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# A Scoping Review on the Epidemiology of Orthobunyaviruses of Canadian Public and Animal Health Relevance in the Context of Vector Species

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## Abstract

**Background:** Mosquito-borne orthobunyaviruses are a growing priority for public and animal health in Canada. It is anticipated that disease incidence will increase due to a warming climate, given that habitats are expanding for reservoir hosts and vectors, particularly in Canada. Little is known about the ecology of primary vectors that perpetuate these orthobunyaviruses, including the viral transmission cycle and the impact of climatic and landscape factors.

**Methods:** A scoping review was conducted to describe the current state of knowledge on the epidemiology of orthobunyaviruses relevant to Canada. The Preferred Reporting Items for Systematic Reviews and Meta-Analyses extension for Scoping Reviews guidelines was used to characterize studies focused on vector species. A literature search was conducted in six databases and gray literature. Eligible studies characterized orthobunyavirus epidemiology related to vector species, including viral competency, geospatial distributions, seasonal trends, and/or risk factors.

**Results:** A total of 1734 unique citations were identified. Screening of these citations revealed 172 relevant studies, from which 87 studies presented primary data related to vectors. The orthobunyaviruses included Cache Valley virus (CVV), Jamestown Canyon virus (JCV), Snowshoe Hare virus (SHV), and La Crosse virus (LACV). Surveillance was the predominant study focus, with most citations representing the United States, specifically, LACV surveillance in Tennessee, followed by CVV and JCV in Connecticut. Orthobunyaviruses were detected in many mosquito species across multiple genera, with high vector specificity only being reported for LACV, which included *Aedes triseriatus*, *Aedes albopictus*, and *Aedes japonicus*. Peridomestic areas were positively associated with infected mosquitoes compared with dense forests. Orthobunyavirus infections, coinfections, and gut microbiota affected mosquito feeding and breeding behavior.

**Conclusion:** Knowledge gaps included Canadian surveillance data, disease modeling, and risk projections. Further research in these areas, especially accounting for climate change, is needed to guide health policy for prevention of orthobunyaviral disease.

**Keywords:** orthobunyaviruses, mosquito-borne zoonoses, vector, epidemiology, surveillance, climate

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## Introduction

CACHE VALLEY VIRUS (CVV), Jamestown Canyon virus (JCV), La Crosse virus (LACV), and Snowshoe Hare virus (SHV) are mosquito-borne orthobunyaviruses (*Peribunyaviridae* family) that are endemic in North America, and can cause viral meningoencephalitis in humans (Evans and Peterson, 2019; Gill et al., 2019; Rust et al., 1999). Cache Valley virus can cause lethal congenital deformities in animals, predominantly sheep (Chung et al., 1990; Edwards et al., 1997). Orthobunyaviruses are the second leading cause of morbidity from domestic arboviral infections in both Canada and the United States, and can predispose patients to chronic sequelae (Fagre et al., 2023; Public Health Agency of Canada, 2023; Soto et al., 2022; Vahey et al., 2021). Infections are likely underdiagnosed (Dimitrova et al., 2011; Makowski et al., 2011), and since reporting is based on passive surveillance, the true health burden of orthobunyaviral diseases is unknown (Totten et al., 2019).

Range expansion of orthobunyaviral vectors due to climate change has been identified as an emerging public health risk, with establishment already noted for *Aedes (Ae.) albopictus* in the temperate climates of Vermont, the United States and Ontario, Canada (Giordano et al., 2020; Khan et al., 2020; Kulkarni et al., 2015; Ludwig et al., 2019; Ogden et al., 2019; Vermont Department of Health, 2024). As such, there is a need to prioritize orthobunyavirus epidemiology research.

These four mosquito-borne zoonoses have distinct sylvatic cycles. The white-tailed deer (*Odocoileus virginianus*) is considered the main vertebrate reservoir for CVV and JCV (Blackmore and Grimstad, 1998; Boromisa and Grimstad, 1987; Issel et al., 1972), while the Eastern chipmunk (*Tamias striatus*) and snowshoe hare (*Lepus americanus*) are the primary hosts for LACV and SHV, respectively (Cully et al., 1992; Cully et al., 1991; Hoff et al., 1969). The vectors also vary across the viruses. *Aedes triseriatus* is considered the primary vector for transmitting LACV, with *Ae. albopictus* and *Ae. japonicus* potentially important secondary LACV vectors (Bara et al., 2016; Harris et al., 2015; Westby et al., 2015). Conversely, for the other three orthobunyaviruses, a wide range of mosquito species across genera are associated with viral transmission (Andreadis et al., 2014; Andreadis et al., 2008; Heard et al., 1991; McMillan et al., 2020; Walker et al., 1993).

Mosquito-borne diseases subsequently arise from complex and highly sensitive interactions between the pathogen, vector, host, and environment. Alterations to this dynamic ecological balance can significantly affect transmission dynamics. Such examples include (1) competition either between mosquito species in the same geographic location or between multiple pathogens within an individual mosquito (Bevins, 2008; Grim, 2006); (2) climatic changes that impact the development duration of the mosquito and the extrinsic incubation period of the virus; (3) land use changes that alter interaction frequencies between vectors and hosts (Armstrong et al., 2017; Bara and Muturi, 2015; Khan et al., 2020; Swanson et al., 2000); (4) genetic reassortment within the virus that changes virulence, vector competency, or host range (Baker et al., 2021; Borucki et al., 1999), or (5) a combination of several of these factors.

These complex relationships are well studied for West Nile virus (WNV), resulting in robust surveillance and preventive measures for mitigating disease (Andreadis et al., 2004;

Andreadis et al., 2001; Drebot et al., 2003; Giordano et al., 2018; Giordano et al., 2017; Nosal and Pellizzari, 2003). However, the transmission cycle is not well understood for orthobunyaviruses in Canada, particularly the vector species involved. Studies have investigated the profile of mosquito vectors in Canada, but viral testing is minimal and inconsistently reported (Drebot, 2015). This scoping review aims to describe the current state of knowledge on the epidemiology of orthobunyaviruses of Canadian public and animal health relevance in the context of vector species, including climate change impacts on the ecology, distribution, and exposure risk in orthobunyavirus vectors.

## Methods

The methods were previously described in Bergevin et al. (2024). In brief, the protocol was established *a priori* (in Doc. S1 of Bergevin et al., 2024) and guided the process for the literature search, screening, and data characterization, all of which adhered to the Preferred Reporting Items for Systematic Reviews and Meta-Analyses extension for Scoping Reviews (PRISMA-ScR) guidelines and methodological framework (Peters et al., 2015; Tricco et al., 2018). A literature search was performed up to March 12, 2021 in six databases comprised of primary research articles related to medicine, public health, science, and the environment.

