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Weather and Land Cover Influences on Mosquito Populations in Sioux Falls, South Dakota

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Abstract

This study compared the spatial and temporal patterns of *Culex tarsalis* Coquillett and *Aedes vexans* Meigen populations and examined their relationships with land cover types and climatic variability in Sioux Falls, SD. Between 24 and 30 CDC CO₂-baited light traps were set annually in Sioux Falls from May to September 2005–2008. Land cover data were acquired from the 2001 National Land Cover Dataset and the percentages of selected land cover types were calculated within a 600-m buffer zone around each trap. Meteorological information was summarized from local weather stations. *Cx. tarsalis* exhibited stronger spatial autocorrelation than *Ae. vexans*. Land cover analysis indicated that *Cx. tarsalis* was positively correlated with grass/hay, and *Ae. vexans* was positively correlated with wetlands. No associations were identified between irrigation and the host-seeking population of each species. Higher temperature in the current week and 2 wk prior and higher precipitation 3–4 wk before collection of host-seeking adult mosquitoes had positive influences on *Cx. tarsalis* abundance. Temperature in the current week and rainfall 2–3 wk before sampling had positive influences on *Ae. vexans* abundance. This study revealed the different influences of weather and land cover on important mosquito species in the Northern Great Plains region, which can be used to improve local vector control strategies and West Nile virus prevention efforts.

Keywords

West Nile virus; *Culex tarsalis*; *Aedes vexans*; weather; land cover

West Nile virus (family *Flaviviridae*, genus *Flavivirus*, WNV) was first detected in the northern Great Plains (NGP) in 2002 and caused a significant regional outbreak in 2003. In subsequent years, the NGP has continued to be a hot spot for WNV, with the highest long-term incidence of WNV neuroinvasive disease in the United States (Lindsey et al. 2008). During the postoutbreak years from 2004 to 2009, 11% of the total number of all human

cases in the United States were reported from South Dakota, which made up <0.3% of the national population. Research in the eastern and midwestern United States has emphasized the importance of *Culex pipiens* L. as a key vector of WNV in urban and suburban areas (Hayes et al. 2005, Kilpatrick et al. 2005, Turell et al. 2005, Hamer et al. 2009). In contrast, South Dakota has a substantial rural population, and mosquito communities are dominated by two species: *Culex tarsalis* Coquillett and *Aedes vexans* Meigen (Easton et al. 1986). *Cx. tarsalis* is considered an important WNV vector in many areas of the western United States (Goddard et al. 2002, Bell et al. 2005, Turell et al. 2005, Bolling et al. 2007, Nielsen et al. 2008). *Ae. vexans* is an abundant nuisance mosquito, but it is also a suspected bridge vector of WNV (Turell et al. 2005).

WNV amplification in avian host communities and transmission to humans are both mediated by blood-feeding behavior of vectors and the degree of exposure to infected mosquitoes. Although the risk of human infection is influenced by multiple factors, vector abundance is a key determinant that is frequently used as an indicator of vector-borne disease risk (Ebel et al. 2005, Bolling et al. 2009). Temporal patterns of mosquito abundance are sensitive to seasonal weather patterns and interannual climatic variability (Reiter 2001). Temperature affects the dynamics of vector populations by influencing the larval developmental rate, the length of the gonotrophic cycle, and mosquito survival, and these factors in turn influence biting rate. In northern latitudes, early spring temperatures also affect the timing of the onset of mosquito activity. Besides temperature, sufficient rainfall is required to create breeding habitats. Relative humidity influences both the survival and flight performance of mosquitoes (Rowley and Graham 1968, Ye et al. 2007).

Previous studies demonstrated the influences of weather on numerous mosquito species in a variety of environments. For example, seasonal ARIMA models showed the lagged effects of cooling degree-days and precipitation on *Ae. vexans* and *Cx. pipiens* in Erie County, NY (Trawinski and Mackay 2008). In New Jersey, *Culex* spp. abundances were associated with warmer temperature and higher precipitation in the previous month (Degaetano 2005). The size of the spring population of *Cx. tarsalis* in California has been positively correlated with warmer winter temperature, higher spring/winter precipitation, and deeper snow pack (Reisen et al. 2008). Weather conditions not only affect vector populations but also influence the virus dynamics within the mosquito. Reisen et al. (2006) have determined that 14.3°C is the threshold temperature for WNV replication in infected *Cx. tarsalis* and that the extrinsic incubation period (EIP) decreases with increasing temperature. Higher temperature tends to increase larval development rates, shorten the gonotrophic cycle, and reduce EIP simultaneously, thereby increasing transmission risk.

