West Nile Virus in the Permanent-Resident Bird Community of a Fragmented Ohio Landscape

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CHAPTER 5

WEST NILE VIRUS IN THE PERMANENT-RESIDENT BIRD COMMUNITY OF A FRAGMENTED OHIO LANDSCAPE

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ABSTRACT.—We surveyed the permanent-resident bird community of a fragmented Ohio landscape for West Nile virus (WNV) antibodies to determine which species carried antibodies, what percentage of the individuals in each species carried antibodies, and whether antibodies were retained from one year to the next. Eight of 20 species carried antibodies in at least one year. For species with >10 captures, the seroprevalence ranged from <1% in Downy Woodpeckers (*Picoides pubescens*) to 33% in Northern Cardinals (*Cardinalis cardinalis*). About 10 young-of-the-year were seropositive each year, which indicates the presence of active viral transmission in the preceding summer. All four seropositive birds from year one that were recaptured in year two were seropositive again, indicating that in at least two species, antibodies may persist. These results suggest that permanent-resident birds are either largely unaffected by WNV or are generally susceptible to mortality when infected with it. The exception is the Northern Cardinal, which may be an important reservoir species for the virus. Seroprevalence in Northern Cardinals was high in both years, and females had higher seroprevalence than males. *Received 30 April 2005, accepted 23 November 2005.*

RESUMEN.—Estudiamos una comunidad permanentes de aves residentes en una región fragmentada del estado de Ohio para detectar cuales especies de aves eran portadoras de anticuerpos del virus del Oeste del Nilo (VON), así como determinar que porcentaje de individuos en cada especies eran portadores de anticuerpos y si estos anticuerpos eran conservados de un ano al otro. De 20 especies de aves, ocho eran portadoras de anticuerpos en al menos un año. Para las especies con mas de 10 capturas, el rango de la sero-frecuencia fue de menos del 1% en *Picoides pubescens* hasta 33% en *Cardinalis cardinalis*. Alrededor de 10 juveniles fueron sero-positivos cada año, lo que indica la presencia de una infección viral activa en el verano anterior. Las cuatro aves sero-positivas del año uno que fueron recapturadas en el año dos fueron sero-positivas nuevamente, indicando que en al menos dos especies, los anticuerpos pueden subsistir. Estos resultados sugieren que las aves residentes son ampliamente no afectadas por el VON o que son por lo general susceptibles a mortalidad cuando son infectadas con el virus. La excepción es *Cardinalis cardinalis*, la cual puede ser un hospedero importante para el virus. La sero-frecuencia en *Cardinalis cardinalis* fue alta en ambos años, y las hembras tuvieron una sero-frecuencia mayor que los machos.

SINCE WEST NILE virus (WNV) appeared in North America, researchers have studied its effects on several different groups of birds (Beckwith et al. 2001, Bernard et al. 2001, McLean et al. 2001, Komar et al. 2003). They have studied migrants to determine how the virus spreads (Rappole et al. 2000), summer residents to determine how and when the virus emerges, and susceptible groups like corvids to determine why some birds are so much more vulnerable to the virus than others (Steele et al. 2000). Some studies have systematically investigated the antibody status of the breeding bird population to determine which species might carry some resistance to WNV and act as a potential reservoir for the

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disease (Ringia et al. 2004, Godsey et al. 2005). These studies did not specifically focus on permanent residents, nor did they look at the same community for more than one year.

Permanent residents may be important for a number of reasons. They are the most reliable indicators of local viral emergence. In various migrants, the virus may have been contracted along the migration route. Permanent residents experience the entire mosquito season, including the peak abundances of a number of species known to transmit the virus. Permanent residents also provide a baseline for determining the role of migrants in WNV transmission. By evaluating WNV activity before migrants arrive, researchers can accurately gauge the amount of viral activity attributable to the new arrivals. Finally, if birds are the reservoir for overwintering WNV, then some of the most likely candidates for triggering re-emergence the following year are permanent residents.