In addition, gray literature searches were performed in Google, Google scholar, five theses repositories, and government health agency websites representing the national, provincial/statewide, and local levels. Searches included terms related to CVV, JCV, LACV, SHV, another orthobunyavirus referenced in the context of Canada, or a vector or host species reported in the context of a relevant orthobunyavirus. Multiple techniques were implemented to validate the literature search, including bibliography evaluations of seminal papers and review articles.

Citations identified were uploaded into reference management software (Zotero; Center for History and New Media, George Mason University, Fairfax, VA) and deduplicated. Citations were next uploaded to an online systematic review management program (Distiller SR; Evidence Partners, Ottawa, Canada) for additional deduplication and relevance screening. Citations were included if published during or after 1999. This year was chosen because it was when the first human case of WNV was detected in North America, which led to robust improvements in mosquito surveillance and arbovirus detection methods (Drebot et al., 2003; Ford-Jones et al., 2002).

Eligible citations were defined as primary studies, in English or French, and had an epidemiologic focus. Despite interest in orthobunyaviruses of relevance in Canada, no geographic restrictions were placed to fully capture the current knowledge base on these viruses. Eligibility was evaluated first by title/abstract followed by full-text screening. Included citations were then characterized (in Doc. S1 of Bergevin et al., 2024). All screening and data characterization were performed by two independent reviewers, and if agreement was not met, a third reviewer was consulted. All extracted data were exported from Distiller SR in spreadsheet format for analysis and visualization using Excel, ver. 16.3 (Microsoft Corp., Redmond, WA) and RStudio, ver. 2023.03 (Posit software, PBC: Integrated Development for R; Boston, MA).

During data characterization, it became apparent that vector- and host-related data could not adequately be reported in a single scoping review due to the breadth of relevant data captured. Since the relevant studies reported solely on host-related or vector-related findings, with minimal exceptions, the studies were characterized in a way to prevent double reporting. One publication presented epidemiologic data related to host species, including incidence, geospatial distribution of prevalence, risk factors associated with vertebrate host species, and seasonal trends (Bergevin et al., 2024). This article focuses on orthobunyaviruses in the context of vector species, including the viral transmission cycle and the impact of climatic and landscape factors.

## Results

### General characteristics

The literature search identified 1734 unique citations. Following title/abstract and full-text screening, 172 relevant citations were identified, of which 87 citations (51%) presented primary data pertaining to vector species. A subset of these vector studies applied a broader perspective by investigating additional aspects of the transmission cycle, including environmental factors ( $n=23$ , 26%), deeper analyses of the orthobunyaviruses ( $n=26$ , 30%), or host surveillance in overlapping geographic regions ( $n=11$ , 13%) (Supplementary Fig. S1).

Among the 87 studies that presented vector data (Supplementary Data S1), all in English, 77 (89%) were peer-reviewed primary publications, and 10 (11%) were gray literature studies comprised of a conference proceeding (CVV focused) (Langer-Curry et al., 2005), a state department public health report (LACV focused) (Byrd et al., 2018), and 8 theses ( $n_{LACV}=7$ ,  $n_{JCV,SHV}=1$ ) (Bassett, 2014; Caldwell, 2004; Grim, 2006; Henry, 2016; Morton, 2003; Ramaswamy, 2015; Scheffel, 2006; Troyano, 2009).

Seventy-one studies investigated a single orthobunyavirus, and 16 studies assessed multiple orthobunyaviruses (Fig. 1). LACV was investigated most often (69%) and predominantly in isolation. In contrast, JCV and SHV were more often investigated in combination with other orthobunyaviruses. For CVV, the studies were split between focusing on the individual virus and in combination with other orthobunyaviruses.

The number of publications trended upward over time, with half the citations published in 2013 or later, and the most

prolific year being 2020 (nine studies) (Fig. 2). Vector surveillance and virus detection studies were most common ( $n=49$ ). A subset of these studies further explored virus phylogeny ( $n=18$ ). Spatiotemporal risk factor analysis ( $n=33$ ) was evaluated in relation to geographic distribution or seasonal patterns of vectors and viruses. Pathogen transmission studies ( $n=31$ ) explored vector competency ( $n=20$ ), bloodmeal analysis ( $n=7$ ), and/or coinfection effects on orthobunyavirus transmission ( $n=5$ ).

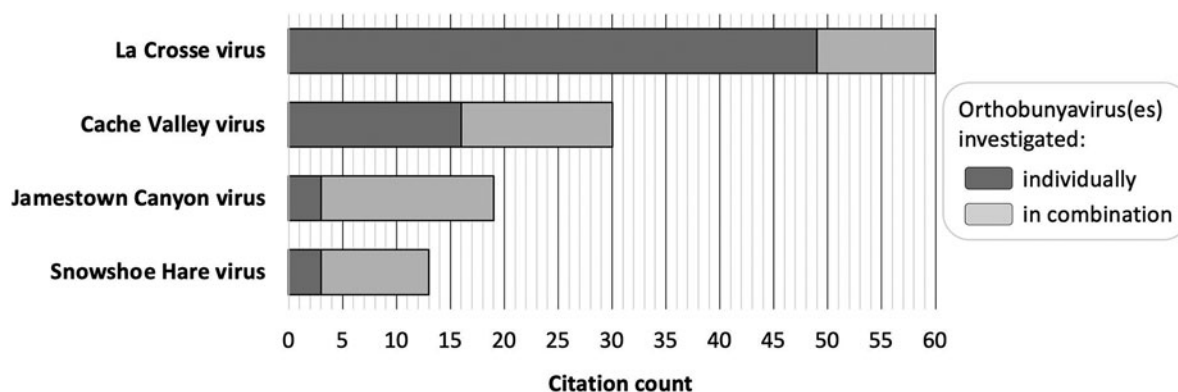
Environmental risk factors were investigated for associations between habitat or weather and vector abundance/composition ( $n=20$ ). Research topics published more recently included forecasting ( $n=5$ ) and methodology papers focused on either vector trapping strategies ( $n=3$ ) or virus detection within vectors ( $n=4$ ). Only one paper focused on prevention measures, specifically, infection deterrents in mosquitoes (Eastepp et al., 2012).

