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RESEARCH ARTICLE

Linking weather conditions and winter tick abundance in moose

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Abstract

Climate change may modify species distribution to higher latitudes, resulting in potential changes of parasite diversity and transmission dynamics in areas where animals might not be locally adapted to these new parasite species. In addition, climate change may increase the frequency and severity of infestations of parasites that are already present in a region, by promoting the development and survival of infectious stages. Over the last decades, the number of moose (*Alces americanus*) infested by winter ticks (*Dermacentor albipictus*) has increased in eastern Canada, possibly because milder climatic conditions are increasing winter tick survival. Our main objective was to determine which meteorological variables are more likely to influence winter tick load on moose. We compiled several weather variables that may limit winter tick survival and explored which weather variables, or their interactions, influenced the winter tick load of 4,100 hunted moose from 2013 to 2019 in Québec, Canada along a latitudinal gradient. Winter tick load in fall decreased with the maximum number of consecutive days in spring with average daily temperatures below −15°C and with the number of consecutive days in summer with a relative humidity <80% when snowmelt in spring was earlier. These results suggest that cold temperatures and prolonged periods of low humidity, amplified by early

snowmelt, limit the survival of adult female ticks and eggs, thus limiting their subsequent load on moose during the following fall. With climate change, precipitation increases and warm temperatures occur earlier in spring and are more frequent in summer. Our results suggest that climate change may have a positive long-term influence on winter tick abundance in the environment and thereby increase winter tick load on moose, which could lead to a significant decrease in moose body condition and survival.

Climate change is expected to have consequences for numerous animal species by shifting or expanding their distribution range to higher latitudes or altitudes (Berggren et al. 2009, White et al. 2018). Consequently, the range of parasites that animals host and parasite diversity in a given region, may be positively influenced by climate change (Hoar et al. 2012). This change in parasite diversity could be of importance for native species that might not be locally adapted to newly invading parasites (Merino and Møller 2010). Climate change is also expected to influence the physiology of the free-living stages of different parasite families (e.g., nematodes, ticks), their development, reproduction and fecundity, and mortality, leading to major changes in the host–parasite interface such as increased parasite loads in wildlife (Altizer et al. 2013). Changes in weather conditions may increase the transmission period of the infective larval stage of parasites and accelerate their development, resulting in an increase in the number of parasites, prevalence, and intensity of infections (Kutz et al. 2005). This is the case for several species of ectoparasites, for which warmer temperatures have a positive influence on their life cycle and promote their geographical expansion (Leighton et al. 2012).

The range expansion of the winter tick (*Dermacentor albipictus*) in the northeastern United States and western Canada is well documented and is a major threat to moose (*Alces americanus*) health (Musante et al. 2007, Samuel 2007, Bergeron and Pekins 2014). Over the past decades, intensity of winter tick infestations on moose have increased in northeastern Canada, as in the United States (Jones et al. 2019), potentially because of shallower snow cover and warmer temperatures in comparison to historical conditions. In addition, moose populations have increased in some regions of Québec, Canada, over the past decades (Lefort and Massé 2015), potentially allowing ticks to multiply and expand their range in the province. Moose are particularly affected by winter tick infestations compared to other cervids because of their lack of adaptation to this ectoparasite. Compared with other cervids, moose are less effective at grooming because they do not have an internal timing mechanism for programmed grooming (Mooring and Samuel 1998). Instead, the discomfort caused by the presence of adult ticks prompts moose to groom and rub against trees more intensely, which can cause loss of fur, at the detriment of feeding (Skorupka 1999). In addition, rutting occurs earlier in the fall for moose than for other cervids, and moose move over great distances during that period, which is also the period during which winter tick larvae start questing (Samuel 2004).

The winter tick is a 1-host tick with a 1-year life cycle that involves 4 different development stages: in fall, from September to November, larvae wait in the vegetation to climb on a passing host; in winter, from January to March, nymphs feed on the blood of their host, molt into adults, and mate; in spring, from March to May, engorged females drop on the ground to lay eggs; and finally in summer, from June to August, eggs mostly stay on the ground. Larvae hatch around late August and climb on vegetation and the cycle starts again (Healy et al. 2018). During fall, spring, and summer, winter ticks are more likely to be vulnerable to weather conditions because they are not protected against the environment by the host. While eggs are more likely to die under low humidity conditions

(Yoder et al. 2016), larvae and adult females are more sensitive to cold temperatures and to the presence of persistent snow cover in spring (Drew and Samuel 1985, Powers and Pekins 2020).

