

Climate change and the potential for range expansion of the Lyme disease vector *Ixodes scapularis* in Canada

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Abstract

We used an *Ixodes scapularis* population model to investigate potential northward spread of the tick associated with climate change. Annual degree-days $>0^{\circ}\text{C}$ limits for *I. scapularis* establishment, obtained from tick population model simulations, were mapped using temperatures projected for the 2020s, 2050s and 2080s by two Global Climate Models (the Canadian CGCM2 and the UK HadCM3) for two greenhouse gas emission scenario enforcements 'A2' and 'B2' of the Intergovernmental Panel on Climate Change. Under scenario 'A2' using either climate model, the theoretical range for *I. scapularis* establishment moved northwards by approximately 200 km by the 2020s and 1000 km by the 2080s. Reductions in emissions (scenario 'B2') had little effect on projected range expansion up to the 2050s, but the range expansion projected to occur between the 2050s and 2080s was less than that under scenario 'A2'. When the tick population model was driven by projected annual temperature cycles (obtained using CGCM2 under scenario 'A2'), tick abundance almost doubled by the 2020s at the current northern limit of *I. scapularis*, suggesting that the threshold numbers of immigrating ticks needed to establish new populations will fall during the coming decades. The projected degrees of theoretical range expansion and increased tick survival by the 2020s, suggest that actual range expansion of *I. scapularis* may be detectable within the next two decades. Seasonal tick activity under climate change scenarios was consistent with maintenance of endemic cycles of the Lyme disease agent in newly established tick populations. The geographic range of *I. scapularis*-borne zoonoses may, therefore, expand significantly northwards as a consequence of climate change this century.

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1. Introduction

Ixodes scapularis Say (1821) is a vector of a number of tick-borne zoonoses including Lyme disease, which currently infects in the order of 20,000 people a year in the USA

(CDC, 2003). For many terrestrial arthropod species, a northward range expansion is expected in response to projected climate change (Root et al., 2003). Were *I. scapularis* to follow this trend, the zoonotic diseases it transmits (Lyme borreliosis, human babesiosis and anaplasmosis: Thompson et al., 2001) may present an enhanced public health challenge for Canada, whose southeastern border lies at the northern edge of the tick's range (CDC, 1999). Whether or not changes in the geographic distribution of vector-borne diseases will occur with climate change is much debated. For some diseases there are grounds for such concerns (Peterson and Shaw, 2003), while for others, outcomes of climate change may be minor compared to

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changes in risk factors such as wealth and lifestyle of target human populations, and alterations to habitats and ecosystems (Hay et al., 2002; Tanser et al., 2003). Analyses using a statistical model have suggested that the geographic range of *I. scapularis* may extend north with climate change (Brownstein et al., 2005). However, these analyses rest on identification of locations suitable for *I. scapularis* in the USA and the question remains as to how far and how significantly in terms of public health, could *I. scapularis* extend north into Canada with climate change.

A coincidence of factors may mean that further spread of *I. scapularis* into Canada is particularly likely and significant for human health. First, the highest incidence of Lyme disease occurs in the northeastern states of the USA, where the densities of *I. scapularis* populations are the highest (CDC, 1999) and these states border some of the most densely populated regions of Canada. Second, *I. scapularis* are carried into Canada each spring by northward migrating birds (Scott et al., 2001). Third, habitats containing high densities of suitable hosts for *I. scapularis* and rodent reservoirs for tick-borne zoonoses are already widespread in highly populated regions of southeastern Canada (Banfield, 1977; Gallivan et al., 1998). Fourth, a dynamic model of *I. scapularis* populations suggested that increasing temperature (associated with climate change) could increase the potential for immigrating ticks to establish resident, endemic tick populations (Ogden et al., 2005).

At the northern end of the tick's range, environmental temperature rather than day length-dependent diapause is the main determinant of intersstadial development rates of engorged *I. scapularis* in the field (Ogden et al., 2004). In model simulations, the colder the environment the longer are intersstadial development times and total generation times, and so the greater is the proportion of ticks that die before reproducing. A theoretical limit of temperature conditions for establishment of self-sustaining *I. scapularis* populations were obtained, at which tick mortality in each cohort is greater than fecundity. Mean annual degree-days $>0^{\circ}\text{C}$ ($\text{DD}>0^{\circ}\text{C}$) was found to be a convenient index of the seasonally variable temperature conditions used in model simulations, which allowed us to quantify and map the current potential geographic range of temperature conditions suitable for *I. scapularis* establishment in Canada. Temperature effects on development rates and on activity of host seeking ticks, may also determine the seasonal activity patterns of different tick instars (Ogden et al., 2005). The current pattern of seasonal activity of immature *I. scapularis* in northeastern USA (nymphs questing in spring and larvae in summer) is thought to drive efficient transmission cycles of some tick-borne zoonoses (Yuval and Spielman, 1990). Our findings have raised three important questions regarding potential effects of projected climate change: (i) will the tick's range increase significantly? (ii) will the threshold number of immigrating ticks needed for establishment be reduced? and (iii) will the seasonal timing of activity of different tick instars allow endemic cycles of tick-borne pathogens (including *Borrelia*

burgdorferi sensu stricto, the agent of Lyme borreliosis) to establish with new endemic *I. scapularis* populations?