Several study designs were utilized across the eligible citations. Observational studies represented the majority, both descriptive ( $n=41$ ) and analytical ( $n=20$ ). Experimental studies ( $n=30$ ) were also captured, including randomized control trials related to mosquito surveillance or trapping effectiveness ( $n=5$ ) (Eastwood et al., 2020a; Henry, 2016; Tamini et al., 2021; Urquhart et al., 2016; Williams et al., 2007), challenge trials related to vector competency ( $n=23$ ), and methodology studies that explored viral detection techniques ( $n=4$ ) (Armstrong et al., 2011; Kinsella et al., 2020; Ngo et al., 2006; Pabbaraju et al., 2009).

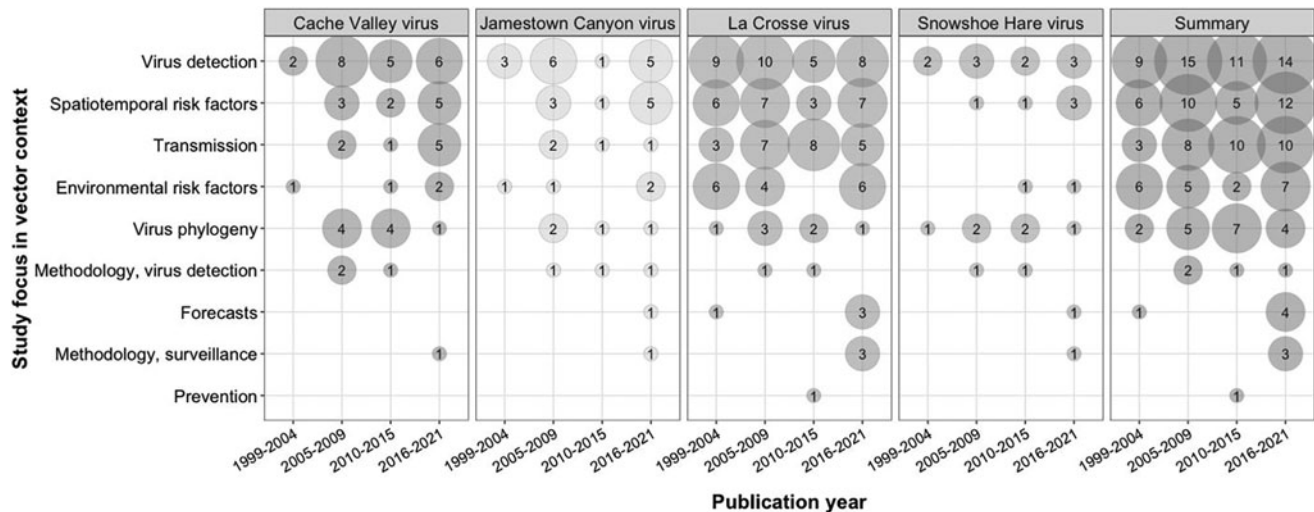
Geographic representation of field data was primarily focused on North America, representing 20 states within the continental United States, 4 provinces in Canada, and 2 states in Mexico (Fig. 3). Eighty-eight percent of the studies ( $n=61$ ) focused on the United States. The remaining 12% consisted of five studies in Canada (Bassett, 2014; Carson et al., 2017; Ludwig et al., 2023; Pabbaraju et al., 2009; Williams et al., 2007), and three studies in Mexico (Blitvich et al., 2012a; Farfan-Ale et al., 2010; Farfan-Ale et al., 2009). (Citation allocations per country and state/province are detailed in Supplementary Data S2.)

### Geographic distribution of orthobunyavirus in vectors

CVV was detected in mosquitoes in 10 states or provinces across all three countries (Fig. 3). Only Montana (USA) was negative for CVV, but midges were surveilled rather than



**FIG. 1.** Frequency of vector-related studies ( $n=87$ ) that evaluated an orthobunyavirus individually (dark gray,  $n=71$ ) versus in combination with at least one additional orthobunyavirus (light gray,  $n=16$ ).



**FIG. 2.** Bubble plot of the study focus versus publication year stratified by virus ( $n=87$  citations). Categories were not mutually exclusive regarding focus or virus type, as exemplified in the summary counts. Circle size corresponds to the number of citations. Publications in 2021 captured the literature up to March only.

mosquitoes, which are the natural vector species (Johnson et al., 2014). JCV was only detected in the continental United States, specifically six states (Fig. 3). LACV was also only detected in the continental United States, specifically 10 states. Extensive focus was given to the central Appalachia region of the United States (Tennessee, Virginia, West Virginia, North Carolina), which is considered a hotspot for La Crosse encephalitis (LACE) in humans (Fig. 3).

SHV was only detected in Newfoundland, Canada, and North Dakota, the United States (Anderson et al., 2015; Bassett, 2014; Carson et al., 2017). In summary, all four orthobunyaviruses were predominantly detected in the eastern United States. The remaining regions either did not detect virus in field-caught vectors, or investigated other factors that impact orthobunyavirus transmission without directly testing for a virus. (Regional allocations of citations are detailed in Supplementary Data S2.)

Only two studies conducted surveillance outside North America. One study detected orthobunyavirus from mosquitoes sampled in Russia that were serologically classified as SHV, but sequence analysis demonstrated a distinction from the North American strains (Vanlandingham et al., 2002). The other study conducted arbovirus surveillance in Greenland and Svalbard, Norway, but detected no orthobunyaviruses, which the authors attributed to either insignificant viral activity or a poor experimental design (Mullerova et al., 2018).