Climate change can increase the occurrence of favorable conditions for the development and survival of winter tick free-living stages, leading to an expansion of the distribution of winter tick towards the north, or an increase in the intensity of winter tick infestations in areas where it is already present. These changes in winter tick–moose relationships could have detrimental impacts on the health of individual moose and eventually on moose population dynamics. Our main objective was to explore the effects of different weather variables and densities of moose populations on winter tick infestation levels on moose in Québec. Because each developmental stage of the winter tick occurs during successive seasons, we expected that inter-regional and interannual variations in moose winter tick load would be linked to the prevailing weather conditions during each season, so that tick load would be higher in regions and during years with weather conditions favorable to the survival of the free-living stages of winter tick. We expected that a later spring snowmelt, an increasing number of consecutive days with non-optimal relative humidity conditions during summer, and an earlier date for the first snow in fall would decrease winter tick load on moose.

STUDY AREA

The study area encompassed >1,000,000 km^2 in Québec, including 17 independent hunting zones with different moose densities and climatic conditions (Table 1; Figure 1). The vegetation in the southern part of the study area was dominated by sugar maple (*Acer saccharum*)–American basswood (*Tilia americana*) and sugar maple–yellow birch (*Betula alleghaniensis*) domains. The northern part of the study area was populated by balsam fir (*Abies balsamea*)–yellow birch, balsam fir–white birch (*Betula papyrifera*), and black spruce (*Picea mariana*)–moss domains (Saucier et al. 2010). The study area is also occupied by white-tailed deer (*Odocoileus virginianus*) in more southern areas and wolves (*Canis lupus*) north of the St. Lawrence River. Land use varies from agricultural lands in the south to public forests in the north. Elevation ranges from sea level to 1,200 m and consists mainly of gently rolling hills. From south to north, the mean minimum daily temperature in winter varied from −10°C to −30°C and the mean maximum daily temperature in summer from 30°C to 15°C (Ministère de l'Environnement et de la Lutte contre les Changements Climatiques 2020). Based on aerial surveys conducted by the Québec Ministère des Forêts, de la Faune et des Parcs (MFFP; Lefort and Massé 2015) moose density at the scale of hunting zones varied from 0.5 moose/10 km^2 to 9.0 moose/10 km^2 (Table 1).

METHODS

Data collection

We used the winter tick counts conducted by the MFFP on the carcasses of moose harvested during the sport hunting season between 15 September and 15 November in 2013-2019 (*n* = 4,100). We assessed the number of winter ticks per moose by counting tick larvae on 3 parts of the body (shoulder, wither, and buttock on 1 side of the animal) along 4 10-cm vertical transects (total of 12 transects; Sine et al. 2009). We used the number of winter ticks counted along the 12 transects as an indicator of moose winter tick load for statistical analyses.

We estimated moose density in each hunting zone using the most recent aerial survey conducted by the MFFP, between 2000 and 2010 (Lefort and Massé 2015). Crews conducted surveys in 6 km^2 by 10 km^2 rectangular plots using the stratified-random block or double census technique (Courtois 1991). The aircraft flew each survey block along flight lines spaced 500 m apart, at an altitude of 110 m and at a speed of 160 km/hour. Crews counted and sexed moose <24 hours after mapping moose yards. The aerial surveys occurred between early January and mid-February because moose are more visible during this period. Aerial surveys conducted by the MFFP usually meet the precision objective to estimate the densities with a confidence interval of <20% with α = 0.10.

TABLE 1 Administrative regions along with their hunting zones, estimated moose population density (moose/ 10 km^2), years of sampling, and the number of moose sampled for winter ticks in Québec, Canada, 2013–2019. Regions are presented according to their spatial distribution, from south to north. We estimated moose population densities with aerial surveys (Lefort and Massé 2015). Average number of winter ticks represents the mean number of ticks counted along the 12 transects of each moose sampled.

Administrative region	Hunting zone	Estimated moose population density (moose/10 km^2)	Years of sampling	Number of moose sampled	Average number of winter ticks per moose
Estrie	4	1.4	2013, 2015–2019	175	29
Chaudière-Appalaches	3	6.0	2013, 2015, 2017–2019	233	22
Centre-du-Québec	7	2.7	2015, 2016, 2019	16	34
Mauricie	14	2.6	2013, 2015–2019	62	5
	15	1.8	2013, 2015–2019	57	6
	26	2.9	2013, 2015–2019	135	11
Capitale-Nationale	27	5.7	2013, 2015–2019	230	9
Outaouais	10	1.5	2013, 2017–2019	20	9
	11	1.4	2013, 2017–2019	25	8
Bas-Saint-Laurent	2	9.0	2013–2019	1,648	18
Abitibi	12	2.5	2013, 2017–2019	55	6
	13	2.7	2013, 2016–2019	287	5
Gaspésie	1	8.0	2013–2019	1,069	18
Saguenay	18	1.3	2013–2019	128	0
Nord-du-Québec	16	1.7	2015, 2017–2019	63	1
	17	0.8	2013–2015, 2018, 2019	8	1
	22	0.5	2013–2019	17	1

