

Predicted Northward Expansion of the Geographic Range of the Tick Vector *Amblyomma americanum* in North America under Future Climate Conditions

Irina Sagurova,¹ Antoinette Ludwig,² Nicholas H. Ogden,² Yann Pelcat,² Guillaume Dueymes,¹ and Philippe Gachon^{1,3}

¹ESCCER (Étude et Simulation du Climat à l'Échelle Régionale) centre, Université du Québec à Montréal, Montréal, Québec, Canada

²Public Health Risk Sciences Division, National Microbiology Laboratory, Public Health Agency of Canada, Saint-Hyacinthe, Québec, Canada

³Strategic Research Chair on Hydro-Meteorological Risks under Climate Change, Department of Geography, Université du Québec à Montréal, Montréal, Québec, Canada

BACKGROUND: The geographic range of the tick *Amblyomma americanum*, a vector of diseases of public health significance such as ehrlichiosis, has expanded from the southeast of the United States northward during the 20th century. Recently, populations of this tick have been reported to be present close to the Canadian border in Michigan and New York states, but established populations are not known in Canada. Previous research suggests that changing temperature patterns with climate change may influence tick life cycles and permit northward range expansion of ticks in the northern hemisphere.

OBJECTIVES: We aimed to estimate minimal temperature conditions for survival of *A. americanum* populations at the northern edge of the tick's range and to investigate the possibility of range expansion of *A. americanum* into northern U.S. states and southern Canada in the coming decades.

METHODS: A simulation model of the tick *A. americanum* was used, via simulations using climate data from meteorological stations in the United States and Canada, to estimate minimal temperature conditions for survival of *A. americanum* populations at the northern edge of the tick's range.

RESULTS: The predicted geographic scope of temperature suitability [$\geq 3,285$ annual cumulative degree days (DD) $> 0^\circ\text{C}$] included most of the central and eastern U.S. states east of longitude 110°W , which is consistent with current surveillance data for the presence of the tick in this region, as well as parts of southern Quebec and Ontario in Canada. Regional climate model output raises the possibility of northward range expansion into all provinces of Canada from Alberta to Newfoundland and Labrador during the coming decades, with the greatest northward range expansion (up to 1,000 km by the year 2100) occurring under the greenhouse gas (GHG) emissions of Representative Concentration Pathway (RCP) 8.5. Predicted northward range expansion was reduced by approximately half under the reduced GHG emissions of RCP4.5.

DISCUSSION: Our results raise the possibility of range expansion of *A. americanum* into northern U.S. states and southern Canada in the coming decades, and conclude that surveillance for this tick, and the diseases it transmits, would be prudent. <https://doi.org/10.1289/EHP5668>

Introduction

Anthropogenic climate change (Cook et al. 2013; IPCC 2018) is likely to drive changes in the geographic ranges of arthropod disease vectors, including those of tick vectors in North America (Ogden et al. 2005; Minigan et al. 2018; Springer et al. 2015). This likelihood is because the survival of tick populations depends on both biotic and abiotic conditions. Temperature plays a critical role in the tick life cycle by determining development rates of eggs and engorged states (Koch 1983) and affecting tick questing activity (Haile and Mount 1987). Subzero air temperatures are not lethal for ticks if they can find refuges in their environment, particularly in the surface layer of the soil (Burks et al. 1996). However, due to its effects on development and activity, temperature determines the length of the tick life cycle. Even where habitats provide refuges from subzero temperatures, a threshold temperature condition occurs below which the tick populations cannot survive, i.e., temperature conditions are too low for the tick to complete its life cycle before it dies, given a particular daily probability that a tick survives (Ogden et al. 2005; Ludwig et al. 2016). Temperature may, therefore, be a limiting factor of the geographic ranges of ticks, and a warming climate

may facilitate their establishment in regions previously climatically unsuitable.

Throughout the 20th century, the geographic range of *Amblyomma americanum* has expanded from the southeastern United States northward to locations in Michigan and New York states that are close to the Canadian border (Springer et al. 2014). This range expansion may have been driven by anthropogenic climate change, which has resulted in a warming trend in the late 20th century in North America (Crowley 2000; Stott et al. 2000; Blunden and Arndt 2019), although there have been no efforts to date to attribute changes in geographic distribution to climate change. This range expansion has had public health impact, at least in terms of increased incidence of spotted fever group rickettsioses (Dahlgren et al. 2016). *A. americanum* is a recognized public health threat, known for its aggressive host-seeking behavior and vector competence for a wide range of zoonotic pathogens, including *Francisella tularensis* (the cause of tularemia; Goddard and Varela-Stokes 2009), *Ehrlichia chaffeensis* (the cause of human monocytic ehrlichiosis; Brouqui 1998), *Rickettsia rickettsii* (the cause of Rocky Mountain spotted fever; Levin et al. 2017) and Heartland virus (Savage et al. 2016). Recently, it has been suggested that the bite of *A. americanum* may trigger red meat allergy (Commins et al. 2011).

A number of studies have assessed associations between *A. americanum* tick population occurrence and density and environmental predictors (Koch and Burg 2006; Schulze et al. 2001; Willis et al. 2012). Studies have also explored the potential effects of climate change on the spatial distribution of the tick (Springer et al. 2015), suggesting possible northward range expansion that may affect northern U.S. states and southern Canada, although *A. americanum* is not yet considered established in Canada and has not been detected in extensive field surveillance conducted in recent years to track the expansion of *I. scapularis* ticks (Bouchard et al. 2015). However, in recent years a small number of specimens, likely imported by migratory birds or travelers, were detected in passive tick surveillance, which suggests that if

Address correspondence to Nicholas H. Ogden, National Microbiology Laboratory, Public Health Agency of Canada, 3200 Sicotte, St. Hyacinthe (QC) J2S 2M2, Canada. Email: Nicholas.ogden@canada.ca

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environmental conditions are, or become, suitable in northern U.S. states and Canada, this tick species could become established (Gasmi et al. 2018). By the end of the 21st century, Canada would “very likely” face a mean annual temperature rise in the range of 2–4°C in comparison with current climate (Romero-Lankao et al. 2014) and potentially higher than 5°C under a high greenhouse gas emissions scenario (Ogden and Gachon 2019). If indeed temperature conditions are a major determinant of the northern limit of the range of this tick, then *A. americanum* may expand its range northward into northern U.S. states and Canada in the future and bring with it the range of diseases and health issues with which it is associated. Consequently, here we evaluate current and future climate suitability for *A. americanum* in the northern United States and Canada to better prepare public health system for possible emergence of these diseases and health issues.

There are two main modeling approaches to understanding and estimating the relationships between environmental variables, such as climate, and the environmental suitability for arthropods, such as *A. americanum*. The most commonly used are “pattern matching” approaches, such as ecological niche modeling that infer environmental suitability from observed species-distribution data. This approach has been used to predict current environmental suitability in North America for *A. americanum* and to project impacts of climate change on the possible geographic distribution of the tick (Bouzek et al. 2013; Springer et al. 2015; Minigan et al. 2018; Kessler et al. 2019; Pascoe et al. 2019). An alternative approach is the use of mechanistic simulation models that identify how environmental factors such as temperature affect population processes in the tick life cycle (Haile and Mount 1987; Mount et al. 1993; Ogden et al. 2005; Ludwig et al. 2016). Both methods have advantages and disadvantages that have been reviewed elsewhere (Mannelli et al. 2016). In previous studies on *I. scapularis* ticks, simulations of a deterministic simulation model calibrated with temperature-dependent parameters were used to define suitable temperature conditions for establishment of tick populations (Ogden et al. 2005) and then to project future spatial distribution of the species under climate change (Ogden et al. 2006, 2008). A similar dynamic population model was developed by Ludwig et al. (2016), which describes the transformations that *A. americanum* ticks undergo as they pass through the four stages of their life cycle (egg, larvae, nymph, and adult). Feeding tick stages are hardening, questing, feeding, and engorged ticks; tick abundance in a specific simulated area depends on seasonally variable environmental conditions, including temperature and day length, while accounting for effects of temperature-independent diapause.

In this study, we used this mechanistic model to investigate the relationship between the size of *A. americanum* tick populations and temperature conditions at 36 locations in southeastern Canada and the eastern United States. From these simulations we defined threshold temperature conditions for tick population survival and evaluated how that the northern limit of the region with suitable climate conditions for the tick in North America may change with climate change.

