Arch Virol
DOI 10.1007/s00705-012-1516-3

BRIEF REVIEW

West Nile virus associations in wild mammals: a synthesis

J. Jeffrey Root

Received: 20 June 2012 / Accepted: 15 September 2012

Abstract Exposures to West Nile virus (WNV) have been documented in a variety of wild mammals in both the New and Old Worlds. This review tabulates at least 100 mammal species with evidence of WNV exposure. Many of these exposures were detected in free-ranging mammals, while several were noted in captive individuals. In addition to exposures, this review discusses experimental infections in terms of the potential for reservoir competence of select wild mammal species. Overall, few experimental infections have been conducted on wild mammals. As such, the role of most wild mammals as potential amplifying hosts for WNV is, to date, uncertain. In most instances, experimental infections of wild mammals with WNV have resulted in no or low-level viremia. Some recent studies have indicated that certain species of tree squirrels (*Sciurus* spp.), eastern chipmunks (*Tamias striatus*), and eastern cottontail rabbits (*Sylvilagus floridanus*) develop viremia sufficient for infecting some mosquito species. Certain mammalian species, such as tree squirrels, mesopredators, and deer have been suggested as useful species for WNV surveillance. In this review article, the information pertaining to wild mammal associations with WNV is synthesized.

Introduction

The first isolation of West Nile virus (WNV; family *Flaviviridae*, genus *Flavivirus*) was documented in Omogo in the West Nile District of Uganda from an adult woman [103]. Subsequently, the virus has been described to be widely distributed in parts the Old World, such as Africa, the Middle East, Asia, southern Europe, and elsewhere [114]. During the summer of 1999, WNV was first detected in the Western Hemisphere in the northeastern U.S. [80]. The virus spread rapidly across the continental U.S. [69] and expanded its range north into Canada by 2001 [24] and southwardly into the Caribbean basin and Mexico between 2001 and 2002 [52]. The virus is thought to have reached the South American continent by 2004 [52]. Although WNV activity is strictly limited to lineage 1 viruses in the New World, lineage 2 viruses occur in various parts of the Old World [5, 78], and additional lineages have been proposed [78].

The natural enzootic cycle of WNV is thought to occur largely among birds and mosquito vectors [56]. Mammals have generally been presumed to be dead-end hosts because they typically produce short-duration viremia that is below the threshold for infecting most mosquito species [7]. For example, horses are known to be commonly exposed to WNV, which can be associated with morbidity and mortality; however, their low viremia of short duration during experimental infections suggest that they are unlikely amplifying hosts [12]. Nonetheless, many reports have suggested that several species of wild mammals are commonly exposed to WNV, occasionally with high associated seroprevalence rates. Some recent experimental studies have documented viremia of $> 10^{5.0}$ pfu/mL in select species of mammals. This level has been commonly used as a threshold suggesting that a minimum level is required to infect select mosquito species through blood meals [51]. Overall, the general consensus on the trivial roles mammals play in the epidemiology of WNV may be due to a lack of inquiry rather than a lack of importance [66].

The objective of this paper was to provide a comprehensive review of WNV activity in wild mammals. In

J. Jeffrey Root (✉)
US Department of Agriculture, National Wildlife Research Center, 4101 La Porte Ave, Fort Collins, CO 80521, USA
e-mail: jeff.root@aphis.usda.gov

Published online: 02 December 2012

addition, the potential roles of wild mammals in the ecology of WNV are discussed. Due to space limitations, Kunjin virus and the Australian continent are not focused on in this paper. For the purposes of this review, natural exposures to WNV are defined as detections of antibodies, virus, viral RNA, or other forms of detection. When suitable/possible, common and scientific names have been updated to reflect modern taxonomy following *Mammal Species of the World* [112]. As reviewed elsewhere, caution must be used when interpreting serologic results from locations where multiple group B arboviruses exist [38]. Many of the older studies cited in this paper used a single assay for antibody detection, some of which are prone to cross-react with other flaviviruses. As such, some antibody detections reviewed in this paper are presented for completeness, but it is acknowledged that some of these reports could represent false positive cross-reactivity.

Natural exposures of wild mammals to West Nile virus

The data presented below represent a synthesis of natural exposures of wild mammals to WNV. For the sake of completeness, reports associated with captive wildlife are also presented in key situations, as zoos and similar facilities have been proposed as potential sentinel sites for emerging pathogens [61].

WNV in rodents

WNV exposures have been detected in diverse wild rodent species from multiple regions. Rodents represent a taxonomic group with one of the highest number of reported species exposed. Some of the earliest observations of WNV exposures in wild mammals were obtained from rodents during the 1960s. Many of the tests used for rodent antibody assessments, especially older accounts, are prone to cross-reactivity and, therefore, should be interpreted with caution. A summary of natural WNV exposures of rodents is presented in Table 1.

Squirrels

Dead and sick tree squirrels have become ubiquitous signs of WNV activity in some regions of the U.S. [39, 50, 76]. Exposures have been detected in fox squirrels (*Sciurus niger*) [8, 39, 50, 76, 91–93], eastern gray squirrels (*Sciurus carolinensis*) [21, 33, 39, 55, 91], western gray squirrels (*Sciurus griseus*) [76], and a red squirrel (*Tamiasciurus hudsonicus*) [91]. Some of these exposures have been detected in dead or moribund squirrels, while many others have come from healthy squirrels that have developed antibodies to WNV following their exposures. High antibody prevalence rates of nearly 50 % have been reported for fox squirrels and eastern gray squirrels [91]. Additional WNV infections have been reported from "squirrels" in Arizona, Kansas, and Wyoming [70, 71]. However, the species identifications were not presented for these animals. Overall, WNV exposures in tree squirrels have been presented from at least thirteen states and the District of Columbia in the contiguous U.S. Additional WNV exposures from a non-tree squirrel comes from the European ground squirrel (*Spermophilus citellus*), in which antibodies were detected in nine specimens from Austria [102].

The reasons why tree squirrels appear to be more commonly exposed to WNV when compared to other sympatric mammal species is undetermined; however, aspects of their behavioral ecology have been suggested to increase their chance of exposure to mosquito vectors [91]. For example, the activity and feeding behavior of *Culex pipiens* complex mosquitoes in tree canopies in Tennessee [96] suggest potential increased exposure to tree squirrels. Tree squirrels have been proposed as useful tools for monitoring WNV activity [76, 91], as these animals provide localized evidence of WNV activity [76]. However, when antibodies are used to monitor WNV activity, the age structure of populations will need to be accounted for [91], young animals will need to be utilized [33], or a longitudinal approach, such as mark-recapture sampling, may be required [93] to overcome bias generated by studying animals potentially exposed during previous years.

Chipmunks

WNV exposures have been documented in eastern chipmunks (*Tamias striatus*) on two occasions in New York and Maryland, USA [33, 63]. However, a multi-state study including New York, Pennsylvania, and Ohio failed to detect WNV antibodies in any of the >30 eastern chipmunks sampled [91]. It has been suggested that limited mosquito exposures or the potential for lethal WNV infections in eastern chipmunks may account for the low seroprevalence observed in this species [33]. Due to their small size, dead chipmunks are less likely to be recovered during surveillance efforts when compared to larger tree squirrels.

Rats

Exposures of WNV to Old World rat species are fairly diverse, with many exposures detected in *Rattus* spp. For example, antibodies to WNV were detected in brown rats (*Rattus norvegicus*) and/or roof rats (*R. rattus*) in Pakistan, Israel, Austria, Tunisia, central Africa, and Madagascar [2, 13, 16, 19, 30, 37, 102], from *R. rattus alexandrius* in

Table 1 Natural exposures of wild rodents to West Nile virus

Common name	Scientific name	Detection type	Location	Reference
Fox squirrel	*Sciurus niger*	Antigen; viral RNA	MI, USA	[50]
		Antigen; viral RNA	IL, USA	[39]
		Antibodies	CO, OH, USA	[91]
		Antibodies	CO, USA	[92]
		Antibodies; viral RNA	CO, USA	[93]
		Viral RNA	CA, USA	[76]
		Antibodies	IA, USA	[8]
Eastern gray squirrel	*Sciurus carolinensis*	Not specified	NY, USA	[55, 63]
		Antigen; viral RNA	IL, USA	[39]
		Antibodies	NY, PA, USA	[91]
		Antibodies	LA, USA	[21]
		Antibodies	MD, D of C, USA	[33]
Western gray squirrel	*Sciurus griseus*	Antibodies	CA, ID, USA	[76]
Red squirrel	*Tamiasciurus hudsonicus*	Antibodies	NY, USA	[91]
European ground squirrel	*Spermophilus citellus*[a]	Antibodies	Austria	[102]
Eastern chipmunk	*Tamias striatus*	Not specified	NY, USA	[63]
		Antibodies	MD, USA	[33]
Hispid cotton rat	*Sigmodon hispidus*	Antibodies	LA, USA	[21]
Roof rat and subspecies	*Rattus rattus*	Antibodies	Pakistan	[37]
		Antibodies	LA, USA	[21]
		Antibodies	Madagascar	[30]
		Antibodies	Tunisia	[13]
		Antibodies	Central Africa	[16]
	R. rattus frugivorus	Antibodies	Egypt	[1]
	R. rattus alexandrius	Antibodies	Israel	[2]
Brown rat	*Rattus norvegicus*	Antibodies	Israel	[2]
		Antibodies	Egypt	[1]
		Antibodies	Pakistan	[19]
		Antibodies	Austria	[102]
		Antibodies	MD, D of C, USA	[33]
Rat	*Rattus* sp.	Antibodies	LA, USA	[91]
African arvicanthis	*Arvicanthis niloticus*	Virus	Nigeria	[49]
		Antibodies[b]	Kenya	[43]
Common dasymys	*Dasymys incomtus*	Antibodies[b]	Kenya	[43]
Kaiser's aethomys	*Aethomys kaiseri*	Antibodies[b]	Kenya	[43]
Rusty-bellied brush-furred rat	*Lophuromys sikapusi*[c]	Antibodies[b]	Kenya	[43]
Black-tailed thallomys	*Thallomys nigricauda*	Antibodies[b]	Kenya	[43]
Common metad	*Millardia meltada*	Antibodies	Pakistan	[19]
Guenther's vole	*Microtus guentheri*[d]	Antibodies	Israel	[2]
Bank vole	*Myodes glareolus*[e]	Virus	Hungary	[73]
		Antibodies	Austria	[102]
		Antibodies	Italy	[59]
Common vole	*Microtus arvalis*	Antibodies	Romania	[25]
Meadow jumping mouse	*Zapus hudsonius*	Antibodies	NY, USA	[91]
Peromyscus mice	*Peromyscus* spp.	Antibodies	NY, OH, USA	[91]
White-footed mouse	*Peromyscus leucopus*	Antibodies	MD, D of C, USA	[33]
House mouse	*Mus musculus*	Antibodies	CO, USA	[91]
		Antibodies	D of C, USA	[33]

