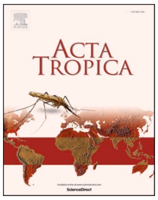
Acta Tropica 261 (2025) 107512

Contents lists available at ScienceDirect

Acta Tropica

journal homepage: www.elsevier.com/locate/actatropica



Modeling the lagged and nonlinear effects of weather conditions on abundance of *Culex tarsalis* mosquitoes in Saskatchewan, Western Canada using a bi-dimensional distributed lag nonlinear model

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ARTICLE INFO

Keywords:
Cx. tarsalis mosquitoes
Abundance of mosquitoes
Weather conditions
Saskatchewan
Distributed lag nonlinear model

ABSTRACT

The establishment of West Nile Virus (WNV) competent vectors continues to pose a major public health challenge in Canada, especially in the south. While studies have examined the association between weather conditions and the abundance of mosquitoes over trap weeks, there is limited research on the effects of weather conditions on the abundance of *Culex tarsalis* (*Cx. tarsalis*) mosquitoes for a lapse of time beyond the trap week in Saskatchewan, Western Canada. To address this gap, we analyzed provincially available weekly mosquito trap and coincident meteorological station data in Saskatchewan from 2010 to 2021 using a bi-dimensional distributed lag and nonlinear model. Data indicate that 171,141 *Cx. tarsalis* mosquitoes were trapped across much of Saskatchewan, from 2010 to 2021. *Cx. tarsalis* were found to be most abundant between weeks 26 and 35 (July and August) and peaked in weeks 30 and 31. Based on the WNV-positive pools, mosquito infection rates increased from week 23 to 36. While weekly average maximum air temperatures between 20 °C and 30 °C were associated with more *Cx. tarsalis* across all lags (0 – 8 weeks), higher weekly average minimum air temperatures had a strong and immediate effect that diminished over longer lags. Higher weekly average rainfall amounts (> 20 mm) were associated with fewer *Cx. tarsalis* mosquitoes across all lags, while average weekly rainfall between 8 and 20 mm was strongly associated with a high abundance of *Cx. tarsalis* mosquitoes over longer lags (5 -7 weeks). Additionally, increasing wind speed was associated with lower abundance of *Cx. tarsalis* across all lags. Findings identified nonlinear lag associations for weekly average maximum air temperature and rainfall, but linear associations for weekly average minimum air temperature and wind speed. Identified lags and thresholds for temperature, rainfall, and wind speed at which mosquito abundance peaked could help to inform public health authorities in timing of vector control measures to prevent WNV transmission.

1. Introduction

Mosquitoes are the deadliest creatures on the earth, responsible for approximately half a million deaths each year through the spread of a variety of disease causing pathogens (World Health Organization (WHO), 2017). There are around 3500 mosquito species worldwide, but only a limited number may carry and transmit infectious pathogens that cause diseases to humans, including malaria, dengue, West Nile Virus (WNV), chikungunya, and several kinds of viral encephalitis (Ng et al., 2019). *Aedes, Anopheles*, and *Culex* mosquitoes are the most common carriers and transmitters of pathogens to people (Ng et al., 2019).

Historically, colder climates in Canada have limited the circulation of mosquito-borne pathogens. However, due to climate change, regions in Canada, as in other temperate countries, are becoming more conducive to mosquito development and the transmission of infectious pathogens (Ng et al., 2019; Ogden et al., 2022; Gizaw et al., 2024). This shift in climate is evident in ongoing changes observed in Canada (Zhang et al., 2019) and incremental increase in temperatures in Canada due to

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https://doi.org/10.1016/j.actatropica.2024.107512
Received 10 October 2024; Received in revised form 23 December 2024; Accepted 23 December 2024

climate change already supports broader establishment of WNV in the country. The predominant WNV vectors in Canada are *Culex pipiens* (*Cx. pipiens*), *Culex restuans* (*Cx. restuans*), and *Culex tarsalis* (*Cx. tarsalis*) (Moua et al., 2021; Colpitts et al., 2012; Ciota, 2017). *Cx. pipiens* and *Cx. restuans* are well adapted to urban environments and are the predominant WNV vectors in Eastern Canada (Rosenkrantz, 2022). Conversely, *Cx. tarsalis* prefer grassland and agricultural areas and are the predominant vector in the Prairies and Western Canada (Rosenkrantz, 2022).

Climatic factors such as temperature (Dodson et al., 2012; Reisen, 1995), rainfall (Koenraadt and Harrington, 2008; Valdez et al., 2017b), relative humidity (Hafez et al., 1993; Sauer et al., 2022), and wind speed (Holmes and Benoit, 2019; Lahondère, 2023; May 1979) affect the biological processes and physiological functions of *Cx. tarsalis.* The life-cycle parameters of *Cx. tarsalis* mosquitoes such as egg viability, larval development, feeding behavior, and fecundity are strongly influenced by temperature (Moser et al., 2023b; Shocket et al., 2020). Warmer temperatures generally accelerate larval development and reduce the time to adult emergence, promoting faster life cycles (Moser et al., 2023b; Shocket et al., 2020). Within a moderate temperature range (typically around 25–30 °C), *Cx. tarsalis* exhibits active metabolic rate, prompting more frequent blood-feeding. After a successful blood meal, higher temperatures (within the optimal range) facilitate faster digestion of blood, efficient energy utilization, and higher egg production rates (Reisen, 1995; Henn et al., 2008). However, extreme temperature can reduce feeding and impair reproductive physiology, leading to reduced egg production and viability, while cooler temperatures diminish their ability to locate or feed on hosts and slow development significantly, resulting extended larval period (Moser et al., 2023b; Shocket et al., 2020).

Rainfall also plays a significant role in the ecology of *Cx. tarsalis* mosquitoes, impacting their breeding habitats and population dynamics. *Cx. tarsalis* mosquitoes lay eggs in standing water, so rainfall directly increases breeding opportunities by creating or replenishing pools, ponds, and other stagnant water bodies (Brust, 1990; Walton et al., 2009; Baspaly, 2003). Consistent moisture levels in breeding sites due to periodic rainfall promote larval survival and development. If rainfall is infrequent or water evaporates quickly, larvae may die before reaching adulthood (Eisenberg, 1992). On the other hand, excessive rainfall can wash away development pools, eggs, and larvae (Koenraadt & Harrington, 2008).

Relative humidity during summer months also influences mosquito population dynamics (Brown et al., 2023b). Many of the mosquito life-traits such as egg production, larval emergence from eggs, pupae development, survival of adults, as well as adult activity and host-seeking behaviors are regulated by increasing relative humidity (de Almeida Costa et al., 2010; Asigau and Parker, 2018; Zwiebel and Takken, 2004), whereas low humidity may cause eggs to desiccate and diminish adult activity (Day, 2016; Holmes and Benoit, 2019), despite the fact that mosquito species respond differently to relative humidity, for instance, *Cx. tarsalis* mosquitoes prefer low humidity for their activity (Stuart, 2020; Baril et al., 2023b).

Similarly, wind speed influences the reproduction and distribution of mosquitoes. Winds flowing in the same direction as mosquito flights let mosquitoes migrate vast distances into new locations (Adeleke et al., 2022). However, high wind speed lowers mosquito host-seeking activity by influencing mosquito flight range and patterns, which in turn affects reproduction capacity (Cardé, 2015). Wind speed also influences mosquito physiology by affecting water loss and thermoregulation. Higher wind speeds can lead to greater evaporation rates, which can dehydrate mosquitoes more quickly, impacting their survival, especially in dry conditions, such as the prairies in Canada. Additionally, strong winds can lower the ambient temperature around a mosquito’s body, influencing its thermoregulation and potentially affecting its ability to function in colder conditions (Holmes & Benoit, 2019; Lahondère, 2023; May 1979).

