Cross-Correlation Map Analyses Show Weather Variation Influences on Mosquito Abundance Patterns in Saginaw County, Michigan, 1989–2005

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ABSTRACT Weather is important determinant of mosquito abundance that, in turn, influences vectorborne disease dynamics. In temperate regions, transmission generally is seasonal as mosquito abundance and behavior varies with temperature, precipitation, and other meteorological factors. We investigated how such factors affected species-specific mosquito abundance patterns in Saginaw County, MI, during a 17-yr period. Systematic sampling was undertaken at 22 trapping sites from May to September, during 1989–2005, for 19,228 trap-nights and 300,770 mosquitoes in total. *Aedes vexans* (Meigen), *Culex pipiens* L. and *Culex restuans* Theobald, the most abundant species, were analyzed. Weather data included local daily maximum temperature, minimum temperature, total precipitation, and average relative humidity. In addition to standard statistical methods, cross-correlation mapping was used to evaluate temporal associations with various lag periods between weather variables and species-specific mosquito abundances. Overall, the average number of mosquitoes was 4.90 per trap-night for *Ae. vexans*, 2.12 for *Cx. pipiens*, and 1.23 for *Cx. restuans*. Statistical analysis of the considerable temporal variability in species-specific abundances indicated that precipitation and relative humidity 1 wk prior were significantly positively associated with *Ae. vexans*, whereas elevated maximum temperature had a negative effect during summer. *Cx. pipiens* abundance was positively influenced by the preceding minimum temperature in the early season but negatively associated with precipitation during summer and with maximum temperature in July and August. *Cx. restuans* showed the least weather association, with only relative humidity 2–24 d prior being linked positively during late spring–early summer. The recently developed analytical method applied in this study could enhance our understanding of the influences of weather variability on mosquito population dynamics.

KEY WORDS West Nile virus, *Aedes vexans*, *Culex pipiens*, *Culex restuans*, cross-correlation map

West Nile virus (family *Flaviviridae*, genus *Flavivirus*, WNV) invaded the United States in 1999 and first produced an outbreak in Michigan in 2002 (www.cdc.gov). Although epidemic transmission declined in the following years, we have shown that WNV was still circulating in Michigan at the site of the current study (Chuang et al. 2011). Because >60 mosquito species can transmit WNV in the United States, local-level vector ecology is important in determining infection risk. *Culex* species are recognized to be among the most important enzootic and epidemic vectors of WNV (Turell et al. 2005).

Mosquito abundance is often measured by trap catch, a variable that is strongly influenced by ambient temperature and precipitation, both primary contributors to the prevailing meteorological conditions of weather variations in any region (Reiter 2001, Barker et al. 2003, Degaetano 2005). Mosquito abundance is considered an important indicator of mosquito-borne diseases (Ebel et al. 2005, Bolling et al. 2009). Because of the complexity of vector–host interactions, the most abundant vector does not always pose the highest risk. WNV transmission risk should be greater under conditions where vector activity overlaps with human residence or natural reservoirs. Although vector infection prevalence is another critical indicator, delays in testing for virus may make this indicator less useful than vector abundance in forecasting mosquito-related transmission early warning. Meteorological measurements have been associated with variation in mosquito abundance in various field studies (Reisen et al.

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2008, Trawinski and Mackay 2008, Ruiz et al. 2010), suggesting utility in developing early warnings.

Various analytic methods have been used to evaluate mosquito abundance patterns in different locations. Time-series analyses have been used, for example, to show associations between degree-day cooling and *Culex pipiens-restuans* complex population dynamics (Trawinski and Mackay 2008) in Erie County, NY. A recent study conducted in northeastern Illinois demonstrated a strong temporal association between increased air temperature and WNV infection in *Culex pipiens* L. and *Culex restuans* Theobald (Ruiz et al. 2010). Furthermore, Wang et al. (2011) have demonstrated predictable *Culex pipiens-restuans* abundance by using mean degree-day and precipitation at specific time lags in Ontario, Canada. These and other studies highlight the significance of weather influences on WNV vector mosquito populations, and also the variability in different geographic settings.