2. Materials and methods

To answer these questions, first we obtained $\text{DD}>0^{\circ}\text{C}$ scenario maps for Canada to examine how the geographic limits for *I. scapularis* establishment obtained in a previous study (Ogden et al., 2005) may change with climate change scenarios for three future projections: the 2020s, the 2050s and the 2080s. Second, we used the *I. scapularis* population model (Ogden et al., 2005) to simulate tick populations at four sites in Ontario, Canada under the climate change scenarios. These simulations were used to: (i) investigate how tick survival, at the current known northern limit of ticks, may change with climate change, affecting the ease with which new populations establish; and (ii) investigate the seasonal activity periods for different tick instars at the current, and future projected, northern edge of the ticks range.

2.1. Mapping mean degree-days $>0^{\circ}\text{C}$ under climate change scenarios

We obtained maps of $\text{DD}>0^{\circ}\text{C}$ under climate change scenarios for Canada, on which to contour the $\text{DD}>0^{\circ}\text{C}$ limits for *I. scapularis* established previously (Ogden et al., 2005), and compare the current geographic range of these limits with the ranges projected for the coming decades. To do this, grid-point data of projected daily maximum and minimum temperatures were obtained from two Global Climate Models (GCMs) for the most recent 30-year climatic 'normal' (1971–2000), and three future 30-year projections (centred on the 2020s, 2050s and 2080s). We used the outputs of the second version of the Coupled Global Climate Model (CGCM2) of the Canadian Centre for Climate Modelling and Analysis (Flato et al., 2000; Flato and Boer, 2001), and the UK Hadley Centre's HadCM3, a coupled atmosphere-ocean general circulation model (Gordon et al., 2000; Pope et al., 2000). The spacing of the grid points was approximately 3.7° latitude and longitude (Canadian model), and 2.5° of latitude by 3.75° of longitude (UK model). We obtained output from these models that incorporated estimated forcing due to emissions of greenhouse and other gases calculated in two scenarios (emission scenario forcings 'A2' and 'B2') for global economic change for the coming decades as defined by the Intergovernmental Panel on Climate Change (IPCC, 2000). Briefly, in scenario 'A2' the future world is very much as it is at present: very heterogeneous with a continuously increasing population, regionally oriented economic development and fragmented per capita economic growth and technological change (IPCC, 2000). In scenario 'B2' the emphasis is on local solutions to economic, social and environmental sustainability, intermediate levels of economic development and a lower population growth rate than 'A2'. Projected greenhouse gas emissions are considerably lower in scenario 'B2' than in scenario 'A2' (IPCC, 2000). For each GCM and each emissions scenario, $\text{DD}>0^{\circ}\text{C}$ were calculated at each grid point by accumulating the daily positive mean

temperature values throughout the whole year. In each case, the process was repeated for all 30 years of the three future time periods and the climatic ‘normal’ of each period at each grid point was obtained by averaging 30 years of annual $DD > 0^{\circ}\text{C}$. The grid-point data were contoured using version 8 of SURFER software package (Golden Software, Inc., Golden, Colorado, USA). The mapped contours were the annual $DD > 0^{\circ}\text{C}$ values at which *I. scapularis* populations died out in model simulations (and the standard errors around these values) obtained by Ogden et al. (2005). In this study we mapped the theoretical geographic limits for *I. scapularis* establishment under two annual regimes of temperature, with (e.g. southern Ontario: $DD > 0^{\circ}\text{C}$ limit = 3063) and without (e.g. inland Quebec: $DD > 0^{\circ}\text{C}$ limit = 2826) local effects of water bodies such as the Great Lakes on the annual cycle of temperature, as previously described (Ogden et al., 2005). The $DD > 0^{\circ}\text{C}$ limits for *I. scapularis* establishment we used for mapping were obtained by regressing the annual maximum numbers of adult ticks at model equilibrium against $DD > 0^{\circ}\text{C}$ for a number of meteorological stations in Canada that provided temperature data to run the model simulations (Ogden et al., 2005). The intercept of the linear regression line with the x -axis provided the $DD > 0^{\circ}\text{C}$ at which deterministic die-out of the tick populations occurred. To check whether these limits remained the same under our climate change scenarios, we used results of 12 model simulations run using temperature data generated for the selected Ontario meteorological stations under climate change scenarios (see the following section). The $DD > 0^{\circ}\text{C}$ limit (x -axis intercept) for each future time period was obtained using linear regressions in S-Plus 2000 Professional Release 3 (Boston, Mass.) in which the number of feeding adult ticks at model equilibrium was the outcome variable and the $DD > 0^{\circ}\text{C}$, for each station at each time period, was the explanatory variable.