In addition to weather conditions, the abundance of *Cx. tarsalis* mosquitoes and their life cycles can be influenced by various non-climate factors, such as land cover, agricultural practices, and population density of nonhuman hosts (e.g., birds) (Adelman et al., 2022). The amount of appropriate vegetation and habitat type (e.g., marsh habitats and grasslands) are critical factors for survival and abundance of *Cx. tarsalis* mosquitoes. *Cx. tarsalis* mosquitoes prefer grasslands, terrestrial water, and agricultural areas (Lothrop & Reisen, 2001; Adelman et al., 2022; Dunphy et al., 2019). Water associated with irrigation, including ditches and hoof prints creates ideal habitats for *Cx. tarsalis* to lay and hatch eggs (Rosenkrantz, 2022; Bradford, 2005; Dunphy et al., 2019). However, the majority of Saskatchewan agriculture is not irrigation-based (Government of Canada, 2024). The abundance of *Cx. tarsalis* mosquitoes is also affected by bird populations because *Cx. tarsalis* mosquitoes have a feeding preference for birds (Dunphy et al., 2019; Turell et al., 2005). Moreover, birds are primary hosts of WNV, serving as a reservoir for infection of mosquitoes, so detecting the virus in dead birds is a good indicator to determine whether people in particular areas are at risk of WNV (Ferraguti et al., 2023; Vidaña et al., 2020). Even though the Saskatchewan Ministry of Health does not use dead birds as an indicator for WNV circulation in the province (Government of Saskatchewan, 2024a), the Canadian Cooperative Wildlife Health Centre (CCWHC) conducts a national surveillance program testing selected dead birds for WNV. In Saskatchewan, anywhere from 2 (in 2021) to 70 (in 2014) birds were tested and up to 13 samples (out of a total of 53 in 2013) were identified as positive for WNV. The highest positive test rates were 58 % (out of 19 tests in 2017) and 50 % (out of 8 tests in 2016), with 0–8 % positive tests in 2011 (8 %), 2012 (7 %), 2014 (3 %), and 2021 (0 %). Positive test rates in other years within this study period ranged from 14 to 25 % (Supplementary Table S1) (Canadian Cooperative Wildlife Health Centre (CCWHC), 2024).

In general, the effect of meteorological conditions on mosquito population dynamics is non-linear and delayed, occurring after any weather anomalies (Lowe et al., 2018; Lebl et al., 2013). The effect of weather factors on adult mosquitoes is cumulative on the immature stages and newly emerged adults, i.e., effects on egg laying and hatching, larvae emerging from eggs, development of pupae, and emergence of adult mosquitoes (Dom, 2019; Aznar et al., 2013). It is, therefore, important to identify the major atmospheric drivers, lag periods, and appropriate model formulations that account for local weather conditions and mosquito abundance. Where a specific occurrence of exposure events affects the outcome (e.g., weather-related infectious diseases such as mosquito-borne diseases and vector abundance), for a lapse of time well beyond the event period, the distributed lag nonlinear model (DLNM) is highly recommended (Gasparrini, 2011; Gasparrini et al., 2010; Bhaskaran et al., 2013). However, this model is not commonly utilized by researchers, especially in Environmental Epidemiology. While there are studies that have analyzed the association between weather conditions and the abundance of mosquitoes in the Canadian prairies (Alberta, Saskatchewan, and Manitoba) using a linear mixed model (LMM) (Chen et al., 2013) and Generalized Linear Mixed Models (GLMMs) (Baril et al., 2023a), there is limited research on the lagged effects of weather conditions on the abundance of *Cx. tarsalis* mosquitoes in Saskatchewan, Western Canada. To address these gaps, meteorological data and weekly mosquito traps in Saskatchewan from 2010 to 2021 were analyzed using a bi-dimensional distributed lag and nonlinear model to investigate the lagged and nonlinear effects of weather conditions on the abundance of *Cx. tarsalis* mosquitoes. The archived weather information is publicly available through Environment and Climate Change Canada (Environment and Climate Change Canada, 2023) while the mosquito data was provide through the Ministry of health within the province of Saskatchewan (Saskatchewan Ministry of Health, 2023). The use of DLNM in this research is novel because the model can describe delayed and nonlinear effects of weather variables on the abundance of *Cx. tarsalis* both along the usual space of the predictors and in the additional dimension of the lags. These lag effects are not addressed by the traditional generalized linear models (GLMs) and generalized additive models (GAMs) (Salazar et al., 2021), even if GAMs and GLM are the standard models for time series analysis in environmental epidemiology (Gudziunaite et al., 2023; Imai & Hashizume, 2015; Jbilou & El Adlouni, 2012).

2. Methods

2.1. Study area

This study was conducted in Saskatchewan, Western Canada. In Saskatchewan, *Cx. tarsalis* is the primary competent vector of WNV and it is abundant in the southern areas of the province when weather conditions are hot and dry. Currently, the Saskatchewan Ministry of Health captures mosquitoes and reports out across four ecological risk areas (Mixed-Grass Prairie, Moist Mixed-Grass Prairie, Boreal Transition, and Boreal Forest), representing 13 regional health authorities (RHA) and 26 communities (Fig. 1 and Table 1). The southern portion of the province consists of a larger area of preferred habitat and therefore higher numbers of *Cx. tarsalis* mosquitoes than the north. These southern regions are also susceptible to seasonal flooding due to low topography and poorly developed drainage systems. The frequency and severity of floods has increased in recent years due to climate change, which is expected to bring more frequent and intense storms (Pattison-Williams et al., 2018). This may result in overflow of mosquito habitats and dilution of nutrients. In the study period (from 2010 to 2021), the highest number of *Cx. tarsalis* mosquitoes were captured in Mixed Grassland type ecoregions, which are semi-arid regions in the south, dominated by agriculture. *Cx. tarsalis* activity is rare in the Boreal type ecoregions (Government of Saskatchewan, 2024b), consisting of increasing forest habitats and cooler temperatures to the north.

The Ministry of Health captured *Cx. tarsalis* mosquitoes from 174 trap locations during the study period (from 2010 to 2021). The

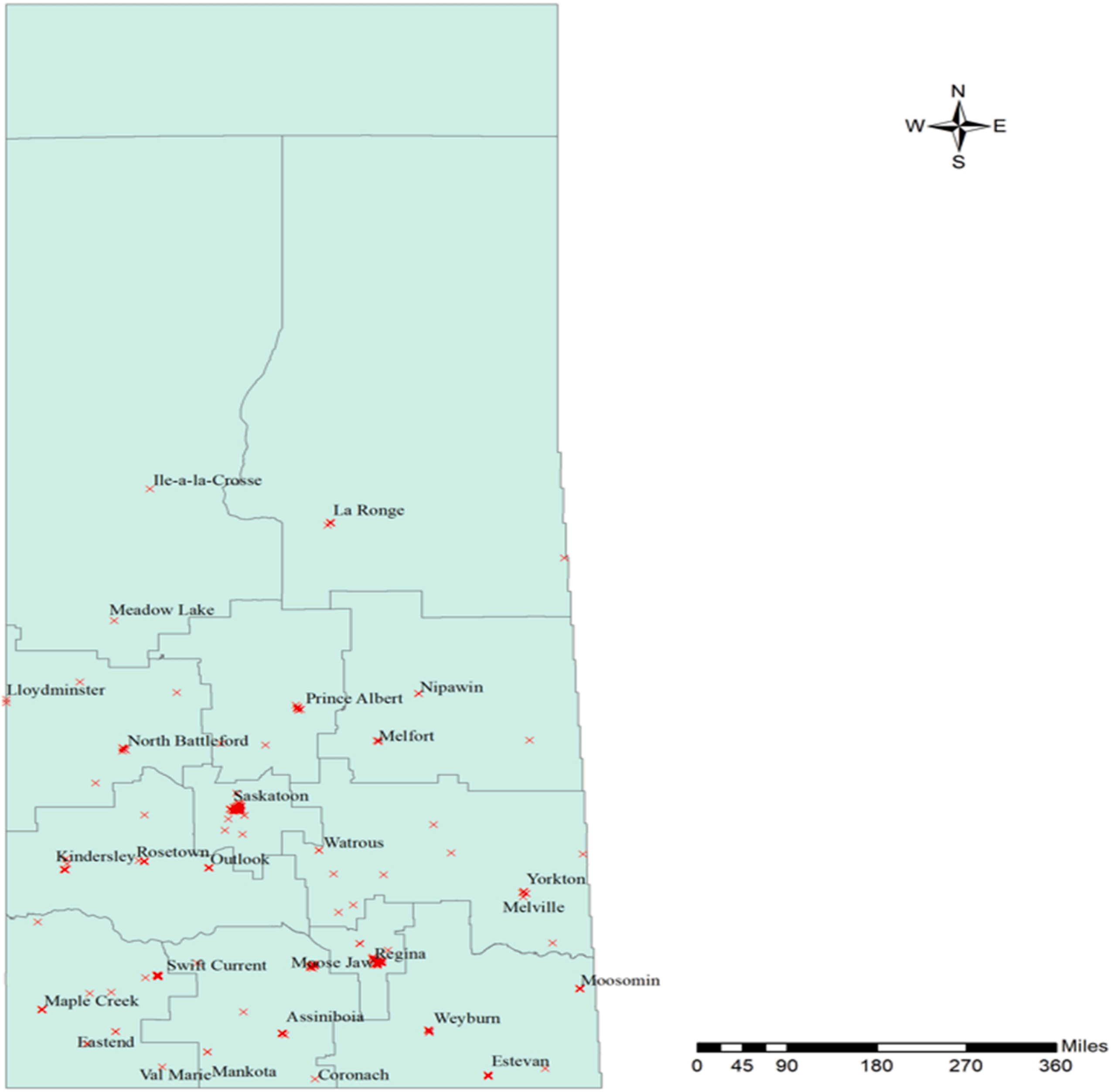

Fig. 1. Mosquito trap sites in Saskatchewan, Western Canada during the study period. Base map was obtained from the Government of Canada Open Portal (GOVERNMENT OF CANADA 2020. Saskatchewan COVID-19 Zones. Available at https://open.canada.ca/data/dataset/ebf56611-d45d-b8a8-eec3-a5c1b52aeec6. Accessed on 26 August 2024).

