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Drought-Induced Amplification of Local and Regional West Nile Virus Infection Rates in New Jersey

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ABSTRACT This study looked at the influence of interannual variations in temperature and precipitation on seasonal mosquito abundances, the prevalence of West Nile virus (family *Flaviviridae*, genus *Flavivirus*, WNV) in the northeastern United States, and the capacity for local mosquito communities to maintain and transmit WNV, defined as vector community competence. Vector and virus surveillance took place within Middlesex County in New Jersey over two transmission seasons (2010 and 2011). Drought conditions during the 2010 season were associated with significant increases in the number of blood-fed *Culex* spp. mosquitoes collected per week, and significant increases in vector community competence, or the ability of local vector communities to transmit WNV, when compared with the wetter and milder 2011 season. These increases were associated with significantly higher weekly WNV infection rates in *Culex* spp. (i.e., *Culex pipiens* L. and *Culex restuans* L.) during the 2010 drought season. On a larger scale, the positive influence of drought on the amplification of WNV was also confirmed at the state level where early seasonal (June–July) increases in temperature and decreases in precipitation were strongly correlated with increases in yearly WNV infection rates over a 9-yr period (2003–2011). These data suggest that there may be clear temperature and precipitation thresholds beyond which epidemic levels of WNV transmission occur.

KEY WORDS drought, West Nile virus, vector community competence, *Culex pipiens*, climate change

West Nile virus (family *Flaviviridae*, genus *Flavivirus*, WNV), first introduced in North America in 1999, has become the most economically and medically important active arbovirus in the United States. Clinically, over the last decade ≈1.8 million people were infected with WNV, resulting in 12,852 cases of encephalitis and meningitis and 1,308 deaths (Kilpatrick 2011). However, compared with the human consequences of infection, the impact of the virus on local wildlife populations has been much more serious. Overall, millions of birds have died from WNV infection, with some species experiencing regional population declines of >50% (LaDeau et al. 2007). The immense economic, public health, and wildlife importance of WNV has stimulated much research on the spatial and temporal risks of transmission. Several investigations have suggested that interannual and long-term climate variability may have a direct influence on the seasonality and intensity of WNV transmission (Epstein 2001, Dohm et al. 2002, Landesman et al. 2007, Ruiz et al. 2010). These studies have addressed the effects of a wide variety of climatic variables, including temperature, precipitation, relative humidity, total degree heating and cooling days, and others (Bolling et al. 2005, Miramontes et al. 2006, Brown et al. 2008, Ruiz

et al. 2010). Although several climate variables have been shown to influence the epidemiology of WNV, temperature and precipitation have emerged as the strongest predictors of viral activity (Landesman et al. 2007, Pecoraro et al. 2007, Ruiz et al. 2010).

Globally, temperatures haven risen steadily over the past 50 yr, and are expected to increase by approximately 1.0–3.5°C by 2100 (Karl et al. 1995). In the United States, daily temperatures have already increased by >0.70°C (Hansen et al. 2010), most of which occurred over the past 30 yr (Watson et al. 1996, Githeko et al. 2001). The current and projected increases in regional and global temperatures are fueling concern about the influence of global warming on the spread and amplification of vector-borne diseases (Githeko et al. 2001, Lafferty 2009). Global increases in temperature are projected to affect the distribution and transmission of mosquito-borne diseases by positively affecting the biology and ecology of the pathogen and its vector species. In regards to WNV, increased temperatures have been shown to increase larval mosquito growth rates, decrease the length of the gonotrophic cycle, and increase viral infection and dissemination rates, as well as increasing the evolutionary rate of the virus (Meyer et al. 1990, Dohm et al. 2002, Reisen et al. 2006, Kilpatrick et al. 2008, Paz and Albersheim 2008). Increases in temperature have

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also been positively correlated with mosquito abundances in Seattle, WA (Pecoraro et al. 2007), and were the strongest temporal predictor of increased infection rates in *Culex pipiens* L. and *Culex restuans* L. in Illinois (Ruiz et al. 2010). These factors, taken together, suggest that increases in seasonal and yearly temperatures lead to increased transmission efficiency and enzootic infection rates, and ultimately lead to an increase in disease risk.

Unlike temperature, the impacts of climate change on regional and global precipitation patterns cannot be described by a simple linear relationship. Modern precipitation patterns are shifting toward the extremes, with more frequent heavy rainfalls and fewer lighter precipitation events (Groisman and Easterling 1994, Karl et al. 1996, Knapp et al. 2008, IPCC 2012). These extremes between wet and dry may also be key predictors of increased or decreased WNV activity. Landesman et al. (2007) reported that human WNV outbreaks are preceded by above-average rainfall in the eastern United States and below average rainfall in the western United States during the prior year. Despite the potential duality of the influence of precipitation on WNV, below-average levels of precipitation seem to be a much stronger temporal predictor of increased WNV activity than above-average levels of precipitation. Seasonal drought periods have been associated with past WNV outbreaks in Europe, New York, Russia, and Israel (Epstein and Defilippo 2001). More recently, it was also reported that seasonal dry conditions precede increases in clinical WNV cases in the southern United States (Shaman et al. 2005), and in Illinois, lower precipitation values were the strongest spatial predictor of mosquito infection rates (Ruiz et al. 2010). Additionally, increased precipitation can negatively affect *Culex* spp. (i.e., *Cx. pipiens* and *Cx. restuans*) abundances, the main enzootic and bridge vector species for WNV in much of the United States (Bernard and Kramer 2001, Andreadis et al. 2004). One explanation for this negative effect is that large rainfalls have a flushing effect on larval container habitats (Geery and Holub 1989, Koenraadt and Harrington 2008). This flushing effect could decrease the ability of local mosquito communities to maintain and transmit WNV by decreasing the community presence of competent enzootic and bridge vector species. However, a lack of precipitation would allow water bodies to eutrophy, which could result in an increase in the community presence of *Culex* spp. because of their preference to oviposit in organically polluted and eutrophic water bodies (Lampman et al. 1996, Jacob et al. 2009).

