

The roles of mosquito and bird communities on the prevalence of West Nile virus in urban wetland and residential habitats

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Abstract This study investigated the impacts of urban wetlands and their adjacent residential environments on the transmission dynamics of West Nile virus (WNV) within the state of New Jersey (USA). A working hypothesis was that urban wetlands decrease the local prevalence of WNV through the dilution effect from increased bird diversity, and through relative reductions in the numbers of competent avian host and mosquito species commonly associated with WNV. Surveys of mosquito and bird communities were undertaken at six urban wetlands and their adjacent residential environments over two seasons (2009, 2010). The community compositions of both avian and mosquito species differed significantly across habitats, and over relatively short geographical distances. Residential areas contained significantly higher proportions of WNV-competent mosquito species (31.25 ± 5.3 %; e.g. *Culex pipiens* and *Culex restuans*), and WNV-competent avian host species (62.8 ± 2.3 %, e.g. House Sparrow and American Robin) when compared to adjacent urban wetlands (13.5 ± 2.1 %; 35.4 ± 2.1 % respectively). Correspondingly, WNV infection rates within local *Culex spp.* populations indicate that WNV was more prevalent within residential areas (28.53/1000) compared to wetlands (16.77/1000). Large urban wetlands (>100 ha) produced significantly lower weekly WNV infection rates in local *Culex spp.* ($6.67 \pm 2.84/1000$) compared to small (<15 ha) wetlands ($22.57 \pm 6.23/1000$). Avian species richness was also influenced by patch size. Large urban wetlands contained significantly more species than small wetland patches. These results confirm that the community compositions of mosquito and avian hosts are important drivers in WNV infections, and that the ecological conditions that favor transmission are more strongly associated with urban residential environments than with adjacent urban wetlands.

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Introduction

In 1910 only 10 % of the world's population lived in urban areas. This figure is now over 50 % and is predicted to reach 70 % by 2050 (Grimm et al. 2008; Seto and Shepherd 2009). The rapid and sustained increase in the number of people living within urban areas has led to a drastic alteration of the physical environment of urban landscapes over the last century (McDonnell and Pickett 1990; Grimm et al. 2000; Zipperer and Pickett 2001). These alterations have severely impacted the preservation, structure, and function of urban wetlands within developing areas (Mahan et al. 2000; Azous and Horner 2001; Boyer and Polasky 2004). Nevertheless, urban wetlands are still the most common type of natural area remaining within many urban areas where they contribute substantially to the enhancement and functionality of urban environments (Manuel 2003; Ehrenfeld 2004). Urban wetlands store floodwaters, maintain water quality, cycle nutrients, and are the main repositories of plant and animal biodiversity within urban areas (Guntenspergen and Dunn 1998; Ehrenfeld 2004; Faulkner 2004).

Despite the potential benefits of urban wetlands, there can be significant local opposition from landowners because urban wetlands are thought to produce and harbor disamenities, such as nuisance animals, unpleasant odors, and high abundances of insects and pests (Doss and Taff 1996). Aggravating these negative sentiments, and putting additional strain on the conservation of urban wetlands, is the concern about urban wetlands and their potential link to increased incidences of human West Nile virus (WNV) infections.

WNV is a single-stranded RNA virus belonging to the family Flaviviridae that includes several important arboviruses, such as Dengue, Japanese encephalitis, and Yellow fever (Lanciotti et al. 1999). Ecologically, WNV is a mosquito-borne human, equine, and avian neuropathogen that is primarily maintained in an enzootic cycle between ornithophilic mosquitoes and local avian hosts (Campbell et al. 2002). WNV was first introduced into the United States in 1999 in New York City (Nash et al. 2001). After its introduction WNV spread rapidly across North America with major economic, public health, and wildlife consequences (LaDeau et al. 2007; Peterson and Hayes 2008). Between 1999 and 2010, ~1.8 million people were infected resulting in 12,852 cases of encephalitis/meningitis and 1308 deaths (Kilpatrick 2011). Local and regional avian populations have fared much worse. Overall, millions of birds have died from WNV infection with certain species experiencing regional population declines of >50 % (LaDeau et al. 2007). During its rapid spread WNV has become increasingly associated with anthropogenically modified areas, particularly urban landscapes (Diuk-Wasser et al. 2006; Pecoraro et al. 2007; Bradley et al. 2008; Brown et al. 2008). Within highly developed areas WNV has been linked to urban green-spaces (Brownstein et al. 2002); particularly in New York City where Rappole et al. (2000) reported that the outbreak of WNV in 1999 occurred at urban sites near wetlands where ornithophilic mosquitoes, migratory birds, and humans are in close contact.

The link between WNV and urban wetlands seems feasible enough given that urban wetlands, and their surrounding urban habitats, can provide potential breeding habitats for competent vector species (e.g. *Culex pipiens* and *Culex restuans*), as well as nesting habitat for common avian hosts implicated in WNV transmission (e.g. American robin and house sparrow). Urban wetlands may also help maintain WNV locally by recruiting immunologically naive birds into an area, since some species of birds develop long-term immunity to WNV (Hamer et al. 2008; Nemeth et al. 2009). However, in contrast to acting as a reservoir

for WNV, wetlands have also been shown to decrease the prevalence of WNV within local mosquito populations. Ezenwa et al. (2007) found that WNV infection rates among *Culex spp.* mosquitoes declined with increasing wetland cover. Furthermore, urban wetlands are the main repositories of biodiversity within urban landscapes (Ehrenfeld 2004). Increased diversity, particularly avian diversity, has been shown to decrease the prevalence of WNV (Allan et al. 2009). This information, combined with the anthropogenic nature of WNV and its primary vector and avian host species, strengthens the possibility that urban wetland areas may decrease the prevalence of WNV. Given these two contrasting views, the true role urban wetlands play in WNV transmission needs to be fully understood.

