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West Nile Virus in North American Wildlife

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ABSTRACT: Since the invasion of the mosquito-borne, West Nile virus (WNV) into North America in New York City (NYC) in 1999, the distribution of the virus has expanded throughout most of the continent during the ensuing years, causing mortality in hundreds of thousands of native and exotic birds and producing tens of thousands of equine and human cases. The initial outbreaks in the NYC area in 1999 were intense in local bird populations, with small outbreaks in humans and equines. Then, WNV spread north and south from this focal area during the next 2 years. The northward and southward sequence of dissemination continued as WNV began to encompass the remainder of the continent. Migrating birds are thought to be one of the major contributors to the rapid dissemination of this mosquito-borne virus. The temporal and spatial pattern and rapidity of the continental spread of WNV, as detected by the national surveillance system, match the semi-annual migratory movements of hundreds of millions of North American birds. The subsequent dissemination of the virus to Canada, the Caribbean, Mexico, Central America, and now South America fits this method of spread as well.

The strain of WNV introduced into the U.S. had increased virulence for North American birds, which quickly became apparent after its introduction and from the subsequent avian epizootics it caused. More than 200 species of birds experienced mortality, especially corvid species such as the American crow, blue jay, and several species of magpies, and recently the greater sage grouse. These species were particularly susceptible to this virulent strain of virus, as demonstrated in experimental studies and from dramatic die-offs during the summer virus transmission seasons. Bird mortality from WNV peaks during August-September at the height of the mosquito-transmission period but extends from April to November each year in some states. This mortality in crows and other corvid species was used as a sensitive sentinel system to detect the presence and movement of the virus through a public health reporting and laboratory testing national surveillance program. Mammal species were frequently infected, and some suffered mortality. The nationwide bird mortality from WNV infections was dramatic in North America during the last 7 years, but the actual impact of the mortality on bird populations is not known because of the insensitivity of national population data available on birds. Few regional declines in bird populations have been detected; however, the impact of WNV on local populations of crows and sage grouse has been observed in some localities. The geographical distribution of WNV activity is not continuous across local landscapes, and unexposed birds can then serve as a source to repopulate local impacted areas when overall populations are high.

West Nile virus persists through the winter periods and reappears annually in the spring in temperate regions of the continent. The mechanisms responsible for this recrudescence are unique and largely unknown. Focusing on these overwintering locations with targeted mosquito control could suppress early season initiation of virus transmission and possibly prevent subsequent summer amplification. Integrated pest management aimed at controlling mosquito populations is currently the only effective approach to control this disease.

KEY WORDS: avian hosts, disease, North America, surveillance, West Nile virus, wildlife

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INTRODUCTION

West Nile virus (WNV) is a mosquito-transmitted virus infection of birds that historically was distributed throughout Africa, Middle East, Europe, and western Asia (Murgue *et al.* 2002). The virus has been responsible for human epidemics within its historical range, but the virus strains there did not cause noticeable mortality in native birds (Work *et al.* 1955), including in hooded crows (*Corvus corone*), until 1997-1998 when mortality in domestic geese (Swayne *et al.* 2001) and in migrating white storks (*Ciconia ciconia*) was reported in Israel (McLean *et al.* 2002, Malkinson *et al.* 2002). The exotic WNV was introduced into the United States in 1999 from the Middle East (Lanciotti *et al.* 1999) and initiated an epizootic in local birds, followed by a human epidemic in the New York City (NYC) area (CDC 1999). The disease outbreak in humans and birds expanded out from the epidemic center in Queens in NYC. Infected dead birds, predominantly American crows (*Corvus brachy-*

rhyngchos), were reported out to a 160-km² area in 22 counties in New York, New Jersey, and Connecticut surrounding NYC during the transmission season of 1999 (Eidson *et al.* 2001). The strain of WNV introduced into the U.S., likely from Israel, was particularly virulent to birds, especially to species of Corvidae, and has caused significant avian mortality (McLean *et al.* 2001, 2004).

The American crow emerged as a valuable indicator of WNV presence in the northeastern U.S. because of its high susceptibility to infection with WNV. Dead crows became an ideal sentinel for public health surveillance, because the crow is a conspicuous species even when sick or dead, is widely distributed throughout the U.S. and southern Canada, is relatively local, and is found in multiple habitats— thus more easily seen and reported by the public (McLean 2002). Enhanced surveillance for the detection of WNV dissemination out of the original focus in NYC area was subsequently established, utilizing mortality in crows as a sentinel system for WNV activity.

In addition, public health departments and mosquito and vector control districts began using the occurrence and intensity of WNV-positive crows to make public health decisions about human risk.

