Journal of Medical Entomology, 62(3), 2025, 621–632
https://doi.org/10.1093/jme/tjaf021
Advance Access Publication Date: 21 February 2025
Research

ENTOMOLOGICAL SOCIETY OF AMERICA
SHARING INSECT SCIENCE GLOBALLY

OXFORD

Vector/Pathogen/Host Interaction, Transmission

Host-feeding behavior of mosquitoes (Diptera: Culicidae) in North Dakota, 2003 to 2006

John F. Anderson[1,*], Angela Bransfield[1], Michael J. Misencik[1], Sydney Jones[2], Andy J. Main[3], Philip M. Armstrong[1], Theodore G. Andreadis[1], and Goudarz Molaei[1,2]

[1]Department of Entomology and Center for Vector Biology & Zoonotic Diseases, The Connecticut Agricultural Experiment Station, New Haven, CT, USA
[2]Department of Epidemiology of Microbial Diseases, Yale School of Public Health, New Haven, CT, USA
[3]Biology Department, American University in Cairo, AUC Avenue, PO Box 74, New Cairo, 11835, Egypt

[*]Corresponding author. Department of Entomology and Center for Vector Biology & Zoonotic Diseases, Connecticut Agricultural Experiment Station, 123 Huntington St. 06511, New Haven, CT, USA (Email: mjrfarm@aol.com).

Subject Editor: Lawrence Hribar

Received on 24 November 2024; revised on 16 January 2025; accepted on 30 January 2025

Mosquitoes are abundant near temporary, semipermanent, and permanent water in North Dakota and are associated with human and veterinary diseases. Little is known about the feeding habits of mosquitoes as related to the transmission of arboviruses. We report on the identification of vertebrate hosts of 9 species of mosquitoes collected in 2003 to 2006. Blood meals of 1,223 from 9 mosquito species were identified to vertebrate species by PCR assays using the mitochondrial *cytochrome b* gene. *Aedes dorsalis* (Diptera: Culicidae) and *Culiseta inornata* fed only on mammals, and *Aedes vexans* fed almost exclusively on mammals. *Aedes trivittatus* fed significantly more on mammals than on birds. *Culex tarsalis* acquired blood meals from the most diverse group of vertebrates, frequently fed on American Robins, and did not exhibit a seasonal shift of feeding on birds to mammals. The extensive feeding of *Cx. tarsalis* on passerine birds and the isolation of West Nile virus (WNV) from 2 specimens that had fed on passerines supports their role in horizontal transmission of WNV. This species also transmits western equine encephalitis virus. Host feeding by *Ae. trivittatus, Ae. vexans, Cs. inornata,* and *Ae. dorsalis* in relation to their possible importance in transmission of trivittatus virus, Cache Valley virus, Jamestown Canyon virus, Potosi virus, or snowshoe hare virus is presented. The identification of host feeding behavior pattern of specific species of mosquitoes enhances our understanding of the enzootic and epizootic nature of 7 viruses in North Dakota.

Keywords: blood-meals, arbovirus, vectors, mosquito, North Dakota

Introduction

Aedes vexans (Meigen) (Diptera: Culicidae) and *Culex tarsalis* Coquillett (Diptera: Culicidae) are the 2 most important species of mosquitoes in North Dakota (Anderson et al. 2015). *Aedes vexans* is dominant and represented 82.9% of more than 3 million specimens collected and identified in eastern and western North Dakota in 2003 to 2006. This species readily attacks humans (Horsfall et al. 1973). The percentage of *Cx. tarsalis* identified was 2.7% and reached peak average numbers per trap-night of 300. Although it infrequently feeds on humans (Thiemann et al. 2012), this species is considered the primary vector of West Nile virus (WNV; Flaviviridae: *Flavivirus*) because of its consistently high infection rates and competency (Turell et al. 2005, Thiemann et al. 2012).

At least 47 species of mosquitoes have been identified in North Dakota (Post and Munro 1949, Darsie and Anderson 1985, Darsie and Ward 2005, Anderson et al. 2023), and 8 arboviruses have been isolated from 13 different mosquito species (Karabatsos 1985, Anderson et al. 2015). Six of these viruses, western equine encephalomyelitis virus (WEEV; Togaviridae: *Alphavirus*) (Leake 1941), WNV (Borchardt et al. 2010), St. Louis encephalitis virus (SLEV; Flaviviridae: *Flavivirus*) (Luby 1979), Cache Valley virus (CVV; Peribunyaviridae: *Orthobunyavirus*) (Sexton et al. 1997), Jamestown Canyon virus (JCV; Peribunyaviridae: *Orthobunyavirus*) (Shepard and Armstrong 2023), and snowshoe hare virus (SSHV; Peribunyaviridae: *Orthobunyavirus*) (Walker and Yuill 2023) have been reported to cause human disease in North Dakota or elsewhere in North America.

© The Author(s) 2025. Published by Oxford University Press on behalf of Entomological Society of America. All rights reserved. For commercial re-use, please contact reprints@oup.com for reprints and translation rights for reprints. All other permissions can be obtained through our RightsLink service via the Permissions link on the article page on our site—for further information please contact journals.permissions@oup.com.

Downloaded from https://academic.oup.com/jme/article/62/3/621/8029747 by ESA Member Access user on 07 May 2026

Knowledge of host interactions of mosquito species may assist in understanding the enzootic cycling and epidemic/epizootic transmission of arboviruses (Tempelis 1975). Accordingly, we report the molecular identification of blood meals of 9 species of mosquitoes collected in eastern and western North Dakota, 2003 to 2006 (Anderson et al. 2015) and relate their host interactions to the arboviruses that have been reported.

Materials and Methods

Collection of Mosquitoes

The trapping of mosquitoes in Cass, Nelson, Richland, and Williams Counties in North Dakota in 2003 to 2006 has been described previously (Anderson et al. 2015). Mosquitoes were collected with Centers for Disease Control (CDC) miniature light traps baited with dry ice (Model 512; John W. Hock Co., Gainesville, FL), and with mosquito magnet experimental (MMX) traps (American Biophysics Corp., East Greenwich, RI) from July 4 to September 26 in 2003, June 8 to October 6 in 2004, May 24 to September 29 in 2005, and June 8 to September 7 in 2006. Traps were placed in rural areas of Cass, Nelson, and Richland Counties, within the City of Fargo in Cass County, and in rural areas immediately outside of Williston in Williams County (Fig. 1). Fargo is on the western side of the Red River, separating North Dakota and Minnesota, and Williston is near the North Dakota and Montana border. Nelson and Richland Counties are in eastern North Dakota (Anderson et al. 2015).

Traps were set in the field and collected the following morning. Mosquitoes were anesthetized or killed with dry ice or at low temperatures and transferred into glass vials sealed with a rubber stopper and gas-proof tape or in Mason jars sealed with a lid and wrapped with gas-poof tape. Mosquitoes were kept at dry ice temperatures or −80 °C and shipped on dry ice by overnight mail to the Connecticut Agricultural Experiment Station (CAES) in New Haven, CT. Mosquitoes were identified to species and recorded by date and collecting site (Carpenter and LaCasse 1955, Barr 1958, Darsie and Ward 1981, 2005, Andreadis et al. 2005). Each mosquito with blood was separated, placed into a 1.5-ml vial, appropriately labeled, and stored at −80 °C.

Blood Meal Identification

DNA was extracted from the blood of individual engorged female mosquitoes using the DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA). The abdomen of each engorged specimen was added to a 1.5-ml microcentrifuge tube, to which 180 µl of ATL buffer and 20 µl of proteinase K were added and thoroughly vortexed. Tissues were lyzed overnight at 56 °C following the protocol for the purification of total DNA from animal tissues (Qiagen). Extracted DNA was used as a template in the polymerase chain reaction assay. Primers were based on vertebrate mitochondrial *cytochrome b* gene sequences using established protocols (Ngo and Kramer 2003, Molaei et al. 2006a, 2006b, 2007). PCR amplicons were purified using the QIAquick PCR Purification Kit (Qiagen). Double-stranded DNA sequencing was performed using the sequencer 3730xl DNA Analyzer (Applied Biosystems) at the DNA Analysis Facility on Science Hill, Yale University, New Haven, CT. Sequences were annotated using ChromasPro version 1.22 (Technelysium Pty Ltd., Tewantin, Queensland, Australia) and identified by comparison to available sequences at the National Center for Biotechnology Information GenBank DNA sequence database using BLAST search (BLASTN) (https://blast.ncbi.nlm.nih.gov/Blast.cgi?PROGRAM=blastn&PAGE_TYPE=BlastSearch&LINK_LOC=blasthome).