Methods

We ran simulations of the dynamic population model (Ludwig et al. 2016) using climate data from each of 36 meteorological stations located in southeastern Canada and northeastern United States (from latitudes 35 to 60°N, and from longitudes 55 to 95°W) to define a temperature threshold for survival of *A. americanum* populations. Under current climate, the region where the meteorological stations are located (Figure 1) is characterized by a north–south latitudinal gradient in temperature (being warmer in the south) with temperatures also being higher the closer that

the stations are to the Atlantic coastline. The deduced temperature threshold was used to evaluate the tick’s potential range in the United States and Canada under future climatic conditions. Our focus was investigating possible northward range expansion of the tick, but northward contraction of the southern limit of the tick may also be possible. If so then the impact on distribution in the southern United States may be small because the tick is likely established in Mexico at present (Sosa-Gutierrez et al. 2016), but further studies targeted to the southern part of the tick’s range are required to explore this impact.

Determining a Lower Temperature Threshold for *A. americanum* Population Survival

Model calibration and simulations. In this study, we used a dynamic population model of *A. americanum* (Ludwig et al. 2016) in STELLA version 10.0.2 (High Performance Systems, Inc.) to estimate the number of ticks, once the model reached equilibrium after an 85-y simulation, at each of 36 sites in eastern North America (Table 1). The logic of the modeling approach is that as cold temperatures in winter do not greatly affect tick mortality rates as long as the woodland habitats provide appropriate refuges (Brunner et al. 2012), and climatic changes would likely act mostly through temperature effects on tick activity, rates of development, and thus life cycle length. Given constant per capita mortality rates of the ticks, a lower climatic temperature threshold will exist at which the life cycle of the tick reaches a length such that the probability that a larvae survives to be a mated, egg-laying, adult female falls below 1, i.e., the basic reproduction number (R_0) of the tick falls below 1, and self-sustaining populations cannot persist (Ogden et al. 2014).

The model comprises 14 states corresponding to stages or phases in the tick life cycle. These stages are eggs, questing (i.e., host-seeking) larvae, feeding larvae, engorged larvae, questing nymphs, feeding nymphs, engorged nymphs, questing adult females, feeding adult females and engorged and egg-laying adult females, plus a “hardening” phase for newly hatched larvae, and newly molted nymphs and adults (Figure 2). Temperature affects tick questing activity as well as the duration of development from one tick life stage to the next: from engorged females to egg laying (the preoviposition period), egg development to hatching of larvae (the preeclosion period), development of engorged larvae to questing nymphs, and development of engorged nymphs to adults. All parameters were the same as those in Ludwig et al. (2016) with the exception of mortality rates among feeding ticks. The proportions of feeding ticks of each stage that die due to grooming were adjusted to produce realistic adult tick infestations of deer in comparison with observations (a maximum 50–75 adult ticks per deer in U.S. locations; e.g., Bloemer et al. 1988, Durden et al. 1991), when the numbers of deer and rodent hosts were set at those seen in 2 km² in parts of the eastern United States where the hosts are abundant (Ogden et al. 2005).

a) Mortality rate of feeding larvae

$$0.65 + \left(0.049 * \ln \left(1.01 + \frac{FeedL}{HostL} \right) \right)$$

b) Mortality rate of feeding nymphs

$$0.45 + \left(0.049 * \ln \left(1.01 + \frac{FeedN}{HostN} \right) \right)$$



Figure 1. Geographic locations of the 36 meteorological stations (using abbreviations of the station names) that provided temperature and day-length data for the dynamic population model simulations. QC, Quebec, ON, Ontario, NL, Newfoundland and Labrador, NB, New Brunswick, NS, Nova Scotia.

c) Mortality rate of feeding adults

$$0.35 + \left(0.049 * \ln \left(1.01 + \frac{FeedA}{HostA} \right) \right) * \frac{12}{10}$$

- FeedL* = Number of feeding larvae
- FeedN* = Number of feeding nymphs
- FeedA* = Number of feeding adults
- HostL* = Number of hosts for larvae (200 rodents)
- HostN* = Number of hosts for nymphs (200 rodents)
- HostA* = Number of hosts for adults (40 deer)

The values on the left-hand side of the equations are the proportions of feeding ticks of each stage that die due to grooming. The right-hand side components describe additional mortality due to density dependent effects on increasing grooming and possible density-dependent acquired resistance to ticks

(Ludwig et al. 2016) calibrated as for *I. scapularis* ticks (Ogden et al. 2005) in the absence of data specifically for *A. americanum*.

Simulations were run with tick development and questing activity rates calculated for each meteorological station (as described in Ludwig et al. 2016), using the following site-specific historical climate data: The monthly mean temperatures (climatological values computed over the 1981–2010 period) were provided by Environment and Climate Change Canada (ECCC) (http://climate.weather.gc.ca/climate_normals/) for Canadian sites and by the National Oceanic and Atmospheric Administration (<https://www.ncdc.noaa.gov/cdo-web/datatools/normals>) for sites in the United States. The mean annual number of DD > 0°C (mean DD > 0°C) was used as an index of the annual temperature conditions at a site for comparison with the numbers of ticks at model equilibrium. Mean DD > 0°C values for the 1981–2010 period were taken from the ECCC website (http://climate.weather.gc.ca/climate_normals/) for Canadian sites and calculated using daily mean temperature provided by the National Centers for Environmental Information website of the NOAA (<https://www.ncdc.noaa.gov/cdo-web/datatools/normals>) for sites in the United States. Day length also affects questing activity of *A. americanum* (reviewed in Ludwig et al. 2016), and for the simulations, day-length data for 2010 for

Table 1. Meteorological stations that provided temperature data for simulations with their location, altitude, mean number of degree days > 0°C (DD > 0°C) and maximum number of feeding larvae at equilibrium in simulations of the dynamic population model of *A. americanum*.

Station	Location (°N and °W)	Altitude (m)	Mean DD > 0°C	Maximum feeding larvae at equilibrium ^d
Canada				
Ontario				
Barrie WPCC	44°22'N, 79°41'W	221.0	3,274.9	0*
Cornwall	45°00'N, 74°44'W	64.0	3,542.7	217,154
Drummond Centre	45°01'N, 76°15'W	145.0	3,182.9	0
Hamilton A	43°10'N, 79°56'W	237.7	3,439.7	30,410
London Int'l Airport	43°01'N, 81°09'W	278.0	3,431.6	17,203
Ottawa Macdonald-Cartier Int'l A	45°19'N, 75°40'W	114.0	3,285.2	12,204
Peterborough Trent U	44°22'N, 78°18'W	198.1	3,280.2	0*
Sault Ste Marie A	46°29'N, 84°30'W	192.0	2,725.9	0
Sudbury A	46°37'N, 80°47'W	348.4	2,786.1	0
Toronto Lester B. Pearson Int'l A	43°40'N, 79°37'W	173.4	3,530.0	164,968
Québec				
Bromptonville	45°29'N, 71°57'W	130.0	3,052.0	0
Chapais 2	49°47'N, 74°51'W	396.2	2,136.4	0
Farnham	45°18'N, 72°54'W	68.0	3,274.3	0
Hemmingford Four Winds	45°04'N, 73°43'W	61.0	3,289.4	0*
Montreal/Pierre Elliott Trudeau Int'l A	45°28'N, 73°45'W	36.0	3,349.3	54,080
Quebec/ Jean Lesage Int'l A	46°48'N, 71°23'W	74.4	2,785.7	0
Rimouski	48°27'N, 68°31'W	35.7	2,651.6	0
Trois Rivières Aqueduc	46°23'N, 72°37'W	54.9	3,027.1	0
New Brunswick				
Fredericton A	45°52'N, 66°31'W	20.7	2,933.2	0
Moncton A	46°06'N, 64°41'W	70.7	2,830.0	0
Saint John A	45°19'N, 65°53'W	108.8	2,682.5	0
Prince Edward Island				
Charlottetown A	46°17'N, 63°07'W	48.8	2,824.9	0
Nova Scotia				
Halifax Stanfield Int'l A	44°52'N, 63°30'W	145.4	2,994.0	0
Sydney A	46°10'N, 60°02'W	61.9	2,727.7	0
Yarmouth A	43°49'N, 66°05'W	43.0	2,958.7	0
United States				
Albany Int'l A	42°44'N, 73°47'W	85.3	3,639.0	353,952
Columbus Ohio State University A	40°04'N, 83°04'W	275.8	4,173.9	1,060,376
Concord Municipal A	43°07'N, 71°17'W	105.5	3,343.4	57,345
Detroit City A	42°24'N, 83°00'W	190.8	3,924.6	1,054,015
Frankfort Capital City A	38°11'N, 84°54'W	245.1	4,723.6	2,010,296
Harrisburg Capital City A	40°13'N, 76°51'W	103.6	4,336.1	1,315,079
Hartford Bradley Int'l A	41°56'N, 72°40'W	53.3	3,944.4	908,993
Lansing Capital City A	42°46'N, 84°34'W	256.3	3,623.6	330,843
Raleigh A	35°53'N, 78°46'W	126.8	5,849.1	2,828,503
Richmond Int'l A	37°30'N, 77°19'W	50.0	5,457.0	3,020,711
Trenton Mercer Co A	40°16'N, 74°48'W	56.1	4,377.5	1,320,764

Note: A, airport; and Int'l A, international airport.