2.2. Generation of ‘site-specific’ climate change scenarios

The CGCM2 climate change scenarios (using emissions scenario ‘A2’) were expressed as monthly mean changes, from the model’s baseline climate (1961–1990) to the three future 30-year climatic periods. Simple linear interpolation translated the grid-point scenarios into monthly mean changes specific for each of four sites in Ontario. Populations of *I. scapularis* are already established close to two of the sites, Chatham ($42^{\circ} 23' \text{N}$ $82^{\circ} 12' \text{W}$) and Picton ($44^{\circ} 01' \text{N}$ $77^{\circ} 07' \text{W}$), while temperature conditions are thought to be currently too cold to support *I. scapularis* at Wiarton ($44^{\circ} 45' \text{N}$ $81^{\circ} 06' \text{W}$) and the more northerly Timmins ($48^{\circ} 34' \text{N}$ $81^{\circ} 23' \text{W}$). The projected site-specific monthly mean changes were used to simulate future daily weather data using a stochastic weather generator, LARS-WG (Semenov and Barrow, 1997; Semenov and Brooks, 1999), as a downscaling tool (Freybuss et al., 1995). LARS-WG was calibrated using > 25 years of historical daily weather observations obtained for each of the sites from the climatological archives of the Meteorological Service of Canada, Environment Canada. For each site LARS-WG

generated sets of 30 years of daily maximum and minimum temperatures and 24-h precipitation, centered on the 2020s, 2050s and 2080s. Thirty years of daily mean temperatures were calculated (the average of daily maximum and minimum temperatures) and averaged to produce a monthly temperature ‘normal’ as well as a mean annual $DD > 0^{\circ}\text{C}$ for each site at each time period. This standard method (Guttman, 1989) created projected temperature normals comparable with the current (1971–2000) temperature normals previously used as input for the *I. scapularis* population model (Ogden et al., 2005). The projected temperature normals were then used to calculate tick development rates for the *I. scapularis* population model and served as direct input affecting tick activity in the model (as previously described; Ogden et al., 2005). Model simulations were then run for each location for each future time period. The annual maximum number of adult ticks at model equilibrium was used as an index of tick survival for comparisons amongst sites and time periods. The monthly proportions of the annual total number of feeding ticks of each instar (at model equilibrium) in each simulation were plotted to compare seasonal tick activity periods.

3. Results

3.1. Geographic limits for *I. scapularis* under climate change scenarios

Both CGCM2 and HadCM3 projected a northwards expansion of the range of the $DD > 0^{\circ}\text{C}$ limit for *I. scapularis* establishment derived from the tick model, that was evident by the 2020s, marked by the 2050s and wide by the 2080s (Fig. 1). The $DD > 0^{\circ}\text{C}$ maps obtained from both CGCM2 and HadCM3 placed the current potential northern limit for *I. scapularis* establishment further south than that mapped directly from 1971–2000 observed data from Canadian meteorological stations (Ogden et al., 2005). Two *I. scapularis* populations known to be established in Ontario are located north of the geographic limit of temperatures suitable for *I. scapularis* predicted by these climate models (Fig. 1). The HadCM3 may be the less realistic of the two models for the Canadian context, because only by the 2020s did the $DD > 0^{\circ}\text{C}$ limits mapped under HadCM3 projections reach those mapped directly from 1971 to 2000 observed data (Ogden et al., 2005). Both models, however, projected similar rates of change in the theoretical northern limit of *I. scapularis* and for simplicity we describe output from CGCM2 in the following. Under both the ‘A2’ and ‘B2’ emission scenarios, by the 2020s the projected range of the tick included most of heavily populated Ontario (south of Georgian Bay in Lake Huron), Quebec south of Quebec City, all of Nova Scotia and Prince Edward Island, much of New Brunswick and southern Manitoba and Saskatchewan (Fig. 1). By the 2050s, the projected range encompassed most of Canada east of the Rockies and south of latitude 50°N (south of 55°N in the case of Saskatchewan and Manitoba), possibly with the exception of Newfoundland. Under the ‘A2’ emission scenario, temperatures in most of central and eastern Canada south of 53°N , including