Table 1
Mosquito trap locations by RHA and community in Saskatchewan in 2010–2021.

Ecological risk areas	RHA	Community	Number of trap sites											
			2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Mixed-Grass Prairie	Cypress	Maple Creek	2	2	2	2	1	3	2	2	2	2	2	2
		Swift Current	2	2	2	2	2	2	2	2	2	2	2	2
		Val Marie	1	1	1	1	1	–	–	–	–	–	–	–
		Eastend	1	–	–	–	–	–	–	–	–	–	–	–
	Five Hills	Assiniboia	2	2	2	2	2	2	2	2	2	2	2	2
		Moose Jaw	8	6	6	7	7	7	4	4	4	4	4	4
	Heartland	Kindersley	2	2	2	2	2	3	2	2	3	1	1	1
		Outlook	1	1	–	–	–	–	–	–	–	–	–	–
		Rosetown	2	2	2	2	2	–	–	–	–	–	2	1
	Regina Qu’Appelle	Moosomin	1	1	1	1	1	1	1	1	1	1	1	1
		Regina	14	16	16	15	18	18	6	5	5	5	5	5
	Sun Country	Estevan	3	3	3	3	3	3	3	3	3	3	3	3
		Weyburn	2	2	3	3	3	2	2	2	2	2	2	2
		Coronach	1	1	–	–	–	–	–	–	–	–	–	–
Moist Mixed-Grass Prairie	Sunrise	Yorkton	2	2	2	2	2	2	2	2	2	2	3	2
		Melville	2	2	2	–	–	1	1	1	1	1	1	1
	Prairie North	North Battleford	2	2	1	2	2	1	1	1	1	1	1	1
		Lloydminster	1	1	1	1	1	2	1	1	1	1	1	1
		Meadow Lake	1	1	–	–	–	–	–	–	–	–	1	–
	Saskatoon	Saskatoon	11	11	11	11	11	14	5	5	5	5	5	5
		Watrous	2	2	–	–	–	–	–	–	–	–	–	–
Boreal Transition	Prince Albert	Prince Albert	4	4	5	5	4	4	2	2	2	2	2	1
	Kelsey Trail	Melfort	1	2	1	2	2	2	1	1	1	1	1	–
Boreal Forest	Mamawetan Churchill River	Creighton	1	1	–	–	–	–	–	–	–	–	–	–
		La Ronge	1	1	2	2	2	–	–	–	–	1	1	–
	Keewatin Yatthe	Ile-a-la-Crosse	1	1	–	–	–	–	–	–	–	–	–	–

maximum distance between the trap locations and meteorological stations in each respective community was 12.15 km with an average distance of 5.5 km (Table 2).

2.2. Study variables and data sources

The outcome variable of this study was the abundance of *Cx. tarsalis* mosquitoes. Mosquito abundance is a measure of the relative quantity of mosquitoes in a specific area during a sampling period. It is calculated by dividing the total number of mosquitoes captured for a specific species by the number of trapping nights during a given sampling period and is expressed as the number of mosquitoes per trap per night. Data for *Cx. tarsalis* mosquitoes were made available from the Department of Epidemiology and Surveillance, Ministry of Health, Government of Saskatchewan, upon request (Saskatchewan Ministry of Health, 2023). The Ministry of Health catches *Cx. tarsalis* mosquitoes every week during the mosquito season (June to September) using New Jersey light traps (without CO_2) and CDC miniature light traps baited with dry ice (The National Collaborating Centre for Infectious Diseases (NCCID), Todoric et al., 2022), placed in predetermined areas throughout various communities (Fig. 1 and Table 1). The trapped mosquitoes are then pooled by trap date and by species, with up to 50 mosquitoes sampled for WNV testing. If WNV is detected in one or more mosquitoes collected from a specific trap, the pools tested for the virus are considered positive (Government of Saskatchewan, 2023). The number of positive pools can be used as a proxy indicator for WNV activity, although it is not a fully reliable measure. Instead, the number of positive pools is used to calculate more relevant indices, such as the mosquito minimum infection rate (MIR) (Bell et al., 2005). The Saskatchewan Ministry of Health determined the level of risk in mosquitoes by using infection rates in mosquitoes (Government of Saskatchewan, 2024b). Mosquito MIR, commonly reported as the number of infected per 1000 tested is the number of positive pools divided by the total number of mosquitoes tested (Ducrocq et al., 2022).

Table 2
Distance between mosquito trap sites and meteorological stations in each respective community.

Distance between trap sites and meteorological stations	Percent of trap sites
<5.5 km	45.9
5.5–10 km	50
>10 km	4.1

The environmental exposure variables of the current study were air temperature (°C), rainfall (mm), relative humidity (%), and wind speed (km/h). Daily meteorological data recorded at the closest meteorological stations to traps were obtained from Environment and Climate Change Canada (Environment and Climate Change Canada, 2023). To be consistent with the weekly mosquito trap data, weekly averages were derived for each weather variable.

2.3. Statistical analysis

A bi-dimensional distributed lag and nonlinear model (DLNM) was used to study the lagged and nonlinear effects of weather conditions on the abundance of *Cx. tarsalis* mosquitoes. This type of model is particularly useful in the fields of epidemiology, environmental science, and economics, where the relationships between variables are often complex and dynamic. This approach relies on the construction of a crossbasis, a bi-dimensional functional space formed by integrating two sets of basis functions that characterize the relationships in the predictor and lag dimensions (Gasparrini, 2011; Gasparrini et al., 2010). The bi-dimensional crossbasis function was represented by quadratic B-splines with 5 degrees of freedom and three internal knots set at equal distances. Because the mosquito trap data were highly scattered, we employed the negative binomial distribution function. The model is of the form:

$$Y_t = negative\ bionomial\ (\mu_t),\ t = 1,\ 2,\ 3,\ \ldots\ldots\ldots\ldots,\ n$$

$$\begin{aligned}&\mathit{Average\ of\ Cx.tarsalis\ per\ trap\ night}\\&= \alpha + \sum_{l=1}^{L}\beta_1(\mathit{Tmax}_t,\ l) + \sum_{l=1}^{L}\beta_2(\mathit{Tmin}_t,\ l) + \sum_{l=1}^{L}\beta_3(\mathit{Tmean}_t,\ l) + \sum_{l=1}^{L}\beta_4(\mathit{Rainfall}_t,\ l)\\&+ \sum_{l=1}^{L}\beta_5(\mathit{RH}_t,\ l) + \sum_{l=1}^{L}\beta_6(\mathit{Wind\ speed}_t,\ l) + \mathit{ns}(\mathrm{week} + \lambda) + \mathit{Year} + \varepsilon_t\end{aligned}$$

where t is the trap week, Y_t is average of *Cx. tarsalis* per trap night in trap week t, α is the model intercept; $Tmax_t,\ l$; $Tmin_t,\ l$; $Tmean_t,\ l$; $Rainfall_t,\ l$; $RH_t,\ l$; and $Wind\ speed_t,\ l$ are the matrices obtained by applying the DLNM to weekly average maximum temperature, weekly average minimum temperature, weekly average mean temperature, weekly average rainfall, weekly average relative humidity, and weekly average wind speed; $\beta_1,\ \beta_2,\ \beta_3,\ \beta_4,\ \beta_5,$ and β_6 are the coefficients of weekly average maximum temperature, weekly average minimum temperature, weekly average mean temperature, weekly average rainfall, weekly average relative humidity, and weekly average wind speed matrices, l is the lag weeks; L is the maximum lag; $ns(\mathrm{week},\ \lambda)$ is the natural cubic spline smoothing function of weeks; and ε_t is error term. The model was adjusted by using a quadratic B-spline function for weekly average maximum temperature, weekly average mean temperature, weekly average rainfall, and weekly average relative humidity with a maximum lag of 8 weeks, whereas linear function was used for weekly average minimum temperature and wind speed with a maximum lag of 8 weeks.