Studying the same community in multiple years allows researchers to determine how susceptible the community is to infection. Obviously, each breeding season brings a new generation of susceptible birds once eggs hatch, assuming that females with antibodies do not pass these antibodies to their young. But the number of susceptible adults may decline if these adults retain antibodies from previous infections. Few data exist on the persistence of antibodies to WNV in wild bird populations.

West Nile virus first appeared in Ohio in 2001, and by 2002 it had spread to all counties in the state (Mans et al. 2004). We have been looking at the demographics of a community of permanent-resident birds in isolated woodlots in north-central Ohio since 1993. Because WNV should affect the demography of the birds in our study area, we began investigating the antibody status of our study population.

We predicted that if WNV is present in an area during the summer, then some of the permanent-resident species should be infected. Although some of the infected birds probably die, others may be entirely unaffected by the virus. Some should develop antibodies to the virus, and we should be able to detect some of those antibodies in the winter. We therefore began collecting blood samples from the mixed species flocks of permanent-resident birds that we band in Ohio woodlots in the winter. Our goals were to identify species that carried WNV antibodies, determine what percentage of individuals of affected species carry antibodies, and determine whether birds carrying antibodies one year are still carrying them the next year. We also sought to identify patterns in antibody status based on sex or year.

Methods

The study area consisted of 52 woodlots and riparian-corridor forested plots located in southern Crawford County, Ohio. We have been studying the winter resident birds in these woodlots since the winter of 1992–1993. The woodlots are generally small, ranging in size from 2.5 to 31 ha, and are surrounded by agricultural fields that make up >90% of the landcover. The fields are used for row crops in the summer, primarily corn and soybeans.

To capture birds, we placed a feeder in a woodlot for a week. We then used mist nets and traps at the feeder to catch all or most of the birds present in the woodlot. Until the winter of 2002–2003, all birds caught were banded with a federal band and released. Starting in 2002–2003, we also took a blood sample before release. Blood samples were obtained by brachial puncture. When possible, we took 100 μL of blood. We collected blood in serum separator tubes and kept it cold until we could centrifuge and freeze the sample.

Serum of live birds was submitted to the Ohio Department of Health Vector-Borne Disease Lab where it was tested for the presence of WNV-specific IgG antibodies using ELISA protocols of Arbovirus Laboratories (Ebel et al. 2002).

We looked at a number of possible patterns of antibody status. In most species, so few individuals carried antibodies that comparisons between males and females were not possible. The same held true for comparisons between years. For White-breasted Nuthatches, however, we could test for a difference in number of seropositive juveniles between the two winters. For Northern Cardinals, we could test for a difference in seroprevalence between males and females over the entire study period. (Scientific names of all study species are given in Table 1.)

In both cases, we used a chi-square test of independence. For White-breasted Nuthatches, we tested whether the number of seropositive juveniles had changed between years. For Northern Cardinals, we looked at whether males or females were more often seropositive. For both, we took a P value less than 0.05 to be significant, with one degree of freedom.

Results

Over two years, we tested 20 species for antibodies to WNV. Of the 20, 8 species had at least one individual test positive during at least one year (Table 1). Percentages of birds positive for

TABLE 1. Number of birds of each species captured in the winters of 2002–2003 and 2003–2004, with number of individuals that tested positive for WNV antibodies in parentheses.