In addition to meteorological conditions, the geographic distribution of mosquito activity is influenced by breeding habitat availability and bloodmeal-seeking behavior that link different mosquito species to specific land cover types. One study indicated that urban land use was associated with *Cx. pipiens/Culex restuans* Theobald populations in New York (Trawinski and Mackay 2010). In contrast, *Cx. tarsalis* is associated with rural habitats in California (Reisen et al. 2009). Spatial variability in climate is another important factor, particularly in mountainous regions. Barker et al. (2009a) reported that in Colorado, *Ae. vexans* and *Cx. tarsalis* were less abundant in cooler, high-elevation foothill and mountain areas than at lower elevations on the plains. Their study also suggested that *Cx. tarsalis* disperses along river corridors in the Great Plains region, with movement obstructed by the Continental Divide. A recent study demonstrated the associations between high WNV incidence and environmental factors, including irrigated crop-land, temperature, and precipitation, in the NGP and posed the hypothesis that these relationships reflected the ecological niche of *Cx. tarsalis* (Wimberly et al. 2008). However, the direct linkages

between vector population and environmental factors have not been well studied in this region.

The latest genetic study on *Cx. tarsalis* identified three regional population clusters, with South Dakota belonging to the Midwest cluster that is distinctive from the Pacific and Sonoran clusters that encompass Western Colorado and California (Venkatesan and Rasgon 2010). Whether these genetic differences influence mosquito behavior and habitat associations is unknown. Furthermore, the NGP has an environment that is distinctive from California and Colorado, where much of the previous research on *Cx. tarsalis* has been carried out. In particular, most of the NGP has lower temperatures, a shorter mosquito season, and lacks the large mountain ranges and steep elevational gradients found in California and Colorado. Large portions of the eastern Dakotas are dominated by groundwater hydrology, with extensive shallow aquifers and numerous small wetlands that are highly dynamic and sensitive to climatic variability. Most landscapes in the NGP are heterogeneous mosaics of multiple land uses, including croplands, pastures, hayfields, and conservation lands. Irrigated agriculture is relatively uncommon compared with the Central Valley of California and northeastern Colorado. To understand the risk of disease transmission in the high WNV incidence region of the NGP, more detailed studies of vector ecology are required.

This study focused on Sioux Falls, SD, and its environs, capitalizing on extensive mosquito trapping conducted by the Sioux Falls Health Department. There were three main objectives: 1) determine the relative influences of temperature, precipitation, and relative humidity on the temporal patterns of mosquito abundance in Sioux Falls, SD; 2) determine the relative influences of major land cover types on the spatial patterns of mosquito abundance in Sioux Falls; and 3) contrast these relationships for two mosquito species—*Cx. tarsalis*, the primary vector of WNV in the region, and *Ae. vexans*, an important nuisance mosquito.

Materials and Methods

Mosquito Data Collection

Sioux Falls is the major metropolitan area in the southeastern part of South Dakota, with a population of 157,935 in 2009. The city is located on the border of Minnehaha and Lincoln counties; these counties are classified as mixed rural and rural, respectively (Isserman 2005). The Big Sioux River passes through Sioux Falls. The rural landscapes surrounding the city are comprised of croplands, pastures, and hayfields, with patches of forests concentrated in parks, bottomlands, shelterbelts, and farmsteads. The climate of Sioux Falls is characterized by humid summers and cold winters, with the majority of precipitation occurring between April and September. There are 2,603 ha of agricultural land with permits for irrigation in Minnehaha and Lincoln counties, and these irrigated lands make up <1% of the total land area. Temperatures vary from -16.7 to -4.4°C in winter and from 16.1 to 30.0°C in summer, and average annual snowfall and rainfall are 998.2 and 627.4 mm, respectively (National Climate Data Center, Asheville, NC).