In most of the above-mentioned studies, the influence of temperature and precipitation were based on annual metrics, e.g., yearly human or enzootic WNV infection rates, or relied upon laboratory experiments (Dohm et al. 2002, Reisen et al. 2006, Landesman et al. 2007, Ruiz et al. 2010). Few studies have incorporated the local and regional impacts of temperature and precipitation on the population and community dynamics of local vector species. The purpose of this study was to examine the seasonal influences of tem-

perature and precipitation on seasonal mosquito abundances, the ability of local mosquito communities to maintain and transmit WNV, which we define as vector community competence, and yearly WNV infection rates at both the local and regional levels. The data from this study come from field surveys of local mosquito communities and the prevalence of WNV within *Culex* spp. populations over two complete transmission seasons (2010–2011) in central New Jersey. At a larger regional scale, analysis of the long-term influence of precipitation and temperature on yearly WNV infection rates used statewide infection and climate data from nine transmission seasons (2003–2011).

Materials and Methods

Study Sites. We surveyed local mosquito populations and the prevalence of WNV at 12 sites located within Middlesex County in New Jersey between 2010 and 2011. Six sites were urban natural areas, primarily urban wetlands, and six sites were located within urban residential and commercial areas. All of the study sites fell within the Piedmont physiographic province, within the Arthur Kill (409.7 km²), or Lower Raritan (910.7 km²) water management areas (WMAs). Urban lands cover 83% of Arthur Kill and 58% of the Lower Raritan WMA; wetland area covers <4.5% and <18%, respectively (NJDEP GIS 2009).

Mosquito Collection. Two active trapping methods were used to monitor host-seeking adult female mosquitoes and the presence of blood-fed *Culex* spp. (i.e., *Cx. pipiens* and *Cx. restuans*). Adult host-seeking mosquitoes were collected using CO₂ baited CDC miniature light traps (John W. Hock Company, Gainesville, FL). Gravid mosquitoes were collected using CDC gravid traps (John W. Hock Company) baited with a hay infusion consisting of 0.5 kg (1 lb) of hay to 114 liters (30 gal) of tap water that was allowed to incubate for at least 5 d. Both trap types were set at least 1 h before sunset and collected the next morning. Mosquitoes were collected weekly June–September during both seasons. Because of the difficulty in correctly distinguishing between *Cx. pipiens* and *Cx. restuans* morphologically, and the lack of *Culex salinarius* (Coquillett) within our traps, collected *Culex* spp. were grouped for statistical analyses as the *Cx. restuans*–*Cx. pipiens* group.

West Nile Virus Testing. The dominant and most tested vector species for WNV in New Jersey are *Cx. restuans* and *Cx. pipiens*, which made them the focal species for WNV testing. In 2010 and 2011 *Cx. restuans* and *Cx. pipiens* mosquitoes were pooled and tested for WNV-viral RNA by TaqMan RT-polymerase chain reaction (PCR) assays according to established protocols (Lanciotti et al. 2000, Farajollahi et al. 2005) in collaboration with the Cape May County Department of Mosquito Control (Cape May, NJ) labs. In 2010 and 2011, only gravid trap collections were tested. Testing gravid trap collections is considered to be a more reliable method of viral surveillance than testing light trap collections (Williams and Gingrich 2007). Infection rates for each season were calculated using max-

Table 1. Summary of individual vector competence values and community dominance values (Berger and Parker 1970) for each mosquito vector species used to generate the vector community competence indices for the 2010 and 2011 collection seasons

Species	Enzootic vector competence value ^a	Bridge vector competence value ^a	Overall competence value	2010 Berger-Parker index of dominance ^{b,c}	2011 Berger-Parker index of dominance ^{b,c}
<i>Ae. albopictus</i>	0.20	1.00	0.60	0.026	0.055
<i>Ae. vexans</i>	0.00	0.50	0.25	0.408	0.362
<i>Culex</i> spp.	1.00	0.50	0.75	0.299	0.226
<i>Cq. perturbans</i>	0.20	0.25	0.23	0.006	0.005
<i>Och. canadensis</i>	0.00	0.50	0.25	0.002	0.008
<i>Och. japonicus</i>	0.20	1.00	0.60	0.045	0.011
<i>Och. triseriatus</i>	0.00	0.50	0.25	0.003	0.011

Overall competence values are derived from the average of each species enzootic and bridge vector competence values.