We identified the meteorological station (n = 48) closest to the harvest location of each moose sampled for tick counts (Figure 1). We obtained data of several weather variables known or suspected to influence the survival of winter tick during their free-living stages. We compiled each weather variable separately for spring (Mar–May), summer (Jun–Aug), and fall (Sep–Nov) for each year and each meteorological station. We compiled data on 1) average relative humidity (%), 2) average minimum and maximum daily relative humidity (%), 3) average temperature (°C), 4) average minimum and maximum daily temperatures (°C), and 5) maximum number of consecutive days with non-optimal temperature and humidity for winter tick survival. The non-optimal relative humidity threshold was <80% (Knülle 1966, Yoder and Spielman 1992), while the non-optimal temperature thresholds were ≤−15°C in spring (Drew and Samuel 1986), <15°C and >35°C in summer (Wilkinson 1967), and <0°C in fall (Drew and Samuel 1985). We determined the date of the complete melting of snow in spring and the date of the first snow in fall based on snow depth data recorded at the weather station. Finally, we calculated the number of annual cumulated degree-days (sum of the mean monthly temperatures multiplied by the number of days in the month, when the mean monthly temperature was >6°C), and the number of thermal degree-days (number of hours with a temperature >6°C, summed for the year; Wilkinson 1967, Zarnke et al. 1990). We compiled all variables from the National Operational Hydrologic Remote Sensing Center (https://www.nohrsc.noaa.gov, accessed 8 Jun 2020).
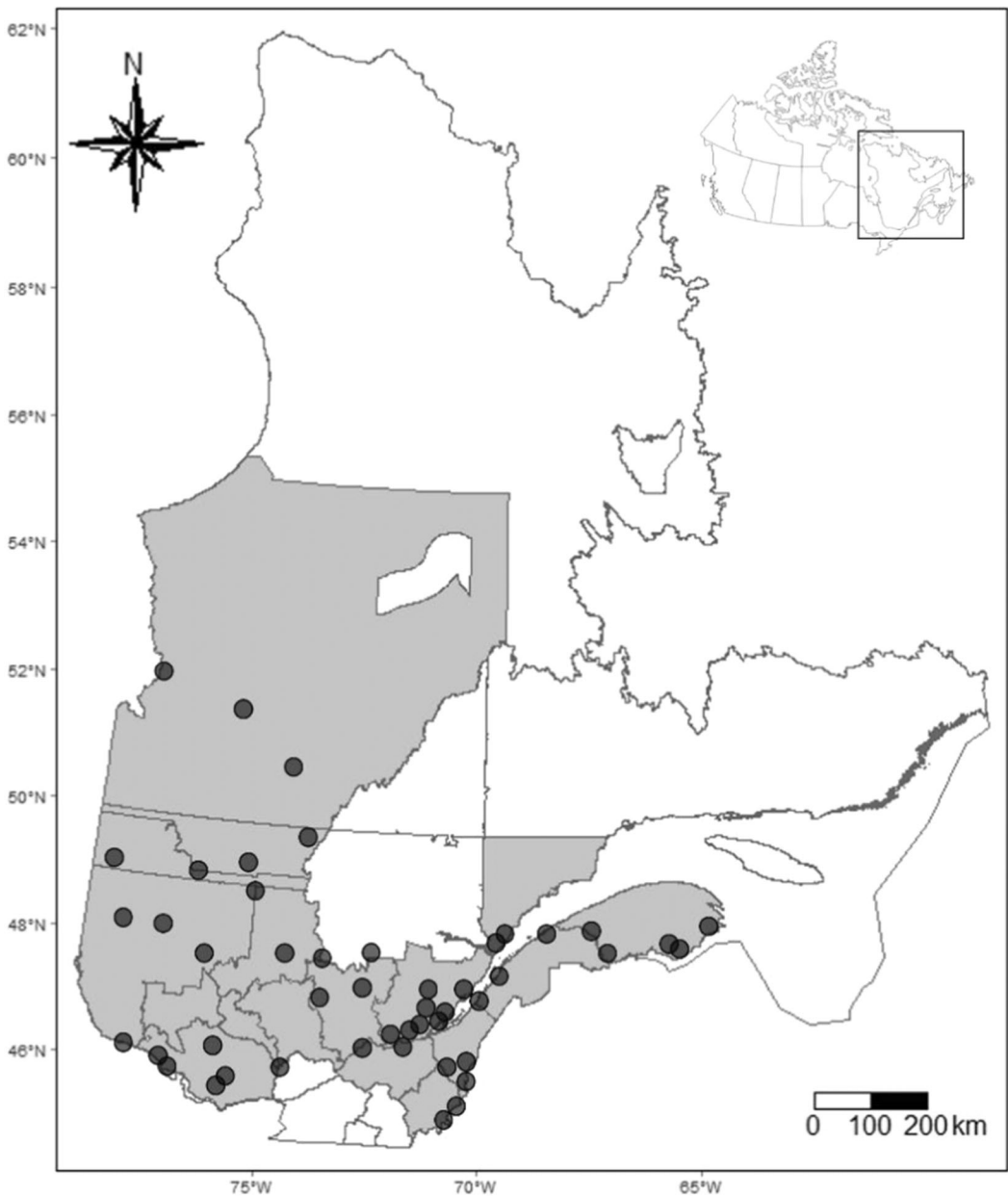
FIGURE 1 Study area in Québec, Canada. Grey areas depict 17 moose hunting zones where tick sampling occurred in 2013–2019. Black dots represent 48 meteorological stations used to collect weather data.

