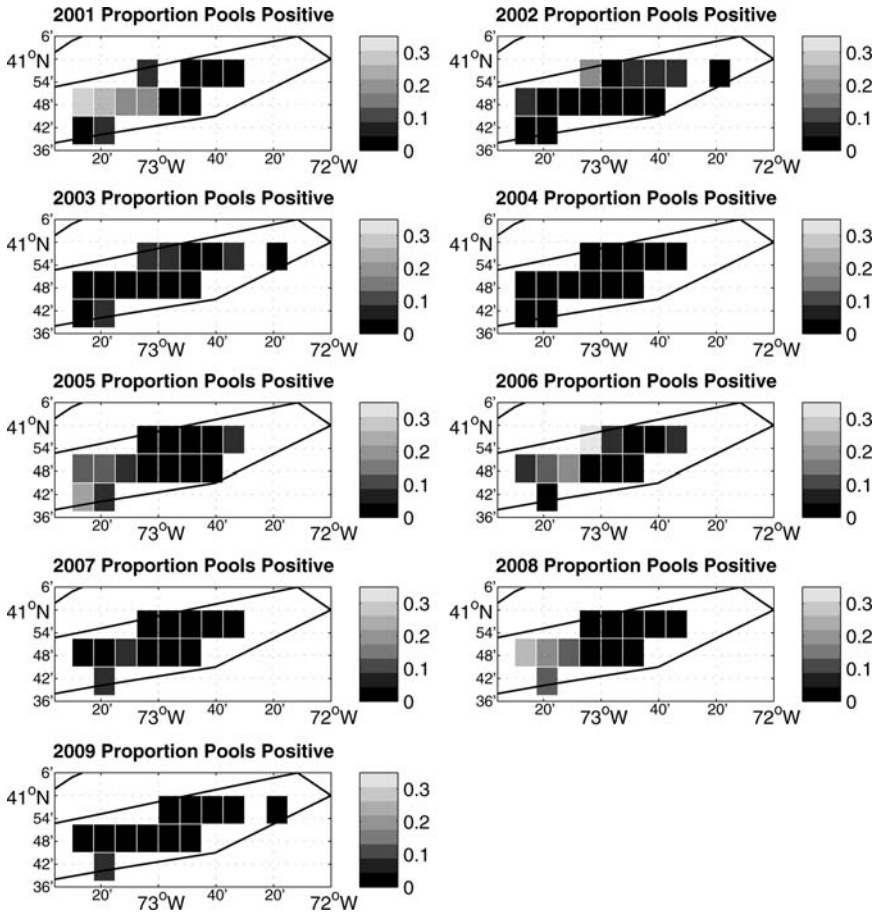
Fig. 2. Yearly proportion of *Culex* pools testing WNV positive in each NLDAS grid cell area of Suffolk County. Only grid cell-years with WNV-tested *Culex* pools and Mosaic hydrology model simulations are shown.

ture, which greatly controls rates of evaporation and transpiration from the land surface.

Due to these west–east gradients of both WNV activity and environmental conditions, it was considered possible that the GLM analysis would merely identify the covariability of these spatial features, i.e., that more WNV-positive pools occur where temperatures are warmer and the land surface wetness (i.e., RZSM and L1SM) is reduced. To account for this covariability, we performed two additional analyses: 1) we divided the county at 73° W into western and eastern portions and repeated the GLM analysis on each independently; and 2) we repeated the GLM analysis by using local monthly anomalies of the meteorological and hydrological conditions.

For the second analysis, at each grid cell, we subtracted the 2001–2009 monthly average (i.e., monthly climatology) from the monthly time series:

$$T'_{(x,y,mn)} = T_{(x,y,yr,mn)} - \overline{T}_{(x,y,mn)} \qquad [1]$$

where $T'(x,y,yr,mn)$ is the monthly anomaly of some environmental condition T at location (x,y) for year yr and month mn. $\overline{T}(x,y,mn)$ is the monthly value of T

averaged over all years (2001-2009) at location (x,y) such that

$$\overline{T}_{(x,y,mn)} = \frac{\sum_{yr = 2001}^{2009} T_{(x,y,yr,mn)}}{9} \qquad [2]$$

By using anomalies, mean spatial gradients of hydrological and meteorological conditions are removed, and we can examine the effects of local deviations from typical local conditions on WNV activity.