Considerable temporal, spatial, and environmental variation in WNV transmission ecology suggests that local-level, detailed studies may provide insight into how weather and climate influence the dynamics of the relevant mosquito vector species. The Saginaw County Mosquito Abatement Commission (SCMAC) has maintained a mosquito surveillance system since 1982, with multiple traps set each year to monitor seasonal dynamics in mosquito abundance. Accordingly, we analyzed this extensive, multiyear, countywide mosquito surveillance data base from Saginaw County, MI, to explore the effects of weather variation on species-specific abundances. Advanced and visualized time-series statistical methods were used to enhance our understanding of meteorological measurements and the abundance of three major mosquito species there. The goal was to develop insight into seasonal dynamics that might prove useful to mosquito control efforts, and possibly to reduce WNV risk.

Materials and Methods

Study Location. Saginaw County, MI (43° 22′N, 83° 59′W) is located in east central Michigan (2,113-km^2 [816-mi^2] area), with a population of 200,169 (2010 census). The city of Saginaw is the largest urbanized area, comprising >25% of the county's total population. Roughly two thirds of the land cover (use) is considered agricultural, with crops dominated by corn (*Zea mays* L.), soybean [*Glycine max* (L.) Merr.], sugar beet (*Beta vulgaris* L.), dry bean (*Phaseolus vulgaris* L.), wheat (*Triticum aestivum* L.), and alfalfa (*Medicago sativa* L.).

Mosquito Sampling. The SCMAC was established in 1977 to control vectors of St. Louis encephalitis virus and nuisance mosquitoes. To monitor mosquito abundance efficiently and consistently, in 1982 SCMAC established a countywide, standardized trapping system. New Jersey Light traps (NJLTs) were set up at sites near the homes of residents who were willing to help operate these traps to collect adult mosquitoes at night. NJLTs were set every Monday, Wednesday, and Friday from mid-May to September (weeks 19–37) of every year. Most trapping sites were placed at the same or nearby places during the 17-yr period, with more traps being added in recent years. To maintain reliability and consistency in our study, analyses occurred from 1989 to 2005, and 22 trap sites with consistent locations were included here (Fig. 1).

Mosquitoes identified to species according to standard morphological criteria by using authoritative keys and references (Darsie and Ward 1981) and were counted. Overall, 40 mosquito species were identified and counted during the 17-yr study period. Here, we focused research on the primary nuisance species *Aedes vexans* (Meigen) and two vectors of St. Louis encephalitis virus and West Nile virus, *Cx. pipiens* and *Cx. restuans* (Turell et al. 2001, Ebel et al. 2005, Hamer et al. 2008).

Weather Data. Meteorological data were obtained from local weather stations via the CD-ROM (National Climatic Data Center [NCDC] Cooperative Station Data, 1850–2006) published by the NCDC provided by National Oceanic and Atmospheric Administration. Saginaw County has several weather stations that record weekly, daily, or even hourly meteorological measurements within the county; however, most weather stations do not have complete records during the entire study period. Only Saginaw MBS International Airport weather station possessed comprehensive meteorological data, including daily maximum temperature (Tmax), daily minimum temperature (Tmin), daily total precipitation (Precip), and average daily relative humidity (RH) during this period. Daily weather measurements from the MBS weather station, located in north central Saginaw County (43° 32′ N, 84° 05′ W) at 201-m elevation, were used in our study (Fig. 1). The mean distance between the weather station and the mosquito trap sites was 13.0 miles (range, 3.9–39.1 km [2.4–24.3 miles]).

Statistical Analyses. The 17-yr (1989–2005), 19,228 trap-night mosquito abundance time series was analyzed to explore associations with varying meteorological conditions, an approach summarized in Fig. 2. Conventional time-series analyses usually consider influences on single time lag unit; however, this might not capture meteorological effects on mosquito abundance if preceding conditions contributed to breeding and survival over weeks to months. Thus, our long-term mosquito database was analyzed using recently proposed methods (Curriero et al. 2005, Shone et al. 2006). This graphical approach visualizes possible relationships between weather factors and subsequent vector populations using specific time intervals by plotting cross-correlation maps (CCMs).