Table 1 continued

Common name	Scientific name	Detection type	Location	Reference
Western Mediterranean mouse	*Mus spretus*	Antibodies	Spain	[14]
		Antibodies	Morocco	[15]
Unidentified mouse	*Mus* sp.	Antigen	Guinea	[53]
		Antibodies	Tunisia	[13]
Northeast African spiny mouse	*Acomys cahirinus*[f]	Antibodies	Egypt	[1]
Eastern spiny mouse	*Acomys dimidiatus*[f]	Antibodies[g]	Egypt	[99]
Field mouse	*Apodemus* sp.	Antibodies	Austria	[102]
Long-tailed field mouse	*Apodemus sylvaticus*	Antibodies	Tunisia	[13]
Maghreb garden dormouse	*Eliomys munbyanus*[h]	Antibodies	Tunisia	[13]
Unidentified praomys	*Praomys* sp.	Antibodies	Central Africa	[16]
Wagner's dipodil	*Dipodillus dasyurus*	Antibodies[g]	Egypt	[99]
Greater Egyptian gerbil	*Gerbillus pyramidum*	Antibodies	Israel	[2]
Unidentified gerbil	*Gerbillus* sp.	Antibodies	Tunisia	[13]
Indian gerbil	*Tatera indica*	Antibodies	Pakistan	[19]
Indian desert jird	*Meriones hurrianae*	Antibodies	Pakistan	[19]
Bushy-tailed jird	*Sekeetamys calurus*	Antibodies[g]	Egypt	[99]
Common hamster	*Cricetus cricetus*	Antibodies	Austria	[102]
Common gundi	*Ctenodactylus gundi*	Antibodies	Tunisia	[13]
Woodchuck	*Marmota monax*	Antibodies	MD, USA	[33]
"Rodents"	Not reported	Antibodies	Hungary	[72]
		Not reported	NY, USA	[68]

[a] Listed in original paper as *Citellus citellus*

[b] Note: Sera were generally insufficient to conduct confirmatory tests

[c] Reported as *Lophuromys sikapusi*, but *Mammal Species of the World* indicates that eastern distribution limits are unresolved [112]

[d] Reported in original paper as *Microtus guntheri*

[e] Reported in original papers as *Clethrionomys glareolus*

[f] Reported in original papers as *Acomys cahrines cahirinus* and *Acomys cahirinus dimidatus* for references [1] and [99], respectively

[g] Note: Antibodies were determined by HI tests and were of low titer. The authors concluded that the small number of rodents with antibodies and the low HI titers are insignificant

[h] Reported in original paper as *Eliomys tunetae*

Israel [2], and *R. rattus frugivorus* and brown rats in Egypt [1]. In addition, virus has been isolated from African arvicanthis (aka grass rat; *Arvicanthis niloticus*) collected from a Sudan woodland vegetative zone in Nigeria [49], and exposures have been detected in the common metad (*Millardia meltada*), also known as the soft-furred rat, collected in Pakistan [19]. A serosurvey in Kenya detected WNV antibodies in African arvicanthis, common dasymys (*Dasymys incomtus*), Kaiser's aethomys (*Aethomys kaiseri*), a rusty-bellied brush-furred rat (*Lophuromys sikapusi*), and a black-tailed thallomys (*Thallomys nigricauda*); however, sera were generally insufficient to conduct confirmatory tests for these species [43]. In the New World, exposures have been primarily limited to Old World rat species of the genus *Rattus*, with antibodies detected in brown rats from Maryland and Washington DC [33], roof rats from Louisiana [21], and *Rattus* species from Louisiana [91]. In addition, antibody-positive hispid cotton rats (*Sigmodon hispidus*) were sampled in Louisiana [21].

Mice

Reported exposures of Old World mice to WNV are limited. WNV antibody detections have been reported in the western Mediterranean mouse (*Mus spretus*) in Spain [14] and Morocco [15], in a field mouse (*Apodemus* sp.) from Austria [102], and in a long-tailed field mouse (*Apodemus sylvaticus*), Maghreb garden dormice (*Eliomys munbyanus*), and unidentified *Mus* sp. in Tunisia [13], in a northeast African spiny mouse (*Acomys cahirinus*) and an eastern spiny mouse (*Acomys dimidiatus*) from Egypt [1, 99], and in unidentified praomys (*Praomys* sp.) from central Africa [16]. Further, viral antigen has recently been reported in an unidentified *Mus* sp. mouse from Guinea

[53]. Similar to the Old World, reported WNV exposures of mice found in the New World are limited. Antibodies to WNV have been detected in *Peromyscus* spp. in the eastern U.S., house mice in the central and eastern U.S., and a meadow jumping mouse (*Zapus hudsonius*) in the eastern U.S. [33, 91].

Other rodents

Additional WNV exposures, mostly in the Old World, have been occasionally documented in other rodent species. These included WNV exposures in an Indian gerbil (*Tatera indica*) and Indian desert jird (*Meriones hurrianae*) from Pakistan [19], a bushy-tailed jird (*Sekeetamys calurus*) and a Wagner's dipodil (*Dipodillus dasyurus*) from Egypt [99], a greater Egyptian gerbil (*Gerbillus pyramidum*) and Guenther's vole (*Microtus guentheri*) from Israel [2], a bank vole (*Myodes glareolus*) and "rodents" from Hungary [72, 73], additional bank voles from Italy and Austria [59, 102], and from a common vole (*Microtus arvalis*) collected in Romania [25]. In addition, WNV antibodies have been detected in the sera of common hamsters (*Cricetus cricetus*) from Austria [102], and in a common gundi (*Ctenodactylus gundi*) and an unidentified gerbil (*Gerbillus* sp.) from Tunisia [13]. Additional rodent WNV exposures were reported in a woodchuck (*Marmota monax*) sampled in Maryland [33] and in "rodents" from New York [68]. Overall, only limited testing of rodents for WNV has been conducted, particularly in the New World, when compared to birds and domestic animals.

WNV in wild carnivores and mesocarnivores

Detections of WNV antibodies in wild carnivores and mesocarnivores have become fairly common over the last decade in North America. Some species have been afflicted with severe disease, primarily in captive situations, following WNV infection, while disease in other species has not been routinely reported. The potential roles of various peridomestic mesocarnivores in WNV amplification cycles have been proposed as important questions [23], likely due to the additional public-health burden these species could foster if they are reservoir competent. Further, mesopredators have been proposed as potentially useful sentinels for monitoring WNV activity in delineated areas [6]. A summary of natural WNV exposures of carnivores and mesocarnivores is presented in Table 2.

Striped skunks

The first detection of WNV exposure in a striped skunk (*Mephitis mephitis*) was reported from Connecticut [63]. Additional exposures were reported in this species sampled in Wyoming, with a high antibody prevalence rate of 63 % [6], thereby suggesting that striped skunks are commonly exposed to WNV in this area. An additional 90 striped skunk sera tested from Arizona, California, Louisiana, and Texas did not yield evidence of WNV antibodies [6].

Canids

Only limited WNV exposures have been detected in wild canids, although this may be due to lack of sampling rather than a lack of exposures. Antibodies to WNV have been detected in coyotes (*Canis latrans*) during two different studies in Wisconsin, with an antibody prevalence rate of 27 % during a 2003-2004 sampling period [22], 0 % during a 2004-2005 sampling period, and increasing to 10 % during a 2005-2006 sampling period [23]. An additional example of a canid exposed to WNV comes from the red fox (*Vulpes vulpes*), as a single red fox was documented to be antibody positive in Wisconsin [22]. Other wild canids, such as the gray fox (*Urocyon cinereoargenteus*), have been tested for WNV exposure but none were found to have been exposed [6].

Raccoons

Raccoons (*Procyon lotor*) have been commonly shown to be exposed to WNV in many regions of the U.S. Feral populations in the Old World may have a similar fate. Raccoon infections with WNV were first reported from New York during 2000 [68]. Subsequently, antibody detections in raccoons were reported in 2005 from Pennsylvania [91] and Louisiana [21]. Additional antibody detections have been documented in raccoons from Wisconsin, Louisiana, Wyoming, Maryland, Washington DC, and Iowa [6, 8, 22, 23, 33].

Bears

Antibodies to WNV have been documented from a small percentage of American black bear (*Ursus americanus*) sera collected from New Jersey [27]. In addition, WNV antibodies have been detected in brown bear (*Ursus arctos*) sera collected from Croatia [62].

Virginia opossum

The Virginia opossum (*Didelphis virginiana*) is a marsupial and is therefore not a member of the mammalian order Carnivora. However, it is considered a North American mesocarnivore. Virginia opossums have exhibited widespread WNV exposures. Antibodies to WNV have been detected in this species from New York, Ohio, Pennsylvania, Louisiana, Wisconsin, Texas, Wyoming, Maryland, Washington DC, and Iowa [6, 8, 21–23, 33, 91]. The

Table 2 Natural exposures of wild and zoo members of the order Carnivora to West Nile virus

Common name	Scientific name	Detection type	Location	Reference
Striped skunk	*Mephitis mephitis*	Not specified	CT, USA	[63]
		Antibodies	WY, USA	[6]
Raccoon	*Procyon lotor*	Antibodies	PA, USA	[91]
		Antibodies	WI, USA	[22]
		Antibodies	LA, USA	[21]
		Antibodies	LA, WY, USA	[6]
		Antibodies	MD, D of C, USA	[33]
		Antibodies	WI, USA	[23]
		Antibodies	IA, USA	[8]
		Not reported	NY, USA	[68]
Red panda	*Ailurus fulgens*	Antibodies	NY, USA	[61]*
Brown bear	*Ursus arctos*	Antibodies	Multiple, Croatia	[62]
American black bear	*Ursus americanus*	Antibodies	NJ, USA	[27]
Polar bear	*Ursus maritimus*	Antibodies, Viral RNA	Toronto, Canada	[26]*
Wolf	*Canis* sp.	IHC, Viral RNA	IL, USA	[60]*
	Canis lupus	IHC, Viral RNA	Québec, Canada	[57]*
Red fox	*Vulpes vulpes*	Antibodies	WI, USA	[22]
Coyote	*Canis latrans*	Antibodies	Yucatan State, Mexico	[29]*
		Antibodies	WI, USA	[22]
		Antibodies	WI, USA	[23]
Jaguar	*Panthera onca*	Antibodies	Yucatan State, Mexico	[29]*
Snow leopard	*Uncia uncia*[a]	Antibodies	NY, USA	[61]*
Cougar	*Puma concolor*[b]	Antibodies	US (not specified)	[48]*
Tiger	*Panthera tigris*[b]	Antibodies	US (not specified)	[48]*
Lion	*Panthera leo*[b]	Antibodies	US (not specified)	[48]*
Civet	Not reported	Antibodies	Ethiopia	[3]
Harbor seal	*Phoca vitulina*	Not reported	NJ, USA	[85]*

* = animal living in a zoo or captive outdoor animal facility

[a] Reported in original paper as *Panthera uncia*

[b] Scientific names were not listed in the original document. These names are assumed to be correct based on the common names listed in the original document. Blood samples were collected from private collections

peridomestic nature of this species in some situations may make it a useful species for monitoring WNV activity.