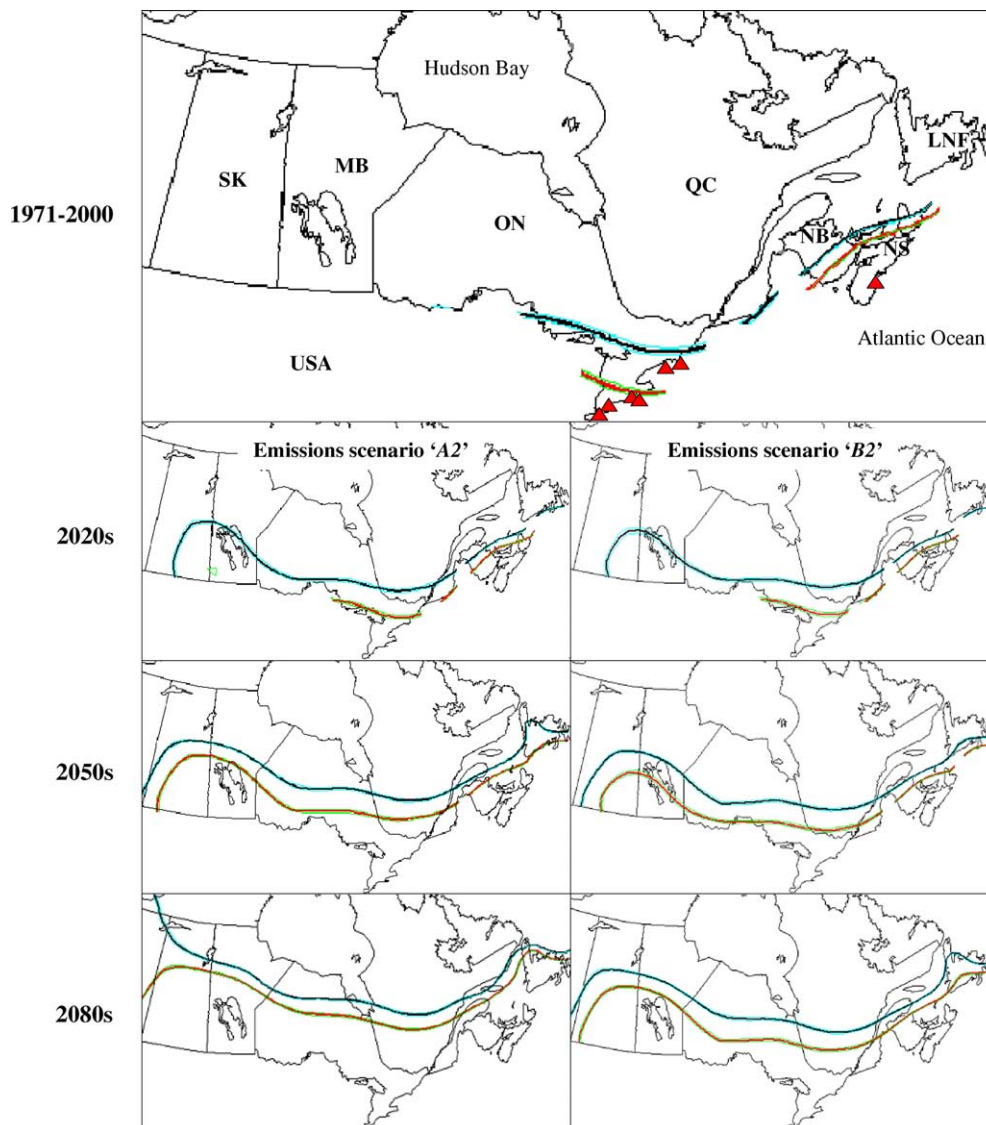


Fig. 1. Model-derived temperature limits for *Ixodes scapularis* establishment in Canada using mean annual degree-days $>0^{\circ}\text{C}$ as an index under current (1971–2000) and projected climate obtained from the CGCM2 global climate model. The red and dark blue lines represent limits in regions affected and unaffected (respectively) by summer cooling by the Great Lakes (Ogden et al., 2005). Upper and lower standard errors of the model derived degree-days $>0^{\circ}\text{C}$ limits are also mapped (pale blue lines around the dark blue line, and green lines around the red line). In the larger map (in which limits are contoured on a map of 1961–1990 output from the CGCM2), locations of known resident populations of *I. scapularis* in Canada are indicated by red triangles, and Provinces are identified as SK, Saskatchewan; MB, Manitoba; ON, Ontario; QC, Quebec; NB, New Brunswick; NS, Nova Scotia and LNF, Labrador and Newfoundland. The columns of smaller maps show temperature limits for *I. scapularis* establishment contoured on maps of temperatures projected for the 2020s, 2050s and 2080s by the CGCM2. In the left-hand column of maps projected temperatures were obtained using emissions scenario ‘A2’, and in the right hand column, the projections were obtained under emissions scenario ‘B2’.