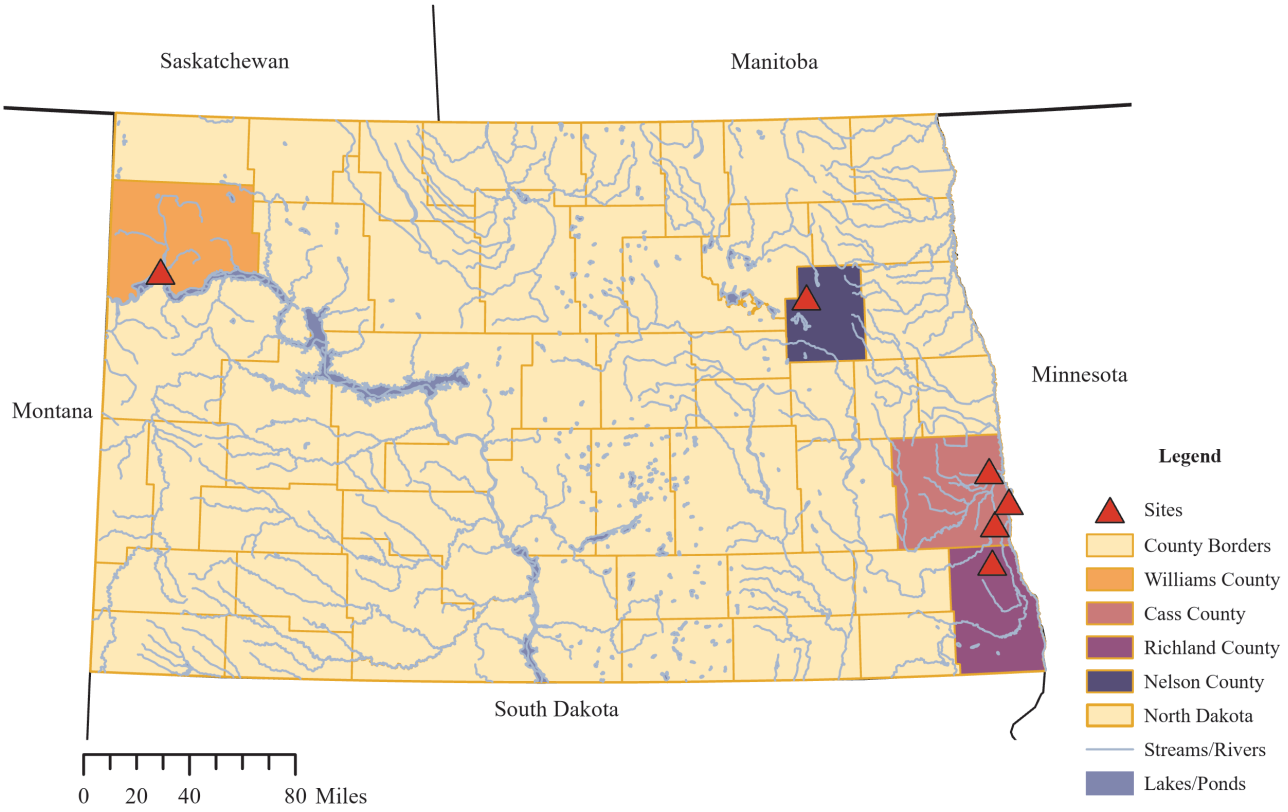

Fig. 1. Mosquito collection sites in North Dakota, 2003 to 2006.

Downloaded from https://academic.oup.com/jme/article/62/3/621/8029747 by ESA Member Access user on 07 May 2026

Virus Isolation

After removal of the abdomen of each engorged specimen for blood meal identification, the remainder of the mosquito, including the head and thorax, was returned to its labeled vial, immediately placed on dry ice, and later transferred to a −80 °C freezer. Viral isolations in Vero cells were attempted from individual specimens (Anderson et al. 2015). The QIAamp viral RNA mini kit protocol (Qiagen, Valencia, CA) was used to extract RNA from a 70-µl sample of infectious Vero cell-growth medium. West Nile virus was identified by a TaqMan reverse transcriptase-polymerase chain reaction (RT-PCR) assay (Lanciotti et al. 2000).

Data Analysis

Fisher's exact test was performed using the procedure of Oyvind Langsrud (https://www.langsrud.com/stat/fisher.htm). Chi-square analyses were performed according to https://www.bmj.com/about-bmj/resources-readers/publications/statistics-square-one/8-chi-squared-tests. To determine if a shift in feeding behavior occurred in *Cx. tarsalis* in North Dakota, as had been reported elsewhere (Reeves et al. 1963, Tempelis 1975), a negative binomial regression was employed, a standard approach in ecological studies for analyzing count data with overdispersion (Stoklosa et al. 2022). This method modeled the *Cx tarsalis* feeding patterns on mammals and birds over 14 wk (weeks 23 to 37) while accounting for the variability in the data. Time was modeled as a continuous predictor, host species (mammals or birds) as categorical predictors, and the dependent variable was the number of mosquitoes feeding on host species at each time period. The model was developed using the *MASS* package in R software (version 2022.12.0 + 353).

Multinomial logistic regression modeling was used to assess the odds of different mosquito species feeding on specific host populations relative to the feeding patterns of the most common mosquito in North Dakota. This method is appropriate for analyzing individual choice among a set of J alternatives, with the characteristics of the individual as the explanatory variable (Hoffman and Duncan 1988). In this model, host species served as the dependent variable, with mosquito species as the primary predictor variable. The model was adjusted to account for temporal (date of mosquito collection in weeks) and spatial (mosquito trapping sites) variability, To reduce collinearity among predictors, mosquito species and trapping sites with fewer than 10 observations were excluded, and correlation coefficients among predictor variables were examined. To ensure sufficient sample size, all bird hosts were grouped into a single "grouped-bird" category due to their relatively lower frequency compared to individual mammalian species. The final model included the mosquito species *Cs. inornata*, *Cx. tarsalis*, *Ae. trivittatus*, *Ae. dorsalis*, and *Ae. vexans*, along with the most common mammalian host species (white-tailed deer, cattle, horse, and eastern cottontail) and the grouped-bird category. White-tailed deer were the most commonly fed-on host and served as the host reference group. *Aedes vexans* is the dominant species in North Dakota and was used as the reference group for mosquitoes (Anderson et al. 2015). Model selection was conducted using Akaike information criterion (AIC) scores, confirmed with Bayesian information criterion (BIC) scores, and evaluated using pseudo-R^2. Odds ratios (OR) with 95% confidence intervals (CI) were calculated to assess the strength of associations between mosquito and host species. The final model was developed using the *nnet* package in R software (version 2022.12.0 + 353). It is important to note that the odds ratios derived from this regression analysis reflect relative feeding, not absolute feeding of mosquito species for one host over another; this limitation is inherent to logistical regression models.

Results

A total of 1,223 blood meals were successfully analyzed from 9 species of mosquitoes, of which 5 species had 114 to 504 specimens examined (Tables 1 and 2, Fig. 2). These were obtained from 3,580,610 mosquitoes collected in Cass, Richland, and Nelson Counties in eastern North Dakota in 2003 to 2005 and in Williams County in 2004 to 2006 in western North Dakota. Vertebrate hosts were identified from 73.9% of 1,655 examined blood meals.

Mosquitoes fed on a variety of mammalian and bird species (Tables 1 and 2, Fig. 3). *Aedes dorsalis* (Meigen) ($n = 114$) and *Culiseta inornata* (Williston) ($n = 160$) fed only on mammals (Tables 1 and 2, Figs. 4 and 5). *Aedes vexans* ($n = 504$) fed almost exclusively on mammals and only rarely imbibed avian blood. *Aedes trivittatus* (Coquillett) (n = 235) fed on 6 bird species but fed significantly more on mammals (chi-square = 223.35, def.=17, $P < 0.001$). *Culex tarsalis* ($n = 194$) fed readily on both mammals ($n = 90$) and birds ($n = 104$). Chi-square analysis comparing bird and mammal feedings showed no significant difference (chi-square = 15.732, def.=14, $P = 0.10$). *Aedes sticticus* (Meigen) ($n = 10$), *Aedes triseriatus* (Say) ($n = 2$), *Aedes flavescens* (Muller) ($n = 1$), and *Aedes melanimon* Dyar ($n = 3$) fed on mammals.

In eastern North Dakota, 92.3% of *Ae. dorsalis* ($n = 39$), 60.0% *Ae. sticticus* ($n = 10$), 43.0% *Ae. trivittatus* ($n = 145$), 83.0% *Ae. vexans* ($n = 363$), and 94.6% of *Cs. inornata* ($n = 37$) fed on large wild or domestic mammals in the order Artiodactyla and on horses, order Perissodactyla (Table 1, Fig. 4). Lagomorphs, particularly eastern cottontail rabbits, were fed upon by *Ae. trivittatus* and *Ae. vexans* 32.4% and 9.1% of the time. Carnivores and rodents were less frequent hosts. *Aedes trivittatus* ($n = 1$), *Ae. vexans* ($n = 3$), and *Cx. tarsalis* ($n = 1$) fed on humans.

Culex tarsalis ($n = 119$) fed on 18 species of birds in 5 orders ($n = 73$) and 13 species of mammals in 6 orders ($n = 46$) in eastern North Dakota (Table 1, Fig. 4). Thirteen species of passerines were identified. American Robin ($n = 19$, 16.0%) and House Sparrow ($n = 17$, 14.3%) were the most common hosts. Mourning Doves ($n = 8$, 6.7%), order Columbiformes, were also frequently identified. This species fed on 6 different mammalian orders. White-tailed deer ($n = 15$, 12.6%) and horses ($n = 8$, 6.7%) were the most frequent hosts.

Six of seven species of mosquitoes in western North Dakota fed exclusively or extensively on mammals (Table 2, Fig. 5). The orders Artiodactyla and Perissodactyla were the primary hosts for *Ae. dorsalis* ($n = 75$, 98.6%), *Ae. vexans* ($n = 141$, 97.2%), and *Cs. inornata* ($n = 123$, 99.9%). *Aedes flavescens* ($n = 1$) and *Ae. melanimon* ($n = 3$) also fed on large mammals. Eighty-three of 90 specimens (92.2%) of *Ae. trivittatus* fed on 10 species of mammals. The orders Artiodactyl (61.2%), Carnivora (12.1%), and Lagomorpha (17.8%) were the primary hosts. Seven specimens fed on non-passerine species of birds.

