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DOES THE ROOSTING BEHAVIOR OF BIRDS AFFECT TRANSMISSION DYNAMICS OF WEST NILE VIRUS?

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Abstract. The potential role of many urban passerine birds in the transmission of West Nile virus (WNV) is well-documented by studies on host competency, seroprevalence in wild birds, and identification of vector blood meal source. In contrast, the impact of bird behavior on transmission dynamics is largely unexplored. Bird roosting (perching) behavior may be a critical component regulating WNV transmission because of the crepuscular/nocturnal feeding behavior of *Culex* mosquitoes, the primary vectors of WNV. We used radio telemetry to determine the roosting behavior of American crows (*Corvus brachyrhynchos*) and northern cardinals (*Cardinalus cardinalus*). On average, healthy crows moved slightly shorter distances between roosts than viremic crows, 1,038.3 meters versus 1,255.5 meters, while cardinals only moved 54.7 meters. Given the average movements of crows and cardinals between roosts, crows, which are viremic for five days, could spread the virus throughout a mean ± SE area of 20.84 ± 0.79 km^2, while viremic cardinals would, on average, only spread the virus over a mean ± SE area of 0.03 ± 0.01 km^2. Because the crow population in Illinois is decreasing at a rate of 11.5% per year and up to 35.6% per year in certain locations, crows are becoming scarce in some areas, thus reducing their role as wild bird sentinels. We suggest that if crows are important in dispersing WNV, large decreases in their abundance will shift transmission cycles to a more focal nature because of the differences in roosting behavior of crows compared with other urban birds, such as cardinals.

INTRODUCTION

Birds are the primary reservoir hosts of West Nile virus (WNV) and mosquitoes, primarily species in the genus, *Culex,* are the main vectors.[1,2] Because *Culex* mosquitoes feed at dusk and when it is dark,[3] most birds are roosting (perching) when they come in contact with mosquitoes. Therefore, understanding avian roosting behavior is crucial to understanding which species may be most important in maintaining and amplifying WNV. Currently, little is known about how faithful birds are to a particular roost, how far individuals travel between roosts, and how often individuals roost by themselves or communally. Species that roost communally in several different roosts over a relatively short period of time and travel large distances between roosts may be more likely to disperse WNV over greater distances. In contrast, species that are highly faithful to a particular roost and do not roost communally may be important in the focal maintenance of virus activity. Birds that roost communally may be more likely to amplify WNV because the more birds in a location the more carbon dioxide is also produced and therefore a greater signal to mosquitoes. Bird-to-bird transmission is most likely to occur in a situation where birds are close proximity for an extended period.

We investigated the roosting behavior of two bird species that may be very important in the transmission dynamics of WNV, particularly in the Midwest; American crows (Corvus *brachyrhynchos*) and northern cardinals (*Cardinalus cardinalus*). Since WNV was first detected in New York in 1999, crows have been the primary bird species associated with WNV transmission activity and human risk.[4] Public heath departments use dead crows as sentinels of WNV activity.[4–6] The reason crows are linked with WNV is that they experience extremely high mortality when infected with WNV,[7,8] and based on laboratory tests, they are highly competent hosts.[9,10] The average viremia lasted for 3.5 days in a study by Komar and others[10] and 4–5 days in a study by Weingartl and others.[11] Crows typically die within seven days of being infected with WNV.[9] Furthermore, when healthy and infected crows have been confined together, bird-to-bird transmission has been documented.[9,12] Crows also develop particularly high titers of the virus,[10–12] with the highest three days post-infection.[11]

Understanding the movement of crows provides valuable information on how far individuals travel and how quickly WNV may spread across an area as a result of viremic crows infecting mosquitoes in new geographic areas. Based on an analysis of movements of healthy crows in east-central Illinois, Yaremych and others suggested that crows occupy a diurnal home range of 7.6 km^2 and may potentially infect mosquitoes over this area if viremic crows exhibited normal movements.[13] However, a better understanding of the role of crows in dispersing the virus may be gained through analysis of crow movement at the time when they are most likely to encounter mosquitoes at nocturnal roosts. Furthermore, analysis of the movement of crows that later die of WNV infection may provide specific data on differences in movement of sick versus healthy crows and implications for transmission and dispersal of the virus. Because WNV causes neurologic problems,[14] viremic individuals may behave differently than healthy individuals.