^a The potential of each species to transmit WNV enzootically (i.e., maintenance vector) and as a bridge vector (i.e. epizootic vector) are based on the results of Turell et al. (2001, 2005).

^b Berger-Parker index of dominance values are calculated as $d = N_i/N$, where N_i is the number of individuals of the i th species, and N is total number of individuals overall.

^c Berger-Parker index of dominance values are represented as weekly averages.

imum likelihood estimation MLE with 95% confidence intervals by using the PooledInfRate version 3.0 add-in (Biggerstaff 2006) for Microsoft Excel and minimum infection rate (MIR) methods when MLE could not be used. State mosquito collections between 2003 and 2009 were tested for WNV-viral RNA at the New Jersey Department of Health and Senior Services Public Health Epidemiology Laboratories (Trenton, NJ) and the Cape May County Department of Mosquito Control (Cape May, NJ) by using RT-PCR TaqMan techniques as outlined above.

Vector Community Competence Values. Changes in vector community competence values in relation to intra-annual variations in temperature and precipitation were used to determine how seasonal differences in climatic conditions affected the ability of local vector communities to transmit and maintain WNV. These values were calculated based on the abundance of each vector species within each habitat using CDC light trap collections because of the similarity between habitats ($F_{1,30} = 0.29$; $P = 0.59$); and exclusivity of gravid trap collections for *Culex* spp. mosquitoes. Community competence values were calculated based on the community presence and the capacity of individual vector species to serve as enzootic or bridge vectors for WNV. Competent vector species were chosen based on the ability of each species to serve as an enzootic or bridge vector for WNV based on the results of Turell et al. (2001, 2005). Each individual species was then assigned a competence value ranging from zero to one based on their ability to acquire and transmit WNV enzootically and act as a bridge vector (Table 1). These values were then combined with the community dominance values for each vector species calculated using the Berger-Parker index of dominance (Berger and Parker 1970, Magurran 2004). The result is a measure of the capacity of the vector community to transmit and maintain WNV locally. Competent vector species included *Culex* spp. (i.e., *Cx. pipiens*, *Cx. restuans*), *Aedes albopictus* (Skuse), *Ochlerotatus japonicus* (Theobald), *Aedes vexans* (Meigen), *Ochlerotatus canadensis* (Theobald), *Ochlerotatus triseriatus* (Say), and *Coquillettidia perturbans* (Walker).

Climate Data. Daily climate data for the 2003–2011 collection seasons were obtained through the Office of

the New Jersey State Climatologist (<http://climate.rutgers.edu/njwxnet/index.php>) and the Utah State Climate Center (<http://climate.usurf.usu.edu/index.php>), which provide access to National Weather Service Cooperative observation stations. For local analyses, climate data were obtained from the New Brunswick, NJ, weather station, which was the station nearest to a majority of our trap sites. For statewide analyses, daily climate data were averaged across 23 weather stations (Supp Table 1 [online only]).

Statistical Methods. Paired t -tests were used to evaluate significant differences between 2010 and 2011 weekly temperature, precipitation, and vector abundance averages. Correlations between species site abundances were analyzed using Pearson product correlation coefficients. Linear regression was performed using the R statistical package (R software), to evaluate the independent relationships between yearly and weekly temperature and precipitation differences and yearly WNV infection rates in *Culex* spp. For the statewide analysis, variations in temperature (daily maximum and daily minimum) and precipitation (daily and weekly lagged totals) were analyzed against cumulative yearly statewide WNV infection rates in *Culex* spp. Infection results were obtained through The Center for Vector Biology Surveillance system (Center for Vector Biology, Rutgers University). Over the nine seasons being analyzed (2003–2011) 25,677 pools of *Culex* spp. were submitted for testing resulting in 2,959 positive results (Table 2).

Results

Climatic Differences Between Years. There were significant differences in overall seasonal daily maximum temperatures ($t_{242} = -2.72$, $P = 0.007$) and seasonal daily precipitation values ($t_{242} = 2.03$, $P = 0.043$) between 2010 and 2011 (Fig. 1). Overall, the average daily maximum temperature during 2010 ($30.16 \pm 4.26^\circ\text{C}$) was 1.5°C higher than it was in 2011 ($28.66 \pm 4.33^\circ\text{C}$). Monthly, the temperature difference was greatest in June ($t_{58} = -2.26$, $P = 0.027$). In 2010 June had an average daily maximum temperature 2.19°C higher (29.94 ± 3.65) than June in 2011 (27.75 ± 3.81). Precipitation in 2011 averaged 3.5 mm

Table 2. Summary of cumulative yearly local and statewide West Nile virus testing results

Level	Yr	No. of pools	No. of mosquitoes	No. of positive pools	MIR
Local	2010	100	4,119	54	13.11 ^a
	2011	125	3,666	15	4.09 ^a
State	2003	3,099	83,392	272	3.26
	2004	2,007	63,667	208	3.27
	2005	2,155	74,650	214	2.87
	2006	1,994	74,334	184	2.48
	2007	2,447	82,282	255	3.10
	2008	3,395	117,142	476	4.06 ^a
	2009	3,915	150,780	294	1.95
	2010	3,113	104,116	641	6.16 ^a
	2011	3,552	118,224	415	3.51

^a Minimum infection rate >4.0 indicates that WNV is being transmitted at an epidemic level within avian host and vector communities.

more daily precipitation (6.10 ± 17.20 mm) compared with 2010 (2.6 ± 7.7 mm). Monthly, August experienced the greatest difference ($t_{60} = 2.50$, $P = 0.018$) with 2011 experiencing on average 13.0 mm more daily precipitation (14.1 ± 28.8 mm) compared with 2010 (1.1 ± 2.9 mm).