The Sioux Falls Health Department maintains multiple CDC CO₂-baited light traps (John W. Hock Company, Gainesville, FL) during the mosquito season from May to September. The numbers of traps were 24 in 2005, 36 in 2006, 42 in 2007, and 42 in 2008. Mosquito traps were set every day from Monday to Thursday, and the samples were collected the next day (from Tuesday to Friday). Mosquito species were identified based on morphological characteristics. Several traps in rural areas that were added after 2006 were removed from the analysis to avoid a potential location bias, so the trap numbers were 24 in 2005 and 30 in the other years.

Land Cover Data

We used remotely sensed land cover data to map spatial patterns of mosquito habitats. Land cover data were acquired from the 2001 National Land Cover Database as a 30-m raster GIS data set. To analyze the relationships between vector activity and landscape characteristics, we summarized land use by using buffers with different sizes around each trap. The buffer radii were 200, 400, 600, 800 m, and 1 km. The percentage of pixels in each land cover type was calculated for each buffer size. Five major land cover types in Sioux Falls were summarized from the 16 classes in the original database. The five land cover types were urban, cultivated crops, grass/hay, forest, and wetland. Urban was composed of developed areas at different levels of intensity, which included residential areas, commercial/industrial regions, and mixtures of constructed materials and vegetation. The cultivated crops type included annual crops, primarily corn and soybeans. The grass/hay type included pastures and hayfields dominated by graminoid or herbaceous vegetation. The forest type consisted of deciduous, evergreen, and mixed forests combined. The wetland type included herbaceous and woody wetlands with herbaceous or shrub vegetation where the soil was saturated or covered with water. A database of irrigation permits and the geographic coordinates of their associated water draw points were obtained from the South Dakota Department of Environment & Natural Resources.

Weather Data

Meteorological information was summarized from three weather stations within or near Sioux Falls: The first weather station was located at the Sioux Falls Airport (43° 34' N, 96° 43' W) in the northern part of the city, The second weather station was north of the city (43° 44' N, 96° 37' W) at the U.S. Geological Survey Earth Resources Observation and Science Center, and is part of the U.S. climate reference network. The third weather station is operated by the High Plains Regional Climate Center's Automatic Weather Data Network and is located in Dell Rapids (43° 46' N, 96° 45' W). The measurements from these three weather stations were averaged. Hourly measurement of temperature, rainfall, and relative humidity were summarized as weekly means (for temperature and humidity) and sums (for precipitation). Temporal lags ranging from the current week (lag = 0) to 4 wk before the collection of host-seeking adult mosquito (lag = 4) were included in the analysis.

Analysis

Mosquito abundances were summarized as the mean number of females per trap night for the four collection nights in each week. In the spatial/temporal analyses and regression models, the raw trap counts were log-transformed (raw trap counts + 1) before the weekly mean was calculated. To analyze the spatial pattern of the mosquito population, mosquito traps were georeferenced and species-specific annual mosquito abundances were mapped. The mapping was done using ArcGIS 9.3 (ESRI, Redlands, CA). Mantel tests were performed to evaluate the spatial autocorrelation for each species using the ade4 package in the R statistical environment, version 2.11. The relationships between mosquito populations and land cover types were evaluated by Pearson correlation coefficients for different buffer sizes (200–1,000-m radius) and in different years. We used multivariate mixed models to analyze the influences of land cover and weather variables with different time lags (weeks) on the female mosquito abundance in the study area. After evaluating the percentage of each land cover type within different buffers, the differences among the buffer sizes were minor so we used the 600-m buffer in the regression models. In the full model, we treated mosquito traps as repeated measurements in the 4 yr, and intercepts were set as random effects to control for variation among traps in each year. A first order autoregressive term (female mosquito abundance in the previous week) was included in the models to adjust for the effect of temporal autocorrelations in consecutive weeks. Spatial autocorrelation also was incorporated by including a random effect that modeled spatial covariance among the

trap sites using a spatial exponential structure. The Euclidean distances between traps were measured using Cartesian coordinates based on an Albers Equal-Area Conic projection. The severity of multicollinearity of independent variables was quantified by the variance inflation factor (VIF) before running the models. We found high multicollinearity ($VIF > 10$) for many land cover variables, so multiple models were required to analyze them separately. There were five different full models for each species. Each full model included all weather variables, a first order autoregressive term and one of the five land cover variables. The effects of land cover types were summarized for each of these full models.