Results

Analysis of the entire record (2001-2009 for all of Suffolk County) indicates that the eight best-fitting GLMs are combinations with five explanatory variables (Table 2). All of these models indicate that wetter land surface conditions during winter (January–March), drier land surface conditions during summer (June–August), increased April temperatures, increased May precipitation, and low March–April specific humidity favor a higher percentage of WNV-
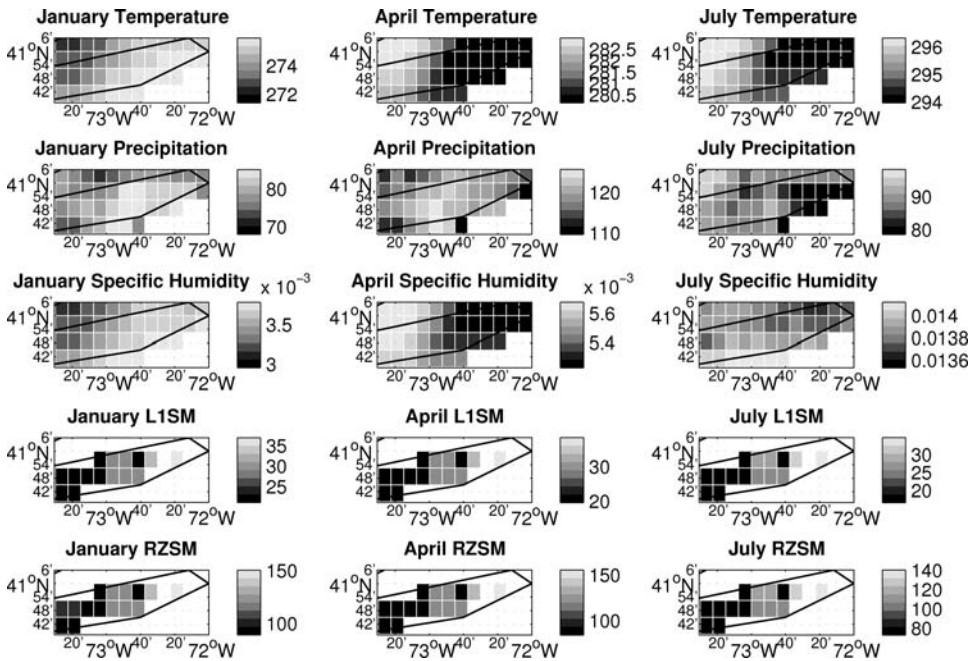
Fig. 3. Monthly averages of temperature (Kelvin), precipitation (kilograms per square meter), specific humidity (kilograms per kilogram), L1SM (kilograms per square meter), and RZSM (kilograms per square meter) on Long Island, including Suffolk County, for January, April, and July, 2001–2009.

positive *Culex* pools for that same year in a given grid cell. These findings suggest that wetter winter conditions (positive L1SM or RZSM effect), wetter and hotter spring conditions (positive precipitation and temperature effects), and drier summer conditions (negative L1SM or RZSM effect) all favor the enzootic transmission of WNV among *Culex* vectors and vertebrate amplification hosts.

The 10 best-fitting GLMs were all subjected to LOOTCV. All LOOTCV models produce parameter estimates with the same sign combinations and of the same general magnitude as their counterpart full GLMs. In fact, for all 10 best-fit models (Table 2), all LOOTCV parameter estimates are well within a factor of 2 of the full GLM model parameter estimates and most are within 25% (the median deviation is 18.6%). Generally, the LOOTCV parameter estimates also remain statistically significant ($P < 0.05$). There are some exceptions. For omission of 2001, 2005, or 2008, the specific humidity parameter estimate for one of the 10 best-fitting models fails to reach this level of significance. For 2006 omission, the winter land surface wetness in three of the eight five-variable models fails to reach this level of significance, as does the summer land surface dryness for one of the eight models, and precipitation in the three-variable model.