Recently, there has been focus on species other than crows (or corvids) as potentially important reservoirs of WNV (i.e., American robins [*Turdus migratorius*]).[1] In the Midwest, one bird species with the highest seroprevalence is the northern cardinal.[15,16] Northern cardinals in Georgia and Florida had the highest prevalence of WNV antibodies among passerine birds,[17] and cardinals in Louisiana have been suggested to be the primary amplifying hosts.[18] West Nile virus is known to cause some mortality in a wide range of bird species, including northern cardinals (www.cdc.gov).[18] Although northern cardinals were not included in an experimental infection study by Komar and others,[10] three of the five most competent avian hosts were non-corvids (i.e., common grackle [*Quiscalus quis-*

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cula], house finch [*Carpodacus mexicanus*], and house sparrow [*Passer domisticus*]). Northern cardinals were also among the most frequently fed upon species by several *Culex* mosquitoes as determined by blood meal analysis.[1,19] There is growing body of evidence that non-corvid passerines are involved in the transmission cycle of WNV, primarily based on the observation that in some areas where crow populations have significantly decreased,[20] WNV activity is still relatively high. If the roosting behavior of crows is responsible for the amplification and spread of the virus throughout an area, and if the roosting behavior of crows is different from other species, then once the crow population is severely reduced the WNV activity will decrease and/or the transmission dynamics will change.

We documented the roosting behavior of American crows and northern cardinals and recorded how far they moved between roosts from one night to the next. We also determined whether the roosting behavior of viremic crows differed from that of healthy individuals and how far a viremic crow may move and spread the virus. We investigated whether crow and cardinal populations were experiencing declines and discuss how population declines of crows may affect the transmission dynamics of WNV.

MATERIALS AND METHODS

The roosting behavior of crows and cardinals was determined during the period when WNV activity is the highest in Illinois, July through September.[21] This study was conducted during the 2002, 2003, and 2004 WNV seasons in Champaign County, Illinois. The area is comprised of the adjacent cities of Champaign and Urbana surrounded by large areas of agriculture. Crows were captured using Australian crow traps,[22] primarily while feeding in the agricultural areas owned by the University of Illinois south of Champaign-Urbana (South Farms). Crows were leg-banded with United States Fish and Wildlife Service bands, and a two-gram radio transmitter (JDJC Corp., Fisher, IL) was attached. Most transmitters were mounted to the rachis of the central tail feather using sutures and epoxy. Two transmitters were applied as neck collars.[8,13] The average battery life of a radio transmitter is three months.

Radio-tagged crows were tracked using vehicle-mounted twin Yagi antennas (Primus Inc., Joliet, IL). Roosts were defined as those areas where crows were located between 11:00 PM and 4:00 AM. We located the roosts of radio-tagged crows as often as possible. On average, we obtained roost location on each individual six of every seven days. Once a roosting crow was located, its position was recorded using Global Positioning Systems. Roosts were generally cohesive and their boundaries easily distinguished. Roosts were considered to be separate if the most peripheral individuals in each roost were at least one kilometer from each other. We calculated the distance between roosts as a straight line distance between the roosting locations of a bird in each roost. The average area used by a viremic crow was calculating as the area of the circle around the point where the crow died to the furthest average roosting location.

Every radio-tagged crow that was found dead was submitted to the University of Illinois, College of Veterinary Medicine Veterinary Diagnostic Laboratory for necropsy. This laboratory conducted a gross necropsy and an immunohistochemical evaluation of major organs to determine if the individual was infected with WNV, and then determined the cause of death based on the gross neocropsy and immunohistochemical results. Because all radio-tagged crows were tracked daily, it is likely that we recovered dead crows within 24 hours of their death. We were assuming that WNV progressed in these birds as has been recorded in crows held in captivity.[10–12] Therefore, we documented roosting behavior for the five days prior to death, which encompasses the time when crows are most viremic.

Northern cardinals were studied from July to September 2005 in the same area of Champaign-Urbana. Cardinals were captured using mist nets and potter walk-in traps. Once captured, a 1.2-gram transmitter was attached to their tail. These radio-tagged cardinals were tracked using a hand-held receiver. Roosting locations were determined by locating these radio-tagged birds between 11:00 PM and 4:00 AM an average of six of every seven nights.