#### *Orthobunyavirus detection by vector species*

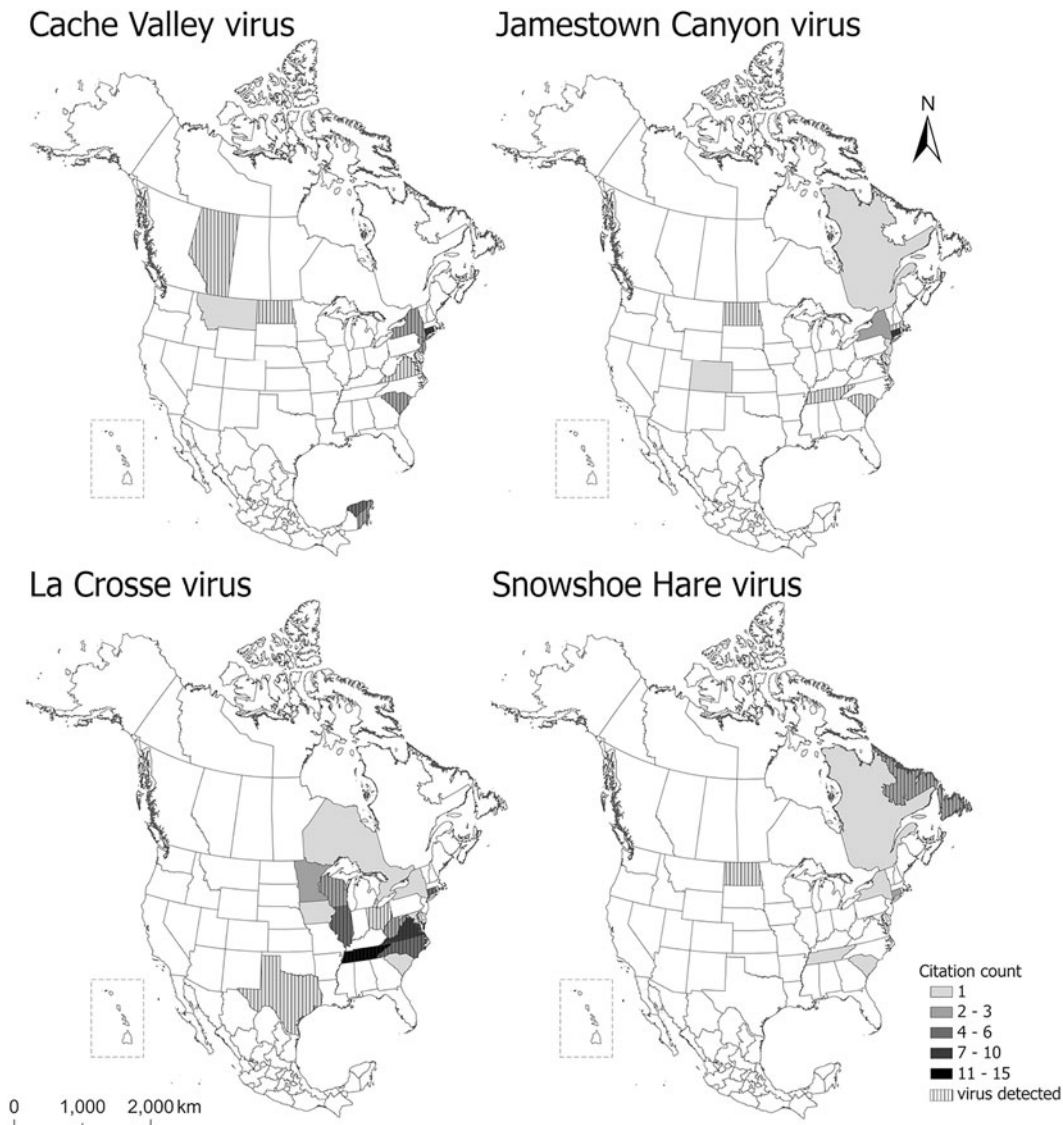
Natural infection with an orthobunyavirus was surveilled in 43 citations (49%, 43 of 87 citations) that cumulatively tested 86 hematophagous arthropod species, including 85 mosquito species (Diptera: Culicidae) and 1 biting midge (Diptera: Ceratopogonidae). Among the mosquito surveillance studies, eight analyzed secondary data based on trapping protocols that either targeted general arbovirus testing (Armstrong et al., 2017; Ngo et al., 2006; Ortiz et al., 2005; Takeda et al., 2003; Wozniak et al., 2001) or specifically, Eastern equine

encephalitis virus (EEEV) and/or WNV (Anderson et al., 2015; Molaei et al., 2009; Petrucci et al., 2020).

At least one orthobunyavirus was detected in nearly half the mosquito species tested (44%, 37 of 85 mosquito species), but no midges were infected with an orthobunyavirus (Johnson et al., 2014; Reeves and Miller, 2013) (Fig. 4). CVV was most tested, representing 79 mosquito species (93%, 79 of 85 mosquito species), of which 24 species (30%, 24/79) across 7 genera were positive for CVV, and 1 midge species (*Culicoides sonorensis*) that was negative. The species most reported to be positive for CVV included *Ae. japonicus* (80%, 4 of 5 citations), *Ae. cinereus* (80%, 4/5), and *Ae. trivittatus* (75%, 6/8). JCV was detected in 33 of 59 mosquito species (56%) distributed across the same 7 genera as CVV, although the species differed slightly.

The mosquitoes most reported for JCV were *Ae. cantator* (100%, 4 of 4 citations), *Ae. trivittatus* (83%, 5/6), and *Ae. stricklandi* (75%, 6/8). Fewer species of mosquito were positive for LACV (17%, 9 of 53 mosquito species), and only *Ae. triseriatus* was predominantly positive (55%, 11 of 20 citations). Few studies reported mosquitoes naturally infected with SHV (10%, 6 of 63 mosquito species), and mostly in *Ae. abserratus* (67%, 2 of 3 citations), *Ae. punctor* (67%, 2/3), and *Ae. pionips* (67%, 2/3).

Viral testing was based on molecular tests (88%, 38 of 43 citations), immunology assays (53%, 23/43), and/or virus isolation (35%, 15/43). Most studies used multiple techniques to confirm a natural infection (65%, 28/43), and 2 studies (5%, 2/43) did not report testing methods (Morton, 2003; Swanson et al., 2000). All studies determined the mosquito species based on morphology, and three studies confirmed with molecular techniques. Similar landscapes were represented across surveillance studies, which included urban and rural environments across woodlots, wetlands, grasslands, and regions with stagnant water. Other aspects of the methodologies varied greatly, including trap types and trapping duration relative to the season (*i.e.*, first to last month), time period per trap (*i.e.*, hours to weeks), and number of collections per season.



**FIG. 3.** Geospatial representation of vector field data collected for orthobunyavirus analysis ( $n=69$ ), per province or state in North America. Citation counts varied across virus (Cache Valley virus=23, Jamestown Canyon virus=17, La Crosse virus=51, Snowshoe Hare virus=10) and correspond to the intensity of color per designated region. Note: Hawaii is not to scale. Shapefiles were obtained from Statistics Canada, United States Census Bureau, and Instituto Nacional de Estadística y Geografía for Mexico. (Citation allocations as well as regions where virus was detected are detailed in Supplementary Data S2.).