SURVEILLANCE

During the initial bird surveillance in 1999, 17,339 dead birds were reported and 5,697 (33%) were crows; 295 of 671 (44%) dead birds tested were laboratory-confirmed WNV positive, and of these 269 (89%) were crows (Eidson *et al.* 2001). After the initial expansion of WNV activity in the NYC area in 1999, the virus survived through the temperate winter and reappeared within the epicenter focal area in May 2000. A multi-state surveillance network was established to track the movement of the virus (CDC 2000). This surveillance consisted of:

- 1) Enhanced passive reporting of human clinical cases,
- 2) Enhanced passive reporting of equine clinical cases,
- 3) Mosquito collection and testing,
- 4) Regular antibody testing of captive sentinel birds (chickens), and
- 5) Dead bird reporting and dead bird collection and testing.

The surveillance data from each state were submitted to a national surveillance data base, ArboNET, and were verified and updated weekly (Marfin *et al.* 2001). New molecular technology to detect virus/antigen in specimens (real-time polymerase chain reaction, RT-PCR) provided rapid testing of birds and mosquitoes and aided in tracking the movement of the virus (Lanciotti *et al.* 2000). Sensitive and specific serologic testing provided rapid detection and subsequent confirmation of human and equine cases and for detection of antibody in wild birds (Ebel *et al.* 2002, Jozan *et al.* 2003). The type and extent of the dead bird surveillance varied across the nation, with some states such as New York testing any bird species submitted (Bernard *et al.* 2001), while other states like Connecticut tested only crows (Hadler *et al.* 2001). After several years, many states only tested crows and other corvid species such as blue jays (*Cyanocitta cristata*) until they detected the first positive bird in a county, and then ceased testing for the year. Other states continued testing throughout the year, to monitor the first appearance of WNV and the subsequent increase in intensity of virus transmission as the season progressed, to more accurately predict human risk of infection.

In 2000, WNV activity expanded to 12 states and the District of Columbia; 12,961 dead birds were submitted for WNV testing, with 4,305 (33.3%) found infected. Crows comprised 58% of the birds tested and 89% of the WNV positive birds; 50.4% of the 7,580 crows tested were infected (Marfin *et al.* 2001). In New York, 68% of the positive birds were crows and the remaining 32% of the positives were among 59 other bird species (Bernard *et al.* 2001). The geographical expansion of WNV in North America continued during the next 3 years, reaching all but 1 of the 48 continental states, 7 provinces in Canada, Mexico, and countries in the Caribbean and Central America.

The rapid expansion of WNV to the southeastern and midwestern states in 2001 was likely aided by the seasonal movement of migratory birds that move along 4

major migratory corridors in North America each season between breeding areas in the north and wintering areas in the south. Dissemination of WNV by migratory birds became more apparent as the virus spread throughout the Mississippi Flyway and the Central Flyway to the west in 2002 (Campbell 2003). The rapid spread and expansion in the Great Plains states, to the Rocky Mountains in 2003, farther westward to the Pacific states during 2004-2005, and south to the Caribbean Islands and Mexico, was further evidence of the role of migratory birds in disseminating WNV.

During the 7 years since WNV entered and spread throughout the U.S., it had a broad host range, infecting and causing mortality in 53,268 birds of 284 native and exotic bird species, both free-ranging and captive, 122 mammals of 26 species, and 2 outbreaks in captive alligators (Farnon 2006). Human cases have declined from the peak in 2003 (Hayes 2004) but continue to occur throughout the U.S. (Figures 1, 2). American crows were the dominant species found positive (>50% in American crows) for the first 3 years, and blue jays and other corvid species became prominent as the virus moved westward from the original introduction site. Virus-positive crows were the first indication of WNV in an area and were the earliest seasonal surveillance event, 4-8 weeks before any other surveillance information. In 2002, dead birds were the first to be reported in 62% of positive counties, and finding a WNV-positive bird before August 1 was a good predictor of subsequent human cases (Guptill *et al.* 2003).