We denoted Y_i as daily mosquito population counts with $i = 1,\ldots,874$ representing trapping days from 15 May 1989 to 16 September 2005. X_i was the time series of the weather data. The association between mosquito abundance and meteorological factors was evaluated by calculating lagged Pearson correlation coefficients $corr(Y_i, f(X_{i-a,\ i-b}))$, using a positive lag a, b with $b \geqq a$. The function $f\,(X_{i-a,\ i-b})$ was taken to be average of the values X_{i-a}, $X_{i-a+}1,\ldots X_{i-b}$ for each weather variable. Mosquito population counts were

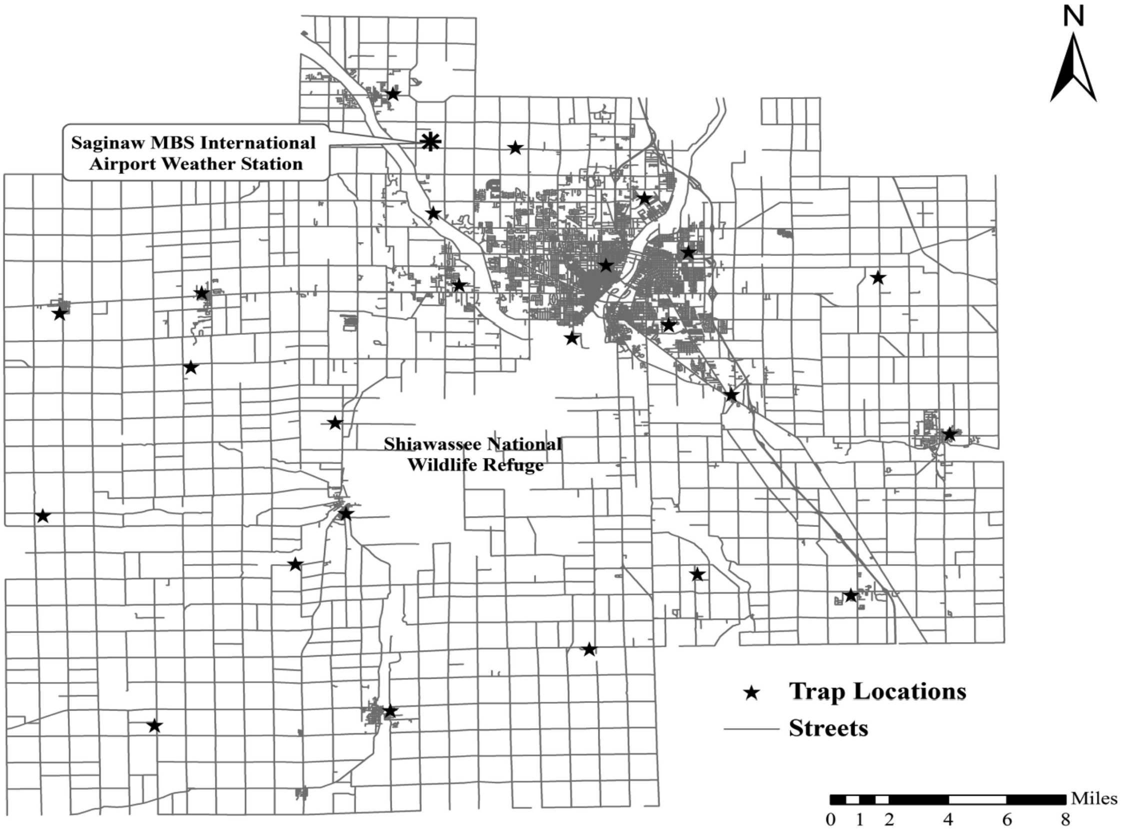

Fig. 1. Locations of NJLTs and the weather station in Saginaw County, MI, used to obtain mosquito and meteorological data during 1989–2005.

natural log-transformed [$\log(Y_i + 1)$] before calculating the correlation coefficient because the raw data were highly skewed. The summary function was set as average total daily Precip, average daily Tmax, average daily Tmin, and average daily RH. Separate CCMs were generated by mosquito species monthly. Lag zero weather was not used as a covariate because that would primarily reflect the effect of weather on trapping probability, rather than on population abundance. At sufficiently long lag periods, the weather will be approximately independent of the lag zero weather and therefore can influence trap counts only through abundance.