Other carnivores

Antibodies to WNV have been detected in an unidentified civet from Ethiopia [3]. This appears to be one of the first published accounts of WNV exposure in a wild carnivore.

WNV in other wild mammalian species

Several additional wild mammalian species have shown evidence of WNV exposure. Some of these represent a single example or a few examples of exposures in a particular taxonomic group. A summary of natural WNV exposures in these species is presented in Tables 3, 4, 5.

Chiropterans

Reports of WNV infections in chiropterans have been widely documented in the New and Old Worlds. Evidence of WNV exposure has been reported in big brown bats (*Eptesicus fuscus*) from New York and Illinois [11, 55, 63], in the little brown myotis (*Myotis lucifugus*) in New York, Maryland, and New Jersey [33, 55, 63, 81], a northern myotis (*Myotis septentrionalis*) sampled in New Jersey [81], and in Mexican free-tailed bats (*Tadarida brasiliensis*) collected in Louisiana [20]. In the Old World, antibodies were detected in Egyptian rousettes (*Rousettus aegyptiacus*) from Israel and Uganda [2, 101], unidentified rousette(s) (*Rousettus* sp.) from central Africa [16], malagasy flying foxes (*Pteropus rufus*) from Madagascar [30], Angolan soft-furred fruit bats (*Lissonycteris angolensis*) collected in Kenya [101], dusky pipistrelles (*Pipistrellus hesperidus*) from Tunisia [13], and unidentified free-tailed bats (*Tadarida* sp.) from central Africa [16]. Antibodies to WNV were described from three additional bat species in Uganda, which included little free-tailed bats (*Chaerephon pumilus*), Angola free-tailed bats (*Mops condylurus*), and a single African straw-colored fruit bat (*Eidolon helvum*) [98, 101]. Further, WNV was isolated from a Leschenault's rousette (*Rousettus leschenaultii*) in India [79]. Additional WNV exposure accounts comes from unidentified "bats"

Table 3 Natural exposures of bats to West Nile virus

Common name	Scientific name	Detection type	Location	Reference
Big brown bat	*Eptesicus fuscus*	Not specified	NY, USA	[55, 63]
		Antibodies	IL, USA	[11]
Little brown myotis	*Myotis lucifugus*	Not specified	NY, USA	[55, 63]
		Antibodies	MD, USA	[33]
		Antibodies	NJ, USA	[81]
Northern myotis	*Myotis septentrionalis*	Antibodies	NJ, USA	[81]
Mexican free-tailed bat	*Tadarida brasiliensis*	Antibodies	LA, USA	[20]
Unidentified free-tailed bat	*Tadarida* sp.	Antibodies	Central Africa	[16]
Egyptian rousette	*Rousettus aegyptiacus*[a]	Antibodies	Israel	[2]
		Antibodies	Uganda	[101]
Leschenault's rousette	*Rousettus leschenaultii*[b]	Virus	India	[79]
Unidentified rousette	*Rousettus* sp.	Antibodies	Central Africa	[16]
Malagasy flying fox	*Pteropus rufus*	Antibodies	Madagascar	[30]
Little free-tailed bat	*Chaerephon pumilus*[c]	Antibodies	Uganda	[98]
Angola free-tailed bat	*Mops condylurus*[c]	Antibodies	Uganda	[98]
African straw-colored fruit bat	*Eidolon helvum*	Antibodies	Uganda	[98, 101]
Angolan soft-furred fruit bat	*Lissonycteris angolensis*	Antibodies	Kenya	[101]
Dusky pipistrelle	*Pipistrellus hesperidus*[d]	Antibodies	Tunisia	[13]
"Bat"	Not reported	Antibodies	Egypt	[106]
		Not reported	WI, USA	[70]
		Virus	India	[46]
		Antibodies	Egypt	[46]
		Antibodies	Ethiopia	[3]
		Antibodies	Central Africa	[16]
		Not reported	NY, USA	[68]

[a] Reported in original paper as *Russettus aegypticus* [2]

[b] Reported in original paper as *Rousettus leschenaulti*

[c] Reported in original paper as *Tadarida pumila* and *Tadarida condylura*

[d] Reported in original paper as *Pipistrellus kuhli*. *Mammal Species of the World* [112] indicates that *Pipistrellus kuhlii* does not include African populations and is referred to as *hesperidus*. The same reference also indicates that there has been some discussion about the correct spelling of *kuhlii* [112]

in New York, Wisconsin, India, Egypt, central Africa, and Ethiopia [3, 16, 46, 68, 70, 106]. The antibody detection in four of 48 unidentified bats from Egypt [106] appears to be one of the first published accounts of WNV exposure in a wild mammal.

Soricomorphs

The literature on WNV in soricomorphs is scant. However, antibodies were detected in Asian house shrews (*Suncus murinus*) from India [47], white-toothed house shrews (*Crocidura russula*) in Spain [14], and a Zaphir's shrew (*Crocidura zaphiri*) in Ethiopia [3]. Several African giant shrews (*Crocidura olivieri*), described in the original paper as *C. occidentalis*, had antibodies reactive with WNV; however, sera were generally insufficient to conduct confirmatory tests on this species [43]. Additional accounts of WNV antibodies in unidentified shrews (*Crocidura* sp.) were described in central Africa [16]. Antibodies reactive with WNV in a non-shrew member of the order Soricomorpha, the Roman mole (*Talpa romana*), have been reported from Italy [59]. Other workers have unsuccessfully attempted to detect WNV antibodies in shrew sera from the New World [91].

Lagomorphs

Detections of WNV antibodies have been published for lagomorph species, primarily in the Old World, with detections occurring in European rabbits (*Oryctolagus cuniculus*) in France [58] and presumably in Austria (e.g., *Oryctolagus* sp.) [102]. WNV antibodies have been reported in European hares (*Lepus syriacus*), presumably now considered to be *Lepus europaeus*, from Israel [2] and from the Czech Republic [44, 45]. An unidentified rabbit and hare yielded evidence of WNV antibodies in Greece [54], and WNV infections were confirmed in three unidentified rabbits from New York [68]. In addition, a black-tailed jackrabbit (*Lepus californicus*) in California tested positive for WNV [76].

Artiodactylids

West Nile virus activity has been detected in a variety of artiodactylids. In the U.S., WNV exposures have been reported in white-tailed deer (*Odocoileus virginianus*) in many regions, with antibodies detected in New Jersey and Iowa [28, 95], and viral RNA detected in Georgia from a three-year-old male with a history of signs of disease, such

Table 4 Natural exposures of nonhuman primates to West Nile virus

Common name	Scientific name	Detection type	Location	Reference
Ring-tailed lemur	*Lemur catta*	Antibodies	NY, USA	[61]*
		Antibodies	Madagascar	[30, 104]
Milne-Edward's sportive lemur	*Lepilemur edwardsi*	Antibodies	Madagascar	[30, 89]
Brown lemur	*Eulemur fulvus*[a]	Antibodies	Madagascar	[30]
Weasel lemur	*Lepilemur mustelinus*[b]	Antibodies	Madagascar	[30]
Verreaux's sifaka	*Propithecus verreauxi*	Antibodies	Madagascar	[30]
Coquerel's sifaka	*Propithecus coquereli*	Antibodies	Madagascar	[17]
Barbary macaque	*Macaca sylvanus*	Virus isolation, viral RNA, antibodies	Toronto, Canada	[74]*
Baboon	Papio cynocephalus anubis[c]	Antibodies	Toronto, Canada	[74]*
	Papio spp.	Antibodies	LA, USA	[87]*
Japanese macaque	Macaca fuscata	Antibodies	Toronto, Canada	[74]*
Rhesus monkey	*Macaca mulatta*	Antibodies	LA, USA	[87]*
Southern pig-tailed macaque	*Macaca nemestrina*	Antibodies	LA, USA	[87]*
		Antibodies	LA, USA	[42]*
Common chimpanzee	*Pan troglodytes*	Antibodies	Congo	[75]
		Antibodies	Central Africa	[16]**
Unidentified monkey	*Cercopithecus* sp.	Antibodies	South Africa	[46]
		Antibodies	Central Africa	[16]**
Greater spot-nosed monkey	*Cercopithecus nictitans*	Antibodies	Central Africa	[16]
Patas monkey	*Erythrocebus patas*	Antibodies	Central Africa	[16]**
Sooty mangabey	*Cercocebus atys*	Antibodies	GA, USA	[18]*
Unknown mangabey	*Cercocebus* sp.	Antibodies	Central Africa	[16]**
Potto	*Perodicticus potto*	Antibodies	Central Africa	[16]
Prince Demidoff's bushbaby	*Galago demidoff*[d]	Antibodies	Central Africa	[16]

* = animal living in a zoo or captive outdoor animal facility

** = assumed to be captive but translation/article is unclear

[a] Reported in original paper as *Lemur fulvus*

[b] Reported in original paper as *Lepilemur mustellinus*

[c] Listed in original paper as olive baboons (*Papio cynocephalus anubis*). *Mammal Species of the World* [112] recognizes the olive baboon (*Papio anubis*) and the yellow baboon (*Papio cynocephalus*) as different species

[d] Reported in original paper as *Galago demidoffi*

as ataxia and tremors [67]. Thus, deer have been proposed as a useful serosurveillance animal for monitoring WNV activity [95]. A greater number of artiodactylid species with WNV exposures have been reported from the Old World. For example, WNV antibodies have been detected in European roe (*Capreolus capreolus*), fallow deer (*Dama dama*), red deer (*Cervus elaphus*), and red sheep (*Ovis aries*) hunted in Moravia, Czech Republic [44, 45]. In addition, a dated account of antibodies in an unidentified "antelope" in central Africa was published over four decades ago [16].

Antibodies have been detected in wild boar/feral swine (*Sus scrofa*) in both hemispheres. These exposures were documented in Florida, Georgia, and Texas in the U.S. [32], and in Moravia in the Czech Republic [36, 44, 45].

Perrissodactylaids

Antibodies to WNV have been detected in sera from feral horses (*Equus caballus*) from Nevada during the last decade, with nearly 1,400 horses sampled during the multi-year study period [31]. A single animal was antibody positive during 2004, but none were positive during 2005-2006 [31]. This trend changed during the latter part of the decade of collection, as during 2008 and 2009, antibody prevalence rates were 19 and 7.2 %, respectively [31].