The purpose of this study was to investigate the immediate impacts of urban wetlands and their adjacent urban environments on the local transmission dynamics of WNV within the northeastern United States. This analysis compares the transmission dynamics of WNV within two habitats over a finer-scale (~500 m) than has been performed previously (Ezenwa et al. 2006; Loss et al. 2009; Bowden et al. 2011). The primary hypothesis is that urban wetlands decrease disease risk for WNV by negatively influencing the ability of local avian host and mosquito communities to maintain and transmit WNV. We believe this occurs in two ways: through the *dilution effect*, and through decreases in the community presence of competent mosquito and avian host species. The dilution effect is based on the diversity of the avian host communities within each habitat and posits that more diverse host communities contain more incompetent disease hosts, thus decreasing disease transmission by directing mosquito blood meals away from more competent host species (Ostfeld and Keesing 2000; Schmidt and Ostfeld 2000; Swaddle and Calos 2008; Keesing et al. 2010). The dilution effect has been shown to occur in relation to WNV (Ezenwa et al. 2006; Allan et al. 2009), and based on the increased avian diversity associated with urban forest fragments and other natural areas compared to more developed areas (Bessinger and Osborne 1982; Tilghman 1987; Jokimaki and Suhonen 1993; Clergeau et al. 1998; Cam et al. 2000) we believe there is strong evidence that the dilution effect may be occurring within urban wetland areas.

In addition to the dilution effect, urban wetlands may decrease the prevalence of WNV by decreasing the community presence of competent avian host species, as well as enzootic and bridge mosquito species associated with WNV. Natural wetland areas have been shown to contain a greater species richness of non-passerine species compared to developed areas, increases in which have been negatively related to mosquito and human infection rates (Ezenwa et al. 2006). Furthermore, increasing the level of urbanization in an area selects for omnivorous, granivorous, and cavity nesting avian species, while leading to an increase in avian biomass and a reduction in diversity (Blair 1996; Miller et al. 2003; Crooks et al. 2004; Chace and Walsh 2006). These processes lead to increases the abundance of common avian host species implicated in WNV transmission, such as the American robin, northern cardinal, and the house sparrow (Komar et al. 2001; Apperson et al. 2002; Kilpatrick et al. 2006) within urban environments compared to more natural areas (Bradley et al. 2008; Diuk-Wasser et al. 2010). In addition to decreasing the community presence of competent avian host species, urban wetlands should also decrease the community presence of competent vector species. Most mosquito species implicated as competent WNV vectors are strongly associated with urban landscapes. In the Northeast, the primary enzootic and bridge mosquito species for WNV, *Culex pipiens* and *Culex restuans*, are strongly associated with urban environments (Bernard and Kramer 2001; Andreadis et al. 2004; Molaei et al. 2006), as are several possible WNV bridge mosquitoes, including *Aedes albopictus* and *Ochlerotatus japonicus* (Sardelis and Turell 2001; Sardelis et al. 2002; Farajollahi and Nelder 2009). All of these species are container-breeding species that breed readily in a variety of artificial water sources that are abundant within urban environments (Costanzo et al. 2005;

Bevins 2007). In contrast, urban wetlands are dominated by major floodwater species, such as *Aedes vexans*, *Ochlerotatus canadensis*, *Ochlerotatus cantator*, and *Ochlerotatus trivittatus*, which have a minimum, if any, role in the enzootic transmission of WNV (Turell et al. 2005). By decreasing the community presence of competent avian host and vector mosquito species the enzootic and incidental transmission of WNV to humans should be decreased within wetland areas.

To test our predictions, we compared mosquito and avian host diversity, the community presence of competent WNV avian host and mosquito species, and the prevalence of WNV within urban wetlands and their adjacent urban residential areas in central New Jersey (USA) during the 2009 and 2010 transmission seasons (June–September). Our study is the first to examine the dynamics of host diversity and community presence of competent mosquito and host species on the transmission of WNV between two uniquely different, but inseparable, urban habitats at the local level. Studies of this kind could have invaluable implications in an ever developing world facing the globalization of anthropophilic vectors (e.g. *Ae. albopictus*) and the diseases they transmit.

Materials and methods

Survey sites

All of our study sites fall 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 2007). To direct our research to the relationship between urban wetland patches and urban disease risk, we selected wetlands surrounded predominately by medium-high (0.5–0.125 acres/unit) density housing (Hasse and Lathrop 2008). The urban wetland patches are dominated by secondary deciduous swamps (e.g., *Acer rubrum*, *Liquidambar styraciflua*, *Quercus spp.*, and *Fraxinus pennsylvanica*), scrub-shrub, and emergent plant assemblages associated with saturated to seasonally flooded landscapes (Cowardin et al. 1979). In total, six urban wetlands, consisting of small (<15 ha), medium (15–30 ha), and large (>30 ha) wetland patches were surveyed (Table 1). All sites were located within Middlesex and Union counties in central New Jersey (Fig. 1).

Avian surveys

Wetland avian survey locations were selected along a 400 m×400 m sampling grid that was established within each wetland. Residential survey locations were selected along a 500 m residential buffer that was created around each wetland boundary. During the breeding season (May 15–July 15), avian wetland surveys were conducted at each point along the 400×400 sampling grid; residential avian sample points were placed every 400 m along the residential buffer. Within each wetland, 1–15 avian points were sampled (35 total), and 10–12 residential avian points were sampled (68 total) around each wetland (Table 1). Each wetland and residential point was visited two to three times during the breeding season. During each visit, observers conducted 10-minute point count surveys.