Due to the independence of land cover and weather effects, there were very similar coefficients for weather variables in the full models. For parsimony, only two land cover types (grass/hay and wetland) that were statistically significant in the full models were selected for further analysis in the next set of final models. We also tested whether distance to the nearest irrigation draw point had a statistically significant effect when added to the models containing weather and land cover variables. To determine the relative importance of different weather variables, four alternative models were compared for each mosquito species: model 1 contained all statistically significant weather variables ($P < 0.05$) from the full model; model 2 contained only temperature and rainfall variables; model 3 contained only rainfall and humidity variables; and model 4 contained only the temperature and humidity variables. We used Akaike's Information Criterion (AIC) to assess relative goodness-of-fit of these models, penalized for the number of parameters. All statistical models were analyzed in SAS 9.2 (SAS Institute, Cary, NC) by using the GLIMMIX procedure.

Results

The mean annual abundance of *Ae. vexans* summarized across all traps varied from 7.63 to 65.76 mosquitoes per trap night. *Aedes vexans* was most abundant in 2005 and 2008 and less abundant in 2006 and 2007 (Table 1). *Culex tarsalis* showed a smaller inter-annual variation in abundance (2.43–8.67 mosquitoes per trap night) and was most abundant in 2005 and 2007 and less abundant in 2006 and 2008 (Table 1).

The temporal patterns of weekly mosquito abundance are shown in Fig. 1. *Aedes vexans* usually emerged earlier in the spring (weeks 17–19) than *Cx. tarsalis*. A bimodal seasonal pattern occurred in *Ae. vexans*, with peaks in summer and early fall. The *Cx. tarsalis* population started to increase in mid-June (weeks 20–23) and climbed rapidly to a peak in July (weeks 26–30). Early emergence was observed in 2007 for both species, especially for *Cx. tarsalis*, which may have been the result of warmer temperature in early spring (Fig. 1a). The warmer temperatures could have accelerated larval development and then triggered earlier population emergence. There was no obvious relationship between rainfall and mosquito abundance except for the heavy precipitation in week 31 of 2006, which might have reduced *Cx. tarsalis* abundance significantly in August (weeks 31–35) because of flushing effects on larval habitats (Fig. 1b).

The spatial patterns of mosquito abundance varied among years. For *Ae. vexans*, abundance was generally higher within city limits (Fig. 2). However, spatial autocorrelation of *Ae. vexans* was statistically significant only in 2005, and Mantel statistics were always lower than those for *Cx. tarsalis* in the same year. *Cx. tarsalis* was concentrated in the suburban and rural regions of the city and showed statistically significant spatial autocorrelation in every year ($P < 0.05$) (Fig. 3). Some traps consistently captured numerous mosquitoes. For example, a trap located northeast of the city limit (Fig. 3, black arrows) always collected many *Cx. tarsalis*, and two traps to the southeast (Fig. 2, black arrows) consistently captured large numbers of *Ae. vexans*.

The percentages of land cover types were similar in the different buffer sizes. Urban was the predominant land cover type (41.96–49.71%) followed by cultivated crops and grass/hay. Forest and wetland each made up $\approx 5\%$ of total. The abundance of *Ae. vexans* was positively correlated with wetlands but had a negative correlation with grass/hay (Fig. 4). *Cx. tarsalis* showed positive correlations with grass/hay and negative correlations with urban (Fig. 5). The correlation with agricultural crop land was minor in our study. It is worth noting that *Cx. tarsalis* correlations with land cover varied in different years. In 2005, the most abundant year for *Cx. tarsalis*, the correlation with cultivated crops was negative (although not statistically significant), and the negative association with urban was close to zero. These relationships were reversed in 2006, when *Cx. tarsalis* was less abundant.