Culex tarsalis ($n = 75$) fed on both mammals (58.7%) and birds (41.3%) in western North Dakota (Table 2, Fig. 5). Cattle ($n = 20$, 26.7%) and deer ($n = 14$, 18.7%) were the most frequent mammalian hosts. Passerines, representing 12 different species, comprised 26.7% of the feedings with the largest number ($n = 7$, 9.3%) recorded from Cedar Waxwing. *Culex tarsalis* fed more on mammals in the west than in the east (Fisher's exact 2-tail test, $P = 0.008$) and

Downloaded from https://academic.oup.com/jme/article/62/3/621/8029747 by ESA Member Access user on 07 May 2026

Table 1. Number (percent) of blood meals identified from 7 species of mosquitoes collected in Cass, Richland, and Nelson Counties, North Dakota, 2003 to 2005.

Host	Mosquito species							
	Aedes dorsalis	*Aedes sticticus*	*Aedes triseriatus*	*Aedes trivittatus*	*Aedes vexans*	*Culex tarsalis*	*Culiseta inornata*	Total
Aves								
Accipitriformes								
Cooper's hawk, *Accipiter cooperii*						2 (1.7)		2 (0.3)
Anseriformes								
American black duck, *Anas rubripes*						1 (0.8)		1 (0.1)
Mallard, *Anas platyrhynchos*				1 (0.7)				1 (0.1)
Columbiformes								
Mourning dove, *Zenaida macroura*				1 (0.7)		8 (6.7)		9 (1.3)
Rock pigeon, *Columba livia*						1 (0.8)		1 (0.1)
Galliformes								
Wild turkey, *Meleagris gallopavo*				8 (5.5)		3 (2.5)		11 (1.5)
Passeriformes								
American goldfinch, *Spinus tristis*						1 (0.8)		1 (0.1)
American robin, *Turdus migratorius*				3 (2.1)		19 (16.0)		22 (3.1)
Black-capped chickadee, *Poecile atricapillus*						1 (0.8)		1 (0.1)
Blue jay, *Cyanocitta cristata*						1 (0.8)		1 (0.1)
Chipping sparrow, *Spizella passerina*				1 (0.7)		6 (5.0)		7 (1.0)
Gray catbird, *Dumetella carolinensis*						1 (0.8)		1 (0.1)
House finch, *Haemorhous mexicanus*						3 (2.5)		3 (0.4)
House sparrow, *Passer domesticus*						17 (14.3)		17 (2.4)
House wren, *Troglodytes aedon*				1 (0.7)		3 (2.5)		4 (0.6)
Marsh wren, *Cistothorus palustris*						1 (0.8)		1 (0.1)
Rose-breasted grosbeak, *Pheucticus ludovicianus*						2 (1.7)		2 (0.3)
Song sparrow, *Melospiza melodia*						2 (1.7)		2 (0.3)
Thrush, *Toxostoma* sp.						1 (0.8)		1 (0.1)
Mammalia								
Artiodactyla								
American bison, *Bison bison*					1 (0.3)			1 (0.1)
Cattle, *Bos taurus*	6 (15.4)			2 (1.4)	25 (6.9)	5 (4.2)	8 (21.6)	46 (6.4)
Sheep, Ovis aries					13 (3.6)		4 (10.8)	17 (2.4)
White-tailed deer, *Odocoileus virginianus*	4 (10.3)	5 (50)		51 (35.2)	161 (44.4)	15 (12.6)	11 (29.7)	247 (34.5)
Wild boar, *Sus scrofa*					1 (0.3)			1 (0.1)
Carnivora								
Cat, *Felis catus*		1 (10)	1 (50)	7 (4.8)	1 (0.3)	1 (0.8)		11 (1.5)
Dog, *Canis familiaris*				4 (2.6)	11 (3.0)	4 (3.4)		19 (2.7)

Downloaded from https://academic.oup.com/jme/article/62/3/621/8029747 by ESA Member Access user on 07 May 2026

Table 1. Continued

Host	Mosquito species							
	Aedes dorsalis	*Aedes sticticus*	*Aedes triseriatus*	*Aedes trivittatus*	*Aedes vexans*	*Culex tarsalis*	*Culiseta inornata*	Total
Raccoon, *Procyon lotor*		1 (10)		5 (3.4)	4 (1.1)	1 (0.8)		11 (1.5)
Red fox, *Vulpes vulpes*					1 (0.3)			1 (0.1)
Lagomorpha								
Eastern cottontail, *Sylvilagus* floridanus	1 (2.6)	1 (10)		47 (32.4)	32 (8.8)	4 (3.4)	1 (2.7)	86 (12.1)
Hare, *Lepus* sp.	2 (5.1)				1 (0.3)	1 (0.8)	1 (2.7)	5 (0.7)
Rabbit, *Sylvilagus* sp.				1 (0.7)				1 (0.1)
White-tailed Jackrabbit, *Lepus townsendii*					3 (0.8)	2 (1.7)		5 (0.7)
Perissodactyla								
Horse, *Equus ferus*	26 (66.7)	1 (10)	1 (50)	10 (6.9)	105 (28.9)	8 (6.7)	12 (32.4)	163 (22.8)
Primates								
Human, *Homo sapiens*				1 (0.7)	3 (0.8)	1 (0.8)		5 (0.7)
Rodentia								
American red squirrel, *Tamiasciurus hudsonicus*					1 (0.3)	1 (0.8)		2 (0.3)
Fox squirrel, *Sciurus niger*						2 (1.7)		2 (0.3)
Groundhog, *Marmota monax*				2 (1.4)				2 (0.3)
Norway rat, *Rattus norvegicus*		1 (10)						1 (0.1)
White-footed mouse, *Peromyscus leucopus*						1 (0.8)		1 (0.1)
Total identified	39	10	2	145	363	119	37	715
No result	42	3	0	100	53	62	31	291

fed on a greater array of vertebrates in eastern and western North Dakota than other mosquito species (Figs. 4 and 5).

Blood-fed *Cx. tarsalis* were collected and identified from June to September. The negative binomial regression model results indicated no statistically significant changes in *Cx. tarsalis* feeding patterns on either birds or mammals over the observed weeks, indicating that a shift in feeding pattern did not occur during this time period. Similarly, there was no significant difference in feeding counts between mammals and birds during this time period (coefficient = −0.11934, $P = 0.747$). We also compared avian feedings ($n = 60$) and mammal feedings ($n = 52$) in June and July with avian feedings ($n = 39$) and mammal feedings ($n = 37$) in August and September. *Culex tarsalis* did not exhibit a shift in feeding on birds and mammals in early or late summer (Fisher's exact 2-tail test, $P = 0.77$).

Four multinomial logistic regression models were tested to examine the relationship between dependent variable (common host species) and the predictor variable (mosquito species) (Table 3). Results indicated an improvement in model fitness upon adding the predictors "date of mosquito collection" and "mosquito trapping site" (MLR: Host ~ Mosquito + Date + Trapping Site; AIC 1402.571). The model demonstrated a Nagelkerke Pseudo R^2 of 81.04% suggesting that the predictor variables explained a substantial portion of the variation in the dependent variable.

The model assessed the feeding patterns of mosquito species on common hosts (birds, cattle, eastern cottontail, and horses) relative to the most common mosquito species, *Ae. vexans*, while controlling temporal and spatial variability (Table 4). The results indicated that compared to *Ae. vexans*, Cx. *tarsalis* displayed a strong preference for feeding on birds over white-tailed deer (OR = 519.25; 95% CI: 122.09 to 2,208.48), though the limited sample size for derived blood meals contributed to wide confidence intervals, underscoring a limitation of the model, though the limited sample size for derived blood meals contributed to wide confidence intervals, underscoring a limitation of the model. Relative to *Ae. vexans*, *Ae. trivittatus* showed a similar preference for feeding on birds compared to white-tailed deer, although this preference was weaker (OR = 20.99; 95% CI: 5.34 to 82.5). In contrast, *Cs. inornata* favored feeding on cattle (OR = 9.79: 95% CI: 4.56 to 21.03) and horses (OR = 4.41; 95% CI: 1.78 to 10.9) relative to the white-tailed deer, compared to *Ae. vexans*. Lastly, *Ae. trivittatus,* showed a preference for feeding on eastern cottontail over white-tailed deer (OR = 5.54; 95% CI: 2.85 to 10.79) compared to *Ae. vexans*.

Isolation of virus was attempted from 1,106 individual blood-fed mosquitoes (*Ae. dorsalis* ($n = 109$), *Ae. sticticus* ($n = 11$), *Cs. inornata* ($n = 173$), *Ae. vexans* ($n = 483$), *Cx. tarsalis* ($n = 192$), *Ae. trivittatus* ($n = 134$), and *Ae. melanimon* ($n = 4$). West Nile virus was isolated from 2 blood-fed *Cx. tarsalis* that had fed on a Cedar Waxwing and

Downloaded from https://academic.oup.com/jme/article/62/3/621/8029747 by ESA Member Access user on 07 May 2026

Table 2. Number (percent) of blood meals identified from 7 species of mosquitoes collected in Williams County, North Dakota, 2004 to 2006.