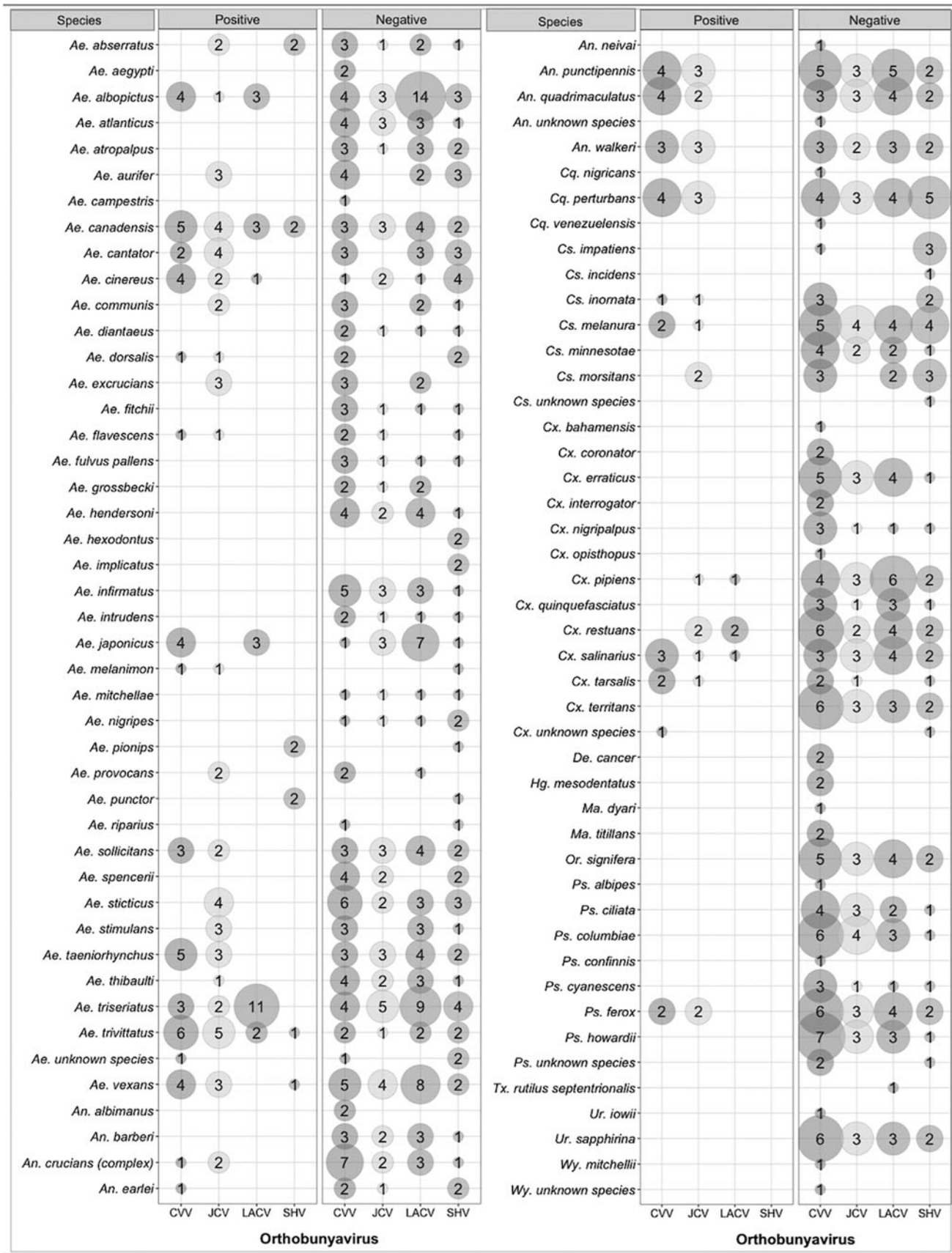
#### *Orthobunyavirus-vector competency testing*

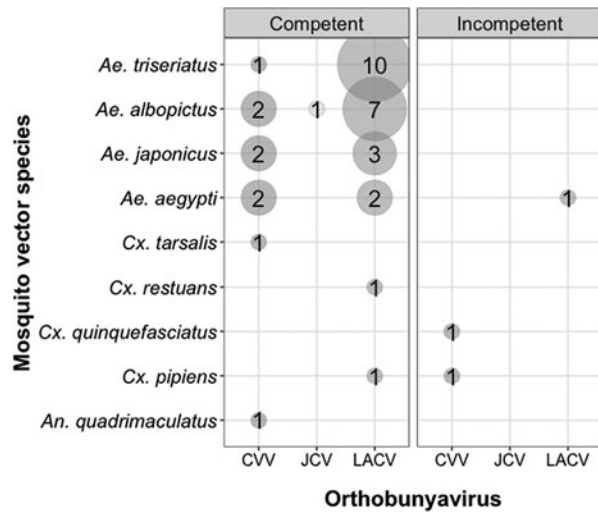
Pathogen transmission in mosquitoes or from mosquitoes to hosts was explored in 13 studies (Fig. 5), although the methods used to verify vector competency varied greatly (Supplementary Table S1). Vertical transmission was confirmed for JCV and LACV either by testing adults that were

reared in the laboratory as field-caught eggs (Gottfried et al., 2002; Reese et al., 2009; Westby et al., 2015) or through experimental infection of adult mosquitoes before copulation (Hughes et al., 2006).

Horizontal transmission of CVV and LACV was confirmed experimentally through forced salivation (Ayers et al., 2019; Ayers et al., 2018; Camille Harris et al., 2015; Chan et al., 2020;

**FIG. 4.** Orthobunyavirus testing results in field-caught mosquito species in North America, reported in citations published from 1999 to March 2021 ( $n=42$  citations). Counts indicate citations and are not mutually exclusive across species. The total number of mosquito species tested varied by virus: CVV=79, JCV=59, LACV=53, SHV=63, and results are presented in alphabetical order based on species name. For mosquito genus shorthand notation, *Ae.*, *Aedes*; *An.*, *Anopheles*; *Cq.*, *Coquillettia*; *Cs.*, *Culiseta*; *Cx.*, *Culex*; *De.*, *Deinocerites*; *Hg.*, *Haemagogus*; *Ma.*, *Mansonia*; *Or.*, *Orthobodomyia*; *Ps.*, *Psorophora*; *Tx.*, *Toxorhynchites*; *Ur.*, *Uranotaenia*; *Wy.*, *Wyeomyia*. CVV, Cache Valley virus; JCV, Jamestown Canyon virus; LACV, La Crosse virus; SHV, Snowshoe Hare virus.





**FIG. 5.** Orthobunyavirus competency testing under laboratory conditions that examined vertical ( $n=3$  citations) and horizontal ( $n=10$  citations) transmission pathways (additional details provided in Supplementary Table S1). For mosquito genus shorthand notation, *Ae.*, *Aedes*; *An.*, *Anopheles*; *Cx.*, *Culex*. CVV, Cache Valley virus; JCV, Jamestown Canyon virus; LACV, La Crosse virus.