Nonhuman primates

Published accounts of wild nonhuman primate exposures to WNV are uncommon and have been primarily associated with Madagascar. Antibodies were detected in a Milne-Edward's

Table 5 Natural exposures of other wild and zoo mammals to West Nile virus

Common name	Scientific name	Detection type	Location	Reference
Asian house shrew	*Suncus murinus*	Antibodies	India	[47]
Greater white-toothed shrew	*Crocidura russula*	Antibodies	Spain	[14]
Zaphir's shrew	*Crocidura zaphiri*	Antibodies	Ethiopia	[3]
African giant shrew	*Crocidura olivieri*[a]	Antibodies[b]	Kenya	[43]
Unidentified shrew	*Crocidura* sp.	Antibodies	Central Africa	[16]
Roman mole	*Talpa romana*	Antibodies	Italy	[59]
White-tailed deer	*Odocoileus virginianus*	Antibodies	NJ, USA	[28]
		Antibodies	IA, USA	[77]*
		Viral RNA	GA, USA	[67]
		Antibodies	IA, USA	[95]
European roe	*Capreolus capreolus*	Antibodies	Moravia, Czech Republic	[44]
		Antibodies	Moravia, Czech Republic	[45]
Fallow deer	*Dama dama*	Antibodies	Moravia, Czech Republic	[44]
		Antibodies	Moravia, Czech Republic	[45]
Red deer	*Cervus elaphus*	Antibodies	Moravia, Czech Republic	[45]
Reindeer	*Rangifer tarandus*	IHC, Viral RNA, antibodies	IA, USA	[77]*
Unidentified antelope	Not reproted	Antibodies	Central Africa	[16]
Mountain goat	*Oreamnos americanus*	Multiple	NE, WY, USA	[86]*
Red sheep	*Ovis aries*[c]	Antibodies	Moravia, Czech Republic	[45]
Feral horse	*Equus caballus*	Antibodies	NV, USA	[31]
Indian rhinoceros	*Rhinoceros unicornis*	Antibodies	NY, USA	[61]*
Asian elephant	*Elephas maximus*	Antibodies	NY, USA	[61]*
		Antibodies[d]	FL, USA	[48]*
Unidentified hyrax	*Dendrohyrax* sp.	Antibodies	Central Africa	[16]
European rabbit	*Oryctolagus cuniculus*	Antibodies	France	[58]
Presumably as above	*Oryctolagus* sp.	Antibodies	Austria	[102]
"Rabbit"[e]	Not reported	Antibodies	Greece	[54]
		Not reported	NY, USA	[68]
European hare	*Lepus europaeus*[f]	Antibodies	Israel	[2]
"Hare"[e]	Not reported	Antibodies	Moravia, Czech Republic	[44]
		Antibodies	Moravia, Czech Republic	[45]
		Antibodies	Greece	[54]
Black-tailed jackrabbit	*Lepus californicus*	Not reported	CA, USA	[76]
Wild boar/feral swine	*Sus scrofa*	Antibodies	Moravia, Czech Republic	[44]
		Antibodies	Moravia, Czech Republic	[45]
		Antibodies	South Moravia	[36]
		Antibodies	FL, GA, TX, USA	[32]
Buru babirusa	*Babyrousa babyrussa*[g]	Antibodies	NY, USA	[61]*
Killer whale	*Orcinus orca*	Viral RNA	TX, USA	[105]*
Bottlenose dolphin	*Tursiops truncatus*	Antibodies	FL, USA	[97]

Table 5 continued

Common name	Scientific name	Detection type	Location	Reference
Virginia opossum	*Didelphis virginiana*	Antibodies	NY, OH, PA, USA	[91]
		Antibodies	WI, USA	[22]
		Antibodies	LA, USA	[21]
		Antibodies	LA, TX, WY, USA	[6]
		Antibodies	MD, D of C, USA	[33]
		Antibodies	WI, USA	[23]
		Antibodies	IA, USA	[8]

* = animal living in a zoo or captive outdoor animal facility

[a] The original paper indicates this animal is the white toothed shrew (*Crocidura occidentalis*). However, *Mammal Species of the World* [112] suggests that this is a synonym of the African giant shrew (*Crocidura olivieri*)

[b] Sera were generally insufficient to conduct confirmatory tests

[c] Reported in original paper as mouflon (*Ovis musimon*)

[d] Scientific names were not listed in the original document. This name is assumed to be correct based on the common names given in the original document. Blood samples were collected from captive collections in Florida

[e] It is unclear from the reference if these animals were captive or wild

[f] Reported in original paper as *Lepus syriacus*

[g] Reported in original paper as *Babyrousa babyrousa*

sportive lemur (*Lepilemur edwardsi*) in Madagascar [30, 89]. In addition, a high percentage of ring-tailed lemurs (*Lemur catta*) were antibody positive in a more recent study in Madagascar, with 94-100 % of animals testing positive by two different assays [104]. In contrast, in an earlier account from Madagascar in which 377 individual lemurs and sifakas from multiple species, including the ring-tailed lemur, were tested, an overall antibody prevalence of approximately 1.9 % was found [30]. Thus, antibodies have also been detected in the weasel lemur (*Lepilemur mustelinus*), brown lemur (*Eulemur fulvus*), and Verreaux's sifaka (*Propithecus verreauxi*), all at very low prevalence levels [30]. Several older accounts of seropositive nonhuman primates have included common chimpanzees (*Pan troglodytes*), unidentified monkeys (*Cercopithecus* sp.), Prince Demidoff's bushbaby (*Galago demidoff*), the potto (*Perodicticus potto*), and the greater spot-nosed monkey (*Cercopithecus nictitans*) from the African continent [16, 46, 75], with antibody prevalence rates of up to 51 % reported for chimpanzees [75].

Hyracoidea

Antibodies reactive with WNV were detected in an unidentified hyrax (*Dendrohyrax* sp.) from central Africa [16].

WNV in wildlife in captive situations

Exposures of mammalian wildlife to WNV in captive situations have been reported on multiple occasions. Primarily, these exposures have been described from New York, Louisiana, Canada, and Mexico, but a few additional exposures have been reported elsewhere, with some interesting cases reported from some marine zoological parks. Data pertaining to WNV associations with captive wildlife are summarized in Tables 2, 4 and 5 (denoted by "*").

New York

Following the 1999 introduction of WNV into the New World, potential WNV activity was noted in the animal collection of the Bronx Zoo/Wildlife Conservation Park as early as August 1999 [61]. A subsequent serosurvey of the animals in the park led to the detection of WNV antibodies in multiple mammals, such as a buru babirusa (*Babyrousa babyrussa*), an Indian rhinoceros (*Rhinoceros unicornis*), two ring-tailed lemurs, two Asian elephants (*Elephas maximus*), two snow leopards (*Uncia uncia*), and a red panda (*Ailurus fulgens*) [61]. The authors suggested that the much higher seroprevalence that they observed in birds, as compared to mammals, was likely related to vector host preferences [61].

Nonhuman primates in the U.S. and Canada

Following a human epidemic of WNV in southern Louisiana, 1,692 serum samples were tested from nonhuman primates housed in an outdoor breeding facility [87]. Antibodies were detected in baboons (*Papio* spp.), rhesus monkeys (*Macaca mulatta)*, and southern pig-tailed macaques (*Macaca nemestrina*), with prevalence rates of

51.4, 39.4, and 20.3 %, respectively [87]. Of interest, antibodies to WNV have been determined to persist in southern pig-tailed macaques for up to 36 months [42]. Additional antibody detections were reported in sooty mangabeys (*Cercocebus atys*) from a nonhuman primate facility in Georgia at a low seroprevalence rate of 6.6 % [18]. None of the 45 rhesus monkeys tested from the same Georgia facility had WNV antibodies [18]. At the Toronto Zoo in Toronto, Canada, a neurologically ill barbary macaque (*Macaca sylvanus*) was diagnosed with a WNV infection [74]. Subsequently, thirty-three nonhuman primates from the zoo were tested for WNV antibodies, with one of seven baboons (*Papio cynocephalus anubis*), two of 16 Japanese macaques (*Macaca fuscata*), and zero of 10 additional barbary macaques testing positive by at least one assay [74].

Anecdotal reports of other captive wildlife

Infections and/or exposures of WNV have been reported from a variety of other captive wildlife from multiple regions of North America. For example, WNV was detected in mountain goats (*Oreamnos americanus*) from Nebraska and Wyoming, which presumably died from their infections [86]. Severe morbidity and a fatal WNV infection in reindeer (*Rangifer tarandus*) have been reported from a captive facility in Iowa [77], and a fatal WNV infection associated with encephalitis and myocarditis was detected in a three-month-old wolf pup (*Canis* sp.), presumably *Canis lupus*, from a private collection in Illinois [60]. An additional case of WNV in a wolf (*C. lupus*), associated with severe renal lymphoplasmacytic vasculitis, was described from a four-month-old captive pup in Québec [57]. Antibodies to WNV were detected from an asymptomatic coyote and a jaguar (*Panthera onca*) from the Meridia Zoo, Yucatan State, Mexico [29]. Additional accounts of WNV antibodies have been reported from captive big cats of the genus *Panthera* and a cougar (*Puma concolor*), all of which were apparently exhibited animals moved to various regions of the U.S., and from elephants associated with captive collections in Florida [48]. A few additional WNV exposures have been described in presumably captive non-human primates from central Africa, with antibody detections in a mangabey (*Cercocebus* sp.), a patas monkey (*Erythrocebus patas*), an unidentified monkey (*Cercopithecus* sp.), and a common chimpanzee (*Pan troglodytes*) [16]. These animals, along with others tested in this reference, often yielded antibodies to multiple viruses tested in a single individual. As such, cross-reactivity may be present in some of these results.

Infections with WNV have not been limited to terrestrial mammals, as WNV infections have been documented in both pinnipeds and cetaceans. For example, following a 10-day illness, a 12-year-old harbor seal (*Phoca vitulina*) died from a WNV infection at a New Jersey State Aquarium [85]. In addition, a WNV infection associated with nonsuppurative encephalitis was confirmed through RT-PCR and sequencing in a killer whale (*Orcinus orca*) from a marine park in Texas [105]. A small percentage of > 100 wild-caught bottlenose dolphins (*Tursiops truncatus*) from the Indian River Lagoon in Florida tested positive for WNV antibodies [97]. Additional marine mammal infections have presumably been reported for harbor seals and monk seals (*Monachus schauinslandi*) in conference proceedings, which have been reviewed elsewhere [48].

Experimental infections

Relatively few experimental infection studies have been conducted on non-domesticated mammals since the discovery of WNV. Some of the recent studies were likely motivated by seroprevalence rates and disease observed in select mammalian species (e.g., *Sciurus* spp.), while others were likely motivated by the potential risks to human health stemming from the synanthropic nature of select mammals. These studies have provided valuable information associated with the potential role of wild mammals in the ecology of WNV.

Which wild mammal species, if any, have the potential for reservoir competence for WNV and which species possess the natural history attributes and behavioral ecology to be commonly exposed to natural vectors of this virus are important questions. It has been suggested that viremia of approximately $10^{5.0}$ pfu/mL is sufficient to infect select mosquito species and subsequently make a vertebrate reservoir competent [51]. However, lower-level viremia has been suggested to be sufficient for infecting some mosquito species at low efficiency [4]. As such, some authors have indicated a range of competence for avian species, with 10^2 to 10^5, 10^5 to 10^8, and 10^9 to 10^{12} pfu/mL of serum representing a low or absent, moderate, and high competence level, respectively [9]. A similar range of competence may be applicable to mammals. At present, no mammals have been determined to develop viremia sufficient to warrant their inclusion in the high competence level (Table 6). However, a limited number of species have been assessed to belong to the moderate competence level, while many have been assessed to be incompetent (Table 6).