Overall, these results indicate that the full model is most sensitive to the exclusion of 2006 from the analysis; however, LOOTCV models that omit 2006 still yield best-fit models and parameter estimates that are similar to the full model. Thus, the LOOTCV findings indicate that 2006 is a critical year for helping to establish the importance of winter (January–March)

wetting and hydrology in general, but the overall results are not unduly sensitive to the exclusion of 2006 or any other year.

RMSE calculated for the LOOTCV predictions for each of the 10 models were slightly larger than full model RMSE, but these differences are <15% (Table 3). Figure 4 shows the LOOTCV predictions for the omitted data for the best-fit GLM (top row of Table 2), as well as the full GLM fit. Both model predictions are plotted in order from least to greatest about which the corresponding observations are scattered. Both the LOOTCV and full GLM predictions perform similarly and successfully discriminate areas and years for which >10% of tested *Culex* pools were positive.

Analysis of the western portion of Suffolk County produces best-fit GLMs that are similar to those for the entire county (model results not shown). The 10 best-fitting GLMs for western Suffolk County are all comprised of three to five variables and tend to include combinations with a wetter winter land surface (January–March); drier April, June, or July land surface; warmer temperatures during April–August; more precipitation during May or August; and less humid conditions during March–August. These findings are generally consistent with the results for the entire county (Table 2).

A similar analysis for the eastern portion of Suffolk County produces few significant models (10 of a possible 34,263 tested combinations). This shortcoming is in part due to the lack of WNV activity in the area. None of the grid cell sites in eastern Suffolk County produce an annual percentage of WNV-positive *Culex* pools >8.5%. Still, seven of the 10 eastern region sig-

Table 2. The 2001–2009 best-fit full GLM results for all of Suffolk County, Long Island, NY

Model	AIC	LISM (lag 1)	LISM (lag 2)	RZSM (lag 1)	RZSM (lag 2)	Temp	Precipitation	Specific humidity
1	344.5	Mar. 0.272 (0.087)	June −0.289 (0.089)			April 1.119 (0.175)	May 0.028 (0.008)	April −2779 (532)
2	344.5			Mar. 0.064 (0.021)	June −0.069 (0.021)	April 1.103 (0.166)	May 0.028 (0.008)	April −2732 (523)
3	350.9	Mar. 0.146 (0.057)	July −0.151 (0.047)			April 1.246 (0.173)	May 0.016 (0.006)	April −3154 (499)
4	351.1	Mar. 0.193 (0.066)	July −0.258 (0.060)			April 0.348 (0.118)	May 0.022 (0.007)	Mar. −2053 (432)
5	351.3	Feb. 0.168 (0.077)	July −0.181 (0.064)			April 1.083 (0.163)	May 0.012 (0.005)	April −2858 (513)
6	351.8			Mar. 0.034 (0.014)	July −0.036 (0.012)	April 1.225 (0.164)	May 0.015 (0.006)	April −3027 (491)
7	352.1			Mar. 0.048 (0.016)	July −0.062 (0.015)	April 0.407 (0.113)	May 0.022 (0.007)	Mar. −1944 (420)
8	353.6	Jan. 0.131 (0.057)	Aug. −0.167 (0.053)			June 0.558 (0.099)	May 0.025 (0.007)	Aug. −245 (121)
9	354.0					May 1.864 (0.226)	May 0.029 (0.006)	May −3580 (512)
10	355.1	May 0.199 (0.096)	July −0.206 (0.087)			April 1.385 (0.204)		April −3924 (723)

Models include up to five variables. Best-fit models are determined by AIC. Columns show the parameter effects associated with each variable, including the month used in the analysis, the parameter estimate, and in parentheses the SE of the parameter estimate. Units are percentage of WNV-positive pools per kilogram per square meter (LISM, RZSM, and precipitation), percentage of WNV-positive per degree Celsius (temperture), and percentage of WNV-positive pools per kilogram (specific humidity).