Species	2002–2003	2003–2004
Mourning Dove (*Zenaida macroura*)	–	2 (0)
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	–	2 (0)
Red-bellied Woodpecker (*M. carolinus*)	29 (1)	38 (0)
Downy Woodpecker (*Picoides pubescens*)	145 (2)	132 (2)
Hairy Woodpecker (*P. villosus*)	10 (1)	14 (0)
Northern Flicker (*Colaptes auratus*)	1 (0)	–
Blue Jay (*Cyanocitta cristata*)	5 (0)	11 (1)
Tufted Titmouse (*Baeolophus bicolor*)	134 (0)	60 (2)
Carolina Chickadee (*Poecile carolinensis*)	99 (0)	74 (0)
White-breasted Nuthatch (*Sitta carolinensis*)	135 (14)	112 (6)
Brown Creeper (*Certhia americana*)	2 (0)	2 (0)
Carolina Wren (*Thryothorus ludovicianus*)	3 (1)	1 (1)
Northern Cardinal (*Cardinalis cardinalis*)	93 (28)	66 (21)
American Tree Sparrow (*Spizella arborea*)	12 (0)	1 (0)
Song Sparrow (*Melospiza melodia*)	3 (0)	–
Dark-eyed Junco (*Junco hyemalis*)	57 (0)	29 (0)
Brown-headed Cowbird (*Molothrus ater*)	–	2 (0)
House Finch (*Carpodacus mexicanus*)	2 (0)	–
Common Redpoll (*Carduelis flammea*)	–	1 (0)
American Goldfinch (*C. tristis*)	14 (0)	–

WNV antibodies in a year ranged from 1.4% in Downy Woodpeckers to 100% in Carolina Wrens. Of species with >10 individuals tested in both years, three species had lower seroprevalence rates the second year (Red-bellied Woodpecker, Downy Woodpecker, and White-breasted Nuthatch). Three species had increased seroprevalence in year two (Tufted Titmouse, Carolina Wren, and Northern Cardinal). Both Dark-eyed Juncos and Carolina Chickadees lacked positive antibody tests in both years. Overall seroprevalence was 6.3% seropositive in the first year, and 6.0% in the second year.

Several individuals were captured in both years. Most of these individuals were negative both years, including Red-bellied Woodpecker (n = 2), Downy Woodpecker (n = 38), Carolina Chickadee (n = 23), and Tufted Titmouse (n = 11). Many White-breasted Nuthatches were also negative both years (n = 35), but three birds were positive both years. A Blue Jay that tested positive in the early spring of 2003 was also positive again in late winter of 2004. Overall, 15.6% of previously seronegative birds returned the second year, whereas 8.5% of seropositive birds returned the second year. The difference in return rates was not significant (χ^2 = 1.61, P = 0.20).

Some juvenile birds tested positive in their first winter. In 2003, 10 juveniles tested positive (3 Northern Cardinals and 7 White-breasted Nuthatches). Nine birds tested positive as juveniles in 2004, including two Downy Woodpeckers, one Tufted Titmouse, one White-breasted Nuthatch, and five Northern Cardinals.

In the first year, 47% (7 of 15) of seropositive White-breasted Nuthatches were hatch-year birds. In the second year, however, only 17% (1 of 6) of seropositive White-breasted Nuthatches were hatch-year birds. Although the drop is substantial, it was not significant.

Over the two years, 24% (21 of 88) of male Northern Cardinals were seropositive. In the same period, 39% (28 of 71) of female Northern Cardinals were seropositive. Females were thus more likely to be seropositive, and this difference was significant (χ^2 = 4.22, P = 0.038).

DISCUSSION

Our work shows that WNV is present in the permanent-resident avian community of Crawford County, Ohio, even after summer surveillance fails to detect the virus (J. S. Marshall

unpubl. data). This suggests that the virus persists at low levels without necessarily emerging in human populations. Our data support the summer surveillance data in that fewer birds were seropositive in the second winter, though about the same number of young-of-the-year were positive in both years. Most of the resident community has generally low seroprevalence rates. Northern Cardinals, however, have notably high seroprevalence rates, which suggests that they may be an important reservoir species for WNV.

Our overall seroprevalence of antibodies matched that found in other large-scale surveys in North America. Ringia et al. (2004) found that 5.3% of their birds were seropositive in Illinois during a year with a major outbreak. Godsey et al. (2005) reported a higher rate of 10.5% seropositive in their work in the southeastern United States. Contrast these results with the 33% of birds carrying antibodies in the 1999 outbreak in New York (McLean et al. 2002), or the 53% of birds carrying antibodies in the 1974 outbreak in South Africa (Murgue et al. 2002). Our results support Ohio Department of Health data showing no outbreak of WNV in humans during the study. However, our data do show that WNV is present even when not detected in humans.