Mosquito Collections. During our study, 11,007 adult mosquitoes in total, consisting of 25 species, were collected from CDC light traps, and an additional 13,407 *Culex* spp. mosquitoes were collected using gravid traps (Table 3). There was a significant ($t_{14} = -3.52$, $P = 0.002$) increase in light trap collections between 2010 (188.2 ± 51.5) and 2011 (545.6 ± 92.3). Conversely, there was a significant decrease ($t_{14} = -2.55$, $P = 0.02$) in yearly gravid trap collections between 2010 (619.7 ± 109.8) and 2011 (274.1 ± 75.2). As is typical for most mosquito communities, a few common species comprised the majority of the collection totals. During both collection seasons *Ae. vexans*, the most abundant floodwater and pest species in the Northeast, dominated our collection totals. *Cx. restuans* and *Cx. pipiens*, the Northeast's most prominent container breeding species, were the second most abundant species overall for both collection seasons. The combined abundances of *Ae. vexans*, *Cx. restuans*, and *Cx. pipiens* accounted for 84.7% of collection totals in 2010 and 64.6% in 2011. Included in the top 10 species based on abundances were *Och. japonicus*, *Ochlerotatus trivittatus* (Coquillett), *Och. triseriatus*, *Och. canadensis*, *Anopheles punctipennis* (Say), *Anopheles quadrimaculatus* (Say), *Uranotaenia sapphirina* (Osten-Sacken), and *Cq. perturbans*.

Overall, yearly mosquito abundances followed a similar pattern between seasons (Fig. 2A). During both seasons mosquito populations were suppressed for most of the summer with the biggest peak in weekly light-trap catches occurring in late September. In contrast to light trap collections for both years, gravid trap collections in 2010 and 2011 both peaked early in the year (June–July) and then gradually decreased throughout the remainder of the season (Fig. 2B). This indicates that early seasonal conditions provided ample oviposition habitat that carried *Culex* spp. populations throughout much of the season.

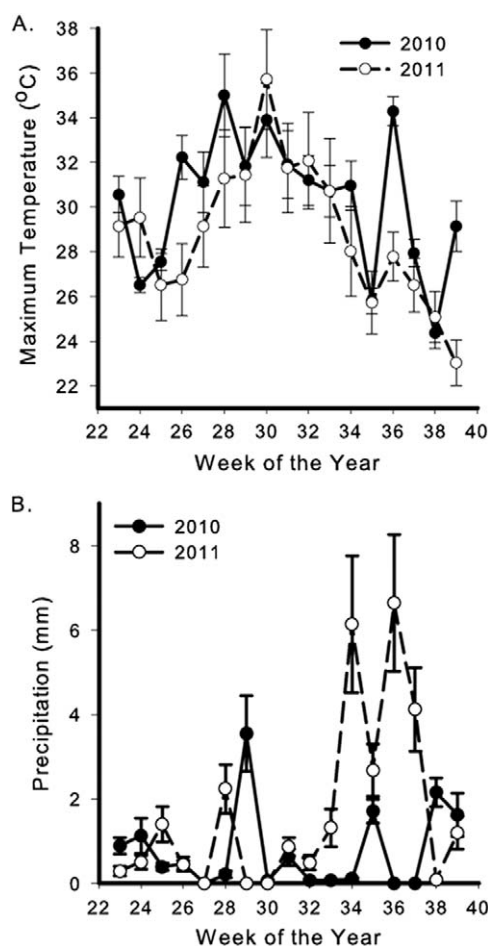


Fig. 1. Seasonal maximum temperature (A) and precipitation averages (B) for the 2010 and 2011 collection seasons (avg \pm SE). Overall, the 2010 season experienced higher weekly maximum temperature averages and lower weekly precipitation totals for most of the year compared with the 2011 season. The x-axis represents United States Center for Disease Control disease weeks.