The population trends of crows and cardinals were determined for the entire state and Cook County, the county with the historically highest WNV activity (www.idph.state.il.us). We did not use Christmas bird count (CBC),[20,23] data because many of the crows in Illinois in winter are migrants. Therefore, the CBC is a poor index of the breeding crow population. We know that at least some of our wintering crows are from northern Michigan because we have radio-tracked two crows from Illinois to areas where they were breeding in northern Michigan (Raim A, unpublished data). We also did not use the breeding bird survey (BBS) because this survey does not sample urban areas, e.g., there are no active BBS routes in Cook County. For determining avian population trends in Illinois, we used the spring bird count (SBC) data, which are available upon request from one of the co-authors (M.P.W.). The SBC has been conducted since 1972 in Illinois, and is conducted by volunteers in all 102 counties on a Saturday that falls between May 4 and May 10. These volunteers record all birds and the number of hours spent by each party in the field. In any given year, there are between 1,100 and 1,600 volunteers in the field. Because of the timing of this census, it provides an ideal index of the breeding crow and cardinal populations in Illinois. Crows in Illinois breed from March through June,[24] and cardinals breed from March through August.[25] This census samples both rural and urban areas, and provides a good index of birds in areas with high WNV activity such as Cook County where they annually have more than 100 volunteers.

The route-regression technique[26] was used to determine the population trend of crows and cardinals. We analyzed the population trend from May 2001, a year before the arrival of WNV, to May 2005, four years after the arrival of WNV. Because decreases in the population could be part of natural fluctuations in the population, we compared the trend after the arrival of WNV to the population trend from 1975 to 2000. In the route-regression technique, a separate trend is calculated for each county (i.e., route) by linear regression. Once county-level estimates of trends are obtained, the overall trend is estimated using the weighted mean of the county trends. Weights are proportional to the total number of individual birds observed in each county. Statistically significant trends were assessed using a one-sample *t*-test comparing the mean slope of the county population trends to zero.

RESULTS

We determined the roosting behavior of 31 American crows and 12 northern cardinals in east-central Illinois by radio telemetry. Of the 31 crows used in this study, 20 died of WNV infection during the study based on necropsy reports, but no radio-tagged cardinals died of WNV infection. All of the crows roosted with at least one other conspecific, while cardinals roosted either by themselves or near their mate. The average distance between where a crow roosted from one day to the next was 1,038.3 meters, with the average largest movement by a crow from one day to the next being 4,153.2 meters. In stark contrast, cardinals moved an average of 54.7 meters between roosts from one day to the next, with the average largest movement by a cardinal being 103.8 meters (Figure 1). The average distance a crow and a cardinal moved between roosts was significantly different ($t = 15.84$, degrees of freedom [df] = 65, $P < 0.01$).

In addition to distance traveled, the average number of roosts used over a five-day period by viremic (1.95) and healthy crows (1.40; individuals that never became infected with WNV during the season) were significantly different ($t = 3.42$, df = 19, $P < 0.01$). The average distance a crow moved between roosts when viremic decreased as the crow neared death, and on the day when it died a crow on average only moved 263.0 meters from where it roosted to where it died (Figure 2). Over the last five days when a crow viremia is highest, they may roost within a mean ± SE area of 20.84 ± 0.79 km^2 or within 2.58 km of where the crow was found dead. Although no cardinals died of WNV infection, if we assume viremic cardinals behave similarly to healthy individuals, then they would have roosted within a mean ± area of 0.03 ± 0.01 km^2.

The crow population throughout the entire state of Illinois experienced a significant decreased of 11.5% per year from 2001 to 2005 ($t = -6.84$, df = 101, $P < 0.01$). The decrease was most severe in Cook County (Chicago area), with a yearly average decrease of 35.6%. However, before the arrival of WNV, the crow population was increasing at a rate of 1.6% per year from 1975 to 2000 ($t = 6.88$, df = 101, $P < 0.01$). Overall, the crow population increased 46.5% from 1975 to 2000 but then decreased 18.3% in the four years after the arrival of WNV. The cardinal population based on the SBC remained stable in Illinois after the arrival of WNV (1.7% increase per year; $t = -0.14$, df = 101, $P = 0.89$). In Cook County, where WNV transmission is the highest based on human and mosquito data, the cardinal population declined decreased at a rate of 2.6% per year. There was no detectable population trend in the cardinal population from 1975 to 2005 (Figure 3).