Tree squirrels

The average peak viremia from all published experimental infections with fox squirrels is approximatley$10^{5.7}$ pfu/mL (Table 6). In addition, a much higher viremia ($10^{8.0}$ pfu/mL)

Table 6 Experimental infections of wild mammals with West Nile virus

Common name	Scientific name	Exposure method	Maximum viremia	Reference
Fox squirrel	*Sciurus niger*	Subcutaneous inoculation	$10^{4.98}$ pfu/mL	[92]
Fox squirrel	*Sciurus niger*	Intramuscular inoculation	$10^{6.1}$ pfu/mL	[83]
		Mosquito bite	$10^{5.3}$ pfu/mL	
Fox squirrel	*Sciurus niger*	Oral exposure	$10^{5.6}$ pfu/mL	[109]
Eastern grey squirrel	*Sciurus carolinensis*	Subcutaneous inoculation	$10^{5.5}$ pfu/mL	[34]
Eastern chipmunk	*Tamias striatus*	Intramuscular inoculation	$10^{7.8}$ pfu/mL	[82]
Eastern cottontail	*Sylvilagus floridanus*	Subcutaneous inoculation	$10^{5.8}$ CID_{50}s/mL[a]	[108]
		Mosquito bite		
"Gerbil"	Not reported	Not reported	Not reported	[46]
Not reported	*Arvicanthis* sp.	Not reported	Not reported	[46]
African white-tailed rat	*Mystromys albicaudatus*	Intracardiac/Intraperitoneal inoculation	None detected	[64]
African arvicanthis	*Arvicanthis niloticus*	Intracardiac/Intraperitoneal inoculation	None detected	[64]
Natal mastomys	*Mastomys natalensis*	Intracardiac/Intraperitoneal inoculation	None detected	[64]
Red veld aethomys	*Aethomys chrysophilus*	Intracardiac/Intraperitoneal inoculation	$10^{1.5}$ (mouse innoc.)	[64]
Southern African vlei rat	*Otomys irroratus*	Intracardiac/Intraperitoneal inoculation	None detected	[64]
Xeric four-striped grass rat	*Rhabdomys pumilio*	Intracardiac/Intraperitoneal inoculation	None detected	[64]
Raccoon	*Procyon lotor*	Subcutaneous inoculation	$10^{4.6}$ pfu/mL	[94]
Rhesus monkey	*Macaca mulatta*	Subcutaneous/intrathalamical inoculations	$10^{3.8}$ LD_{50}/mL	[84]
		Intradermal inoculation	$\leq$100 $TCID_{50}$/mL	[88]
		Intracerebral, intranasal, and intravenous inoculations[a]	Not reported	[103][b]
		Subcutaneous inoculation	$10^{2.0}$/0.02 ml serum (mouse innoc).	[40]
		Subcutaneous and intravenous inoculation	No live virus recovered[c]	[111]
Crab-eating macaque	*Macaca fascicularis*	Subcutaneous inoculation	No live virus recovered[c]	[111]
Bonnet macaque	*Macaca radiata*	Intranasal inoculation	"Low grade"	[35]
Lemur[d]	*Eulemur* spp.	Subcutaneous inoculation	$10^{3.0}$ LD_{50}/mL	[90]
Hamadryas baboon	*Papio hamadryas*	Intradermal inoculation	10^5–10^6 copies/mL[e]	[113]
Grivet	*Chlorocebus aethiops*[f]	Intracerebral inoculation	Not reported	[103]
"Monkey"	Not reported	Aerosol	Not reported	[46]
Big brown bat	*Eptesicus fuscus*	Subcutaneous inoculation	180 pfu/mL	[20]
Mexican free-tailed bat	*Tadarida brasiliensis*	Subcutaneous inoculation	None detected	[20]
African straw-colored fruit bat	*Eidolon helvum*	Intraperitoneal inoculation	None detected	[100]
Egyptian rousette	*Rousettus aegyptiacus*	Intraperitoneal inoculation	Trace	[100]
"Hedgehog"	Not reported	Intracerebral inoculation	Not reported	[103]

[a] It is unclear if this titer is associated with a subcutaneous inoculation or mosquito bite

[b] Note: Animals were reported as "rhesus monkeys" in the original article with no corresponding scientific name. Therefore, these animals are assumed to represent *Macaca mulatta*

[c] No live virus recovered, but PCR-based viremia described as "discrete and short-lived" in *M. mulatta* and undetectable in two *M. fascicularis* that developed fever. *M. fascicularis* were themectomized and/or CD8 T-cell depleted

[d] Note: Reported as *Lemur fulvus fulvus* and *L. fulvus albifrons* in original paper. These are now likely represented by *Eulemur fulvus* and *E. albifrons*. However, no distinction is made in the original paper as to which species was experimentally infected with WNV

[e] Viremia range reported by authors is based on quantitative real-time PCR assay

[f] Reported as African monkey (*Cercopithecus ethiops centralis*) in original paper. *Mammal Species of the World* [112] suggests that *Chlorocebus aethiops* has been used a synonym of *Cercopithecus aethiops*

has been detected in a naturally infected fox squirrel [76]. An experimental infection study has also been conducted on eastern grey squirrels, with a maximum viremia detected of $10^{5.5}$ pfu/mL [34]. High seroprevalence rates have also been reported for these two squirrel species, with overall seroprevalence from multiple states and study sites of nearly 50 % [91]. Thus, these tree squirrel species are commonly exposed to WNV and develop viremia of a moderate level of competence that is sufficient for infecting some mosquito vectors. In addition, based on the detection of viral RNA in select tissues long after the clearance of viremia (e.g., 29 DPI), fox squirrels have been suggested as having the potential to be persistently infected [83].

Eastern chipmunks

Experimentally infected eastern chipmunks yielded moderately high viremia, with up to $10^{7.8}$ pfu/mL detected [82]. However, a lower seroprevalence rate was noted when eastern chipmunks were compared to other mammalian species tested from Maryland [33]. In addition, no antibody-positive eastern chipmunks were detected in three states where this species was sampled, even though these animals were sympatric with antibody-positive tree squirrels [91]. This low seroprevalence suggests that eastern chipmunks may develop fatal WNV infections or are not commonly exposed to appropriate mosquito vectors [33]. During experimental infections, no signs of illness were observed in any chipmunk during 1-8 DPI; however, potential signs of WNV disease were observed during 9-11 DPI, with neurologic symptoms and lethargy as the most common signs of disease observed [82]. Most of these animals were euthanized for humane reasons prior to death so the lethality of WNV infection was not determined with certainty. However, the severity of the disease described [82], along with the additive effects of predation avoidance and the need to forage suggest that WNV infection can certainly be lethal for eastern chipmunks. This may represent a reason why chipmunks have been uncommonly reported as antibody positive in the literature [33].

Eastern cottontails

Eastern cottontails (*Sylvilagus floridanus*) experimentally infected with WNV developed a maximum viremia of $10^{5.8}$ CID_{50}s/mL with no signs of disease detected [108]. The literature on natural WNV infections in rabbits and hares is scant; however, antibodies have been reported from rabbits and hares in Europe and Israel [2, 44, 45, 58]. In addition, a black-tailed jackrabbit was exposed to WNV in U.S. [76], thereby suggesting that leporids are exposed to WNV in both hemispheres of the world. The small number of documented WNV exposures in lagomorphs is surprising, especially if one considers how often several of these species are observed by the general public. However, the lack of disease noted during experimental infection studies [108] suggests that natural infections may go unnoticed by the public. As such, lagomorphs may be exposed to WNV more frequently than has been reported previously.

Baboons

Peak PCR-based viremia titers of 10^5 to 10^6 copies/mL have been reported for baboons (*Papio hamadryas*) at 4 DPI of an experimental infection with WNV [113]. Considering that most reported viremias in nonhuman primates have been low (Table 6), this result is somewhat surprising.

Other species

Other species such as rhesus monkeys, big brown bats, Mexican free-tailed bats, Egyptian rousettes, African straw-colored fruit bats, lemurs (*Eulemur* spp.), and raccoons did not yield significant viremias during experimental infections [20, 84, 88, 90, 94, 100]. Of interest, two of three experimentally infected African straw-colored fruit bats had antibodies in post-inoculation sera with no viremia detected at any time after infection [100]. In addition, one of six African rodent species tested, the red veld aethomys (*Aethomys chrysophilus*), yielded evidence of low-level WNV viremia [64]. Maximum viremias during experimental infections were not reported for several other mammalian species (Table 6). As such, their potential contribution to WNV mosquito cycles is not discussed. With few exceptions, most wild mammals experimentally infected with WNV to date have developed low- (many) or moderate- (few) level viremia.

Conclusions

It is clear that WNV has the potential to infect a great diversity of wild mammalian species in most regions of the world. This review tabulates at least 100 wild mammal species (including those captive in outdoor enclosures) with some evidence of natural exposure, and there are likely several other species exposed to WNV that have not been published or were not discovered during this review. Some species appear to be exposed at much greater frequencies than others, which may involve one or more facets of their behavioral ecology. In addition, these exposures are likely influenced by a diversity of factors, such as age, urbanization, date (e.g., timing within an annual WNV cycle), and vector feeding preferences [33]. In some instances, some mammal species may produce highly localized information associated with WNV activity [76].

The capacity of most wild mammals to be reservoir competent for WNV remains undermined, as this would require many more experimental infection studies or serendipitous viremic wild-caught animals to ascertain. However, studies conducted during the last decade have clearly shown that some mammalian species produce viremia that is sufficient for infecting some mosquito species, although none as of yet have been shown to produce the high-level viremia (e.g., $> 10^8$ pfu/mL) that have been reported for select avian species [51]. However, some recent work suggests that mammals may warrant further scrutiny. First, viremia for fox squirrels and eastern chipmunks has been reported up to 10^8 and $10^{7.8}$ pfu/mL, respectively [76, 82]. Second, a naturally exposed fox squirrel still had a viremia of $10^{5.7}$ pfu/mL three days after a viremia of $10^{8.0}$ pfu/mL, thereby suggesting that this animal maintained a viremia $> 10^{5.0}$ for 4 days [76]. Because experimental infections have only been conducted on a handful of species, it remains to be determined if other wild mammals develop even higher viremia than has been reported previously. Thus far, based on a small number of experimental infections, select members of the rodent family Sciuridae and a single lagomorph species have been the only wild mammalian species yielding strong evidence of having the viremic capacity to make reasonable contributions to WNV mosquito cycles. However, experimental data associated with a recent study on baboons [113] indicate that this species might warrant more attention.