TRANSMISSION AND MORTALITY

Wild avian species are the natural hosts in the transmission cycle of WNV, but all species do not respond the same to virus infections and thus vary in their ability to infect mosquitoes. Therefore, experimental infection studies on various species of birds, including corvid species, were conducted to determine their susceptibility to and reservoir competence for WNV. The fatality rate (number dying of those infected) varied from 100% for American crows and black-billed magpies (*Pica hudsonia*), 83% in blue jays, and 64% in fish crows (*Corvus ossifragus*) to 33% in common grackles (*Quiscalus quiscula*) (Komar *et al.* 2003). A number of other bird species did not suffer mortality. American crows died between days 4-8 post infection and exhibited progressive clinical signs of lethargy, ataxia, unusual posture, inability to perch or stand, recumbency, and death. A further indication of the high mortality rate in crows is the low WNV antibody prevalence detected in free-ranging populations exposed to the virus, suggesting that only a few infected crows survive the disease. Sampling of free-ranging American crows in the NYC area in 1999 found only 1.1% of 175 antibody positive (McLean *et al.*, unpubl. data), 1.2% of 162 crows in New Jersey during 2000-2001 (Jozan *et al.* 2003), and 3.2% of 156 crows in central Illinois (Yaremych *et al.* 2003), for an overall average of 1.8% of 493 crows that were antibody positive.

Direct transmission between infected and uninfected contact American crows and other bird species occurred during these experiments, and the clinical signs and fatality rate were similar in the contact and infected birds

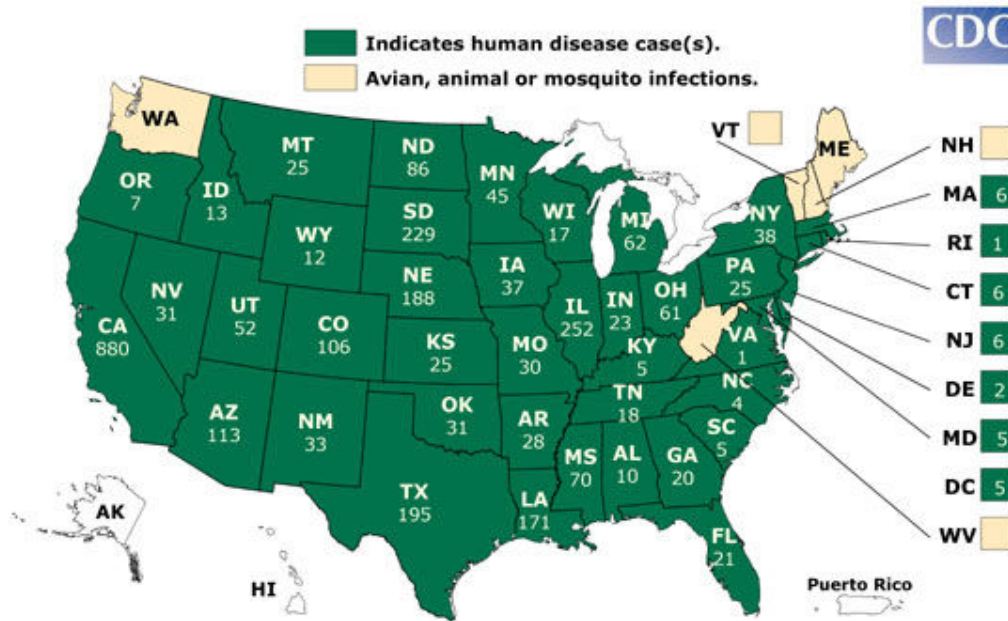


Figure 1. Distribution of West Nile virus activity in the United States, 2005 (CDC 2006).

(McLean *et al.* 2001). Oral transmission of WNV was demonstrated in 5 bird species, and American crows became infected after ingesting the carcasses of a WNV-infected house sparrow (*Passer domesticus*) (Komar *et al.* 2003) and WNV-infected white mice (*Mus musculus*) (R. McLean, unpubl. data). It is not known if direct contact or oral transmission occurs in nature, nor if they are important methods of transmission beyond the normal mosquito transmission route. These could be alternate routes of infection for hawks and owls.

Following WNV infection, many avian species circulate high quantities of virus in their blood (viremia), allowing them to infect mosquitoes, thus making them competent reservoirs (Komar *et al.* 2003). When animals die from infection, it was thought that they were dead-end hosts for the virus and would not contribute to virus transmission. However, crows and other species have viremias of sufficient titers for 3 - 5 days prior to their death to contribute to transmission (reservoir competent) by infecting mosquitoes that feed upon them. Sick and viremic crows would also be more receptive hosts for mosquito feeding, and thus contribute even more to transmission than when they are unaffected and healthy during the early stage of infection. In addition, crows and other species shed WNV through oral and cloacal exudates for days at high titers. For some corvid species, the virus can be detected on oral and cloacal swabs for days after death (Panella *et al.* 2005). A rapid dip-stick test (VecTest, Medical Analysis Systems, Camarillo, CA) was found useful in testing dead corvids, particularly American crows, for WNV infection. This simple test can be used for rapid field evaluation in surveillance programs.