CCM results were generated by plotting the correlation between each mosquito abundance and each weather variable within specific time interval lags (lag a and b). The CCM supported a better interpretation of weather influences on mosquito abundance than traditional cross-correlation plots that only consider one single time lag. The CCM procedure also allows visualization of associations between vector populations and interval lags based on meteorological conditions. An example CCM shown in Fig. 3 indicates the cross-correlations between preceding precipitation and *Ae. vexans* abundance during July, with all combinations of interval time lags (a and b, unit = days).

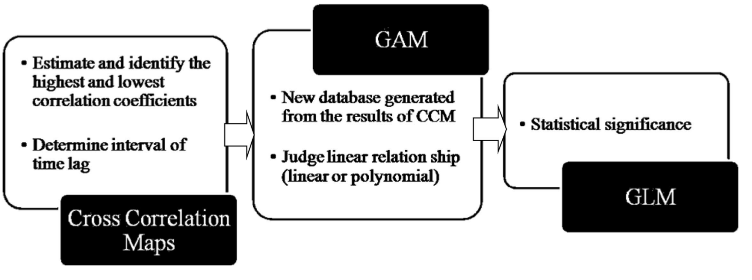

Fig. 2. Flow chart of statistical analyses used in studies of mosquito abundance and weather variability in Saginaw County, MI, during 1989–2005.

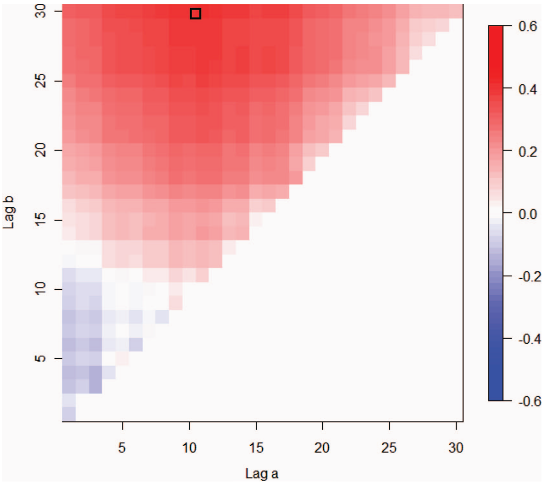

Fig. 3. CCM of *Ae. vexans* abundance and preceding precipitation during July 1989–2005 (black box indicates the area with the highest correlation coefficient). (Online figure in color.)

Pearson's correlation coefficients of multiple combinations of time interval lags are indicated by intensity of red color (positive correlations) and blue color (negative correlations). This visualization permits identification of patterns of lagged associations during the preceding period (30 d in our analysis). All of the CCM analyses for each of the three mosquito species during different months are presented in Supp Figs. 1–5 [online only].

After generating the CCMs, a series of correlation coefficients for each weather variable and time lag was rank ordered. The highest and lowest correlation coefficients were chosen as summary measures of each weather variable and time lag, with the highest and lowest coefficients indicating positive and negative influences, respectively.

To evaluate whether correlations between weather factors and vector populations were linear, we applied the generalized additive model (GAM) with a smooth operator to plot relationships and also to evaluate the equivalent degrees of freedom (EDF). Nonlinearity was considered if the EDF was far from 1 (Faraway 2006). For associations not deemed to be linear, a quadratic term was added to fit the final model. Because of the inherent correlation among many meteorological variables, a variance inflation factor (VIF) was estimated to detect the level of correlation among variables to address collinearity in subsequent regression models. Such collinearity generally should be considered in analyses when VIF is >10 (Kunter et al. 2004). All variables were then analyzed in a generalized linear model (GLM) under a Gaussian distribution. The final species-specific models included all weather variables (Precip, Tmax, Tmin, and RH) under specific lag times. All analyses were completed using the software R version 2.70 (http://www.r-project.org/) and the "mgcv" package was used for the GAM plotting.