Host	Mosquito species							
	Aedes dorsalis	*Aedes flavescens*	*Aedes melanimon*	*Aedes trivittatus*	*Aedes vexans*	*Culex tarsalis*	*Culiseta inornata*	Total
Aves								
Anseriformes								
Blue-winged teal, *Spatula discors*						1 (1.3)		1 (0.2)
Gadwall, *Mareca strepera*						2 (2.7)		2 (0.4)
Mallard, *Anas platyrhynchos*						1 (1.3)		1 (0.2)
Columbiformes								
Mourning dove, *Zenaida macroura*				3 (3.3)		3 (4.0)		6 (1.2)
Galliformes								
Common pheasant, *Phasianus colchicus*					1 (0.7)	2 (2.7)		3 (0.6)
Wild turkey, *Meleagris gallopavo*				3 (3.3)	2 (1.4)	2 (2.7)		7 (1.4)
Passeriformes								
American goldfinch, *Spinus tristis*						1 (1.3)		1 (0.2)
American robin, *Turdus migratorius*						2 (2.7)		2 (0.4)
Black-capped chickadee, *Poecile atricapillus*						1 (1.3)		1 (0.2)
Black-headed grosbeak, *Pheucticus melanocephalus*						1 (1.3)		1 (0.2)
Brown-headed cowbird, *Molothrus ater*						1 (1.3)		1 (0.2)
Cedar waxwing, *Bombycilla cedrorum*						7 (9.3)		7 (1.4)
Gray catbird, *Dumetella carolinensis*						1 (1.3)		1 (0.2)
House wren, *Troglodytes aedon*						2 (2.7)		2 (0.4)
Marsh wren, *Cistothorus palustris*						1 (1.3)		1 (0.2)
Savannah sparrow, *Passerculus sandwichensis*						1 (1.3)		1 (0.2)
Western meadowlark, *Sturnella neglecta*						1 (1.3)		1 (0.2)
Yellow warbler, *Setophaga petechia*						1 (1.3)		1 (0.2)
Piciformes								
Downy woodpecker, *Dryobates pubescens*				1 (1.1)				1 (0.2)
Mammalia								
Artiodactyla								
Cattle, *Bos taurus*	35 (46.7)	1 (100)	2 (66.7)	17 (18.9)	33 (23.4)	20 (26.7)	90 (73.1)	198 (39.0)
Elk, *Cervus canadensis*	1 (1.3)				1 (0.7)			2 (0.4)
Mule deer, *Odocoileus hemionus*	2 (2.7)			5 (5.6)	13 (9.3)		5 (4.1)	25 (4.9)
Pronghorn, *Antilocapra americana*							1 (0.8)	1 (0.2)
Sheep, *Ovis aries*	1 (1.3)			9 (10.0)		1 (1.3)		11 (2.2)
White-tailed deer, *Odocoileus virginianus*	27 (36)			24 (26.7)	75 (53.2)	14 (18.7)	19 (15.4)	159 (31.3)

Downloaded from https://academic.oup.com/jme/article/62/3/621/8029747 by ESA Member Access user on 07 May 2026

Table 2. Continued

Host	Mosquito species							
	Aedes dorsalis	*Aedes flavescens*	*Aedes melanimon*	*Aedes trivittatus*	*Aedes vexans*	*Culex tarsalis*	*Culiseta inornata*	Total
Carnivora								
Cat, *Felis catus*				4 (4.4)		2 (2.7)		6 (1.2)
Dog, *Canis familiaris*				4 (4.4)		2 (2.7)		6 (1.2)
Striped skunk, *Mephitis mephitis*				3 (3.3)				3 (0.6)
Lagomorpha								
Eastern cottontail, *Sylvilagus* floridanus				16 (17.8)	1 (0.7)			17 (3.3)
Perissodactyla								
Donkey, *Equus asinus*						1 (1.3)		1 (0.2)
Horse, *Equus ferus*	8 (10.6)		1 (33.3)		15 (10.6)	2 (2.7)	8 (6.5)	34 (6.7)
Primates								
Human, *Homo sapiens*	1 (1.3)					1 (1.3)		2 (0.4)
Rodentia								
American beaver, *Castor canadensis*				1 (1.1)				1 (0.2)
Fox squirrel, *Sciurus niger*						1 (1.3)		1 (0.2)
Total identified	75	1	3	90	141	75	123	508
No result	23	0	2	61	10	32	13	141

on an American Goldfinch collected in Williams County on 3 August 2004, and 14 August 2004, respectively.

Discussion

Seven of the 9 mosquito species, *Ae. dorsalis, Ae. flavescens, Ae. melanimon, Ae. sticticus, Ae. triseriatus, Ae. vexans,* and *Cs. inornata*, fed exclusively or almost entirely on mammals. *Aedes trivittatus* fed extensively on mammals but also fed on 6 species of birds. *Culex tarsalis* fed equally on mammals and on birds. In a prior study, 7 different viruses were isolated from these 9 species of mosquitoes in 2003 to 2006 (Anderson et al. 2015). We discuss the feeding habits of these mosquitoes in relation to the horizontal acquisition and transmission of their viruses.

Culex tarsalis fed on birds and mammals without a significant shift from avian to mammalian hosts as the season progressed during weeks 23 to 37. The negative binomial regression model suggested that the feeding selection of mosquitoes for birds or mammals remained consistent throughout the study period. Previously, seasonal shifts of *Cx. tarsalis* feeding on birds in the spring to feeding on mammals in mid-summer and later have been recorded in California, resulting in an increased risk in transmission of WEEV to humans and domestic animals (Reeves et al. 1963, Tempelis et al. 1965, Tempelis 1975).

Culex tarsalis fed on 6 orders of birds, but the largest numbers of feedings were on passerines. American Robins (n = 19) and House Sparrows (n = 17) were most commonly fed upon in eastern North Dakota, and Cedar Waxwings (n = 7) were the most common avian host in western North Dakota. *Culex tarsalis* also fed on 6 orders of mammals, feeding most frequently on white-tailed deer (12.6%) and horses (6.7%) in the east and on cattle (26.7%) and white-tailed deer (18.7%) in the west. Two human feedings from this species were recorded. In eastern North Dakota, the multinomial logistic model revealed that *Cx. tarsalis* readily fed on birds compared to white-tailed deer. This species was reported to feed primarily on white-tailed deer and passerine birds, including American Robin and House Sparrow, in Steele County, North Dakota (Mehus and Vaughan 2013).

West Nile virus was first recorded in North Dakota in 2002 and caused disease in 17 humans followed by 617 human cases in 2003 (https://www.cdc.gov/westnile). Since then, North Dakota along with other Great Plains states have emerged as hot spots for WNV transmission and have the highest long-term incidences of neuroinvasive disease in the United States. *Culex tarsalis* is the primary vector of WNV (Goddard et al. 2002) in the high plains and western states, and birds are the primary amplifiers of this virus (Apperson et al. 2002, Molaei et al. 2006b, Kramer et al. 2008). West Nile virus was isolated from *Cx. tarsalis* (n = 121) in both eastern and western North Dakota in 2003 to 2006 from the middle of June through early September (Anderson et al. 2015), and in the current study, WNV was isolated from 2 blood-fed specimens that fed on an American Goldfinch and a Cedar Waxwing. West Nile virus is transmitted tangentially to horses and humans in subsequent feedings. American Robins and House Sparrows, known to develop viremias (Komar et al. 2003), were identified as frequent hosts in eastern North Dakota and likely, along with other passerine species, are important amplifying hosts.

Culex tarsalis is also a primary vector of WEEV (Hammon and Reeves 1943) and SLEV (Luby 1979). Western equine encephalitis reached epidemic proportions in North Dakota in 1941 (Leake 1941), and WEEV was isolated from 2 pools of *Cx. tarsalis* collected in western North Dakota in 2004 (Anderson et al. 2015). Passerine birds are the primary vertebrate reservoirs of WEEV (Smith et al. 1997).

Culiseta inornata and *Ae. dorsalis* preferentially feed on large mammals in midwestern and western North America, particularly ruminants and horses, and even humans (Shemanchuk et al. 1963, Tempelis 1975a, Anderson and Gallaway 1987), but *Ae. dorsalis* will feed on smaller animals, including birds (Horsfall

Downloaded from https://academic.oup.com/jme/article/62/3/621/8029747 by ESA Member Access user on 07 May 2026