^dAt three sites indicated by asterisks, the number of larvae was declining at the end of the simulations indicating that the populations were dying out. For simplicity, the equilibrium value shown for these sites is zero.

all sites were obtained from the Astronomical Applications Department of the United States Naval Observatory website (<http://aa.usno.navy.mil/data/>).

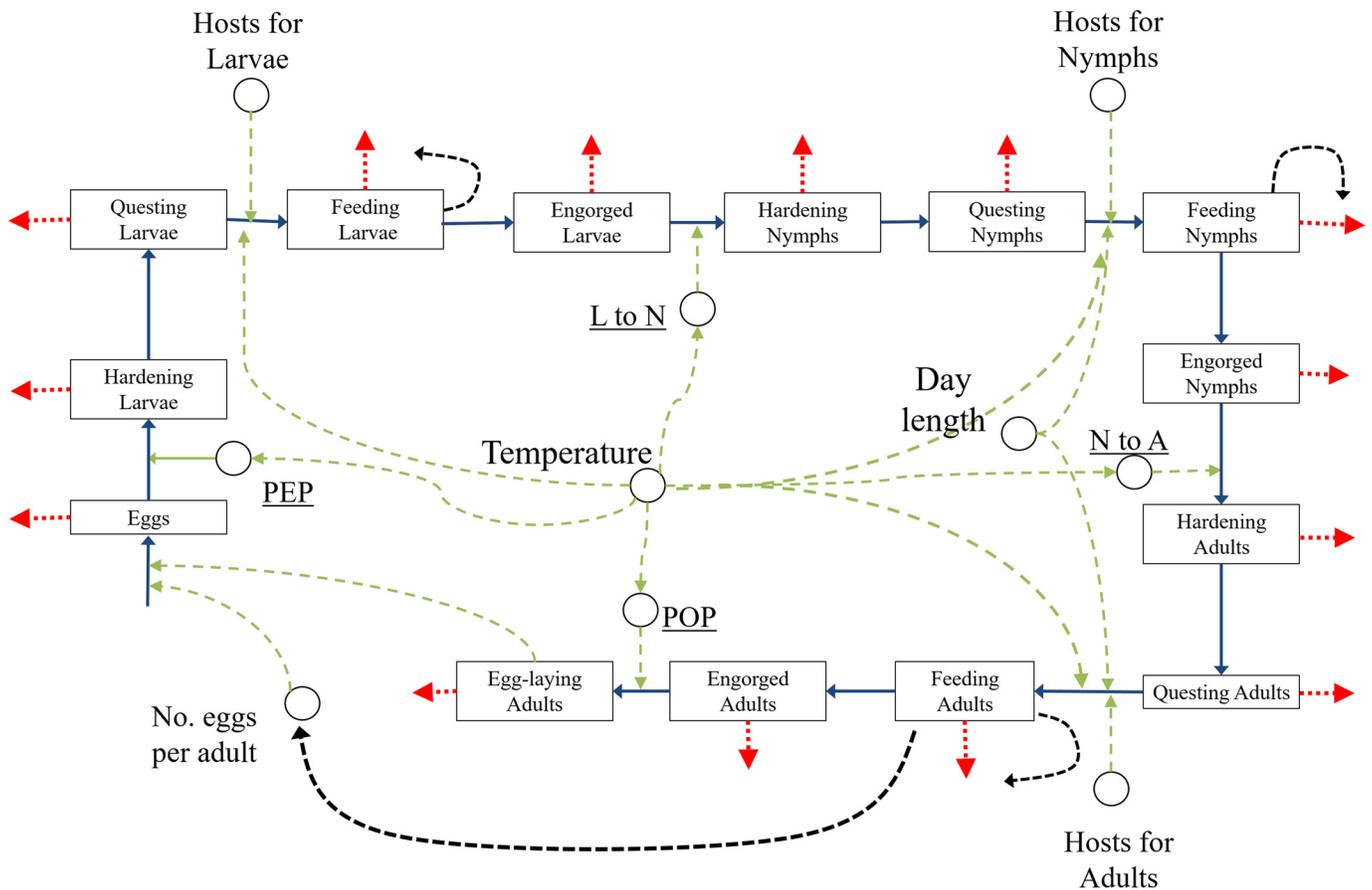
The model output data were managed in R (version 3.4.0; R Development Core Team). A tick population was considered at equilibrium if the maximum annual numbers of ticks of a particular stage was stable for the 10 y at the end of the 85-y simulation period. Sites with zero or crashing populations at the end of the simulation were considered as having a climate unsuitable for *A. americanum*.

DD threshold for tick population survival. As in previous studies (Ogden et al. 2005, 2006; Springer et al. 2015), the mean annual number of DD > 0°C served as an index of the seasonally variable temperature conditions at any particular location. The outcome from the dynamic population model (the maximum annual number of feeding larvae, nymphs, and adult ticks at equilibrium) was the dependent variable in a regression model, where the mean DD > 0°C was an explanatory variable. The Spearman's rank correlation test (Dahmen and Hall 1990) at the 1% significance level ($p < 0.01$) was used to assess the quality of this relationship. From the regression

model, the highest value of DD > 0°C at which the number of ticks in the model was zero was considered to be the lowest temperature threshold for tick population survival. However, simulation results from the individual meteorological stations were also inspected, because DD > 0°C is not a perfect index of how seasonally variable temperature conditions may affect tick population survival (Ogden et al. 2005, and see Results section).

Using this threshold, the predicted current distribution of temperature suitability for *A. americanum* in North America was mapped using gridded observational data series at 10-km resolution from the Australian National University SPLINE (ANUSPLINE) data sets over Canada (Hutchinson et al. 2009; McKenney et al. 2011), and the North American Land Data Assimilation System (NLDAS) data sets over the United States (Xia et al. 2012).

As a sensitivity analysis of variation in the geographic scope of predicted temperature suitability, the limit of the occurrence of temperature suitability was mapped using DD > 0°C values higher and lower than the value selected as described above. The selection of these values was guided by the standard error of the



Legend:

- > Transitions from only life stage or phase to the next
-> Mortality occurring at each life stage or phase
- - -> Temperature and day length influences on tick development and activity
- - -> Density-dependent effects on mortality and reproduction rates

Figure 2. A diagram of the model showing each stage or phase of the tick life cycle as boxes linked by life cycle processes (hatching of eggs, development and molting of ticks) shown by solid arrows. Arrows of different styles indicate mortality that affects each life stage, influences of temperature and day length on life cycle processes, and density-dependent effects on mortality and reproduction rates. Temperature affects questing activity of questing larvae, nymphs, and adults, and acts on development rates from one life stage to the next: the preoviposition period of engorged adult females (POP), the preclosure period of eggs (PEP), and the development of engorged larvae to nymphs (L to N) and from engorged nymphs to adults (N to A). Effects of day length on questing activity were also included in the model.

coefficient in the regression model of number of larvae against $DD > 0^{\circ}\text{C}$.

Empirical validation of the life cycle model. First, the results of 11 simulations run using environmental data from stations in the United States were compared with county-level distribution maps of *A. americanum* in the United States (Springer et al. 2014). Using records from literature and databases published between the years 1898 and 2012, Springer et al. (2014) classified counties as having established *A. americanum* populations (six ticks or two life stages) or reported *A. americanum* (fewer than six ticks of a single life stage or number of ticks not specified), or as *A. americanum* being absent (no report). We considered that counties classified by Springer et al. (2014) as “established” and “reported” as having suitable temperature conditions for survival of *A. americanum* if they were south of counties considered to have “established” *A. americanum* populations. Second, we assessed the extent to which counties that were considered “established” and “reported” by Springer et al. (2014) were within the

geographic range of the region currently predicted to be climatically suitable for the tick, and we measured the sensitivity of the temperature limit to detect “established” and “reported” counties in the United States. Estimates of specificity were not attempted because the data in Springer et al. (2014) are presence only, and because it was expected that temperature suitability for *A. americanum* will have a much wider geographic scope than the complete ecological niche that includes characteristics of habitat and host densities.