Results

In total, 22 mosquito trapping sites produced 874 trap observations from 15 May 1989 to 16 September 2005, resulting in 19,228 trap-nights and 300,770 mosquitoes. The average number of mosquitoes per trap-night for the entire period was 4.90 for *Ae. vexans,* 2.12 for *Cx. pipiens,* and 1.23 for *Cx. restuans.* The pattern of mosquito abundance varied by species (Fig. 4); however, populations of *Ae. vexans,* the most abundant species, peaked in June–July and gradually decreased, *Cx. pipiens* abundance was elevated until July and decreased thereafter, and *Cx. restuans* abundance was greatest in June and then immediately declined. Mosquito abundances varied by year, with annual average abundances for 1989–2005 of 1.73–13.07 for *Ae. vexans,* 1.26–4.35 for *Cx. pipiens,* and 1.02–1.17 for *Cx. restuans.*

The monthly species-specific CCMs indicated different meteorological influences on mosquito abundances. The results of monthly CCMs were summa-

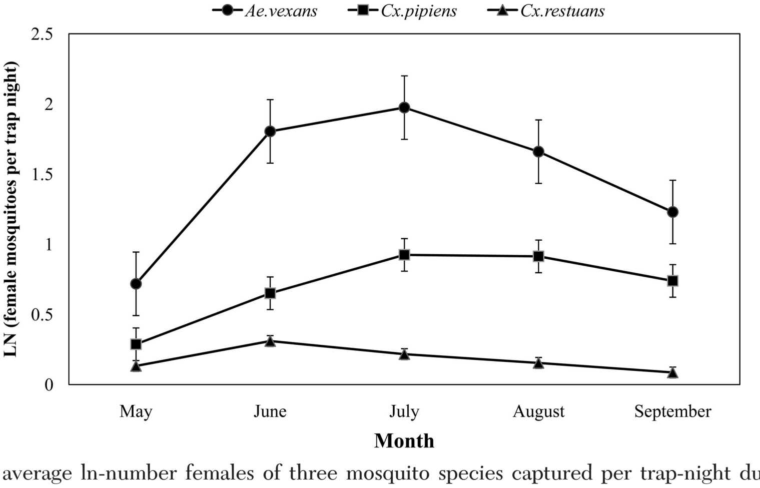

Fig. 4. Monthly average ln-number females of three mosquito species captured per trap-night during 1989–2005 in Saginaw County, MI.

Table 1. Correlation coefficients of mosquito abundance and weather variables for three mosquito species sampled from 1989 to 2005 in Saginaw County, MI

Weather variable	May		June		July		Aug.		Sept.	
	Lag[a]	Correlation[b]	Lag	Correlation	Lag	Correlation	Lag	Correlation	Lag	Correlation
Ae. vexans										
Precip	4–30	0.26	7–30	0.46	11–30	0.42	7–30	0.50	6–21	0.55
Tmax	1–24	0.51	21–23	0.15	10–30	−0.23	6–24	−0.43	17–26	−0.32
Tmin	1–25	0.55	13–27	0.42	17–25	0.19	20–22	−0.18	8–17	0.42
RH	1–25	0.17	5–27	0.43	9–25	0.46	7–26	0.61	4–27	0.55
Cx. pipiens										
Precip	22	0.13	7–24	0.30	1–20	−0.32	1–6	−0.23	22–24	−0.29
Tmax	1	0.31	22–23	0.26	15–27	−0.24	4	−0.22	1	0.38
Tmin	1–25	0.40	13–25	0.45	29–30	0.18	4	−0.18	20–21	0.38
RH	23	0.24	3–20	0.37	5–15	−0.21	2	−0.11	20	0.18
Cx. restuans										
Precip	18	0.26	8–25	0.24	14–23	−0.16	10–15	−0.15	14	−0.20
Tmax	1	0.16	5–7	−0.26	1–28	−0.41	11–17	−0.23	20–22	−0.18
Tmin	19	0.21	22	0.15	1–26	−0.47	11–29	−0.20	27–30	0.23
RH	3–25	0.36	4–21	0.31	28–30	0.16	14–30	0.19	4	0.17

[a] Unit of lag is days.
[b] The highest Pearson correlation coefficient from CCM (critical value is 0.195 for $P = 0.05$ with two-sided test without adjusting for multiple testing).

rized as correlation coefficients and time lag for three species (Table 1; Supp Figs. 1–5 [online only]). Preceding Precip was critical for *Ae. vexans* populations in every month, especially after May, and the strength of the correlations increased over the season. Both prior Tmax and Tmin values also were positively correlated with *Ae. vexans* abundance in late spring; however, the effect of Tmax reversed after June. RH was associated with *Ae. vexans* patterns in a manner similar to that of Precip.