Newfoundland, were projected to be suitable for *I. scapularis* establishment in the 2080s. Labrador and Northern and Eastern Quebec were predicted to remain unsuitable for tick establishment under any scenario but suitable temperatures may extend much further north in Alberta and Saskatchewan, reaching the Great Slave Lake region of North West Territories. The rate of expansion of the northern limits of temperature suitable for *I. scapularis* establishment was similar under both ‘A2’ and ‘B2’ emission scenarios, using either the CGCM2 or HadCM3 climate model, up to the 2050s. Between the 2050s and 2080s, however, the rate of expansion of the limits was lower under the ‘B2’ scenario than

under the ‘A2’ scenario. The relationship between $\text{DD}>0^{\circ}\text{C}$ and the maximum numbers of feeding adult female ticks (in surviving populations) at equilibrium in the location-specific model simulations, was strong and linear (Fig. 2, $\beta=0.33$, $\text{SE}=0.02$, $P<0.0001$, $R^2=0.96$). The x-axis intercept was $2875 \text{ DD}>0^{\circ}\text{C}$, closer to the intercept obtained using data from meteorological stations in inland Quebec (Ogden et al., 2005) that are mostly unaffected by summer cooling by water bodies. These findings suggest that the geographic extent of temperature conditions suitable for *I. scapularis* establishment remain within the bounds mapped in Fig. 1. The $2826 \text{ DD}>0^{\circ}\text{C}$ limit for establishment of *I. scapularis* (dark blue line in

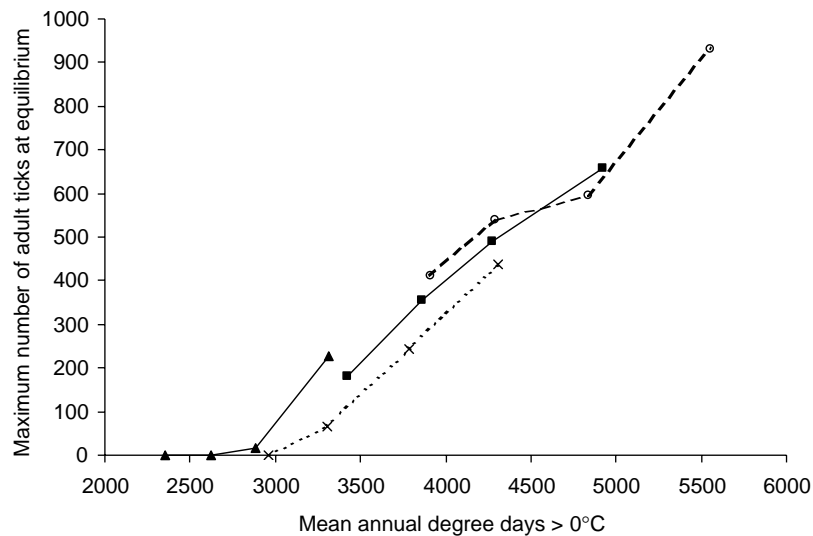


Fig. 2. Increases in the simulated maximum annual number of adult ticks at model equilibrium with increases in the mean annual number of degree-days $> 0^{\circ}\text{C}$, for selected meteorological stations in Ontario. Crosses indicate values for Wiarton, triangles for Timmins, squares for Picton and circles for Chatham. The values are (going from left to right) for 1971–2000 normals and years representative of the 2020s, 2050s and 2080s, respectively.

Fig. 1) may be the more accurate after the 2020s, however, because tick populations established in more northerly locations are less likely to be influenced by summer cooling by the Great Lakes (Ogden et al., 2005).