Viral shedding, although less likely than more traditional mechanisms associated with mosquito cycles, may have the potential to perpetuate some WNV activity. For example, positive oral swabs, fecal samples, and/or urine samples have been detected in tree squirrels during experimental infection studies [34, 83, 92]. These observations, along with the demonstration of successful oral WNV transmission in fox squirrels [109] and successful predator-prey transmission in a domestic mammal [4], suggest that viral shedding and other alternative routes of transmission should not be completely discounted as a potential transmission mechanism of this virus among mammals.

The role of persistent WNV infections in the epidemiology of this virus in mammals is undermined. However, some reports suggest that WNV may be present in certain species long after their viremia has cleared. For example, WNV was isolated from urine and oral swabs of fox squirrels up to 17 and 22 DPI, respectively, and WNV RNA was detected in kidney tissue up to 29 DPI [83]. In a second study based on oral exposure of WNV, viral RNA was detected in select tissues (i.e., salivary gland and/or kidney) from multiple squirrels during 65-72 DPI [109]. Virus was detected in select organs of some experimentally infected rhesus macaques > 160 DPI; however, changes in the virus were noted [84]. Others have noted that experimentally infected golden hamsters (*Mesocricetus auratus*) yielded persistent WNV shedding in urine for up to 8 months, during which changes were reported in the virus [107]. Additional studies are warranted to assess any role long-term or persistent infections play in non-traditional WNV cycles [109], as ingestion of virus-laden urine and predator-prey transmission have been speculated as potential transmission scenarios [110]. Notably, predator-prey transmission has been documented in domestic cats fed WNV-infected mice [4], and oral transmission has been reported in a variety of vertebrates [51, 109].

Nonviremic transmission of WNV between mosquitoes has been described from mosquitoes co-feeding on laboratory mice, suggesting that a large number of vertebrates could potentially play a role in mosquito infections [41]. If this commonly occurs in wild mammals in natural settings, many species could play a role in WNV epidemiology.

Due to their potential for site fidelity, non-migratory habits, and ease of observation, select mammals have been proposed as good sentinel animals for WNV in local situations [76, 91]. For example, dead and moribund tree squirrels have been successfully used for WNV surveillance, with the dynamics of WNV infections in tree squirrels reflecting that of dead birds [76]. In addition, serology of mammals can also be used for the surveillance of WNV in certain situations [33, 91, 93, 95].

Disease caused by WNV infection in wild mammals has varied widely, both at the inter- and intraspecific levels. For example, signs of disease were uncommon in experimental infections of tree squirrels [34, 83, 92]; however, WNV-infected tree squirrels with severe disease have been commonly reported in natural settings from multiple regions [39, 50, 76]. The reason for this discrepancy is unclear. However, experimental studies could show varying results from natural infections and from other experimental studies for several reasons. For example, crows (*Corvus brachyrhynchos*) experimentally infected with North American and Old World strains of WNV had higher viremia titers and death rates when infected with the former [10]. In addition, others have noted different responses in birds experimentally infected with Saint Louis encephalitis virus when exposed to a virus of varying doses and passage history [65].

Age may play a role in the severity of infections in some mammal species. For example, many WNV-positive tree squirrels in California were juvenile animals in 2005; however, the authors were unable to assess if young animals were more susceptible to severe WNV infections than adults or if their observation was due to the timing of late litters of young animals [76]. Additional juvenile mammals have been reported with severe disease associated with WNV infection. Of interest, two wolf pups, ages 3 and

4-months-old, succumbed to WNV infection during the last decade [57, 60]. In contrast, severe disease in older mammals has also been reported, as acute neurologic disease associated with WNV infection has been described in a 25-year-old barbary macaque [74]. Overall, data related to age effects of disease associated with WNV infection in nonhuman mammals is inadequate and could be an important topic for future study.

As has been suggested previously, this review indicates that most wild mammals will likely only play a minor role in WNV epidemiology. At present, no mammals have been shown to yield the high-level viremia noted in some avian species. However, the scant number of experimental infection studies that have been conducted to date on wild mammals suggests that this topic has not been rigorously evaluated. As such, more experimental infection studies are warranted in key mammalian species, especially studies pertaining to ubiquitous peridomestic mammals. Based on experimental evidence from the New World, Old World tree squirrels in WNV endemic areas would be an excellent choice for future evaluations of the reservoir competence of wild mammals.

Acknowledgments I thank K. Bentler and R. McLean for excellent reviews of an earlier version of this manuscript, and A. Lavelle for assistance in obtaining literature. The opinions and conclusions of this article are those of the author and do not necessarily represent those of the U.S. Department of Agriculture.

References

1. Abdel-Wahab KS, Imam IZ (1970) Antibodies to arboviruses in rodent sera. J Egypt Public Health Assoc 45:370–375
2. Akov Y, Goldwasser R (1966) Prevalence of antibodies to arboviruses in various animals in Israel. Bull World Health Organ 34:901–909
3. Andral L, Brès P, Sérié C, Casals J, Panthier R (1968) Etudes sur la fièvre jaune en Ethiopie. 3. Etude sérologique et virologique de la faune sylvatique. Bull World Health Organ 38:855–861
4. Austgen LE, Bowen RA, Bunning ML, Davis BS, Mitchell CJ, Chang GJJ (2004) Experimental infection of cats and dogs with West Nile virus. Emerg Infect Dis 10:82–86
5. Bakonyi T, Ivanics É, Erdélyi K, Ursu K, Ferenczi E, Weissenböck H, Nowotny N (2006) Lineage 1 and 2 strains of encephalitic West Nile virus, Central Europe. Emerg Infect Dis 12:618–623
6. Bentler KT, Hall JS, Root JJ, Klenk K, Schmit B, Blackwell BF, Ramey PC, Clark L (2007) Serologic evidence of West Nile virus exposure in North American mesopredators. Am J Trop Med Hyg 76:173–179
7. Blitvich BJ (2008) Transmission dynamics and changing epidemiology of West Nile virus. Anim Health Res Rev 9:71–86
8. Blitvich BJ, Juarez LI, Tucker BJ, Rowley WA, Platt KB (2009) Antibodies to West Nile virus in raccoons and other wild peridomestic mammals in Iowa. J Wildl Dis 45:1163–1168
9. Bowen RA, Nemeth NM (2007) Experimental infections with West Nile virus. Curr Opin Infect Dis 20:293–297
10. Brault AC, Langevin SA, Bowen RA, Panella NA, Biggerstaff BJ, Miller BR, Komar N (2004) Differential virulence of West Nile strains for American crows. Emerg Infect Dis 10:2161–2168
11. Bunde JM, Heske EJ, Mateus-Pinilla NE, Hofmann JE, Novak RJ (2006) A survey for West Nile virus in bats from Illinois. J Wildl Dis 42:455–458
12. Bunning ML, Bowen RA, Bruce Cropp C, Sullivan KG, Davis BS, Komar N, Godsey MS, Baker D, Hettler DL, Holmes DA, Biggerstaff BJ, Mitchell CJ (2002) Experimental infection of horses with West Nile virus. Emerg Infect Dis 8:380–386
13. Chastel C, Rogues G, Beaucournu-Saguez F (1977) Enquête séro-épidémiologique mixte arbovirus-arénavirus chez les petits mammifères de Tunisie. Bull Soc Pathol Exot Filiales 70:471–479
14. Chastel C, Launay H, Rogues G, Beaucournu JC (1980) Infections à arbovirus en Espagne: enquête sérologique chez les petits mammifères. Bull Soc Pathol Exot Filiales 73:384–390
15. Chastel C, Launay H, Bailly Choumara H (1982) Infections à arbovirus au Maroc: sondage sérologique chez les petis mammifères du nord du pays. Bull Soc Pathol Exot Filiales 75:466–475
16. Chippaux-Hyppolite C, Chippaux A (1969) Contribution à l'étude d'un réservoir de virus animal dans le cycle de certains arbovirus en Centrafrique. I. Etude immunologique chez divers animaux domestiques et sauvages. Bull Soc Pathol Exot Filiales 62:1034–1045
17. Clerc Y, Rodhain F, Digoutte JP, Albignac R, Coulanges P (1982) Le programme exploratoire arbovirus de l'Institut Pasteur de Madagascar: bilan 1976–1980. Arch Inst Pasteur Madagascar 49:65–78
18. Cohen JK, Kilpatrick AM, Stroud FC, Paul K, Wolf F, Else JG (2007) Seroprevalence of West Nile virus in nonhuman primates as related to mosquito abundance at two national primate research centers. Comp Med 57:115–119
19. Darwish MA, Hoogstraal H, Roberts TJ, Ahmed IP, Omar F (1983) A sero-epidemiological survey for certain arboviruses (Togaviridae) in Pakistan. Trans R Soc Trop Med Hyg 77:442–445
20. Davis A, Bunning M, Gordy P, Panella N, Blitvich B, Bowen R (2005) Experimental and natural infection of North American bats with West Nile virus. Am J Trop Med Hyg 73:467–469
21. Dietrich G, Montenieri JA, Panella NA, Langevin S, Lasater SE, Klenk K, Kile JC, Komar N (2005) Serologic evidence of West Nile virus infection in free-ranging mammals, Slidell, Louisiana, 2002. Vector Borne Zoonotic Dis 5:288–292
22. Docherty DE, Samuel MD, Nolden CA, Egstad KF, Griffin KM (2006) West Nile virus antibody prevalence in wild mammals, Southern Wisconsin. Emerg Infect Dis 12:1982–1984
23. Docherty DE, Samuel MD, Egstad KF, Griffin KM, Nolden CA, Karwal L, Ip HS (2009) Short report: changes in West Nile virus seroprevalence and antibody titers among Wisconsin mesopredators 2003–2006. Am J Trop Med Hyg 81:177–179
24. Drebot MA, Lindsay R, Barker IK, Buck PA, Fearon M, Hunter F, Sockett P, Artsob H (2003) West Nile virus surveillance and diagnostics: a Canadian perspective. Can J Infect Dis 14:105–114
25. Duca M, Duca E, Buiuc D, Luca V (1989) Studiul seroepidemiologic şi virologic al prezenţei unor arbovirusuri pe teritoriul Moldovei, 1961–1982. Rev Med Chir Soc Med Nat Iasi 93:719–733
26. Dutton CJ, Quinnell M, Lindsay R, Delay J, Barker IK (2009) Paraparesis in a polar bear (*Ursus maritimus*) associated with West Nile virus infection. J Zoo Wildl Med 40:568–571
27. Farajollahi A, Panella NA, Carr P, Crans W, Burguess K, Komar N (2003) Serologic evidence of West Nile virus infection in black bears (*Ursus americanus*) from New Jersey. J Wildl Dis 39:894–896