Sensitivity analysis of mortality rates. The sensitivity of simulation outcomes of tick models of this type to changes in parameter values has been extensively studied (Ogden et al. 2005; Wu et al. 2013; Ludwig et al. 2016), and mortality rates of both feeding and questing ticks are key parameters determining the numbers of ticks at model equilibrium. Values for these parameters in the *A. americanum* model are estimated from other tick species, so it is important to assess how changes in the values may affect the number of ticks at equilibrium in simulations. For example, if

mortality rates are set higher than those actually occurring in nature, in simulations the number of ticks would be artificially low. This possibility is not of great importance for our objectives here unless it affects the temperature threshold for *A. americanum* population survival deduced from the simulations at the meteorological stations. To explore this possibility, we performed a local sensitivity analysis to assess the impact of increasing and decreasing mortality rates of parasitic and nonparasitic tick stages on the model outcome of the numbers of feeding larvae at equilibrium. Feeding larvae were chosen over feeding nymphs and adults because feeding larvae had the most linear relationship with $DD > 0^{\circ}\text{C}$ above the threshold value for population survival. The model was run as before for 85 y with temperatures and day-length data for four meteorological stations (Ottawa and Hamilton in Canada, and Albany and Detroit in the United States) that have temperature conditions close to the deduced $DD > 0^{\circ}\text{C}$ limit for *A. americanum* population survival. For each meteorological station, three simulations were run: one with mortality rates unchanged, one with mortality rates increased by 5%, and one with mortality rates decreased by 5%. The outcomes of the simulations (maximum annual number of larvae at model equilibrium) were then explored graphically to see if changing the mortality rates altered the intercept of the relationship between $DD > 0^{\circ}\text{C}$ and number of larvae.

Potential Distribution Changes under Future Climate

We estimated future spatial distribution of the estimated $DD > 0^{\circ}\text{C}$ limit for *A. americanum* populations over North America using average values of daily mean temperature simulations over North America from an ensemble of six regional climate model (RCM) simulations in order to minimize uncertainties related to intramodel variability. These RCM simulations are part of the *COordinated Regional climate Downscaling EXperiment* (CORDEX; Mearns et al. 2017) under the initiative of the World Climate Research

Programme's Working Group on Regional Climate and the Working Group on Coupled Modelling. Each simulation covers the 1971–2000, 2011–2040, 2041–2070, and 2071–2100 periods and is available at a horizontal resolution of approximately 50 km. Our series of climate projections are based on two Representative Concentration Pathways (RCPs), RCP4.5 and RCP8.5 (Van Vuuren et al. 2011), to represent uncertainties about future greenhouse gas emissions. RCP4.5 is a medium stabilization scenario leading to a stable radiative forcing level of $4.5^{\circ}\text{W}/\text{m}^2$ by the year 2100 (relative to the year 1750; Moss et al. 2010). RCP8.5 is a high emission scenario leading to a rising radiative forcing level of $8.5^{\circ}\text{W}/\text{m}^2$ by the year 2100 (Van Vuuren et al. 2011). The six simulations of RCMs driven by various global climate models are described in Table 2.

Potential changes in temperature trends leading to possible changes of the range of *A. americanum* were projected both at local and regional scales. First, we estimated short and mean term evolution of $DD > 0^{\circ}\text{C}$ for the 36 meteorological stations at which simulations were run to identify the time period at which future temperature conditions become favorable for *A. americanum* establishment. The ensemble mean values for each station were computed from the six RCM simulations using average values of four RCM grid points surrounding each station, each historical period, and RCP scenario. Second, future geographic distributions of the $DD > 0^{\circ}\text{C}$ limit for *A. americanum* population survival were mapped according to the RCM simulation results. To achieve this, the mean $DD > 0^{\circ}\text{C}$ was calculated for each 50-km grid cell of North America, for each RCM simulation, and for each time period and RCP scenario. The RCM data were interpolated by inverse distance weighting (IDW) in ArcGIS (version 10.4; ESRI) to allow the deduced $DD > 0^{\circ}\text{C}$ limit for *A. americanum* population survival to be mapped as a smoothed isotherm. The northern extent of the deduced $DD > 0^{\circ}\text{C}$ limit for *A. americanum* was mapped for each time period and RCP scenario according to the geographic distribution of the mean $DD > 0^{\circ}\text{C}$

Table 2. The regional climate models (RCMs) and driving models used to perform simulations of historic (1971–2000) and future (2011–2040, 2041–2070, 2071–2100) temperature trends over North America.

Simulation number	Regional Climate Model			Global Climate Model (driving conditions)		
	Name	Responsible institution	References	Name	Responsible institution	References
1	Canadian Regional Climate Model (CRCM5)	Université du Québec à Montréal, Canada	Martynov et al. 2013; Šeparović et al. 2013	Second generation Canadian Earth System Model (CanESM2)	Canadian Centre for Climate Modelling and Analysis (CCCma) of Environment and Climate Change Canada (ECCC), Canada	http://climate-modelling.canada.ca/
2	Canadian Regional Climate Model (CRCM5)	Université du Québec à Montréal, Canada	Martynov et al. 2013; Šeparović et al. 2013	Fifth version of Max Planck Institute Earth System Model (ECHAM5/MPI-M&MPI-ESM-LR)	Max Planck Institute for Meteorology, Germany	https://www.mpimet.mpg.de/
3	Canadian Regional Climate Model (CanRCM4)	CCCma of ECCC, Canada	Scinocca et al. 2016	Canadian Regional Climate Model (CanRCM4)	CCCma of ECCC, Canada	
4	High Resolution Limited Area Model (HIRHAM5)	Danish Meteorological Institute, Denmark, and Alfred Wegener Institute Foundation for Polar and Marine Research, Germany	Bøssing Christensen et al. 2007	High Resolution Limited Area Model (HIRHAM5)	Danish Meteorological Institute, Denmark and Alfred Wegener Institute Foundation for Polar and Marine Research, Germany	Bøssing Christensen et al. 2007
5	Rosby Centre regional atmospheric model (RCA4)	Rosby Centre, Sweden	Strandberg et al. 2015	CanESM2	CCCma of ECCC, Canada	http://climate-modelling.canada.ca/
6	Rosby Centre regional atmospheric model (RCA4)	Rosby Centre, Sweden	Strandberg et al. 2015	EC-EARTH	ICHEC, Ireland	Hazeleger et al. 2010

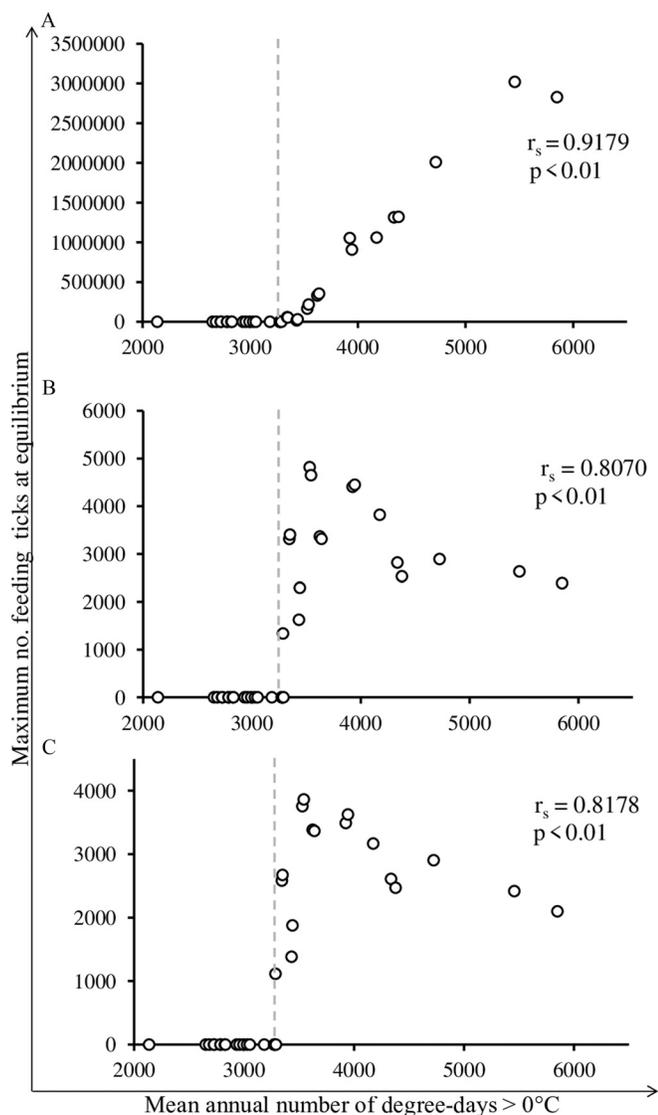


Figure 3. Maximum number of feeding larvae (panel A), nymphs (panel B) and adults (panel C) at equilibrium plotted against the mean annual number of degree days $> 0^\circ\text{C}$ ($\text{DD} > 0^\circ\text{C}$), for the meteorological stations that provided temperature data for the simulations. The dashed line indicates the lower temperature threshold for *A. americanum* population survival estimated in the study (3,285 $\text{DD} > 0^\circ\text{C}$).

obtained in the RCM ensemble projections. Maps were also produced plotting the 10th, 50th, and 90th percentiles of the RCM ensemble projections to explore variations among RCM outputs as a source of uncertainty in projections.