Table 3. RMSE of the LOOTCV GLMs versus RMSE of the full best-fit GLMs

Model	LOOTCV RMSE	Full GLM RMSE
1	4.68	4.23
2	4.79	4.23
3	4.65	4.35
4	4.75	4.35
5	4.70	4.35
6	4.66	4.36
7	4.73	4.37
8	5.04	4.40
9	5.08	4.48
10	4.57	4.46

The models are ordered as in Table 2. Units are annual percentage of WNV-positive *Culex* pools.

nificant GLMs (i.e., all parameter estimates significant at $P < 0.05$) select for wetter land surface conditions during either March or May, drier land surface conditions during June or July, hotter March or April temperatures, and increased precipitation during May. These relationships are consistent with those found for the whole of Suffolk County (Table 2).

We also repeated the GLM analysis for the whole of Suffolk county by using local monthly anomalies of meteorological and hydrological conditions (equation 1). Seven of the 10 best-fitting anomaly GLMs included wetter land surface conditions during either March or May, drier land surface conditions during June or July, hotter April temperatures, increased precipitation during March or May, and lower specific humidity during April. Again, these findings are generally consistent with the results for the entire county (Table 2).

Some spatial autocorrelation of the annual percentage of WNV positive *Culex* pools exists among grid cell sites in Suffolk County (Fig. 5, top). The best-fitting GLMs account for much of this spatial autocorrelation; this model diminution of the spatial autocorrelation is evident in the correlogram of the model residuals (Fig. 5, bottom). Nonetheless, we did perform simultaneous autoregression (SAR) with the GLM (Haining 1990; Shaman et al. 2010). The best-fitting models produced within the SAR GLM framework were in fact weaker (higher AIC and deviance) than the best-fitting models produced with the GLM (Table 2). These findings indicate that hydrological and meteorological variables provide a better constraint of the spatial structure of the field than inclusion of a simple distance-weighted spatial autoregressive term.

Discussion

Our findings indicate that meteorological and hydrological conditions provide a robust constraint on the spatial and temporal variability of WNV among pools of *Culex* mosquitoes in Suffolk County. The best-fitting GLMs indicate that wetter winter land surface conditions, warmer spring temperatures, increased spring precipitation, and drier early summer land surface conditions all favor the increased prevalence of WNV among *Culex* vectors. Based on tem-
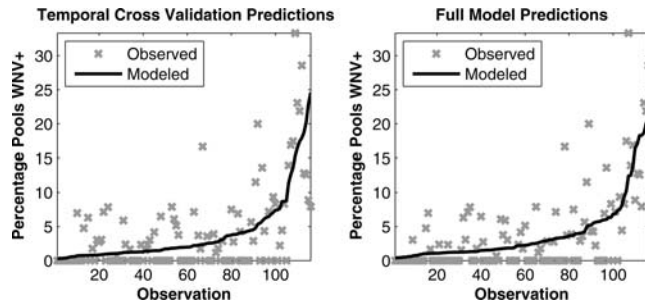
Fig. 4. LOOTCV GLM predictions for the best-fit parameter combination (left; top line of Table 2). Full GLM predictions for the same best-fit parameter combination (right). The observations and GLM predictions are plotted and ordered in pairs by the latter variable from least to greatest.

poral cross-validation and spatially partitioned analysis these associations seem robust in both time and space.