During fall migration (August 15–October 31), avian surveys were conducted using line transects. Line transects were selected for migration surveys because they have been shown to increase the number of species detected during migration (Wilson et al. 2000), when birds are no longer singing and thus may be less detectable on point counts. Within the wetland

Table 1 Summary of wetland sites and survey summaries for avian point counts and mosquito collection sites for each season (2009/2010)

Site	Size (hectares)	County (NJ)	Water Type/Types	Year Surveyed
Large 1	267.1	Middlesex	Seasonally Flooded/ Saturated Partially Drained/ Ditched	2009/2010
Large 2	182.1	Union	Temporally Flooded/ Seasonally Flooded	2009
Small 1	8.36	Middlesex	Saturated	2009/2010
Small 2	11.33	Union	Saturated	2009
Medium 1	24.7	Middlesex	Saturated Partially Drained/Ditched	2010
Medium 2	27.1	Middlesex	Saturated	2010
	Avian Wetland Survey Points Breeding ^a / Migration ^b	Avian Residential Survey Points Breeding ^a /Migration ^b	Wetland Mosquito Survey Points 2009/2010	Residential Mosquito Survey Points 2009/2010
Large 1	15/15	12/6	2/4	2/4
Large 2	11/11	12/6	2	2
Small 1	1/3	10/6	2	2/4
Small 2	2/2	11/6	2	2
Medium 1	3/0	11/0	2	2
Medium 2	3/0	12/0	2	2

^a Avian breeding season surveys were conducted using point count methods

^b Avian migration surveys were conducted using line-transect methods

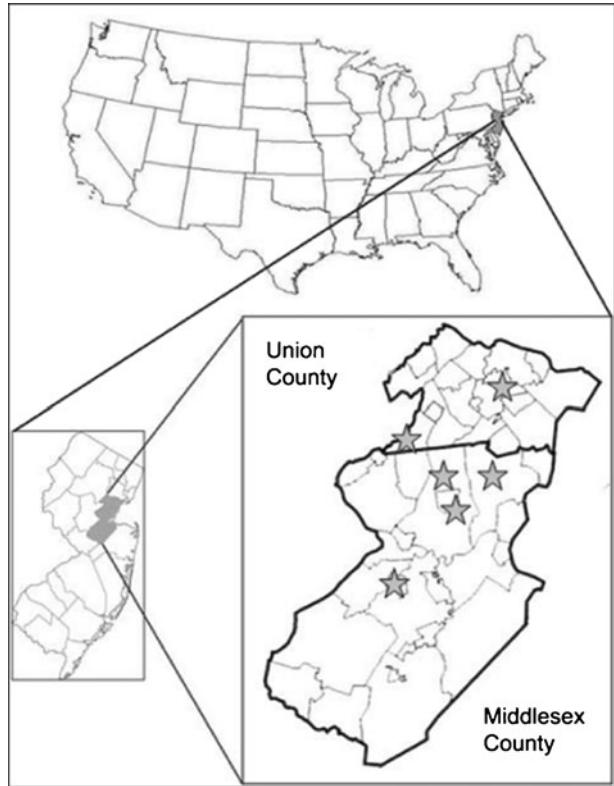
areas, transects began at the same point locations used for breeding season surveys, and extended 200 m in a random direction. For residential transects, we selected a subset of 6 points, and transects extended 200 m as close as possible to the 500 m buffer line. Migration surveys were not conducted for the two medium sized sites in 2010. A total of 37 wetland and 24 residential transects were surveyed (Table 1). Line transect surveys were conducted three (2010) to four (2009) times during fall migration. During each transect survey, observers walked the transect line and recorded the distance and direction to all birds detected.

All surveys were conducted between one half hour before sunrise, and four hours after sunrise, on days with no precipitation and wind speeds less than 12 mph (Ralph et al. 1993). To account for biases in population measures resulting from imperfect detectability, data collection methods for point counts and line transects were designed for distance sampling (i.e., 400 m grid; Buckland et al. 2001, 2004) and time-depletion (removal) analyses (Farnsworth et al. 2002). Observers recorded all birds heard or seen in ten one-minute intervals, and measured exact distance, when possible, using a laser rangefinder. Observers also recorded observation type (heard, seen, heard and seen, or overflight), as well as basic weather information (wind speed, temperature, sky condition) and time of day.

Mosquito collection and identification

Wetland mosquito survey sites consisted of 2–4 survey points located along the 400×400 m avian grid 100 m from the edge of the wetland, and 2–4 corresponding residential sites

Fig. 1 Urban wetland and residential site locations within Union and Middlesex counties in the state of New Jersey (USA). Shaded grey stars represent the approximate location of urban wetland and residential site locations for both avian and mosquito surveys conducted in 2009 and 2010



located along the 500 m avian survey buffer line. Two active trapping methods were used to monitor host-seeking adult female mosquitoes and the presence of blood-fed *Culex spp.* mosquitoes within each habitat. For 2009 and 2010 adult host-seeking mosquitoes were collected using CO₂ baited CDC miniature light traps (John W. Hock Company). Gravid mosquitoes were collected using CDC gravid traps (John W. Hock Company) baited with a hay infusion consisting of 1 lb (0.5 kg) of hay to 30 gal (114 L) of tap water that was allowed to incubate for at least 5 days. Both trap types were set at least one hour before sunset and collected the following morning. Mosquitoes were collected weekly June–September. This time frame allows us to analyze early seasonal transmission patterns and infection rates during the peak in both human clinical cases and infection rates in local mosquito populations, which usually occur between July and mid-September each year (Andreadis et al. 2004; Kilpatrick et al. 2006). Upon returning to the lab, captured mosquitoes were frozen (−20 °C) approximately 30 min prior to being identified to species using stereomicroscopes (Darsie and Ward 1981; Andreadis et al. 2005). Due to the difficulty in correctly distinguishing between *Culex pipiens* and *Culex restuans* morphologically, and the lack of *Culex salinarius* within our traps, collected *Culex spp.* were grouped for statistical analyses as the *Cx. restuans/pipiens* group.

WNV testing and statistical analyses

The dominant and most tested mosquito species for WNV in New Jersey are *Cx. restuans* and *Cx. pipiens*, which made them our focal species for WNV testing. *Cx. restuans/pipiens*

pools were tested in 2009 using VecTest, an antigen panel assay (Microgenics Corporation, Fremont CA), which produces similar results to those of reverse transcription polymerase chain reaction (RT-PCR) techniques (Siirin et al. 2004). *Cx. restuans/pipiens* were tested in pools of up to 50 mosquitoes from collections from both habitats. Light trap and gravid trap pools were tested separately. In 2010 mosquito pools were tested for WN-viral RNA by TaqMan RT-polymerase chain reaction (PCR) assays following established protocols (Lanciotti et al. 2000; Farajollahi et al. 2005) in collaboration with the Cape May County Department of Mosquito Control. Due to the lack of precipitation during the 2010 season, and subsequent poor catch rates in light trap collections, we only tested gravid trap *Cx. restuans/pipiens* collections in 2010. All statistical analyses based on mosquito collections were done using the R statistical software (R Development Core Team 2008). Infection rates (IR) were calculated using maximum likelihood estimation (MLE) with 95 % confidence intervals 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.