The length of lag weeks was determined based on the number of days it takes *Cx. tarsalis* mosquitoes to complete their life cycle, plus the mean adult life span. It has been reported that the mean development time to adult for *Cx. tarsalis* mosquitoes under field conditions in southern Manitoba is between 20 and 25 days (Buth et al., 1990) and the mean adult life span in north America is 27 days (Moser et al., 2023a), we used a maximum of 8 weeks lag period, which is a plausible period of time that includes the combined time for egg hatching, larval development to adult mosquitoes, and adult life span. Table 3 summarizes the length of lag weeks, variable basis, and basis for lag for each weather variable.

The Akaike Information Criterion (AIC) was used to choose the best model. The goal of the AIC is to balance the goodness of fit of the model with its complexity, penalizing models that are too complex. Generally, models with the lowest AIC value provided the best fit (Supplementary Table S2) (Akaike, 1974). Sensitivity analysis was also performed to assess the robustness of model parameters to changing degree of freedoms for exposure-response and varying smooth functions. The results of the analysis showed that the model parameters were robust to changing degrees of freedom (3 to 5). All the statistical analyses were performed in R statistical software v4.3.2 (R Core Team, 2023) using the "dlnm" package (Gasparrini, 2011; Gasparrini et al., 2010).

Table 3
Choice of lag period, variable basis, and basis for lag for each climatic variable.

Variable	Lag period	Basis for variable	Basis for lag
Weekly average maximum temperature	8	Quadratic B-spline	Quadratic B-spline
Weekly average minimum temperature	8	Linear	Linear
Weekly average mean temperature	8	Quadratic B-spline	Quadratic B-spline
Weekly average rainfall	8	Quadratic B-spline	Quadratic B-spline
Weekly average relative humidity	8	Quadratic B-spline	Quadratic B-spline
Weekly average wind speed	8	Linear	Linear

3. Results

3.1. Descriptive analysis

A total of 2920,533 mosquitoes were trapped in Saskatchewan from 2010 to 2021. Out of these total captured mosquitoes, 171,141 (5.9 %) were *Cx. tarsalis*, where the highest number of *Cx. tarsalis* mosquitoes were captured in the southern part of the province (Fig. 2). The highest number of *Cx. tarsalis*, 74,575 (43.6 %) were captured in 2010 (Table 4). However, the number of *Cx. tarsalis* mosquitoes captured decreased from year to year in the study period (Table 4 and Fig. 3A). In Saskatchewan, *Cx. tarsalis* mosquitoes were abundant in weeks 26 to 35 (i.e., July and August), where the highest number of mosquitoes trapped in weeks 30 and 31 (Fig. 3B). Supplementary Fig. S1 presented the number of trapped mosquitoes in each community by year. Moreover, a total of 6713 *Cx. tarsalis* mosquito pools were tested for WNV from 2010 to 2021 and 284 pools were found positive, where the highest annual MIR was reported in 2012 (12.9) (Table 4). In the study period, WNV-positive mosquitoes were captured early in the mosquito season and the infection rate increased from week 23 to 36 (Fig. 3C).

In weeks 23–36, the weekly average mean air temperature was 17.4 °C, while the weekly average minimum air temperature was 10.4°C and the weekly average maximum air temperature was 24.3 °C. During the same period, the weekly average rainfall ranged from 0 mm to 38 mm with a mean of 3 mm, whereas the weekly average wind speed ranged from 0 km/h to 143.9 km/h, with a mean of 36.3 km/h. The weekly average relative humidity ranged from 81 to 100 %, with a mean of 95.5 % in weeks 23 to 36 in the study period.

3.2. Associations between weather conditions and number of Cx. tarsalis captured in the mosquito season

In the current study, and based on the above DLNM model, the abundance of *Cx. tarsalis* mosquitoes was statistically associated with weekly average maximum air temperature, weekly average minimum air temperature, weekly average rainfall, and weekly average wind speed (Figs. 4–7 and Table 5). However, the weekly average mean air temperature and weekly average relative humidity did not show a clear relationship with *Cx. tarsalis* abundance, as illustrated in the 3D and contour plots (Supplementary Figs. S2 and S3). The association between the weekly average maximum air temperature and the average of *Cx. tarsalis* mosquitoes trapped per night is not linear (Fig. 4A and 4B). Air temperatures between 20 and 30 °C were associated with higher numbers of *Cx. tarsalis* throughout the lag weeks (0–8 weeks), where the effect was strong between 25 °C and 29 °C in shorter lags. On the other hand, air temperatures below 20°C and 30°C were associated with a lower number of *Cx. tarsalis* mosquitoes across all lags compared with the reference temperature of 24.4 °C (mean of the observed maximum temperature in the study period). The cumulative effect (lag 0–8 weeks) of weekly average maximum air temperature on the abundance of *Cx. tarsalis* mosquitoes was highest at a temperature of 27°C (β: 1.64, 95 % CI: 0.97, 2.31) and declined in temperatures below and above 27 °C (Table 5).

The effects of weekly average minimum air temperature on the abundance of *Cx. taraslis* mosquitoes in 8 weeks lag period was linear

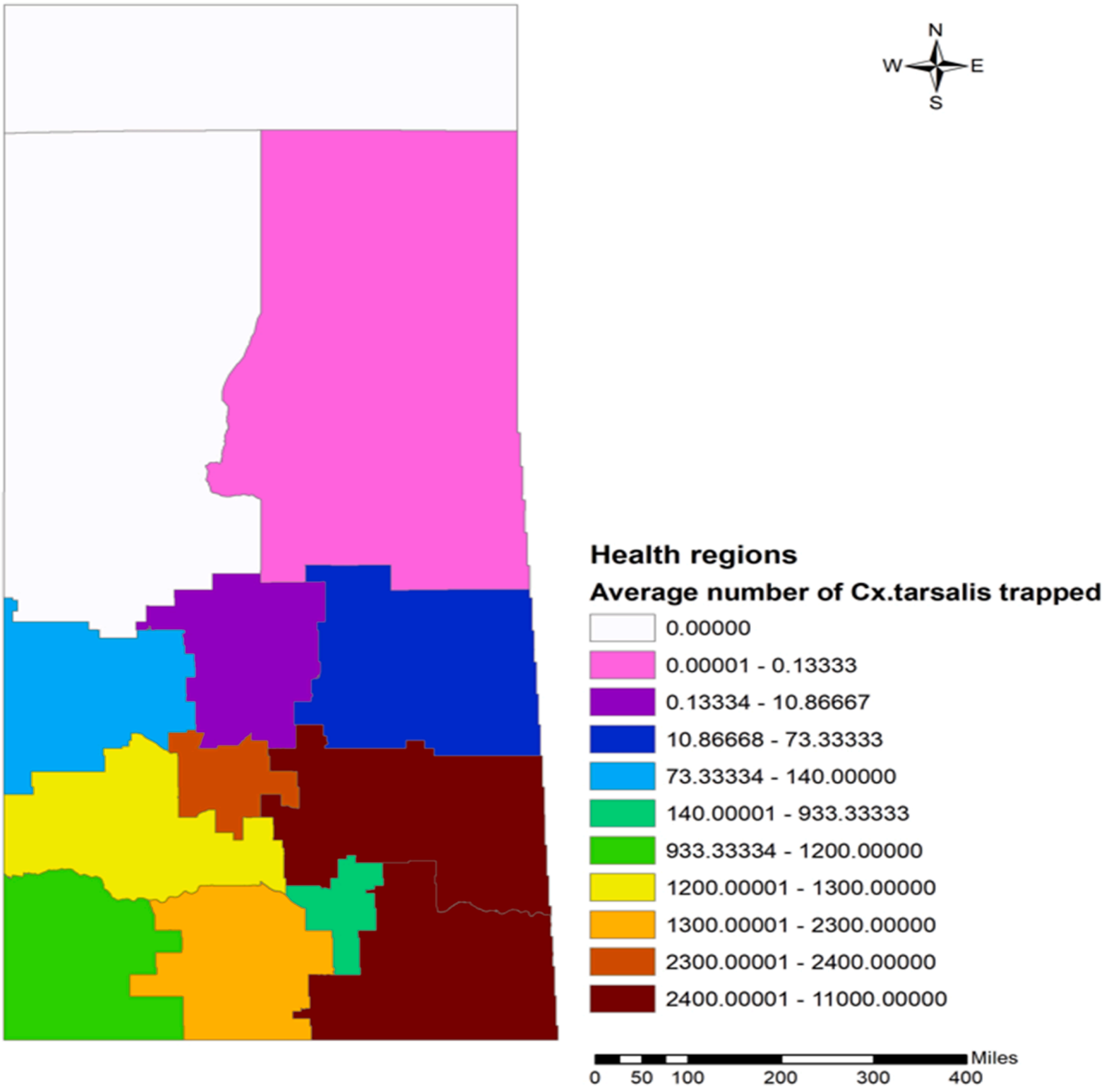

Fig. 2. Average number of *Cx. tarsalis* mosquitoes trapped in Saskatchewan, Western Canada during the study period. Base map was obtained from the Government of Canada Open Portal (GOVERNMENT OF CANADA 2020. Saskatchewan COVID-19 Zones. Available at https://open.canada.ca/data/dataset/ebf56611-d45d-b8a8-eec3-a5c1b52aeec6. Accessed on 26 August 2024).