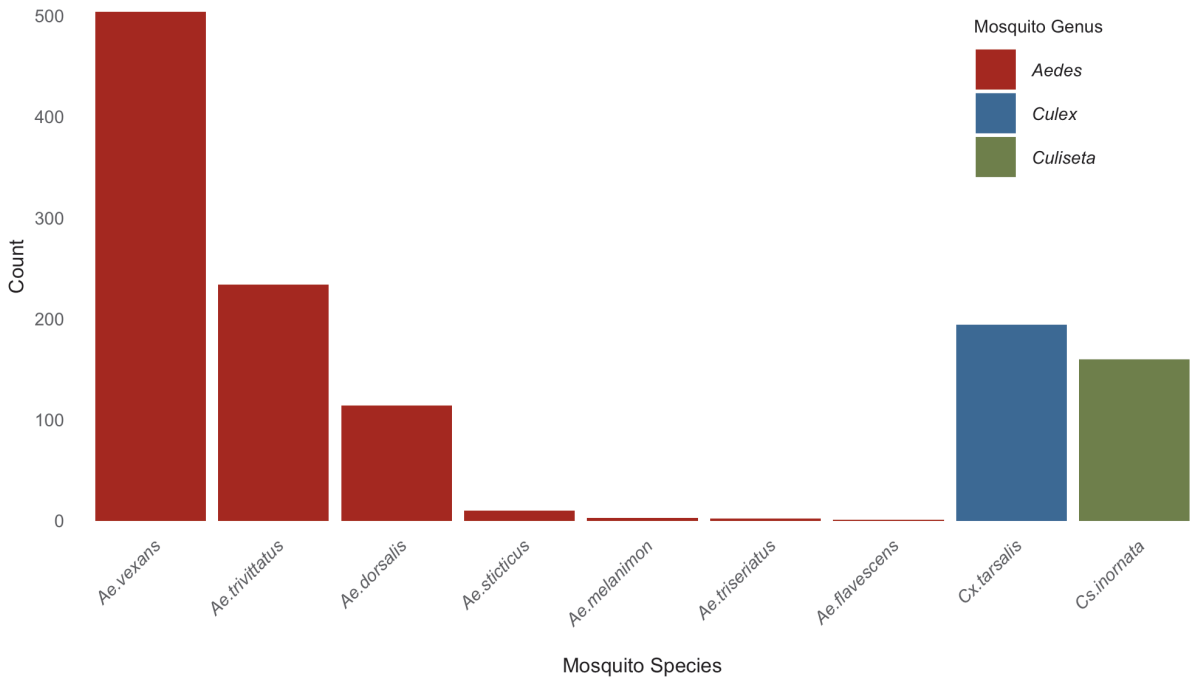

Fig. 2. Counts of blood meals from different mosquito species. Species are grouped by genus in order of frequency. Within the genus *Aedes,* species are ordered by frequency.

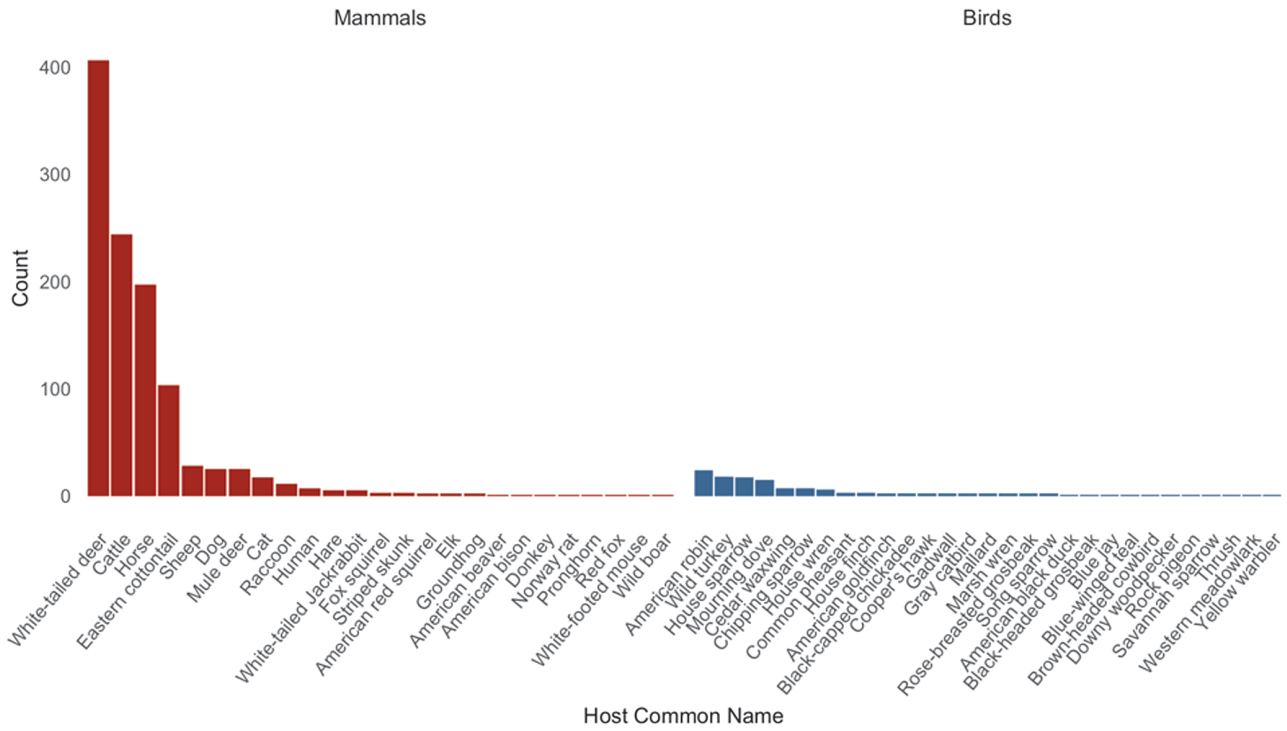

Fig. 3. Counts of blood meals from different host species. Species are grouped as mammal or bird in order of frequency-count.

1955, Shemanchuk et al. 1963). In our study, *Cs. inornata* and *Ae. dorsalis* fed entirely on mammals, particularly horses, white-tailed deer, and cattle. Selection of specific animal hosts is often dependent on their relative abundance (Anderson and Gallaway 1987), although in our study, the multinomial logistic model revealed that *Cs. inornata* was more likely to feed on cattle than white-tailed deer.

Four arboviruses, CVV, WNV, JCV, and Potosi virus (POTV; Peribunyaviridae: *Orthobunyavirus*), were isolated from *Cs. inornata* and *Ae. dorsalis* in North Dakota (Anderson et al. 2015). *Cs. inornata* is competent to transmit CVV, WNV, and JCV (Corner et al. 1980, Kramer et al. 1993, Turell et al. 2005), and *Ae. dorsalis* is competent to transmit WNV (Turell et al. 2005). White-tailed deer are likely propagative hosts for CVV, JCV, and POTV (Neitzel and

Downloaded from https://academic.oup.com/jme/article/62/3/621/8029747 by ESA Member Access user on 07 May 2026

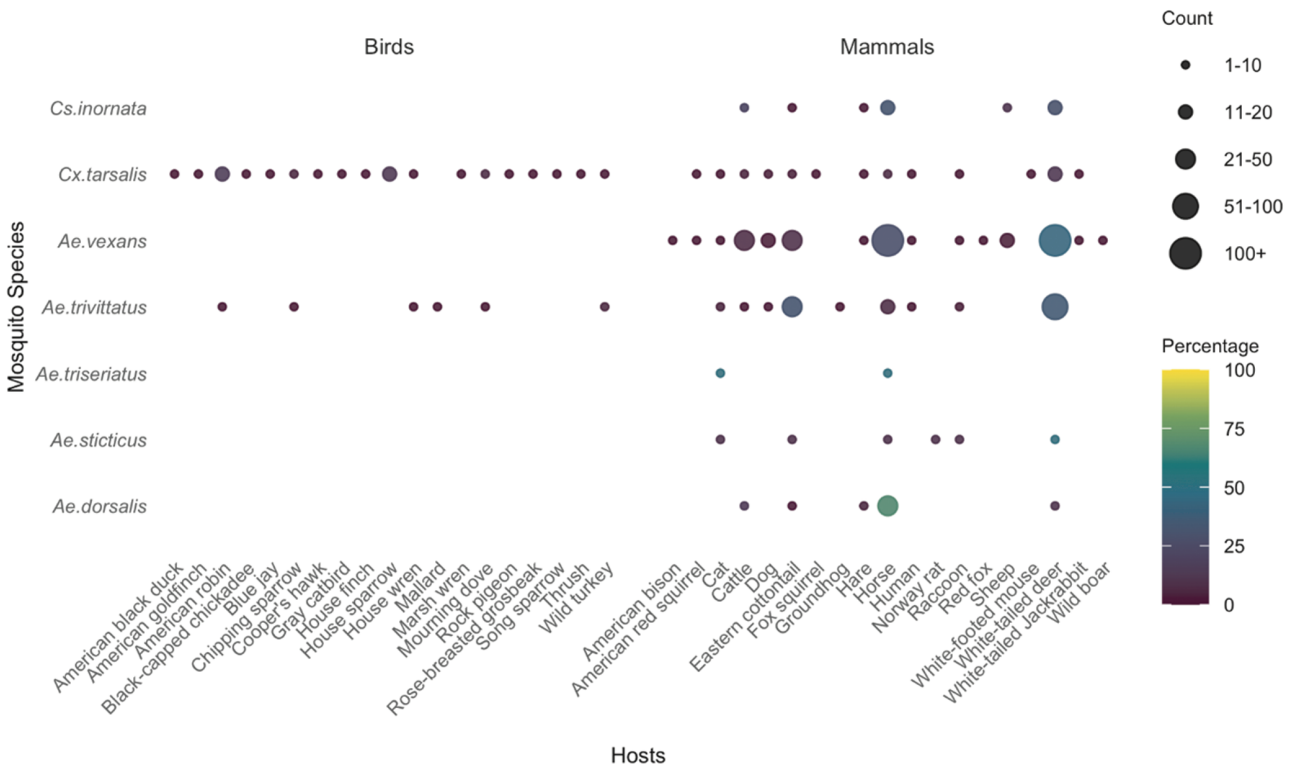

Fig. 4. Blood meals identified from mosquito species collected in Cass, Richland, and Nelson Counties, North Dakota, 2003 to 2005. Counts of hosts for specific mosquito species are identified by the size of the dot. The insert in the upper right shows the range of the count by size of the dot. The percentage of hosts fed upon by a specific mosquito species are identified by the color of the dot. The insert in the lower right shows the heat map.