Cx. pipiens was less affected by meteorological conditions than *Ae. vexans.* Preceding temperature, especially Tmin, impacted abundance of this species in May and June, with no apparent associations thereafter. Precipitation and RH seemed to have only minor influences on *Cx. pipiens,* with rainfall producing a negative impact after July (Table 1; Supp Figs. 1–3 [online only]).

Cx. restuans showed similar weather-associated patterns as those of *Cx. pipiens,* although abundance was not as strongly influenced. Preceding RH in May and June was positively associated with *Cx. restuans* abundance, whereas a negative effect of preceding Tmax and Tmin was observed in summer.

After evaluating the linear relationship between mosquito abundance and weather conditions by the generalized additive models, only one model required a quadratic term be added to fit that model (negative Precip effect for *Cx. pipiens* in July). The results of VIFs for all the meteorological variables indicated no significant collinearity (data not shown).

The final statistical models indicated different significant patterns of weather effects on these three vectors (Table 2). For *Ae. vexans,* elevated Precip 2–3 wk prior was significantly associated with increased abundance of this species throughout the sample period. Similarly, higher Tmin lagged 2–3 wk was positively associated with *Ae. vexans* for the early season, whereas elevated preceding Tmax produced a negative effect on abundance after July (Table 2). The range of Tmin in Saginaw County was between −2.8 and 20.0°C in May, and for Tmax was between 13.3 and 38.3°C in summer. The influence of RH was weaker, but with a pattern that was similar to that for Precip.

Weather associations for *Cx. pipiens* indicated that higher Tmin roughly 3 wk prior had a positive impact on adult abundance of this species early in the season (May and June) (Table 2; Supp Figs. 1 and 2 [online only]). This temperature association disappeared during summer, with higher Tmax showing negative effects in July and August. Interestingly, elevated Precip seemed to have no influence on *Cx. pipiens* abundance early in the reproductive season, but a negative impact after July (Supp. Fig. 3 [online only]). Similar to Precip, lagged RH during late spring also was associated with adult *Cx. pipiens* abundance. Thus, Precip and RH seemed to have different influences on *Ae. vexans* and *Cx. pipiens.*

For *Cx. restuans,* additional associations with weather variables were found (Table 2). Elevated RH 3 d to 3 wk prior was associated with increased abundance for most of the reproductive season, but especially in May and June. When the RH was >75%, the effect became stronger (data not shown). Interestingly, Precip had no obvious effect on this species. As with the other two species, elevated Tmax was negatively associated with this mosquito's population.

According to the adjusted R^2 values, the extent to which mosquito abundance was explained by weather factors was highly species-dependent. *Ae. vexans* seems more sensitive to the weather variability than two other species (Table 2).

Discussion

This study used an analytical approach to mosquito abundance data that uncovered strong relationships with meteorological events and weather. Indeed, our approach revealed relationships between weather variability and mosquito abundance through statistical

Table 2. Analysis of vector abundance and weather variables for three mosquito species sampled from 1989 to 2005 in Saginaw County, MI

Weather variable	May			June			July			Aug.			Sept.		
	β		Lag[a]	β		Lag	β		Lag	β		Lag	β		Lag
Ae. vexans															
Precip	0.13	***	4–30	0.115	***	7–30	0.059	***	11–30	0.074	***	7–30	0.076	***	6–21
Tmax	0.102		1–24	−0.022		21–23	−0.15	***	10–30	−0.125	***	6–24	−0.127	**	17–26
Tmin	0.243	*	1–25	0.168	***	13–27	0.154	***	17–25	0.002		20–22	0.09		8–17
RH	0.039		18–26	0.179	***	5–27	0.129	**	9–25	0.15	***	7–26	0.029		4–27
Adj. R^2		0.41			0.44			0.32			0.48			0.46	
Cx. pipiens															
Precip	0.001		22	0.026		7–24	−3.296	**	1–20	−0.018	***	1–6	−0.013	**	22–24
							1.933	[b]							
Tmax	−0.128		1	0.005		22–23	−0.106	***	15–27	−0.039	**	4	0.045	***	1
Tmin	0.287	**	1–25	0.112	***	13–25	0.013		29–30	0.005		4	0.037	*	20–21
RH	0.025	*	23	0.141	***	3–20	−0.076	**	5–15	−0.011		2	0.021		20
Adj. R^2		0.28			0.39			0.36			0.21			0.45	
Cx. restuans															
Precip	0.006		18	0.013		8–25	−0.014		14–23	−0.005		10–15	0		14
Tmax	−0.002		1	−0.048	***	5–7	−0.058		1–28	−0.037		11–17	−0.033		20–22
Tmin	0.013		19	0.014		22	−0.212	***	1–26	−0.05		11–29	0.051	*	27–30
RH	0.1	**	3–25	0.086	***	4–21	0.037	**	28–30	0.064	*	14–30	0.016		4
Adj. R^2		0.15			0.18			0.25			0.13			0.21	