28. Farajollahi A, Gates R, Crans W, Komar N (2004) Serologic evidence of West Nile virus and St. Louis encephalitis virus infections in white-tailed deer (*Odocoileus virginianus)* from New Jersey, 2001. Vector Borne Zoonotic Dis 4:379–383
29. Farfán-Ale JA, Blitvich BJ, Marlenee NL, Loroño-Pino MA, Puerto-Manzano F, García-Rejón JE, Rosado-Paredes EP, Flores-Flores LF, Ortega-Salazar A, Chávez-Medina J, Cremieux-Grimaldi JC, Correa-Morales F, Hernández-Gaona G, Méndez-Galván JF, Beaty BJ (2006) Antibodies to West Nile virus in asymptomatic mammals, birds, and reptiles in the Yucatan Peninsula of Mexico. Am J Trop Med Hyg 74:908–914
30. Fontenille D, Rodhain F, Digoutte JP, Mathiot C, Morvan J, Coulanges P (1989) Les cycles de transmission du virus West-Nile à Madagascar, Océan Indien. Ann Soc Belg Med Trop 69:233–243
31. Franson JC, Hofmeister EK, Collins GH, Dusek RJ (2011) Short report: Seroprevalence of West Nile virus in feral horses on Sheldon National Wildlife Refuge, Nevada, United States. Am J Trop Med Hyg 84:637–640
32. Gibbs SEJ, Marlenee NL, Romines J, Kavanaugh D, Corn JL, Stallknecht DE (2006) Antibodies to West Nile virus in feral swine from Florida, Georgia, and Texas, USA. Vector Borne Zoonotic Dis 6:261–265
33. Gómez A, Kilpatrick AM, Kramer LD, Dupuis Ii AP, Maffei JG, Goetz SJ, Marra PP, Daszak P, Aguirre AA (2008) Land use and West Nile virus seroprevalence in wild mammals. Emerg Infect Dis 14:962–965
34. Gómez A, Kramer LD, Dupuis Ii AP, Kilpatrick AM, Davis LJ, Jones MJ, Daszak P, Aguirre AA (2008) Experimental infection of eastern gray squirrels (*Sciurus carolinensis*) with West Nile virus. Am J Trop Med Hyg 79:447–451
35. Goverdhan MK, Kulkarni AB, Gupta AK, Tupe CD, Rodrigues JJ (1992) Two-way cross-protection between West Nile and Japanese encephalitis viruses in bonnet macaques. Acta Virol 36:277–283
36. Halouzka J, Juricova Z, Jankova J, Hubalek Z (2008) Serologic survey of wild boars for mosquito-borne viruses in South Moravia (Czech Republic). Vet Med (Praha) 53:266–271
37. Hayes CG, Baqar S, Ahmed T, Chowdhry MA, Reisen WK (1982) West Nile virus in Pakistan. 1. Sero-epidemiological studies in Punjab Province. Trans R Soc Trop Med Hyg 76:431–436
38. Hayes CG (1988) West Nile Fever. In: Monath TP (ed) The Arboviruses: epidemiology and ecology. CRC Press, Boca Raton, pp 59–88
39. Heinz-Taheny KM, Andrews JJ, Kinsel MJ, Pessier AP, Pinkerton ME, Lemberger KY, Novak RJ, Dizikes GJ, Edwards E, Komar N (2004) West Nile virus infection in free-ranging squirrels in Illinois. J Vet Diagn Invest 16:186–190
40. Henderson BE, Cheshire PP, Kirya GB, Lule M (1970) Immunologic studies with yellow fever and selected African group B arboviruses in rhesus and vervet monkeys. Am J Trop Med Hyg 19:110–118
41. Higgs S, Schneider BS, Vanlandingham DL, Klingler KA, Gould EA (2005) Nonviremic transmission of West Nile virus. Proc Natl Acad Sci USA 102:8871–8874
42. Hukkanen RR, Liggitt HD, Kelley ST, Grant R, Anderson DM, Hall RA, Tesh RB, DaRosa APT, Bielefeldt-Ohmann H (2006) West Nile and St. Louis encephalitis virus antibody seroconversion, prevalence, and persistence in naturally infected pig-tailed macaques (*Macaca nemestrina*). Clin Vaccine Immunol 13:711–714
43. Johnson BK, Chanas AC, Shockley P, Squires EJ, Gardner P, Wallace C, Simpson DIH, Bowen ETW, Platt GS, Way H, Parsons J, Grainger WE (1977) Arbovirus isolations from, and serological studies on, wild and domestic vertebrates from Kano Plain, Kenya. Trans R Soc Trop Med Hyg 71:512–517
44. Juřicová Z (1992) Protilátky proti arbovirům u lovné zvěre odchycené na Moravě. Vet Med (Praha) 37:633–636
45. Juřicová Z, Hubálek Z (1999) Serological surveys for arboviruses in the game animals of southern Moravia (Czech Republic). Folia Zool 48:185–189
46. Karabatos N (ed) (1985) International catalogue of arboviruses, including certain other viruses of vertebrates, 3rd edn. American Society of Tropical Medicine and Hygiene, San Antonio
47. Kaul HN, Venkateshan CN, Mishra AC (1976) Serological evidence of arbovirus activity in birds and small mammals in Japanese encephalitis affected areas of Bankura District, West Bengal. Indian J Med Res 64:1735–1739
48. Keller M (2005) Development of a competitive inhibition enzyme-linked immunosorbent assay (CI ELISA) for serosurvey of wildlife species for West Nile virus emphasizing marine mammals. Veterinary Medicine. University of Florida, p 102
49. Kemp GE, Causey OR, Setzer HW, Moore DL (1974) Isolation of viruses from wild mammals in West Africa, 1966–1970. J Wildl Dis 10:279–293
50. Kiupel M, Simmons HA, Fitzgerald SD, Wise A, Sikarskie JG, Cooley TM, Hollamby SR, Maes R (2003) West Nile virus infection in eastern fox squirrels (*Sciurus niger*). Vet Pathol 40:703–707
51. Komar N, Langevin S, Hinten S, Nemeth N, Edwards E, Hettler D, Davis B, Bowen R, Bunning M (2003) Experimental infection of North American birds with the New York 1999 strain of West Nile virus. Emerg Infect Dis 9:311–322
52. Komar N, Clark GG (2006) West Nile virus activity in Latin America and the Caribbean. Rev Panam Salud Publica 19:112–117
53. Konstantinov OK, Diallo SM, Inapogi AP, Ba A, Kamara SK (2006) The mammals of Guinea as reservoirs and carriers of arboviruses. Med Parazitol (Mosk):34–39
54. Koptopoulos G, Papadopoulos O (1980) Zooanthroponoses in Greece. A serological survey for antibodies to the arboviruses of tick-borne encephalitis and West Nile. In: Vesenjak-Hirjan J (ed) Arboviruses in the Mediterranean Countries, Zbl Bakt Suppl 9. Gustav Fischer Verlag, Stuttgart, pp 185–188
55. Kramer LD, Bernard KA (2001) West Nile virus infection in birds and mammals. Ann N Y Acad Sci 951:84–93
56. Kramer LD, Styer LM, Ebel GD (2008) A global perspective on the epidemiology of West Nile virus. Annu Rev Entomol 53:61–81
57. Lanthier I, Hébert M, Tremblay D, Harel J, Dallaire AD, Girard C (2004) Natural West Nile virus infection in a captive juvenile Arctic wolf (*Canis lupus*). J Vet Diagn Invest 16:326–329
58. Le Lay-Rogues G, Arthur CP, Vanderwalle P, Hardy E, Chasterl C (1990) Wild rabbit, *Oryctolagus cuniculus* L., and arboviruses in southeast France. Results of two serologic investigations. Bull Soc Pathol Exot 83:446–457
59. Le Lay Rogues G, Valle M, Chastel C, Beaucournu JC (1983) Petits mammiferes sauvages et arbovirus en Italie. Bull Soc Pathol Exot 76:333–345
60. Lichtensteiger CA, Heinz-Taheny K, Osborne TS, Novak RJ, Lewis BA, Firth ML (2003) West Nile virus encephalitis and myocarditis in wolf and dog. Emerg Infect Dis 9:1303–1306
61. Ludwig GV, Calle PP, Mangiafico JA, Raphael BL, Danner DK, Hile JA, Clippinger TL, Smith JF, Cook RA, McNamara T (2002) An outbreak of West Nile virus in a New York City captive wildlife population. Am J Trop Med Hyg 67:67–75
62. Madić J, Huber D, Lugović B (1993) Serologic survey for selected viral and rickettsial agents of brown bears (*Ursus arctos*) in Croatia. J Wildl Dis 29:572–576