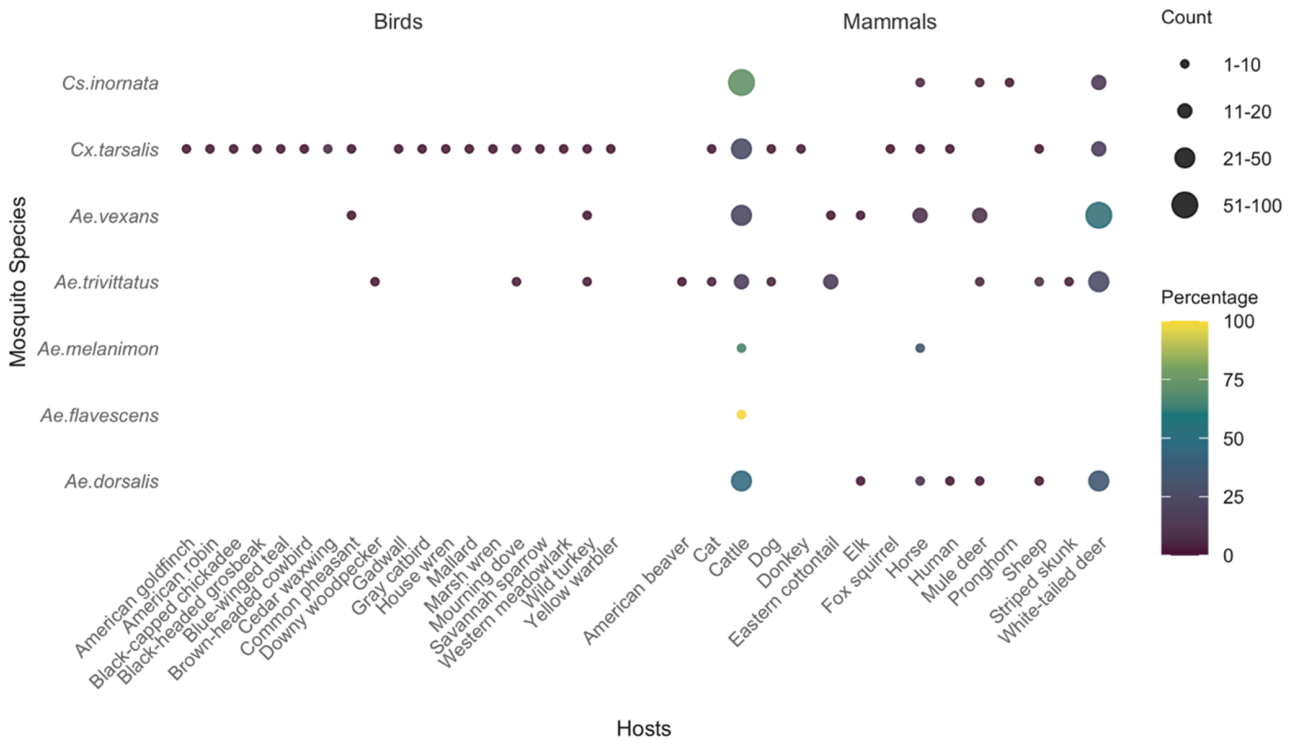

Fig. 5. Blood meals identified from mosquito species collected in Williams County, North Dakota, 2004 to 2006. Counts of hosts for specific mosquito species are identified by the size of the dot. The insert in the upper right shows the range of the count by size of the dot. The percentages of hosts fed upon by a specific mosquito species are identified by the color of the dot. The insert in the lower right shows the heat map.

Downloaded from https://academic.oup.com/jme/article/62/3/621/8029747 by ESA Member Access user on 07 May 2026

Table 3. Multinomial logistic regression model fitting information.

Model	AIC	BIC	−2 Log Likelihood
Host ~ 1	2,402.275	2,421.413	1,197.138
Host ~ Mosquito	2,062.287	2,157.977	1,011.144
Host ~ Mosquito + Date	1,999.624	2,191.002	959.812
Host ~ Mosquito + Date + Trapping Site	1,402.571	1,881.017	601.286

Table 4. Bloodmeal counts of mosquito species on host species in multinomial logistic regression.

[1]Host Species	[2]Mosquito Species	β	St. Error	Odds Ratio	95% Confidence Interval	
					Lower	Upper
[3]Bird	(Intercept)	−1.63	0.9	0.2	0.03	1.15
	Cx. tarsalis	6.25	0.74	**519.25**	122.09	2,208.48
	Ae. trivittatus	3.04	0.7	**20.99**	5.34	82.5
Cattle	(Intercept)	−0.85	0.58	0.43	0.14	1.34
	Ae. dorsalis	0.9	0.43	**2.47**	1.07	5.69
	Cs. inornata	2.28	0.39	**9.79**	4.56	21.03
	Cx. tarsalis	0.9	0.42	**2.46**	1.07	5.66
	Ae. trivittatus	−0.65	0.49	0.52	0.2	1.36
Eastern Cottontail	(Intercept)	−1.89	0.87	**0.15**	0.03	0.84
	Ae. dorsalis	−0.32	1.1	0.73	0.08	6.28
	Cs. inornata	−1.05	1.07	0.35	0.04	2.87
	Cx. tarsalis	0.32	0.67	1.38	0.37	5.16
	Ae. trivittatus	1.71	0.34	**5.54**	2.85	10.79
Horse	(Intercept)	−1.85	1.1	0.16	0.02	1.36
	Ae. dorsalis	1.2	0.45	**3.32**	1.38	8.02
	Cs. inornata	1.48	0.46	**4.41**	1.78	10.9
	Cx. tarsalis	−0.66	0.54	0.52	0.18	1.49
	Ae. trivittatus	−1.73	0.45	**0.18**	0.07	0.43

[1]White-tailed deer is the reference group.
[2]*Aedes vexans* is the reference group.
[3]*Aedes dorsalis* and *Cs. inornata* did not feed on birds; these species were removed.

Grimstad 1991, McLean et al. 1996, Blackmore and Grimstad 1998, Hughes et al. 2023, Shepard and Armstrong 2023), although many other mammals have been seropositive (Hughes et al. 2023, Shepard and Armstrong 2023). *Culiseta inornata* and *Ae. dorsalis* likely become infected with these 3 viruses while acquiring blood from white-tailed deer in North Dakota. Their propensity for feeding on large mammals suggests that *Cs. inornata* and *Ae. dorsalis* are not important vectors for WNV.

Aedes vexans has a predisposition for large mammals such as cattle, horses, and white-tailed deer and readily attacks humans (Horsfall et al. 1973, Tempelis 1975), but it also feeds on small to medium-sized mammals and even birds (Edman 1971, Hayes et al. 1973, Magnarelli 1977, Molaei and Andreadis 2006). In our study, it acquired blood from 14 and 6 species of mammals in eastern and western North Dakota, respectively. White-tailed deer, mule deer, horses, cattle, dogs, sheep, and cottontail rabbits were the primary hosts.

Two hundred 89 isolates of CVV ($n = 92$), JCV ($n = 58$), POTV ($n = 4$), SSHV ($n = 3$), trivittatus virus (TVTV; Peribunyaviridae: Orthobunyavirus) ($n = 77$), and WNV ($n = 55$) were made from *Ae. vexans* in North Dakota in 2003 to 2006. *Aedes vexans* is moderately susceptible to WNV, individual mosquitoes with a disseminated infection can transmit the virus by bite and may be a potentially important bridge vector (Turell et al. 2005), and likely was involved in the transmission of WNV to humans in Cass County, North Dakota, in 2003, where the risk of *Ae. vexans* transmitting WNV to humans was 73.6% (Anderson et al. 2015). This species may have become infected by feeding on passerine birds, although we did not identify this species feeding on passerines, or it may have acquired the virus by feeding on mammals such as squirrels, which develop high viremias (Root et al. 2006, Platt et al. 2008). The aggressive feeding of *Ae. vexans* on humans and their exceptionally high abundance, where numbers averaged 4,000 or more per trap during weeks 25 to 29 in eastern North Dakota and, in western North Dakota, averaged 30,000 per trap in week 28, contributes to their risk of transmitting WNV (Anderson 2023).

The frequent feeding of *Ae. vexans* on large animals suggests this mosquito is likely transmitting CVV, JCV, and POTV, which may be amplified among large mammals in North Dakota, as we stated earlier in this discussion for *Cs. inornata*.

Snowshoe hares and squirrels are likely reservoirs for SSHV (Artsob 1981, McLean 1981, Walker and Yuill 2023). The snowshoe hare virus was isolated from *Ae. vexans* and *Ae. trivittatus* in North Dakota (Anderson et al. 2015). Lagomorphs, particularly eastern cottontail rabbits, were fed upon by *Ae. vexans* and *Ae. trivittatus*, but their role as reservoirs has not been established. Other lagomorphs and squirrels are also abundant.