Table 4

Number of mosquitoes captured during the mosquito season in the study period (2010 to 2021 in Saskatchewan, Western Canada.

Year	All species trapped	Number of *Cx. tarsalis* trapped	Number of *Cx. tarsalis* tested	Number of pools tested	Number of positive pools	Number of *Cx. tarsalis* of positive pools	MIR
2010	427,551	74,575	52,283	1415	9	378	0.2
2011	346,646	20,552	21,238	763	21	152	1
2012	231,271	3597	3501	442	45	88	12.9
2013	357,179	10,690	9899	636	36	1253	3.6
2014	441,508	12,111	11,751	597	19	857	1.6
2015	198,865	7671	7286	536	16	611	2.2
2016	308,862	21,188	14,354	591	68	2656	4.7
2017	71,698	3322	3316	421	10	291	3
2018	132,473	15,426	15,424	682	51	1767	3.3
2019	198,876	1047	1047	200	0	0	0
2020	101,592	160	158	70	0	0	0
2021	104,012	802	802	360	9	53	11.2

MIR: Mosquito minimum infection rate.

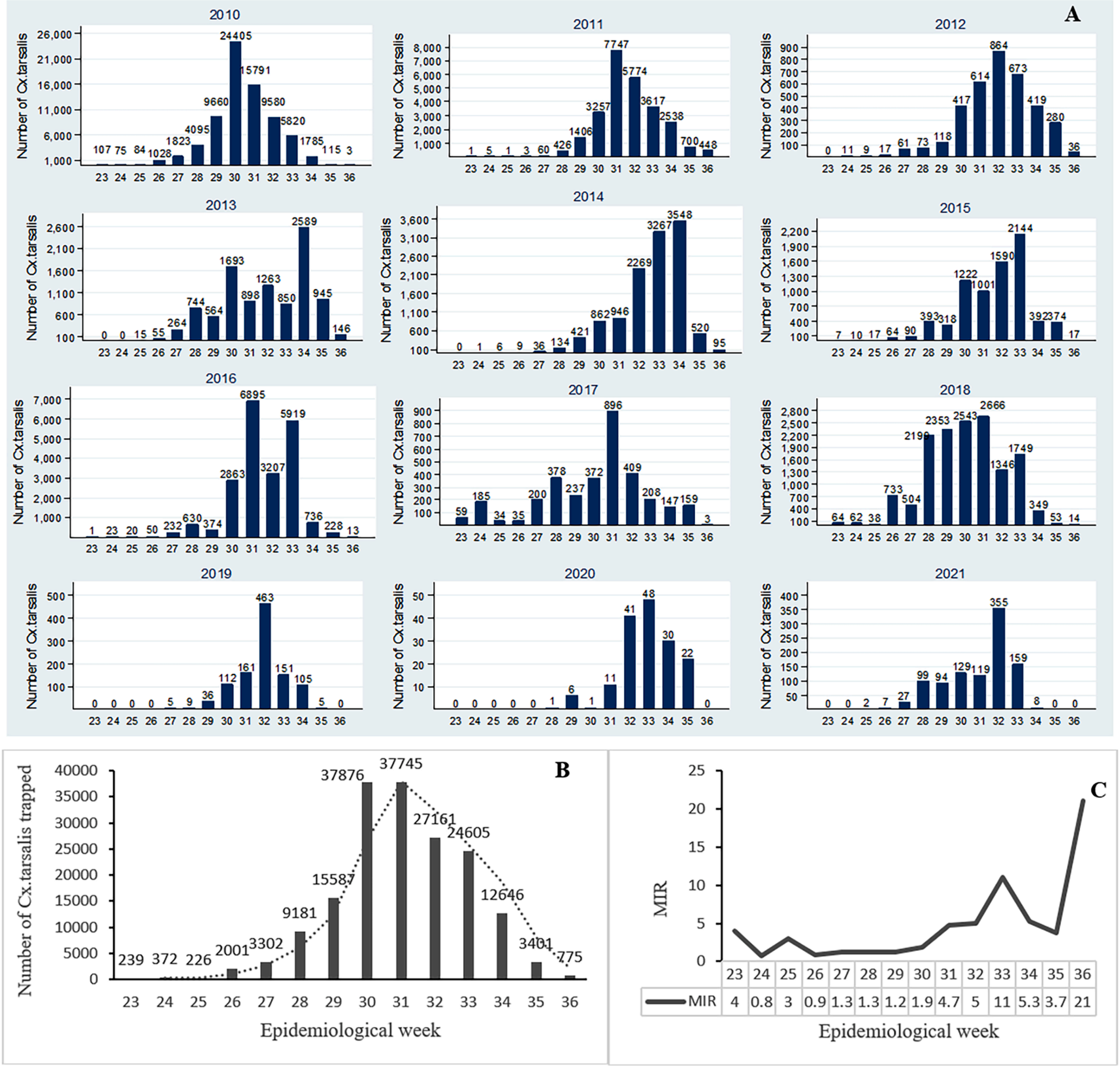

Fig. 3. Number of *Cx. tarsalis* mosquitoes trapped by epidemiological weeks (week 23–36) in each year (A), number of *Cx. tarsalis* mosquitoes trapped by epidemiological weeks (week 23–36) (B) in the study period, and mosquito minimum infection rate (MIR) by epidemiological week (week 23–36) in the study period (C) in Saskatchewan, Western Canada. Note: Graphs are on different scales for better visualization.

compared with a reference value of 14.3 °C, which is the baseline temperature for *Cx. tarsalis* in cold regions (Fig. 5A). Weekly average minimum air temperatures between the reference temperature and 26 °C showed a positive association. The 3D plot (Fig. 5A) shows a very strong and immediate effect of high temperatures (between 20 and 26 °C) and a diminished effect over longer lags and cold temperatures. As the contour plot (Fig. 5B) shows, cold temperatures below the reference temperature are associated with zero number of *Cx. tarsalis* mosquitoes in the entire lag weeks. The cumulative effect of weekly average minimum air temperature on the abundance of *Cx. tarsalis* mosquitoes decreases as temperature decreases. Compared with the reference temperature of 14.3 °C, the cumulative effect to the 99th percentile of the weekly average minimum air temperature (16 °C) was 1.32 (β: 1.32, 95 % CI: 0.97, 1.67), 5.18 (β: 5.18, 95 % CI: 3.81, 655) to 99.9th percentile (21 °C), and was 22.16 (β: 22.16, 95 % CI: 4.72, 39.60) to 100th percentile (26 °C) (Table 5).

The association between weekly average rainfall and abundance of *Cx. tarsalis* mosquitoes is not linear (Fig. 6A and 6B). Weekly average rainfall, between approximately 8 and 20 mm in longer lags (lag 5–7), was strongly associated with a high abundance of *Cx. tarsalis* mosquitoes even if this effect is diminished over 4 to 0 lag weeks. On the other hand, higher weekly average rainfall (> 20 mm) in the entire lag weeks is associated with a lower number of *Cx. tarsalis* mosquitoes. Compared with a reference value of 1.9 mm, which is the mean of the weekly average rainfall recorded in the mosquito season in the study period, the cumulative exposure (lag 0 – 8 weeks) to 99.9th percentile of rainfall (31 mm) was −98.91 (β: −98.91, 95 % CI: −187.29, −10.53), 3.70 (β: 3.70, 95 % CI: 0.68, 6.72) to 99th percentile (12 mm), and 2.75 (β: 2.75, 95 %