3.2. Tick survival and seasonality under climate change scenarios

For areas currently suitable for tick establishment (e.g. Chatham and Picton), using temperature data obtained from the output of CGCM2 under the ‘A2’ emissions scenario, the *I. scapularis* population model predicted an increase in the equilibrium number of ticks of between 30 and 100% by the 2020s, depending on location, with tick numbers increasing between two- and four-fold by the 2080s (Fig. 2). These changes represent declines in total annual mortality of ticks due to a shortening of the tick’s lifecycle consequent of the combined effects of more favorable temperatures for host-seeking activity and shorter duration of development for engorged ticks and eggs. The simulated seasonality of different tick instars for the sites where *I. scapularis* are currently established in Ontario (e.g. Chatham using 1971–2000 temperature normals) and at the northern limit of range expansion (e.g. for Timmins using projected temperature for the 2050s) follow the pattern currently observed in Ontario (Ogden et al., 2005, Fig. 3a and e, respectively). In this pattern, which permits establishment of endemic cycles of *B. burgdorferi sensu stricto* (Lindsay et al., 1997), the main activity period for nymphs is in spring and early summer, while the main activity period for larvae is late summer. In simulations for Chatham and Picton, as projected temperatures increased, larvae became active earlier in the year due to increased egg-to-larva development rates. At the same time, increased larva-to-nymph development rates and autumn

temperatures more favorable for tick activity, meant that progressively more larvae active in summer were able to feed, moult and become actively host-seeking nymphs in autumn of the same year (Fig. 3b–d).

4. Discussion

There is a general consensus amongst GCMs in the direction and degree of projected temperature and precipitation change for Canada (IPCC, 2001). The CGCM2 and HadCM3 output we used here are not ‘outlier’ projections for climate change in Canada in comparisons with that of other models and the ‘A2’ emission scenario is considered the most realistic if the world remains much as it is today (IPCC, 2001). In our study, there was consensus amongst GCMs and the emissions scenarios that a northern expansion of temperature conditions favorable for self-sustaining populations of *I. scapularis* will occur. In tick populations simulated under projected temperature conditions, the relationship between abundance and $\text{DD} > 0^{\circ}\text{C}$ was similar to that when simulations were run using real historical temperature data (Ogden et al., 2005). Therefore, it is reasonable to use $\text{DD} > 0^{\circ}\text{C}$ limits obtained previously as a representation of the limit for *I. scapularis* establishment under climate change scenarios.

These observations, combined with the potential degree of increase in tick survival in the region immediately south of these theoretical temperature limits, suggest considerable potential for northward expansion of the range of this tick even as early as the 2020s. Our findings are distinct from those of Brownstein et al. (2005), who indicated that the potential expansion of the northern range of ‘climatically suitable habitat’ for *I. scapularis* would be minimal from the present time to the 2050s and only between the 2050s and 2080s would significant range expansion occur. This discrepancy may in