Relative abundance of competent vector species in wetland vs. residential areas

Competent mosquito 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. (2005). The relative abundance of these species within each habitat was determined using the Berger-Parker index of dominance (Berger and Parker 1970; Magurran 2004). This value represents the community dominance of each species within each habitat. These values were calculated based on the abundance of each mosquito species within each habitat using CDC light trap collections due to the similarity between habitats ($F_{1,30}=0.2954$, $P=0.59$), and exclusivity of gravid trap collections for *Cx. restuans/pipiens*. Competent mosquito species included *Cx. restuans/pipiens*, *Ae. albopictus*, *Oc. japonicus*, and *Ochlerotatus triseriatus*. Commonly encountered incompetent mosquito species, based on their inability to act as enzootic or bridge vectors in the wild (Turell et al. 2005), included *Ae. vexans*, *Oc. cantator*, *Ochlerotatus grossbecki*, *Ochlerotatus abserratus*, and *Oc. trivittatus*. Even though *Ae. vexans* has been implicated as a bridge vector for WNV, over a 3 year time span (2008–2010) 681 pools of *Ae. vexans* were submitted for WNV testing in the state of New Jersey with only one pool returning a positive result (Center for Vector Biology, Rutgers University 2010). Given the low prevalence of WNV within *Ae. vexans* in our study area *Ae. vexans* was determined to be a poor vector species for WNV within our study.

Relative abundance of competent avian host species in wetland vs. residential areas

Although WNV has been detected in at least 326 bird species (CDC 2010), only 44 species have been studied by experimental infection (reviewed in Kilpatrick et al. 2007). Komar et al. (2003) and Kilpatrick et al. (2007) have used a slightly different approach to calculate the host competency index, the sum of the daily probabilities that a mosquito biting a bird will become infectious for WNV. For the purposes of our study, we selected species with a host competence index greater than 1.0, in both studies, as ‘competent’. All other species were considered ‘non-competent’; however, many of these species have not been rigorously tested and thus host competency might not be unknown. For our study, competent species include American Crow, American Robin, Blue Jay, Common Grackle, House Finch, and House Sparrow. This analysis does not take into account mosquito feeding preferences, which may be important in WNV transmission dynamics (Kilpatrick et al. 2006). To examine any potential differences in detectability between competent avian vs. non-competent avian host

species, and between wetland vs. urban habitats, we ran a series of *a priori* models in program DISTANCE 6.0 (Thomas et al. 2009). Models included constant detectability across habitat (wetland vs. urban) and species competency (competent vs. non-competent), and various combinations of habitat and competency as covariates. Avian model selection was determined using an information-theoretic approach (Burnham and Anderson 2002), in which we selected the model with the lowest Akaike's Information Criterion (AIC). Results of distance sampling on avian surveys indicated that the best model for estimating detection probabilities, based on AIC criteria, included constant detectability across habitat and competency; therefore, we did not correct for differences in detectability and used the raw counts for all subsequent analyses.

To compare host availability for WNV, we examined indices of relative and absolute abundance of competent and non-competent avian species at wetland and surrounding residential sites during the breeding season and fall migration. For each competent species, we calculated the relative abundance as the total number of observations for that species at a particular site, divided by the total number of observations for all species at that site, and then summed across species to get a total relative abundance for competent species. We used ANOVA (PROC GLM) in SAS ver. 9.2 (SAS Institute 2008) to identify differences in the proportion of competent species between urban and residential sites. As an index of absolute abundance, we calculated the mean number of individuals recorded per transect per survey, and used ANOVA to identify any differences in overall abundance between wetland and surrounding residential areas.

Avian diversity in wetland vs. residential areas

To address our dilution effect hypothesis we employed several diversity indexes, which included species richness, Shannon-Weaver index, and Simpson's diversity index. Avian species richness was calculated as the total number of species observed (across all points/transects and surveys) during breeding season and fall migration surveys for both 2009 and 2010. The Shannon-Weaver and Simpson's diversity indices were calculated based on the total number of observations for each species averaged across all survey points at each wetland and residential location. All diversity indices were calculated and analyzed separately for breeding and fall migration surveys. ANOVA was used to identify differences in diversity measures between urban wetlands and adjacent residential areas, and among different wetland size classes. We used Pearson's product-moment correlation coefficient and linear regression methods to examine the correlation between avian diversity measures, WNV infection rates, and wetland patch size.

Results

The relative abundance of competent vector species in wetland vs. residential areas

Residential sites contained significantly higher proportions of competent mosquito species during both the 2009 ($t_{14} = -3.69$, $P = 0.005$) and 2010 ($t_{18} = -4.05$, $P < 0.001$) collection seasons compared to wetland areas (Fig. 2a). In 2009 competent mosquito species accounted for an average of 39 % of weekly residential mosquito collections compared to 23 % within wetland sites. In 2010 both these numbers increased with competent species comprising 60 % of residential populations and 26 % of wetland populations. Increases in the proportion of competent species within residential sites is primarily explained by increases in the