Statistical analyses

We performed a preliminary principal component analysis (PCA) to assess the relationships among the different weather variables to avoid using highly correlated variables in the final model. We then tested if the retained weather variables from the PCA influenced the number of winter ticks on moose. Because we wanted to consider the effect of variables one by one and we used an exploratory approach, we performed stepwise model selection by

Akaike's Information Criterion (AIC) with the function stepAIC() (MASS package; Ripley et al. 2020) in R version 4.0.2 (R Core Team 2020) with a generalized linear mixed model using template model builder (glmmTMB package; Magnusson et al. 2020) and a binomial negative family to account for over-dispersion. We selected the model with the least number of parameters within a ΔAIC of 2.

The initial model included the weather variables selected in the preliminary PCA analysis for each season, the date of snowmelt in spring, and the date of the first snow in fall. We also included weather variables from spring and summer of the previous year to assess possible time-lags effects. Adult female winter ticks that drop off the moose in spring can survive a year in the forest and eggs can cyst for 1 year before hatching if conditions are not optimal for their survival (K. Oyen, University of Cincinnati, personal communication). In addition to the weather variables, we also added the regional moose population density to the model. Because winter tick load is expected to increase over the fall sampling period, we included date of the tick survey as a covariate. Based on our predictions, we tested the interactions between mean temperature and mean humidity, and between the maximum number of days with non-optimal temperature and non-optimal humidity for each season of the current and previous year. We considered all 2-way interactions among the following variables: date of snow melt in spring, the maximum numbers of days with non-optimal humidity in summer, and date of the first snow in fall. Finally, based on AIC corrected for small sample size (AIC$_c$), we included the hunting area, weather station, and year as random intercepts in the model to account for temporal and spatial variation (Figure S1, available in Supporting Information). Because there were no ticks counted in the Saguenay area and we wanted to determine the effects of weather variables on the intensity of winter tick load on moose, we removed this region from the analyses. We standardized all continuous variables (mean = 0, SE = 1) to facilitate model convergence and interpretation of effects. Collinearity between all variables and all statistical assumptions were verified and fulfilled.

RESULTS

The PCA revealed that 5 groups of weather variables could be formed using the first 2 axes, which explained 70% of the variance (Figure 2). Consequently, we retained 1 variable from each group to run the models: mean relative humidity, mean temperature, maximum number of consecutive days with non-optimal relative humidity for winter tick survival, maximum numbers of consecutive days with non-optimal temperature for the survival of winter tick, and annual cumulated degree-days (Figure 2; Table S1, available in Supporting Information).

The model with the least number of parameters within a ΔAIC of 2 (Table S2 and S3, available in Supporting Information) had 19 variables, 4 of which had confidence intervals that did not overlap with zero (Table 2). Winter tick load was positively correlated with the sampling date (Table 2; Figure 3) and negatively correlated with the number of consecutive days when the average daily temperature was <−15°C in spring (Table 2; Figure 4). Winter tick load was also modulated by the interaction between the maximum number of consecutive days when maximal relative humidity in summer was <80% and the date of snowmelt in spring (Table 2). The number of winter ticks on moose in fall decreased with the maximum number of consecutive days with relative humidity <80% in the previous summer and more so when the date of snowmelt was earlier in spring (Figure 5). All weather variables measured during fall had confidence intervals that overlapped with zero, although we observed a positive trend between mean fall humidity and winter tick load of moose (Table 2; Figure 6A). The random intercept of hunting zone had a variance of 0.70 (Table 2) and the station and year had a variance of 0.54, suggesting that spatial variation in winter tick loads on moose was about 1.3 times greater than the temporal effect (Figure S1). Similarly, we noted a positive trend between moose population density and winter tick load (Table 2; Figure 6B). The dispersion parameter for the negative binomial model was 1.04, which means that the winter tick counts had a slight overdispersion that was controlled for with the negative binomial family.