The extensive wild bird mortality associated with WNV and its occurrence within backyards in suburban and urban neighborhoods is unique among most avian diseases (except for house finch conjunctivitis) and was

alarming to the public. Among avian biologists, this mortality also raised concern as a possible serious threat to populations of some migratory and non-migratory avian species. American crows and other highly susceptible bird species such as the threatened greater sage grouse (*Centrocercus urophasianus*) have a high fatality rate from WNV infection, and these species could be suffering mortality significant enough to affect populations (McLean 2004, Walker *et al.* 2004). Up to 82% of greater sage grouse with radio collars died from WNV in 2003 in 2 states and in Alberta, Canada (Naugle *et al.* 2004), and experimental studies confirmed the high mortality rate of sage grouse from WNV infections (Clark *et al.* 2006). Data from the breeding bird survey show that American crow densities in midwestern and northeastern states increased during the last several decades and were in record numbers at certain sites in the NYC area prior to the invasion of WNV. A recent decline in survey trend data for New York is evident. The regional abundance of such a susceptible host species likely improved the chances for the introduced virus to survive and rapidly amplify. The patchy distribution and variable intensity of WNV transmission would leave pockets of unexposed and viable bird populations to rebuild those severely affected areas, if WNV activity does not persist in the region.

SPATIAL AND TEMPORAL PATTERNS

The spatial distribution of WNV transmission is heterogeneous and clustered, as determined by critical interacting factors that influence transmission, particularly host and vector distribution and where they overlap within optimum habitats that support transmission. These patterns are generally not evident from the surveillance data, because positive birds, mosquitoes, and equine and human cases are reported at the county level. Counties usually represent multiple habitats over varying sizes of

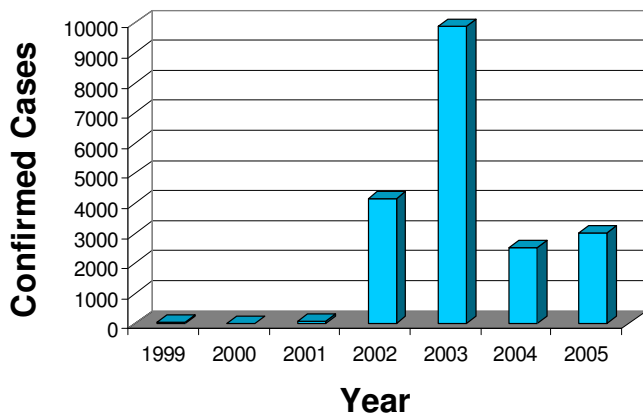


Figure 2. West Nile virus confirmed human cases in the U.S.

geographical areas and varying human concentrations, all of which affect reporting. A pattern was evident in the northeastern states in 2000, where there were differences in the reported intensity of infections in American crows statewide between the adjacent states of New York and Connecticut. Of the 1,732 crows tested in New York, 47% were WNV infected (Bernard *et al.* 2001), compared to 70% of 1,574 crows tested in Connecticut (Hadler *et al.* 2001). The spatial distribution of reported WNV activity in crow populations within these 2 states reflected the discontinuous distribution of transmission (Beckwith *et al.* 2002). The highest intensity of positive crows was concentrated in the south around the 1999 focus in the NYC area in both states, but declined dramatically northward toward the rural upstate New York and Connecticut, where positive crow reports were scattered and diffused. Even at a lower scale, national surveillance data could show 2 adjacent counties with the same number of positive birds, and yet the spatial distribution could be quite different, with the positive birds in one county distributed throughout the county; whereas, in the other county, positive birds could be in a single focus or cluster. Similar variable patterns in reporting of positive birds were observed in other states, such as Arizona and California (Levy 2005, Kramer 2006).

Temporal patterns of transmission are seasonal, with peaks of amplification determined by reproductive cycles of vector and host species, residency status of avian species, and latitudinal weather patterns. The seasonal patterns in the northern states occur during late summer and are shortened by the cessation of mosquito activity during the late fall to the early spring period; whereas, in southern states from Florida to California, mosquitoes actively feed throughout the year. In these states with warmer climates, WNV transmission is sustained almost continuously year round (Tesh *et al.* 2004), with peaks occurring during the fall. Because of this continuous transmission, these states likely serve as annual sources of WNV for northward migratory birds in the spring to become infected, and then introduce or re-introduce the virus to northern states during their migration. However, the southward movement of mosquito-borne viruses by fall migration of infected birds is more prominent, because of the late summer seasonal peaks of WNV

transmission in the northern states; these birds become infected before or during their southward migration (Stamm and Newman 1963).