Aedes vexans was also associated with TVTV. Seventy-seven isolations were made from specimens collected in both eastern and western North Dakota from the second week of June through the first week of August (Anderson et al. 2015). Cottontail rabbits and fox squirrels are reservoir hosts for this virus in Iowa (Pinger et al. 1975). Both these mammals are abundant in North Dakota. *Aedes vexans*, although primarily feeding on large mammals, feeds also on smaller mammals (Magnarelli 1977, Nasci 1984), and in eastern North Dakota, we recorded 8.8% of the feedings to be on cottontail rabbits. *Aedes vexans* may be acquiring TVTV from rabbits.

Aedes trivittatus feeds primarily on mammals, but it is more opportunistic than *Ae. vexans* and feeds on a wider range of hosts (Pinger and Rowley 1975, Nasci 1984). Cottontail rabbits were the primary hosts (68.2%) in central Iowa (Pinger and Rowley 1975). In our study, this species fed frequently on white-tailed deer and cottontail rabbits in eastern and western North Dakota, and, in the western part, it also fed extensively on cattle. The multinomial logistic regression model showed *Ae. trivittatus* fed more often on eastern cottontail compared to *Ae. vexans*.

Five viruses CVV ($n = 2$), JCV ($n = 12$), SSHV ($n = 1$), TVTV ($n = 295$), and WNV ($n = 3$) were identified from the 313 isolates from *Ae. trivittatus* in North Dakota in 2003 to 2006, with TVTV comprising 94.2% and JCV 3.8% of the isolations (Anderson et al. 2015). The frequent feedings of *Ae. trivittatus* on cottontail rabbits in Iowa (Pinger and Rowley 1975) and in our study, as well as the identification of neutralizing antibodies in rabbits and fox squirrels (Pinger et al. 1975), suggest that *Ae. trivittatus* may obtain TVTV from these mammals in North Dakota. The propensity of *Ae trivittatus* to feed on deer and the isolation of JCV and CVV from *Ae. trivittatus* in North Dakota suggest that, *Ae. trivittatus* could be acquiring and transmitting these 2 viruses among white-tailed deer, although competency is not known. While *Ae. trivittatus* is

Downloaded from https://academic.oup.com/jme/article/62/3/621/8029747 by ESA Member Access user on 07 May 2026

competent to transmit WNV (Turell et al. 2005) and fed on passerine birds in our study and others (Pinger and Rowley 1975, Molaei et al. 2008), the relatively few isolations indicate that *Ae. trivittatus* may be an infrequent vector. As mentioned previously, *Ae. trivittatus* may also be involved in the transmission of SSHV (Walker and Yuill 2023).

Acknowledgments

We thank Loida Tobias, Silka Tobias, David Benth, Chris Bean, and Jacquelin Stenehjem for collecting mosquitoes and sending them on dry ice to our laboratory. Jacquelin Stenehjem made arrangements for the Williston Vector Control, District 1, to collect mosquitoes. The Williston Vector Control Board allowed us to have their employees collect mosquitoes and to use their facilities. Gary Brewer, Chairman, Department of Entomology, North Dakota State University, provided helpful suggestions and arranged the use of their laboratories and equipment and for the employment of Loida and Silka Tobias. We thank many North Dakota citizens for allowing us to trap mosquitoes on their properties, including William Barker of North Dakota State University, who enabled us to trap mosquitoes at the Ekre Ranch. The following provided superb technical assistance at the Connecticut Agricultural Experiment: Bonnie Hamid, Amanda Rahmann, Michael Vasil, Terrill Goodman, John Shepard, Michael Thomas, Elizabeth Alves, Tanya Petruff, Clare Secker-Walker, Leah Heibi, Alyson Florek, Charles McGee, Susan McKnight, Sarah Reef, Leigh Cash, and Michael Olson. John Shepard and Michael Thomas verified the identities of selected specimens. We thank the Yale University StatLab for consultation for the statistical analysis.

Author contributions

John Anderson (Conceptualization [equal], Funding acquisition [equal], Investigation [equal], Writing—original draft [equal], Writing—review & editing [equal]), Angela Bransfield (Investigation [equal], Writing—review & editing [equal]), Michael Misencik (Investigation [equal], Writing—review & editing [equal]), Sydney Jones (Formal analysis [equal], Writing—original draft [equal]), Andy Main (Investigation [equal], Writing—review & editing [equal]), Philip Armstrong (Investigation [equal], Writing—review & editing [equal]), Theodore Andreadis (Funding acquisition [equal], Investigation [equal], Writing—review & editing [equal]), and Goudarz Molaei (Conceptualization [equal], Methodology [equal], Writing—review & editing [equal])

Funding

This work was supported in part by USDA Specific Cooperative agreement 58-6615-1-218 and by Laboratory Capacity for Infectious Diseases Cooperative Agreement U50/CCU116806-01-1 from the Centers for Disease Control and Prevention.

Conflicts of interest. None declared.

References

Anderson RA, Gallaway WJ. 1987. The host preferences of *Culiseta inornata* in southwestern Manitoba. J. Am. Mosq. Control Assoc. 3:219–221.

Anderson JF, Main AJ, Armstrong PM, et al. 2015. Arboviruses in North Dakota, 2003-2006. Am. J. Trop. Med. Hyg. 92:377–393. https://doi.org/10.4269/ajtmh.14-0291

Anderson JF, Main AJ, Armstrong PM, et al. 2023. Seasonality of mosquitoes in North Dakota, 2003-2006, with four new state records. J. Am. Mosq. Control Assoc. 39:68–74. https://doi.org/10.2987/23-7118

Andreadis TG, Thomas MC, Shepard JJ. 2005. Identification guide to the mosquitoes of Connecticut. Bull. Conn. Agric. Exp. Stn 966:1–173.

Apperson CS, Harrison BA, Unnasch TR, et al. 2002. Host-feeding habits of *Culex* and other mosquitoes (Diptera: Culicidae) in the Borough of Queens in New York City, with characters and techniques for identification of *Culex* mosquitoes. J. Med. Entomol. 39:777–785. https://doi.org/10.1603/0022-2585-39.5.777

Artsob H, 1981. California encephalitis (CE). In: Steele JH, Beran GW, editors. Handbook Series in Zoonoses. Section B: Viral Zoonoses. Boca Raton, FL: CRC Press. p. 150–154.

Barr AR. 1958. The mosquitoes of Minnesota (Diptera: Culicidae: Culicinae). Univ. Minn. Agric. Exp. Sta. Tech. Bull. 228:1–154.

Blackmore CG, Grimstad PR. 1998. Cache Valley and Potosi viruses (Bunyaviridae) in white-tailed deer (*Odocoileus virginianus*): experimental infections and antibody prevalence in natural populations. Am. J. Trop. Med. Hyg. 59:704–709. https://doi.org/10.4269/ajtmh.1998.59.704

Borchardt SM, Feist MA, Miller T, et al. 2010. Epidemiology of West Nile virus in the highly epidemic state of North Dakota, 2002-2007. Public Health Rep. 125:246–249. https://doi.org/10.1177/003335491012500213

Carpenter SJ, LaCasse WJ. 1955. Mosquitoes of North America (North of Mexico). Berkeley: University of California Press. p. 360.

Corner LC, Robertson AK, Hayles LB, et al. 1980. Cache Valley virus: experimental infection in *Culiseta inornata*. Can. J. Microbiol. 26:287–290. https://doi.org/10.1139/m80-048

Darsie RFJr, Anderson AW. 1985. A revised list of the mosquitoes of North Dakota, including new additions to the fauna. J. Am. Mosq. Control Assoc. 1:76–79.

Darsie RFJr, Ward RA. 1981. Identification and geographic distribution of mosquitoes of North America, north of Mexico. Mosq. Syst. 1:1–313.

Darsie RF, Jr., Ward RA. 2005. Identification and geographical distribution of the mosquitoes of North America, North of Mexico. Gainesville: University Press of Florida. p. 383.

Edman JD. 1971. Host-feeding patterns of Florida mosquitoes I. *Aedes*, *Anopheles*, *Coquillettidia*, *Mansonia* and *Psorophora*. J. Med. Entomol. 8:687–695. https://doi.org/10.1093/jmedent/8.6.687

Goddard LB, Roth AE, Reisen WK, et al. 2002. Vector competence of California mosquitoes for West Nile virus. Emerg. Infect. Dis. 8:1385–1391. https://doi.org/10.3201/eid0812.020536

Hammon WM, Reeves WC. 1943. Laboratory transmission of western equine encephalomyelitis virus by mosquitoes of the genera *Culex* and *Culiseta*. J. Exp. Med. 78:425–434. https://doi.org/10.1084/jem.78.6.425

Hayes RO, Tempelis CH, Hess AD, et al. 1973. Mosquito host preference studies in Hale County, Texas. Am. J. Trop. Med. Hyg. 22:270–277. https://doi.org/10.4269/ajtmh.1973.22.270

Hoffman SD, Duncan GJ. 1988. Multinomial and conditional logit discrete-choice models in demography. Demography 25:415–427. https://doi.org/10.2307/2061541

Horsfall WR. 1955. Mosquitoes-their bionomics and relation to disease. New York: The Ronald Press Company. p. 723.

Horsfall WR, Fowler HW, Moretti LJ, et al. 1973. Bionomics and embryology of the inland floodwater mosquito *Aedes vexans*. Urbana: University of Illinois Press.p. 211p.

Hughes HR, Kenney JL, Calvert AE. 2023. Cache Valley virus: an emerging arbovirus of public and veterinary health importance. J. Med. Entomol. 60:1230–1241. https://doi.org/10.1093/jme/tjad058

Karabatsos N. 1985. International catalogue of arboviruses, including certain other viruses of vertebrates. San Antonio,Texas: American Society of Tropical Medicine and Hygiene for The Subcommittee on Information Exchange of the American Committee On Arthropod-borne Viruses. p. 1147.