FIGURE 2 Principal component analysis on the relationships between 12 candidate weather variables used to represent the environmental conditions that could influence the survival rates of the free-living stages of winter tick during 3 consecutive seasons (ellipses): spring (Mar–May), summer (Jun–Aug), and fall (Sep–Nov). These variables were collected from 48 weather stations in 16 different moose hunting zones in Québec, Canada, 2013–2019. This figure shows relationships among mean daily relative humidity (mean_hum), mean minimum daily relative humidity (mean_hum_min), mean maximum daily relative humidity (mean_hum_max), mean daily temperature (mean_temp), mean minimum daily temperature (mean_temp_min), mean maximum daily temperature (mean_temp_max), number of thermal degree-days (ATDD), number of annual cumulated degree-days (AADD), maximum number of consecutive days with non-optimal humidity (consecutive_humnogood), sum of days with non-optimal humidity (sumhumnogood), maximum number of consecutive days with non-optimal temperature (consecutive_tempnogood), and the sum of days with non-optimal temperature (sumtempnogood). Dim1 is the first dimension of the principal component explaining 35.7% of the variance, and Dim2 is the second dimension of the principal component explaining 34.4% of the variance.

DISCUSSION

Weather and seasonality influence variation in prevalence and intensity of ectoparasites in host populations (Parola et al. 2008, Estrada-Peña et al. 2012, Eisen et al. 2016). Our results revealed that weather conditions in spring and summer were the most likely meteorological factors affecting winter tick load on moose the following fall. In spring, blood-engorged female ticks drop of moose to lay eggs on the ground. Adult female ticks are resistant to harsh conditions and can survive temperatures down to −15°C (Drew and Samuel 1986), but our results indicated that winter tick load on moose in fall decreased with prolonged periods with temperature <−15°C during the previous spring. Researchers of a study on another tick species reported that some ticks can survive cold shock but estimated a lethal temperature threshold between −18°C and −20°C (Sands et al. 2021). Tick survival likely declines

TABLE 2 Coefficients (β) and their 95% confidence intervals of variables in the most parsimonious model explaining winter tick load in moose sampled (n = 4,100) in Québec, Canada, 2013–2019. Coefficients are scaled (mean = 0, SD = 1). Variables with confidence intervals that do not overlap zero are indicated with an asterisk.

Variables	β	95% CI Lower	95% CI Upper
Intercept	2.34	1.71	2.97*
Sampling date	0.19	0.16	0.23*
Density	0.37	−0.03	0.77
Cumulated annual degree-days	0.06	−0.10	0.22
Number of consecutive days with temperature <−15°C in spring	−0.18	−0.34	−0.02*
Number of consecutive days with temperature <−15°C in spring of previous year	−0.01	−0.17	0.15
Number of consecutive days <80% relative humidity in spring	0.01	−0.16	0.16
Number of consecutive days <80% relative humidity in spring of previous year	−0.06	−0.21	0.08
Spring mean humidity of previous year	−0.04	−0.20	0.13
Date of snowmelt	0.01	−0.14	0.16
Number of consecutive days <80% relative humidity in spring × number of consecutive days with temperature <−15°C in spring	−0.03	−0.16	0.10
Number of consecutive days <80% relative humidity in spring of previous year × number of consecutive days with temperature <−15°C in spring of previous year	−0.07	−0.20	0.06
Date of snowmelt × number of consecutive days <80% relative humidity in summer	0.15	0.04	0.26*
Number of consecutive days <80% relative humidity in summer	−0.12	−0.26	0.03
Number of consecutive days <80% relative humidity in summer of previous year	−0.05	−0.19	0.08
Number of consecutive days with temperature <15°C in summer	−0.07	−0.25	0.11
Number of consecutive days with temperature <15°C in summer of previous year	−0.04	−0.20	0.12
Number of consecutive days <80% relative humidity in summer of previous year × number of consecutive days with temperature <15°C in summer of previous year	−0.01	−0.12	0.10
Number of consecutive days <80% relative humidity in summer × number of consecutive days with temperature <15°C in summer	−0.07	−0.09	0.22
Fall mean humidity	0.12	−0.01	0.26

with harsh late winters (i.e., several consecutive days with temperature <−15°C), when tick females are on the ground, leading to a lower abundance of female ticks that could lay eggs in the environment. This lower abundance of females likely translates into a lower number of larvae that could hatch and climb on moose the following fall.