The final statistical models contained three different types of variables. The first type of variable was a first order autoregressive term that was the female mosquito number in the previous week. The second type included weather variables that were weekly average temperature, weekly total rainfall, and weekly average relative humidity at a range of temporal lags from 0 to 4 wk. The third type of variable was two land cover types that were statistically significant in the full models. *Ae. vexans* had a significant positive association with wetlands ($P < 0.05$) and a negative association with grass/hay ($P < 0.05$) (Table 2). *Cx. tarsalis* had a significant positive association with grass/hay ($P < 0.05$) (Table 2).

The final regression models indicated that temperature in the current week and 1 wk before the collection of adult mosquitoes significantly affected *Cx. tarsalis* abundance (Table 3). Rainfall 3–4 wk prior also had positive associations, but the temperature 3 wk prior and humidity in the current week had negative associations with the abundance of *Cx. tarsalis* host-seeking females. Multimodel comparisons demonstrated that temperature was the most important component related to *Cx. tarsalis* abundance (AIC difference, 281.1 for the model excluding temperature; Table 3). For *Ae. vexans*, rainfall 2–3 wk prior and temperature in the current week had positive influences on mosquito abundance. The negative relationship with temperature 2 wk prior might reflect the inverse correlation between the temperature and rainfall. Relative humidity had a negative impact in the current week and a positive association 3 wk prior (Table 4). Multimodel comparisons demonstrated that rainfall was the most important factor in the models of *Ae. vexans* abundance (AIC difference, 276.98 for the model excluding rainfall; Table 4). *Cx. tarsalis* had a positive association with grass/hay in the final models but no statistically significant relationship with wetlands (Table 3). In contrast, *Ae. vexans* had a positive association with wetlands but no statistically significant association with grass/hay (Table 4). Both species had weak associations with distance to irrigation that were not statistically significant at the $P < 0.05$ level (data not shown). Therefore, the distance to irrigation variable was not included in the final models.

Discussion

This study analyzed the spatial and temporal patterns of *Ae. vexans* and *Cx. tarsalis* abundance and their relationships with land cover and climatic variability in Sioux Falls, SD, from 2005 to 2008. Female host-seeking mosquitoes were captured in this study through the use of CDC CO₂ light traps, so their abundances reflected the bloodmeal-seeking behavior of these species. The results indicated that environmental factors influenced the two mosquito species in different ways. *Ae. vexans* occurred in greater numbers than *Cx. tarsalis* and was most abundant in proximity to wetlands. In contrast, *Cx. tarsalis* was most abundant in landscapes dominated by grasslands, pasture, and hay. Vector control in Sioux Falls is partially dependent on the monitored mosquito counts, but the amount of treatments is constrained by budgetary limitations. Although these vector control efforts have an impact on mosquito populations, we were not able to obtain detailed data on control levels to include in our models. Therefore, we assumed that the influences of vector control activities

were captured by the random error term and the spatial covariance term in our mixed effects model.

Previous studies found that *Cx. tarsalis* breed in agricultural habitats and seek bloodmeals in developed areas in Colorado (Winters et al. 2008) and that *Cx. tarsalis* was dominant near agricultural areas in California (Nielsen et al. 2008). Furthermore, studies in California (Reisen et al. 2009) and Colorado (Eisen et al. 2010) have found that *Cx. tarsalis* abundance and WNV incidence are spatially associated with rural landscapes dominated by irrigated agriculture. A regional analysis of WNV incidence in the NGP similarly found that incidence during the 2003 outbreak was higher in counties with a higher percentage of the population living in rural areas and a higher percentage of irrigated land (Wimberly et al. 2008). However, the results of our finer-scale analysis emphasize that *Cx. tarsalis* abundance in eastern South Dakota is not generically associated with rural or agricultural habitats, but more specifically with landscapes dominated by perennial grass cover, particularly lands used for grazing and hay production. In contrast, associations with row crop agriculture were weak and nonsignificant. Furthermore, we did not find statistically significant associations with distance to irrigation. These findings reflect the land use patterns of eastern South Dakota, which is dominated by rain-fed agriculture with limited irrigation, as well as the distinctive ecology of *Cx. tarsalis*.