Komar N, Langevin S, Hinten S, et al. 2003. Experimental infection of North American birds with the New York 1999 strain of West Nile virus. Emerg. Infect. Dis. 9:311–322. https://doi.org/10.3201/eid0903.020628

Kramer LD, Bowen MD, Hardy JL, et al. 1993. Vector competence of alpine, Central Valley, and coastal mosquitoes (Diptera: Culicidae) from California for Jamestown Canyon virus. J. Med. Entomol. 30:398–406. https://doi.org/10.1093/jmedent/30.2.398

Kramer LD, Styer LM, Ebel GD. 2008. A global perspective on the epidemiology of West Nile virus. Annu. Rev. Entomol. 53:61–81. https://doi.org/10.1146/annurev.ento.53.103106.093258

Downloaded from https://academic.oup.com/jme/article/62/3/621/8029747 by ESA Member Access user on 07 May 2026

Lanciotti RS, Kerst AJ, Nasci RS, et al. 2000. Rapid detection of West Nile virus from human clinical specimens, field-collected mosquitoes, and avian samples by a TaqMan reverse transcriptase-PCR assay. J. Clin. Microbiol. 38:4066–4071. https://doi.org/10.1128/JCM.38.11.4066-4071.2000

Leake JP. 1941. Epidemic of infectious encephalitis. Pub. Health Rep. 56:1902–1905. https://doi.org/10.2307/4583872

Luby JP. 1979. St. Louis encephalitis. Epidemiol. Rev. 1:55–73. https://doi.org/10.1093/oxfordjournals.epirev.a036214

Magnarelli LA. 1977. Host feeding patterns of Connecticut mosquitoes (Diptera: Culicidae). Am. J. Trop. Med. Hyg. 26:547–552. https://doi.org/10.4269/ajtmh.1977.26.547

McLean DM, 1981. California group viral infections of Canada. In: Steele JH, Beran GW, editors. Handbook series in zoonoses. Section B: viral zoonoses. Boca Raton, FL: CRC Press. p. 107–111.

McLean RG, Kirk LJ, Shriner RB, et al. 1996. The role of deer as a possible reservoir host of Potosi virus, a newly recognized arbovirus in the United States. J. Wildl. Dis. 32:444–452. https://doi.org/10.7589/0090-3558-32.3.444

Mehus JO, Vaughan JA. 2013. Molecular identification of vertebrate and hemoparasite DNA within mosquito blood meals from eastern North Dakota. Vector Borne Zoonotic Dis. 13:818–824. https://doi.org/10.1089/vbz.2012.1193

Molaei G, Andreadis TG. 2006. Identification of avian- and mammalian-derived bloodmeals in *Aedes vexans* and *Culiseta melanura* (Diptera: Culicidae) and its implication for West Nile virus transmission in Connecticut, U.S.A. J. Med. Entomol. 43:1088–1093. https://doi.org/10.1603/0022-2585(2006)43[1088:IOAAMB]2.0.CO;2

Molaei G, Oliver J, Andreadis TG, et al. 2006a. Molecular identification of blood-meal sources in *Culiseta melanura* and *Culiseta morsitans* from an endemic focus of eastern equine encephalitis virus in New York. Am. J. Trop. Med. Hyg. 75:1140–1147. https://doi.org/10.4269/ajtmh.2006.75.1140

Molaei G, Andreadis TG, Armstrong PM, et al. 2006b. Host feeding patterns of *Culex* mosquitoes and West Nile virus transmission, northeastern United States. Emerg. Infect. Dis. 12:468–474. https://doi.org/10.3201/eid1203.051004

Molaei G, Andreadis TG, Armstrong PM, et al. 2007. Host feeding pattern of *Culex quinquefasciatus* (Diptera: Culicidae) and its role in transmission of West Nile virus in Harris County, Texas. Am. J. Trop. Med. Hyg. 77:73–81. https://doi.org/10.4269/ajtmh.2007.77.73

Molaei G, Andreadis TG, Armstrong PM, et al. 2008. Host-feeding patterns of potential mosquito vectors in Connecticut, U.S.A.: molecular analysis of bloodmeals from 23 species of *Aedes*, *Anopheles*, *Culex*, *Coquillettidia*, *Psorophora*, and *Uranotaenia*. J. Med. Entomol. 45:1143–1151. https://doi.org/10.1603/0022-2585(2008)45[1143:hpopmv]2.0.co;2

Nasci RS. 1984. Variatons in the blood-feeding patterns of *Aedes vexans* and *Aedes trivittatus* (Diptera: Culicidae). J. Med. Entomol. 21:95–99. https://doi.org/10.1093/jmedent/21.1.95

Neitzel DF, Grimstad PR. 1991. Serological evidence of California group and Cache Valley virus infection in Minnesota white-tailed deer. J. Wildl. Dis. 27:230–237. https://doi.org/10.7589/0090-3558-27.2.230

Ngo KA, Kramer LD. 2003. Identification of mosquito bloodmeals using polymerase chain reaction (PCR) with order-specific primers. J. Med. Entomol. 40:215–222. https://doi.org/10.1603/0022-2585-40.2.215

Pinger RR, Rowley WA. 1975. Host preferences of *Aedes trivittatus* (Diptera: Culicidae) in central Iowa. Am. J. Trop. Med. Hyg. 24:889–893. https://doi.org/10.4269/ajtmh.1975.24.889

Pinger RR, Rowley WA, Wong YW, et al. 1975. Trivittatus virus infections in wild mammals and sentinel rabbits in central Iowa. Am. J. Trop. Med. Hyg. 24:1006–1009. https://doi.org/10.4269/ajtmh.1975.24.1006

Platt KB, Tucker BJ, Halbur PG, et al. 2008. Fox squirrels (*Sciurus niger*) develop West Nile virus viremias sufficient for infecting select mosquito species. Vector Borne Zoonotic Dis. 8:225–233. https://doi.org/10.1089/vbz.2007.0182. https://www.ncbi.nlm.nih.gov/pubmed/1824096

Post RL, Munro JA. 1949. Mosquitoes of North Dakota. N. D. Agr. Expert. Sta. Bimonthly Bull 11:173–183.

Reeves WC, Tempelis CH, Bellamy RE, et al. 1963. Observations on the feeding habits of *Culex tarsalis* in Kern County, California, using precipitating antisera produced in birds. Am. J. Trop. Med. Hyg. 12:929–935. https://doi.org/10.4269/ajtmh.1963.12.929

Root JJ, Oesterle PT, Nemeth NM, et al. 2006. Experimental infection of fox squirrels (*Sciurus niger*) with West Nile virus. Am. J. Trop. Med. Hyg. 75:697–701. https://doi.org/10.4269/ajtmh.2006.75.697

Sexton DJ, Rollin PE, Breitschwerdt EB, et al. 1997. Life-threatening Cache Valley virus infection. N. Engl. J. Med. 336:547–549. https://doi.org/10.1056/NEJM199702203360804

Shemanchuk JA, Downe AER, Burgess L. 1963. Hosts of mosquitoes (Dipter: Culicidae) from the irrigated areas of Alberta. Mosq. News 23:336–341.

Shepard JJ, Armstrong PM. 2023. Jamestown Canyon virus comes into view: understanding the threat from an underrecognized arbovirus. J. Med. Entomol. 60:1242–1251. https://doi.org/10.1093/jme/tjad069

Smith JF, Davis K, Hart MK, et al. 1997. Viral encephalitides. In: Sidell, FR., Takafuji, ET and Franz, DR, editors. Medical aspects of chemical and biological warfare. Washington, D. C: Borden Institute, Walter Reed Army Medical Center. p. 561–589.

Stoklosa J, Blakey RV, Hui FKC. 2022. An overview of modern applications of negative binomial modelling in ecology and biodiversity. Diversity 14:320. https://doi.org/10.3390/d14050320

Tempelis CH. 1975. Host-feeding patterns of mosquitoes, with a review of advances in analysis of blood meals by serology. J. Med. Entomol. 11:635–653. https://doi.org/10.1093/jmedent/11.6.635

Tempelis CH, Reeves WC, Bellamy RE, et al. 1965. A three-year study of the feeding habits of *Culex tarsalis* in Kern County, California. Am. J. Trop. Med. Hyg. 14:170–177. https://doi.org/10.4269/ajtmh.1965.14.170

Thiemann TC, Lemenager DA, Kluh S, et al. 2012. Spatial variation in host feeding patterns of *Culex tarsalis* and the *Culex pipiens* complex (Diptera: Culicidae) in California. J. Med. Entomol. 49:903–916. https://doi.org/10.1603/me11272

Turell MJ, Dohm DJ, Sardelis MR, et al. 2005. An update on the potential of North American mosquitoes (Diptera: Culicidae) to transmit West Nile virus. J. Med. Entomol. 42:57–62. https://doi.org/10.1093/jmedent/42.1.57

Walker ED, Yuill TM. 2023. Snowshoe hare virus: discovery, distribution, vector and host associations, and medical significance. J. Med. Entomol. 60:1252–1261. https://doi.org/10.1093/jme/tjad128

Downloaded from https://academic.oup.com/jme/article/62/3/621/8029747 by ESA Member Access user on 07 May 2026