Results

Survival Threshold under Current Climate

Simulations of population dynamics. Model simulations with temperature data for 1981–2010 resulted in die-out of tick populations in 16 sites in Canada, located in New Brunswick, Nova Scotia, northern Quebec, and Ontario (Table 1); hence these regions were considered unsuitable for *A. americanum* under current climate conditions. Simulated tick populations at three other sites in Canada (Barrie, Peterborough, and Hemmingford) survived, but their size gradually decreased over the 85-y simulation period, and current climatic conditions at these sites were also considered unsuitable. Climatic conditions of all other sites in the

United States, five sites in southern Ontario, and one in southern Quebec permitted tick populations to reach equilibrium (Table 1).

D-D threshold for tick population survival. There is a statistically significant positive correlation between $\text{DD} > 0^\circ\text{C}$ and the simulated maximum number of larvae ($r_s = 0.9179$, $p < 0.001$), nymphs ($r_s = 0.8070$, $p < 0.01$) and adults ($r_s = 0.8178$, $p < 0.01$) at the sites. The relationship between temperature and tick abundance was linear for larvae and polynomial for nymphs and adults (Figure 3) associated with the negative relationship between temperature and tick activity at high temperatures that particularly constrain nymphal and adult tick activity (Haile and Mount 1987). The linear relationship between larvae and $\text{DD} > 0^\circ\text{C}$ [$(1,276.3 \times \text{DD} > 0^\circ\text{C}) - (4.23 \times 10^6)$] suggested a limit of 3,318 $\text{DD} > 0^\circ\text{C}$ for *A. americanum* population survival. However, at the Ottawa site, simulated tick populations persisted at very low numbers, even though the $\text{DD} > 0^\circ\text{C}$ at this site (3,285.2 $\text{DD} > 0^\circ\text{C}$) was slightly lower than the limit obtained from regression. At Ottawa, summers are warmer and winters are cooler than at sites nearby (e.g., Hemmingford) at which simulated populations did not survive, even though $\text{DD} > 0^\circ\text{C}$ at these sites was slightly greater than at Ottawa. This aspect underscores that $\text{DD} > 0^\circ\text{C}$ is a simplified index of the seasonally variable temperature conditions at a site (see Ogden et al. 2005 for further discussion of this topic), and to be cautious in our assessments of risk of *A. americanum* range expansion, we considered 3,285 $\text{DD} > 0^\circ\text{C}$ as the lower temperature limit for survival of populations of this tick. Associated with the parameterization of the activity–temperature relationship (Haile and Mount 1987), tick abundance became inversely proportional to temperature sites with $\text{DD} > 0^\circ\text{C}$ of 4,000 or more. The geographic distribution of gridded observed $\text{DD} > 0^\circ\text{C}$ data for 1981–2010 suggests that the northern limit of the range of *A. americanum* in northeastern North America is south of the Canadian provinces of Ontario and Quebec (Figure 4), although much of New England was predicted to be currently unsuitable. Further west (to approximately longitude 110°W) the northern limit for the ticks was predicted to be within those states bordering Canada, while high-altitude regions, such as the Appalachian and Rocky Mountains, were predicted to be unsuitable (Figure 4). Temperature suitability on the Pacific coast was predicted to extend into southern British Columbia, although there are no known populations of *A. americanum* west of the Rocky Mountains (Springer et al. 2014). The standard error of the coefficient in the regression model of number of larvae against $\text{DD} > 0^\circ\text{C}$ was 4.5% of the value of the coefficient. The northern geographic extent of predicted current temperature suitability was also mapped using $\text{DD} > 0^\circ\text{C}$ for population survival set at 4.5% greater (3,433 $\text{DD} > 0^\circ\text{C}$) or lower (3,137 $\text{DD} > 0^\circ\text{C}$) than the selected limit. Variation in the value of $\text{DD} > 0^\circ\text{C}$ had a relatively minor impact (in the order of ± 50 km) on the predicted area of temperature suitability (see Supplemental Material Figure S1).

Empirical validation of predicted temperature limit. Model simulations suggested temperature suitability at all the 11 meteorological stations in the United States, and possible *A. americanum* presence has been identified in the counties in which 8 of these stations occur according to tick records (Springer et al. 2014) (Table 3). When comparing the geographic extent of tick records data (Springer et al. 2014) with temperature suitability predicted by the modeled limit for *A. americanum*, all but one (Presque Isle county in Northern Michigan) “established” counties (652/653) were within the geographic range of temperature conditions predicted as suitable for the tick, i.e., the temperature limit had a sensitivity of 99.8% in predicting “established” counties. More counties were considered as “reported” for the tick in the upper Midwest and in New England, where temperature was predicted to be too cold for *A. americanum* populations, but even

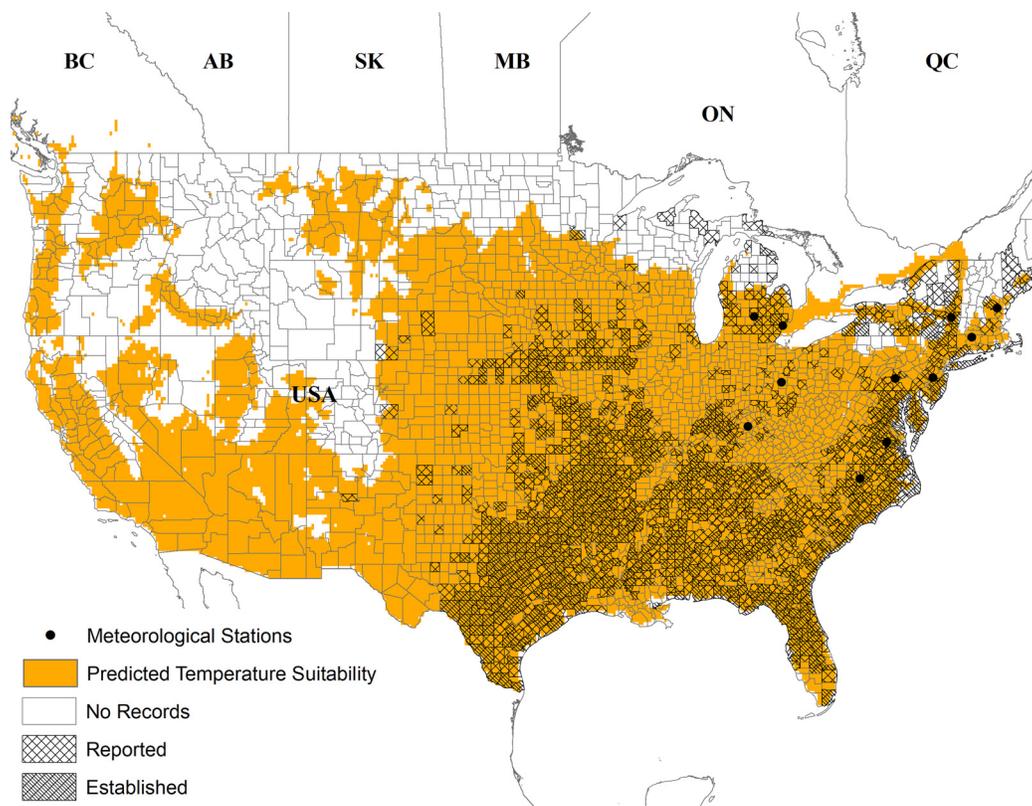


Figure 4. Regions of Canada and the United States predicted as having temperature conditions suitable for *A. americanum* population survival ($\geq 3,285$ degree days $> 0^{\circ}\text{C}$) under current climate (1981–2010 normals), computed from observed ANUSPLIN NLDAS data at approximately 10-km resolution. U.S. counties identified as having “reported” and “established” *A. americanum* according to Springer et al. (2014) are shown (respectively) by light and heavy cross-hatching. Locations of the 11 meteorological stations in the United States that provided temperature and day-length data for the dynamic population model simulations are also shown.

so, the temperature limit predicted suitability for 634 of the 647 counties with a “reported” status (Figure 4), providing a sensitivity of 98.0% in predicting “reported” counties and 98.9% sensitivity in predicting “established” plus “reported” counties (1,286 out of 1,300). There were 1,389 U.S. counties east of 110°W that were predicted as having suitable temperature, but without records of *A. americanum* populations.

Sensitivity analysis of mortality rates. Simulation results for Ottawa, Hamilton, Albany, and Detroit were obtained with a 5% variation of on-host and off-host tick mortality to evaluate the potential effect of uncertainty of mortality parameters on model outcomes. As expected, increasing mortality rates reduced tick numbers, and reducing mortality rates increased them; however, as the temperature conditions approached the limit for population persistence, the effect of changing mortality rates became very small (Figure 5). Therefore, although variations in mortality rates varied the numbers of ticks above the threshold for population persistence, they did not greatly affect the predicted $\text{DD} > 0^{\circ}\text{C}$ limit for population die-out.