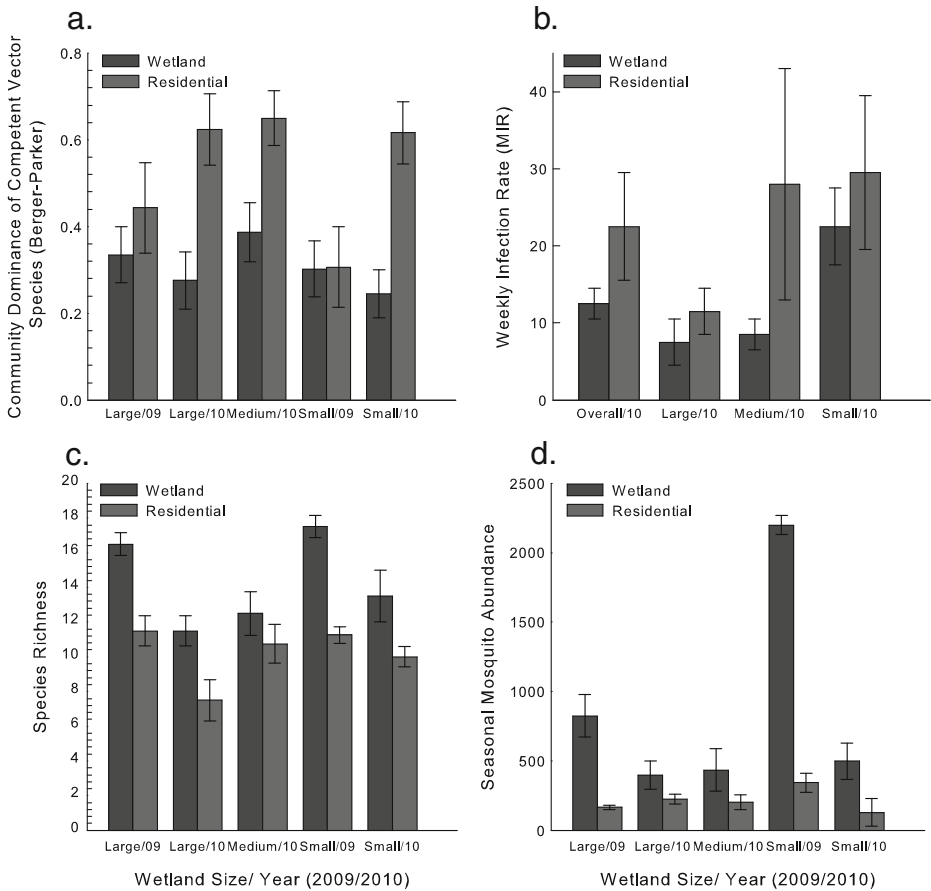


Fig. 2 Community dominance of competent mosquito species (a), weekly WNV infection rates (b), seasonal mosquito abundances (c) and mosquito species richness (d) for each habitat type and wetland size classification. All values are represented as mean \pm SE

community dominance indices of urban associated species, such as *Cx. restuans/pipiens* and *Ae. albopictus* (Fig. 3). In addition to having a lower community presence of competent mosquito species, wetland communities were more productive in terms of the number of mosquito species they supported and the number of mosquitoes they produced (Fig. 2c, d) compared to residential sites across all wetland size classes. Small wetlands were particularly productive producing significantly more ($t_{10} = -8.24$, $P < 0.001$) mosquitoes than large wetland patches.

Relative abundance of competent avian host species in wetland vs. residential areas

As with mosquito communities, urban wetland sites experienced a decreased community presence of competent WNV avian host species compared to adjacent urban residential sites during both breeding season and fall migration surveys (Fig. 4a, b). During the breeding season, competent species accounted for an average of 32 % of all birds recorded at wetland sites in 2009 and 33 % in 2010, significantly lower than the 59 % observed at residential

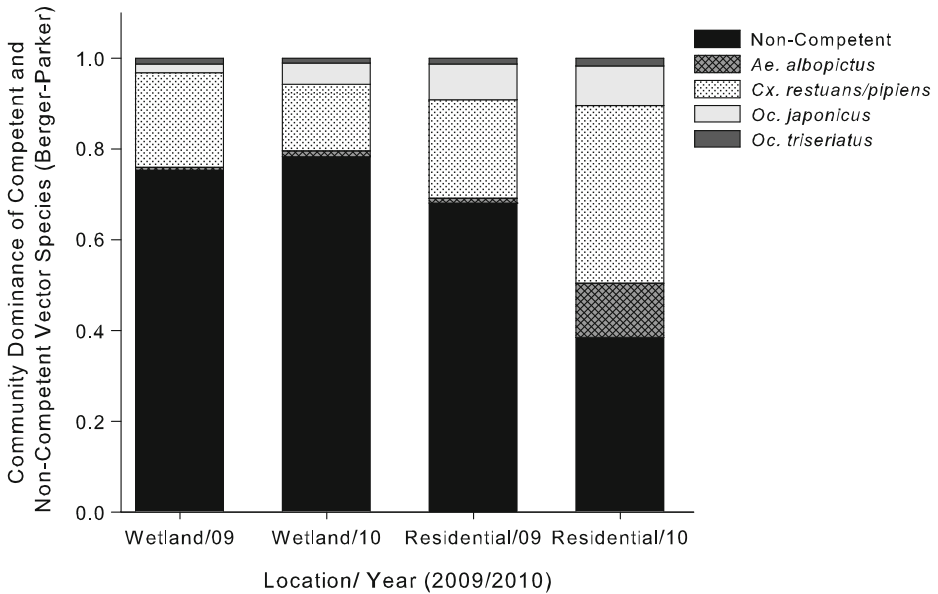


Fig. 3 Community dominance of competent and non-competent mosquito species within urban wetland and residential habitats

sites in 2009 ($F_{1,6}=7.14$, $P=0.037$) and the 58 % observed in 2010 ($F_{1,6}=11.14$, $P=0.016$). Similarly, competent species accounted for an average of 31 % of the total fall count in 2009 and 39 % in 2010, significantly lower than the 53 % observed at residential sites in 2009 ($F_{1,6}=8.02$, $P=0.030$) and 72 % in 2010 ($F_{1,2}=19.48$, $P=0.048$). Across both years and seasons, competent species accounted for 35.4 % of the total count at wetland sites and 62.8 % of the total count at residential sites. Additionally, estimates of absolute abundance indicate that fewer birds were observed per point/transect at wetland sites than in surrounding residential areas during the 2009 breeding season ($F_{1,170}=5.76$; $P=0.018$), 2010 breeding season ($F_{1,172}=7.68$; $P=0.0062$), and 2010 fall migration ($F_{1,88}=8.23$; $P=0.0052$). There was no difference in the number of birds observed during 2009 fall migration ($F_{1,218}=1.98$; $P=0.16$). The smaller number of birds, coupled with the lower proportion of competent species in wetlands, suggests that WNV risk would be lower in wetlands compared to surrounding residential areas. Interestingly, the stronger presence of competent avian host species within residential sites corresponded to increases in competent urban associated species, primarily the house sparrow (Fig. 5), which was virtually absent from wetland sites. This increase was seen during both breeding season and fall migration surveys. These results indicate that the house sparrow has a stronger community presence within residential sites compared to wetlands sites during the entire transmission season.