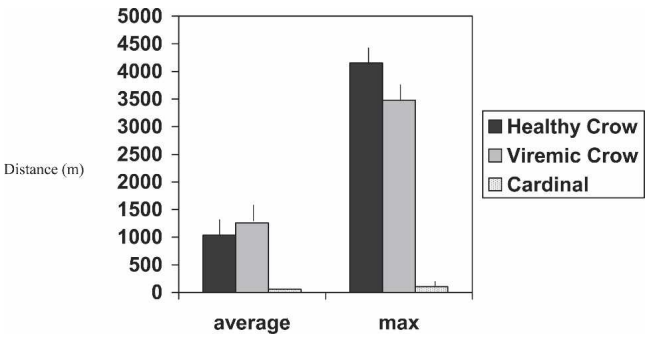

FIGURE 1. Mean ± SE distance between roosts for rows and cardinals from one day to the next and maximum (max) distance an individual moved between roosts from one day to the next.

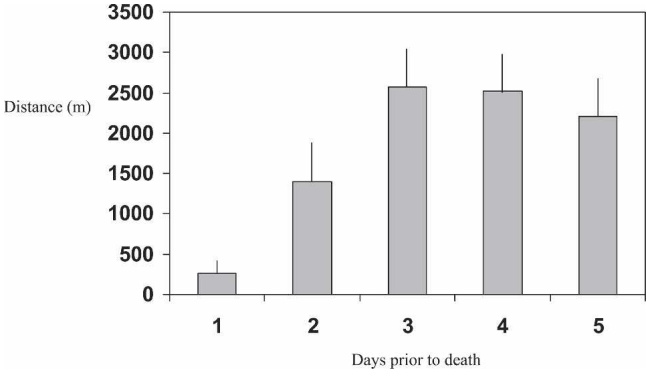

FIGURE 2. Mean ± SE distance from where a crow was found dead to where it roosted the five nights before it died.

DISCUSSION

American crows exhibit roosting behavior that is ideal for the spread of WNV throughout an area because they always roost communally, roost at several different locations, and roost with different individuals. This behavior could result in mosquitoes in several different areas having access to potentially viremic crows. Bird-to-bird transmission may also contribute to why crows are important in transmission dynamics. Although bird-to-bird transmission of WNV in crows has only been observed in the laboratory, American crows exhibit many of the behaviors that may result in bird-to-bird transmission of the virus. West Nile virus has been found in feather pulp,[27] and allopreening could facilitate bird-to-bird transmission, especially during molt when the feather pulp would be most abundant. In Illinois, crows molt between June and September[24] which corresponds to the peak of WNV activity. Crows are known to shed the virus from their oral cavity and cloaca.[10] Because crows always roost communally, they may be exposed to WNV more than other species, most of which do not roost communally when WNV transmission is most active.

One of the interesting results of our study on roosting behavior is that viremic crows use more roosts than healthy crows. This may seem counter-intuitive because sick birds would generally seem less likely to move around. The data show that infected birds used the same roosts as healthy birds until one or two days before they died. Because individuals often forage several kilometers from where they roost, it is possible they became sufficiently ill during the day and were unable to return to their usual roosting site that evening. Our radio telemetry data indicate that the night before their death they tend to roost at the nearest roost site. In some situations, it was unclear whether a crow had died before roosting, or died during the night.

In contrast to crow behavior, which may be dispersing WNV by one to four kilometers per night, the roosting behavior of cardinals is more consistent with focal WNV activity. Because cardinals do not move very far between roosts and do not roost communally, there is less possibility of bird-