Potential Range Expansion under Climate Change

According to grid point data extracted from the RCM ensemble, all but one of the 25 Canadian sites (Chapais in northern Quebec) investigated here will become climatically suitable for *A. americanum* during the course of the 21st century (Table 4). However, two locations (Quebec City and Rimouski) were only predicted to have suitable climate when the RCP8.5 scenario was used by the climate models. Regional warming trends over North America projected by the RCMs (see Supplementary

Material Figure S2) resulted in similar increases in $\text{DD} > 0^{\circ}\text{C}$, and result in similar potential range expansion under medium- (RCP4.5) and high-emission (RCP8.5) scenarios until the end of the 2060s. At the end of the century (the 2071–2100 period,) potential range expansion under the conditions of these emission scenarios starts to diverge substantially due to more pronounced warming under the RCP8.5 scenario (i.e., higher $\text{DD} > 0^{\circ}\text{C}$) in comparison with the RCP4.5 scenario (see Supplementary Material Figure S2). Therefore, under both emission scenarios, *A. americanum* establishment may become possible in all northern U.S. states from Montana eastward, and in southern parts of the Canadian Prairie Provinces (Alberta, Saskatchewan, and Manitoba), and southern parts of eastern Canada including eastern Ontario, southeastern Québec, southern Nova Scotia, and southern New Brunswick by the end of the 2011–2040 period. Further and similar northward expansion of the range of temperature suitability was predicted under both emissions scenarios for the 2041–2070 period. However, projected range expansion was considerably greater under the RCP8.5 emissions scenario, and in the western regions of the tick’s range (Figure 6), for the 2071–2100 period. In that period, climate suitability was predicted to extend to up to latitude $51\text{--}54^{\circ}\text{N}$ (depending on longitude), a northward range expansion of 500–1,000 km (also depending on longitude) from current. Under the RCP4.5 emission scenario, climate suitability was predicted to extend to up to latitude $46\text{--}52^{\circ}\text{N}$, a northward range expansion of 250–500 km, depending on longitude, from current.

The uncertainty in future climate projections from the different models is shown using the distribution of suitable temperature

Table 3. The presence of *A. americanum* populations in dynamic population model simulations for 11 U.S. meteorological stations in comparison with observational evidence (from Springer et al. 2014) of *A. americanum* in the county where each station is located.

Station	County	State	Tick populations present in:	
			Simulations	Observed data
Albany Int'l A	Albany	New York	Yes	Yes
Columbus Ohio State University A	Franklin	Ohio	Yes	No
Concord Municipal A	Merrimack	New Hampshire	Yes	Yes
Detroit City A	Wayne	Michigan	Yes	Yes
Frankfort Capital City A	Franklin	Kentucky	Yes	No
Harrisburg Capital City A	Dauphin	Pennsylvania	Yes	Yes
Hartford Bradley Int'l A	Hartford	Connecticut	Yes	No
Lansing Capital City A	Ingham	Michigan	Yes	Yes
Raleigh Airport	Wake	North Carolina	Yes	Yes
Richmond Int'l A	Richmond	Virginia	Yes	Yes
Trenton Mercer Co A	Mercer	New Jersey	Yes	Yes

Note: A, airport; and Int'l A, international airport.

using the 10th, 50th, and 90th percentiles of the ensemble of RCM projections (Figure 7). The greatest intermodel variation was for projections for the Prairie Provinces of Canada (Alberta, Saskatchewan, and Manitoba) and when model outputs were obtained using the RCP8.5 scenario for the 2071–2100 time period.

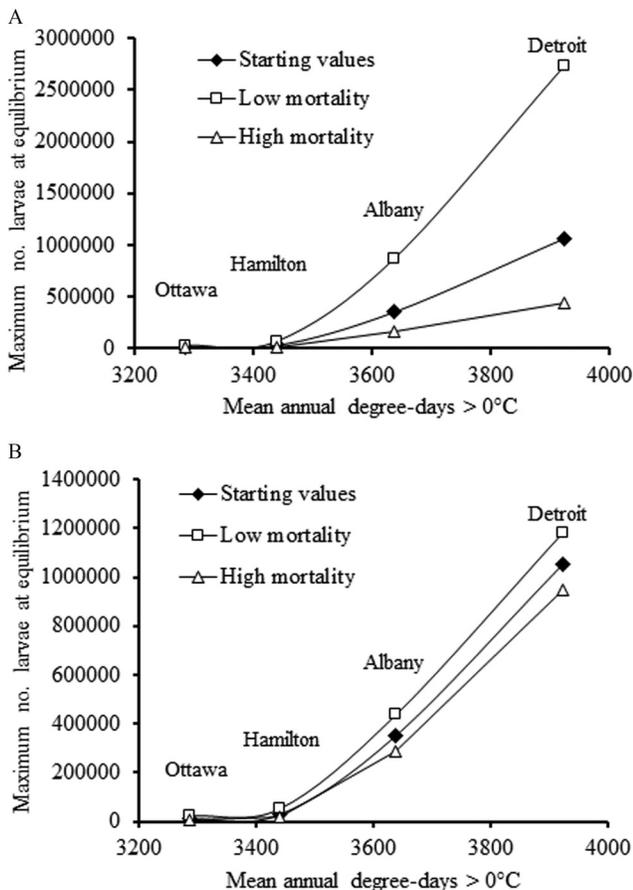


Figure 5. Relationship between the maximal number of feeding larvae at equilibrium and the mean annual degree days resulting from modification of mortality rates of feeding (panel A) and nonfeeding (panel B) stages of *A. americanum*. For each meteorological station (Ottawa, Hamilton, Albany, and Detroit), the results of three simulations are shown: one using starting values for the basal daily mortality rates, and one each using basal daily mortality rates 5% above and below starting values.

Discussion

In this study, using a deterministic population model we sought to identify a lower temperature threshold for persistence of *A. americanum* populations that may define the northern limit for populations of this tick. We then explored how climate change may affect the northern extent of the geographic range of this tick by northward expansion of the area of climatic suitability in North America. Our results suggest considerable potential for northward range expansion of the tick throughout the 21st century.

Our simulations with modified mortality rates among feeding ticks reproduced results of the study of Ludwig et al. (2016), with respect to suitability of current temperature conditions in southeastern Canada for *A. americanum* populations, and suggest that the region of current temperature suitability extends into southwestern Quebec and southern Ontario.

The simulation results for meteorological stations in the United States were consistent with *A. americanum* occurrence based on passive surveillance at eight sites but were not consistent for three sites (Hartford, Connecticut; Franklin, Kentucky; and Franklin, Ohio) that were predicted to be suitable for tick establishment but had no documented evidence of tick presence according to Springer et al. (2014). Evidence of *A. americanum* populations has been found at locations further north than these three sites (Springer et al. 2014). Therefore, the absence of ticks from the counties in which the sites occur may reflect the influence of environmental factors that were not accounted for by the model, such as suboptimal habitat, relative humidity, or host densities (Koch 1983; Lancaster Jr and McMillan 1955). However, detection of tick populations in Springer et al. (2014) was by passive surveillance, and it may be that there are indeed *A. americanum* populations present but undetected (Barrett et al. 2015). The predicted current range of climatic suitability in the central and eastern regions of the United States is also consistent with observations. Temperature suitability was also predicted to extend west of the Rocky Mountains. To our knowledge, populations of the tick have not been found here (Springer et al. 2014). Precisely why this absence is the case is not known; other essential environmental factors for *A. americanum* tick population survival (woodland habitat, relative humidity, host densities) are likely present (Pascoe et al. 2019), so perhaps the mountains and the prairies are a physical barrier to dispersal of this tick. When comparing the predicted range of temperature suitability in North America against surveillance data, Presque Isle county in Michigan is the only county that has been identified as having “established” *A. americanum*, yet it has temperature conditions predicted to be unsuitable for the tick. However, this county was considered “established” on the basis of passive tick surveillance

Table 4. Future mean annual number of degree days $>0^{\circ}\text{C}$ (DD $> 0^{\circ}\text{C}$) from ensemble mean values computed from six regional climate models projections under RCP4.5 and RCP8.5 scenarios, extracted from four grid points located close to the 36 meteorological stations.