We also observed an interaction between relative humidity and timing of snowmelt on moose winter tick load. Winter tick load on moose decreased with the number of consecutive days with relative humidity <80% in summer and this trend was exacerbated when snowmelt occurred earlier in spring. This result suggests that early snowmelt may intensify desiccation of winter tick eggs during summer. Early snowmelt is generally caused by warmer temperatures earlier in the season, which results in lower soil moisture in early summer compared to the wetter soil in summer associated with later snowmelt in spring (Blankinship et al. 2014). Early snowmelt can have numerous consequences that could contribute to a drier summer, such as earlier runoff that will reduce flows in summer (Barnett et al. 2005) or increased stress on plants that will cause less evapotranspiration (Rungee et al. 2019). Later snowmelt, however, more often results in wetter soil in spring and increases the evaporation rate during summer,
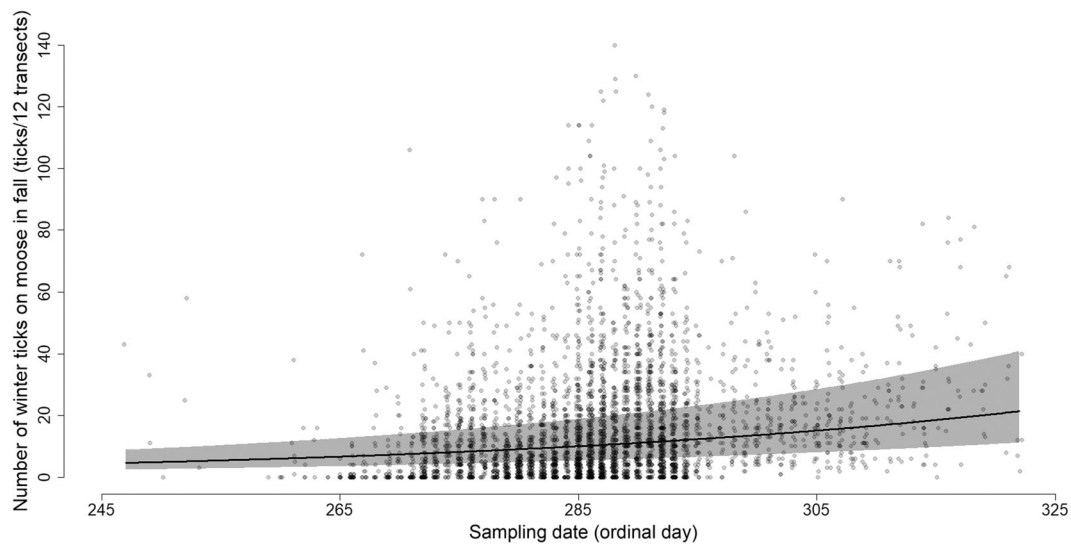
FIGURE 3 Predictions with 95% confidence intervals (in grey) from the most parsimonious model describing the number of winter ticks on moose in fall in relation with the sampling date in Québec, Canada, 2013–2019. Dots represent raw data.
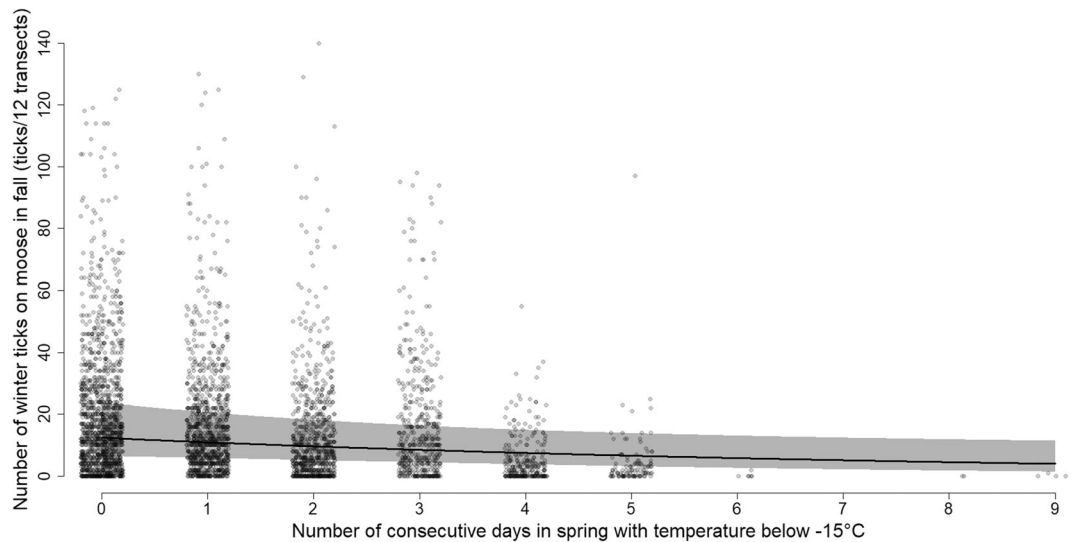