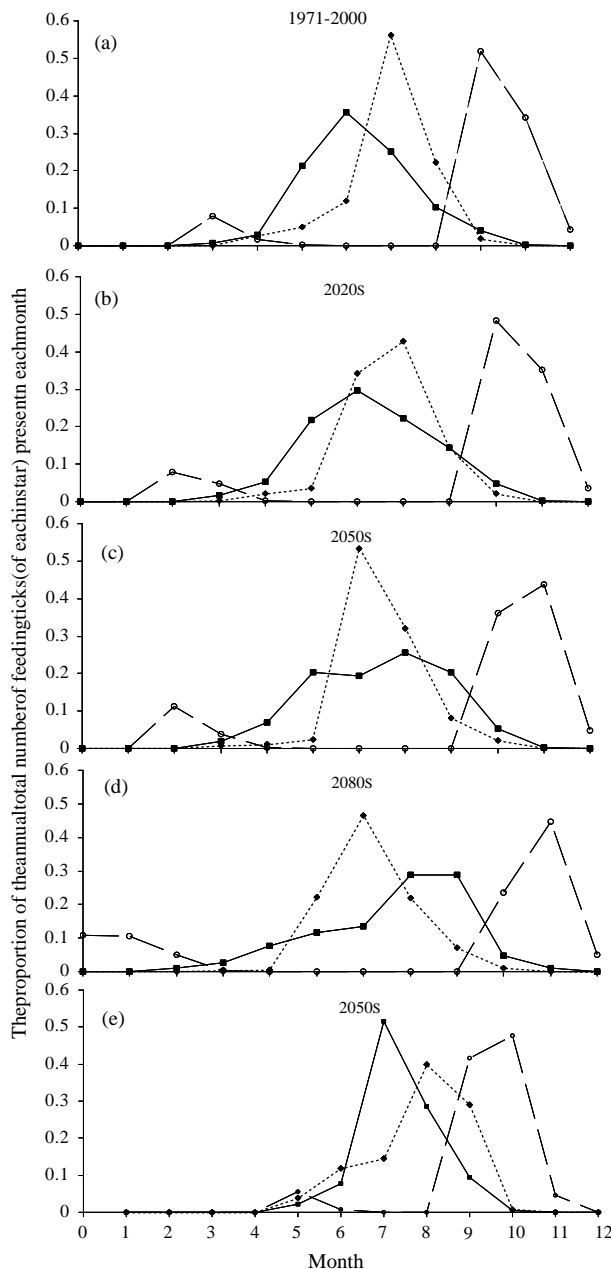


Fig. 3. The simulated seasonality of larval (dotted line), nymphal (solid line) and adult (dashed line) *Ixodes scapularis* at Chatham, Ontario (graphs a–d), close to a current *I. scapularis* population on the shore of Lake Ontario (Morshed et al., 2003), and at Timmins, Ontario (e), where *I. scapularis* are not established. Monthly variations in tick numbers are shown as the monthly proportions of the annual total number of feeding ticks at model equilibrium. Graphs (a)–(d) represent simulations using current (1971–2000) temperature normals and using projected temperature conditions for years representative of the 2020s, 2050s and 2080s, respectively. Note that the activity period for larvae steadily advances over this time period, while the proportion of nymphs active in summer-autumn increases. Graph (e) shows the seasonality of different instars in 2050s when ticks first become established at the northern edge of their potential range at this time.

part be due to over-estimation (by 300–500 km) of the current northern range of ‘climatically suitable habitat’ by the statistical model of Brownstein et al. (2005). Our limits derived from the *I. scapularis* population model are much further south and more in line with the known actual northern

limit of established *I. scapularis* populations (Fig. 1 Ogden et al., 2005). Also, the GCM used by Brownstein et al. (2005) was CGCM1, while we used the more recent CGCM2 as well as the current IPCC greenhouse gas emission scenarios (IPCC, 2000), which could have had an effect on the different projections.

Coincidence of a number of additional factors may translate potential into actual range expansion of *I. scapularis* and result in emergence of tick-borne zoonoses as a more important public health problem in south central and southeastern Canada. First, northward migrating birds are carrying *I. scapularis* into Canada each spring (Scott et al., 2001), a theoretically very efficient means of extending the range of *I. scapularis* (Madhav et al., 2004). A large biomass of birds migrates into Canada having passed through the northeastern and north central states of the USA, where *I. scapularis* occur at high densities (CDC, 1999), at the time of year when nymphal *I. scapularis* are active. In the last decade more than 2000 adult *I. scapularis* have been found by members of the public in locations in Canada from Alberta to Newfoundland and voluntarily submitted to public health organisations for identification (L.R. Lindsay, unpublished data). Only 56 ticks were submitted from locations where field studies revealed the existence of established *I. scapularis* populations (L.R. Lindsay, unpublished data), inferring that most ticks submitted by the public were derived from engorged nymphs carried on migratory birds.

Our study suggests that tick abundance in *I. scapularis* populations towards the northern edge of the current range (e.g. the population close to Picton) will increase considerably with projected climate change, doubling by the 2020s. Although the gradient of the relationship between tick abundance and $DD > 0^{\circ}\text{C}$ varies with host finding success (Ogden et al., 2005), the increased tick abundance in simulations indicates substantially increased tick survival because tick abundance is regulated in the model by density-dependent processes (Ogden et al., 2005). The threshold number of ticks immigrating on birds for establishment of new populations in suitable habitats is, therefore, likely to decline and establishment of tick populations in warmer regions of southeastern Canada may become more common, perhaps as early as the 2020s.

Second, emergence of Lyme disease in the northeastern USA has been associated with land use changes that increased the density of white-tailed deer (*Odocoileus virginianus*: hosts of adult *I. scapularis*) in habitats with abundant rodents, which are reservoirs of *B. burgdorferi* sensu stricto and hosts for immature ticks (Thompson et al., 2001). The geographic range of white-tailed deer is wide in Canada, extending east–west from the Maritime Provinces through to British Columbia and from the USA border north into all heavily populated south-eastern Canada (Banfield, 1977). At least in Ontario and Quebec, white-tailed deer abundance is often greater than seven per square kilometre, which has been considered the minimum density for detectable *I. scapularis* populations in the USA (Gallivan et al., 1998; Rand et al., 2003; Québec, ministère des ressources naturelles et de la faune: http://www.fapaq.gouv.qc.ca/fr/faune/plan_ges_cerf.htm). With the exception of Newfoundland

(which is thought devoid of *Peromyscus* spp. and white tailed deer; Banfield, 1977), rodent reservoirs hosts for the causal agents of Lyme and other zoonoses (either *Peromyscus leucopus* or *Peromyscus maniculatus*; Donahue et al., 1987; Rand et al., 1993) are also widespread in Canada.