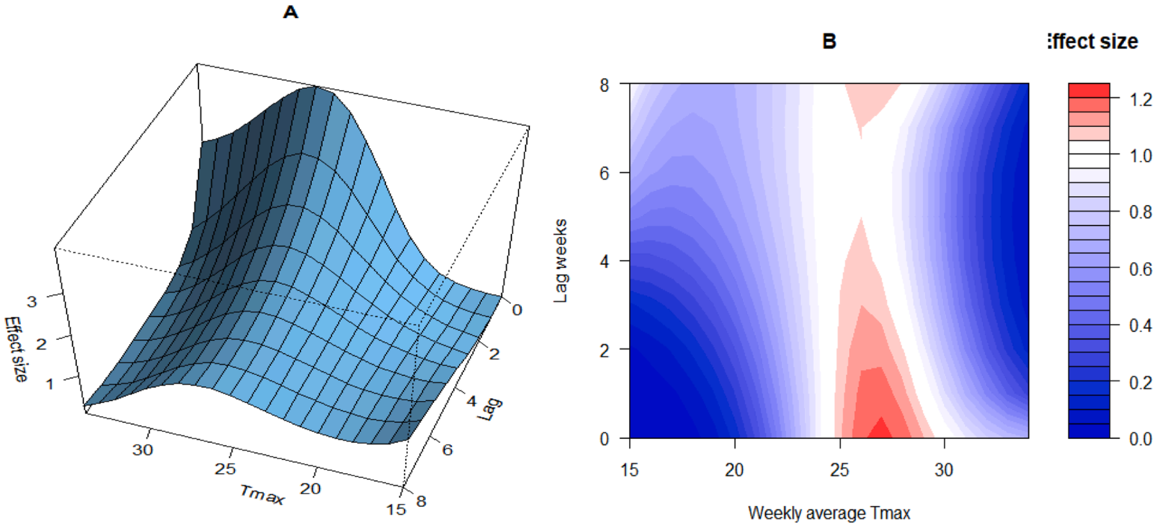

Fig. 4. The lagged effect of weekly average maximum air temperature on *Cx. tarsalis* mosquitoes in Saskatchewan (A is a 3D plot and B a contour plot offer a comprehensive summary of the bi-dimensional exposure-lag-response association). The effect is estimated with reference to 24.4 °C. Effect size in the plots is the regression coefficient.

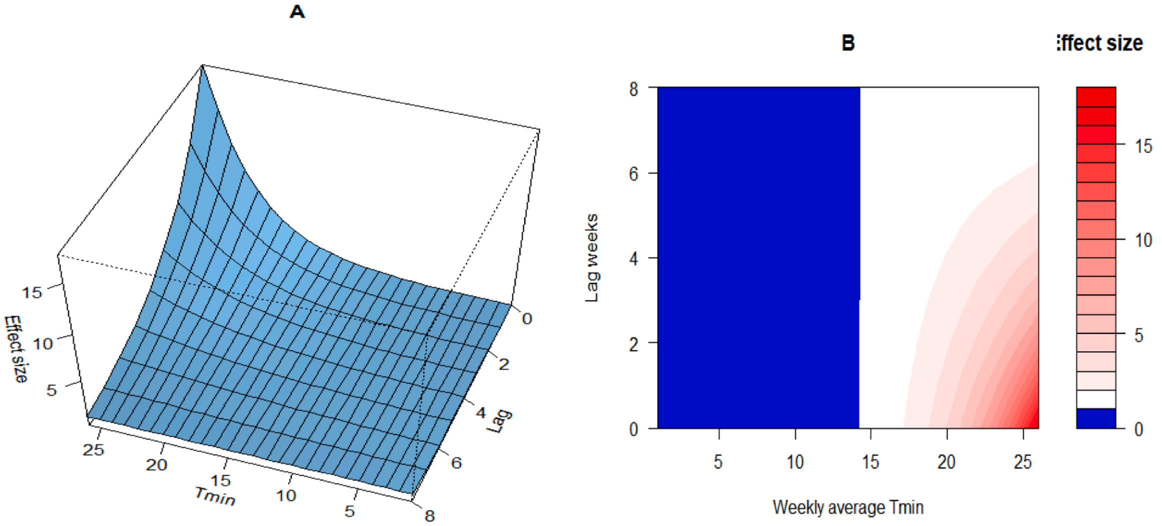

Fig. 5. The lagged effect of average weekly minimum air temperature on *Cx. tarsalis* mosquitoes in Saskatchewan (A is a 3D plot and B a contour plot offer a comprehensive summary of the bi-dimensional exposure-lag-response association). The effect is estimated with reference to 14.3 °C. Effect size in the plots is the regression coefficient.

CI: 1.04, 4.46) to 97.5th percentile (8 mm) (Table 5).

In general, an increasing wind speed over lag 0 to 8 is associated with a lower abundance of *Cx. tarsalis* mosquitoes (Fig. 7A and &B), with maximum effect achieved at lag 0 to 2. As provided in Table 5, the cumulative effect (lag 0 – 8 weeks) of weekly average maximum wind speed on the abundance of *Cx. tarsalis* mosquitoes decreases as the wind speed increases. The cumulative effect was 1.24 (β: 1.24, 95 % CI: −1.76, 4.24) at the 1st percentile (7 km/h) and 0.71 (β: 0.71, 95 % CI: 0.69, 0.73) at the 99th percentile (65 km/h) compared with the highest wind speed recorded in the study period, i.e., 143.9 km/h (Table 5).

4. Discussion

This study was conducted to model the lagged and nonlinear effects of weather conditions on the abundance of *Cx. tarsalis* mosquitoes in Saskatchewan, Western Canada using a bi-dimensional distributed lag nonlinear model. From 2010 to 2021, a total of 171,141 *Cx. tarsalis* mosquitoes were trapped, with the highest number, 74,575 (43.6 %), recorded in 2010. The number of *Cx. tarsalis* mosquitoes caught dropped year after year during the study period. Even though it is widely acknowledged that rising temperatures in temperate regions increase the abundance of mosquitoes (Ewing et al., 2016; Reinhold et al., 2018), the reduction in mosquito population in the studied region could be attributed to drought or insufficient rainfall. The southern Saskatchewan region, the area where most of the mosquito trap data are reported, is highly prone to drought (Wheaton et al., 2016; Sumaiya et al., 2021), e.g., notable droughts occurred during 2015 (7671 *Cx. tarsalis* were trapped) (Wheaton et al., 2023), 2017 (3322 *Cx. tarsalis* were trapped) (Hadwen and Schaan, 2017; Hoell et al., 2020), 2020 (160 *Cx. tarsalis* were trapped) (Umphlett et al., 2022), and 2021 (802 *Cx. tarsalis* were trapped) (Wheaton et al., 2023; Umphlett et al., 2022) in the study period. The magnitude, frequency, and duration of drought in the area are expected to be high in the future due to climate change (Wheaton et al., 2016; Sumaiya et al., 2021). However, the effect of drought on *Cx. tarsalis* mosquitoes is dependent on the availability of minimum amounts of water. *Cx. tarsalis* mosquitoes can thrive in drought

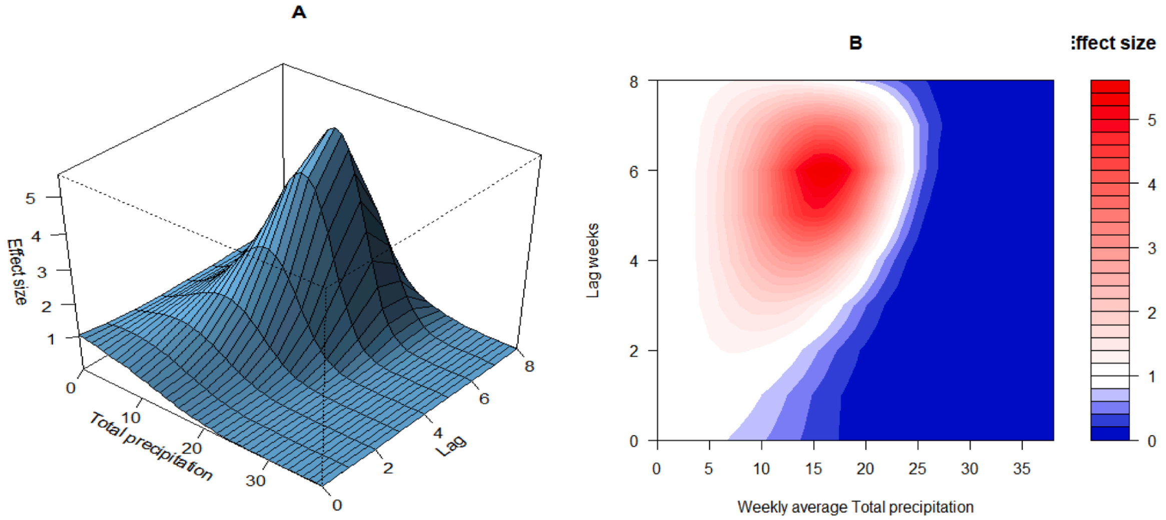

Fig. 6. The lagged effect of weekly average rainfall on *Cx. tarsalis* mosquitoes in Saskatchewan, Western Canada (A is a 3D plot and B a contour plot offer a comprehensive summary of the bi-dimensional exposure-lag-response association). The effect is estimated with reference to 1.9 mm, mean of the observed rainfall. Effect size in the plots is the regression coefficient.