Station	RCP4.5			RCP8.5		
	2011–2040	2041–2070	2071–2100	2011–2040	2041–2070	2071–2100
Canada						
Ontario						
Barrie WPC	3,572.5	3,869.4	4,029.8	3,458.8	3,883.2	4,426.9
Cornwall	3,608.4	3,901.5	4,056.2	3,426.0	3,853.7	4,398.6
Drummond Centre	3,684.9	3,979.4	4,137.4	3,523.3	3,952.3	4,498.7
Hamilton A	4,107.4	4,415.9	4,584.2	3,958.0	4,401.0	4,964.0
London Int'l Airport	4,061.7	4,370.3	4,538.0	3,949.5	4,389.1	4,952.7
Ottawa Macdonald-Cartier Int'l A	3,502.8	3,796.3	3,951.6	3,342.8	3,762.2	4,304.4
Peterborough Trent U	3,709.0	4,017.1	4,177.4	3,612.4	4,048.4	4,598.6
Sault Ste Marie A	3,134.0 ^a	3,432.6	3,587.1	3,063.6 ^a	3,458.5	3,994.0
Sudbury A	3,012.9 ^a	3,302.5	3,452.5	2,934.8 ^a	3,326.7	3,850.3
Toronto Lester B. Pearson Int'l A	3,848.3	4,155.7	4,321.1	3,742.2	4,177.8	4,733.7
Québec						
Bromptonville	3,117.7 ^a	3,395.5	3,534.9	2,998.9 ^a	3,408.7	3,927.3
Chapais 2	2,151.4 ^a	2,395.2 ^a	2,516.2 ^a	2,061.2 ^a	2,393.6 ^a	2,852.7 ^a
Farnham	3,602.2	3,899.1	4,048.1	3,399.3	3,827.2	4,372.4
Hemmingford Four Winds	3,580.7	3,874.0	4,022.6	3,382.1	3,809.7	4,352.0
Montreal/Pierre Elliott Trudeau Int'l A	3,585.0	3,886.2	4,035.7	3,391.2	3,817.4	4,365.5
Québec/ Jean Lesage Int'l A	2,852.8 ^a	3,129.4 ^a	3,266.9 ^a	2,717.7 ^a	3,104.6 ^a	3,613.9
Rimouski	2,691.5 ^a	2,963.8 ^a	3,093.3 ^a	2,610.1 ^a	2,989.8 ^a	3,493.2
Trois Rivières Aqueduc	3,169.0 ^a	3,452.7	3,596.7	3,019.5 ^a	3,421.7	3,950.9
New Brunswick						
Fredericton A	3,203.9 ^a	3,485.2	3,628.1	3,058.9 ^a	3,464.8	3,992.1
Moncton A	3,404.7	3,691.8	3,844.8	3,264.2	3,694.7	4,255.1
Saint John A	3,862.6	4,159.6	4,326.9	3,626.9	4,085.5	4,669.7
Prince Edward Island						
Charlottetown A	3,471.0	3,787.3	3,958.0	3,331.0	3,806.7	4,420.8
Nova Scotia						
Halifax Stanfield Int'l A	3,865.6	4,161.5	4,326.1	3,682.8	4,156.4	4,752.6
Sydney A	3,285.9	3,594.5	3,769.1	3,163.1 ^a	3,656.3	4,281.4
Yarmouth A	4,413.2	4,715.0	4,900.0	4,203.0	4,711.9	5,328.0
United States						
Albany Int'l A	3,816.3	4,103.4	4,252.5	3,635.0	4,074.3	4,618.0
Columbus Ohio State University A	4,788.6	5,075.8	5,244.4	4,603.0	5,067.8	5,629.3
Concord Municipal A	3,883.9	4,179.5	4,332.1	3,708.2	4,152.6	4,705.5
Detroit City A	4,360.4	4,660.5	4,833.9	4,240.9	4,676.9	5,237.9
Frankfort Capital City A	5,408.8	5,677.1	5,852.8	5,199.8	5,679.4	6,234.6
Harrisburg Capital City A	4,717.1	4,997.6	5,158.6	4,501.6	4,967.4	5,534.7
Hartford Bradley Int'l A	4,409.8	4,691.5	4,852.7	4,189.1	4,641.5	5,204.3
Lansing Capital City A	4,266.4	4,567.6	4,741.5	4,105.4	4,552.0	5,123.3
Raleigh A	6,156.2	6,409.7	6,568.1	5,910.7	6,370.9	6,925.0
Richmond Int'l A	5,818.8	6,085.4	6,242.8	5,564.1	6,030.4	6,595.6
Trenton Mercer Co A	5,065.6	5,342.0	5,509.2	4,864.5	5,330.8	5,910.3

Note: A, airport; and Int'l A, international airport.

^aValues below the deduced minimum of 3,285 DD $> 0^{\circ}\text{C}$ for survival of *A. americanum* populations.

data (Walker et al. 1998). Similarly, 13 counties in the northern United States identified as positive for *A. americanum* using the “reported” criteria, were also predicted as having unsuitable temperature conditions. Again, though, for these counties *A. americanum* populations were detected by passive tick surveillance methods (Means and White, 1997; Keirans and Lacombe, 1998; Walker et al. 1998). Locations identified as positive for tick populations based on passive surveillance may be false positives due to the presence of “adventitious” ticks that can be dispersed long distances out of tick populations by hosts such as migratory birds (Gasmí et al. 2018). In the absence of active field surveillance in these locations it is currently impossible to fully confirm whether tick populations are present in the counties identified as “reported” or “established.” Thus, we considered that the temperature threshold estimated for *A. americanum* identified here may be able to define the northern limit of the geographic range of the tick, although further field surveillance is needed to confirm this.

The model was sensitive to variations in the mortality rates of feeding and nonfeeding ticks, for which we have no accurate estimates. However, variations in these mortality rates had a very

small impact on the estimated lower limit for population survival, which was 3,285 DD $> 0^{\circ}\text{C}$. This DD threshold is higher than that estimated for *I. scapularis* (Ogden et al. 2005), which is consistent with the observed spread of *I. scapularis* tick populations into Canada in advance of *A. americanum*.

Northward range expansion of *A. americanum* is expected with climate change on the assumption that cold temperature conditions are the main limiting factor at present. Projected range expansion was not quite as dramatic as that projected for *I. scapularis* (Ogden et al. 2006). Day length affects host-seeking activity of *A. americanum* (Haile and Mount 1987), but not that of *I. scapularis* (Durden et al. 1996), and it remains to be investigated to what extent this aspect may result in differences of range expansion between these species. The predicted range expansion in the United States may have limited public health impact as in general regions of high population density are within the current geographic range of the region of temperature suitability (see <https://www.census.gov/history/www/reference/maps/> vs. Figure 4). However, possible range expansion into parts of Canada close to the U.S. border was predicted from Alberta eastward into

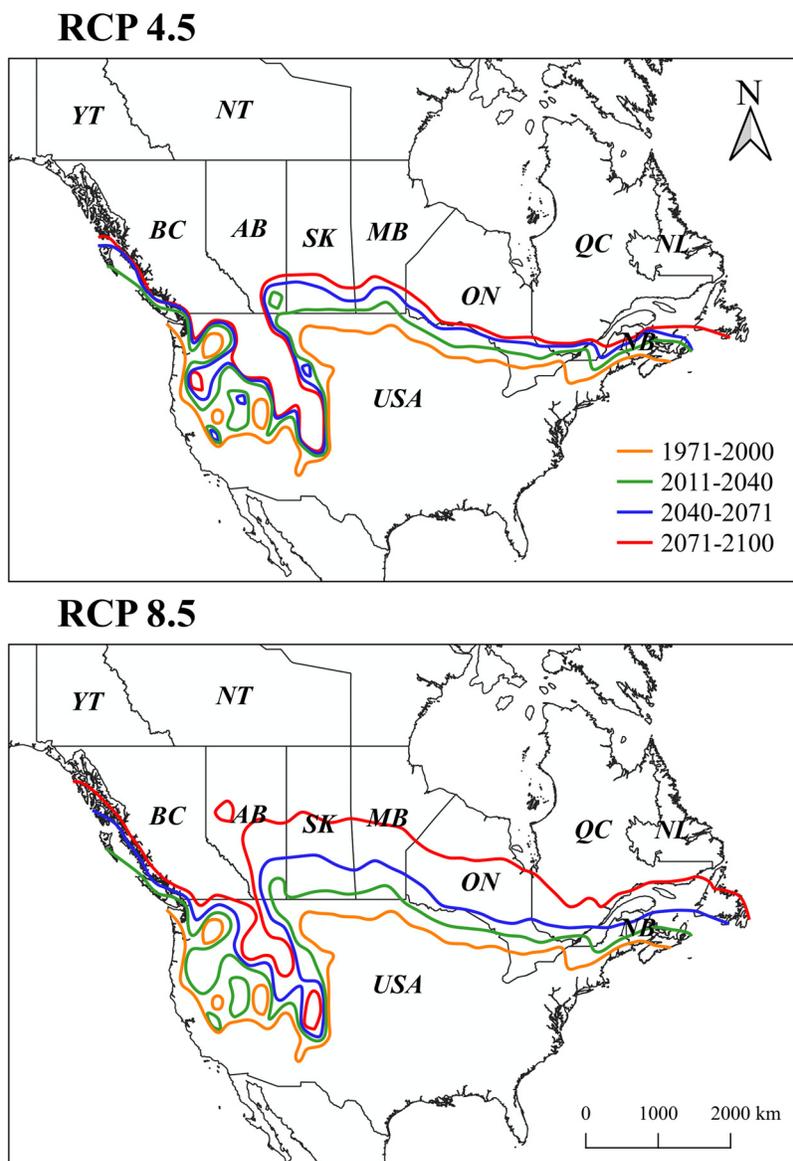


Figure 6. Geographic location of the lower temperature threshold (3,285 degree days $>0^{\circ}\text{C}$) for *A. americanum* survival during the 1971–2000, 2011–2040, 2041–2070, and 2071–2,100 periods computed from ensemble mean values of six Regional Climate Models under RCP4.5 (upper panel) and RCP8.5 (lower panel) scenarios.