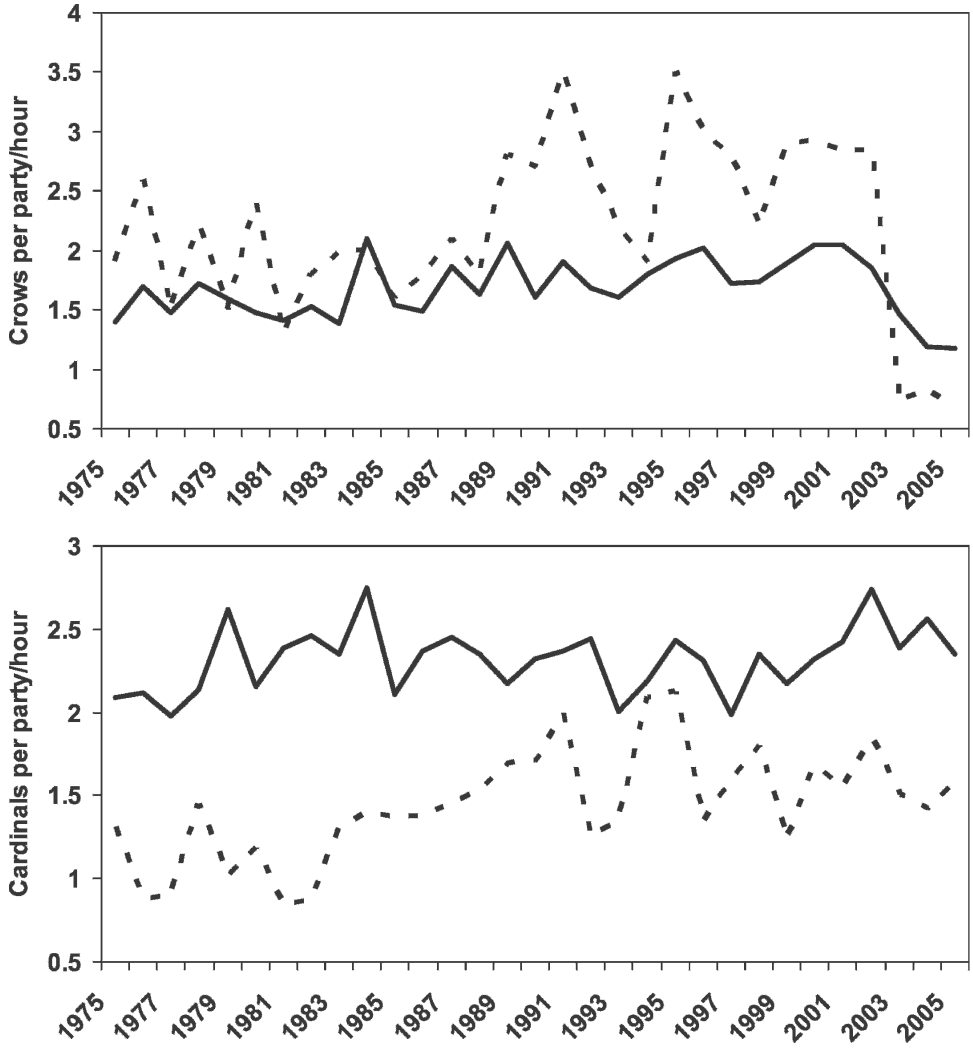

FIGURE 3. Crow and cardinal population decrease throughout Illinois (**solid line**) and in Cook County (Chicago area, **dashed line**). The population trends were determined using Spring Bird Count data.

to-bird transmission. However, given their abundance in urban habitats and fidelity to roost sites, cardinals or other passerines like house sparrows may be important reservoir hosts in the focal maintenance or amplification of WNV transmission.

The density of dead crows has been suggested to be a means of predicting the area of highest risk for human cases.[4] If crows were the sole reservoir host for WNV, then one may expect that the WNV infection rates in mosquitoes and the number of human cases would decrease as crows die out from WNV-induced mortality. Clearly, this is not the case in Illinois, which had a resurgence in WNV in Cook County in 2005 despite a continuing downward trend in crow abundance. It seems more plausible that crows are important dispersers of WNV throughout an area, especially since the average distance between roosts was slightly greater than a kilometer. Therefore, a dramatic decrease in the crow population might not affect the amplification of WNV, but could change the rate of spread to adjoining areas. That is, the transmission dynamics would then change to reflect the roosting behavior of the major reservoir hosts. Assuming WNV is maintained throughout the winter by infected, overwintering mosquitoes,[28–31] then in the absence of infected crows dispersing WNV, transmission activity may be expected to be more focal. Although the roosting behavior for many common species is poorly described, it is generally assumed that species such as American robins, house sparrows, and mourning doves (*Zenaida macroura*) are roosting at or near their breeding territories. However, house sparrows and mourning doves do occasionally roost in groups, but not to the extent to which crows roost communally. Once a crow population is extirpated or severely reduced in an area, you would expect transmission activity to show a slower spread from one area to the next and instead expect more focal hot spots maintained by the breeding species in that area.