West Nile virus activity, as indicated by the yearly percentage of WNV-positive *Culex* pools, tends to be greater in western Suffolk County (Fig. 2) where summer temperatures are hotter and hydrological conditions are drier year-round (Fig. 3). In fact the year-to-year variability of hydrological conditions at any grid cell is much less than the east–west differences among grid cells (data not shown). However, the anomaly analysis presented here accounts for

Fig. 5. (Top) Correlation of annual percentage of *Culex* pools testing positive for WNV among Suffolk County grid cell sites plotted as a function of distance, 2001–2009. (Bottom) Same as for top but calculated for the residuals of the best-fit GLM for all of Suffolk County (see Table 2). The line with circles shows the average correlation at each distance.

these spatial differences of environmental conditions and the results of this analysis are similar to that of the full GLM.

Although the anomaly analysis is revealing, it is worth noting that mosquitoes do not respond to anomalies, per se (e.g., monthly anomalies of temperature). Mosquitoes respond to the actual ambient temperatures. If the environmental conditions in the western portion of the island are more hospitable to a given *Culex* species, then using monthly anomalies, which to a certain extent weights all localities equally, is not as informative as using raw monthly data. However, that the anomalies and raw data generally produce similar results indicates that the associations between WNV activity and meteorological and hydrological conditions are not merely a consequence of their common spatial covariability with some other "real" driver.

In truth, the best-fitting five-variable GLMs delineate relationships more complex than a simple east–west gradient. The inclusion of wet winter land surface conditions, even though year-round conditions are drier in the west than in the east, also indicates that these multivariable models capture the effects of local interannual (temporal) variability on WNV activity. If these GLMs were merely describing the geographic trend of WNV activity, then they would select for drier winter conditions.

The results with the two Mosaic model estimates of soil moisture conditions, L1SM and RZSM, were very similar. This indicates that future analyses need only include one of these measures.

Biological Implications. These findings have several biological implications. One could envision that the wet winter conditions and warm wet spring conditions facilitate earlier *Culex* mosquito activity and an early increase of mosquito abundance. Drier summers might then favor the congregation of birds and mosquitoes around remaining eutrophic water resources that support *Cx. pipiens* and *Cx. restuans* breeding. This might enable enzootic amplification of WNV among the congregated vectors and hosts (Shaman 2007). Previous analyses also have found evidence of heightened WNV activity in Suffolk County when water resources during summer are limited (Rochlin et al. 2009). These inferences of how meteorological and
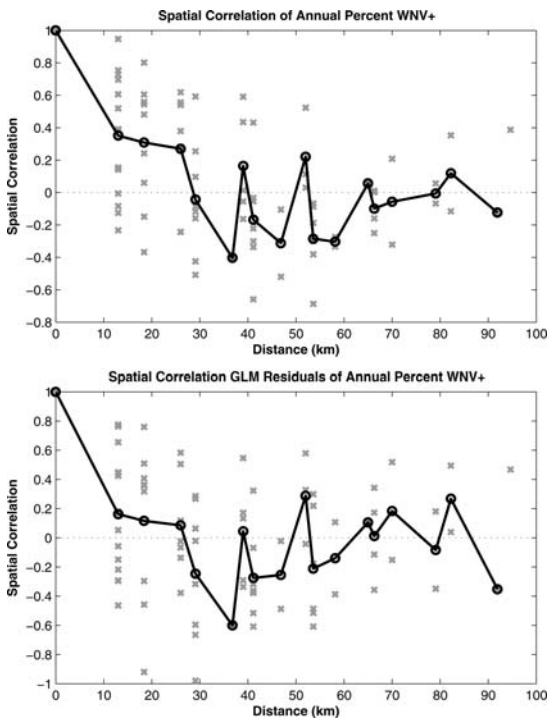
hydrological conditions affect *Culex* biology and WNV transmission need to be further tested in the field.