West Nile virus in wetland vs. residential areas

Following a similar pattern to that of the community presence of competent avian host and vector species, WNV was more prevalent in *Cx. restuans/pipiens* populations from residential sites than from urban wetland sites (Table 2). In 2009 the prevalence of WNV in *Cx. restuans/pipiens* populations within both wetland and residential habitats was minimal. We

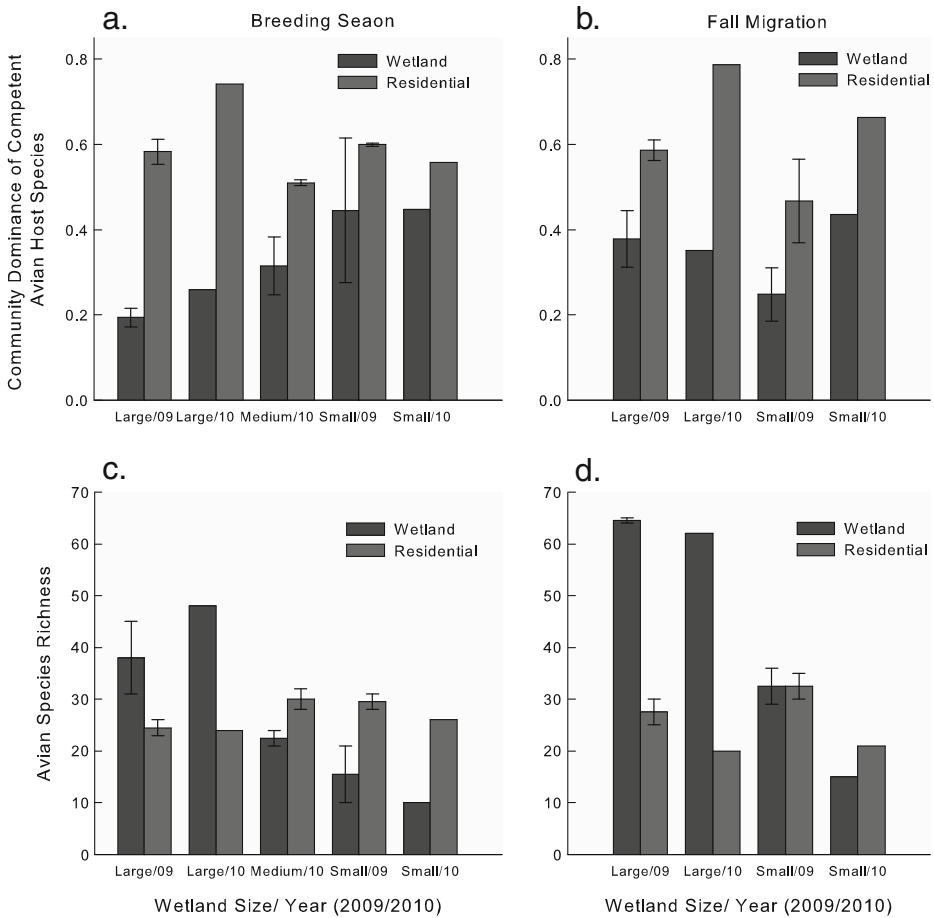


Fig. 4 The community presence of competent avian host species (a, b) and avian species richness (c, d) during breeding season and fall migration surveys for each habitat type and wetland size classification. Breeding season data were collected using point-count methods and fall migration data were collected using line-transect methods. All values are represented as mean ± SE

tested a total of 87 pools containing 1754 *Cx. restuans/piapiens* mosquitoes, and only one pool tested positive for WNV. However, in 2010 WNV was highly prevalent at all of our trap sites. We tested 100 gravid trap pools containing 4119 *Cx. restuans/piapiens* mosquitoes with 54 pools returning positive results for both primers (34 residential, 20 wetland).

Wetland sites had a maximum likelihood estimated (MLE) infection rate of 15.89 (per 1000), and residential sites had an MLE infection rate of 22.08. In addition, the month of August had a substantially higher overall infection rate (35.52) than July (13.54) or September (14.58). This is in agreement with previous findings that WNV infection rates peak in mid to late summer (Kilpatrick et al. 2006; Bolling et al. 2009). In relation to patch size, we found that the size of the wetland patch can significantly influence the presence of WNV. Large wetland sites and their adjacent residential areas had the lowest WNV infection rates, whereas small wetland sites had significantly higher weekly infection rates than either medium ($t_{22}=-2.32, P=0.038$) or large ($t_{22}=-2.30, P=0.036$) wetland patches (Fig. 3b).