FIGURE 4 Predictions with 95% confidence intervals (in grey) from the most parsimonious model describing the number of winter ticks on moose in fall in relation to the maximum number of consecutive days in spring with average daily temperature below −15°C in Québec, Canada, 2013–2019. Dots represent raw data.

resulting in wetter conditions during summer (Small 2001). In summer, tick eggs are in development and particularly vulnerable to desiccation (Rechav and Von Maltzahn 1977). Numerous studies conducted in controlled conditions investigated the capacity of different species of *Ixodes* ticks to survive under different humidity conditions (Rodgers et al. 2007, Yoder et al. 2016). These studies have shown that eggs and freshly hatched larvae can survive during 24 hours of low relative humidity, but their survival rate is reduced when exposed to dry air during extended periods (Rodgers et al. 2007). Optimal relative humidity for several tick species has been identified as >80%, as tick
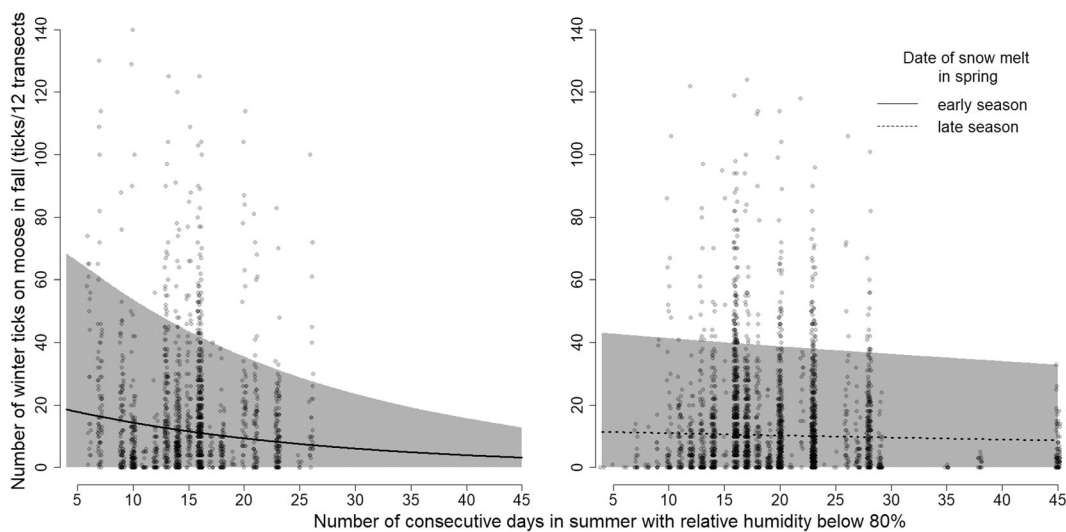
FIGURE 5 Predictions with 95% confidence intervals (in grey) from the most parsimonious model describing the number of winter ticks on moose in fall in relation to the maximum number of consecutive days in summer with relative humidity <80% for early (25 Apr) and late (15 May) snow melt in spring in Québec, Canada, 2013–2019. Dots represent raw data.
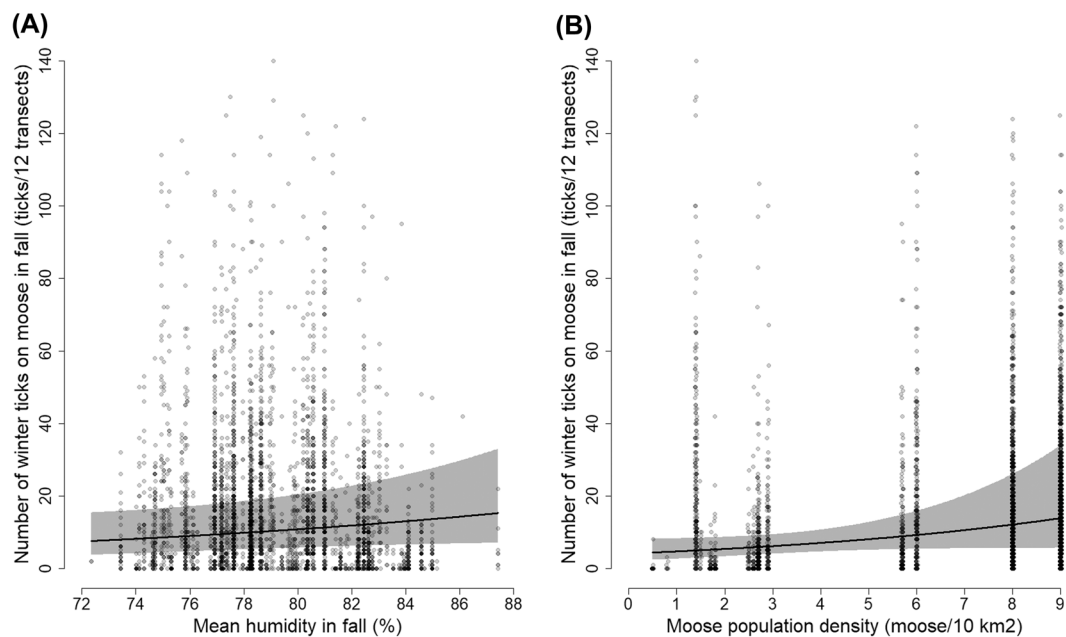