The linkage between mosquito abundance and breeding habitat is contingent upon the host-seeking behavior of different species. In previous studies, *Cx. tarsalis* has been shown to travel distances in excess of 10 km to find bloodmeals or locate oviposition sites (Milby et al. 1983, Reisen et al. 1992). Our findings showed that spatial patterns of *Cx. tarsalis* were positively correlated with landscapes dominated by grass/hay in a year when the species was less abundant (2006), but the correlations were lower in a year when this mosquito was comparatively abundant (Fig. 5). These results may reflect an interaction between mosquito abundance and dispersal. During the year (2006) with the lowest abundance, environmental conditions may have been less favorable for mosquito growth or adult survival, so that mosquito activity was concentrated close to breeding habitats. In contrast, mosquitoes may have survived longer and dispersed to more distant regions in the year (2005) with more favorable environmental conditions. Shaman et al. (2003) hypothesized that in Florida, mosquito vectors of Saint Louis encephalitis virus were restricted to densely vegetated habitat during drought periods and dispersed more broadly after periods of continuous rainfall. Similar effects may occur in eastern South Dakota, where surface water availability is highly sensitive to interannual climatic fluctuations. Additional years of data will be required to more rigorously assess the influences of weather on spatial associations between mosquito abundance and breeding habitats in the northern Great Plains.

Barker et al. (2009b) showed that adult mosquito abundance had no monotonic association with distance to larval habitat for *Cx. tarsalis* for distances up to 400 m, compared with a negative association for *Ae. vexans*. This finding suggests that *Ae. vexans* populations are likely to be more concentrated close to their breeding habitat, whereas *Cx. tarsalis* abundance does not depend on the distance from breeding sites <400 m away. In contrast, we found that both *Cx. tarsalis* and *Ae. vexans* had statistically significant spatial associations with habitats measured within a range of buffer sizes from 200 m to 1 km. Furthermore, we found that *Cx. tarsalis* exhibited higher spatial autocorrelation than *Ae. vexans*, which may reflect dispersal limitations and stronger spatial associations with breeding habitats. However, our study was not designed to specifically address questions related to dispersal, and additional field studies are needed to clarify the dispersal behavior of *Cx. tarsalis* in the northern Great Plains. Wind speed and direction, connectivity via river corridors and other dispersal habitat, and patterns of host availability are also important factors that should be considered.

Seasonal weather patterns influenced the abundances of both mosquito species. Rainfall 2–3 wk before mosquito sampling was the most important determinant of *Ae. vexans* abundance. This mosquito is known as a floodwater breeder and can be extremely abundant near inundated areas during summer. Other environmental factors, such as the temperature, are also critical (Schafer and Lundstrom 2006). The time from hatching to adult emergence varies 1 to 3 wk and increases with decreasing temperature (Becker et al. 2003). In our analysis, the strongest influence was rainfall 2 wk before mosquito sampling, which is concordant with the previous findings. Another study indicated *Ae. vexans* abundance was correlated with the interaction of cooling degree-days/precipitation and evapotranspiration (Trawinski and Mackay 2008). Shaman et al. (2002) showed the positive linkage between *Ae. vexans* abundance and a wetness index. Our models captured the positive influences of both temperature and precipitation at biologically plausible time lags that could provide for a basis for planning vector control activities. Although *Ae. vexans* is susceptible to WNV infection, it does not play a very important role in the enzootic cycle due to its low infection rate and feeding preference for mammals instead of birds (Bell et al. 2005, Molaei and Andreadis 2006).

In contrast, *Cx. tarsalis* is the principal WNV vector in the Great Plains region and West Coast due to its high vector competence (Goddard et al. 2002, Turell et al. 2005) and feeding behavior. This vector is ornithophilic in early season and its feeding behavior shifts to bite both birds and mammals when the population increases in summer (Kilpatrick et al. 2006, Kent et al. 2009). This shifting behavior allows *Cx. tarsalis* to serve as an amplification vector in late spring and also as a bridge vector to transmit WNV to humans and other animals in summer and fall. Our analysis showed that temperature in the preceding week is the most important factor triggering increases in *Cx. tarsalis* abundance. *Cx. tarsalis* prefers newly created standing water pools, ditches, or pond edges with organic nutrient covered by grass and vegetation, and larval development is strongly influenced by temperature (Beehler and Mulla 1995, Reisen et al. 1995, Zou et al. 2006). The oviposition behavior of *Culex* spp. is attracted to water with high levels of organic substrates (Bentley and Day 1989). Large open water bodies or running water, such as rivers, are not suitable habitat because of low nutrient concentrations and high predator abundance (Mercer et al. 2005). For this reason, rainfall is required to create temporary water pools, and the accumulation of organic matter determines whether female *Cx. tarsalis* lay eggs on the pools. This time interval is reflected in our models as the 3–4-wk lag between rainfall and increases in *Cx. tarsalis* abundance.