Most permanent residents had low or no antibody seroprevalence. Similar surveys, however, have not reported seropositive birds in the winter mixed flocks that we studied (Ringia et al. 2004, Godsey et al. 2005). Indeed, with the exception of Black-capped Chickadees (*Poecile atricapillus*) or Carolina Chickadees, few of these birds have even been caught. Anecdotal evidence suggested that chickadees might be negatively affected by WNV, but we found no support for this in antibody data. This may reflect the lack of antibody formation in chickadees, the death of all infected birds, or the loss of antibodies formed (Main et al. 1988). The seropositive Tufted Titmouse caught in 2004, however, may indicate the potential for parid involvement in the WNV cycle.

By and large, however, the permanent residents that make up the mixed-species flock in the winter in our study area (primarily Carolina Chickadees, Tufted Titmice, Downy Woodpeckers, and White-breasted Nuthatches) carry few antibodies. Assuming that these species form antibodies and do not simply die after infection, our results suggest that these birds are not particularly involved in WNV transmission, with the possible exception of the White-breasted Nuthatch. All of these species are cavity-nesters, and the cavity may provide a measure of protection against mosquitoes (Edman and Kale 1971). These birds may also be active in areas less frequented by mosquitoes carrying WNV. Comparisons of areas in which mosquitoes and birds are active, including surveys of nest sites, would help determine why these species seem less involved in WNV transmission.

The Northern Cardinal, on the other hand, had far and away the highest seroprevalence among species sampled in significant numbers. Several other studies have found high seroprevalence for WNV antibodies. Ringia et al. (2004) found that Northern Cardinals had the second-highest seroprevalence among passerines (12.4%). Godsey et al. (2005) found a seroprevalence in Northern Cardinals of 75%, but on a sample size of only four birds. Bernard et al. (2001) also found a Northern Cardinal with virus in New York in 2000. All these studies, including ours, point to Northern Cardinals as an important species in the WNV cycle, though nobody yet knows whether or not Northern Cardinals are a competent host for WNV (Godsey et al. 2005).

The reasons for high seroprevalence in Northern Cardinals also remain unclear. Compared with most of the other species in our study, the Northern Cardinal is the only open-cup nester. This may mean that Northern Cardinals are more vulnerable to mosquitoes. Mans et al. (2004) reported that 92% of their WNV-positive mosquito pools in Ohio in 2002 were *Culex* species. Novak et al.'s (1981) studies of mosquito distribution showed *Culex* species feeding both in the canopy and near the ground, but preferring habitats with overhanging grape vines. We have found many Northern Cardinal nests in bushes covered by grape vines (J. S. Marshall pers. obs.), so Northern Cardinals may be particularly vulnerable to mosquitoes carrying WNV. Other studies have also reported fairly high seroprevalence in other shrub-nesting species, particularly American Robins (*Turdus migratorius*) and various mimids (Ringia et al. 2004, Godsey et al. 2005). This may suggest that nesting ecology plays an important role in the WNV transmission cycle in birds. Again, however, all these birds may be active in areas that have abundant mosquito populations.

Our results regarding differential seroprevalence in male and female Northern Cardinals may support the idea that nest sites are important areas of virus transmission. Other surveys of antibodies in birds have reported no differences in seroprevalence between males and females (Ringia et al. 2004, Godsey et al. 2005). Yaremych et al. (2004) also reported no sex-based difference in mortality in American Crows (*Corvus brachyrhynchos*) in Illinois. Our work represents the first reported sex-based difference in WNV antibody seroprevalence. This may represent a difference in exposure to WNV-carrying mosquitoes during the nesting cycle. Only females incubate, and while incubating, they may be less prone than a roosting male to move when harassed by mosquitoes. On the other hand, males may also be more likely to die when infected. Vertebrate males tend to have higher disease rates than females, potentially because testosterone is a known immunosuppressant (Yaremych et al. 2004). We have no evidence that male Northern Cardinals suffer higher mortality rates than females, but it is an alternate explanation for the pattern we see.