Vector Community Competence Values. Inter-annual variations in temperature and precipitation were associated with significant differences in community competence values between years (Fig. 3A). Overall, despite producing less mosquitoes because of severe drought conditions, the 2010 season still produced significantly ($t_{14} = 3.01$, $P = 0.006$) higher weekly vector community competence values (0.38 ± 0.06) compared with 2011 (0.30 ± 0.08). In all, the 2010 season produced higher weekly community competence values for every week of collections. In addition, the weekly site abundances of major container-breeding species were significantly correlated with each other during the hot and dry 2010 season, but not during the wet and mild 2011 season (Table 4). In 2010 the weekly site abundances of *Culex* spp. were positively correlated to the weekly site abundances of *Och. japonicus* ($r = 0.60$, $P = 0.03$), but not *Ae. albopictus*

Table 3. Weekly and seasonal totals for the 12 most common species collected during the 2010 and 2011 collection seasons

Species/wk	Weekly collection summary for 2010																Total
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38		
<i>Ae. albopictus</i>	1	2	1	4	5	3	3	22	0	0	10	10	2	1	11	75	
<i>Ae. vexans</i>	24	38	55	13	39	56	37	97	34	20	69	186	184	358	800	2,010	
<i>An. punctipennis</i>	8	9	4	9	13	16	3	21	14	6	18	2	7	13	4	147	
<i>An. quadrimaculatus</i>	3	4	5	1	4	0	1	4	2	1	2	0	0	0	0	27	
<i>Cq. perturbans</i>	2	1	1	0	4	0	0	2	0	0	0	0	0	0	0	10	
<i>Culex</i> spp.	52	56	31	17	38	20	14	18	18	31	21	7	23	10	25	381	
Gravid <i>Culex</i> spp.	731	1,292	1,419	1,341	928	471	498	448	514	184	341	297	356	191	284	9,295	
<i>Och. canadensis</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Och. japonicus</i>	7	7	0	1	3	4	4	6	12	1	14	10	2	2	1	74	
<i>Och. triseriatus</i>	0	0	2	0	0	1	0	0	1	0	2	1	0	0	0	7	
<i>Och. trivittatus</i>	0	11	6	0	16	10	1	1	0	0	0	0	0	0	0	45	
<i>Ur. sapphirina</i>	0	1	0	0	1	0	0	3	0	0	1	0	4	0	1	11	
Light-trap totals ^a	103	132	109	47	128	113	65	175	83	64	139	216	222	384	843	2,823	
Species/wk	Weekly collection summary for 2011																Total
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38		
<i>Ae. albopictus</i>	2	0	0	11	7	0	7	22	32	25	18	22	42	15	25	228	
<i>Ae. vexans</i>	9	140	276	133	321	61	70	77	78	49	62	1,184	726	747	247	4,180	
<i>An. punctipennis</i>	6	35	29	9	64	134	105	111	86	38	74	58	47	48	8	852	
<i>An. quadrimaculatus</i>	0	2	6	2	2	2	0	3	2	0	11	6	2	2	4	44	
<i>Cq. perturbans</i>	1	6	12	1	3	12	14	5	10	3	9	0	1	0	77	154	
<i>Culex</i> spp.	78	156	133	45	75	32	48	61	34	31	50	121	119	101	24	1,108	
Gravid <i>Culex</i> spp.	316	814	1,011	492	338	155	205	155	232	117	80	53	62	49	33	4,112	
<i>Och. canadensis</i>	2	34	7	1	1	0	0	0	0	0	0	0	0	0	0	45	
<i>Och. japonicus</i>	0	4	16	6	7	1	4	4	1	0	6	5	1	8	2	65	
<i>Och. triseriatus</i>	0	11	3	3	13	7	7	2	0	0	1	4	2	3	3	59	
<i>Och. trivittatus</i>	8	4	5	12	3	10	3	0	0	1	0	53	10	9	11	129	
<i>Ur. sapphirina</i>	0	1	5	5	4	41	42	257	327	142	368	39	10	7	2	1,250	
Light-trap totals ^a	109	393	492	233	500	300	300	542	570	303	599	1,500	971	969	403	8,184	

Abundances are represented as the total number of female mosquitoes of each species collected per week by using CDC miniature light traps baited with CO₂, except gravid *Culex* spp. that were collected using CDC gravid traps baited with a hay infusion.

^a Light-trap totals include all species collected.

($r = 0.10$, $P = 0.74$), which was never captured in large numbers.

Local Influence of Temperature and Precipitation on Yearly Infection Rates. In addition to being associated with higher weekly gravid trap collections and vector community competence values, the 2010 season produced significantly higher levels of WNV infection compared with the 2011 season (Table 2). Overall, the 2010 season produced higher weekly infection rates for 10 of 11 wk of testing (Fig. 3B). This led to an average weekly MIR of 18.44/1000 during the 2010 season, which is significantly greater ($t_{10} = 3.24$, $P = 0.004$) than the average weekly infection rate produced during the milder 2011 season (4.09/1000). Seasonally, August produced higher overall infection rates during both the 2010 (35.52) and 2011 (14.63) seasons compared with July (13.34, 1.31) and September (14.58, 4.29). Despite the substantial increase in infection rates during the 2010 season there were no significant correlations between infection rates and weekly temperature and precipitation averages, a trend which also carried over to the 2011 season.