Third, *I. scapularis* populations are already established in the Carolinian forests of southern Ontario (Lindsay et al., 1998; Morshed et al., 2003) and these forests are also likely to spread northwards with climate change (IPCC, 1998). The pace of northwards spread of these forests is not likely to be limiting, however, on the spread of *I. scapularis*, which are clearly capable of surviving in coniferous woodlands in Nova Scotia (Ogden et al., 2005) and perhaps in northern boreal type forests (Lindsay et al., 1995).

The accuracy of mean DD>0 °C limits alone in projecting the future geographic range of *I. scapularis* is limited for a number of reasons. First, mean DD>0 °C is not a perfect index of how seasonal variations in temperature may affect the survival of *I. scapularis* in different locations (Ogden et al., 2005). Second, the projected range limits are for tick populations in habitats in which tick survival is similar to the maple forest at Long Point, Ontario (Ogden et al., 2005). More arid habitats such as some central Canadian prairies are unlikely to support *I. scapularis* and may become drier with climate change (IPCC, 2001, 1998), limiting western spread of *I. scapularis* even if temperature conditions become more suitable. Third, changes in rainfall with climate change are very likely to affect survival of tick populations by affecting activity of host-seeking ticks (Randolph and Storey, 1999). Rainfall effects are not included in the model because they remain to be quantified for *I. scapularis*, but clearly, within the projected ranges *I. scapularis* could only establish where habitat and rainfall make adequate levels of moisture available for the ticks. For much of Ontario, Quebec and the Maritimes, annual precipitation is expected to increase but projections for rainfall are far less certain than those for temperature (IPCC, 2001, 1998). In as yet unpublished projections of rainfall in southeastern Canada, local variability in the annual precipitation (from current values) was very high. Therefore, even if we were directly able to model effects of rainfall on tick survival, we could not confidently extrapolate regional projections for rainfall to a more local scale. Changes in rainfall patterns resulting in increases in droughts and heavy rainfall events (IPCC, 2001, 1998) are likely to reduce tick survival and inhibit spread of the ticks' range into some regions. Lastly, our limits do not account for stochastic extinctions of the tick populations. Despite these limitations, our conclusion is that increased temperatures with climate change could permit a potentially wide expansion of the northern range of *I. scapularis*. Consistent with this, the number of populations of *I. scapularis* in Canada has risen from one to seven in the last decade, all in the warmest regions of Ontario and Nova Scotia (Ogden et al., 2005), during a period when the first evidence of climate change may have been seen (Parmesan and Yohe, 2003).

At the expanding northern edge of the range of *I. scapularis*, the seasonal pattern of activity of larval and nymphal *I. scapularis* was consistent with that observed in the field, which supports transmission cycles of *B. burgdorferi* sensu stricto (Lindsay et al., 1997; Fig. 3). In these cycles, infective nymphs active in spring and early summer infect rodents, which in turn infect larvae that are active in mid to late summer. Infected larvae molt into infective nymphs by the following spring to begin the cycle again (Yuval and Spielman, 1990). Our model suggests that as temperatures increase, larvae are active and feed earlier in the year and increasing proportions of nymphs become active and feed in autumn of the year they fed as larvae. Observed variations in seasonality of immature *I. scapularis* at different latitudes in the USA tend to support our model-generated patterns. The pattern generated for projected temperatures at Chatham, Ontario in the 2050s (Fig. 3c) is similar to that recently observed in Maryland, USA (Hofmeister et al., 1999), and that generated for Chatham in the 2080s (Fig. 3d) is similar to that observed in Georgia, USA (Oliver, 1996). Greater overlap in larval and nymphal activity (e.g. Chatham in the 2020s, Fig. 3b) may enhance transmission cycles of *I. scapularis*-borne pathogens that are efficiently transmitted from rodents to ticks for only short periods (Randolph, 2001), such as *Anaplasma phagocytophilum* (Bown et al., 2004; Massung et al., 2004). Transmission models are needed to investigate these effects more fully, and again there is uncertainty in these projections because variations in future rainfall are also likely to influence seasonal tick activity (Vail and Smith, 2002).

We conclude that there is considerable potential for the range of *I. scapularis* to expand northwards with projected climate change. The seasonality of different tick instars in newly established populations is likely to support transmission cycles of *B. burgdorferi* sensu stricto, so expansion in the geographic range of public health risk due to tick-borne zoonoses such as Lyme borreliosis, is likely to accompany the range expansion of the tick. Gaps in our knowledge of *I. scapularis* ecology and uncertainty about aspects of climate change do, however, limit the precision of mapped future ranges.

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