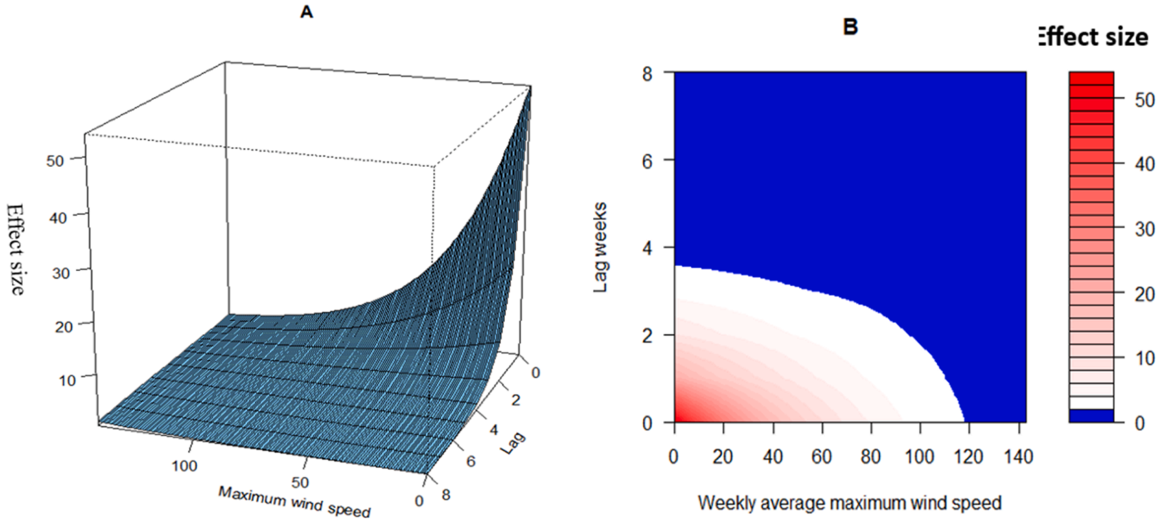

Fig. 7. The lagged effects of weekly average maximum wind speed on *Cx. tarsalis* mosquitoes in Saskatchewan (A is a 3D plot and B a contour plot offer a comprehensive summary of the bi-dimensional exposure-lag-response association). The effect is estimated with reference to 143.9 km/h. Effect size in the plots is the regression coefficient.

conditions as long as rainfall, wind, and humidity conditions are sufficient to create and maintain stagnant pools (Bradford, 2005).

Our study suggested that air temperatures between 14 °C and 30 °C across all lag weeks were positively associated with the abundance of *Cx. tarsalis* mosquitoes in the studied region, where the highest association was observed between 25 °C and 29 °C and a high abundance of *Cx. tarsalis* mosquitoes was recorded between weeks 26 and 35. *Cx. tarsalis* has a temperature threshold of 14 °C to 35 °C (Roth et al., 2010; Henn et al., 2008; Reisen, 1995; Paz, 2015); however, ambient temperatures exceeding 30 °C limit larval survival (Reisen, 1995). Warmer temperatures combined with wetter weather provide more habitats for *Cx. tarsalis* mosquitoes to reproduce and grow faster. Warmer temperatures allow female mosquitoes to lay eggs more frequently because their metabolism increases as temperature warms, making them more active and likely to seek blood, which contains protein required for more frequent and rapid egg development (Vorhees et al., 2013). Moreover, *Cx. tarsalis* mosquitoes complete their life cycle more quickly in warmer weather. For example, temperature increases from 16 °C to 24 °C increased the rate of culex mosquito development by an average of 2.9-fold, while increases from 24 °C to 32 °C increased it by an average of 2.3-fold (Ciota et al., 2014). The average time to emergence varied from 29 days at 16 °C to 9 days at 28 °C (Ciota et al., 2014). On the other hand, cold temperatures below 14°C and hot temperatures above 30 °C are negatively associated with the abundance of *Cx. tarsalis* mosquitoes. Lower temperatures generally limit metabolic rates and thus growth rate. Low temperatures can induce mortality in immature stages, with the deadly effect of cold temperature being greatest at late developmental stages (fourth instar larvae and pupae). Similarly, temperatures exceeding 30 °C may result in increased mortality of mosquito eggs, larvae, and adults (Reisen et al., 2014b; Moser et al., 2023b).

The current study revealed that summer rainfall has both negative and positive effects on the abundance of *Cx. tarsalis* mosquitoes in the studied region, depending on the amount of rain and the time period in which the mosquitoes develop. The optimal quantity of rainfall, particularly in the longer lags, i.e., the time between egg laying and adult emergence, is highly associated with high mosquito abundance.

Table 5
Overall cumulative association of weather variables and average of *Cx. tarsalis* mosquitoes per trap night in Saskatchewan, Western Canada.

Weather variables	Average of *Cx. tarsalis* per trap night	
	Unadjusted β with 95 % CI	Adjusted β with 95 % CI
Weekly average maximum air temperature		
1st percentile (17 °C)	−17.26 (−23.61, −10.91)	−8.31 (−11.96, −4.66)
2.5th percentile (18 °C)	−12.13 (−15.17, −9.09)	−7.91 (−10.38, −5.44)
10th percentile (20 °C)	−7.31 (−8.66, −5.96)	−5.95 (−7.07, −4.82)
25th percentile (22 °C)	−3.26 (−3.89, −2.63)	−3.18 (−3.75, −2.61)
75th percentile (26 °C)	0.84 (0.39, 1.29)	1.35 (0.94, 1.76)
76th percentile (27 °C)	0.71 (0.02, 1.40)	1.64 (0.97, 2.31)
90th percentile (29 °C)	−1.32 (−2.38, −0.26)	0.46 (−0.56, 1.48)
97.5th percentile (31 °C)	−6.08 (−7.77, −4.39)	−3.78 (−5.31, −2.25)
99th percentile (33 °C)	−14.00 (−17.66, −10.33)	−11.96 (−15.02, −8.90)
Weekly average minimum air temperature		
1st percentile (4 °C)	−9.84 (−12.02, −7.66)	−7.97 (−10.07, −5.87)
2.5th percentile (5 °C)	−8.89 (−10.85, −6.93)	−7.20 (−9.10, −5.30)
10th percentile (7 °C)	−6.98 (−8.51, −5.45)	−5.65 (−7.14, −4.16)
25th percentile (9 °C)	−5.07 (−6.19, −3.95)	−4.10 (−5.18, −3.02)
75th percentile (12 °C)	−2.20 (−2.89, −1.51)	−1.78 (−2.25, −1.31)
90th percentile (13 °C)	−1.24 (−1.51, −0.97)	−1.01 (−1.28, −0.74)
97.5th percentile (15 °C)	0.67 (0.51, 0.83)	0.54 (0.40, 0.68)
99th percentile (16 °C)	1.62 (1.27, 1.97	1.32 (0.97, 1.67)
99.9th percentile (21 °C)	6.41 (4.99, 7.82)	5.18 (3.81, 6.55)
100th percentile (26 °C)	13.42 (11.40, 15.44)	22.16 (4.72, 39.60)
Weekly average rainfall		
1st percentile (0 mm)	0.70 (−1.56, 0.16)	0.23 (−0.73, 1.19)
50th percentile (1 mm)	−0.38 (−0.69, −0.07)	−0.01 (−0.38, 0.36)
75th percentile (3 mm)	0.57 (0.32, 0.57)	0.23 (−0.08, 0.54)
90th percentile (5 mm)	1.76 (1.09, 2.43)	1.09 (0.32, 1.85)
97.5th percentile (8 mm)	3.50 (1.81, 5.19)	2.75 (1.04, 4.46)
99th percentile (12 mm)	4.56 (1.21, 7.91)	3.70 (0.68, 6.72)
99.5th percentile (15 mm)	3.44 (1.34, 8.22)	1.86 (−2.59, 6.31)
99.9th 99th percentile (31 mm)	−63.00 (−136.70, −10.70)	−98.91 (−187.29, −10.53)
Weekly average maximum wind speed		
1st percentile (7 km/h)	1.24 (−1.76, 4.24)	–
2.5th percentile (12 km/h)	1.19 (−1.69, 4.07)	–
10th percentile (22 km/h)	1.10 (−1.57, 3.77)	–
25th percentile (32 km/h)	1.01 (−1.44, 3.46)	–
50th percentile (40 km/h)	0.94 (−1.33, 3.21)	–
75th percentile (46 km/h)	0.89 (−1.25, 3.03)	–
90th percentile (53 km/h)	0.82 (−1.16, 2.60)	–
97.5th percentile (60 km/h)	0.76 (−1.08, 2.60)	–
99th percentile (65 km/h)	0.71 (0.69, 0.73)	–

This is because rainfall plays a key role in producing and maintaining the wet breeding locations required for egg laying, hatching, and development (Chowell et al., 2019; Marini et al., 2016; Valdez et al., 2017a; Karki et al., 2016; Chandra & Mukherjee, 2022). On the other hand, heavy rainfall in the entire lag weeks is associated with a lower number of *Cx. tarsalis* mosquitoes. This is because heavy rains can wash away eggs and larvae (Koenraadt and Harrington, 2008). Many vector breeding areas are likely to be overwhelmed and washed out during severe rainfall events, and excessive rainfall can also dilute nutrients in standing water (Jones et al., 2012; Koenraadt and Harrington, 2008; Shand et al., 2016). Moreover, a lower amount of rainfall in shorter lags contributed to the abundance of *Cx. tarsalis* mosquitoes in the studied region. This could be because increased near-surface humidity caused by rainfall promotes mosquito flight activity and host-seeking behavior (Shaman & Day, 2007; 2005).