Regional Influence of Temperature and Precipitation on Yearly Infection Rates. State-wide, early seasonal drought conditions (i.e., increased temperature and decreased precipitation) preceded high transmission seasons. Each season experiencing epidemic transmission levels (MIR > 4) over the past 9 yr (Table 2) in New Jersey experienced drought conditions (daily high temperature averages >29.0°C and

daily precipitation averages <4.0 mm) early in the season (June–July). Correlation analyses reveal that early seasonal increases in daily maximum temperatures between June and July were significantly positively correlated with yearly infection rates ($r = 0.75$, $P = 0.021$), whereas early seasonal increases in daily precipitation totals over the same time period were significantly negatively correlated ($r = -0.85$, $P = 0.004$) with yearly WNV infection rates (Fig. 4). In addition, linear regression analyses reveal that increases in daily precipitation totals averaged between the months of June and July were the strongest temporal predictor of yearly WNV activity, explaining 67% of the variation in yearly infection rates ($R^2 = 0.67$, $P = 0.004$). Increases in daily maximum temperatures averaged between the months of June and July were also a strong temporal predictor of yearly WNV activity, explaining 50% of the variation in yearly infection rates ($R^2 = 0.50$, $P = 0.021$). Combined, the interaction between early seasonal daily maximum temperatures and daily precipitation totals explained 69% ($R^2 = 0.69$, $P = 0.003$) of the yearly variation in WNV infection rates in *Culex* spp. These data show that early seasonal temperature and precipitation averages can be strong predictors of yearly WNV activity.

Discussion

The results of this study support the importance of intra-annual variations in temperature and precipita-

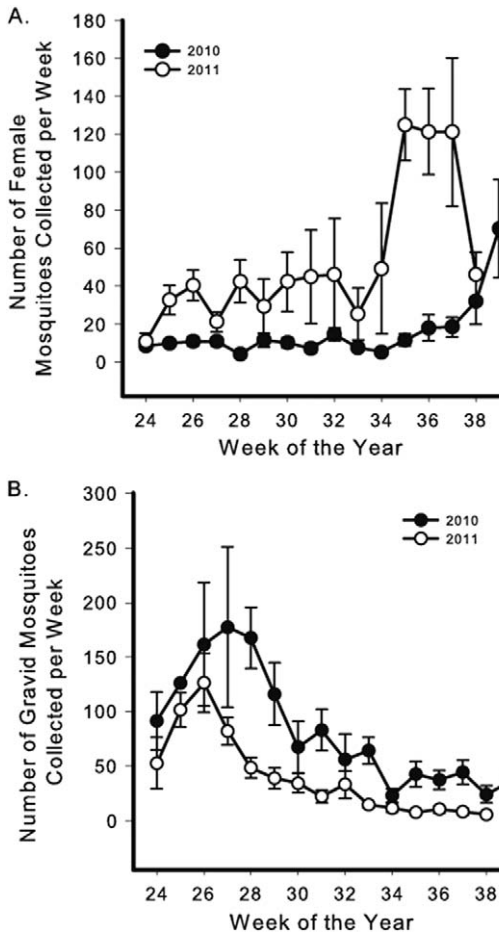


Fig. 2. Seasonal light-trap (A) and gravid-trap abundances (B) for the 2010 and 2011 collection seasons (avg \pm SE). Overall, 2011 produced higher weekly light-trap collections compared with the 2010 season, whereas the 2010 season produced higher weekly gravid trap collections compared with the 2011 season. Furthermore, light-trap and gravid trap abundances peaked at opposite times in the season during both years. Light-trap collections peaked late in the year, whereas gravid trap collections peaked early in the year. Light-trap collections represent the number of female host-seeking mosquitoes collected per week, whereas gravid-trap collections represent the number of successfully blood-fed female *Culex* spp. mosquitoes collected per week. The x-axis represents United States Center for Disease Control disease weeks.

tion on local vector population dynamics and the seasonal prevalence of WNV, as well as the importance of interannual variations in temperature and precipitation on regional yearly infection rates. Our primary finding is that seasonal conditions associated with drought (i.e., increased temperatures and decreased precipitation totals) correspond to epidemic transmission levels at both the local and regional levels. These data confirm the association between drought and the amplification of WNV as reported by others (Epstein and Defilippo 2001, Shaman et al. 2005). These find-