FIGURE 6 Predictions with 95% confidence intervals (in grey) from the most parsimonious model describing the number of winter ticks on moose in fall in relation to A) the mean relative humidity in fall and B) the moose population density in Québec, Canada, 2013–2019. Dots represent raw data.

survival starts to significantly decrease under this threshold (Knülle 1966, Rechav and Von Maltzahn 1977, Rodgers et al. 2007). When relative humidity values are <80%, the air is not saturated enough to allow ticks to uptake moisture and they die from desiccation (Stafford 1994). Our results expand this knowledge and suggest that humidity is an important limiting factor for the development of winter tick eggs in natural environments.

Furthermore, winter ticks exhibit significant resilience to varying humidity conditions. For example, off-host larvae and adult female winter ticks can survive underwater conditions, suggesting a considerable adaptability to different moisture levels (Sullivan et al. 2022). Additionally, larvae are characterized by specific water balance attributes that are essential for their survival off-host, particularly under conditions of varying humidity (Yoder et al. 2016). These findings indicate that, similar to other tick species, winter ticks are likely to experience survival challenges under low humidity conditions.

Desiccation of questing larvae during autumn could also have influenced moose winter tick load, as we observed a positive trend between relative humidity in fall and the number of winter ticks on moose. Previous reports showed that desiccation was also detrimental to Ixodidae larval development, where larvae hatching from eggs exposed to dry conditions had a shorter lifespan than larvae hatched from eggs exposed to optimal conditions of humidity (Sutherst and Bourne 2006). Larvae will limit the duration of questing when relative humidity is not optimal to minimize the negative effect of drought (Knap et al. 2009, Ogden and Lindsay 2016). In line with this, winter tick larvae may be influenced by environmental conditions, including humidity, that can influence their questing and host-seeking behaviors (Yoder et al. 2017). Therefore, it is likely that greater relative humidity could result in greater winter tick loads on moose in fall, aligning with our observations.

Host population density is a key factor determining whether a parasite species could infect and persist in a defined host population (Takemoto et al. 2005). High host density and frequency of contacts between hosts result in a greater risk of parasite transmission and greater parasite loads at individual and population levels (Ryder et al. 2007). Our results showed a positive and strong trend between winter tick load on moose and moose population density. Social contacts between animals are generally rare in moose, with the exception of the mating season and mother-calf relationships (Miquelle et al. 1992). Therefore, higher density in this system represents more available hosts, which increases the chances that winter tick larvae will find a host in fall. In addition, moose in eastern Canada often form small groups in late fall-early winter that can be maintained over winter, which could create areas of greater infestation risk in the following fall. Consequently, higher moose densities hold a large potential to maintain and promote larger tick populations.

RESEARCH IMPLICATIONS

Our study was influenced by both spatial and temporal variation in climate and was based on a relatively short time series of winter tick counts. Nevertheless, we assessed the potential influence of several weather variables, and their interplay, on the intensity of winter tick load on moose in their natural ecosystem. This is an important step to better understand winter tick–moose dynamics and the reported increase in the intensity of winter tick infestations in moose populations in northeastern North America. Nonetheless, winter tick counts in our study did not cover the entire tick questing period, which reduced our ability to infer the effect of certain variables, especially on larvae in fall. In a context of climate change, where weather is changing, this would translate into more favorable conditions for ticks, which will probably improve the survival and development of tick eggs in summer and the survival of adults in spring. Our study opens new avenues for future research assessing the potential synergistic effects of weather on winter tick dynamics and factors controlling their intensity and prevalence.

ACKNOWLEDGMENTS

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Our research was conducted using data collected on carcasses of moose harvested during the sport hunting season and no live animals were handled. Moose density in each hunting zone was estimated using the most recent aerial surveys conducted by the Québec government.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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