Wind speed is negatively associated with the abundance of *Cx. tarsalis* mosquitoes in the study area. The maximum effect of low wind speed on the abundance of *Cx. tarsalis* mosquitoes is reached at the trap week and increasing wind speed over lags 0 to 8 is associated with a lower abundance of *Cx. tarsalis* mosquitoes. Wind speed is associated with the abundance of *Cx. tarsalis* mosquitoes for different reasons. One reason is that wind speed influences the distribution, flight, and dispersal activity of mosquitoes. High wind speed reduces the flight activities and host-seeking behavior of *Cx. tarsalis* mosquitoes by dispersing CO_2 (Cardé, 2015; Karki et al., 2016), resulting in reduced blood-feeding and oviposition, and consequently, a reduction in reproductive capability, i.e., fewer eggs will be produced by females throughout their lifetime, and the next mosquito generation will be smaller (Stilianakis et al., 2016). The second mechanism is the deadly impact of wind-induced waves in aquatic reservoirs. Wind-induced waves in aquatic reservoirs kill mosquitoes in their aquatic stages (Endo & Eltahir, 2018). Third, high wind speed can inhibit mosquito establishment in their climatic niche (Larsen, 2010). Furthermore, at high wind speeds, mosquitoes are not actively flying and therefore not being collected in the traps (Reisen et al., 2003).

It is documented that relative humidity influences the abundance of mosquitoes (Brown et al., 2023a; de Almeida Costa et al., 2010; Cai et al., 2023; Lega et al., 2017). Relative humidity of 40 to 90 % is associated with improved longevity, survival, egg production, desiccation tolerance, and mosquito activity. Humidity levels above 90 % and below 40 %, on the other hand, are associated with lower mosquito survival rates (Lyons et al., 2014; Brown et al., 2023b). However, abundance of *Cx. tarsalis* mosquitoes was not statistically associated with relative humidity in the current study, which is in line with findings of other studies (Baril et al., 2023b; Drakou et al., 2020; Asigau and Parker, 2018). *Cx. tarsalis* mosquitoes generally prefer hot and dry conditions (relatively low humidity) (Stuart, 2020; Baril et al., 2023b). Laboratory-based studies also confirmed that *Cx. tarsalis* mosquitoes prefer relatively low humidity (Reinhold et al., 2022; Dodson et al., 2012). However, very dry conditions, e.g., weekly average rainfall below approximately 8 mm, was associated with a low abundance of *Cx. tarsalis* mosquitoes in Saskatchewan.

Even though, the development of WNV in mosquitoes is expected in temperate regions during summer because warmer summer temperatures promote faster pathogen replication (McDermott, 2022; Reisen et al., 2014a; Kilpatrick et al., 2008) and shorten the extrinsic incubation period (Agarwal et al., 2017; Reisen et al., 2014a), WNV-infected mosquitoes are captured early in the mosquito season in Saskatchewan. The presence of WNV-positive mosquitoes in the early season may indicate that the virus overwintered in diapause insects and that pathogen development occurred in the spring, resulting in a large number of infected mosquitoes in the early transmission season (Kampen et al., 2021; Rudolf et al., 2017; Nasci et al., 2001). Mosquito infections during the early transmission season can lead to spread of the virus in the spring as well as long-term disease establishment (Nasci et al., 2001; Andreadis et al., 2010). For example, in Canada, the incidence of mosquito-borne diseases has increased by around 10 % over the previous 20 years due to the increasing length of transmission seasons caused by changing climates (Ludwig et al., 2019).

Findings of this study provide valuable insights for authorities involved in mosquito control in Saskatchewan and beyond to optimize mosquito surveillance and intervention timing, improve resource allocation, and enhance public health alerts and risk communication. Understanding how weather variables such as temperature, rainfall, humidity, and wind speed influence abundance of *Cx. tarsalis* mosquitoes over time can help predict periods of peak abundance. This allows for informed trap deployment and more precise and timely interventions, such as the application of larvicides or adulticides, to suppress mosquito populations before they become a public health concern. The lagged effects identified by the model can pre-empt and therefore significantly reduce the time lag between population surges and control actions, enhancing the efficiency of mosquito management efforts. Targeting interventions during peak abundance of mosquitoes rather than a continuous approach can help public health and mosquito control authorities to better allocate resources to areas at higher risk during specific weather conditions. Moreover, understanding the weather patterns that precede mosquito abundance can help public health authorities to inform individuals to use personal preventative measures, e.g., using repellents and avoiding outdoor activities at peak times.

This study had some limitations. First, although trap counts provide a good indicator of the relative abundance of mosquitoes and their host-seeking behaviors during the trapping time, they may not always correspond to total mosquito abundance since not all mosquitoes are captured by light traps. A variety of factors influence trapping efficiency, including the number and type of traps, timing of traps, equipment concerns (such as batteries), and weather factors (McCardle et al., 2004; Vezenegho et al., 2015). Second, the impact of meteorological conditions on mosquito biology and behavior was not examined. Third, we did not adjust for non-climatic variables, such as land use and bird populations which are linked to adult mosquito abundance and infection rates (Adelman et al., 2022), the latter because available WNV bird population data cannot be associated with specific regions or traps.

5. Conclusion

The current study confirmed that the weather conditions at and beyond the trap weeks (in our case within the 8 weeks before the trap weeks) affect the abundance of *Cx. tarsalis* mosquitoes in Saskatchewan. Warmer temperatures (weekly average air temperature between 25 °C and 29 °C) over the 8 weeks lag period, wetter weather (weekly average rainfall between 8 mm and 20 mm) in longer lags, and no wind or low wind speed in shorter lags were associated with the abundance of *Cx. tarsalis* mosquitoes in the studied region, where the association was nonlinear for weekly average maximum air temperature and rainfall, but linear for weekly average minimum air temperature and wind speed. Generally, warmer temperatures combined with wetter weather provide favorable conditions for growth and development of the immature stages of *Cx. tarsalis* mosquitoes and adult mosquitoes prefer hot and dry conditions. These findings identified could help public health authorities prevent transmission of WNV by timing their vector control measures to coincide with a weather-driven increase in mosquito activity. Finally, if there are ways to include information around bird populations and potential small-scale change in land-use, these could be helpful for any further analysis.

Availability of data and materials

The mosquito trap data can be accessed through requests directly to the Saskatchewan Ministry of Health. The meteorological data is publicly available on Environment and Climate Change Canada website.

Funding sources

This work is funded under the Global Water Futures program, which is through the Canada First Research Excellence Fund. Funders did not have roles in the study design; collection, management, analysis, and interpretation of data; writing of the report; and the decision to submit the report for publication.

CRediT authorship contribution statement

Zemichael Gizaw: Conceptualization, Methodology, Data curation, Formal analysis, Visualization, Writing – original draft. **Cuauhtémoc Tonatiuh Vidrio-Sahagún:** Writing – review & editing, Writing – original draft. **Alain Pietroniro:** Conceptualization, Methodology, Data curation, Visualization, Writing – review & editing, Funding acquisition, Writing – original draft. **Corinne J. Schuster-Wallace:** Conceptualization, Methodology, Data curation, Visualization, Writing – review & editing, Funding acquisition, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgment

Authors wish to acknowledge Environment and Climate Change Canada and Saskatchewan Ministry of Health for providing us the meteorological and mosquito trap data. Authors also would like to acknowledge Dr. Jeff Armstead, Director of Digital Strategy and Dr. Bijay Adhikari, Manager of Epidemiology and Surveillance, Government of Saskatchewan for helping us to access weekly mosquito trap data in Saskatchewan.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.actatropica.2024.107512.

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