***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.
[a] Unit of lag is days.
[b] Quadratic term.

methods not routinely used in vectorborne disease research. The association of meteorological variables under specific time-interval lags produced more robust inferences than analyses that only focus on effects under single, predefined time lags. By applying these visualized cross-correlation methods, we were able to identify various specific weather associations and presumed duration influences during spring and summer for each of these three mosquito species.

Ae. vexans was the most abundant mosquito in Saginaw County. Its population was highly associated with prior rainfall in a linear pattern, a finding that is consistent with other field studies on the ecology of this species. Female *Ae. vexans* oviposit at sites that are likely to be inundated in the future; hence, this mosquito's designation as a "flood-water species" (Strickman 1980, Hayes et al. 1985). Larvae usually hatch rapidly after intense rainfall, with larval and pupal development being temperature-dependent. Our study showed that higher preceding Tmin was linked with increased *Ae. vexans* captures early in the season. Elevated Tmax during the early summer, however, was associated with later decline in abundance, suggesting that longevity of both adults or larvae might be influenced by the higher temperature (>30°C). Daily mosquito survival rates reported in other studies indicated that survival probability increases from 0.82 to 0.90 at 9 versus 20°C and decreases to 0.04 at a temperature of 40°C (Horsfall 1955, Martens et al. 1995). This phenomenon was observed in all three species in our study and is consistent with generally nonlinear relationships in mosquito ecology at the environmental extremes. The importance of RH seemed to be similar to that of rainfall, two weather variables that are highly correlated. Trawinski et al. (2008) applied seasonal ARIMA models to analyze the same three species in Erie County, NY, also demonstrating an association between climatic indicators and mosquito abundances. They showed that *Ae. vexans* abundance predictions can be improved significantly by adding meteorological variables to their models. Our results also suggest that *Ae. vexans* was more sensitive to variations in weather than were the two *Culex* species.

Previous investigations have suggested that *Ae. vexans* represents more of a nuisance than an important WNV vector. Before the introduction of WNV into North America, *Ae. vexans* was considered a possible vector based on both field and laboratory studies (Turell et al. 2005, Anderson et al. 2006, Tiawsirisup et al. 2008). However, mammals are the principal host on which *Ae. vexans* feeds, although birds make it a potential bridge vector (Tiawsirisup et al. 2008). In Saginaw County, the minimum infection rate of *Ae. vexans* was low in our field investigations (Chuang et al. 2011). Nevertheless, this species should continue to be monitored carefully because it is so abundant in the area, and vector control can be temporally focused according to the preceding precipitation.

Cx. pipiens has been recognized as a potentially important vector of WNV in many settings (Turell et al. 2005, Hamer et al. 2008), including Saginaw County (Chuang et al. 2011). This species showed responses to weather variables that were different from the other species. Higher Precip within the previous 3 wk seemed to have a negative impact on *Cx. pipiens* during summer and early fall. Our study also demonstrated that temperature was important for *Cx. pipiens* populations, both early and late in the activity season (Tmin in Table 2). Nevertheless, high RH still seemed advantageous to adult *Cx. pipiens* abundance early in the season, even if their eggs may not have hatched as rapidly after elevated rainfall, as was observed with *Ae. vexans.*