The residency status of birds in northern breeding areas influence which species are more likely to transport these viruses southward during fall migration; i.e., summer resident birds have a higher probability of becoming infected before they migrate than do transient migratory species, which are present for only a very short time as they pass through areas where there is active transmission (Crans *et al.* 1994). There are obviously mechanisms in addition to the northward movement of WNV by migratory birds in the spring that initiate summer transmission cycles, since positive birds, particularly crows, are found WNV-positive during early spring. Positive birds have appeared during early spring in a number of states at the beginning of the mosquito reproduction and feeding period and before most of the migratory birds arrive, indicating there are other mechanisms for the “overwintering” of WNV besides annual re-introduction (Guptill *et al.* 2003). Continuous transmission by active mosquitoes, and vertical transmission in *Culex p. quinquefasciatus* through their eggs to adult mosquitoes, appear to be important mechanisms in California (Reisen *et al.* 2006). Other methods of overwintering of WNV are being investigated or suggested, such as infected overwintering ticks or other arthropod vectors (Hutcheson *et al.* 2005), and possibly latent and relapsing infections in birds (Crans *et al.* 1994, Reisen *et al.* 2006). The overwintering locations are important in initiating early virus transmission and serving as a local source of virus for amplification and dissemination.

CONTROL

Mosquito-transmitted viral diseases of birds such as WNV are spatially and temporally dynamic, because most of the natural bird host species are not sedentary, and thus it becomes difficult to predict where virus transmission is and will be occurring. This uncertainty makes it problematical in targeting specific control efforts to reduce transmission; therefore, disease control methods for WNV are generally applied over larger areas. However, if over-wintering sites have been identified, then specific targeted control can be applied early at these sites to prevent amplification and dissemination. Once virus transmission is elevated in the bird-mosquito transmission cycle, control efforts are aimed at interrupting or stopping transmission (CDC 2000). The avian host species are obviously an important component of the cycle, but population reduction of birds would not be feasible for most species, with the exception of some peri-domestic species like house sparrows and pigeons in urban centers and some rural species such as blackbirds that form large flocks (McLean *et al.* 2002). However, the timing of such bird control would make it ineffective, because the flocking behavior occurs more during the fall and winter months when transmission is low or no longer occurs, and the need for disease control is during the peak period of transmission in the summer months, to prevent or reduce human risk. Also, massive killing of birds would not be an acceptable alternative. The weakest link in the transmission cycle is mosquitoes, which can be

attacked effectively because they are sedentary, their habitats generally identifiable, and some chemical and biological compounds can be applied to control mosquitoes (CDC 2000, Moore *et al.* 1993).

Mosquito control is accomplished best through an integrated pest management approach in community-wide programs (CDC 2000). The risk of WNV transmission is determined from real time surveillance to identify mosquito breeding sites. Once sites are identified, source reduction to clean up potential breeding sites, or treating the sites with chemical or biological agents to control mosquito larvae, are conducted in the spring to prevent or suppress mosquito production and reduce subsequent adult mosquito populations and virus amplification. If these methods are not effective and heightened transmission occurs during the summer, the infected adult mosquitoes are the direct risks to the human population and thus the new target for control under potential epidemic conditions. Ground and aerial application of low-volume insecticides are required to control adult mosquito populations to suppress transmission in affected areas (Moore *et al.* 1993). The availability and use of equine vaccines has greatly reduced the number of equine cases from WNV (USDA 2006), although cases still occur in areas where the vaccines are not in wide use, particularly in newly affected states (Kramer 2006). The extralabel use of equine vaccines has had mixed and limited results in protecting avian species against WNV infection (Turell *et al.* 2003, Nusbaum *et al.* 2003, Johnson 2005).

CONCLUSION

After the exotic WNV entered the U.S. in 1999, it rapidly disseminated throughout North America and has become established as an enzootic disease. National surveillance documented the expansion, utilizing dead birds as sentinels and indicators of virus activity, and migratory birds likely participated in the rapid spread of the virus throughout the continent. Few invasive diseases have had the broad and intense impact on human, animal, and wildlife health that WNV has had in a short period of time. The high virulence of the introduced strain of WNV was a major contributing factor for the easy establishment and expansion, and it was responsible for the significant number of human and equine cases, as well as the high mortality among bird populations. The virulence of the virus has not changed during the last 7 years and may not in the near future. Targeted mosquito control is the only method now available to suppress local virus transmission and reduce human risk. Equine vaccines have contributed to the reduction in equine cases, wherever they were used. West Nile virus will likely remain enzootic throughout the continent, with periodic outbreaks whenever and wherever the conditions are conducive for increased virus transmission. The invasion of South America has started, and WNV may soon become a problem for countries there.

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