Grim, 2006; Troyano, 2009; Yang et al., 2018) or by virus detection in body parts (Bara et al., 2016; Reeves and Miller, 2013). Only one study confirmed vector competency using a host, by assessing infection status of a naïve host (suckling mice) that was fed upon by LACV-infected mosquitoes (*Ae. japonicus* and *Ae. triseriatus*) (Sardelis et al., 2002). No studies investigated vector competency for SHV.

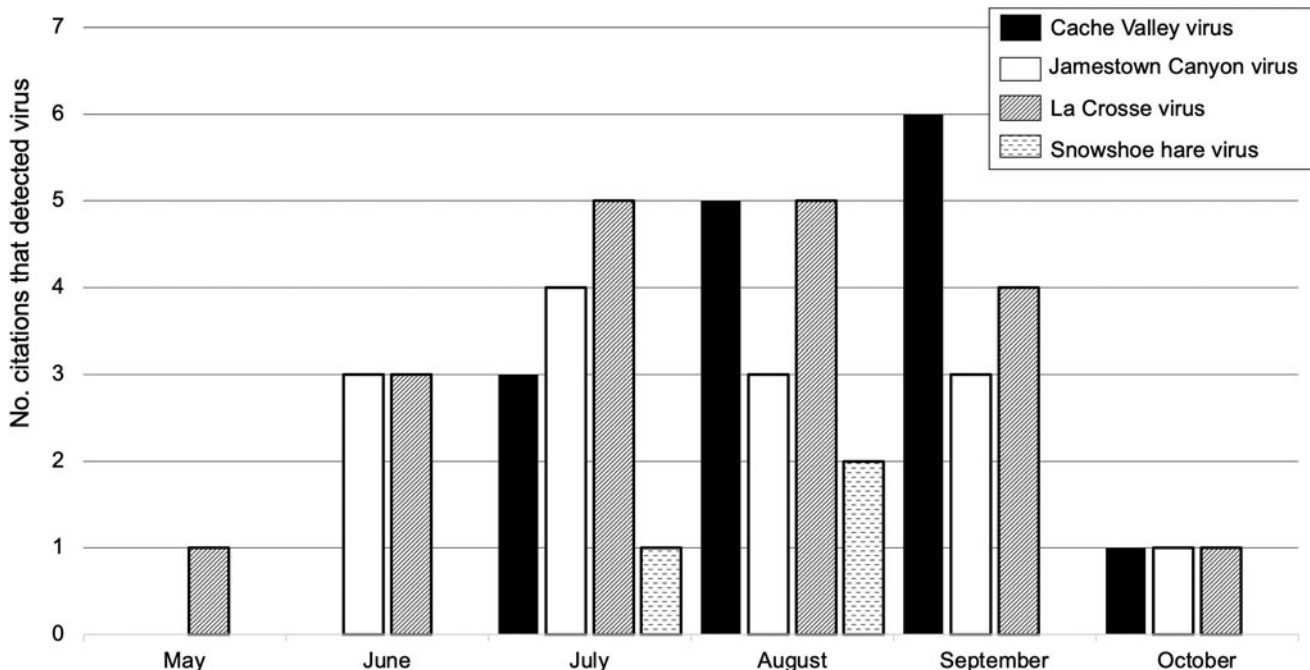
### Seasonal distribution of orthobunyavirus in vectors

Distinct seasonal trends were observed in terms of when viral agents were detected from mosquito vectors (Fig. 6). LACV was detected throughout the mosquito season from May to October (Eastwood et al., 2020b; Harris et al., 2015; Nasci et al., 2000; Scheidler et al., 2006; Westby et al., 2015), while SHV was only detected in July and August (Anderson et al., 2015; Carson et al., 2017). The peak period for JCV detection in mosquitoes was in July and coincided with peak mosquito abundance (Anderson et al., 2018; Anderson et al., 2015; Andreadis et al., 2008; McMillan et al., 2020).

On the contrary, CVV detection in mosquitoes peaked in August and September when mosquito abundance was significantly reduced (Anderson et al., 2018; Anderson et al., 2015; Andreadis et al., 2014; McMillan et al., 2020; Ngo et al., 2006; Ortiz et al., 2005). Although the majority of studies captured in this scoping review conducted orthobunyavirus surveillance, only 13 studies reported the specific week or month that viruses were isolated from mosquito pools.

### Vector bloodmeal analysis

Bloodmeal analysis was conducted for 32 mosquito species considered important arbovirus vectors, with the aim of identifying vertebrate species that may serve a critical role as enzootic amplifiers for orthobunyavirus transmission (Supplementary Table S2) (Anderson et al., 2018; Caldwell, 2004; Molaei et al., 2009; Molaei et al., 2008; Murdock et al., 2010; Tamini et al., 2021; Westby et al., 2015). The majority of mosquito species (27 of 32) were trapped in Connecticut, and the remaining 5 species were from Colorado, North Carolina, or Tennessee.



**FIG. 6.** Seasonal trends of orthobunyavirus detection in mosquito surveillance among studies that conducted temporal analysis ( $n=13$  citations). Mosquito trapping season varied by study, with June through August represented in all studies, and May, September, and/or October only represented in a subset. Note: citation counts indicate at least one virus isolation was detected, not the absolute number of detections per citation.

Thirty mosquito species fed on mammals, predominantly white-tailed deer (*O. virginianus*). Eight of these mosquito species also fed on birds, predominantly Passeriformes. Four species were simply opportunistic feeders (*Culex territans*, *Ae. canadensis*, *Ae. cantator*, and *Uranotaenia sapphirina*) (Anderson et al., 2018; Molaei et al., 2008). In summary, mosquito species that were most commonly infected with an orthobunyavirus (Fig. 4) were primarily mammalophilic (Supplementary Table S2).

### Risk factors

Four categories were identified among 39 studies that explored risk factors associated with exposure to vectors and/or orthobunyavirus (Table 1, references included in Supplementary Table S3). In cases where the outcome was exposure to vectors only, the vectors served as proxies for orthobunyavirus exposure, because the vector surveillance data represented hotspots for human cases. There were five times more studies that focused on risk factors associated with LACV ( $n=32$ ) than studies that investigated risk factors associated with CVV ( $n=5$ ), JCV ( $n=6$ ), or SHV ( $n=2$ ).