Newfoundland, that encompass some of the most highly populated parts of this country (<https://www150.statcan.gc.ca/n1/pub/91-214-x/2015000/section04-eng.htm#a1>). The projected range expansions in the ecological niche model studies of Springer et al. (2015) and Raghavan et al. (2019), were more modest than those here. In the current study, only temperature was considered, although the ecological niche models considered other climatic variables, and indeed these variables may limit range expansion of the tick. However, both models of Springer et al. (2015) and Raghavan et al. (2019) consider the whole range of the tick (rather than focusing on the northern limit) and rather underestimate environmental suitability in northern states in comparison with the observational data in Springer et al. (2014). The simulation model in our study uses experimental data on temperature effects on tick development rates and activity (and other aspects of the tick life cycle), so the temperature limits identified by the model are “real” inasmuch as those experimental data are representative of *A. americanum* across its geographic range. If they are representative, the lower temperature

limit obtained should be a more accurate than that obtained from ecological niche models for a number of reasons. The ecological niche models of *A. americanum* use surveillance data that has not been systematically collected and use “presence” data based on passive surveillance, which may be falsely positive due to the presence of adventitious ticks. In addition, the niche models consider a wide range of climatic variables, including temperature, that are assumed to limit the species range, but the assumptions are rarely supported by empirical evidence. For example, Peterson and Raghavan (2017) used the minimum temperature of the coldest month as one bioclimatic variable in an ecological niche model for *I. scapularis*. Empirical data (Brunner et al. 2012) suggest this variable is unlikely to be limiting for *I. scapularis*, so its inclusion is likely because it correlates with other environmental variables. However, only greater field surveillance data can determine which method is most accurate at identifying the northern range of the tick.

As anticipated, there was only a slight difference between projections made using the RCP4.5 and RCP8.5 emissions

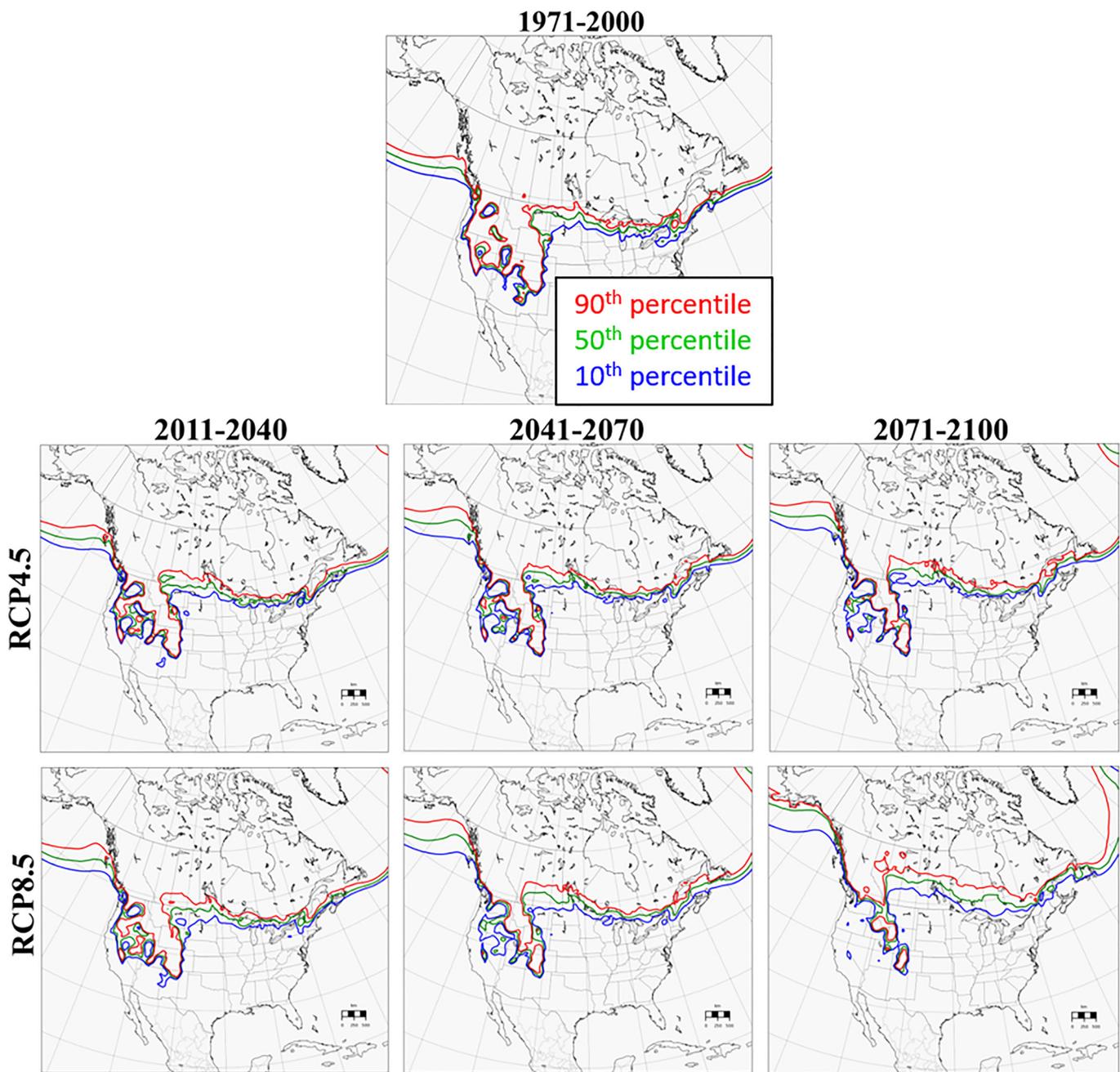


Figure 7. Intramodel variability in an ensemble of six Regional Climate Model (RCM) simulations at 50-km resolution and its effect on the location of the lower temperature threshold (3,285 degree days $>0^{\circ}\text{C}$) for *A. americanum* survival in North America in 1971–2000, 2011–2040, 2041–2070, and 2071–2100, under RCP4.5 and RCP8.5 scenarios. Lines indicating the 10th, 50th, and 90th percentiles of the RCM simulated values are shown.

pathways up to the 2060s, but thereafter, projected range expansion was much greater under RCP8.5. All climate models projected future temperatures that would permit northward range expansion, but there was marked variation among the models in the degree of projected warming, particularly in the last decades of the 21st century and when the models used RCP8.5.

At sites with higher temperatures (i.e., $\geq 4,000\text{DD} > 0^{\circ}\text{C}$), simulated tick population abundance declined associated with parameterization of reduced host-finding activity according to observations of Haile and Mount (1987). Therefore, very high temperatures may be detrimental to *A. americanum* populations. In the ecological niche model studies of Springer et al. (2015) and Raghavan et al. (2019), northward range expansion of the geographic range of *A. americanum* was accompanied by possible

northward contraction of the southern limit of the tick as those regions become hotter than the historical range of climate conditions.

In summary, we have used a simulation model approach to estimate the minimum temperature conditions for the survival of *A. americanum* populations. Using this information, we have identified the possible current extent of temperature suitability in northern North America. We have also identified the possible northern extent of temperature suitability for this tick according to climate projections for the 21st century. The future extent of the northern limit varied according to the emission scenario and regional climate model. The establishment of *A. americanum* in northern U.S. states, and in the densely populated parts of southeastern and south-central

Canada, is plausible in the coming decades, provided that other aspects of the ecological niche of the tick are present. These results suggest that maintaining systematic passive or active surveillance, or both types, for *A. americanum* in these regions would be prudent.

Acknowledgments

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