Negative temperature effects at 2-wk lags occurred in both species (Tables 3 and 4) which might indicate nonlinear associations with temperature. For example, extremely high temperature can reduce mosquito survival and result in the production of less offspring. A recent study in California also showed that summer *Cx. tarsalis* abundance was negatively associated with spring–summer temperature (Reisen et al. 2008). Similarly, relative humidity showed a negative influence in the current week for both species, although the effects were relatively minor. As with temperature, these negative relationships may reflect nonlinearity. High humidity could increase the mosquito survival (Clements 1963), but beyond a threshold extremely high humidity might indicate incoming rainfall and therefore limit the dispersal of adult mosquitoes. The potential for negative impacts of extreme weather conditions on vector abundance and disease transmission requires further study.

Our study provides comparative insight into the temporal and spatial distribution of two important mosquito species and their relationships with land cover and weather in southeastern South Dakota. This improved understanding of mosquito ecology could help to enhance the efficiency of vector control efforts and disease prevention. Host-seeking activity of these species was studied in Colorado, where *Cx. tarsalis* activity was highest 1.2–4.5 h after sunset and *Ae. vexans* was highest 0.8 h before and 6.5 after sunset (Godsey et al.

2010). These findings indicated the overlap of host-seeking activity of the two species after sunset. Our study further emphasizes that each species has a distinctive environmental niche and is associated with a different suite of weather conditions and landscape characteristics. Furthermore, given the unique climate, land use, and hydrology of the NGP, the details of these environmental relationships will probably differ from other regions of the western United States where *Cx. tarsalis* is the primary WNV vector. Vector control agencies can take advantage of these associations to anticipate the timing and spatial location of population increases and target vector control activities in more efficient ways.

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Fig. 1. Temporal patterns of weekly mosquito abundance and temperature (a) and rainfall (b).

Fig. 2. Spatial pattern of log-transformed *Ae. vexans* abundance (log-transformed annual female mosquitoes per trap night; red indicates impervious surfaces). (Online figure in color.)

Fig. 3. Spatial patterns of log-transformed *Cx. tarsalis* abundance (log-transformed annual female mosquitoes per trap night; red indicates impervious surfaces). (Online figure in color.)

Fig. 4. Correlations between log-transformed *Ae. vexans* abundance and land cover within different buffer sizes (the critical value is 0.388 for 2005 and 0.361 for 2006–2008 for P value = 0.05 under a two-sided test).

Fig. 5. Correlations between log-transformed *Cx. tarsalis* abundance and land cover within different buffer sizes (the critical value is 0.388 for 2005 and 0.361 for 2006–2008 for P value = 0.05 under a two-sided test).

Table 1

Summary statistics for yearly mosquito abundance

Yr	Cx. tarsalis			Ae. vexans		
	Total	Mean ^a	SE ^b	Total	Mean	SE
2005	14,048	8.67	1.51	97,050	65.76	12.46
2006	5,071	2.43	0.31	40,471	17.26	4.29
2007	15,728	6.16	1.04	19,199	7.63	0.91
2008	9,285	3.92	0.59	64,871	26.19	4.54

^a Raw female mosquitoes per trap night.

^b Number of traps was 24 in 2005 and 30 from 2006 to 2008.