In Illinois, this pattern of more focal activity and less dispersal may be starting to occur. Crows have been decreasing throughout the state but their decrease is most precipitous in Cook County (i.e., Chicago area). In 2002, there was a statewide outbreak of WNV with Cook County having the most human cases. However, we can be reasonably certain that WNV transmission occurred throughout northern, central, and southern counties because of the number of horse cases and detection of pools of WNV-positive *Culex* (www.idph

TABLE 1

Data was retrieved from the Illinois Department of Public Health webpage on 12/8/05*

Year	2001	2002	2003	2004	2005
No. of counties	7	100	77	62	52
No. of human cases	0	884	54	60	248

* The number of counties that had birds, mosquitoes, or horses that tested positive for West Nile virus (WNV) since WNV was first detected in Illinois. The third row is the number of human cases reported to the department for each year.

.state.il.us/ and Table 1). After this initial outbreak, which at the time was the largest outbreak of WNV every recorded, fewer counties reported activity in mosquitoes, dead WNV-positive birds, and human cases. Most of the activity was relatively localized in the northeastern part of the state (i.e., Cook County). In 2005, Illinois experienced a resurgence of WNV; however, unlike the outbreak year of 2002, the activity has remained focal within the state with fewer counties detecting WNV and more than half of the cases being in Cook County (Table 1). Even within Cook County, it was evident there were areas of very high and very low activity (www.idph .state.il.us/ and Novak R, unpublished data).

Although WNV is undoubtedly influenced by other biologic and meteorologic factors, additional research in areas with relatively large and small crow populations is needed to determine if decreases in crows will alter the transmission dynamics and/or dispersal rate of WNV. Although American crow is the predominate corvid of central North America, other species such as jays, magpies, and ravens may also be important in the transmission dynamics of WNV in western North America (www.westnile.ca.gov).

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West Nile virus (WNV) is a single-stranded RNA virus that causes West Nile fever. It is a member of the family Flaviviridae, specifically from the genus Flavivirus, which also contains the Zika virus, dengue virus, and yellow fever virus. West Nile virus is primarily transmitted by mosquitoes, mostly species of Culex. The primary hosts of WNV are birds, so that the virus remains within a "birdâ€“mosquitoâ€“bird" transmission cycle. The arrival of West Nile virus (WNV) in North America has led to interest in the interaction between birds, the. ampliï¬cation hosts of WNV, and Culex mosquitoes, the primary WNV vectors. American robins (Turdus mi-. gratorius) are particularly important ampliï¬cation hosts of WNV, and because the vector Culex mosquitoes are. primarily nocturnal and feed on roosting birds, robin communal roosting behavior may play an important role. in the transmission ecology of WNV.Â Second, the roosting behavior of juvenile robins is likely to. differ from that of adults. Juvenile robins are less efï¬cient at.Â roosts affects seasonal patterns of WNV transmission, varia-. tions in the detection of WNV in mosquitoes should be cor-. related with variations in communal roosting by robins. Antibodies to West Nile virus in asymptomatic mammals, birds, and reptiles in the Yucatan Peninsula of Mexico. The American Journal of Tropical Medicine and Hygiene 74: 908â€“914.Google Scholar. Fernandez-Salas, I, Contreras-Cordero, JF, Blitvich, BJ, Gonzalez-Rojas, JI, Cavazos-Alvarez, A, Marlenee, NL, Elizondo-Quiroga, A, Lorono-Pino, MA, Gubler, DJ, Cropp, BC, Calisher, CH and Beaty, BJ (2003). Serologic evidence of West Nile Virus infection in birds, Tamaulipas State, Mexico. Vector-Borne and Zoonotic Diseases 3: 209â€“213.CrossRef Google Scholar PubMed.Â Experimental transmission of West Nile virus (Flaviviridae: Flavivirus) by Carios capensis ticks from North America. Vector-Borne and Zoonotic Diseases 5: 293â€“295.CrossRef Google Scholar PubMed.