Risk factors related to vector ecology were most studied ( $n=24$  citations, Table 1). Positive associations were reported between exposure to competent vectors and types of land cover, but the relationships were unique to mosquito species. Positive associations were found between *Ae. albopictus*, *Coquillettidia perturbans*, or *Ae. japonicus* abundance and residential/urban areas, and between *Ae. triseriatus* abundance and forests (Bara and Muturi, 2015; Barker et al., 2003a; Barker et al., 2003b, Bewick et al., 2016; Ludwig et al., 2023; Nasci et al., 2000; Tamini et al., 2021; Troyano, 2009) or peridomestic areas with outdoor artificial containers (Byrd et al., 2018; Nasci et al., 2000; Tamini et al., 2021).

A positive correlation was also identified between vector abundance and weather factors (e.g., increased cumulative precipitation, current and lagging seasonal temperatures, and elevation) (Ghataka et al., 2019; Haddow et al., 2009; Ludwig et al., 2023; Nance et al., 2018; Nasci et al., 2000; Reed et al., 2019).

Conversely, when weather effects on vector susceptibility to orthobunyaviruses were considered, a large negative cor-

relation was reported between seasonal precipitation and vectors infected with CVV or JCV (Takeda et al., 2003). Frequency of encounters between wildlife reservoirs and infected mosquito vectors was also explored. No relationships were identified; this failure was attributed to the high abundance of wildlife populations in all study regions (Andreadis et al., 2014; Andreadis et al., 2008; Caldwell, 2004; Scheidler et al., 2006).

Mosquito species and abundance were also commonly assessed as risk factors for increased viral exposure ( $n=24$  citations). Most of these studies surveilled LACV vectors, and confirmed that endemic regions were strongly associated with an abundance of *Ae. albopictus*, *Ae. japonicus*, and *Ae. triseriatus* (Barker et al., 2003a; Byrd et al., 2018; Caldwell, 2004; Erwin et al., 2002; Fryxell et al., 2015; Harris et al., 2015; Jones et al., 1999; Nasci et al., 2000; Reed et al., 2019; Rowe et al., 2020; Scheffel, 2006; Tamini et al., 2021; Troyano, 2009; Westby et al., 2015). However, studies that compared vector abundance and species diversity between LACV hotspots (i.e., based on human LACE cases) and control sites (i.e., no cases reported) that were considered ecologically similar, reported no difference in mosquito composition or abundance between sites (Caldwell, 2004; Scheffel, 2006).

Trends in vector specificity for other orthobunyaviruses were not observed. Rather, mosquito species heterogeneity across multiple genera was consistently reported in endemic regions for CVV and JCV (based on arbovirus surveillance) (Andreadis et al., 2014; McMillan et al., 2020; Takeda et al., 2003).

Associations were also explored between mosquito activity patterns and population dynamics, and exposure levels to orthobunyavirus vectors ( $n=8$  citations, Table 1). Time of day was identified as a risk factor for exposure to LACV vectors, in that *Ae. triseriatus*, *Ae. albopictus*, and *Ae. japonicus* were significantly more active during evening and nighttime hours compared with daytime, suggesting a higher risk of host infection at nighttime if exposed to these vectors (Urquhart et al., 2017).

Nutritional deprivation had no effect on the prevalence of LACV infection or dissemination rates for *Ae. albopictus* (Westby et al., 2016), but being infected with LACV did alter certain activities depending on the mosquito species. Shorter

TABLE 1. RISK FACTORS EVALUATED IN ASSOCIATION WITH EXPOSURE TO ORTHOBUNYAVIRUS VECTORS AND/OR LIKELIHOOD OF MOSQUITO INFECTION

Risk factors investigated in context of vectors	No. of citations				
	All viruses	CVV	JCV	LACV	SHV
Vector ecology (e.g., habitat, surrounding landscape and wildlife reservoir populations, climatic factors including temperature, precipitation)	24	4	5	18	2
Mosquito species and abundance	24	4	2	20	—
Vector bionomics (e.g., blood-feeding behavior, diel period, nutritional deprivation, parity, interspecies competition, or behavior changes due to orthobunyavirus infection)	8	2	2	5	—
Individual vector factors (e.g., orthobunyavirus transmission rate changes due to midgut microbiota or pathogenic coinfections)	5	—	—	5	—
Total citations	39	5	6	32	2

The methods used to evaluate risk factors varied greatly across studies, and included various analytical techniques ( $n=32$ , citations in bold in Supplementary Table S3) or descriptive measures ( $n=7$  citations in Supplementary Table S3). Risk factor categories are not mutually exclusive.

CVV, Cache Valley virus; JCV, Jamestown Canyon virus; LACV, La Crosse virus; SHV, Snowshoe Hare virus.



and more frequent feedings were observed in LACV-infected *Ae. triseriatus*, suggesting increased horizontal transmission by this primary vector (Jackson et al., 2012). However, no change was observed in longevity or fecundity in either LACV-infected *Ae. triseriatus* or *Ae. albopictus* (Costanzo et al., 2014; Reese et al., 2009). More importantly, when also accounting for interspecies competition between these two vectors, despite *Ae. triseriatus* being more likely to become infected with LACV, its population decreased with the introduction of the invasive *Ae. albopictus* (Bevins, 2008).

Further, disease modeling that accounted for interspecies competition between these two species reported a diluting effect on LACV prevalence when both species were established versus the presence of only *Ae. triseriatus* populations (Bewick et al., 2016).

The final risk category assessed individual vector factors on increased virulence ( $n=5$  citations, Table 1). Dual infection with LACV and *Dirofilaria immitis* (heartworms, another common mosquito-borne pathogen in LACV endemic regions) was reported to enhance LACV dissemination and transmission rates in *Ae. albopictus* but not in *Ae. triseriatus* (Grim, 2006; Troyano, 2009). Mosquito midgut bacteria and fungi also affected viral infection and dissemination rates in LACV vectors (Muturi et al., 2016).

## Discussion

This scoping review, which focused on the epidemiology of orthobunyaviruses of relevance to Canada, characterized 87 studies published between 1999 and March 2021 related to vectors and virus transmission. The number of citations per year trended upward over the study period. LACV was investigated twice as often as CVV and three times more often than JCV or SHV. Most citations were surveillance studies that were highly concentrated geographically and nearly all in the United States. Most LACV studies represented Tennessee, and the remaining three orthobunyaviruses were most frequently surveilled in Connecticut, although SHV was never detected. Few studies surveilled orthobunyaviruses or vectors in Canada.