Table 2

Mixed effect model results of land cover influences on mosquito abundance from the full models

Land cover (600-m buffer) ^a	<i>Ae. vexans</i>		<i>Cx. tarsalis</i>	
	Standardized estimate	95% CI	Standardized estimate	95% CI
Urban (51.8%)	2.21	−2.00 to 6.42	−2.72	−5.45 to 0.004
Deciduous forest (4.1%)	1.52	−2.62 to 5.67	−0.88	−3.75 to 1.99
Grass/hay (16.3%)	−4.11 *	−8.15 to 0.07	3.79 *	1.15–6.43
Cultivated crops (25.5%)	−0.39	−4.60 to 3.83	0.67	−2.23 to 3.57
Wetland (0.87%)	5.79 *	1.67–9.91	0.8	−2.19 to 3.79

^a Summarized from multiple regression models that were adjusted for weather variables at lags of 0–4 wk, a first order temporal autoregressive variable, a random intercept, and an exponential spatial covariance structure.

* $P < 0.05$.

Table 3
Mixed effects model results of weather and land cover influences on *Cx. tarsalis* from the final models

Variable ^a	Model 1			Model 2			Model 3			Model 4		
	Standardized estimate	95% CI		Standardized estimate	95% CI		Standardized estimate	95% CI		Standardized estimate	95% CI	
First order autoregressive												
Mos_lag1	29.28	27.42–31.13		29.54	27.70–31.39		38.29	36.71–39.88		29.31	27.44–31.17	
Weather												
Temp	7.57	5.08–10.06		9.06	6.60–11.52					6.11	3.62–8.59	
Temp_lag1	13.47	10.54–16.41		13.32	10.36–16.29					14.21	11.25–17.18	
Temp_lag2	– 6.34	–9.05 to 3.62		– 8.74	–11.37 to 6.10					– 5.95	–8.69 to 3.21	
Rainfall_lag3	4.45	3.02–5.89		4.31	2.87–5.75		4.75	3.22–6.27				
Rainfall_lag4	4.42	2.94–5.91		3.48	2.02–4.94		2.92	1.36–4.49				
Relative humidity	– 4.77	–6.40 to 3.14					– 4.34	–5.95 to 2.73		– 3.55	–5.16 to 1.95	
Land cover												
Grass/hay	4.27	1.56–6.98		4.30	1.65–6.96		2.71	0.88–4.52		4.23	1.52–6.93	
Wetland	1.90	–0.82 to 4.62		1.88	–0.78 to 4.54		1.22	–0.59 to 3.02		1.90	–0.82 to 4.61	
AIC		5,431.93			5,449.86			5,713.03			5,474.14	
AIC difference					17.93			281.1			42.21	

^aVariables in the models were selected from the full models according to statistical significance ($P < 0.05$; shown in bold) and only grass/hay and wetland were included as land cover variables.

Table 4
Mixed effects models results of weather and land cover influences on *Ae. vexans* from the final models

Variable ^a	Model 1			Model 2			Model 3			Model 4		
	Standardized estimate	95% CI		Standardized estimate	95% CI		Standardized estimate	95% CI		Standardized estimate	95% CI	
First order autoregressive												
Mos_lag1	45.6	43.13–48.08		46.21	43.72–48.69		50.84	48.62–53.06		42.73	40.16–45.29	
Weather												
Temp	22.9	19.71–26.08		21.03	17.98–24.08					23.15	19.77–26.53	
Temp_lag2	– 15.03	–18.26 to 11.79		– 15.09	–18.08 to 12.11					– 11.25	–14.65 to 7.84	
Rainfall_lag2	18.84	16.73–20.94		18.08	15.97–20.19		19.09	16.94–21.24				
Rainfall_lag3	3.26	1.11–5.41		4.82	2.72–6.91		2.85	0.61–5.08				
Relative humidity	– 4.99	–7.28 to 2.72					– 6.82	–9.05 to 4.60		– 3.82	–6.23 to 1.40	
RH_lag3	7.52	5.22–9.81					3.25	0.94–5.56		6.00	3.66–8.34	
Land cover												
Grass/hay	–2.83	–6.60 to 0.94		–2.81	–6.49 to 0.88		–2.57	–5.73 to 0.58		–3.22	–7.28 to 0.83	
Wetland	4.85	1.04–8.66		4.78	1.24–10.34		4.15	0.96–7.34		5.16	1.06–9.26	
AIC		7,235.19			7,264.57			7,407.92			7,512.17	
AIC difference					29.38			172.73			276.98	

^aVariables in the models were selected from the full models according statistical significance ($P < 0.05$, shown in bold) and only grass/hay and wetland were included as land cover variables.