The present study also provides some insights into antibody persistence. Although we recaptured few previously seropositive birds, those that we recaptured were all still carrying antibodies. McIntosh et al. (1969) showed that WNV antibodies prevent reinfection, even when deliberately exposed to virus. Thus, the persistent antibodies should protect our birds from future WNV infection. This is especially promising in the case of the Blue Jay that carried persistent antibodies. Although each year's new birds provide a fresh source of susceptible individuals, persistent antibodies will protect adults and limit the population of susceptible individuals.

Also of note is the lower return rate for seropositive birds. Although the difference was not significant, seropositive birds returned at half the rate of seronegative birds. This suggests that the virus may cause physiological damage or impose energetic costs that reduce the survival of infected birds even if they recover. Future work may improve our ability to detect such survival effects.

The general seroprevalence in the community was fairly constant between years. Although human cases were not present in the study area in either year, the background seroprevalence suggests that the virus remains in the study area, given the unlikelihood that many of the birds we sampled came from very far outside the area. Further, the presence of hatch-year birds with antibodies confirms that at least some virus transmission occurred in the breeding seasons between our study periods.

Interestingly, the summer of 2004 saw the greatest number of reported avian cases of WNV in Crawford County during the study period. The preliminary results from the following winter, however, show a tremendous drop in seroprevalence. No woodpeckers, White-breasted Nuthatches, or Tufted Titmice were seropositive, and the seroprevalence of Northern Cardinals had dropped to ~10% (J. S. Marshall and D.A. Zuwerink unpubl. data). It may be that WNV is slowly disappearing from the study area because conditions have not promoted an outbreak, and that we are seeing the last seropositive birds from the initial outbreak.

All these results should be viewed with certain caveats in mind. First, the antibody test used by the Department of Health tends to cross-react with St. Louis encephalitis (SLE) antibodies. Therefore, a few of our seropositive birds may have carried antibodies to SLE but not WNV. Few of our study species were likely to be exposed to SLE in Ohio, however (R. G. McLean pers. comm.), so this particular problem should not change our general findings.

Although one might conclude that species with a high number of seropositive individuals are particularly susceptible to WNV infection, other interpretations are possible. To test positive, a bird has to be bitten by a WNV-infected mosquito, the virus has to infect the bird, and the bird has to recover from the infection. A high seroprevalence rate may indicate that the birds are preferred by mosquitoes carrying WNV (Apperson et al. 2004), that the birds live in areas frequented by infected mosquitoes, or that the birds have high native resistance to the disease, allowing high survival rates. Although a large number of birds may have survived infection, a large number may have died.

A low seroprevalence rate, on the other hand, also has several possible explanations. Few Blue Jays tested positive for antibodies, but given that corvids have high mortality rates following WNV infection (Bernard et al. 2001, McLean et al. 2001), this low seroprevalency may be the result of the

death of infected birds. On the other hand, the birds with no antibodies may be poor hosts for the disease. In such cases, instead of indicating vulnerability, low antibody presence indicates native resistance. Other birds may develop no antibodies in response to WNV or, if antibodies develop, they may be lost by our winter sampling period. Main et al. (1988) found that Black-capped Chickadees carrying Eastern Equine Encephalomyelitis (EEE) antibodies had almost all lost those antibodies by the next year. In general, antibody titers decrease over time (Emord and Morris 1984). Finally, if species with high seroprevalence rates are preferred by mosquitoes or are in preferred mosquito habitat, species with low seroprevalence rates may be less-preferred species or in less-preferred habitat.

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