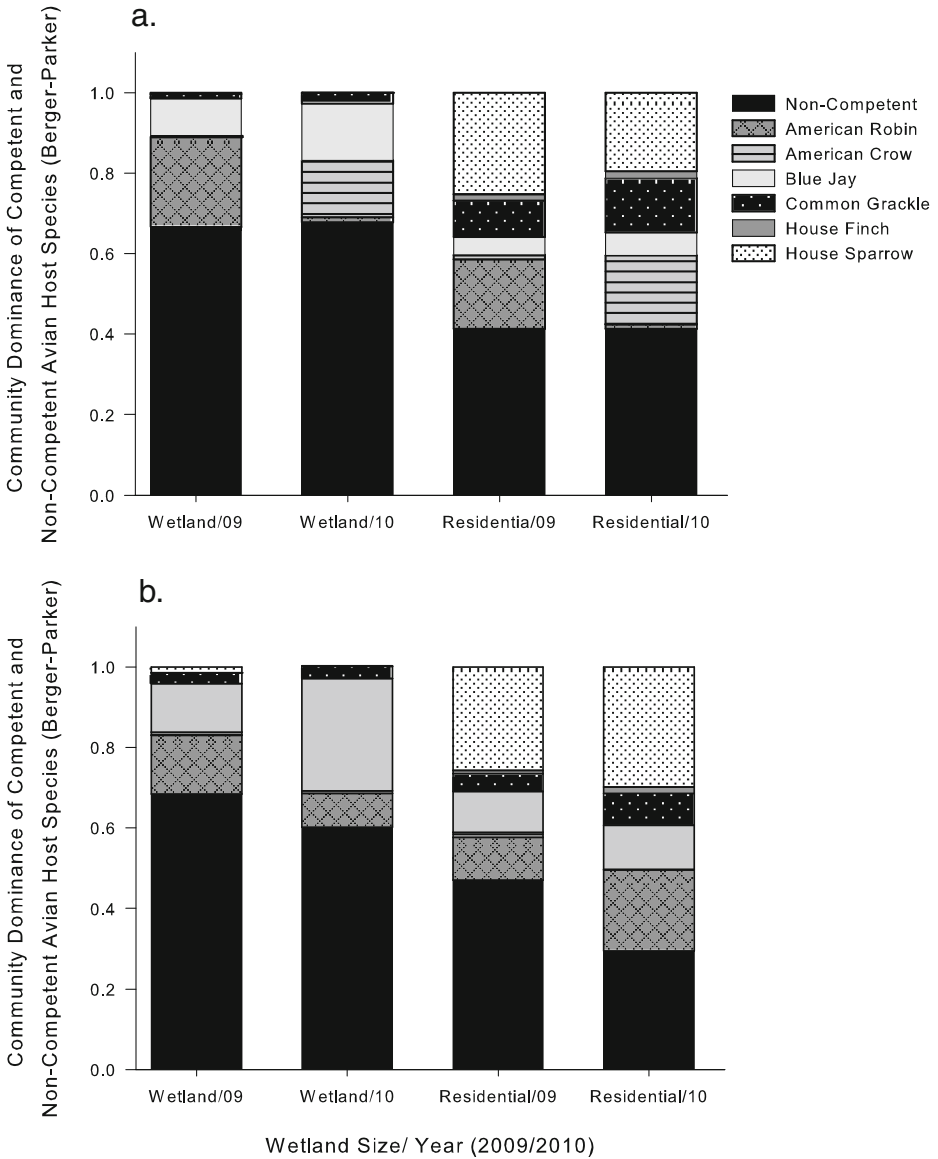


Fig. 5 The community dominance of competent and non-competent avian host species in urban wetland and residential habitats during breeding season (a) and fall migration (b) surveys. Breeding season data were collected using point-count methods and fall migration data were collected using line-transect methods

Relationship between avian diversity and infection rates in wetland vs. residential areas

We found no significant relationships between any measure of avian diversity and WNV infection rates within urban wetland or urban residential areas based on correlation analyses using Pearson’s product–moment correlations or linear regression methods. Overall, species richness was our best indicator of the impact of host diversity on WNV as it produced the

Table 2 West Nile Virus infection rates in *Culex* spp. (*Culex restuans*, *Culex pipiens*) populations within wetland and residential sites for each size class, and for each month of testing during the 2010 season. Infection rates calculated using PooledInfRate 3.0 (Biggerstaff 2006)

Wetland size/month	Infection rate	95 % CI	Number of pools	Number of positive pools	Number of individuals
Wetland					
Overall	15.89	10.47–23.60	50	24	2076
Large	7.09	2.34–17.53	13	4	643
Medium	15.58	6.05–36.69	25	11	946
Small	28.81	14.88–57.23	12	9	487
Residential					
Overall	22.08	15.31–31.61	50	30	2043
Large	13.43	5.71–28.82	13	6	559
Medium	24.47	12.08–54.37	26	14	1047
Small	51.74	28.63–151.74	11	10	437
Month					
July	13.34	8.61–20.14	46	22	2210
August	35.52	23.75–54.11	33	24	1182
September	14.58	6.82–28.83	21	8	727

largest correlation value and smallest p-value ($r=-0.51$, $P=0.061$). Shannon-Weaver and the Simpsons index calculations resulted in small correlation values ($r<0.13$) and large p-values ($P>0.20$) when analyzed against infection rates. Species richness was also our best indicator of the impact of patch size on host diversity. We found a strong positive relationship between wetland size and avian richness ($r=0.72$, $P<0.001$) with significant differences occurring between large and small wetland sites during breeding ($F_{2,5}=10.80$, $P=0.019$) and fall migration ($F_{2,4}=11.89$, $P=0.018$) surveys. Overall, large wetland sites contained greater species richness than their surrounding residential areas during both breeding and fall migration (Fig. 4c, d) surveys, but this pattern was not seen at small and medium sized wetland sites. Due to the small number of sites in each size class, the difference is statistically significant only for Fall 2009 ($F_{1,2}=210.62$, $P=0.0047$), but a similar pattern of greater richness in wetland areas was observed for large sites during all seasons.