Characterization of the surveillance studies revealed several takeaway messages. First, isolating virus from positive mosquito pools is an extremely rare occurrence (Andreadis et al., 2014; McMillan et al., 2020), especially if traps are not positioned in ecological areas suitable for orthobunyavirus vectors. More intensive surveillance efforts in peridomestic, agricultural, and rural residences alongside forests may facilitate identifying important orthobunyavirus vectors by better representing their habitats. Orthobunyavirus surveillance would also benefit from complementary studies that surveil vertebrate hosts in overlapping geographies to more accurately capture the viral prevalence in a region (Bergevin et al., 2023; Blitvich et al., 2012b; Boromisa and Grimstad, 1987; Carson et al., 2017; Cully et al., 1991; Dupuis et al., 2021).

Concurrently enhancing mosquito surveillance efforts in potential hot spots of disease cases has the potential to rapidly identify primary vectors in designated locales, as has been successfully demonstrated with LACV vectors in the Appalachia region, the United States (Bewick et al., 2016; Haddow et al., 2011; Harris et al., 2015; Urquhart et al., 2016).

Additional surveillance techniques may also increase the likelihood of detecting an orthobunyavirus, such as compo-

nents that can attach to standard adult mosquito traps and collect mosquito saliva or excreta for pooled virus testing (L'Ambert et al., 2023; Meyer et al., 2019). These methods could be a cost-effective solution to complement the widely distributed and well-established ongoing vector and arbovirus surveillance efforts. However, the value of these novel techniques in the field is limited due to potential degradation of the virus prior to analysis or the difficulty in identifying the mosquito species that was the source of the virus detected in saliva or excreta samples.

A second key takeaway is that consistent strategies for mosquito surveillance methodology would facilitate comparisons across studies (Gu et al., 2008). This review highlighted variation in surveillance methodology and reporting, which included trap types, trapping frequency and duration per season, targeted times of day, and landscapes represented. These differences could lead to biased reporting of mosquito species as well as misrepresent arbovirus transmission risk. This may explain the inconsistent results when isolating virus from the multitude of field-caught mosquito species. Surveillance methodology must be robust and well documented, given the crucial role these data serve in parameterization of disease models and as public health transmission risk indicators (Bewick et al., 2016; Ghataka et al., 2019; Rowe et al., 2020).

Interestingly, there were no mosquito-borne disease projection studies captured in this review. This is alarming for Canada, given that CVV, JCV, and SHV are endemic, but little is known about the ecology and risk factors that may exacerbate orthobunyaviral transmission (Tjaden et al., 2018). Further, disease incidence will likely increase due to factors such as urban sprawl, increased global travel and trade, and an evolving climate conducive to an extended season for mosquitoes and viral transmission (Franklins et al., 2019; Skinner et al., 2023), but the rate of change is unknown. These findings necessitate further research on orthobunyaviral disease modeling and projections under climate change, to better understand and prepare for pressures placed on human and animal health systems.

Viral transmission was also investigated by experimental competence studies. However, these studies were few and focused predominantly on LACV vectors, exotic mosquito species (*Ae. albopictus*, *Ae. aegypti*), or species of the *Culex* genus commonly implicated with transmitting WNV (Andreadis et al., 2001; Drebot et al., 2003). While virus isolation from a vector may suggest transmission competency, it is not sufficient (Dieme et al., 2022). Competency studies are warranted to identify primary vectors. It was surprising how few studies sought to identify the primary vectors in endemic regions for CVV, JCV, or SHV.

Furthermore, as with surveillance studies, there was great variation in the competence methodologies, which limited comparisons and extrapolation of results to natural settings. In fact, only 1 of 13 studies applied the gold standard technique (Wu et al., 2022) for assessing vector competency by using a naïve vertebrate host (Sardelis et al., 2002). Consistent metrics that enable repeatable studies whereby only the mosquito species were to vary would expedite our understanding of the transmission cycles for the various orthobunyaviruses (Wu et al., 2022). Standardizing vector competency studies may also enhance our knowledge of horizontal versus vertical transmission in the maintenance of

enzootic orthobunyavirus cycles, and further, how climate change may impact those cycles.

There were some limitations in this study. Virus isolation and vector competency results may have under-represented certain mosquito species or endemic regions because of the restricted time frame of eligible citations. However, reviews on similar subject matter that were not restricted by publication date reported similar trends to what was reported in this scoping review (Day et al., 2023; Harding et al., 2019; Hughes et al., 2023; Shepard and Armstrong, 2023; Waddell et al., 2019; Walker and Yuill, 2023). This suggests that the takeaways from this review are not greatly impacted by the exclusion of citations due to publication date.

Relevant research may also have been excluded due to the screening inclusion criteria that required that the methods and results be reported in the context of an orthobunyavirus rather than only the vector itself. The extensive validation measures taken during the literature searches did identify a small number of excluded citations that investigated relevant vectors, particularly *Ae. albopictus*. However, these studies evaluated the vector in the context of West Nile, yellow fever, dengue, or zika virus, and were modeling papers that explored the climate change effects on projected geographic distribution of the vector itself and not in relation to the pathogen (Chen et al., 2013; Laporta et al., 2023; Ogden et al., 2014). Still, extensive research on this mosquito vector was characterized in this review based on other studies that framed the research in an orthobunyavirus context.

## Conclusion

North American orthobunyaviruses are widespread in Canada and the United States based on vector and arbovirus surveillance. However, these time- and labor-intensive studies require very large quantities of mosquito pools to be able to detect virus when present. A multifaceted research approach is necessary for a better understanding of orthobunyavirus epidemiology. In Canada, this is critical given the impact of orthobunyaviruses on human and animal health, and the relatively small number of studies conducted in surveillance, cluster detection, and disease risk projections. Considering the impact that climate change is forecasted to have within Canada, which will likely further promote orthobunyavirus transmission, research is needed to guide future public and animal health efforts to mitigate disease.

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## Authors' Contributions

M.d.B. contributed to conceptualization (lead); data curation (lead); methodology (lead); formal analysis (lead); project administration (supporting); visualization (lead); writing—original draft (lead); writing—review and editing (lead). V.N. and K.M.C. assisted with conceptualization

(supporting); methodology (supporting), formal analysis (supporting); project administration (lead); resources (equal); writing—review and editing (supporting); funding acquisition (equal). T.S. supported with data curation (supporting), writing—review and editing (supporting). A.L. performed formal analysis (supporting); writing—review and editing (supporting). P.M. contributed to writing—review and editing (supporting). S.M. assisted with writing—review and editing (supporting), funding acquisition (lead).

## Author Disclosure Statement

The authors declare no competing financial or intellectual interests that could have influenced the work reported in this study.

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## Supplementary Material

Supplementary Data S1  
Supplementary Data S2  
Supplementary Table S1  
Supplementary Table S2  
Supplementary Table S3  
Supplementary Figure S1

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