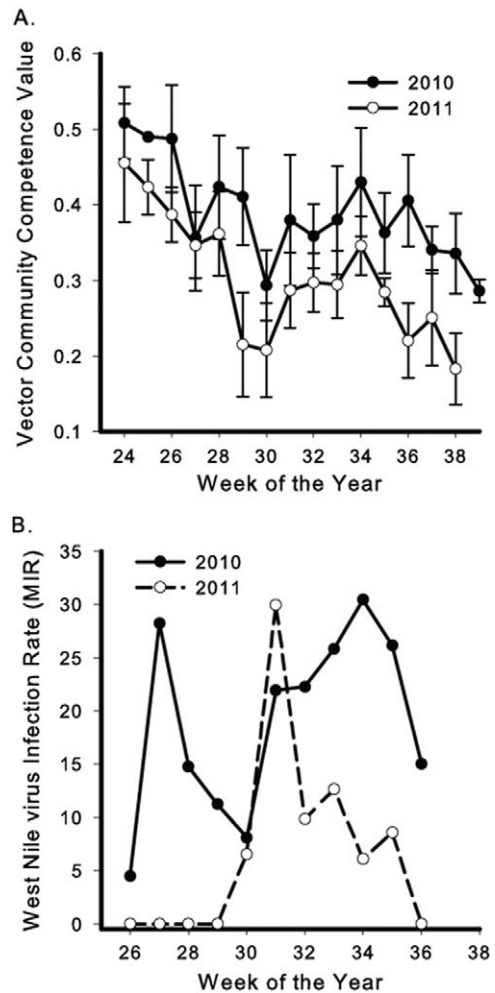


Fig. 3. Seasonal vector community competence values (A) and West Nile virus infection rates (B) for the 2010 and 2011 seasons. Vector community competence values (avg \pm SE) are based on the community presence and ability of individual vector species to act as enzootic or bridge vector species for WNV. WNV infection rates are represented as weekly MIR in *Culex* spp. (*Cx. restuans* and *Cx. pipiens*) populations. Overall, the 2010 season produced higher weekly vector community competence values and weekly WNV infection rates for all but 1 wk of collections compared with the 2011 season. The x-axis represents United States Center for Disease Control disease weeks.

ings may also extend to other encephalitic mosquito-borne diseases known to respond positively to drought, including Saint Louis encephalitis virus (family *Flaviviridae*, genus *Flavivirus*) that has a transmission cycle that is similar to WNV (Shaman et al. 2002).

The principal mechanisms behind the increase in infection rates at the local level during the 2010 season was an increase in the number of successfully blood-fed *Culex* spp. collected per week, and an increase in the community presence of virally competent vector species in response to drought. Increases in the number of successfully blood-fed *Culex* spp. in response to

Table 4. Species-site correlations between *Culex* spp. and other prominent container inhabiting species (i.e., *Ae. albopictus* and *Och. japonicus*) and *Ae. vexans*, the most abundant floodwater species in the Northeast

Yr	Species	Species-site Pearson's product moment correlations	
		<i>r</i>	<i>P</i>
2010	<i>Culex</i> spp./ <i>Och. japonicus</i>	0.6	0.03*
	<i>Culex</i> spp./ <i>Ae. albopictus</i>	0.10	0.74
	<i>Culex</i> spp./ <i>Ae. vexans</i>	-0.06	0.805
2011	<i>Culex</i> spp./ <i>Och. japonicus</i>	0.19	0.52
	<i>Culex</i> spp./ <i>Ae. albopictus</i>	0.10	0.73
	<i>Culex</i> spp./ <i>Ae. vexans</i>	0.19	0.52

There were positive significant site correlations between container inhabiting species (i.e. *Culex* spp. and *Och. japonicus*) during the 2010 collection season but not during the 2011 season. These data demonstrate that both site specific qualities and seasonal climate differences influence the site abundances of individual vector species.

* $P < 0.05$.

increased temperatures may be because of shortened developmental times and increased rates of oviposition activity, ultimately leading to increased biting rates (Strickman 1988, Ruiz et al. 2010). The importance of the relationship between increased oviposition activity and increased WNV activity in response to temperature has also been confirmed by Reisen et al. (2006). Resien and his colleagues reported that enzootic WNV activity in *Culex tarsalis* Coquillett, the primary vector of WNV in the western United States, began after the length of both the gonotrophic cycle and the extrinsic incubation period (EIP) decreased in response to increased temperature. Conversely, the increase in weekly vector community competence values may be attributed to a lack of precipitation. A lack of precipitation may have increased the community presence of WNV-competent vector species by creating a strong spatial synchronicity between competent vector species (i.e., *Culex* spp. and *Och. japonicus*) through larval habitat stabilization. *Culex* spp. and *Och. japonicus* are both prominent urban container-breeders (Sardelis et al. 2002, Andreadis et al. 2004, Molaei et al. 2006, Farajollahi and Nelder 2009), and unlike floodwater species, they are subject to flushing effects in larval habitats in response to large precipitation events (Geery and Holub 1989, Koenraadt and Harrington 2008). Furthermore, a lack of precipitation would allow water bodies to eutrophy, which could result in an increase in the community presence of *Culex* spp. because of their preference to oviposit in organically polluted and eutrophic water bodies (Lampman et al. 1996, Jacob et al. 2009). Therefore, drought conditions may not only decrease the community presence of less competent floodwater species (Turell et al. 2005) but also may increase the presence of virally competent vector species within an area.

At the state level, early seasonal (June–July) increases in temperature and decreases in precipitation related to drought support epizootic transmission levels within *Culex* spp. (*Cx. restuans* and *Cx. pipiens*) populations through a dichotomous process. This pro-