63. Marfin AA, Petersen LR, Eidson M, Miller J, Hadler J, Farello C, Werner B, Campbell GL, Layton M, Smith P, Bresnitz E, Cartter M, Scaletta J, Obiri G, Bunning M, Craven RC, Roehrig JT, Julian KG, Hinten SR, Gubler DJ, Hilger T, Jones JE, Lehman JA, Medlin K, Morris T, Perilla MJ, Sutliff S, Withum D, Sorhage F, Tan C, Beckett G, Gensheimer K, Greenblatt J, Montero J, Galbraith P, Tassler P, DeMaria A, Matyas B, Timperi R, Bandy U, Breslosky T, Andreadis T, McCarthy T, Backenson B, Hagiwara Y, Kramer L, Morse D, Wallace B, White D, Willsey A, Wong S, Cherry B, Fine A, Kellachan J, Kulakasera V, Poshni I, Rankin J, Hathcock L, Wolfe D, Roche J, Jenkins S, Levy M, MacCormack JN, Gibson J, Blake P, Kramer S, Lance-Parker S, Conti L, Hopkins RS, Oliveri R, Lofgren JP, Woernle CH, Currier M, Slavinski S, Kelso K, Rawlings J (2001) Widespread West Nile virus activity, eastern United States, 2000. Emerg Infect Dis 7:730–735
64. McIntosh BM (1961) Susceptibility of some African wild rodents to infection with various arthropod-borne viruses. Trans R Soc Trop Med Hyg 55:63–68
65. McLean RG, Mullenix J, Kerschner J, Hamm J (1983) The house sparrow (*Passer domesticus*) as a sentinel for St. Louis encephalitis virus. Am J Trop Med Hyg 32:1120–1129
66. McLean RG, Ubico SR, Bourne D, Komar N (2002) West Nile virus in livestock and wildlife. Curr Top Microbiol Immunol 267:271–308
67. Miller DL, Radi ZA, Baldwin C, Ingram D (2005) Fatal West Nile virus infection in a white-tailed deer (*Odocoileus virginianus*). J Wildl Dis 41:246–249
68. MMWR (2000) Update: West Nile Virus Activity—Eastern United States, 2000. Morb Mortal Wkly Rep 49:1044–1047
69. MMWR (2002) Provisional surveillance summary of the West Nile virus epidemic—United States, January–November 2002. Morb Mortal Wkly Rep 51:1129–1133
70. MMWR (2004) West Nile Virus Activity—United States, November 3–8, 2004. Morb Mortal Wkly Rep 53:1050–1051
71. MMWR (2006) West Nile Virus Activity—United States, January 1–August 15, 2006. Morb Mortal Wkly Rep 55:879–880
72. Molnár E, Gresíková M, Kubásova T, Kubinyi L, Szabó JB (1973) Arboviruses in Hungary. J Hyg Epidemiol Microbiol Immunol 17:1–10
73. Molnár E, Gulyás MS, Kubinyi L, Nosek J, Kozuch O, Ernek E, Labuda M, Grulich I (1976) Studies on the occurrence of tick-borne encephalitis in Hungary. Acta Vet Acad Sci Hung 26:419–437
74. Ølberg RA, Barker IK, Crawshaw GJ, Bertelsen MF, Drebot MA, Andonova M (2004) West Nile virus encephalitis in a barbary macaque (*Macaca sylvanus*). Emerg Infect Dis 10:712–714
75. Osterrieth PM, Deleplanque-Liegeois P (1961) Presence d' anticorps vis ∼ a∼vis des virus transmis par arthropodes chez le chimpanze (*Pan troglodites*). Comparaison de leur etat immunitaire a celui de l'homme. Ann Soc Belg Med Trop 1:63–72
76. Padgett KA, Reisen WK, Kahl-Purcell N, Fang Y, Cahoon-Young B, Carney R, Anderson N, Zucca L, Woods L, Husted S, Kramer VL (2007) West Nile virus infection in tree squirrels (Rodentia: Sciuridae) in California, 2004–2005. Am J Trop Med Hyg 76:810–813
77. Palmer MV, Stoffregen WC, Rogers DG, Hamir AN, Richt JA, Pedersen DD, Waters WR (2004) West Nile virus infection in reindeer (*Rangifer tarandus*). J Vet Diagn Invest 16:219–222
78. Papa A, Bakonyi T, Xanthopoulou K, Vázquez A, Tenorio A, Nowotny N (2011) Genetic characterization of West Nile virus lineage 2, Greece, 2010. Emerg Infect Dis 17:920–922
79. Paul SD, Rajagopalan PK, Sreenivasan MA (1970) Isolation of the West Nile virus from the frugivorous bat, *Rousettus leschenaulti*. Indian J Med Res 58:1169–1171
80. Petersen LR, Roehrig JT (2001) West Nile virus: a reemerging global pathogen. Emerg Infect Dis 7:611–614
81. Pilipski JD, Pilipski LM, Risley LS (2004) West Nile virus antibodies in bats from New Jersey and New York. J Wildl Dis 40:335–337
82. Platt KB, Tucker BJ, Halbur PG, Tiawsirisup S, Blitvich BJ, Fabiosa FG, Bartholomay LC, Rowley WA (2007) West Nile virus viremia in eastern chipmunks (*Tamias striatus*) sufficient for infecting different mosquitoes. Emerg Infect Dis 13:831–837
83. Platt KB, Tucker BJ, Halbur PG, Blitvich BJ, Fabiosa FG, Mullin K, Parikh GR, Kitikoon P, Bartholomay LC, Rowley WA (2008) Fox squirrels (*Sciurus niger*) develop West Nile virus viremias sufficient for infecting select mosquito species. Vector Borne Zoonotic Dis 8:225–233
84. Pogodina VV, Frolova MP, Malenko GV (1983) Study on West Nile virus persistence in monkeys. Arch Virol 75:71–86
85. ProMED-mail (2002) West Nile virus update 2002-USA (28). ProMED-mail Archive number 20021031.5674
86. ProMED-mail (2002) West Nile virus, Caprine and Ovine-USA (NE) (04). ProMED-mail Archive number 20020920.5368
87. Ratterree MS, Travassos da Rosa APA, Bohm RP Jr, Cogswell FB, Phillippi KM, Caillouet K, Schwanberger S, Shope RE, Tesh RB (2003) West Nile virus infection in nonhuman primate breeding colony, concurrent with human epidemic, southern Louisiana. Emerg Infect Dis 9:1388–1394
88. Ratterree MS, Gutierrez RA, Travassos Da Rosa APA, Dille BJ, Beasley DWC, Bohm RP, Desai SM, Didier PJ, Bikenmeyer LG, Dawson GJ, Leary TP, Schochetman G, Phillippi-Falkenstein K, Arroyo J, Barrett ADT, Tesh RB (2004) Experimental infection of rhesus macaques with West Nile virus: level and duration of viremia and kinetics of the antibody response after Infection. J Infect Dis 189:669–676
89. Rodhain F, Clerc Y, Albignac R, Ricklin B, Ranaivosata J, Coulanges P (1982) Arboviruses and lemurs in Madagascar: a preliminary note. Trans R Soc Trop Med Hyg 76:227–231
90. Rodhain F, Petter JJ, Albignac R (1985) Arboviruses and lemurs in Madagascar: experimental infection of *Lemur fulvus* with yellow fever and West Nile viruses. Am J Trop Med Hyg 34:816–822
91. Root JJ, Hall JS, McLean RG, Marlenee NL, Beaty BJ, Gansowski J, Clark L (2005) Serologic evidence of exposure of wild mammals to flaviviruses in the central and eastern United States. Am J Trop Med Hyg 72:622–630
92. Root JJ, Oesterle PT, Nemeth NM, Klenk K, Gould DH, McLean RG, Clark L, Hall JS (2006) Experimental infection of fox squirrels (*Sciurus niger*) with West Nile virus. Am J Trop Med Hyg 75:697–701
93. Root JJ, Oesterle PT, Sullivan HJ, Hall JS, Marlenee NL, McLean RG, Montenieri JA, Clark L (2007) Fox squirrel (*Sciurus niger*) associations with West Nile virus. Am J Trop Med Hyg 76:782–784
94. Root JJ, Bentler KT, Nemeth NM, Gidlewski T, Spraker TR, Franklin AB (2010) Experimental infection of raccoons (*Procyon lotor*) with West Nile virus. Am J Trop Med Hyg 83:803–807
95. Santaella J, McLean R, Hall JS, Gill JS, Bowen RA, Hadow HH, Clark L (2005) West Nile virus serosurveillance in Iowa white-tailed deer (1999–2003). Am J Trop Med Hyg 73:1038–1042
96. Savage HM, Anderson M, Gordon E, McMillen L, Colton L, Delorey M, Sutherland G, Aspen S, Charnetzky D, Burkhalter K, Godsey M (2008) Host-seeking heights, host-seeking activity patterns, and West Nile virus infection rates for members of the *Culex pipiens* complex at different habitat types within the hybrid zone, Shelby County, TN, 2002 (Diptera: Culicidae). J Med Entomol 45:276–288
97. Schaefer AM, Reif JS, Goldstein JD, Ryan CN, Fair PA, Bossart GD (2009) Serological evidence of exposure to selected viral,

bacterial, and protozoal pathogens in free-ranging atlantic bottlenose dolphins (*Tursiops truncatus*) from the Indian River Lagoon, Florida, and Charleston, South Carolina. Aquat Mamm 35:163–170
98. Shepherd RC, Williams MC (1964) Studies on viruses in East African bats (Chiroptera). 1. Haemagglutination inhibition and circulation of arboviruses. Zoonoses Res 3:125–139
99. Sherif NEDH (2007) Serological evidence of antibodies to certain arboviruses in desert rodent sera in Egypt. Egypt J Hosp Med 28:342–346
100. Simpson DI, O'Sullivan JP (1968) Studies on arboviruses and bats (Chiroptera) in East Africa. I. Experimental infection of bats and virus transssion attempts in *Aedes* (*Stegomyia*) *aegypti* (Linnaeus). Ann Trop Med Parasitol 62:422–431
101. Simpson DI, Williams MC, O'Sullivan JP, Cunningham JC, Mutere FA (1968) Studies on arboviruses and bats (Chiroptera) in East Africa. II. Isolation and haemagglutination-inhibition studies on bats collected in Kenya and throughout Uganda. Ann Trop Med Parasitol 62:432–440
102. Sixl W, Kock M, Withalm H, Stunzner D, Sixl-Voigt B (1989) Serological investigations of small mammals in waste disposal sites in Austria. Geographia Medica Suppl 2:65–68
103. Smithburn KC, Hughes TP, Burke AW, Paul JH (1940) A neurotropic virus isolated form the blood of a native of Uganda. Am J Trop Med Hyg 20:471–492
104. Sondgeroth K, Blitvich B, Blair C, Terwee J, Junge R, Sauther M, VandeWoude S (2007) Assessing flavivirus, lentivirus, and herpesvirus exposure in free-ranging ring-tailed lemurs in southwestern Madagascar. J Wildl Dis 43:40–47
105. St. Leger J, Wu G, Anderson M, Dalton L, Nilson E, Wang D (2011) West Nile virus infection in killer whale, Texas, USA, 2007. Emerg Infect Dis 17:1531–1533
106. Taylor RM, Work TH, Hurlbut HS, Rizk F (1956) A study of the ecology of West Nile virus in Egypt. Am J Trop Med Hyg 5:579–620
107. Tesh RB, Siirin M, Guzman H, Travassos Da Rosa APA, Wu X, Duan T, Lei H, Nunes MR, Xiao SY (2005) Persistent West Nile Virus infection in the golden hamster: studies on its mechanism and possible implications for other flavivirus infections. J Infect Dis 192:287–295
108. Tiawsirisup S, Platt KB, Tucker BJ, Rowley WA (2005) Eastern cottontail rabbits (*Sylvilagus floridanus*) develop West Nile virus viremias sufficient for infecting select mosquito species. Vector Borne Zoonotic Dis 5:342–350
109. Tiawsirisup S, Blitvich BJ, Tucker BJ, Halbur PG, Bartholomay LC, Rowley WA, Platt KB (2010) Susceptibility of fox squirrels (*Sciurus niger*) to West Nile virus by oral exposure. Vector Borne Zoonotic Dis 10:207–209
110. Tonry JH, Xiao SY, Siirin M, Chen H, Travassos Da Rosa APA, Tesh RB (2005) Persistent shedding of West Nile virus in urine of experimentally infected hamsters. Am J Trop Med Hyg 72:320–324
111. Wertheimer AM, Uhrlaub JL, Hirsch A, Medigeshi G, Sprague J, Legasse A, Wilk J, Wiley CA, Didier P, Tesh RB, Murray KO, Axthelm MK, Wong SW, Nikolich-Žugich J (2010) Immune response to the West Nile virus in aged non-human primates. PLoS ONE 5:e15514
112. Wilson DE, Reeder DM (2005) Mammal species of the world. A taxonomic and geographic reference, 3rd edn. Johns Hopkins University Press, Baltimore
113. Wolf RF, Papin JF, Hines-Boykin R, Chavez-Suarez M, White GL, Sakalian M, Dittmer DP (2006) Baboon model for West Nile virus infection and vaccine evaluation. Virology 355:44–51
114. Zeller HG, Schuffenecker I (2004) West Nile virus: an overview of its spread in Europe and the Mediterranean basin in contrast to its spread in the Americas. Eur J Clin Microbiol Infect Dis 23:147–156