The importance of *Cx. pipiens* to WNV transmission in the United States is considerable (Marra et al. 2003, Turell et al. 2005). In another study, we demonstrated that WNV infection rates in Saginaw County are high in *Cx. pipiens* (Chuang et al. 2011). Birds are the primary hosts of this vector, yet it also feeds on mammals, including humans (Marra et al. 2003, Turell et al. 2005). One recent study on *Cx. pipiens* feeding preferences indicated that 16% of blood meals were from mammals, of which 83% were from humans (Hamer et al. 2009). Thus, *Cx. pipiens* could have important roles as both an amplifying vector among avian populations and a bridge vector to humans. In Saginaw County, the temporal pattern of WNV infection in *Cx. pipiens* was similar to that of dead birds identified by (Chuang et al. 2011), suggesting transmission between this mosquito species and birds. Tmin early in the transmission season was a good indicator of *Cx. pipiens* abundance during the following month, perhaps providing insights into the timing and intensity of future vector control measures.

The role of *Cx. restuans* in WNV transmission also has been demonstrated elsewhere (Andreadis et al. 2001, Sardelis et al. 2001). In Saginaw County, *Cx. restuans* abundance peaked in June and was much lower than the two other species. The abundance crossover phenomenon between *Cx. pipiens* and *Cx. restuans* was observed in central Illinois, a pattern apparently influenced by Tmax (Kunkel et al. 2006). In that study, the abundance of *Cx. restuans* peaked in the early summer and then simultaneously decreased with the increasing abundance of *Cx. pipiens.* A similar "crossover" was not detected in Saginaw County; however, the seasonal abundance of these two mosquito species showed similar patterns. Interestingly, *Cx. restuans*, in our study, was more abundant early in the season when preceding RH was higher. Preferred breeding habitats for *Cx. restuans* are shaded temporary ground pools, woodland pools, or discarded tires, with survival and development depending on organic nutrients within the pools (Beier et al. 1983, Reiskind et al. 2004). Unlike the two other species, *Cx. restuans* was not affected by most short-term weather variation except for RH. The low capture rate might reduce the power to detect significant relationships. In Saginaw County, we previously showed that WNV infection rates of this species were higher in the late spring and early summer (Chuang et al. 2011), which is also true with its abundance. *Cx. restuans* might be an important vector for enzootic transmission of WNV in this area.

To analyze the relationship between weather variability and mosquito abundance, consistent databases for both are needed. The SCMAC provided a high-quality mosquito database covering many years. However, some limitations of this study were unavoidable. The NJLTs were maintained by residents in the area, placing 14 of the trapping sites close to more urbanized habitats, and the other eight sites in more rural settings. The impact of meteorological variables on adult mosquito abundance was based on weather station data; however, we did not directly identify how weather influenced development and survival of eggs, larvae, pupae, or adults. The environmental factors that influence mosquito abundance are extremely complicated so the associations might not be explained well solely using climatic variables. The complexity also was reflected by the moderate R^2 values ($<50\%$) in the results that indicates the mosquito abundance should be influenced by other factors. In addition to meteorological conditions, habitat, land cover (use), human activity, and survival probability of overwintering eggs (*Aedes* spp.) or adults (*Culex* spp.) could be affecting mosquito populations and should be considered in future studies. Use of trap counts as an indirect indicator of mosquito population is another limitation. We are unable to analyze the accuracy of this indicator, so causal inferences are difficult to make.

Because of the complex interactions of mosquito ecology and environmental conditions, the correlation coefficients of many time lag intervals were very similar and no single significant time period was identified from our results. However, this is not surprising, because changes occur continuously over the time course of the entire season of mosquito activity. In general, summarizing the lag relationship by the location of the largest absolute value in the CCM could be inadequate, for example, because such a summary can only describe the largest mode of a bimodal CCM. In the same manner that one should look at a scatterplot to determine whether a single correlation coefficient provides a reasonable summary of its shape, so one should consider each CCM to evaluate how well the selected window summarizes the relationships between lags. We provide all the CCMs in the supplement to allow readers to do so.

Our study intended to estimate the associations of preceding meteorological events and mosquito abundances, thereby enhancing our understanding of mosquito ecology and disease risk in the study area. However, more detailed entomological studies are needed to better understand the ecologies of major mosquito species in other settings. Combining the latest remote sensing data that might provide more environmental measurements could improve the ability to forecast mosquito population dynamics in these and other settings.

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