Discussion

Anthropogenic environmental changes have drastically increased the prevalence of zoonotic pathogens, especially vector-borne diseases, over the last decade (Ostfeld et al. 2002; Patz et al. 2004; Allan et al. 2009). Of these changes, urbanization is one of the most influential in relation to vector-borne diseases because it can affect the richness and diversity of many animals and insects that play key roles in disease transmission. In the case of WNV, transmission relies upon the local interactions occurring between multiple species of host that sustain the pathogen and several to many species of vector that transmit the pathogen (Keesing et al. 2006). The success or failure of disease transmission between these two interacting species groups is greatly impacted by habitat fragmentation and heterogeneity (Smith et al. 2004). There is no better environment to study the influence of habitat fragmentation and heterogeneity on the transmission dynamics of WNV than within urban

ecosystems. Urban ecosystems provide the unique opportunity to study a multitude of habitat types separated by mere meters of distance. More pointedly, urban mosaics provide the opportunity to address how habitat fragmentation and heterogeneity involving urban wetlands and their adjacent residential/commercial areas may influence the transmission of WNV and disease risk to local human populations. To address this question we investigated the immediate influence of habitat type and patch size on the relationships between avian host diversity, vector abundance, and prevalence of WNV over a finer spatial scale than has been used in previous studies (Schmidt and Ostfeld 2000; Ezenwa et al. 2006; Loss et al. 2009; Bowden et al 2011).

Our data support the idea that WNV transmission responds to environmental and anthropogenic features of urban environments (Bertolotti et al. 2008; Hamer et al. 2011; Loss et al. 2009). The community composition of both bird and mosquito species changed significantly across the permeable barrier separating urban wetlands from their adjacent residential surroundings. As expected given the anthropogenic nature of WNV residential areas had the highest WNV infection rates within *Cx. restuans/pipiens* populations, while also containing a significantly larger community presence of competent bird and mosquito species compared to wetland areas. Overall, residential mosquito communities contained a stronger community presence of the primary enzootic and bridge vector species present in the Northeast, such as *Cx. restuans*, *Cx. pipiens*, *Ae. albopictus*, and *Oc. japonicus*, when compared to their wetland counterparts. A similar pattern was seen for avian species. Highly competent host species, such as the house sparrow and the American robin were more strongly associated with residential areas than with wetlands during both the breeding and fall migration seasons. More importantly, wetlands did not sustain many highly competent avian host species that were concurrently abundant within residential sites, the most notable of which was the house sparrow. House sparrows have been shown to be strong amplifying and reservoir hosts for WNV in North America (Komar et al. 2003; Nemeth et al. 2009). Even though some studies have shown that house sparrows are rarely feed upon relative to their abundance compared to the American robin (Kilpatrick et al. 2006; Hamer et al. 2009), its absence from wetland sites is striking and may have lessened the capacity of wetland avian communities to maintain and transmit WNV locally.

There is evidence that the dilution effect may be occurring within large (>100 ha) urban wetlands which contain significantly richer avian communities, and which had the lowest WNV infection rates when compared to small (<15 ha) and medium (15–40 ha) sized wetland patches. The effects of patch size on avian species richness in our study is in agreement with previous studies investigating the effects of patch size on avian diversity in forested areas, grasslands, salt marsh and freshwater wetlands (Ambuel and Temple 1983; Blake and Karr 1984; Brown and Dinsmore 1986; Askins et al. 1990; Faaborg et al. 1995; McIntyre 1995; Shriver et al. 2004). In addition to the effects on avian diversity, there was an inverse relationship between patch size and infection prevalence within local *Cx. restuans/pipiens* populations. Small urban wetland sites had significantly higher weekly infection rates than large urban wetland sites. This pattern is similar to that reported by Ezenwa et al. (2007) who found that WNV infection rates within *Culex spp.* decreased with increasing wetland cover when analyzing the effect of land cover variation on vector density, amplification host abundance, and host community composition. Interestingly, the influence of patch size and habitat fragmentation extends beyond WNV. Allan et al. (2003) studying the influence of forest fragmentation on the prevalence of Lyme disease discovered that there were significant linear declines in both nymphal tick infection prevalence and nymphal tick density with increasing patch size. These authors concluded that Lyme disease risk drastically increases in response to decreasing forest patch size. Furthermore, Brownstein et al.

(2005) reported a positive link between forest fragmentation and both tick density and Lyme disease infection prevalence using satellite imagery to analyze the influence of patch size and isolation in regards to disease risk for Lyme disease. The results of these studies, combined with the results of our study, confirm that patch size and habitat fragmentation, primarily isolation, can substantially influence the prevalence of both mosquito and tick-borne diseases of medical importance.

In addition to the influence of habitat type and patch size, seasonal variations in climatic conditions dramatically influenced seasonal WNV infection rates. The substantial increase in WNV infection rates within both wetland and residential habitats during the 2010 collection season compared to the 2009 season occurred during a prolonged period of seasonal drought in the Northeast. Between June–September of 2010 the state of New Jersey experienced moderate to extreme drought conditions, whereas most of the 2009 season was classified as very moist to extremely moist based on the Palmer Drought index (NOAA 2012). Seasonal drought periods have been associated with past WNV outbreaks in Europe, New York City, Russia, and Israel (Epstein and Defilippo 2001). More recently, it was reported that seasonal drought conditions precede increases in clinical WNV and Saint Louis encephalitis virus cases in the southern US (Shaman et al. 2002; Shaman et al. 2005). Based on these results drought conditions appear to have resulted in the increase in yearly WNV infection rates experienced in our study. This may have occurred due to the aggregation of host and vector species around remnant water sources during periods of drought that facilitates the epizootic amplification of the virus in local vector and host populations (Shaman et al. 2005).

In summary, the results of this study show that the prevalence of WNV is directly related to the community presence of competent avian host and mosquito species, and this is heavily influenced by patch size and habitat type. Overall, our results lead to the conclusion that urban wetlands, especially large (>100 ha) urban wetlands, decrease disease risk for WNV by decreasing the community presence of both competent avian host and mosquito species while increasing the diversity of local avian host communities. These findings were the direct result of examining the dynamics of host diversity and the community presence of competent mosquito and host species on the transmission of WNV at the abrupt intersection of two uniquely different, but inseparable, urban habitats. Studies of this kind will become increasingly pertinent in an ever developing world facing the resurgence and emergence of medically important arboviruses (e.g. Dengue, WNV, Yellow fever) and the anthropophilic vectors (e.g. *Ae. albopictus*, *Aedes aegypti*) which transmit them.

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Conflict of interest The authors declare that they have no conflict of interest.

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