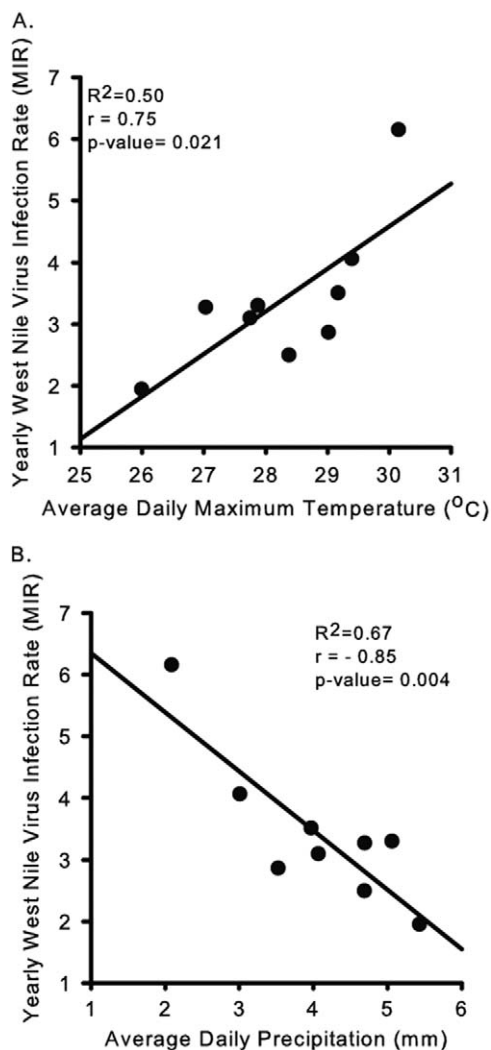


Fig. 4. Relationships between yearly West Nile virus infection rates and early seasonal (June–July) daily maximum temperature (A) and daily precipitation (B) averages. Temperature and precipitation are represented as weekly averages. WNV infection rates are represented as cumulative yearly infection rates within *Culex* spp. (*Cx. pipiens*, *Cx. restuans*) pools submitted to the state of New Jersey from 2003 to 2011. These figures show that early seasonal drought conditions (i.e., increased temperatures and decreased precipitation totals) are strongly associated with increases in yearly WNV infection rates in *Culex* spp. in New Jersey.

cess revolves around the positive impacts of increased temperature and decreased precipitation events during the primary amplification and transmission phases of WNV in the Northeast. Much like the annual transmission cycle of Saint Louis encephalitis virus (Shaman et al. 2002), the seasonal transmission cycle of WNV in the Northeast can be divided into four primary phases: March–April, reemergence; May–June, early transmission; July–August, primary transmission; and September–October, late transmission. Thus, June and July represent critical transmission periods for

WNV. Subsequently, processes which favor the transmission of disease over this time period could elevate transmission from endemic to epidemic levels. The dichotomous relationship between temperature and precipitation may seem counterintuitive because increases in monthly precipitation lead to increases in the abundance and type of aquatic larval habitats, which result in an increase in mosquito abundance (Shaman et al. 2002, 2006; DeGaetano 2005; Shaman and Day 2006). However, as we have shown above drought conditions significantly increase the community presence of competent vector species while decreasing the community presence of less competent floodwater species, such as *Och. canadensis* and *Ochle-rotatus cantator* (Coquille), which have virtually no role in the enzootic amplification of WNV (Turell et al. 2005). This occurs because the majority of floodwater species prefer to feed on mammalian hosts, whereas *Cx. pipiens* and *Cx. restuans* are ornithophilic (Turell et al. 2001, Turell et al. 2005). Thus, when increased temperatures and decreased precipitation totals co-occur, as experienced during the 2010 season, it results in epizootic levels of transmission, as seen in both our local and regional analyses. This is a similar conclusion to that of Shaman et al. (2011) who reported that drier early summer conditions during the months of June and July were associated with increases in WNV among *Culex* vectors in Long Island, NY.

There is a very clear temperature and precipitation threshold (daily high temperature averages $>29.0^{\circ}\text{C}$ and daily precipitation averages $<4.0\text{ mm}$) over which epidemic levels ($\text{MIR} > 4.0$) of transmission occur in New Jersey. Above this threshold, there is evidence of increased physical contact between vector and host species involved in WNV transmission (i.e., fewer available water sources, increased feeding rates, and increased vector density). Thus, the increased physical contact between vector and host as they aggregate around scarce resources, similar to what occurred during the 2010 season, would facilitate epizootic WNV amplification. A similar dynamic was responsible for the increase in WNV activity in the southern United States during early drought conditions which resulted in the aggregation of *Culex nigripalpus* (Theobald) and wild birds, and lead to epizootic WNV amplification and high levels of WNV transmission (Shaman et al. 2005).

In conclusion, several authors have warned that global climate warming will increase the distribution and emergence of a wide variety of infectious diseases (Sutherst 1993, Martens et al. 1995, Lindsay et al. 1998, Patz et al. 1998, Harvell et al. 2002). These assumptions have been supported by a number of studies demonstrating the positive impacts of global climate change on a wide range of infectious diseases (Patz et al. 1998, Martens et al. 1999, Reiter 2001, Rydzanicz et al. 2006). In our study we have shown that drought conditions (i.e., increased temperatures and decreased precipitation), the frequency and severity of which are predicted to increase because of global climate change (Sheffield and Wood 2008, Allen et al. 2010, IPCC

2012), are associated with increases in the prevalence of WNV. Furthermore, although socioeconomic conditions and anthropogenic activities may also be important in the distribution and emergence of WNV and other infectious diseases (Ruiz et al. 2007, Bradley et al. 2008, Zell et al. 2008, Lafferty 2009, Randolph 2009), our study confirms that seasonal variations in climatic conditions have a strong impact on the prevalence of vector-borne diseases.

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