The overall east–west spatial gradient of WNV activity in Suffolk County (Fig. 2) may in part be due to the strong spatial gradients of mean meteorological and hydrological conditions (Fig. 3). These conditions no doubt influence the distribution and local composition of *Culex* mosquito species. For example, if the environmental conditions, including the prevalence of saltwater marshes, in western Suffolk County favor a higher ratio of *Cx. pipiens* and *Cx. restuans* to *Cx. salinarius;* and if *Cx. pipiens* and *Cx. restuans* are the more efficient enzootic vectors of WNV, then western Suffolk County would logically have more WNV activity. Such environmental influences on *Culex* species composition may occur in both space and time, because local year-to-year changes in the environment may make an area more or less hospitable to the proliferation of each *Culex* species. It is thus possible that hydrological and meteorological conditions affect the spatial–temporal distribution of WNV activity not only by modulating the breeding success, rates of activity, and contact with avian amplification hosts of a given *Culex* species but also by changing local *Culex* and avian host species composition. This potential linkage between environmental conditions and species composition across Suffolk County needs to be explored further and compared with other potential drivers, including differences in flora, water management practices (e.g., the distribution of catch basins), and land use practices.

The meteorological and hydrological conditions favorable to WNV activity, as determined here, may provide a means for identifying which *Culex* species is principally responsible for WNV amplification in Suffolk County. That is, by determining the *Culex* species that thrives best through a wet winter, wet and warm spring, and dry summer, it could be inferred that this species is the dominant enzootic vector when WNV prevalence increases. Of course, this issue also could be examined in the laboratory by pooling *Culex* mosquito collections by species, rather than genus, before assaying for WNV.

Our analysis focuses on WNV presence among pools of assayed *Culex* mosquitoes, a metric that does not necessarily correspond directly with WNV transmission rates to humans. Maintenance of WNV in the North American environment is generally attributed to enzootic transmission among ornithophilic *Culex* mosquitoes and avian hosts. A hypothesized switch of the feeding preference of *Cx. pipiens* from birds to mammals during summer (Spielman 2001) may enable this mosquito species to act as both enzootic and bridge vector. Other *Culex* species also have been shown to seasonally switch from blood feeding on avian to mammalian hosts (Edman and Taylor 1968) or to feed more generally on both birds and mammals (Niebylski and Meek 1992; Apperson et al. 2004). The degree to which *Cx. pipiens, Cx. restuans*, and *Cx. salinarius* participates in the transmission of WNV to humans will depend on mosquito feeding patterns, individual species vector competence, and the avail-able host species composition, as well as environmental conditions.

Prediction of WNV Activity. Documentation of amplification in the field, even on a limited basis, can be difficult, costly, and time-consuming. Analyses, such as the one presented here, provide preliminary insight into how WNV transmission dynamics respond to the intraseasonal and interannual variability of meteorological and hydrological conditions. The findings suggest that the gross distribution of WNV is linked to climate, which in part determines habitat and *Culex* species distribution and prevalence. Furthermore, the year-to-year variability of WNV activity is associated with local meteorological and hydrological conditions and WNV amplification is most closely linked to these conditions at specific times of years.

Figure 4 illustrates both the utility and limitations of the best-fit model. The GLM predictions are able discriminate areas with the greatest WNV activity from those with lesser activity. All grid cell-years with >10% observed WNV positive *Culex* pools are partitioned to the right in each plot and, for the full GLM, are associated with predictions of >5% WNV-positive *Culex* pools. This indicates that the GLM can identify areas at risk for intense WNV activity. However, observations of 1-10% WNV-positive *Culex* pools are scattered throughout all levels of GLM prediction, which indicates that the model is not capable of distinguishing moderate WNV activity from no WNV activity at all.

Accurate identification of areas at risk for greater than moderate WNV activity could ostensibly help public health planning and WNV control. The best-fit GLM has built-in lead times in that all meteorological and hydrological conditions associated with WNV activity occur before the peak WNV transmission season (Fig. 1). Thus, GLM predictions of WNV activity could be used to develop control strategies that more effectively reduce infectious mosquito numbers and WNV transmission to humans. The next steps will be to validate this model prognostically in the coming years and then use it to focus control measures in both space and time.

Acknowledgments

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